# Approaching the Negative is not Avoiding the Positive: FNIRS, ERP and fMRI Studies on the Approach-Avoidance Task

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Dipl.-Psych. Lena Helene Ernst
aus Bühl

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Dekan: Prof. Dr. Wolfgang Rosenstiel

1. Berichterstatter: Prof. Dr. Martin Hautzinger

2. Berichterstatter: Prof. Dr. Andreas J. Fallgatter

3. Berichterstatter: Prof. Dr. Ute Habel (Aachen)

# Für Hanna

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# **Abstract**

Approaching positive and avoiding negative stimuli are fundamental principles of behaviour. Such automatically triggered reactions are essential for survival in the short term, while their conscious regulation guarantees behavioural flexibility in the long term. The Approach-Avoidance Task (AAT) simulates approach-avoidance reactions and – thereby – allows for the assessment of both automatic approach-avoidance tendencies and their regulation. Incompatible conditions (approach negative, avoid positive) comprise a conflict: Automatically elicited compatible reaction tendencies (avoid negative, approach positive) have to be inhibited for performing an alternative reaction. This conflict is reflected in the finding of enhanced reaction times (RTs) in incompatible compared to compatible conditions, so-called stimulus response compatibility effects (SRC effects). The thesis at hand investigated the neuronal (part A) and neuropsychological (part B) correlates of such SRC effects in healthy young adults reacting to positive and negative pictures from the International Affective Picture System (IAPS) as stimuli of general emotional relevance.

Study A1 addressed the contributions of prefrontal areas via functional near-infrared spectroscopy (fNIRS) in 15 participants. Incompatible, regulated reactions compared to compatible, automatic reactions caused stronger activation in right dorsolateral prefrontal cortex (DLPFC), i.e., in one of the main instances for behavioural control in humans.

In 37 participants, study A2 investigated the dependency of this finding on a moderator variable: The gene encoding the enzyme Monoamine Oxidase A (termed *MAOA*-uVNTR) influences affective and cognitive control, which are both required for the regulation of automatic approach and avoidance behaviour. Carriers of the low- compared to the high-expressing genetic variant (*MAOA-L* vs. *MAOA-H*) showed increased regulatory activity in right DLPFC during incompatible compared to compatible conditions as assessed with fNIRS. This might have been a compensatory mechanism for stronger emotional reactions as shown in previous studies and might have prevented any influence of incompatibility on behaviour. In contrast, fewer errors but also lower activity in right DLPFC during the processing of negative compared to positive stimuli indicated *MAOA-H* carriers to have used other regulatory areas. This resulted in slower RTs in incompatible conditions, but – in line with the known better cognitive regulation efficiency – allowed for performing incompatible reactions without activating the DLPFC as the highest control instance. Carriers of one low-

and one high-expressing allele lay as intermediate group between the reactions of the lowand high-expressing groups.

Study B1 assessed event-related potentials (ERPs) in 15 persons for depicting neuropsychological sub-processes underlying behavioural SRC effects. Early attention allocation preparing efficient stimulus classification (N1 ERP) and response inhibition on the level of response representations (N2 ERP) were associated with the solution of the conflict in incompatible conditions. For positive stimuli, these processes were enhanced during the incompatible condition *avoid positive* compared to the compatible condition *approach positive*. Source localization analysis revealed activity in right occipital areas (N1 ERP), and in left DLPFC and insula (N2 ERP) to be neuronal generators of these electrophysiological SRC effects. This neuronal regulation resulted in no influence of incompatibility at the behavioural level. For negative pictures, the reversed pattern was found: There were no electrophysiological SRC effects, but clear behavioural SRC effects in both RTs and error frequency, i.e., participants were faster and made fewer errors during avoiding than approaching negative pictures.

With regard to such neuropsychological sub-processes, study B2 extended the research question for the influence of the personality characteristic goal-oriented pursuit, i.e. of the willingness to actively regulate behavioural responses. The P3 ERP reflecting controlled attention allocation was assessed in 36 healthy participants. For negative pictures, analyses revealed this neuropsychological mechanism to mediate the relation between personality and behaviour: Stronger goal-oriented pursuit was associated with higher controlled attention allocation to the incompatible compared to the compatible condition and – thereby – with less automatic avoidance tendencies in response to negative pictures, i.e., with higher efficiency of regulation.

While these studies applied a common joystick version of the AAT, study A3 used a cued GoNoGo variant developed by the author: The cue event indicated participants (n=34) to prepare a response, while the move event signaled to realize it (Go trials) or to inhibit it (NoGo trials). The NoGo conditions allowed for investigating the inhibition of automatic reaction tendencies without the initiation of another response (classical incompatible conditions, see above). Moreover, the neuronal measurements were extended to the whole brain by functional magnetic resonance imaging (fMRI). For negative pictures, strong

neuronal response preparation at the cue event in the anterior cingulum, insula, thalamus, frontal and parietal cortices was followed by even faster incompatible than compatible reactions. The more negative and arousing participants rated the pictures, the stronger they showed response initiation processes at the move event in the right midbrain and – thereby – the stronger the observed reversed behavioural effects were (mediation analysis). In NoGo conditions, the inhibition of automatically elicited, compatible response tendencies required more regulation via the superior parietal lobule than the inhibition of prepared incompatible reactions. In contrast, for positive pictures, incompatible reactions were mainly regulated at the move event (frontal and parietal cortices) and resulted in prolonged RTs. Missing neuronal regulation effects in the NoGo conditions further indicated positive pictures to elicit only weak compatible approach tendencies.

In sum, these results revealed a higher conflict potential for the incompatible reactions approach negative than for avoid positive. In line with previous literature on phenomena such as the negativity bias, this might indicate avoidance reactions to negative stimuli to be more important than approach reactions to positive stimuli. Most important, study B2 showed the efficiency of solving the conflict in the condition approach negative to depend on cognitive capacities as reflected in controlled attention allocation (P3 ERP) and the personality trait goal-oriented pursuit. Complementary, study A3 revealed a first hint for significant subcortical regulatory contributions. Future studies have to clarify, if this is also the case without the possibility to prepare reactions at the cue event.

These studies revealed first insights into the neuronal correlates of SRC effects in healthy participants reacting to stimuli of general emotional relevance. They are discussed in the context of neuronal and neuropsychological models of behavioural control, but also with regard to explanations of SRC phenomena from cognitive-emotional psychology. In short, the current findings are in accordance with the assumption that top-down control processes – as necessary in incompatible conditions – rely on frontal cortical activity. However, study A3 emphasizes the importance of more elaborated network models also taking into account the cooperation with other structures, such as e.g., the cingulum as influential conflict monitoring instance. The neuropsychological, more functionally orientated approach of part B revealed enhanced attention allocation (N1, P1 and P3 ERPs) and response inhibition processes (N2 ERP) to underlie behavioural SRC effects. Here, differences in the ERPs to positive and negative stimuli are also discussed with regard to disturbing influences of technical task characteristics.

Furthermore, the shown interindividual differences are discussed with regard to previous assumptions of SRC effects constituting universal phenomena. In this context and against the background of pathologically enhanced approach tendencies in addiction disorders, in study A4, participants (n=15) reacted to alcohol and non-alcohol pictures. Here, the left anterior lateral orbitofrontal cortex as part of the general reward system processing secondary rewards showed stronger activation during approaching compared to avoiding alcohol pictures. This difference was positively correlated with participants' expectation about beneficial effects of alcohol in terms of emotional regulation.

Future studies have to show the reliability and validity of these findings. Technical problems as well as advanced data analyses and research questions are discussed in the light of recent developments in cognitive-emotional psychology and neuroscience. Thereby, considerations on the integration of psychological models and neuronal findings via embodiment theories are presented.

# Zusammenfassung

Annäherungsreaktionen an positive Stimuli und das Vermeiden von negativen Stimuli sind grundlegende Verhaltensprinzipien. Diese automatisch ausgelösten Tendenzen sichern wesentlich die Überlebenswahrscheinlichkeit auf kurze Sicht, während hingegen auf lange Sicht nur ihre bewusst gesteuerte Regulation die Flexibilität unseres Verhaltens garantieren kann. Während des Approach-Avoidance Tasks (AAT; englisch für Annäherungs-Vermeidungs Aufgabe) werden Annäherungs- und Vermeidungsreaktionen simuliert. Somit ermöglicht der AAT die Erforschung sowohl automatisch ausgelöster Annäherungs- und Vermeidungstendenzen, als auch deren Regulation. Inkompatible Bedingungen (negativannähern, positiv-vermeiden) stellen eine Konfliktsituation dar: Die automatisch ausgelösten Reaktionstendenzen (negativ-vermeiden, positiv-annähern) müssen unterdrückt und eine alternative Reaktion umgesetzt werden. Dieser Konflikt schlägt sich in längeren Reaktionszeiten (RZ) in den inkompatiblen verglichen zu den kompatiblen Bedingungen nieder; ein Muster, das als Stimulus-Reaktions-Kompatibilitäts Effekte (SRK Effekte) bezeichnet wird. Die vorliegende Dissertation untersuchte in Teil A die neuronalen und in Teil B die neuropsychologischen Korrelate solcher SRK Effekte bei gesunden jungen Erwachsenen, die auf positive und negative Bilder aus dem Katalog International Affective Picture System (IAPS) reagierten, d.h. auf emotionale Stimuli von universeller Gültigkeit.

Studie A1 untersuchte den Beitrag präfrontaler Areale mittels funktioneller Nah-Infrarot Spektroskopie (fNIRS) bei 15 Probanden. Verglichen mit kompatiblen, automatischen Reaktionen gingen inkompatible, regulierte Reaktionen mit einer stärkeren Aktivierung des rechten dorsolateralen präfrontalen Kortex (DLPFK) einher, d.h. mit der stärkeren Aktivierung einer der Hauptinstanzen für Verhaltenskontrolle beim Menschen.

Studie A2 untersuchte die Abhängigkeit dieses Befunds von einer Moderator-Variablen bei 37 Probanden mit fNIRS: Das Gen *MAOA*-uVNTR enkodiert das Enzym Monoaminoxidase A, das affektive und kognitive Kontrolle beeinflusst; beide Kontrollmechanismen sind während der Regulation von automatischen Annäherungs- und Vermeidungstendenzen notwendig. Verglichen mit Trägern der hoch-expressiven Variante (*MAOA-H*), zeigten Träger der gering-expressiven Variante (*MAOA-L*) stärkere regulatorische Aktivität im rechten DLPFK während inkompatibler als während kompatibler Bedingungen. Da frühere Studien in dieser Gruppe stärkere emotionale Reaktivität zeigten, könnte dies einen kompensatorischen Mechanismus abbilden, der jeglichen problematischen

Einfluss der inkompatiblen Bedingung auf die Verhaltensebene verhindert hat. Dagegen waren bei den *MAOA-H*-Trägern weniger Fehler, aber auch eine geringere Aktivität des DLPFK während der Verarbeitung negativer – verglichen mit positiven Reizen – zu beobachten. Dieses Muster könnte auf den Beitrag anderer regulatorischer Areale hinweisen. Deren angenommene Aktivität resultierte in langsameren RZ in inkompatiblen Bedingungen, erlaubte jedoch – in Übereinstimmung mit bisherigen Befunden von besserer kognitiver Regulationsfähigkeit – die Ausführung inkompatibler Reaktionen ohne einen Beitrag des DLPFK als höchster Kontrollinstanz. Die Reaktionen von Trägern eines geringund eines hoch-expressiven Allels lagen zwischen denen der beiden anderen Gruppen.

Studie B1 erfasste ereigniskorrelierte Potentiale (EKPs) in 15 Probanden mit dem Ziel, neuropsychologische Subprozesse abzubilden, die behavioralen SRC Effekten zu Grunde liegen. Frühe Aufmerksamkeitszuteilung zur Vorbereitung effizienter Stimulusklassifikationen (N1 EKP) und Reaktionsinhibition auf der Ebene von Reaktionsrepräsentationen (N2 EKP) waren an der Konfliktlösung in inkompatiblen Bedingungen beteiligt. Diese Prozesse waren erhöht während der inkompatiblen Bedingung *positiv-annähern* verglichen zur kompatiblen Bedingung *positiv-vermeiden*. Eine Quellenlokalisations-Analyse zeigte Aktivität im rechten Okzipitalkortex (N1 EKP) und im linken DLPFK und der linken Insula (N2 EKP) als neuronale Generatoren dieser elektrophysiologischen SRK Effekte auf. Diese neuronale Regulation resultierte in keinerlei problematischem Einfluss der inkompatiblen Bedingung auf die Verhaltensebene. Bezüglich negativer Stimuli war das umgekehrte Reaktionsmuster zu beobachten: Es ergaben sich keine elektrophysiologischen SRK Effekte, aber deutliche behaviorale SRK Effekte, sowohl hinsichtlich der RZ als auch hinsichtlich der Fehlerhäufigkeit, d.h. die Probanden waren schneller und machten weniger Fehler während des Vermeidens negativer Bilder verglichen zum Annähern negativer Bilder.

In Bezug auf diese neuropsychologischen Subprozesse war die Fragestellung in Studie B2 erweitert um den Einfluss des Persönlichkeitszugs *Zielorientiertheit* (Wille, sein Verhalten aktiv zu regulieren). Das P3 EKP bildet die Zuwendung kontrollierter Aufmerksamkeit ab; es wurde in 36 Probanden erfasst. Für die negativen Bilder ergaben die Analysen, dass dieser neuropsychologische Mechanismus die Beziehung zwischen dem oben genannten Persönlichkeitszug und dem Verhalten der Probanden mediierte: Stärkere Ausprägungen von *Zielorientiertheit* gingen einher mit einem höheren Ausmaß an Zuwendung kontrollierter Aufmerksamkeit in inkompatiblen verglichen mit kompatiblen Bedingungen und – dabei – mit

weniger starken automatischen Vermeidungstendenzen, d.h. mit einer höheren Effizienz der Regulation.

Während diese Studien eine gewöhnliche Joystick-Version des AAT einsetzten, wurde in Studie A3 eine GoNoGo Variante mit Hinweisreiz eingesetzt, die von der Autorin eigens für diese Untersuchung entwickelt wurde: Der Hinweisreiz zeigte den Probanden (n=34) an, dass sie die Reaktion vorbereiten sollten, während das Go-NoGo-Signal vermittelte, ob die Reaktion ausgeführt (Go-Durchgänge) oder inhibiert werden sollte (NoGo-Durchgänge). Die NoGo-Durchgänge ermöglichten es, die Inhibition automatischer Reaktionstendenzen zu untersuchen, ohne dass eine andere Reaktion initiiert wurde wie in den klassischen inkompatiblen Bedingungen. Darüber hinaus bezogen sich die neuronale Messungen mit Hilfe funktioneller Magnetresonanztomographie (fMRT) auf Aktivierungen im gesamten Gehirn. Die negativen Stimuli führten zu starker neuronaler Reaktionsvorbereitung bei Präsentation des Hinweisreizes im anterioren Cingulum, in der Insula, im Thalamus, sowie im frontalen und parietalen Kortex. Diese Aktivität wurde gefolgt von einem überraschenden RZ-Muster bestehend aus schnelleren Reaktionen in inkompatiblen als kompatiblen Bedingungen. Je negativer und aufregender die Probanden die Bilder bewerteten, desto stärkere Reaktionsinitiierungs-Aktivität zeigten sie im rechten Mittelhirn und desto stärkere umgekehrte Verhaltenseffekte (Mediationsanalyse). In den NoGo-Durchgängen erforderte die Inhibition der automatisch ausgelösten, kompatiblen Reaktionstendenzen stärkere Regulation im superioren Parietallappen als die Inhibition der vorbereiteten inkompatiblen Reaktionen. In Kontrast dazu wurden die inkompatiblen Reaktionen mit positiven Bildern hauptsächlich zum Zeitpunkt des Go-NoGo Signals reguliert (frontaler und parietaler Kortex) und resultierten in den üblichen längeren RZ. Die fehlenden neuronalen Regulationseffekte in den NoGo-Durchgängen stützten die Interpretation, dass positive Stimuli nur schwache kompatible Annäherungstendenzen auslösten.

Zusammengefasst zeigten diese Ergebnisse ein größeres Konfliktpotential für die inkompatible Bedingung negativ-annähern als für positiv-vermeiden auf. Übereinstimmend mit bisherigen Befunden zu psychologischen Phänomenen wie dem negativity bias (englisch für die häufig bevorzugte Verarbeitung negativer Informationen), könnte dies bedeuten, dass das Vermeiden von negativen Stimuli wichtiger ist als das Annähern an positive Stimuli. Studie B2 ergab, dass die Effizienz der Konfliktverarbeitung in der Bedingung negativannähern kognitiver Kapazität, die als kontrollierte abhängig ist von Aufmerksamkeitszuwendung (P3 EKP) und dem Persönlichkeitszug Zielorientiertheit erfasst wurde. Ergänzend hierzu fanden sich in Studie A3 erste Hinweise für einen bedeutsamen subkortikalen Beitrag zur Regulation. Weitere Studien sind nötig um zu klären, ob ein solcher Mechanismus auch aktiv ist, wenn es keinen Hinweisreiz gibt, der die Vorbereitung der Reaktionen erlaubt.

Die vorliegenden Untersuchungen ergaben einen ersten Einblick in die neuronalen Korrelate von behavioralen SRK Effekten bei gesunden Probanden, die auf universell gültige emotionale Stimuli reagierten. Die Bedeutung dieser Ergebnisse wird vor dem Hintergrund neuronaler und neuropsychologischer Modelle der Verhaltenskontrolle, sowie im Kontext von kognitiv-emotionalen Erklärungsansätzen zu SRK Effekten diskutiert. Die Befunde stimmen mit Annahmen überein, dass Top-Down-Kontrollprozesse (englisch für höher geordnete Kontrollprozesse), die in inkompatiblen Bedingungen nötig sind, über Aktivität im frontalen Kortex erfolgen. Allerdings legen die Befunde in Studie A3 auch ein großes Erklärungspotential komplexerer Netzwerk-Modelle nahe, da diese die Zusammenarbeit mit anderen Hirnstrukturen, wie z.B. dem Cingulum als wichtiger Konflikt-Überwachungs-Instanz, miteinbeziehen. Der mehr funktionell ausgerichtete Untersuchungsansatz in Teil B zeigte erhöhte Aufmerksamkeitszuwendung (N1, P1 und P3 EKP) und Reaktionsinhibition als neuropsychologische Grundlagen von behavioralen SRK Effekten auf. Die hier gefundenen Unterschiede zwischen positiven und negativen Stimuli werden auch hinsichtlich möglicher Störeinflüsse von aufgabenspezifischen Charakteristika des AAT diskutiert.

Weiterhin werden die aufgezeigten interindividuellen Unterschiede in Bezug gesetzt zur bisherigen Annahme, dass SRK Effekte ein stets und allgemein gültiges Verhältnis zwischen Stimuli und Reaktionen abbilden. In diesem Zusammenhang und vor dem Hintergrund pathologisch erhöhter Annäherungstendenzen bei Suchterkrankungen, wurden in Studie A4 zudem 15 Probanden mit Bildern von alkoholischen und nicht-alkoholischen Produkten getestet: Der linke anterior-laterale Orbitofrontalkortex, der zum Belohnungssystem gehört und für die Verarbeitung sekundärer Verstärker zuständig ist, war während des Annäherns alkoholischer Bilder stärker aktiviert als während der Vermeidungsreaktionen. Dabei galt: Je mehr positive, emotionsregulierende Wirkung die Probanden Alkohol zusprachen, desto deutlicher ausgeprägt war dieser Unterschied.

Zukünftige Untersuchungen sollten die Reliabilität und Validität dieser Befunde überprüfen. Mögliche technische Probleme, sowie weiterführende Auswertemethoden und

Fragestellungen werden in Bezug auf neuere Entwicklungen in der kognitiv-emotionalen Psychologie und den Neurowissenschaften erläutert. In diesem Zusammenhang werden eigene Vorschläge zur Integration psychologischer Modelle und neuronaler Befunde mittels Ansätzen aus der Embodiment-Forschung aufgezeigt (englisch für "verkörpertes Wissen", d.h. einer gemeinsamen Ebene von psychologischen Phänomenen und neuronalen Prozessen).

# 1 General Introduction

"Survival depends on the maintenance of the body's physiology within an optimal homeostatic range. This process relies on fast detection of potentially deleterious changes in body state and on appropriate corrective responses." (Damasio & Carvalho, 2013, p. 143, line 1-6). Damasio and Carvalho (2013; see also Damasio, 1994b; Damasio, 1996) suggest such changes of body states as caused by the organisms' needs or by environmental stimuli to result in feelings. This affectively enriched feedback allows for the fast detection of the body changes, since it signals the direction of the shift in the homeostatic balance and indicates appropriate reactions (see also 1.1.3.3, 1.2.1 and 1.2.2).

Approach and avoidance reactions can be seen as fundamental behavioural principles and – thereby – as basic dimensions of such regulatory activity (Carver, 2006). A large part of these reactions is triggered automatically: Quickly grabbing delicious food or staying away from unpleasant situations such as painful visits at the dentist's ensures survival and hedonic fulfilment in the short term. Importantly, human beings have a much broader repertoire of behavioural abilities, since they can control and inhibit immediate impulses, which are disadvantageous for the achievement of long-term goals. Not eating the delicious food for avoiding overweight or going to the dental examination for guaranteeing one's health ensures survival in the long term (cf. Krieglmeyer & Deutsch, 2010).

# 1.1 Approach and avoidance:

# Basic principles of motivation and behaviour

Approach and avoidance are behavioural reactions common to many, if not all living species from worms (e.g. *Caenorhabditis elegans*, Brenner, 1974), molluscs (e.g. *Aplysia*, Kandel & Tauc, 1965; Kandel, et al., 2013, chapter 66) and flies (e.g. *Drosophila*, Tanimoto, et al., 2004) to mammals (for summaries see Schneirla, 1959 and Elliot & Covington, 2001, p. 76 et seq.; cf. also Schandry, 2003, chapter 24). Thereby, reflexes as the most rudimentary forms can even be found in primitive organisms such as e.g. amoebae (Schneirla, 1959).

Konorski (1967) suggested a categorization of reflexes into protective reflexes, "[...] which are thrown into action only in case of emergency [...]" (p. 9, line 12-14) and into

preservative reflexes, "[...] which are absolutely indispensable to the preservation of the organisms (or species) whatever the conditions in which they exist [...]" (p. 9, line 10-12). He further subdivided the preservative reflexes into the dichotomy of appetitive reflexes, when behaviour is directed towards an object (food, sex), and defensive reflexes, when behaviour is directed away from a stimulus (danger, toxin).

In their overview on human approach-avoidance motivation, Elliot and Covington (2001) concluded, "[...] that the distinction between approach and avoidance motivation [...] represents a part of the evolutionary heritage that humans share with organisms across the phylogentic spectrum, is instigated immediately and automatically in response to most if not all stimuli humans encounter, is grounded in the basic neuroanatomical structures of the brain, and concords with the intuitively based knowledge of how humans are motivated in their daily lives." (p. 82,. line 26-32).

Lang et al. (1998) summarized that "These motivational circuits are activated primitively by unconditioned appetitive and aversive stimuli. They determine the general mobilization of the organism, the deployment of reflexive approach and withdrawal behaviors, and mediate the formation of conditioned associations based on primary reinforcement." (p. 659, line 27-31). With regard to more complex human-specific emotions, Lang et al. (1998) suggested that "Pleasant emotions are associated with an appetitive system – the primitive neural mediation of approach, hunger, sexual, and nurturant behavior; unpleasant emotions are driven by a defensive system, primitively associated with withdrawal, escape from pain, and defensive aggression." (p. 659, line 34-38).

The huge variety of human emotions and behaviour is in accordance with the fact that our central nervous system (CNS) is much more complicated than the CNS of any animal. Moreover, the neocortex allows for human-specific regulatory capabilities (e.g. Miller, 2000; see 1.1.2). The following chapters describe theories and experiments on human approach-avoidance behaviour and its regulation. Thereby, chapter 1.1.1 gives an overview of important psychological constructs and chapter 1.1.2 presents investigations on neuronal correlates. Chapter 1.1.3 links and complements these descriptions by offering a more detailed look at the underlying mechanisms.

### 1.1.1 Positive – approach and negative – avoidance:

### Basic evaluation – behaviour relations

The idea of seeking pleasure and avoiding pain as fundamental characteristics of human behaviour can already be found in some of the oldest written transmissions of mankind (cf. Rohls, 1999): It is contained in the Epic of Gilgamesh, the legendary Sumerian king of Uruk from the Early Dynastic Period of Mesopotamia (c. 2900 - 2350 BC; Early Bronze Age; speech of the female divinity Siduri, tablet X; see line 77-91 of the translation by Foster, 2001, p. 75 and p. 205). Furthermore, this statement is a major idea of several philosophical traditions, such as the Indian Lokāyata/Cārvāka school (c. 600 BC - 1200 AC; Turner-Lauck Wernicki, 2010; Shastri, 1957, spec. pp. 14-40; Saran, 1994) and the Chinese Mohism represented by Mo-tzu (c. 400s - 300s BC; Loy, 2007), but also of the classic schools of antique Greek and Roman philosophy (Tilley, 1998): The Cyreanic school probably founded by Aristippus of Cyrene (c. 435 - c. 356 BC; O'Keefe, 2001a) and the Epicureanism founded by Epicurus (341 - 271 BC; O'Keefe, 2001b) established the term hedonism (the greek ἡδονή (hēdonē) means pleasure). Their ideas were further represented by the Roman Lucretius (c. 99 - c. 55 BC; Simpson, 2002; Wiker, 2002, chapter 2), but antagonised by Christianity due to the reduction of the doctrin to dissipation and atheism (Wiker, 2002, chapter 3). However, in the renaissance, the rediscovery of Lucretius' poem De Rerum Natura initiated the reappearance of Epicureanism (Wiker, 2002, chapter 4; Casini, 2012). Thinkers of the Enlightened Absolutism (e.g. Hobbes, 1588-1679) and of the Enlightenment (e.g. the atomist Gassendi, 1592-1655; cf. also Bacon, 1561-1626 and Spinoza, 1634-1677) inserted Epicurean materialism into political philosophy and Christian immaterial interpretations, supported by the general rise of the natural sciences (Wiker, 2002, chapter 6 and 7).

In the Empiricism of the 18<sup>th</sup> and 19<sup>th</sup> centuries, Bentham (1748-1832; Sweet, 2001) and Mill (1806-1873; Heydt, 2006) suggested happiness, i.e., the presence of pleasure and the absence of pain, to guide all forms of human behaviour, whereby many processes happen unconsciously (Motivational or Psychological Hedonism). In contrast, in Normative or Ethical Hedonism with the two major streams Hedonistic Egoism and Hedonistic Utilitarianism, Bentham defined collective happiness as criterion for moral rightness presuming conscious deliberation of goals and action consequences (Sweet, 2001). Contemporary varieties of Hedonism differ with regard to e.g. the definition of pleasure and pain or the meaning of qualitative and conscious aspects (Weijers, 2011; Tännsjö, 2007; Onfray, 1992). This

persistence and recurrence of the concept *approach posivite-avoid negative* over the time emphasizes its potential in explaining human behaviour and motivational tendencies.<sup>1</sup>

The significance of these two basic relations between stimulus evaluation and behaviour was also repeatedly confirmed by findings in experimental psychology: In the presence of positively evaluated stimuli, approach behaviour is facilitated, while, in the presence of negative stimuli, avoidance behaviour is facilitated (e.g. Solarz, 1960; Chen & Bargh, 1999; for a more detailed description see also 1.3, spec. 1.3.2; cf. also Neumann et al. (2005) for facial reactions). This relation is bidirectional: The identification of positive valence (e.g. categorizing positive stimuli as positive) is facilitated when approach-related behaviour such as bending the arm is performed and - vice versa - the identification of negative valence is facilitated, when avoidance-related behaviour such as stretching the arm is performed (Neumann & Strack, 2000; see also end paragraphs of 1.1.3). In general, better performance is known to be associated with congruent stimuli-response pairings (e.g. Kornblum, et al., 1990). Accordingly, positive-approach and negative-avoidance assignments can be interpreted as congruent pairings of stimuli and behaviour, while positive-avoidance and negative-approach assignments can be interpreted as incongruent pairings (for a detailed discussion of the underlying mechanisms see 1.3.2, 10.5.1 and 10.5.2). A variety of emotional and motivational theories describes aspects which are of great relevance for understanding and further investigating this phenomenon.

Several theories assume the evaluative categorization of stimuli and situations, in terms of a positive – negative distinction to constitute a fundamental step in information processing, emotional reaction and response preparation. In different influential emotion theories, such a classification is seen as a necessary sub-process contributing to the final emotion. Wundt (Wundt, 1901, see spec. pp. 92 et seqq.) suggested emotions to be characterized by specific values on the two dimensions valence (original: Lust – Unlust) and arousal (Erregung – Beruhigung). These considerations can be found in many later emotion theories, such as the circumplex of Russell (1980; Barrett & Russell, 1998; unpleasantness – pleasantness, activation – deactivation) and the emotion-motivation theory of Lang (1985; Lang, et al., 1990; negative – positive, high arousing – low arousing). The latter theory also underlies the International Affective Picture System (IAPS) and the self-assessment manikin (SAM; Lang,

<sup>&</sup>lt;sup>1</sup> In general, however, there have been and still are many arguments against the validity of hedonism as explanation for all human behaviours: For example, objections of Prudential Hedonism contain that not all forms of pleasure are valuable for well-being and that pleasure is not the only source of intrinsic value (Weijers, 2011; cf. also Moore (1873-1958), Preston, 2005).

1980; Lang, et al., 2005; Bradley & Lang, 1994). With regard to cognitively orientated theories of emotion, Arnold (1969, see spec. chapter 10) specified the evaluation of the valence of a given situation and its consequences for the individual as the first step of an emotional reaction and Lazarus (1991, see pp. 133-152 and p. 215 et seqq.; cf. also Lazarus, et al., 1970) described it as one part of primary appraisal (goal congruency – goal incongruency). Similarly, Scherer (1984; Scherer, 1986, 1988) suggested an *intrinsic pleasantness check* in his component process model of emotions and the dimensions positive – negative and active/aroused – passive/calm in the Geneva emotion wheel (e.g. Scherer, 2005). These two dimensions are further supported by investigations on the dimensionality of the sematic space of human language. Factor analyses revealed evaluative adjectives to mainly load on *evaluation* and – to a lower extent – on *dynamism* (potency and activity; Osgood, et al., 1957, see chapter 2, pp. 31-75 for an overview on the beginnings of such research). In line with the theoretical considerations, both factors appeared to be bipolar.

Importantly, there is evidence from experimental psychology that the stimulus categorization as either positive or negative occurs automatically. Affective priming effects describe the automatic influences of the valence of a prime stimulus on a following reaction: In the classical experiments (exp.) by Fazio et al. (1986), participants faster categorized adjectives as either positive or negative (original: good or bad), when these stimuli were preceded by a valence congruent word for which participants had strong valence associations. Importantly, such an effect was only obtained, when the stimulus onset asynchrony (SOA) between the prime and the target stimulus was too short to allow for a reaction to the target that could comprise intentional and conscious processing of the prime characteristics (300 ms; exp. 2 and 3). Subsequent studies, which used a huge variety of different verbal and pictorial stimuli as primes and targets, showed the stability and robustness of affective priming effects, as well as their validity when the valence of the target stimuli was not consciously evaluated (for a commented review see Fazio, 2001; for a comment on technical aspects and mechanisms of affective priming see Klauer & Musch, 2003).

Thereby, studies revealing subliminal primes to exert influence on reactions to supraliminal targets most strongly supported the interpretation that the affective evaluation of the prime stimulus is an automatic process (e.g. Greenwald, et al., 1996). Fazio et al. (1986) interpreted these evaluations as *attitudes* (for a more sophisticated definition see 1.1.3).

Discussion arose with regard to the question of attitude strength to constitute a moderating factor of the impact on behaviour. In short, the attitude accessibility model by Fazio et al. (1986; Fazio & Williams, 1986; Fazio, et al., 1989) emphasized that a certain strength of the attitude is necessary to cause influences on behaviour, while Bargh et al. (1992) stated automatic influences regardless of attitude strength (cf. also Bargh, 1997). Furthermore, subsequent research showed automatically activated attitudes to significantly determine processes underlying everyday behaviour such as information processing, decision making and judgemental processes via automatic capture of attention and activation of related categorization options (for reviews see Bargh, 1997 and Fazio, 2001).

The functional value of such automatic attitude activation is seen in the facilitation of reactions to a complex environment: Chen and Bargh (1999) stated that "In our view, the automatic evaluation effect is an adaptive back-up system for those times when conscious processing is elsewhere [...] by itself, evaluation of stimulus as good or bad does not provide a person any adaptive benefit – only if it immediately prepares appropriate responses to the stimulus would it be of any value." (p. 217, line 13-15 and 20-23, left text column). Fazio (2001) concluded that "By forming attitudes, individuals structure their social world into classes of objects that merit either approach or avoidance behaviour [...]." (p.130, line 38-40).

The assumption that the valence assigned to a certain stimulus determines behaviour in terms of a positive-towards and negative-away distinction can be found in many theoretical orientations. Elliot and Covington (2001) gave a detailed overview on this aspect. In short, hedonistic tendencies as fundaments of all human behaviour were already postulated by the pioneer of emotional research James (1842-1910, James, 1890b, see spec. chapter 25). In drive theories, stimuli were assumed to acquire positive or negative valence and to steer behaviour according to the organisms needs (e.g. Miller, 1944). Researchers investigating learning mechanisms also referred to the towards-away distinction, specifically with regard to reinforcement and repetition of behaviours leading to a positive end and weakening and inhibition of behaviour leading to negative consequences (e.g. Thorndike, 1911, see spec. chapter 6; Rotter, 1973, see spec. chapter 5). Several theories described interindividual personality differences to be based on differences in the evaluation of stimuli and the related approach-avoidance behaviour (Eysenck, 1966, see spec. chapter 2; Gray, 1990b, see also 1.1.2; Heider, 1967, see spec. chapter 10).

The Gestalt psychologist Lewin stated that "[...] one might distinguish two large groups of valences according to the sort of initial behavior they elicit: the positive valences (+), those effecting approach; and the negative valences (-), or those producing withdrawal or retreat." (Lewin, 1935, p. 81, line 15-19). In his field theory, Lewin (1938/1968) assumed human behaviour to be a function of psychological constructs such as needs and of environmental constructs such as the characteristics of an object (p. 96: Be=F(P,E), with Be=behaviour, P=individual and E=environment; however, see also the more sophisticated depiction of environmental influences on pp. 107-109): Both, the person as well as the environment characteristics being relevant at a specific moment contribute to the valence assigned to a stimulus and - thereby - to its motivational force (see also Lewin, 1943). This force steers human behaviour in the so-called hodological space (i.e., the available environmental space) for the sake of reaching an aim and releasing tension caused by needs (Lewin, 1938/1968, see spec. pp. 82-86 and pp. 87-109; p. 88: if Va(G) > 0 then  $|f_{P,G}| > 0$  and if Va(G) < 0 then  $|f_{P,G}| > 0$ , with Va(G)=valence of object G and P=individual; see also figure 33 on p. 91). Together with other driving or restraining forces given at the same time, the motivational force constitutes the so-called force field. In case of different competing forces, a response conflict arises (Lewin, 1938/1968, pp. 175-201).

The biphasic emotion theory of Lang et al. (1990) also contains this assumption, that stimulus valence crucially determines the general direction of behaviour by evoking motivational forces<sup>2</sup>: "It is postulated that all affects are primitively associated with either a behavioral set favoring approach, attachment, and consummatory behavior or a set disposing the organism to avoidance, escape, and defense." (p. 377, line 9-13, left text column). Following Frijda (1986, spec. p. 72 et seqq.), Lang et al. (1990; Lang, 1995) defined emotions as action dispositions, preparing the organism for quick appropriate reactions. Lang (1995) suggested this reaction preparation to work via the activation of an approach motivational system in case of positively evaluated stimuli and via an avoidance motivational system in case of negatively evaluated stimuli. Thereby, he assumed a process called motivational priming to result in facilitated approach behaviour towards positive stimuli and facilitated avoidance of negative stimuli: "Specifically, associations, representations, and action programs that are linked to the engaged motivational system have a higher probability of access [...], and conversely, mental events and programs linked to the nonengaged

<sup>&</sup>lt;sup>2</sup> The term *motivation* refers to the impetus, which results from internal needs, cognitive motives and external stimuli (Häcker & Stapf, 2009).

system have a reduced probability and strength of activation." (p. 377, line 20-22 and 24-26, right text column). In other words, the affective evaluation of a stimulus and the subsequent activation of the related motivational system prime or pre-activate behavioural tendencies which are compatible with the stimulus valence.

With regard to concrete motor programs, Lang et al. (1993) reported significant correlations between participants' explicit ratings of valence (pleasure) and activity of two facial muscles as assessed via electromyography (EMG): Positive ratings showed a Ushaped quadratic relationship to the activity of the zygomaticus muscle, the essential muscle for smiling. Thereby, the right arm of the U indicated a positive linear relation, i.e. the more positively participants rated positive IAPS pictures, the stronger activated was their zygomaticus muscle, when the pictures elicited a certain amount of positive affect. And, the more negatively participants rated negative IAPS pictures, the stronger activated was their corrugator muscle, which is fundamentally responsible for frowning (cf. Cacioppo, et al., 1986b; cf. also Neumann, et al., 2005 as described in 1.1.3). Furthermore, several findings associated vertically nodding the head with positive affect and approach motivation, while horizontally shaking the head was linked to negative affect and avoidance motivation (e.g. Wells & Petty, 1980; Tom, et al., 1991). Two other muscles are of specific interest for approach-avoidance behaviour: The flexor muscle is responsible for bending the arm in approaching positive stimuli such as nutrition to the body or for embracing mating partners. In contrast, the tensor muscle is responsible for stretching the arm, i.e., for avoiding stimuli (cf. Cacioppo, et al., 1993). A more critical and sophisticated report of theories and findings on the relation of these arm movements to stimulus evaluation and approach-avoidance tendencies is given in 1.3.1 and 11.2.

### 1.1.2 Correlates in the nervous system

The conceptualization of approaching positive stimuli and avoidaning negative ones as fundamental classes of behaviour led to the hypothesis of specialized nervous systems for their processing (cf. Carver, 2006). Animal and neuroscientific research on mechanisms in the nervous system revealed the following evidences for different, specialized structures.

Examples of appetitive and protective reflexes as most primitive forms of approach and avoidance behaviour are already given in 1.1. Neurophysiological research was also helpful for understanding human defensive reflexes. Lang and colleagues showed the so-called startle eyeblink modulation: The intensity of the startle reflex (a defensive reflex and part of the orienting reflex) was differentially modulated by the individual's affective background (Vrana, et al., 1988; Bradley, et al., 1990). EMG measurements of the musculus orbicularis oculi showed the amplitudes of the sub-component blink reflex elicited by acoustic startle probes (and also visual ones, Bradley, et al., 1990) to be higher, when participants processed negatively valenced stimuli, and to be lower during the presentation of positively valenced material. Importantly, additionally assessed measures of interest (ratings and viewing time) and arousal (ratings and skin conductance) in the study of Bradley et al. (1990) revealed evidence, "[...] that the valence-reflex relationship is not fundamentally attentional and that it is not a nonspecific effect of drive or activation, [...]" (Lang, 1990; p. 383, line 11-13, right text column). Lang and colleagues did not investigate an equivalent reflex for appetitive motivation, such as e.g. salivation. However, the modulation of the startle reflex in both directions - negative-enhanced and positive-reduced - was interpreted as evidence "[...] that emotional valence is a general information-processing category, with sensory, central, and response processing implications." (Lang, et al., 1990, p. 392, line 11-13, right text column). Theses findings further support the assumption of emotional psychologists that stimulus valence is automatically processed (see 1.1.1): Reflexes are automatic reactions, which cannot be voluntarily steered (cf. Grewe, 2001). While their comparability to more complex human behaviour is restricted (see also 11.2), these results show important basic principles. In his biphasic emotion theory, Lang et al. (1990) stated that all affective evaluations are associated with either approach or avoidance behaviour (see 1.1.1) and further, "[...] that affective behavior is organized biphasically at all levels of response complexity, from cognitive events to the exteroceptive reflexes." (p. 381, line 35-37, right text column).

Furthermore, Greenwald et al. (1998) and Hamm et al. (1993) emphasized parallels in the modulatory patterns of the startle response in animals and humans (for a summary of the involved neuronal structures and neurotransmitters see also Birbaumer & Schmidt, 2003, figure 26-14, p. 666). Lang et al. (2000; Lang & Davis, 2006) concluded that defensive reflexes in humans might rely on the same neuronal structures constituting the fear circuit in rats, specifically on the amygdala (e.g. Davis, et al., 1982; Davis, 1992; LeDoux, 1995). This assumption also followed an earlier suggestion of Masterson and Crawford (1982) that

negative affect in humans might be the output of the same defense system underlying avoidance behaviour in animals (see p. 664, last passage of right text column).

By electrically stimulating specific limbic regions, it was possible to gain results not only on brain structures related to fear and avoidance, but also on brain structures related to approach motivation (pleasure centres; Olds, 1956a). Rats frequently to persistently pressed a lever for intracranial self-stimulation, when the electrodes were implanted into the septal area (Olds & Milner, 1954; Olds, 1956b). Subsequent research also using lesioning procedures, drug administration and brain imaging techniques identified the mesolimbic dopaminergic pathway and dopamine (DA) release in its projection area nucleus accumbens/ventral striatum to underlie such incentive motivation causing approach behaviour (for a summary see e.g. Birbaumer & Schmidt, 2003, pp. 640-644). In contrast, electrical stimulation of the hypothalamus/thalamus caused cats to show different types of avoidance behaviour, whereby the avoidance of food (exp. 3) might be seen as the most powerful evidence for unpleasant experiences (Delgado, et al., 1954; cf. also Olds, 1956a). In rats, acetylcholine release in the nucleus accumbens as assessed via in vivo microdialysis was associated with inhibition of behaviour such as e.g. satiation and avoidance of negative conditioned stimuli (Mark, et al., 1992; Hoebel, et al., 2008; cf. Hoebel, et al., 1999). This might be seen as a cholinergic stop system of the DA system, whereby the realization of the motor reactions resulting from its activity depended on a sufficiently high DA level (Hoebel, et al., 2008).

While these investigations and findings presented the two motivational systems as relatively independent constructs, Dickinson and Dearing (1979) extended Konorski's suggestion (Konorski, 1967; see 1.1) and proposed a model also taking into account appetitive-aversive interactions: Findings on counterconditioning procedures led to their model of reciprocal inhibitory interactions between the aversive and appetitive motivational systems (see figure 8.3, p. 214, Dickinson & Dearing, 1979). In humans, the conceptualization of these two systems is even more complicated. In his evolutionary orientated comparison of approach and withdrawal behaviour in animals and humans, Schneirla (1959) summarized that "Much evidence shows that in *all* animals the speciestypical pattern of behavior is based upon biphasic, functionally opposed mechanisms insuring approach or withdrawal reactions [...] in general, what we shall term the *A-type* of mechanism, underlying approach, favors adjustments such as food-getting, shelter-getting, and mating; the *W-type*, underlying withdrawal, favors adjustments such as defense,

huddling, flight, and other protective reactions. Also, through evolution, higher psychological levels have arisen in which through ontogeny such mechanisms can produce new and qualitatively advanced types of adjustement to environmental conditions. Insects are superior to protozoans, and mammals to insects, in that ontogeny progressively frees processes of individual motivation from the basic formula of prepotent stimulative-intensity relationships." (p. 4, line 8-10 and line 12-18; see also the schema on p. 27)<sup>3</sup>.

In general, the extremely well developed prefrontal cortex (PFC) is seen as neural correlate of regulatory control abilities in humans (e.g. Ernst & Fudge, 2009). The electrophysiological research of Davidson (1984; Davidson, et al., 1990; Davidson, et al., 2000) revealed evidence for specialized approach-avoidance systems in terms of hemispheric asymmetry: The frontal cortex of the left hemisphere was proposed to be responsible for approach behaviour (approach system) and the frontal cortex of the right hemisphere to be responsible for avoidance behaviour (withdrawal system). Participants watched short movies containing facial expressions of disgust and happiness. The electroencephalogramm (EEG) revealed disgust to be associated with reduced power  $(\mu V^2/Hz)$  in the alpha band (8-13 Hz) in the right hemisphere compared to the left hemisphere and compared to happy faces in frontal and – less clearly – in anterior temporal regions (Davidson, et al., 1990). For happy facial expressions, significantly reduced alpha power was found in left compared to right anterior temporal regions and compared to disgust movies. Importantly, such a differentiation was not found, when negative and positive films were compared without specifically selecting disgust and happiness.

Further research emphasized, that this asymmetry is not valence-based, but depends on a differentiation between the motivational tendencies of approach and avoidance. Harmon-Jones and Allen (1998) showed anger, i.e., a negative emotion, which often causes approach tendencies, to be associated with reduced alpha power, i.e. with enhanced activity in the left anterior hemisphere (cf. also Berkman & Lieberman, 2010). A meta-analysis of 65 imaging studies on emotional processing supported these interpretations with some restrictions (Wager, et al., 2003; cf. also Feldman Barrett & Wager, 2006). In the lateral PFC, there was no lateralization for avoidance behaviour, but – by tendency – a left-sided lateralization for approach behaviour. Moreover, the medial PFC revealed the unexpected

<sup>&</sup>lt;sup>3</sup> Note that Schneirla (1959) differentiated between the concepts of *approach vs. withdrawal* as elementary behaviour and *seeking vs. avoidance* as evolutionary and developmentally higher ordered forms of behaviour.

pattern of a left lateralization for avoidance behaviour. Such contradicting findings might be understood in the light of another study (Hagemann, et al., 2005), which revealed only 40-50% of anterior asymmetry to be explicable by individual trait differences. Moreover, concentrating on the neocortical level might be too restrictive, since "[...] this neural augmentation developed to better serve survival needs, and anatomy shows clearly that the extended cortex is intimately connected to its motivational subcortical and primitive cortical roots." (Lang, et al., 1998, p. 660, line 24-27).

This fact is taken into account by another theory also assuming specialized neuronal systems for approach and avoidance behaviour. In his Reinforcement Sensitivity Theory (RST), Gray (1981; Gray, 1990b; Gray, 1994) described three fundamental emotion systems (see also the figures on p. 245 & 246 in Gray, 1994), which were re-grouped into two emotional-motivational systems in the revised RST (rRST; Gray & McNaughton, 2000). Gray based his suggestions on results from neuropsychology, conditioning procedures, psychopathology, psychopharmacology, lesion studies and animal research. In the literature cited above, Gray assumed these systems to be existent in both the mammalian and human brain and to be characterized by specific neural structures and cognitive processes determining the final behavioural reactions to reinforcement-related inputs.

At one side, a behavioural approach system, the so called Behavioural Approach System (BAS) deals with appetitive motivation and approach behaviour to positive stimuli and security (Gray, 1990b). A more detailed description of the BAS is given in 9.2, since one of its sub-components was of specific interest for study B2. However, Gray himself concentrated much more on the investigation of the behavioural avoidance system, which deals with aversive motivation and withdrawal or avoidance behaviour (Gray, 1990b; Gray, 1982). It consists of the Behavioural Inhibition System (BIS) and the Fight/Flight/Freeze System (FFFS; Gray & McNaughton, 2000). The FFFS reflects sensitivity to punishment: It is activated by unconditioned stimuli of punishment and non-reward and elicits unconditioned flight behaviour and defensive aggression (Gray, 1990b). The BIS, in contrast, is described as a conflict detection system: It can be seen as a monitor system, which, in case of a mismatch between expected and current state, switches from its comparator function to a regulation process (Gray, 1982, chapter 10; Gray, 1990b). It is responsible for passively approaching security by enhancing attention allocation and by inhibiting ongoing behaviour, i.e., it contributes to the solution of conflicts by facilitating defensive behaviour. Gray (1982) postulated an important role of the BIS in the generation, maintenance and cessation of anxiety and explained the anxiolytic effects of drugs such as benzodiazepines and barbiturates in terms of a downregulation of the BIS (see also Gray & McNaughton, 2000).<sup>4</sup>

With regard to the neuronal level, Gray suggested the limbic system and the basal ganglia to constitute a system for the attainment of goals and to mainly underlie the BAS (Gray, 1995; Gray & McNaughton, 1996; see figure 10, p. 16 of Gray, et al., 1991 for a schematic overview of all included structures and their connections). The limbic structures are responsible for the sensory aspects of goal attainment, namely for recognizing goals, i.e., opportunities to gain positive reinforcers, and for evaluating the consequences of actions. The motor aspects, i.e., the establishment and execution of motor programs, are mediated by the basal ganglia. Thereby, GABAergic (gamma aminobutyric acid), glutamatergic and dopaminergic neurotransmitter projections are involved and the frontal cortex is suggested to coordinate the different subprocesses. Furthermore, Gray (1982; Gray, 1987b; Gray & McNaughton, 2000) suggested the septohippocampal system (SHS), consisting of the hippocampal formation and the medial and lateral septal area, and the Papez circuit to constitute the neuronal basis of the BIS. The orbitofrontal cortex (OFC) is assumed to have influences on the activity of the SHS (see Gray, 1982, figure 10.8, p. 294 for a schematic overview of all included structures and their connections). With regard to neurotransmitter systems, noradrenergic and serotonergic projections were shown to be involved (Gray, 1982, see spec. chapter 11). The FFFS was related to activity in the periaqueductal grey, the hypothalamus and the amygdalae, i.e., to structures associated with primary defensive reactions (Gray, 1987b; Gray & McNaughton, 1996).

In defining his theory, Gray started from the personality dimensions extraversion and neuroticism as suggested by Eysenck (1966; for a comparison see e.g. Matthews & Gilliland, 1999). Following also his own results on the relationship between eye blink conditioning and personality characteristics in humans, Gray (1970; Gray, 1987a) proposed a rotation of the dimension *extraversion* for 30° in direction of the dimension *neuroticism* and renamed it *impulsivity*. The BAS is assumed to be its neurobiologicial basis. Similarly, the dimension *neuroticism* was rotated for 30° in direction of *introversion* (as the other pole of the

<sup>&</sup>lt;sup>4</sup> Other conceptualizations refered to these two systems as Behavioural Activation System (Fowles, 1980; Cloninger, 1987, for a comparison of Cloninger's personality dimensions *reward dependence* and *harm avoidance* to Gray's dimension *impulsivity* and *anxiety* see table 1 on p. 575 of this reference, see also Zuckerman, 2005, pp. 15-26 for a summary of three-dimensional models of personality) or Behavioural Facilitation System (Depue & Collins, 1999) and Withdrawal System (Davidson, et al., 1990), respectively.

extraversion dimension) and renamed anxiety, with the BIS as neurobiological correlate (see also Gray, 1972; Gray, 1981; Pickering, et al., 1999). Elektrophysiological research supported Gray's alteration of Eysenck's personality theory: Bartussek et al. (1993) showed higher amplitudes of the P2, N2 and P3 ERPs in extraverted individuals to auditive stimuli signaling winnings, what is in line with the assumption of a higher reactivity of their BAS; introverted persons showed stronger reactions to losses as hypothesized in terms of a higher reactivity of the BIS. Recent functional magnetic resonance imaging (fMRI) studies showed such interindividual differences to also covary with activity in brain regions related to reward processing (stronger BAS – stronger activity in ventral striatum and OFC, Hahn, et al., 2009) and with the functional connectivity strength between structures associated with punishment (stronger BIS - stronger hippocampus-amygdala connectivity, Hahn, et al., 2010). In the current thesis, the investigation of interindividual differences concentrated on the RST (see study B2). However, it should be noted, that the theories of Davidson and Gray might also be conformable or complemental: Harmon-Jones and Allen (1997) showed higher BAS scores to be associated with relatively stronger left than right hemispheric frontal activity (reduced alpha band activity; cf. also 10.2.3).

### 1.1.3 The link from affective evaluations to behavioural tendencies

This chapter complements the mechanisms of affective evaluations causing approach and avoidance reactions as roughly outlined in 1.1.1 and presents theories linking these mechanisms to their neuronal correlates.

### 1.1.3.1 Emotions and attitudes

Both, affective evaluations and behavioural reaction tendencies are parts of emotions (Scherer, 1990).<sup>5</sup> The term *emotion* is derived from the Latin word *emovere* (to move forth/away), thereby already implicating a link between affect and action (Häcker & Stapf, 2009, p. 255). In modern psychology, there are many theories on emotions (see appendix of Kleinginna & Kleinginna, 1981). Most of these different views represent hybrid theories, i.e., they assume several basic components to be essential for an emotion, whereby they differ

<sup>&</sup>lt;sup>5</sup> I refer to the common distinction of the terms *affect*, *emotion* and *feeling* (see e.g. Otto, et al., 2000): *Affect* simply means the result of the evaluation of the valence of a given situation or stimulus, *emotion* means the entity of affective, cognitive, behavioural, neurophysiological and motivational reactions related to such an evaluation, *feeling* means the subjective, conscious experience of an emotion.

with regard to the question of necessity and causal or sequential relations of the sub-components. Kleinginna and Kleinginna (1981) subsumed the existing definitions in the following way: "Emotion is a complex set of interactions among subjective and objective factors, mediated by neural/hormonal systems, which can (a) give rise to affective experiences such as feelings of arousal, pleasure/displeasure; (b) generate cognitive processes such as emotionally relevant perceptual effects, appraisals, labeling processes; (c) activate widespread physiological adjustments to the arousing conditions; and (d) lead to behavior that is often, but not always, expressive, goaldirected, and adaptive." (p. 355, line 25-32).

This latter statement, that emotions have motivational functions which cause reaction tendencies allowing for quick appropriate responses and – thereby – guaranteeing the organism's survival, was specifically emphasized by evolutionary orientated emotion theorists such as Darwin (1872/1998, see spec. chapters 1-3), McDougall (1908/1926, see spec. chapters 2 and 3) and Plutchik (1980, p. 129: postulate 3 of his theory). The biphasic emotion model of Lang et al. (1990, see 1.1.1) defining emotions as action dispositions is an example for modern theories maintaining these assumptions.

Cognitive emotion theories assume emotion specific action tendencies to be one of the results of cognitive evaluations and part of the final emotion (Arnold, 1969, see spec. pp. 177-182 and pp. 241-248; Frijda, 1986, see spec. pp. 69-94; Lazarus, 1991, see spec. pp. 203 et seqq.; Scherer, 1986). In contrast, based on experimental findings such as the mere exposure effect<sup>6</sup> and the above described affective priming effects, Zajonc (1980) postulated the independence of affective and cognitive systems (separate system model). He refered to such automatic affective processes as *hot cognitions*, a "class of feelings [...] involved in the general quality of behavior that underlies the approach-avoidance distinction." (Zajonc, 1980, p. 152, line 9-11, right text column).

In general, such unspecific behavioural approach-avoidance tendencies resulting from the basic evaluation of the stimulus valence as either positive or negative might be seen as

<sup>&</sup>lt;sup>6</sup> For an overview on attitude effects see e.g. Greenwald and Banaji (1995, pp. 9-10). They describe the main mechanism as a transfer of the evaluation of one object onto another one. In short, *halo effects* mean influences of a known, but irrelevant attribute B on the judgement of a novel attribute A of a stimulus. *Mere exposure effects* mean enhanced liking of a stimulus due to frequent presentations. The term *subliminal attitude conditioning* is used by Greenwald and Banaji (1995) to refer to the valence attribution of a subliminal stimulus to a novel stimulus.

the difference between emotions and attitudes with regard to their relations to behaviour (Neumann, 2003; Campbell, 1963, p. 96; cf. also Wyer Jr., et al., 1999, see spec. p. 7; Clore & Colcombe, 2003, see spec. table 13.2, p. 338). The affective processes investigated in the current thesis represent attitudes and unspecific approach-avoidance tendencies rather than emotions and related specific action tendencies (see also 1.3 and 10.6.2).

The term attitude is derived from the Latin words apto (aptitude, fitness) and acto (postures of the body; Bull, 1968, p. 129). Early working definitions of attitudes already included the aspect of a direct link to behaviour: Critically reviewing the concepts of mental and motor attitudes existing until then, Allport (1935/1967) concluded that "An attitude is a mental and neural state of readiness, organized through experience, exerting a directive or dynamic influence upon the individual's response to all objects and situations with which it is related." (p.810, line 7-10; cf. also the conclusions of McGuire, 1969 (spec. pp. 155-157) on the cognitive-affective-conative components view). Campbell (1963) emphasized the motor aspect even stronger by defining attitudes as acquired behavioural disopositions (see spec. pp. 95 and 96 of this reference). Osgood (1957) summarized that attitudes are implicit, "[...] predispose toward an evaluative response [...]" (p. 189, line 26) and can be seen as "[...] tendencies of approach or avoidance [...]" (p. 169, line 27), since "[...] attitudes can be ascribed to some basic bipolar continuum with a neutral or zero reference point, implying that they have both direction and intensity [...]" (p. 189, line 29 & 30 - p. 190, line 1). "This characterization of attitude as a learned implicit process which is potentially bipolar, varies in its intensity, and mediates evaluative behavior, suggests that attitude is part [...] of the internal mediational activity that operates between most stimulus and response patterns." (Osgood, et al., 1957, p. 190, line 5-9; cf. also Doob, 1947, p. 136). Zajonc and Markus (1982) added that "Since attitudes contain such a substantial affective component, they are likely to have multiple representations – and somatic representations are probably among the more significant ones (p. 130, line 18-21, left text column). In general, cognitive, affective and behavioural components are the classical suggestions for subparts constituting an attitude (Rosenberg & Hovland, 1960; for a description of the development of the concept attitude see Fleming, 1967). For linking all these characteristics to the following theoretical outlines, the definition given by Greenwald and Banaji (1995) might be the most memorable: "Attitudes are favorable or unfavorable dispositions [...]" (p. 7, line 26, left text column).

### 1.1.3.2 Network models: Associative explanations

In the first part of this chapter (see 1.1.1), I described affective priming effects due to automatic attitude activation. With regard to the mediating mechanisms<sup>7</sup>, explanations for semantic priming effects were taken as initial point (e.g. Neely, 1977): These explanations refer to theories which assume conceptual knowledge to be stored in terms of associative networks, i.e., each stimulus feature is a node in a network and the activation of one node spreads to others, thereby activating a complete representation of a stimulus or situation (Anderson & Bower, 1973, see spec. chapters 4,7 and 11; Collins & Loftus, 1975; for a graphical illustration of a network account see 1.2.1). Spreading activation models of semantic memory explain priming effects by activation spreads, whereby the probability of activation spreading from one node to another is the higher the more features accord between the two nodes (Neely, 1977; Lorch, 1982). Bower (1981) suggested emotions and evaluative concepts to be also stored in such networks. He assumed spreading activation to underlie experimental results, which show facilitation effects in case of congruent mood behaviour combinations, such as e.g. recall of affective experiences. In accordance with this view, Fazio (2001; Fazio, et al., 1986) supposed a spread of activation from affective primes to their associated evaluation. Thereby, however, he did not give any details on the further relation to the actual behavioural realization.

Lang (1995) proposed a similar explanation for his startle reflex findings and evaluative behaviour in general. According to his suggestions, such activation spreads also comprise the activation of behavioural concepts and motor programs. Concentrating on the investigation of fear processes, Lang et al. (1983; Lang, 1985) described phobic reactions by means of a network model comprising representations of stimuli, their meaning and the related responses. Later, he extended the basic assumptions of this example to the statements of his bioinformational associative network model (Lang, et al., 1998). There, the first essential aspect is constituted by so-called action memories, i.e., memories of responses including memories of related motor programs and physiological patterns. Thereby, importantly, Lang et al. (1998) suggested the network to also comprise non-

<sup>&</sup>lt;sup>7</sup> Another explanation, the so-called response competition model of priming, followed explanations given for the Stroop effect from parallel response competition models (MacLeod, 1991): The evaluation of the prime prepares the response associated with this stimulus. The target also elicits evaluative processes and associated response tendencies. Reactions are facilitated when the two response tendencies are congruent, since the pre-activation due to the prime has already lowered participants' response threshold for this reaction. In contrast, reactions are inhibited when the two response tendencies are incongruent (Klinger, et al., 2000). See also Klauer and Musch (2003) for an overview of suggested mechanisms.

semantic representational levels – an assumption based on findings on *as if* phenomena (see below for a detailed discussion of their meaning). The second essential aspect of this theory is the assumption that such action memories are "[...] the most primitive of memorial forms [...]" (Lang, et al., 1998, p. 659, line 10-11) and – thereby – part of the network constituting an emotional responses (cf. also Lang, et al., 1983; Lang, 1985).

In 1.1.1, I already described the suggestion of Lang (1995) that evaluative processes activate motivational systems, which – in turn – activate behavioural programs. This specification is another important aspect of his theory, whereby Lang et al. (1998) assumed "[...] that emotion networks include direct connections to the brain's primary motivational systems. These systems are neural circuits that were laid down early in our evolutionary history, in primitive cortex, subcortex and mid-brain, that activate behaviors basic to the survival of individuals and species." (p. 659, line 21-25). However, Lang et al. (1998) did not give any closer details on the nature of these connections between cognitive representations of stimuli (sensory information), meaning (declarative knowledge) and responses (procedural knowledge) with the neuronal motivational circuits (cf. figure 3 of this reference).

### 1.1.3.3 Neuronal level: Damasio's as if body loops

This question was addressed by Damasio, a representative of the view that emotions are not less advantageous for the guidance of human behaviour than rational decisions are (see e.g. Damasio, 1998; Damasio, 1994b; cf. also affect-as-information theories, e.g. Wyer Jr., et al., 1999; Clore, et al., 2001). The high functional value attributed to feelings is the starting point of his somatic marker hypothesis (Damasio, et al., 1991; Damasio, 1994a, chapter 8), a theory on decision making specifically in uncertain situations. There, Damasio postulated the importance of "[...] an emotional mechanism that rapidly signals the prospective consequences of an action, and accordingly assists in the selection of an advantageous response option." (Bechara & Damasio, 2005, p. 339, line 3-5). This theory is described in more detail in 1.2. Here, I concentrate on its core elements, the *body loops* and the *as if body loops*, which origin from the assumption, that homeostatic regulation is essential for survival (see 1 and 12) and that "[...] emotion and the experience of emotion, are the highest-order direct expressions of bioregulation in complex organisms." (Damasio, 1998, p. 84, line 23-25, left text column).

Homeostatic regulation is possible, since the brain as main generator of emotions is connected to the effector organs of the body (cf. Lang, et al., 1998, p. 658 et seq.), whereby "[...] emotions operate along the dimensions of approach or aversion, of appetition or withdrawal." (Damasio, 1998, p. 86, line 33-34, left text column). Damasio, thereby, connected considerations of Darwin (1872/1998), James (1890b; James, 1890a) and the Neural Darwinism of Edelman<sup>8</sup> (Edelman, 1987, see spec. part 3) with findings from modern neurological research in patients with specific brain damages (Bechara & Van Der Linden, 2005; see also 1.2.2). He stated that "An emotion is defined a a collection of changes in body and brain states triggered by a dedicated brain system that responds to specific contents of one's perceptions, actual or recalled, relative to a particular object or event." (Bechara & Damasio, 2005, p. 339, line 13-15). The resulting somatic state, i.e., the triggered physiological modifications (changes in internal milieu and viscera as well as in the musculoskeletal system) are relayed to the brain and "[...] lead to the development of somatic state patterns in brainstem nuclei (e.g., the PBN), and in somatosensing cortices (e.g., insular/SII, SI cortices, and cingulate cortices)." (Bechara & Damasio, 2005, p. 341, line 15-17 and cf. figure 2, p. 342; cf. also figure 1, p. 85, Damasio, 1998). This body loop is assumed to work via the spinal cord, humoral signals and specifically the vagus nerve. Together with cognitive changes related to the emotional state, this feedback forms a complex mental state, namely feelings. Importantly, mental representations of future events can directly activate the somatic state patterns, which are stored in the brainstem nuclei and the insular/SII, SI cortices, thereby re-creating the somatic state, the feeling and the contained information on probable consequences. Since the body is not engaged, Damasio termed this process the as if body loop (Bechara & Damasio, 2005).

In sum, Damasio specified, how the neural level can be seen as the integration centre of stimulus representations, affective evaluations and behavioural preparation. Such a common basis is possible due to the fundamental alliance of brain and body or in other words, due to a common substrate of mind and body, a view following the rationalism of Spinoza (1634-1677; Damasio, 2003, spec. pp. 209-217) and contradicting the dualism of Descartes (1596-1650; Damasio, 1994a, see spec. chapter 11)<sup>9</sup>.

<sup>&</sup>lt;sup>8</sup> Edelman (1987) stated that "[...] the brain is dynamically organized into cellular populations containing individually variant networks [...]" (p. 4, line 36 & 37 - p. 5, line 1), whereby epigenetic mechanisms and frequent repetitions of activation patterns determine the structure and function of these networks (pp. 4-8).

<sup>&</sup>lt;sup>9</sup> Damasio altered Descartes' conclusion "cogito ergo sum" into "I feel, therefore I am" (Damasio, 1994a, chapter 11; cf. also Damasio, 2001).

#### 1.1.3.4 Embodiment theories

The assumption that neuronal activation patterns are the integration basis of all information processing is common to all embodiment theories (for reviews see Niedenthal, et al., 2005b; Niedenthal, et al., 2005a). There, it is suggested that information processing is based on mental representations, i.e. internal symbols, of the processed stimuli. However, in contrast to amodal theories of information processing, memory and emotion such as e.g. the above presented network models, embodiment theories assume knowledge to be embodied, i.e., to be based on bodily states and specific activation patterns in the modality specific systems of the brain (e.g. Barsalou, 1999; Glenberg, 1997; see also Niedenthal, et al., 2005a, p. 23). These systems are the sensory systems responsible for perception, the motor systems responsible for action and introspective systems underlying conscious experiences (Niedenthal, et al., 2005b). Thereby, as suggested by Damasio (1998), reacting to the environment creates a repertoire of such modality-specific responses (online embodiment). These stored embodiments can be re-activated, when the related stimulus is not present, e.g., when perceiving a symbol (offline embodiment; Wilson, 2002, see spec. claim 6, p. 632 et seqq.).

One representative of embodiment theories is the perceptual symbol systems (PSS) theory (Barsalou, 1999), which states that "[...] cognition is inherently perceptual, sharing systems with perception at both the cognitive and the neural levels." (p. 577, line 13-15, left text column) and "[...] that simulations of perceptual, motor, and introspective experience underlie the representation and processing of knowledge." (Niedenthal, et al., 2005b, p. 194, line 48-50, left text column). Thereby, the convergence zone (CZ) theory of Damasio (1989) was taken as neuronal fundament (see Barsalou, 1999, p. 583, left text column and author's response, R1.1, p. 637, right text column). Damasio (1989) proposed simultaneous multiregional neuronal activation to underlie memory processes and cognition in general: Perception of physical structures "[...] occurs in fragmented fashion and in geographically separate cortices located in modal sensory cortices." (p. 39, line 5-6; cf. p. 27, bulletin (1): sensory and motor primary and early association cortices). The integration of these fragments depends on their simultaneous co-activation. Such combinatorial arrangements of synaptic patterns of activity in neuronal ensembles, so-called binding codes, are stored in convergence zones. Convergence zones are the amodal device for triggering simultaneous activation according to these combinations and their neuronal substrates are "[...] association cortices of different orders, both sensory and motor, some limbic structures

(entorhinal cortex, hippocampus, amygdala, cingulate cortices), and the neostriatum/cerebellum [...]" (p. 27, line 18-20, see also p. 45 et seq.). 10

The PSS theory assumes, that the stored modality-specific patterns, so-called simulators, can be re-enacted by simply activating mental representations of a stimulus, whereby the processes do not have to be conscious (see Barsalou, 1999, chapter 2, spec. p. 586; see also figure 2, p. 68 of Barsalou, et al., 2003). Moreover, the PSS theory assumes these simulations to also contain situation specific conceptualizations, so that their activation allows for adequate preparation of action (Barsalou, et al., 2003, p. 70 et seqq.). While this mode of cognition is referred to as deep processing, the alternative mode, the shallow processing, defines the use of superficial representatios at word-level (see Barsalou, 1999, author's response R1.4, p. 639 et seq.).

## 1.1.3.5 The bidirectionality of the link

These considerations comprise the assumption of a bidirectional link between evaluative processes and behavioural tendencies: Online embodiment or the development of simulators describe the acquisition and activation of attitudes via motor reactions. Investigations on facial and body feedback mechanisms revealed facial expressions and body positions to influence feelings (e.g. Strack, et al., 1988<sup>11</sup>), social judgements (e.g. Mussweiler, 2006) and memory processes (e.g. Förster & Strack, 1996<sup>12</sup>). Thereby, affective and cognitive processes, which are compatible with the shown expression or posture, were facilitated or enforced (for reviews see e.g. McIntosh, 1996; Barsalou, et al., 2003). Furthermore, such compatibility was associated with better cognitive performance in secondary tasks, since more processing resources were available (e.g. exp. 3 of Förster & Strack, 1996; Förster & Stepper, 2000). Förster & Strack, 1996 suggested "[...] that our results are consequences of *conceptual*-motor compatibility. This notion states that the activation of thought and feeling

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With regard to perception-independent recall of memories, problem solving, decision-making, planning, creativity and communication, Damasio (1989) stated that "All those functions are predicated on a key operation: the attempted reconstitution of learned perceptuomotor interactions in the form of internal recall and motor performance. Attempted perceptuomotor reconstitution is achieved by time-locked retroactivation of fragmentary records, in multiple cortical regions as a result of feedback activity from convergence zones. The success of this operation depends on attention, which is defined as a critical level of activity in each of the activated regions, below which consciousness cannot occur." (p. 27, line 31-38).

<sup>&</sup>lt;sup>11</sup> The *pen study* showed participants to rate cartoons as more funny, when keeping a pen between their front teeth, what induces a smile, than when keeping it between their lips, what precludes smiling. <sup>12</sup> Participants more likely recognized positive and negative adjectives among new distractors when they had nodded and shook their head during the encoding phase, respectively (exp. 1 and 2).

and the concurrent execution of specific behaviors depends<sup>13</sup> on their natural co-occurrence." (p. 429, line 18-21, left text column). In other words, frequently co-occurring affective evaluations and motor patterns build concepts and the activation of components belonging to the same concept is facilitated.

Offline embodiment or the activiation of simulations by simulators describes the facilitation of motor and cognitive reactions via activated attitudes (Niedenthal, et al., 2005b; for a review see e.g. Dijksterhuis & Bargh, 2001). The studies discussed in 1.3 showed positive attitudes to fasten approach behaviour and negative attitudes to fasten avoidance behaviour. Since these results are the initial point for the investigations of the current thesis, the reader is referred to the detailed description of their design variations in 1.3.1 and mechanisms in 1.3.2. Neumann et al. (2005) showed this facilitation pattern for facial reactions: Latency of EMG signals revealed participants to faster create a smiling (zygomaticus muscle) during the evaluation of positive words and to faster frown (corrugator muscle) during the evaluation of negative words in a categorization task. Furthermore, the activation of approach motivation via flexing the arm (for an exact description of the method see Neumann and Strack (2000) in 1.3.1) was associated with better memory retrieval of famous personalities liked by the participants compared to unpopular personalities. In contrast, avoidance motivation via bending the arm facilitated the generation of disliked names (Förster & Strack, 1997; Förster & Strack, 1998).

Similarly, investigations on more complex affective phenomena such as e.g. mimicry and empathy also revealed evidence for a bidirectional link between emotional evaluation and behaviour (for a review see e.g. Niedenthal, et al., 2005b, pp. 192-194). Thereby, Barsalou et al. (2003) emphasized the importance of embodiment for social behaviour and relationships. While a large number of studies concentrated on affective embodiment processes, it should be noted that the above described conceptualizations of embodiment theories also account for analogue compatibility findings in non-affective and non-social research (see e.g. Barsalou, et al., 2003, p. 62; Barsalou, 1999), though these findings are not relevant for the current thesis. The term *embodiment* simply refers to the assumption of a common neuronal coding basis for perception, memory and action.

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<sup>&</sup>lt;sup>13</sup> grammatical error in the original text

Importantly, bidirectionality of the emotion-behaviour relationship was already assumed by Darwin (1872/1998, see spec. chapters 1-3), when studying emotional expressions in animals and humans. In his opinion, behaviour is not only a consequence of an affective evaluation, but also constitutes a cause of it. Similar assumptions can also be found in the writings of James (1890b, chapter 25), who might be seen as the first researcher clearly stating emotions to constitute embodied phenomena (Lavender & Hommel, 2007b): Relevant stimuli cause bodily reactions, whose perceptual experience represents the emotion (cf. also Schachter & Singer, 1962).

### 1.1.3.6 Common coding view: Theory of Event Coding (TEC)

This statement of James is closely linked to another of his postulates on the bidirectional nature of the relation between the initiation of actions and the perception of action consequences (James, 1890b, pp. 522-528): The *ideo-motor principle* states that actions are represented in terms of codes of their anticipated effects, i.e., as the sensory consequences (kinaesthetic, visual, tactile) that typically result from them (Lotze, 1852, pp. 287-313; for an overview see Stock & Stock, 2004). The second assumption of this principle is that motor reactions can be triggered by these representations of their effects: "Wherever movement follows *unhesitatingly and immediately* the notion of it in the mind, we have ideo-motor action." (James, 1890b, p. 522, line 20-21).

The common coding perspective refers to this principle (Prinz, 1990). Thereby, the Theory of Event Coding (TEC) is a meta-theory of perception and action planning, which claims "[...] that perceiving and action planning are functionally equivalent, inasmuch as they are merely alternative ways of doing the same thing: internally representing external events [...]" (Hommel, et al., 2001, p. 860, left text column, line 37-39). *Perception* refers to the late cognitive products of perceptual processing and *action* to the early cognitive antecedents of action. "TEC's core concept is the event code, which again consists of the codes that represent the distal features of an event [...]." (Hommel, et al., 2001, p. 861, right text column, line 17-19). Sensory information is the feature code from perception and, in an analoguous manner, action-feature codes underlie the representations of actions. Both proximal feature codes converge onto distal, abstract feature codes in a common coding system. This abstract level, whose neuronal basis is not further specified, might be seen as the main difference in comparison to embodiment theories, which suggest a common neuronal and – thereby – concrete and not abstract coding level of perception and action.

However, TEC also assumes synchronization, i.e., the temporal coupling of activating feature codes belonging to one event, as the mechanism of binding or integration. A hierarchical order of such events via higher-order codes ensures their integration into whole scenes. Most relevant for the current thesis, however, is the affectively enriched version of the TEC (Lavender & Hommel, 2007b). There, the parallels between non-affective and affective processing are emphasized, resulting in the final statement that affect is a perceivable stimulus feature similar to other features such e.g. colour or size. Affective feature codes can be part of event coding and – thereby – of action plans, which are cognitively represented in terms of distributed codes of their perceived features. In this context, Lavender and Hommel (2007b) described Damasio's somatic marker hypothesis (Damasio, 1994a) as "[...] a mere extension of Jamesian ideomotor theorising [...]" (p. 1275, line 25), since it attributes to affective codes the same function as the *ideo-motor principle* attributes to perceptual representations of action effects in general: They serve as retrieval cues for actions ensuring the selection of the most appropriate response.

In general, stronger weighting of relevant than irrelevant feature codes takes into account situational demands and is referred to as *attention* in the perceptual domain and as *intention* with regard to action planning (Hommel, et al., 2001). In contrast to automatic, stimulus-induced activations of action codes, these mechanisms are highly relevant for voluntary translations of perception codes into action codes and vice versa. The next chapter gives an overview on the general functionality of automatic and controlled processes, but see also 10.5 for a discussion of these principles in the context of findings of the current thesis.

# 1.2 Automatic and regulated processing:

# Basic concepts in cognitive psychology and neuroscience

A large variety of theories in psychology and neuroscience assumes human behaviour and emotions to result from the interplay of two different families of processes (e.g. Shiffrin & Schneider, 1977; Shiffrin & Dumais, 1981; Shiffrin & Schneider, 1984): At one side, there are processes which occur automatic and fast, at the other side, the distinctiveness of human beings can be subsumed as the possibility to volitionally act, what – at least to some extent – means that automatic reactions can be overridden by planned reactions (for reviews see Smith & DeCoster, 2000; Bargh & Ferguson, 2000; Smith & Neumann, 2005, pp. 289-293).

With regard to attitudes, Greenwald and Banaji (1995) emphasized the importance of unconsciousness components and stated that "*Implicit attitudes* are introspectively unidentified (or inaccurately identified) traces of past experience that mediate favorable or unfavorable feeling, thought, or action toward social<sup>14</sup> objects." (p. 8, line 1-3, right text column).

The MODE model (Motivation and Opportunity as DEterminants) of Fazio (1990) suggests attitudes to influence behaviour via a deliberative, controlled process, when individuals have enough motivation to reflect on the attitude and the future behavioural consequences. According to Fazio (1990), this is the case, when individuals fear costs due to invalid decisions. Furthermore, the opportunity, i.e., the appropriate situational circumstances for realizing the so activated behaviour must also be given (cf. the theory of reasoned action, see spec. chapters 6 and 8 of Fishbein and Ajzen (1975) or the theory of planned behaviour (Ajzen, 1985; Ajzen, 1991)). Elsewise, in the spontaneous processing mode, attitudes influence behaviour in a *theory driven* manner and the attitude strength determines the final impact on behaviour (Fazio, 1990).

Similar theories on automatic and controlled processes, which are of specific relevance for the current thesis, are outlined in detail in the following sections. Before so doing, the usage of several terms needs to be clarified. *Automatic* processes are defined as fast, usually frequently and regularly conducted reactions, which are more or less independent

<sup>&</sup>lt;sup>14</sup> Since most research on attitudes was conducted in social contexts, this definition refers to social objects. However, its implications are also valid for stimuli in general (Greenwald & Banaji, 1995).

from volition and conscious control (Häcker & Stapf, 2009, p. 100-101). *Implicit* reactions refer to covert, internal responses and the term *unconscious* is used for processes, which are not volitionally controllable, since we have no knowledge and awareness about them (Häcker & Stapf, 2009, p. 1042 and pp. 142-144). *Impulsive* reactions designate affective, hormic responses without rational deliberation at their initiation (Häcker & Stapf, 2009, p. 461).

Importantly, automaticity can be seen as consisting of different, relatively independent features which do not necessarily co-occur (Bargh, 1992; for an overview see also Moors & De Houwer, 2006): Automatic processes can be unintentional, autonomous (involuntary), effortless (not attention demanding), uncontrollable, purely stimulus driven, very fast and can occur outside of awareness. Furthermore, the concept of conditional automaticity assumes specific situational prerequisites to be necessary for automatic processes, such as e.g. goals activating related concepts in memory (Bargh, 1992). This statement also implies that the dualism of automatic and controlled processes is not strictly given in most complex situations (see also 10.6.3; Eder, 2011).

In the current thesis, I use the terms *automatic* and *implicit* as synonyms since these concepts largely overlap (Moors & De Houwer, 2006; cf. also De Houwer, et al., 2009a). However, as emphasized by Deutsch and Strack (2006), who refered to the theory on the emotional construct by Russell (2003), the terms *implicit* or *automatic* and *unconscious* should not be used as synonyms, since automatic processes can occur unconsciously, but might be associated with subjective experiences of like or dislike.

### 1.2.1 Cognitive-emotional psychology: Impulsive vs. reflective systems

As already mentioned above (see 1.1.3), research on the relation between affective evaluations and behaviour can be distinguished into research on global approach-avoidance tendencies elicited by rudimentary stimulus evaluation along a positive-negative axis and research on emotion specific behavioural tendencies. Similarly, the theoretical considerations leading Lang to his biphasic emotion theory (see 1.1.1; Lang, et al., 1990; Lang, 1995) included a differentiation between strategic and tactical aspects of motivational behaviour based on technical terms used in warfare (Lang, et al., 1990, p. 380). Lang used the term strategic to describe the global organization of behaviour along the dimension of valence,

i.e., along the global orientation positive-approach and negative-avoidance. Furthermore, a categorization of a given stimulus along the second dimension of affective evaluation, namely the dimension of arousal, ensures energy resources for realizing the behaviour "[...] without specifying exact patterns of action" (Lang, et al., 1990, p. 380, line 36, right text column). In contrast, tactical aspects of motivational behaviour refer to the further shaping of these global orientations with regard to concrete motor patterns depending on context specific requirements. In other words, these two classes of motivational processes are assumed to be sequential, whereby Lang (1995) stated that "It is clear that the contextual tactics of approach and avoidance have become more varied in humans; nevertheless, the strategic frame of appetite and aversion is no less relevant." (p. 373, line 7-10, right text column).

Neumann (2003) combined the idea of such a sequential model of approach-avoidance behaviour with dual-process models of cognitive psychology. He also assumed automatic evaluative processes to activate the approach or the avoidance motivational system. Importantly, this activation is postulated to happen at a representational level. Therefore, the corresponding behaviour is not automatically realized. Rather, subsequent cognitively controlled processes also contribute to the finally shown behaviour. If the activated automatic tendencies are not adequate, human beings have the possibility to inhibit them and to show an alternative response. Neumann (2003) based his suggestion on the faster and more automatized processing of evaluative compared to non-evaluative information (e.g. Bargh, 1997). Moreover, he also refered to emotion theories, which assume evaluative processes to be necessary but not sufficient to elicit emotions: More cognitively impressed processes follow the evaluative processes and determine the final emotion and behaviour (Weiner, 1986, chapter 5; Neumann & Strack, 2000; Ajzen, 1985).

The assumption of such sequential processes explain the variety of emotions and behaviour by an interplay of automatic processes as correlates of evolutionary adaptations and of the human-specific possibility to regulate and inhibit these automatic response tendencies. In cognitive and social psychology, there are many theories suggesting these two modes of information processing to be based on two semi-independent systems. One representative of these so-called dual-process models is the MODE model described above in 1.2. Another widely-used example is the Elaboration-Likelihood-Modell (Petty & Cacioppo, 1986; peripheral and central routes of attitude change; Cacioppo, et al., 1986a; cf. also the heuristic-systematic model of information processing; Chaiken, 1980). A comprehensive

review on dual-process models in several domains, such as social information processing (stereotyping, social judgements), reasoning and memory processes was given by Smith and DeCoster (2000).

The reflective-impulsive model (RIM) of Strack and Deutsch (2004) is the most interesting one for the current thesis. Strack and Deutsch (2004) combined features of different dualprocess models with motivational explanations. Thereby, they "[...] propose the existence of a motivational orientation that acts as a behavioral catalyst and relates valence to approach and avoidance [...]." (p. 222, line 11-14, left text column). In 10 theses, Strack and Deutsch (2004) described the fundamental assumptions of their model. The two systems rely on different representations and information processing styles (theses 1, 4 and 6): The impulsive system contains associative links between stimulus representations (see figure 1) and activates behavioural schemata via activation spreads as described above for network models in general (see 1.1.3.2). In contrast to such automatic reactions, controlled behaviour is initiated by the reflective system after conscious deliberation. Thereby, information processing is based on the semantic relations underlying the reflective system and the truth value assigned to them. Accordingly, the impulsive system works fast and requires only little cognitive capacity, while processes of the reflective system are slower and depend on the allocation of attentional ressources (thesis 3). These two systems operate in parallel, whereby the impulsive system is always activated by the perceptual input; the reflective system, however, is only engaged, when attentional resources are directed to the respective situation (thesis 2). Moreover, the final behaviour is always executed via the activation of sensory-motor clusters in the impulsive system, so-called behavioural schemata. Behavioural control by the reflective system is necessary, when several behavioural schemata are activated at a time or when an automatic reaction tendency has to be inhibited (thesis 5; cf. also 1.2.3, Shallice & Burgess, 1996). Moreover, the link from a decision made by the reflective system to its actual behavioural realization includes a step, which the RIM refers to as intending (thesis 7): This process describes the monitoring of the impulsive system and the environment for identifying adequate conditions which allow for the actual realization of the planned behaviour. According to the RIM, intending bridges temporal delays in behavioural realization without requiring cognitive capacity, but by automatically reactivating the decision and the related behavioural schemata.

Operations of the impulsive system might be accompanied by an experiental state of awareness, "[...] that is, without necessarily knowing its origin, people may experience a

feeling with its distinct phenomenal quality." (Strack & Deutsch, 2004, p. 224, line 22-24, right text column). In contrast, information processing in the reflective system elicits a noetic state of awareness, "[...] which consists of knowledge that something is or is not the case." (Strack & Deutsch, 2004, p. 226, line 10-11, left text column). The impulsive system is orientated in terms of either approach or avoidance motivation preparing the organism for adequate reactions (thesis 8). Homeostatic dysregulation due to deprivation of basic needs leads to the activation of the motivational orientation and behavioural schemata, which allow for its regulation (thesis 10). Cognitive, affective and behavioural operations are facilitated, if they are compatible with the current motivational orientation (thesis 9). Thereby, the link between evaluative processes and behaviour is assumed to be bidirectional (see also 1.1.3) and the motivational orientations are moderators for the execution of behaviour.

The RIM was originally developed to explain social behaviour and the interplay between temptations and self-regulation mechanisms. Its assumptions, however, are suited to also explain behaviour in general as investigated in the current thesis (Strack & Deutsch, 2004). As explained above and depicted in figure 1, the impulsive system is assumed to be an associative network, built up by clusters of representations of stimuli, their valence, and behavioural programs. The more frequently these elements co-occur, the closer the connections between them become and the faster activation disperses within the cluster. Such activation spreads trigger behavioural tendencies automatically according to the emotional valence assigned to a certain stimulus due to prior learning experiences: In general, positive stimuli lead to automatic approach tendencies and negative stimuli to automatic avoidance tendencies, since our everyday lifes contain an endless number of repetitions of these valence-response combinations. Furthermore, the assumption of such a direct link from stimulus evaluation to behaviour can explain why automatic tendencies are activated so fast and strongly. With regard to addiction and anxiety disorders, this theoretical model can be used to explain the pathologically enhanced approach tendencies to addictionrelated stimuli and avoidance tendencies to anxiety-related stimuli, respectively (Deutsch & Strack, 2006; see also 2.2.3).

In healthy individuals, the reflective system controls the impulsive system via two broad mechanisms. First, cognitive control in terms of decision-making directs behaviour by deliberations about the consequences of actions and emotion regulation (Strack & Deutsch, 2004). Second, behavioural control is possible by means of several mechanisms of impulse control such as attention allocation and inhibition of motor responses (Bechara, et al., 2006).

However, the influence of the reflective system is restricted to situations, in which the required cognitive capacity is available (see above), while the impulsive system is always involved in information processing and the resulting reactions. In detail, for over-ruling automatic tendencies, i.e., for performing alternative reactions, the automatically activated affective evaluation and the motor impulse have to be inhibited and a contrary reaction has to be initialized according to a conscious aim, i.e., according to a current content in working memory (WM; Hofmann, et al., 2008; Bechara, et al., 2006). In other words, overcoming automatic reaction tendencies requires cognitive regulation comprising affective regulation, cognitive inhibition as well as maintenance and realisation of WM content.

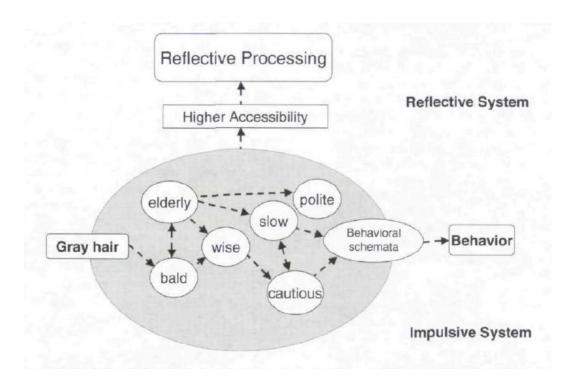


Figure 1: Associative network structure of the impulsive system of the reflective-impulsive model (RIM)

The impulsive system is built up by clusters of stimulus representations. Behavioural schemata are activated via activation spreads from one activated node to the others – thereby – linking affect to action. The example depicts activation of the cluster *elderly*: Perceiving a person with gray hair enhances the accessibility of associated contents and – thereby – facilitates associated behaviour. Modified according to Strack and Deutsch (2004, p. 224).

### 1.2.2 Neuronal models:

### Prefrontal top-down control vs. subcortical bottom-up influences

In 1.1.3, I already described the core elements of Damasio's somatic marker hypothesis, the *body loops* and the *as if body loops* (Damasio, et al., 1991). With regard to decision making in uncertain situations, Damasio et al. (1991; Bechara & Damasio, 2005) suggested somatic marker signals from anticipated affective states to facilitate advantageous responses by allowing for a comparison of future consequences: During decision making, individuals activate mental representations of stimuli, which they anticipate to contribute to future events. These mental representations activate the stored somatic state patterns which previously have been associated with the stimuli (*as if body loop*). The somatic state and the related feeling, the so-called somatic markers, inform the individual about possible consequences of an action. This deliberation process happens mostly outside awareness.

With regard to the neuronal level, Damasio et al. (1991; Damasio, 1998; Damasio, 1996; Bechara & Damasio, 2005) suggested two regions to be of specific interest: Besides the brainstem nuclei and the insular and somatosensory cortices as regions, which store the somatic state patterns, the ventromedial prefrontal cortex (VMPFC) and the amygdalae are crucial instances in decision making. Bechara and Damasio (2005) assumed the amygdalae to be essential for linking affective reactions elicited by current innate or learned positive and negative stimuli (primary inducers) to the related somatic states. The VMPFC, in contrast, is responsible for linking recalls of such primary inducers to the stored somatic state patterns by reconstituting the original somatic state via the activation of somatic effectors in the hypothalamus and brain stem nuclei (Bechara & Damasio, 2005; Damasio, 1996). In line with these hypotheses, lesions or dysfunction of the VMPFC were accompanied by poor decision making under uncertainty (Damasio, et al., 1991).

In healthy individuals, the response associated with the most positive consequences is supported via the influence of somatic markers on brain regions such as the striatum and supplementary motor area (SMA), i.e., on response selection and motor responses (Bechara & Damasio, 2005). Furthermore, Bechara and Damasio (2005) suggested this biasing of actions to be mediated by neurotransmitter systems. They argued that all major neurotransmitter systems (DA, serotonin (5-HT), norepinephrine (NA), acetylcholine (Ach)) have cell bodies in the brainstem and axon terminals in the cerebral cortex. Neurotransmitters modulate the generation of action potentials and – thereby – synaptic

activity of neurons in both cortical and subcortical regions (Bechara & Damasio, 2005). In sum, Damasio states significant impact of affective evaluations on cognitive decision processes, whereby the VMPFC plays an essential role in generating the final product of this interaction.

A leading position of frontal cortical areas in stimulus processing and the following generation of responses is also an important assumption of top-down control models in cognitive neuroscience (see e.g. Miller & D'Esposito, 2005). In general, controlled conscious processing is suggested to involve cortical areas. Thereby, specifically the PFC plays an important role in controlling and regulating behaviour and other brain areas (e.g. Miller, 2000; Koechlin, et al., 2003). In contrast, automatic processes are assumed to be steered by subcortical areas. Cognitive control by the PFC is suggested to be executed via top-down signals influencing neuronal activity in other brain regions (Miller & Cohen, 2001; cf. Curtis & D'Esposito, 2003; see also 1.2.3 for a more detailed description<sup>15</sup>). However, direct evidence for this hypothesis is rare, since it is technically difficult to depict the spatio-temporal dynamics between different brain regions, but necessary to allow for conclusions on causal connections.

Direct evidence for prefrontal top-down control signals came from animal research. There, it is possible to stimulate specific neuron populations (e.g. Moore & Armstrong, 2003) or to impair prefrontal functions by means of cooling (e.g. Fuster, et al., 1985) or surgical techniques such as e.g. split-brain surgery (Tomita, et al., 1999) and to measure the resulting effects on the activity of probably influenced regions. In humans, investigations of patients with prefrontal lesions by means of neuroimaging methods (e.g. ERPs; Chao & Knight, 1998) or studies in healthy participants inducing temporary PFC dysfunctions by application of inhibitory transcranial magnetic stimulation (TMS; e.g. Tupak, et al., 2013) also indicated the PFC to be essential for preferably processing task relevant aspects.

Suggestive evidence for top-down control signals from the PFC was derived from single unit recordings in primates, which tried to assess the relative onset of neural activity across different brain regions (e.g. Rainer, et al., 1998). Feedman et al. (2003) using simultaneous multisite recordings showed neural activity in the inferior temporal cortex (ITC) to preceed

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<sup>&</sup>lt;sup>15</sup> While most investigations of top-down control concentrated on controlled attention allocation, their assumptions and findings are ususally generalized to other cognitive domains.

activity in the PFC during the encoding of the sample stimulus and the following delay in a match-to-category task. However, during the decision phase, PFC activity allowed for distinguishing between match and non-match decisions, while activity in the ITC reappeared. That is consistent with the assumption of top-down control signals biasing the processing of category relevant features. In humans, the onset of blood oxygenation level dependent (BOLD) responses in fMRI can be compared between different brain regions (e.g. Menon, et al., 1998). This is difficult, because the translation from neural signals into the hemodynamic response causes a loss of temporal resolution and because of the so-called *hemodynamic inverse problem* (Heeger & Ress, 2002; Buckner, 2003): There are regional differences in vascular supply, which are difficult to separate from differences in processing related activity.

FMRI data also allow for multivariate analyses and, therefore, for functionally and not only temporally orientated evidence (for an overview see Miller & D'Esposito, 2005). The method of structural equation modelling (SEM) tests for effective connectivity<sup>16</sup> between different regions (e.g. Rowe, et al., 2005). Further developments, the methods of dynamic causal modelling (DCM) and Granger causality mapping (GCM), make less a priori assumptions about the direction of a connection by emphasizing the temporal differences in neural activity. While DCM measures the coupling between different regions (e.g. Mechelli, et al., 2004; Mechelli, et al., 2003), GCM predicts the time series of activity of one region from the time series of another region (e.g. Roebroeck, et al., 2005). In sum, all these techniques revealed findings supporting the role of the PFC as top-down control region (Miller & D'Esposito, 2005).

However, it should be noted, that such top-down control models might not account for all cognitive processes. Alternative explanations rely on recurrent connections (cf. Botvinick & Plaut, 2004) or cognitive branching (Koechlin & Hyafil, 2007; Koechlin & Summerfield, 2007). Moreover, loops of neural activation through the amygdala and the striatum to the PFC might constitute the anatomical basis for powerful bottom-up influences, when affective contents disturbe cognitive control (Dolcos & McCarthy, 2006; Dolcos, et al., 2006; see also Ernst & Fudge, 2009).

<sup>&</sup>lt;sup>16</sup> I do not present studies on functional connectivity, since functional connectivity does not allow for conclusions on causal connections between brain areas. While effective connectivity is defined as the influence of one neuronal system over another, functional connectivity simply means the temporal correlations between spatially remote neurophysiological events (Friston, 1994).

For the current thesis, I concentrated on a specific model, which describes the neuronal systems underlying automatic approach-avoidance reactions and their regulation. The neurobiological triadic model of Ernst et al. (2006; see also Ernst & Fudge, 2009) suggests the ventral striatum to steer automatic approach reactions towards positive stimuli and the amygdala to steer automatic avoidance reactions towards negative stimuli, while the PFC as a main neuronal control instance is responsible for controlled reactions. This model is based on behavioural deficits observed in humans with specific brain lesions, Gray's dual-system theory of behaviour (see 1.1.2), functional neuroimaging research and anatomical connectivity investigations. Lesion studies identified the above mentioned functions as dominant functions of these three structures, though the generalizability of such findings is limited due to the problems associated with this study type, such as e.g. missing pre-lesion baseline measurements or small sample sizes (Meyer-Lindenberg, et al., 2005; Caine & Watson, 2000; Bechara & Van Der Linden, 2005).

In general, neuroimaging studies revealed the ventral striatum to be activated during processing of rewards (e.g. Knutson, et al., 2001; O'Doherty, et al., 2004; Delgado, et al., 2000; Tomer, et al., 2008; cf. also Bichot, et al., 2011 for an electrical stimulation study in monkeys), while the amygdalae and insulae are associated with reactions to aversive, unfavourable stimuli (Cunningham, et al., 2010; Schlund & Cataldo, 2010; Zald & Pardo, 1997; Becerra, et al., 2001). It should be noted, that - although frequently found - these associations are not exclusive (Carretie, et al., 2009; Hamann & Mao, 2002; Schlund & Cataldo, 2010). The functions of the PFC as control instance are more differentiated, since its regional functional specialization is more pronounced (e.g. Koechlin, et al., 2003). Several models assume the dorsolateral prefrontal cortex (DLPFC), which initiates performance adjustments, to constitute the highest control instance of the human brain (e.g. Miller & Cohen, 2001; Ridderinkhof, et al., 2004; Duncan, 2001; Ernst & Fudge, 2009). In contrast, the OFC indicates the affective value ascribed to a specific stimulus (O'Doherty, et al., 2003; Kringelbach & Rolls, 2004; Sescousse, et al., 2010). Moreover, together with other regions in the medial prefrontal cortex, it is responsible for inhibition processes, response reversal and decision making (Schoenbaum, et al., 2007; Damasio, et al., 1991, see also above and 1.1.2; for reviews see Elliott & Deakin, 2005 and O'Doherty, 2007). The anterior medial PFC (frontal pole, Brodmann area (BA) 10) was shown to be important for metacognition (e.g. Gallagher, et al., 2000), self-evaluation (e.g. Amodio & Frith, 2006) and rule formation processes (Brass & Haggard, 2007; Volz, et al., 2003).

Furthermore, Ernst and Fudge (2009) proposed a model extension in terms of sub-triadic formations: The so-called fractal triadic model is a more differentiated version of the triadic model, wherein each of the three nodes is organized in a triadic manner and has heteromodal functions (see figure 2). In other words, each of the three nodes has sub-structures, which are responsible for one of the three functions. This suggestion relies on a variety of findings on the anatomical constitution and the ontogentic development of the structures as well as on their connections with other brain regions and their role in neurotransmission in animals and humans. With regard to the striatum, the anterior parts are associated with approach and the posterior parts with avoidance reactions, while afferent relations from the PFC are responsible for controlling these structures. In the amygdalae, the basolateral nucleus is suggested to process approach and the central nucleus avoidance tendencies; afferent relations from the PFC are also responsible for their control. In the PFC, the DLPFC is assumed to constitute the highest control instance, while the medial OFC is associated with approach and the lateral OFC with avoidance processes.

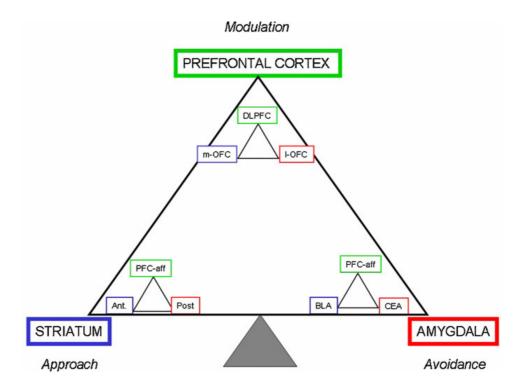


Figure 2: Fractal Triadic Model of neural systems underlying motivated behaviour

The amygdala is seen as the main instance for avoidance behaviour, the striatum initiates approach tendencies and the prefrontal cortex modulates their activity. However, each node of this triad has heteromodal functions, since it comprises sub-structures responsible for one of the three functions (see the text above for details). DLPFC: dorsolateral prefrontal cortex; m-OFC: medial orbital frontal cortex; I-OFC: lateral orbital frontal cortex; PFC-aff: prefrontal cortical afferents; Ant: anterior striatum; Post: posterior striatum; BLA: basolateral amygdala; CEA: central amygdala. Modified according to Ernst and Fudge (2009, p. 376).

# 1.2.3 Neuropsychological and neurophysiological models: Automatic vs. conscious attention allocation and mechanisms of conflict processing

The above presented neuronal models contain assumptions on interactions between different brain regions. However, they are relatively restricted to the assignment of specific brain functions to specific structures. In contrast, neuronal network models and neuropsychological approaches have a more process-oriented focus and allow for disentangling different functional mechanisms. Here, I introduce models of attention allocation and conflict processing, which are of interest for the current thesis and also differentiate between automatic and controlled processes.

Most attention models assume attention to have limited capacity, for which both automatic and regulated processing fight (Broadbent, 1964, spec. chapter 2; Broadbent, 1970; Treisman, 1969). Habitual processes do not need much attentional resources, while new or dangerous situations unintentionally capture attentional resources. For avoiding distracters in the environment to catch attentional resources, human beings have the ability to voluntarily attach attention to a stimulus (e.g. Koch & Ullman, 1985; cf. also James, 1890a, chapter 11). This is especially important for the controlled processing of complex and dangerous situations (e.g. Norman & Shallice, 1986; see also below). ERPs allow to depict the temporal sequence of different attentional processes (for an overview see Gazzaniga, et al., 2002, pp. 255-270; Luck, 1995; cf. also Olofsson, et al., 2008). This is possible due to their high temporal solution in the range of milliseconds. In short, early ERPs such as the N1 and P1 ERP depict automatic attentional processes (e.g. Smith, et al., 2003; Vogel & Luck, 2000), while the later P3 ERP is associated with more controlled attention allocation (Nieuwenhuis, et al., 2005). Besides attentional processes, ERPs also allow for depicting sub-processes of conflict processing in general such as conflict solution mechanisms and response selection (N2 ERP; Folstein & Van Petten, 2008). For a more detailed description of theses processes see also studies A1 and A2 of the current thesis.

With regard to the underlying neuronal structures of automatic (stimulus-driven) and controlled (goal-directed) attention allocation, two separate networks were identified (for a review see Corbetta & Shulman, 2002). A largely right lateralized ventral frontoparietal network, consisting of the inferior frontal cortex and temporoparietal cortex, can be seen as the exogenous orienting system: "One of its key functions is to direct attention to

behaviourally relevant sensory stimuli that are outside the focus of processing." (Corbetta & Shulman, 2002, p. 208, line 58-60, right text column). A bilateral dorsal frontoparietal network, comprising the superior frontal cortex and the intraparietal cortex, is responsible for top-down controlled attention allocation to specific stimulus features. Its activation might indicate the maintaincance of salience maps, whereby Corbetta and Shulman (2002) also hinted to the possibility of integration functions with regard to informative bottom-up signals. The interaction between these two systems might be a cooperative process, whereby the ventral system "[...] serves as an alerting system that detects behaviourally relevant stimuli in the environment, [...]" (Corbetta & Shulman, 2002, p. 211, line 44-45, right text column) and the dorsal sysem contributes more precise information on the stimuli. Otherwise, the ventral system might constitute a *circuit breaker* of the dorsal system, when ongoing cognitive activity, i.e. top-down control, has to be interrupted for reacting to more significant stimuli. Other studies revealed attentional control to also involve activity in the pulvinar nucleus of the thalamus, the basal ganglia, the insular cortex and the anterior cingulate cortex (e.g. Hopfinger, et al., 2000; cf. Desimone, et al., 1990; Koch & Ullman, 1985).<sup>17</sup>

With regard to the mechanism of such attentional top down control, biased competition models of attention suggest these nonsensory networks and areas to influence activity in specific brain regions in such a way, that - among simultaneously presented stimuli - task relevant features are preferably processed (e.g. Desimone & Duncan, 1995; Vecera, 2000). Investigations with positron emission tomography (PET) and fMRI of selective visual attention in humans revealed nonoverlappping subregions in the extrastriate visual cortex to be activated, when subjects selectively attended to the form, colour, speed/motion or location of presented stimuli (e.g. Corbetta, et al., 1991; Mangun, et al., 1997; O'Craven, et al., 1997; cf. also Kastner, et al., 1998; see also Tootell, et al., 1998 for an fMRI investigation on the retinotopical organization of visual spatial attention). Similarly, selectively enhanced activity in the fusiform face area (FFA) was found for attending to faces and in the parahippocampal place area (PPA) for attending to objects (O'Craven, et al., 1999; Gazzaley, et al., 2005). By combining PET with ERPs, Heinze et al. (1994) and Mangun et al. (1997) showed covariations between modulations in the P1 ERP amplitude and in the activity of these areas. This is in line with prior source localization studies of the P1 ERP (e.g. Clark & Hillyard, 1996) and the assumption that controlled attention allocation facilitates visual processing at an early stage in terms of improving the signal-to-noise ratio for attended compared to

<sup>&</sup>lt;sup>17</sup> See the reviews of Posner and Petersen (1990) and Posner and Dehaene (1994) or the results of e.g. Fan et al. (2005) on neuronal systems underlying other attentional domains such as alerting and orienting reactions.

unattended stimuli (Mangun, et al., 1997). The combined fMRI-ERP study of Gazzaley et al. (2005) revealed such facilitation effects to also shorten the latency of the N170 ERP, i.e., to enhance the speed of neuronal processing. Furthermore, this study also showed suppression of neuronal activity for unattended stimuli as previously reported in ERP studies (Luck & Hillyard, 1995; Luck, et al., 1994).

Investigations on the neurophysiology of such attentional top down control by means of cingle cell recordings in monkeys showed enhanced firing rates of neurons in visual areas processing the attended stimulus (e.g. Moran & Desimone, 1985; Spitzer, et al., 1988) and enhanced synchronization of these neuron populations (e.g. Fries, et al., 2008). Further research on the amount and mechanisms of this enhancement supported the biased competion theory: The neuronal response to simultaneously presented stimuli can be described as a weighted average of the response to isolated stimuli and attention strengthened the weights for the attended stimulus for approximately 30% (e.g. Reynolds, et al., 1999; Treue & Maunsell, 1999; Fallah, et al., 2007). Reddy et al. (2009) investigated this attentional bias at the multi-voxel level in an fMRI study in humans. Though results from single neuron level might not be necessarily mirrored at multi-voxel level, since neuronal responses merge to the BOLD signal in a nonlinear way, participants' activity in the FFA, PPA and the occipito-temporal cortex was also shifted by attention for about 30%.

Techniques from computational neuroscience allowed Deco and Rolls (2005) to investigate the dynamics of top-down biased competition and bottom-up influences in a multi-layer model. They concluded that both bottom-up and top-down attentional synaptic inputs to the neuron show linear additivity, while the relation of the top-down input to the neuron's firing rate is nonlinear, thereby, explaining why top-down attention exerts major modulatory effects at intermediate levels of bottom-up input. With regard to the question, how an entire object is preferably processed, Duncan (2001) suggested an adaptive coding model of top-down control: The PFC supports the representations of an object in neuronal systems processing the different objects' properties (cf. also Rossi, et al., 2009). When an object gains dominance in any of these systems, its remaining features are also favoured because multiple brain systems have the tendency to converge to represent related information (see also the integrated competition hypothesis (e.g. Duncan, et al., 1997) and findings on attention related long-range coupling between PFC and visual cortices (e.g. Gregoriou, et al., 2009)).

Another influential model, which also assumes subcortical structures to be essential for automatic processing and the cortical level for more elaborated processing of attended stimuli, was suggested by LeDoux (1994; see also LeDoux, 1996, chapter 6). Based on works investigating neural circuits of fear learning in rats (e.g. Davis, 1992; for a review see also LeDoux, 1995), LeDoux described two systems of processing visual input and initiating an appropriate response, a so-called low road and high road. The low road processes stimuli fast, but unprecisely. However, this enables fast reactions and - thereby - surviving in dangerous situations. The high road enables a detailed analysis of the stimulus, but has the disadvantage of much slower processing. With regard to the neuronal correlates, LeDoux (1994; see also the figure on p. 38 of this reference) suggested sensory information about the visual stimulus to be projected to the thalamus, where this input is compared to information from previous stimuli which were associated with aversiveness. The thalamus sends the result of this comparison to the amygdalae, which can directly initiate flight behaviour. Therefore, this low road is very fast, but also superficial. The high road is suggested to comprise projections from the primary rude analysis in the thalamus to the visual cortex. There, a more detailed analysis is provided. The result of this analysis is also signaled to the amygdalae and from there, to the cingulate gyrus and the VMPFC. So, the response initiated by the low road can be either supported or corrected, depending on whether the fine analysis of the high road confirms the result of the low road or not. Recently, similar processing mechanisms have also been suggested for the auditory domain (Brockelmann, et al., 2011).

Besides attentional control, successful conflict processing also requires the selection of appropriate responses. Norman and Shallice (1986) suggested a psychological model of response selection processes, wherein selection of an action is seen as a competitive process. In difficult situations, several so-called schema control units, which represent responses, are activated at the same time. Norman and Shallice (1986) differentiated between two types of response selection: Contention scheduling is a passive type of selection. Competition between schemas is solved via mutual inhibitory connections. In contrast, the supervisory attentional system (SAS) ensures flexibility of behaviour by voluntarily favouring the selection of certain schema control units. It was suggested to exert executive control via enhanced conscious attention allocation in difficult, novel situations. Its activity is necessary for ensuring the flexibility of behaviour in terms of planning, decision making, corrections of errors, abstraction of logical rules, inhibition and overcoming habitual

responses (Shallice, 1994; Shallice & Burgess, 1996). Imaging studies suggested enhanced activity in the anterior cingulate cortex (ACC) to underlie executive control functions associated with the SAS (e.g. Fan, et al., 2005; for a review see Paus, 2001). The ACC was suggested to modulate the processing in other brain regions in such a way, that it is most efficient given the current task demands (Crottaz-Herbette & Menon, 2006). Its interactions with prefrontal cortical regions ensure enough WM capacity and the initiation of response adaptations, while its interactions with associative cortical regions can amplify activity in one perceptual module over others (Weissman, et al., 2005; Posner & Raichle, 1994, chapter 7, spec. pp. 168-174).

MacDonald et al. (2000) showed a double dissociation between the contributions of the ACC and the DLPFC to cognitive control: In a modified Stroop test, they temporally separated strategic preparation processes related to the given instruction from evaluative processes related to the response. The instruction to name the colour of the presented word, compared to the instruction to read it, caused stronger activity in left DLPFC, but did not influence ACC activity. In contrast, while there were no differences in DLPFC activity, right ACC was more strongly activated during incompatible than compatible colour-naming trials. MacDonald et al. (2000) concluded, that the ACC (BA 24 and 32) is essential for monitoring performance and the DLPFC (BA 9) for the implementation of control. Similar results were obtained by Gehring and Knight (2000), who investigated patients with lesions in DLPFC. The error-related negativity (ERN) is an ERP, which arises after the commission of an error in flanker tasks. It represents performance monitoring related to activity in the ACC as was shown by source localization analyses (e.g. van Veen & Carter, 2002). In their study, Gehring and Knight (2000) did not find alterations in its amplitude compared to the ERN of healthy individuals. However, in contrast to the healthy controls, patients showed no differences in the magnitude of the ERN between incorrect and correct trials, but impairments in corrective behaviour. These results hint to an interaction between the ACC and DLPFC in conflict monitoring and the resulting behaviour.

In their comment on this study, Cohen et al. (2000) defined the key function of the ACC as a conflict monitoring system, i.e. as an evaluation system of response conflicts. Furthermore, such conflicts between different responses need an increase in attentional vigilance to allow for behavioural regulation. Cohen et al. (2000) suggested an increase of responsivity of the noradrenergic brainstem nucleus locus coeruleus (LC) to constitute the mechanism underlying this process (see figure 1 of this reference; see also Usher, et al.,

1999). In the current thesis, the use of fMRI in study A3 allowed for the measurement of activity in both DLPFC and ACC as a subcortical region. For a further elucidation of theories and findings on the contributions of the DLPFC and ACC, specifically with regard to interactions with parietal areas, see also 10.1.2, 10.1.4 and 10.2.4.

# 1.3 Approach-Avoidance Task (AAT)

As described in the previous chapters, a great part of approach-avoidance behaviour happens as automatic reactions. Since such automatic, impulsive processes occur mainly outside from the awareness, they cannot be assessed by participants' explicit reports. Rather, implicit measures are necessary, whereby De Houwer et al. (2009a) defined implicit measures as "[...] a measurement outcome that is causally produced by the to-be-measured attribute in the absence of certain goals, awareness [...]" (p. 350, line 39-41; for a review and statement on normative criteria see De Houwer, et al., 2009a; see also the comments by Gawronski, et al., 2009 and Nosek & Greenwald, 2009 and the reply by De Houwer, et al., 2009b).

The Approach-Avoidance Task (AAT) is a widely used implicit task. Its advantage is the direct assessment of the behavioural component of approach-avoidance impulses. Thereby, both the automatic impulses as well as their deliberative regulation can be assessed (Krieglmeyer & Deutsch, 2010). According to the given instruction, participants either have to approach or to avoid stimuli presented on a computer screen. Currently, there are two popular versions how to implement these behaviours (see figure 3). In the joystick version, participants pull or push a joystick, which enhances and reduces the picture size, respectively (zooming effect; e.g. Rinck & Becker, 2007). In the manikin version, a manikin is moved on the computer screen towards the picture or away from it via pressing a button (e.g. De Houwer, et al., 2001).

In compatible conditions, the instructed behaviour matches implicit reaction tendencies (avoiding negative stimuli or approaching positive ones), while such tendencies have to be inhibited for performing an alternative reaction in incompatible conditions (approaching negative stimuli or avoiding positive ones). As a consequence of this conflict, reaction times are longer in incompatible compared to compatible conditions. These so-called stimulus response compatibility effects (SRC effects) are the main parameter of the AAT and are calculated as (longer) reaction times in incompatible minus (shorter) reaction times (RTs) in compatible conditions (cf. Krieglmeyer & Deutsch, 2010).

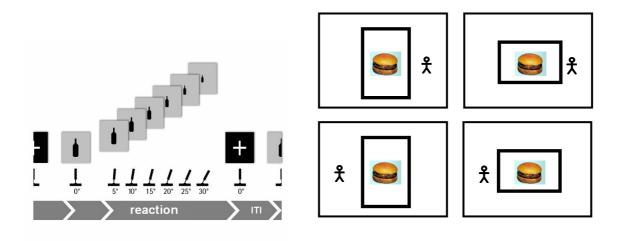


Figure 3: Schematic illustration of two AAT versions

Right panel: Joystick version, avoidance reaction (push movement) with a picture depicting a beverage. Left panel: Manikin version with a positive picture from the International Affective Picture System (IAPS). The four possible arrangements of frame (lengthwise or crosswise) and position of the manikin (right or left) are shown.

### 1.3.1 Origin, development and critical issues

The first mentioning of an experimental investigation on arm movements and their relation to affective processes was given by Münsterberg (1892). In a self-experiment, he tested the accuracy of arm movements towards and away from the body for a specific distance during positive and negative affective states. He concluded that "Es ergibt sich also, dass in der Unlust die Streckbewegungen wesentlich zu klein, die Beugebewegungen zu gross, und umgekehrt in der Lust die Beugebewegungen zu klein, die Streckbewegungen zu gross gemacht werden." (Münsterberg, 1892, p. 223, line 1-5) and further, that "Biologisch ist der Antagonismus zwischen Streck- und Beugetätigkeit offenbar gleichzusetzen dem Gegensatz von Annäherung und Entfernung in Bezug auf äußere Reize." (p. 224, line 4-6).

Since then, researchers used a variety of experimental tasks simulating approach-avoidance behaviour to investigate these processes. Influences of the compatibility of stimulus valence and automatic approach-avoidance tendencies on RTs were described by Solarz (1960) for the first time. Individuals categorized word stimuli as positive and negative

by moving a hand lever to approach or to avoid words cards mounted on a moveable stage. Participants faster initiated compatible than incompatible movements (avoid positive, approach negative words). <sup>18</sup> Chen and Bargh (1999, exp. 1) conceptually replicated this study with a lever and word stimuli presented on a computer screen. Later experiments replaced the lever by a joystick (refered to as simple joystick version, e.g. Chen & Bargh, 1999) and – finally – the feedback joystick version was used (e.g. Rinck & Becker, 2007), wherein the simulation of approach and avoidance also included the zooming effect as already described in 1.3.

# 1.3.1.1 Specific muscle activation account vs. distance regulation account

One interpretation of SRC effects concentrated on effects due to the arm movements per se. The so-called specific muscle activation account suggested a long-term association between stimulus evaluation and motor representations of arm movements to be the underlying mechanism (Cacioppo, et al., 1993; Chen & Bargh, 1999). Accordingly, flexion and extension of the biceps are uniquely associated with approach and avoidance behaviour due to a long life higher order Pavlovian conditioning process, since, in countless repetitions within an individual's life time, arm flexion and extension are closely coupled in time with approaching desirable goods and avoiding undesirable goods, respectively (Cacioppo, et al., 1993; Neumann & Strack, 2000). This interpretation is in line with the assumption of evolutionary based, rigid, hard-wired connections between affective evaluations and instrumental motor responses, as e.g. suggested by the Hard Interface Theory (HIT) of Zajonc and Markus (1984). There, it is assumed that motor reactions are hard representations of affect (compared to affective experience as soft representation). The embodiment perspective described in 1.1.3.4 might be seen as a cognitively orientated descendant of the HIT (Niedenthal, et al., 2005b). Its assumptions imply an explanation of SRC effects in terms of retrieving the neural representations of response tendencies, since, there, body movements per se are not assumed to have representational content.

However, already the results of Münsterberg (1892), which associated arm tension with approach and arm flexion with avoidance behaviour, indicated that such explanations cannot fully account for SRC effects. Several further studies suggested not the muscle activation per

<sup>&</sup>lt;sup>18</sup> Note, that the original question of this study was, whether participants faster learn compatible than incompatible S-R relations, see also 10.5.4.

se, but the regulation of the distance between the subject and the stimulus to be the essential aspect (distance regulation account; Wentura, et al., 2000; Markman & Brendl, 2005; van Dantzig, et al., 2008; Lavender & Hommel, 2007b; Seibt, et al., 2008; Eder & Rothermund, 2008a; Neumann & Strack, 2000, exp. 2). Markman and Brendl (2005) disentangled the effects resulting from muscle activation and distance regulation by presenting a corridor on a computer screen, in which participants' first name was positioned in the middle and positive and negative words either behind the name or in front of it. In case of the word being presented in front of the name, approaching it by moving the lever required extending the arm and avoiding the word required bending the arm. Regardless of the word position, i.e., regardless of the actually conducted movement, participants were faster, when they moved positive words towards the name than away from it and vice versa for negative words.

Van Dantzig et al. (2008) showed neutral responses to become approach-avoidance reactions when they were paired with reducing and enhancing the distance to a stimulus. By pressing one of two keys, participants had to decide, whether presented words were emotional or neutral. Thereby, one key press was always followed by an enlargement of the word size creating the impression of approach and distance reduction, while the other key press caused a decrease of word size creating the impression of avoidance and distance enhancement. As expected, positive words were faster categorized as *emotional* when they were associated with the key press followed by the approach impression. For negative words, this decision was faster, when the key press was followed by the avoidance impression.

Seibt et al. (2008) systematically varied participants' instructions and found SRC effects for both possible reference points, the physical self and the computer screen: In line with the above reported findings from Markman and Brendl (2005), arm flexion was interpreted as approaching and arm tension as avoiding a stimulus, when the physical self (body) was the reference point (exp. 1). In contrast, when the reference point of the reaction was shifted from the participant to the computer screen, approaching the stimulus on the computer screen was identical to a movement away from the physical self of the participant and avoiding the stimulus required a movement towards the participant. The found SRC effect pattern revealed participants to interpret arm flexion as avoiding and arm tension as approaching a stimulus (Seibt, et al., 2008, exp. 3; cf. also exp. 2 of Eder & Rothermund, 2008a). Such a reversed interpretation of arm movements was also shown by Lavender and

Hommel (2007b) with a slightly different experimental setup: Participants moved a doll positioned on the middle plate to a front plate (nearer to the screen, but farther away from their body) and to a back plate (farther away from the screen, but nearer to their body), respectively. Wentura et al. (2000, exp. 3) supported the validity of the distance regulation explanation by replicating these findings with a completely different experimental setup: Participants were instructed to permanently press a key and to release it, when a word appeared on a computer screen, what caused a reduction of the word size. This equalled a withdrawal movement from the screen, but approach to the participant. Another group of participants held their index finger on the response key and pressed it when a word was presented resulting in an enlargement of the stimulus and the impression of approach (for a further description and discussion of this study see also 11.2). In sum, these experiments clearly revealed the aspect of distance regulation to more effectively code approachavoidance tendencies than the instrinsic characteristics of the arm movements: Participants interpreted the required movements dependent on the reference point the movement was directed to (cf. also the classic study of Heider and Simmel (1944) on the interpretation of movements as following or chasing in dependence of the experimental context).

This argumentation also explains why the manikin version of the AAT is efficient. De Houwer et al. (2001, exp. 4) were the first who realized approach-avoidance reactions via the movements of a manikin. In this task version, participants have to press a button to move a manikin towards or away from a stimulus. In other words, moving the manikin regulates the distance between this representative of the participant and the stimulus. However, the distance-regulation account cannot explain all results (cf. the findings of Rotteveel & Phaf, 2004, see below and 10.5.1). Another interpretation of SRC effects concentrated on the representational overlap of stimulus valence and the required response (Lavender & Hommel, 2007b; Eder & Rothermund, 2008a). A detailed discussion of this theory and its meaning for the current thesis is given in 1.3.2 and 10.5.

### 1.3.1.2 Unintentional valence processing

Results were controversial with regard to the question, whether SRC effects arise when the stimulus valence is processed unintentionally. Chen and Bargh (1999, exp. 2) showed faster RTs for compatible reactions using the simple joystick version. There, participants always pushed or pulled a lever (two separate task blocks), i.e., moved it without consciously evaluating the valence of a word stimulus. Similarly, in exp. 3 of Duckworth et al. (2002),

participants were instructed to always approach or avoid the presented images. These images had been generated as novel stimuli, i.e., as stimuli without any explicit conceptual meaning, but had been rated by participants as intuitively positive or negative. Approaching positively and avoiding negatively valenced stimuli, i.e., congruent stimulus-direction combinations caused faster reactions. Furthermore, De Houwer et al. (2001, exp. 4) reported SRC effects in a manikin version, when participants categorized positive and negative words according to their grammatical category (adjective vs. noun). Krieglmeyer et al. (2010) also used this sort of control task and showed significant SRC effects in a feedback joystick version (exp. 2a) and when participants moved a dot on a screen by moving a pen on a writing tablet (exp. 2b). Another masking variant resulting in unintentional processing of the stimulus valence was used by Wiers et al. (2009) in addiction research. Participants were instructed to react according to the format of beverage and IAPS pictures, which were either presented in portrait (lengthwise) or in landscape format (crosswise). Although, the content of the picture was not relevant for solving the task, it clearly influenced participants' reactions. Note, that study A3 of the current thesis is the first investigation, which used this masking variant with IAPS pictures in healthy persons.

The stability of these findings was questioned by Rotteveel and Phaf (2004) using an experimental arrangement with three perpendicular buttons on a vertical stand. Participants started each movement with their hand at the middle button. Therefore, pressing the upper button equalled extending the arm and thereby an avoidance movement, while pressing the lower button equalled bending the arm and thereby an approach movement. The authors only found SRC effects, when participants categorized pictures of positive and negative facial expressions according to their valence (exp. 1), but not when the gender of the depicted person was the categorization criterion (exp. 2). Similarly, Lavender and Hommel (2007b, doll version, see 1.3.1.1) only found SRC effects, when they asked participants to categorize the presented IAPS pictures according to their valence, but not with the instruction to concentrate on the spatial orientation of the pictures. One might suspect the different task versions, stimuli and control instructions to account for the variability of these findings. However, another explanation was given by Krieglmeyer et al. (2010, see also 1.3.3), who suggested the unambiguity of the instruction to be the essential aspect: In the above cited studies, which did not reveal significant SRC effects when the stimulus valence was processed unintentionally, the movements were not clearly instructed as approach and avoidance movements and the reference point of the movement was not clearly specified. Moreover, the TEC suggests another explanation with regard to possible influences of the motivational context. This alternative is discussed in 10.5 together with its relevance for the findings of the present thesis.

# 1.3.1.3 The influence of approach-avoidance reactions on attitude formation

With regard to the bidirectionality of the link between affective evaluation and behaviour as introduced in 1.1.3.5, Cacioppo et al. (1993) used the AAT to show arm flexion and extension to influence attitudes. Thereby, arm flexion was realized as an isometric flexor contraction: Participants had to press with their palms upward on the lower surface of a table. In contrast, arm extension was achieved via pressing the palms downward on the upper surface of the table. During these muscle contractions, participants rated the valence of Chinese ideographs, i.e., of novel, previously neutrally rated stimuli (exp. 1 and 2). Ideographs presented during arm flexion were rated as more positive than during arm extension (cf. also the results of Eder and Klauer (2009) with regard to neutral stimuli). However, when participants did not consciously evaluate the valence, but categorized the stimuli into *simple design* and *complex design* (exp. 3), this effect was no longer existent. Cacioppo et al. (1993) conluded "[...] that motor activation is not the critical factor, but instead it is motor activation in the psychological context of individuals evaluating the attitude stimuli [...]." (p. 10, line 14-17, left text column; cf. Förster & Strack, 1998).

Cretenet and Dru (2004) replicated this study, but also took into account Davidson's theory of hemispheric cortical asymmetry (Davidson, et al., 1990; see 1.1.2). According to the interpretation of Cretenet and Dru (2004), contracting an arm should activate not only contralateral motor regions, but also contralateral adjacent areas: Contracting the right arm should activate the left-hemispheric approach system and contracting the left arm should activate the right-hemispheric avoidance system. Therefore, while Cacioppo et al. (1993) asked participants to use both palms, Cretenet and Dru (2004) tested participants with either the right or the left palm. Congruent conditions, namely extension contraction with the left palm (activating the right – hemispheric avoidance system) and flexion contraction with the right palm (activating the left – hemispheric approach system), led to more positive ratings than incongruent conditions (flexion of right arm and extension of left arm; exp. 1). Simultaneously conducting the two congruent movement conditions caused more positive ratings than simultaneously conducting the two incongruent movement conditions (exp. 2). These findings further supported the general assumption that approach-avoidance reactions

influence attitude formation on neutral stimuli. However, when analyzing the data according to the hand-contraction arrangement as used by Cacioppo et al. (1993), participants' ratings were only moderately different from zero. This was also the case in the study of Cacioppo et al. (1993), what confirmed Cretenet and Dru (2004) in their interpretation, that there is a significant interaction between hand and arm contraction resulting in merely no effects when participants perform a congrurent and an incongruent condition at the same time. While Förster and Strack (1996) proposed the above described hypothesis of conceptual-motor compatibility (see 1.1.3.5), Cretenet and Dru (2004) interpreted their results as showing influences of motor congruency at a lower stage of processing, namely within the motor system (see however 10.5).

Centerbar and Clore (2006) questioned the results of Cacioppo et al. (1993), since participants' pre-exposure to the stimuli might have enhanced their positivity (cf. mere exposure effect in 1.1.3.1) and Duckworth et al. (2002) had shown already subtle differences in the valence ratings of novel stimuli to cause behavioural SRC effects (see 1.3.1.2). Based on valence judgements assessed in a prior study, Centerbar and Clore (2006) differentiated between positive and negative Chinese ideographs. Furthermore, they instructed participants to use their dominant hands, while - otherwise - replicating the proceedings of Cacioppo et al. (1993). Centerbar and Clore (2006) showed the influence of approach-avoidance related muscle contractions on the evaluation of the ideographs to depend on the a priori valence of these stimuli: The ideographs were rated more positively in compatible combinations of motor action and valence (approach positive, avoid negative) compared to incompatible combinations (exp. 1 and 2). Importantly, there were no main effects of the arm position per se, i.e., there was no direct effect of arm contraction on attitude formation for the ideographs. A similar pattern was found, when using the original stimuli of Cacioppo et al. (1993, exp. 3), whereby Centerbar and Clore (2006) interpreted the results for the subset of the most neutrally rated stimuli as indicating absolutely no influence of arm contraction.<sup>19</sup>

However, Friedman and Förster (2000; Friedman & Forster, 2002) showed approach-avoidance reactions to influence affect and related cognitive processes. According to the cognitive tuning theory, individuals' cognitive styles depend on their affective state (Schwarz & Bless, 1991): Negative affect signals a problematic situation inclusive the necessity to

<sup>&</sup>lt;sup>19</sup> I question the validity of this interpretation, since Centerbar and Clore (2006) did not report any post-hoc tests, although figure 2 shows enormous variances and each subset consisted of only 6 ideographs. Future studies specifically concentrating on this aspect and – thereby – using a more appropriate task design might be useful.

systematically process information and to rely on established solutions, thereby, restricting creative problem solving. In contrast, positive affect signals a non-hazardous environment inducing a heuristic processing style and openness to novelty resulting in creative solutions. In accordance with these predictions, arm flexion as assumed to cause positive affect led to a better performance in tasks requiring creative thinking, while arm extension as assumed to induce negative affect facilitated analytic thinking (Friedman & Forster, 2000; Friedman & Forster, 2002).

With regard to the influence of approach-avoidance reactions on attitude formation, Cretenet and Dru (2004) showed that performing arm contractions did not change participants' mood, i.e., that a change of the generalized affective state did not explain the found effects (see also Förster & Strack, 1996, exp. 2 and Cacioppo, et al., 1993, exp. 6). However, for congruent conditions, they discussed the induction of a sense of ease and – thereby – positive feelings not assessed by the used questionnaires to possibly influence participants' ratings. In this context, Cacioppo et al. (1993) concluded that the retrieval of higher order classical conditioning contingencies between movements and motivational orientations from non-declarative memory mediated the found effects (see however 10.5).

## 1.3.2 Stimulus Response Compatibility effects (SRC effects)

The enhanced RTs in incompatible situations were interpreted as consequence of the conflict in these conditions: Automatic, compatible behavioural impulses have to be inhibited and alternative, opposite, uncommon reactions have to be performed. Therefore, the strength of SRC effects was interpreted to reflect the degree of incompatibility, respectively, the strength of automatic behavioural impulses in the compatible condition (Krieglmeyer & Deutsch, 2010; Heuer, et al., 2007).

SRC effects were shown in healthy subjects using positive and negative stimuli. Thereby, word stimuli – mainly adjectives and nouns – were used (e.g. Solarz, 1960; De Houwer, et al., 2001; Eder & Rothermund, 2008a). Other studies prefered the presentation of pictorial stimuli, namely facial expression (e.g. Rotteveel & Phaf, 2004; Roelofs, et al., 2009) and IAPS pictures (Lavender & Hommel, 2007a; Wiers, et al., 2009). Moreover, the AAT was also used to measure approach-avoidance tendencies towards social groups (Neumann, et al.,

2004) and towards goals and temptations (Fishbach & Shah, 2006). See 10.6.2 for a detailed description of these studies and a discussion of the AAT with regard to complex and more ecologically valid behaviour.

The AAT also allows for assessing psychopathological alterations of approach-avoidance tendencies: At one side – reflecting pathologically enhanced avoidance tendencies as associated with anxiety disorders – SRC effects for anxiety-relevant stimuli were found in individuals with enhanced levels of anxiety and anxiety disorders (e.g. Heuer, et al., 2007; Rinck & Becker, 2007). At the other side, SRC effects were shown for addiction related populations. Stimuli closely related to the respective addicted behaviour caused facilitated approach reactions and hindered avoidance behaviour. Such effects were shown for hazardous drinkers (Field, et al., 2008; Wiers, et al., 2009), for persons addicted to heroin (Zhou, et al., 2011) or alcohol (Barkby, et al., 2012; Wiers, et al., 2011; cf. also my own study, which is not part of the current thesis, Ernst, et al., in press; however, see also Spruyt, et al., 2013), for tobacco smokers (Bradley, et al., 2004) and for regular cannabis users (Field, et al., 2006).

While the above described studies and conclusions concentrated on the mode of action, which simulates approach-avoidance behaviour in the AAT (see 1.3.1.1), there is another central question with regard to the mechanisms of SRC effects. Both the motivational view and the evaluative coding view offer suggestions. The explanation from the motivational view is derived from theories of motivated orientation (Neumann & Strack, 2000; Krieglmeyer & Deutsch, 2010; Krieglmeyer, et al., 2010; Chen & Bargh, 1999). As described above (see 1.1.1, 1.1.3.1 and 1.1.3.2), affective stimuli are assumed to facilitate approach-avoidance reactions by eliciting motivational orientations that prepare the organism for appropriate responses (Lang, et al., 1990; Lang, 1995; Lang, et al., 1998; Neumann, 2003). This assumption of behavioural preparedness attributes a higher relevance to valence processing compared to any other psychological process, because it is indispensable for an organism's survival.

Empirical evidence came from exp. 1 of Neumann and Strack (2000). They showed behavioural input to activate the two motivational systems and – thereby – to also influence the valenced-based categorization of words. Participants faster categorized words as positive and negative by left and right button presses, when the approach system was

activated by pressing the palm of the non-dominant hand against the underside of a table (flexion condition) and when the avoidance system was activated by pressing the palm on the top of the table (tension condition), respectively. In exp. 2, Neumann and Strack (2000) showed the same acceleration of RTs, when participants were given the visual impression of moving away or towards the computer screen by presenting a background of increasing (approach) or decreasing (avoidance) concentric circles. In other words, participants only got exteroceptive cues of approach-avoidance reactions, but no proprioceptive cues. This result further supported, that the regulation of the distance to the stimulus and not the movement per se is essential for SRC effects (see also the more detailed description of this aspect in 1.3.1).

The central statement of the motivational view is, that SRC effects allow for conclusions, whether a stimulus is associated with approach or avoidance motivation and, thereby, for conclusions on the positive or negative valence assigned to this stimulus (Krieglmeyer, et al., 2010). Furthermore, the motivational view assumes these relations to be evolutionary or functionally based: "Approach orientation is a preparedness to decrease the distance between the person and an aspect of the environment." and "Avoidance orientation can be conceptualized as a preparedness to increase the distance between the person and the environment." (Strack & Deutsch, 2004, p. 231, right text column, line 14-16 and line 18-20).

With regard to the contribution of automatic and regulated, deliberative processes, the above introduced RIM (see 1.2.1) as a representative of dual-process models from cognitive-emotional psychology implies the following explanation (Strack & Deutsch, 2004): SRC effects might be described as the difference between — on the one hand — the faster activation of usually evoked behavioural schemata via the impulsive system in compatible situations and — on the other hand — the slower process of their inhibition and the initiation of an alternative reaction by the reflective system in incompatible conditions.

The alternative view, the evaluative coding view as derived from the TEC (Hommel, et al., 2001, see 1.1.3.6), does not contain such evolutionary orientated explanations. It uses the term *affective-mapping effect* instead of SRC effect (Eder & Rothermund, 2008a; Lavender &

Hommel, 2007b). This term is based on the assumption that valence has no special status among other stimulus features, such as e.g. colour, size or location. The affectively enriched version of the TEC assumes, that the affective feature codes assigned to an event are part of its coding as are the feature codes for sensory perception and associated motor actions (Lavender & Hommel, 2007b). Together, these sensorimotor units represent action plans, as already suggested by James' *ideo-motor principle* (James, 1890b), which assumes that "[...] a particular action is cognitively represented by codes that refer to how it feels to carry out that action [...]" (Lavender & Hommel, 2007b, p. 1277, line 10-11). The second part of this principle is also affectively extended to the assumption that the activation of such affective codes – as of any other feature code – can initiate the related action.

This is possible due to the overlap of feature codes on the level of more abstract codes in the common coding system. If a stimulus is evaluated as being positive, its representations contain the code *positive valence*. All actions and other stimuli also comprising this code are partially activated, i.e., their prefered processing is primed. Furthermore, the TEC assumes the cognitive representations of approach reactions to contain feature codes of positive affect, since they are usually associated with positive action results (Eder & Klauer, 2009). In an analoguous manner, the representations of avoidance reactions contain feature codes of negative affect. With regard to the AAT, faster RTs for compatible reactions are explained as a facilitation effect resulting from the overlap between the valence code of the stimulus and the valence code of the reaction. In contrast, in incompatible conditions, an action plan not pre-activated by the valence code of the stimulus has to be executed.

Summing up, the central message of the evaluative coding view is the statement, that the mediating mechanism underlying SRC effects is not a motivational orientation as suggested by the motivational view, but valence compatibility. Following this argumentation, SRC effects or – rather – affective mapping effects do not reflect motivational orientations and only imply that the valence codes of a stimulus and a response correspond with each other. Thereby, stimuli and responses are assumed to share a representational space, i.e., to directly interact via their feature representations. In contrast, the motivational view implies an indirect relation with the motivational orientations as mediator between stimulus and response (cf. Krieglmeyer, et al., 2010).

Lavender and Hommel (2007b) directly tested the impact of different feature codes on reactions in the AAT (doll version, for a description see 1.3.1.1). They used IAPS pictures, which were slightly rotated either to the left or right side, i.e., whose representational codes contained the feature codes valence and spatial orientation. In the affective instruction group, the picture valence indicated, whether participants had to conduct approach or avoidance movements. Analyses revealed the expected affective mapping effects. In the spatial instruction group, the orientation of the pictures was the criterion for choosing the appropriate movement direction. Here, no affective mapping effects emerged, but the expected spatial mapping effects. According to previous findings (Bauer & Miller, 1982; Lippa, 1996), human perception-movement relations contain an intrinsic hand axis: Moving the left hand forward equals a movement to the left side, while moving it backwards equals a movement to the right side. For the right hand, the opposite relations hold true. In the used doll version of the AAT, moving the hand with the doll forward means approaching the picture and moving it backwards means avoiding it. Therefore, compatible conditions are approach with the right hand and avoid with the left hand for pictures rotated to the right side and avoid with the right hand and approach with the left hand for pictures rotated to the left side. Analysis revealed significantly shorter RTs for the so definded compatible compared to incompatible conditions, i.e., spatial mapping effects.<sup>20</sup> This latter result showed, that the intention created by the used instruction determined the weighting of the different feature codes, which were associated with a stimulus, and – thereby – the nature of the overlap with possible motor reactions. Furthermore, these findings questioned the status of valence as special and, therefore, automatically and preferably processed stimulus feature.

Although, these conclusions from the evaluative coding view clearly restrict the generalized statements of the motivational view, SRC effects (or affective mapping effects) still allow for conclusions on the valence assigned to a stimulus and its compatibility with approach-avoidance reactions. A more detailed discussion of these aspects is given in 10.5, together with the integration of findings of the current thesis on differences between the processing of positive and negative stimuli.

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<sup>&</sup>lt;sup>20</sup> It should be noted however, that the authors drew this conclusion on the significant main effect of *spatial mapping* as post-hoc test of the significant interaction *spatial mapping* x *response hand*, but did not report the comparisons between compatible and incompatible conditions separately for each hand (cf. figure 6A of Lavender and Hommel (2007b) depicting an asymmetric interaction).

### 1.3.3 Sensitivity, reliability and criterion validity

Until now, there is only one study directly investigating the question of sensitivity, reliability (internal consistency) and criterion-validity: Krieglmeyer and Deutsch (2010) compared the manikin version, the simple joystick verion and the feedback joystick version of the AAT with regard to these parameters at the behavioural level. The manikin task was the most sensitive and – thereby internally valid – AAT version. When participants explicitly processed the valence of presented word stimuli (exp. 1), the manikin task revealed medium to large effect sizes of SRC effects (according to Cohens's d; Cohen, 1977), while the simple joystick task revealed only small SRC effects. When participants categorized the words according to their grammatical category (nouns vs. adjectives), i.e., processed the valence unintentionally (exp. 2), there were small SRC effects in the manikin and feedback joystick version, but no significant SRC effects in the simple joystick task. There were no differences between the versions with regard to their split-half reliability (calculated as Spearman-Brown correlation between odds and even trials;  $r \ge .75$ ). However, the split-half reliability was only satisfactory, when valence was intentionally processed ( $r \le .53$ ). Finally, compared to the feedback joystick task, the manikin task also revealed higher criterion validity (exp. 3).

According to Krieglmeyer and Deutsch (2010), the differences in sensitivity might be due to three reasons. First, recategorization of the required responses in other terms than the instructed response labels could introduce error variance and reduce task sensitivity. Participants might recategorize the responses for simplifying specifically incompatible trials. For example, avoiding a stimulus by pushing the joystick away from one's body might be recategorized as pushing the joystick forward. Similarly, approaching a stimulus by pulling the joystick towards oneself might be internally changed to pulling it backwards, thereby, loosing its relation to approach-avoidance tendencies.<sup>21</sup> Furthermore, compared to the manikin task, the relationship between the concrete reaction and the meaning of the response is fixed, because movements in one direction always equal approach and in the other direction avoidance. This might additionally simplify recategorization processes. With regard to the movements required in the joystick versions, there is also another categorization aspect which could be problematic under specific circumstances: The interpretations of the arm movements can be reversed. Moving a joystick away from one's body simulates an avoidance movement, but also means that the participant moves the hand

<sup>&</sup>lt;sup>21</sup> These alternative response labels were explicitly used as instruction by Chen and Bargh (1999). However, there, SRC effects were found even when participants did not intentionally process the valence of the stimuli (exp. 2).

closer to the stimulus. Similarly, pulling the joystick towards one's body equals an approach movement, but also moves the hand away from the stimulus. The studies cited in 1.3.1.1 showed, that these alternative interpretations of the arm movements can be intentionally induced by changing participants' instructions. There, SRC effects were reversed when the meaning of the joystick movements specified the computer screen and not the participants' body as reference point (Seibt, et al., 2008, exp. 3; Eder & Rothermund, 2008a, exp. 2; cf. also Markman & Brendl, 2005; Lavender & Hommel, 2007b; Wentura, et al., 2000, exp. 3). While Rinck and Becker (2007, exp. 2) showed such an interpretational change to be merely impossible in the feedback joystick task with its zooming effect, Krieglmeyer and Deutsch (2010) suggested this alternative interpretation of push- and pull-movements to be most unlikely in the manikin version.

Furthermore, according to their suggestions, the second reason for the higher sensitivity of the manikin version might be found in the means of distance regulation: In the joystick versions, the position of the object is manipulated, because - independently of the concrete interpretation of the movement - one movement equals taking the object and the other one equals putting it away. In contrast, the manikin version is based on - at least virtual movements of participants' position, since the stick figure as representative of the participant moves towards or away from the stimulus. Krieglmeyer and Deutsch (2010) suggested this behaviour to be more universal and automatised, since it is more similar to highly automatised forms of natural behaviour, such as e.g. withdrawal reflexes (cf. Konorski, 1967; Schneirla, 1959). There, the core element of the defensive behaviour is to move body parts away from the danger and not to remove the critical stimulus or to cause it to remove. Extending this argumentation to approach behaviour, one might describe natural approach reactions rather as moving oneself towards the desired object for getting it than as moving the stimulus. In the context of the motivational view, valenced evaluations might more strongly activate such highly automatised forms of behaviour than initiating manipulations of an object, what might result in stronger SRC effects in the manikin version.<sup>22</sup>

The third important contribution to the sensitivity of the AAT version was constituted by the aspect of consciously or unconsciously processing the valence of the stimuli

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<sup>&</sup>lt;sup>22</sup> Krieglmeyer and Deutsch (2010) further supported their argument on automaticity with the assumption, that the AAT mainly assesses the link between stimulus evaluation and the activation of approach-avoidance schemata, which is a long-term association. In contrast, the translation from the activated schemata into concrete behaviour has short-term characteristics, since it is only established during the measurement (cf. also 10.5.4).

(Krieglmeyer & Deutsch, 2010). Regarding previous controversial results (for a detailed overview see 1.3.1) together with the results of exp. 2 of Krieglmeyer et al. (2010), one might conclude that the mental representation of approach-avoidance behaviour is the crucial factor (Krieglmeyer & Deutsch, 2010). Unintentional evaluations of stimulus valence seem to cause weaker activations of approach-avoidance schemata as indicated by the above described smaller SRC effects. However, De Houwer et al. (2001, cf. Bargh, et al., 1992; see also 1.1.1) suggested stimulus valence to be unintentionally processed in case of activated semantic representations of a stimulus. Following this explanation, Krieglmeyer and Deutsch (2010) postulated the controversial previous results to depend on unambiguous representations of responses as approach and avoidance reactions, i.e., to reflect differences in the study design and the instruction. They stated, that, in principle, valent stimuli are able to trigger approach-avoidance tendencies when participants do not intentionally evaluate stimulus valence. However, it is necessary, that the possible responses are unambiguously mentally represented as approach and avoidance behaviour.

Furthermore, Krieglmeyer and Deutsch (2010) investigated the criterion-validity of the AAT by correlating the strength of SRC effects for spider pictures with self-report questionnaires on fear of spiders (exp. 3). Scores of the spider fear scales and explicit valence ratings of spider pictures were negatively correlated with approach-biases towards spiders (calculated as the difference between approaching minus avoiding spider pictures). In other words, the stronger participants' fear of spiders was and the more negatively they rated the spider pictures, the more strongly they showed a behavioural tendency for avoiding spider pictures. The reversed pattern was found for the butterfly control pictures. This only hold true for the manikin version; in the feedback joystick version, only the explicit ratings, but not the questionnaires were significantly related to the assessed behaviour. Such a higher validity of the manikin version is in line with its higher sensitivity. However, as Krieglmeyer and Deutsch (2010) pointed out, it might also be due to design shortcomings of this study, such as e.g., distortion of self-reports by self-presentation motives, since Rinck and Becker (2007, exp. 1) showed the joystick version to be highly valid: There, SRC effects predicted real behaviour towards spiders in a behavioural assessment test of approach and avoidance reactions. With regard to healthy participants reacting to typical positive and negative stimuli, such evidence of validity is still missing.

For the current thesis, I followed these previous findings and used the feedback joystick version and a variant of the manikin version (see 2.1 and 2.2.2). Moreover, participants of the

current studies were instructed in a clear manner, i.e., the required responses were unambiguously defined as approach and avoidance reactions.

## 1.3.4 Neuronal activity during the AAT

Up to date, there are only a few investigations, which combined the AAT with neuroimaging methods. In fMRI, one research group investigated reactions to facial expressions in healthy participants. Roelofs et al. (2009) observed regulatory activity in left lateral OFC and ventrolateral PFC (VLPFC) during incompatible trials (approach angry faces, avoid happy faces). Volman et al. (2011b) also showed activity in bilateral VLPFC and frontal pole and, moreover, in fusiform gyrus, left supramarginal and inferior parietal gyrus to be enhanced during incompatible conditions. Furthermore, when inhibiting left anterior PFC (aPFC) by means of TMS, Volman et al. (2011a) reported decreased perfusion in bilateral aPFC and posterior parietal cortex, but also increased perfusion in amygdalae and left FFA (continuous arterial spin labeling). More details on these findings and their relation to results of the current thesis can be found in 10.1.3.

With regard to behavioural SRC effects, Roelofs et al. (2009), Volman et al. (2011a) and Volman et al. (2011b) found the expected pattern of faster RTs for compatible reactions, when participants categorized the pictures according to the valence of the facial expressions, but not when participants reacted according to the gender of the presented faces. A more detailed discussion of the results of Volman et al. (2011b) is also given in 10.1.3.

Using EEG/ERPs, van Peer et al. (2007) and van Peer et al. (2009) investigated avoidance reactions of social phobic persons to facial stimuli. They concentrated on the P150 ERP as an ERP specific for the processing of facial expressions, the N2 ERP and the P3 ERP. In high, but not low trait avoidant participants, cortisol administration (i.e. stress induction) elicited behavioural SRC effects for angry faces (faster RTs for avoidance than approach reactions) by increasing RTs in the critical, affect-incongruent condition *approach angry faces* (van Peer, et al., 2007). This might be interpreted as an aggravation of performance, which was accompanied by an enhancement of N2 and P3 ERP amplitudes in the non-critical, affect-congruent condition *avoid angry faces* compared to the affect-incongruent condition *avoid happy faces*. Van Peer et al. (2009) investigated patients with

social anxiety disorders. While there were no effects with regard to the P3 ERP, patients with high levels of social anxiety showed enhanced amplitudes of a component specific for the processing of facial expressions (P150 ERP) after cortisol administration during avoidance compared to approach of both happy and angry faces.

These results were taken as an orientation for the design and methodological decisions of the current studies. However, they are only related to the current thesis to some extent, since their questions concentrated on social emotional behaviour and – thereby – the samples and stimuli differed substantially (see also 10.2).

## 2 Aims and linkage of studies

The thesis at hand investigated the neuronal and neuropsychological correlates of approach-avoidance reactions during the AAT. Regulation processes in incompatible situations (approach negative, avoid positive) were of specific interest, since they are human-specific and guarantee behavioural flexibility. Thereby, the current work aimed to answer questions regarding the underlying neuronal correlates of behavioural SRC effects. While behaviour assessed as RTs and error frequencies is the final outcome of several different psychological processes, neuroimaging and electrophysiological methods allow for disentagling the contributions of specific sub-processes. The current thesis concentrated on sub-processes underlying the reactions of healthy persons to stimuli of general emotional relevance. The following chapters outline the aims and hypotheses of the included six studies as well as the technical details, which were orientated at the above described previous studies.

## 2.1 Basic questions

I combined the above described models from cognitive-emotional psychology and neuroscience to a theoretical framework for the investigations of brain activity during the AAT. Explanations for SRC effects (i.e., for longer RTs in incompatible than compatible conditions) were deduced from both perspectives.

Following the RIM, SRC effects result, because incompatible reactions require the inhibition of approach-avoidance impulses in terms of the reflective system controlling the impulsive system and initiating an alternative reaction (Strack & Deutsch, 2004). As suggested in thesis 8 of the RIM, the impulsive system is orientated in terms of either approach or avoidance motivation. Thereby, the functioning of the impulsive system, namely the activation spreads in its network structure, allow for the fast activation of all representational nodes belonging to one behavioural schema. In other words, the functioning of the impulsive system might be seen as the correlate of the motivational orientation.

Following the neuronal models presented above, such SRC effects might result from prefrontal cortical top-down regulation inhibiting subcortical bottom-up activity (Ernst & Fudge, 2009).

In general, SRC effects might result from a conflict at the response-selection stage, when the intuitive response competes with the instructed response (cf. also 10.2.2). Therefore, from the neuropsychological perspective, response inhibition mechanisms and attentional mechanisms ensuring a different weighting of relevant and irrelevant task features should underlie SRC effects (Norman & Shallice, 1986). Specifically, SRC effects might result from controlled attention allocation regulating effects produced by automatic attention allocation.

Implications from the alternative psychological explanation for SRC effects according to the common coding view (see 1.3.2) are discussed in 10.5. For the sake of clarity and simplicity, I only use the explanation from the RIM as psychological background, when deriving the hypotheses for the different studies. It is more intuitive with regard to the role of motivation. However, when discussing the findings of the present study, this view is expanded by the common coding explanation, which allows for overcoming several of its shortcomings (see 10.5).

Part A of this thesis investigated neuronal correlates of SRC effects from a localization approach by means of functional imaging. In studies A1, A2 and A4, functional near infrared spectroscopy (fNIRS) was used to assess prefrontal cortical activity, including activity of the DLPFC. This optical imaging method (see e.g. Obrig & Villringer, 2003) measures cortical activity in a valid (Plichta, et al., 2007a) and reliable manner (Plichta, et al., 2006; Plichta, et al., 2007b; Schecklmann, et al., 2008), while its limited depth resolution does not allow for depicting subcortical activation in striatum and amygdala as arising from automatic approach-avoidance tendencies. However, fNIRS has several advantages in comparison to fMRI or other imaging methods, specifically the silent working mode and the reduced sensitivity to movement artefacts as might be caused by the arm movements in the joystick AAT. For a more detailed description of these advantages see 4.2. The basic hypothesis of studies A1, A2 and A4 refered to the DLPFC as a main regulation instance of the human brain. The DLPFC was expected to show enhanced regulatory activity in incompatible compared to compatible conditions as neuronal correlate of behavioural SRC effects.

With regard to the AAT, I used a joystick version for all studies including studies from part B, except for study A3. In two different blocks, participants were explicitly instructed to react according to the pictures' valence. Thereby, I tried to ensure that the picture valence was

really attented to (cf. 1.3.1.2). Following the suggestion of Krieglmeyer and Deutsch (2010), approach and avoidance movements were unambiguously instructed by clearly defining participants' physical self as reference point: Bending the arm corresponded to approaching a stimulus and extending the arm to avoiding a stimulus. A zooming effect in terms of enhancing the pictures size, when approaching it, and reducing the picture size, when avoiding it, additionally ensured the unambiguity of the required responses.

In study A3, this approach to assess neuronal correlates was broadened: FMRI was used to measure whole brain activity, i.e., to depict not only cortical but also subcortical activity. For avoiding any movement artefacts, I used a manikin version of the AAT. Again, participants received clear definitions of the possible reactions: Moving the manikin towards the picture stimuli equalled approaching it and moving the manikin away from the picture equalled avoiding it. This task further comprised a new development in terms of a GoNoGo version of the AAT, which is described in detail in 2.2.2. In short, this task version aimed at a closer investigation of the preparation and realization versus inhibition of compatible and incompatible reactions.

In part B (studies B1 and B2), neuropsychological processes were investigated by means of EEG/ERPs, i.e., these studies were orientated at a more process-oriented approach (see also 1.2.3). Due to its high temporal solution in the range of milliseconds, EEG allows for depicting different sub-processes in terms of ERPs. Thereby, in contrast to the localization approach of the neuronal models, ERPs allow for the investigation of the sequence of automatic and controlled processes. Thereby, data analysis concentrated on ERPs depicting unconscious (P1, N1 ERP) and conscious (P3 ERP) attention allocation (Smith, et al., 2003; Vogel & Luck, 2000). Furthermore, the N2 ERP as indicator of conflict processing and inhibition was in the focus of interest (Folstein & Van Petten, 2008). In general, I expected incompatible compared to compatible conditions to elicit higher amplitudes of ERPs indicating attentional regulation and inhibitory processes. A more detailed description of the processes reflected by these ERPs can be found in the introduction sections of studies B1 (8.2) and B2 (9.2). For identifying brain areas generating the electrophysiological effects, I conducted a source localization analysis in study B1. Thereby, the disadvantage of the low spatial resolution was reduced, although the findings of this study should be interpreted in the context of the fMRI findings (study A3).

In all studies, the thesis at hand concentrated on the universality of the investigated processes: The measurements were conducted in healthy persons with negative and positive IAPS pictures, which are stimuli of general emotional relevance (Lang, et al., 2005). I decided to not use facial expressions, since, there, the reason of the emotion might not be clear (cf. Lavender & Hommel, 2007b). In study A3, I also used neutral picture stimuli for investigating the specificity of the reactions to positive and negative stimuli (see also 10.3.5).

Until now, such picture stimuli were only used twice in the AAT (Wiers, et al., 2009; Lavender & Hommel, 2007b). In the study of Wiers et al. (2009), however, the focus of interest lay on another picture set also used in the study, namely pictures of alcohol and non-alcohol products. This study assessed only RTs and revealed heavy social drinking students at genetic risk for alcohol dependence to show generalized approach biases towards alcohol stimuli, but also to positive IAPS pictures, while heavy drinkers not at risk did not show such an effect. The result was interpreted as generalized approach bias towards all sorts of appetitive stimuli. Lavender and Hommel (2007b) found significant SRC effects for the used IAPS pictures, when the pictures' valence was the categorization criterion, i.e., when participants consciously evaluated the valence, but not, when participants concentrated on another feature (spatial orientation of the pictures). Although, Lavender and Hommel (2007b) found generally faster RTs for negative than positive pictures (affective instruction group), they did not compare SRC effects elicited by positive and negative pictures.

However, previous results on the processing of positive and negative stimuli in general clearly revealed fundamental differences between these two valence categories (e.g. Ito, et al., 1998; for details see 10.3.4). In sum, negative stimuli were shown to be preferentially processed. Explanations from an evolutionary perspective suggested them to be more important for survival (e.g. Ohman, et al., 2001). Therefore, the thesis at hand separately analyzed reactions to positive and negative stimuli.

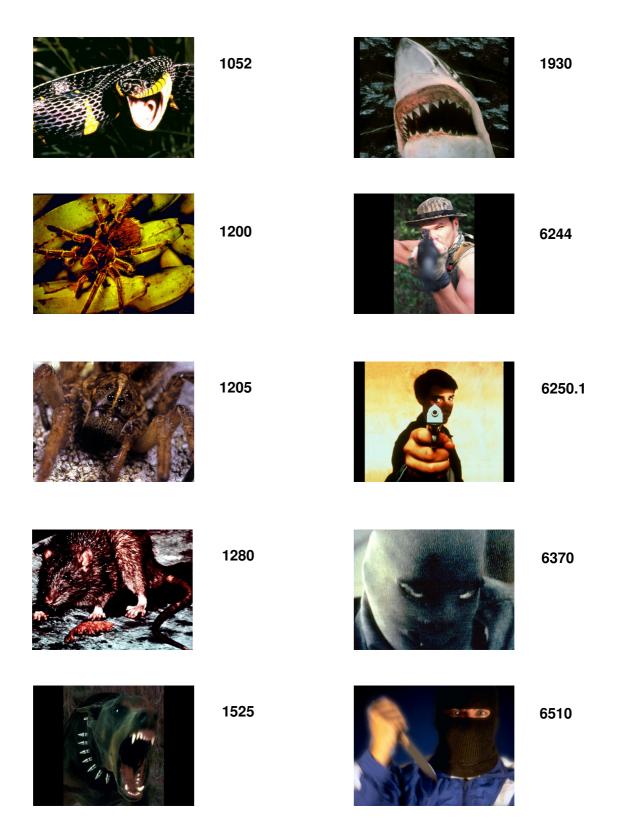


Figure 4: Negative IAPS pictures

This final set was used for studies A2, B2 and A3 (numbers according to the classification of Lang, et al., 2005).

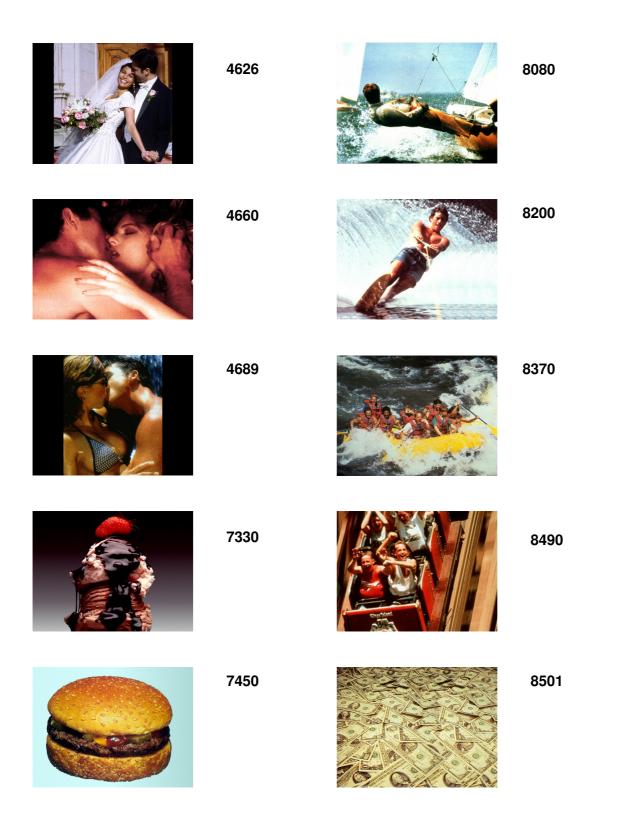


Figure 5: Positive IAPS pictures

This final set was used for studies A2, B2 and A3 (numbers according to the classification of Lang, et al., 2005).



Figure 6: Neutral IAPS pictures

This final set was used for studies A2, B2 and A3 (numbers according to the classification of Lang, et al., 2005).

## 2.2 Development of further questions

The results of the initial studies A1 and B1 led to subsequent questions (studies A2, A3, B2; see table 1 in chapter 3 for an overview on methodological aspects). In short, study A2 investigated interindividual differences in terms of genetic influences as a moderator of regulation processes, while study B2 concentrated on interindividual differences and their role in connecting brain and behaviour in a mediator model. As already mentioned above, study A3 investigated whole brain processes during different conflict stages by means of a GoNoGo version of the AAT.

#### 2.2.1 Interindividual differences

I conducted the initial studies A1 and B1 under the assumption, that approach-avoidance tendencies are universal processes. However, the differences between behavioural and neuronal results indicated possible influences of interindividual differences in stimulus processing (for details see 4.5.1 and 8.5). In general, previous studies showed related processes such as impulses and self-control to be influenced by interindividual differences (Hofmann, et al., 2008; Friese, et al., 2008).

With regard to processes assessed in the AAT, such influences were also suggested by Krieglmeyer and Deutsch (2010): "[...] individual dispositions may moderate how the stimulus is evaluated and to what degree approach or avoidance schemata are activated." (p. 812, left text column, line 31-33). Until now, only one AAT study directly took this consideration into account. Puca et al. (2006) assessed the strength of participants' general approach and avoidance motives via a semiprojective questionnaire (Multi-Motive Grid (MMG), Sokolowski, et al., 2000). Participants moved their forearm towards (approach) or away (avoidance) from words presented on a computer screen. Independently from the valence of the words (positive, negative, neutral), the strength of the avoidance motives significantly modulated the force of participants' reactions (peak force): High expressions of avoidance motives were associated with higher peak force for avoidance than approach movements, while low expressions of avoidance motives were associated with the reversed pattern (exp. 1).

I decided to test for such possible influences of interindividual differences on automatic reactions tendencies and on the regulation efficiency in incompatible AAT conditions.

Thereby, I concentrated on variables, which are related to the processes involved in the AAT, by taking two different approaches: In study A2, a neurobiological moderator approach was chosen to investigate the influence of a genetic factor, namely of the variants of the Monoamin Oxidase A (MAOA) enzyme. In study B2, a neuropsychological mediator approach was used to investigate the influence of the personality variable goal-oriented pursuit.

In study A2, I followed previous studies which used a moderator approach, i.e., which included a variable defining categorical subgroups with different qualities. With regard to the AAT, all the studies investigating pathologically altered reactions can be subsumed under this approach (see 1.3.2). In non-pathological samples, this approach was also taken by van Peer et al. (2007), when categorizing subsamples of persons with low and high expressions of a specific personality trait. Until now, however, there is only one study using a genotype as moderator. A first investigation of genetic influences on reactions in the AAT revealed young adult carriers of a risk genetic variant for alcohol dependency (G-allele of the mu-opioid receptor gene *OPRM1*) to show enhanced approach biases for appetitive stimuli in general (Wiers, et al., 2009b; see also the study description above in relation to the usage of IAPS pictures). Besides their role as risk factors for pathologies, genetic variants regulating the concentration of specific neurotransmitters are also powerful determiners of regional brain activity and connectivity between different areas underlying non-pathological responses (e.g. Meyer-Lindenberg, 2009).

Due to the emotional stimulus content, managing the conflict in incompatible AAT conditions depends not only on cognitive control, but also on the affective response. Previous studies showed variations in the gene encoding *MAOA* (*MAOA*-uVNTR) to significantly determine neuronal activity in regions, which are crucial for affective reactions and regulation, as well as for cognitive inhibition and WM performance. For details on the exact mode of action of *MAOA* on monoaminergic neurotransmitter systems see 5.2 and 5.5. In short, *MAOA-L* carriers show stronger activation of emotionally relevant areas and lower activation of cognitively relevant areas than *MAOA-H* carriers (e.g. Eisenberger, et al., 2007; Passamonti, et al., 2006). In a similar way, participants' reactions in the AAT might depend on this genotype with *MAOA-H* carriers displaying better regulation. The detailed hypotheses are described in 5.2.

In study B2, I extended such moderator approaches by using a mediator model for investigating how a personality characteristic, that strongly determines the efficiency of active behavioural regulation, influences reactions in incompatible AAT-conditions. The personality trait *goal-oriented pursuit* is a sub-dimension of the Behavioural Activation System (BAS) as suggested in Gray's Reinforcement Sensitivity Theory (RST; Gray, 1994; Gray & McNaughton, 2000; see also 1.1.2). It is assessed via the scale BAS-drive (Carver & White, 1994). Goal-oriented pursuit reflects motivated cognitive performance and control of subcortical responses to emotional stimuli by the PFC (Carver & White, 1994; cf. Passamonti, et al., 2008b; Putman, et al., 2010). It is assumed to be associated with better behavioural regulation leading to desired outcomes (Carver & White, 1994). With regard to the AAT, higher BAS-drive scores were expected to be accompanied by less behavioural SRC effects, i.e., by better behavioural regulation.

As mentioned above, I was also interested in the neuropsychological mechanisms underlying such interindividual differences: The parietal P3 ERP is interpreted to reflect the allocation of capacity-limited attentional resources towards relevant situations (Nieuwenhuis, et al., 2005). In this context, I expected SRC effects in the P3 ERP in terms of enhanced amplitudes during correct incompatible compared to compatible AAT reactions. Furthermore, higher P3 ERP amplitudes had been associated with better behavioural performance (e.g. Clayson & Larson, 2011b). Therefore, I expected stronger P3 SRC effects to be accompanied by less pronounced SRC effects at the behavioural level.

Moreover, I expected higher BAS-drive scores to be associated with larger P3 SRC effects, i.e., better behavioural regulation in terms of more conscious attention allocation. Finally, for the first time in research on the AAT, I connected the three components personality, brain and behaviour in terms of a mediator model: The question of study B2 was, whether the influence of interindividual differences in goal-oriented pursuit on behaviour is mediated by the efficiency of cognitive regulation, i.e., whether the amount of controlled attention allocation is a mechanism underlying the impact of this personality trait on behaviour. In other words, higher BAS-drive scores should be associated with less behavioural SRC effects, whereby the association with stronger P3 SRC effects was expected to be the mechanism underlying this relation.

#### 2.2.2 GoNoGo version of the AAT and whole brain activation

For study A3, I developed a new version of the AAT in terms of a GoNoGo task. The task is depicted in the methods section of study A3 (6.3.3). The reaction phase was divided into two events, the cue event indicating the participant to prepare a response and the move event indicating the participant to actually make the prepared response or to inhibit it. The cue event consisted of a picture in a frame, whose format told participants to either approach (portrait format) or to avoid (landscape format) the stimulus. This instruction was reversed for half of the participants. Furthermore, a black little manikin was presented on either left or right side of the picture. The move event consisted of the same arrangement, whereby the manikin was either green (Go conditions) or red (NoGo conditions).

The idea of this development was the further investigation of the conflict underlying SRC effects. Study A3 aimed at the preparation of compatible and incompatible reactions, as well as at their realization versus inhibition. Following the assumptions presented above, the cue event should already elicit neuronal SRC effects: According to the motivational view, the valence of the stimuli should be automatically processed and the valence evaluation should automatically elicit the related motivational tendencies. Therefore, a mismatch between the elicited motivation and the instructed reaction direction should constitute a conflict prior to the actual response. Regulatory SRC effects would indicate a pre-regulation during this anticipation phase. For the move event, in the Go trials, I also expected regulatory SRC effects, when participants had to react, since – despite the assumed pre-regulation – actually performing an incompatible reaction should require regulatory capacities. In contrast, in the NoGo trials, I expected reversed SRC effects, i.e., a shift in the concept of compatibility: Inhibiting compatible reactions should be an incompatible situation; however, not performing an incompatible reaction should be a compatible situation. Thereby, the GoNoGo version allowed for investigating the inhibition of compatible response tendencies without the initiation of an alternative response as is the case in the usual incompatible conditions. Thereby, I was also interested in differences between processing positive and negative stimuli. Following the results of studies A1, A2, B1 and B2 (see 10.3 and 10.4), negative stimuli seemed to have been more important for participants. In the GoNoGo task version, such differences might be specifically pronounced with regard to the assumed pre-regulation processes.

With regard to specificities of the task design, I took into account the findings and suggestions of previous studies described above. First, in contrast to studies A1, A2, B1 and B2, a non-explicit instruction variant was used. Following the studies of e.g., Wiers et al. (2009), participants reacted according to the pictures' frame, i.e., the valence was no longer intentionally processed. The advantage of this instruction variant is, that it does not prepare participants for subsequent compatibility effects (see the discussions of studies A1-B2, e.g., 4.5.1).

Second, the position of the manikin was chosen as left and right from the picture and frame. I did not use the common arrangement of the positions below and above the picture (cf. Wiers, et al., 2009; De Houwer, et al., 2001), since the rating study of Eder and Rothermund (2008a) revealed the response labels *up* and *towards* to be unintentionally associated with the concept *positive*, while *down* and *away* were associated with *negative*. In contrast, *left* and *right* were evaluated as neutral. In accordance with these explicit findings, in a manikin AAT, Krieglmeyer, et al., 2010 (exp. 1) found faster RTs, when approaching the manikin to the picture was equivalent to moving it upwards (manikin started from below the picture) and when avoiding was equivalent to moving the manikin downwards (manikin started from above). In contrast, when the manikin started from above for the approach movement (downwards movement) and from below for the avoidance movement (upwards movement), longer RTs indicated a mismatch between the unintentional evaluation of the response labels and the motivational orientation.<sup>23</sup>

Third, I chose a simultaneous presentation of the picture, the frame (i.e., the instruction) and the manikin for allowing participants to prepare the specific reaction at the cue event. Pressing the left button moved the manikin to the left and pressing the right button moved it to the right. However, dependent on the starting position of the manikin either on the left or on the right side of the picture, these movements equalled approaching or avoiding the stimulus. Therefore, the cue event created an anticipation phase, which allowed participants to prepare the specific response and – thereby – to reduce the error probability. With regard to the move event in NoGo trials, participants really had to process the valence and direction before inhibiting the response, while in a GoNoGo version without a cue event, the red colour of the manikin would allow to omit any response without identifying the actual stimulus

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<sup>&</sup>lt;sup>23</sup> Krieglmeyer et al. (2010) suggested executive control processes to be generally enhanced in the latter arrangement and to mask the influence of bottom-up processes and, thereby, SRC effects.

arrangement. In contrast, the green colour would only indicate to react, while the identification of the correct response would still be necessary.

Fourth, I took a probability of 50% for the frequency of Go and NoGo events. This frequency ensured enough NoGo events for the fMRI analysis and forced participants to concentrate throughout the anticipation phase by causing the greatest possible uncertainty about the required reaction.

Furthermore, neuronal activity was investigated in the entire brain by means of fMRI, not only in cortical regions as done in the fNIRS studies. Until now, this imaging method was used in the studies already mentioned in 1.3.4 (Roelofs, et al., 2009; Volman, et al., 2011b; Volman, et al., 2011a). Specifically with regard to regulation processes in incompatible situations, subcortical regions such as the ACC or the insulae were in the focus of interest (see chapter 6 for details).

## 2.2.3 Approach bias: Learned stimulus response compatibility

As mentioned above (see 1.3.2), in addiction and anxiety disorders approach and avoidance tendencies are pathologically altered, respectively. The question arises, if such alterations are also observable at the neuronal level. Study A4 of the present thesis is a pilot study for investigating such alterations with regard to addiction processes by means of fNIRS.

Dual-process models of impulse and self-control assume approach biases towards addiction-relevant stimuli to be strongly enhanced due to prior positive learning experiences (Deutsch & Strack, 2006). With regard to the neuronal model of approach-avoidance reactions as suggested by Ernst and Fudge (2009), such alterations might be observable in terms of enhanced activity of the ventral striatum during *approaching alcohol* compared to *avoiding alcohol*, depicting the compatibility of the former condition due to heightened positive evaluation of approaching alcohol stimuli (cf. Bechara, 2005). Study A4 investigated these effects in the OFC, which is the only structure of the general reward circuitries that is measurable by fNIRS (Koob & Volkow, 2010). Furthermore, as for the processing of general

positive and negative stimuli, regulation associated DLPFC activity should be enhanced during *avoiding alcohol* compared to *approaching alcohol*, indicating the incompatibility of the former condition.

In the current thesis, I investigated these processes in a sample of healthy young adults with non-problematic drinking amounts and frequencies. Participants reacted to pictures of alcohol and non-alcohol products. These pictures had previously been developed in our laboratory and tested for suitability in another sample. This pilot study was conducted for generally testing the above described neuronal hypotheses. Since alcohol stimuli should not be of general relevance for healthy participants, I expected participants' individual consumption pattern and validation of alcohol to modulate the reactions to alcohol stimuli. In general, the more positive participants perceive alcohol stimuli, the stronger a possible behavioural approach bias should be and the stronger their activation should be during approaching than avoiding alcohol in OFC and during avoiding than approaching alcohol in DLPFC.

# 3 Overview of studies: Methodological aspects

	imaging method	task variant	sample size (n)	analysis	analysis programs
Study A1: Basics: Prefrontal activation patterns in fNIRS	fNIRS	■ Joystick AAT ■ ITI duration 3.5-9 s (jitter) ■ explicit emotion instruction → 2 runs	15	<ul> <li>event-related</li> <li>Gaussian         HRF with         peak time of         6.5s</li> <li>mdRTs</li> </ul>	■ SPSS ■ MATLAB
Study A2: Interindividual differences: MAOA-uVNTR as neurobiological moderator	fNIRS	<ul> <li>Joystick         AAT</li> <li>ITI duration         3.5-9 s         (jitter)</li> <li>explicit         emotion         instruction         → 2 runs</li> </ul>	37  MAOA-L: n = 7  MAOA- LH: n = 8  MAOA-H: n = 22	<ul> <li>event-related</li> <li>Gaussian</li> <li>HRF with</li> <li>peak time of</li> <li>6.5s</li> <li>mdRTs</li> </ul>	■ SPSS ■ MATLAB
Study A3: GoNoGo AAT and whole brain activity	fMRI	<ul> <li>cued         GoNoGo         AAT (cue         event, move         event)</li> <li>ISI duration         2.25 s</li> <li>ITI duration:         stable jitter         + prejitter         (3.5 s-6.5s)</li> <li>implicit         instruction         (frame)</li> <li>5 runs</li> </ul>	34	<ul> <li>event-related</li> <li>Gamma         Function         HRF (2<sup>nd</sup>         order)</li> <li>D-Scores</li> </ul>	<ul> <li>SPSS</li> <li>SPM8</li> <li>GLM_FLE X</li> <li>peak_nii</li> <li>marsbar</li> <li>SPSS PROCESS</li> </ul>
Study A4: learned stimulus- response compatibility (alcohol pictures)	fNIRS	<ul> <li>Joystick         AAT</li> <li>ITI duration         3.5-9 s         (jitter)</li> <li>explicit         emotion         instruction         → 2 runs</li> </ul>	15	<ul> <li>event-related</li> <li>Gaussian         HRF with         peak time of         6.5s</li> <li>mdRTs</li> </ul>	■ SPSS ■ MATLAB

	imaging method	task variant	sample size (n)	analysis	analysis programs
Study B1: Basics: SRC effects in ERPs	ERPs sLORETA	<ul> <li>Joystick         AAT</li> <li>ITI         duration         2.5-4 s         (jitter)</li> <li>explicit         emotion         instruction         → 2 runs</li> </ul>	15	<ul> <li>amplitudes of ERPs</li> <li>mdRTs</li> <li>penalty scores</li> </ul>	<ul><li>SPSS</li><li>MATLAB</li><li>Vision     Analyzer2</li><li>sLORETA</li></ul>
Study B2: Interindividual differences: Controlled attention allocation as neuropsycho- logical mediator	ERPs	■ Joystick AAT ■ ITI duration 2.5-4 s (jitter) ■ explicit emotion instruction → 2 runs	36	<ul> <li>amplitudes of ERPs</li> <li>mdRTs</li> <li>mediation analysis</li> </ul>	<ul> <li>SPSS</li> <li>SPSS</li> <li>PROCESS</li> <li>MATLAB</li> <li>Vision</li> <li>Analyzer2</li> </ul>

Table 1: Overview of the methodological aspects of the included studies

AAT = Approach-Avoidance Task, D-scores = SRC effects corrected for intraindividual variance, ERP = event-related potential, fNIRS = functional near-infrared spectroscopy, fMRI = functional magnetic resonance imaging, HRF = haemodynamic response function, ITI = inter-trial interval, ISI = inter-stimulus interval, *MAOA*-uVNTR = gene encoding monoamine oxidase A (MAOA), mdRTs = median reaction times, SRC effect = stimulus-response compatibility effect

The remaining abbreviations refer to names of analyses programs, which are reported in detail in the methods sections of the respective studies.

## 4 Study A1: Prefrontal activation patterns in fNIRS

The contents of this chapter are published in:

Ernst LH, Plichta MM, Lutz E, Zesewitz AK, Tupak SV, Dresler T, Ehlis A-C, Fallgatter AJ (2013): Prefrontal activation patterns of automatic and regulated approach-avoidance reactions – A functional near-infrared spectroscopy (fNIRS) study. *Cortex*, 49 (1), 131-142.

In the following chapter, study A1 is denominated *study 1*, since the original publication also contains study A4 (refered to as *study 2*).

See 17.1 (organizational remarks) with regard to the formatting of the text (use of abbreviations, headings, etc.) and the rights for publications.

#### 4.1 Abstract

The present pilot study investigated cortical processes during automatic and regulated approach-avoidance reactions for the first time. In 15 healthy volunteers, prefrontal activity was measured with functional near-infrared spectroscopy (fNIRS) during performance of a joystick version of the Approach-Avoidance Task (AAT). In experiment 1, participants approached (pulled towards their body) and avoided (pushed away from their body) positive and negative pictures. Incompatible, regulated reactions (avoid positive, approach negative) compared to compatible, automatic reactions (approach positive, avoid negative) caused stronger activation in terms of a decrease of deoxygenated haemoglobin (HHb) in right dorsolateral prefrontal cortex (DLPFC) (i.e., in one of the main instances for behavioural control in humans).

In the context of pathologically enhanced approach tendencies in addiction disorders and of planned future studies, we presented alcohol and non-alcohol pictures in experiment 2. Here, left anterior lateral orbitofrontal cortex as part of the general reward system processing secondary rewards showed stronger activation in terms of increased oxygenated haemoglobin (O<sub>2</sub>Hb) during approaching compared to avoiding alcohol pictures. This difference was positively correlated with participants' expectation about beneficial effects of alcohol in terms of emotional regulation.

Despite some limitations due to the pilot character of the study, our results suggest that further combinations of the AAT and functional imaging methods will reveal detailed insight into neuronal mechanisms constituting approach-avoidance as basic behavioural principles and into specifically altered sub-processes in alcohol dependence.

## 4.2 Introduction

The basic behavioural principles of approach and avoidance have been investigated by cognitive-emotional psychology as well as neurosciences for gaining insight into mechanisms of behavioural impulses and their control. Both perspectives conceive approach-avoidance behaviour to be constituted of automatically triggered, unconscious processes and more consciously controlled reactions (Hofmann, et al., 2009; Ernst & Fudge, 2009). Indeed, quickly approaching positive stimuli and avoiding negative stimuli are essential for regulating the organism's needs in the short term. On the other hand, human beings often have to regulate those immediate impulses by means of volitional control for achieving long-term goals (Hofmann, et al., 2009). In cognitive-emotional psychology, dual-process models of impulse and self-control assume the automatic and controlled reactions to be processed by two semi-independent systems, an impulsive system and a reflective system, respectively (e.g. Strack & Deutsch, 2004). Imaging studies showed the striatum and amygdala to be mainly associated with automatic approach reactions towards positive stimuli and avoidance reactions towards negative stimuli, respectively (Ernst & Fudge, 2009; Tomer, et al., 2008; O'Doherty, et al., 2004; Cunningham, et al., 2010; Schlund & Cataldo, 2010). However, these subcortical structures do not exclusively process positive, respectively negative stimuli (Carretie, et al., 2009; Hamann & Mao, 2002). Neuroscientific models suggest controlled approach-avoidance reactions to be mediated by the prefrontal cortex (PFC) as a main neural control instance (Ernst & Fudge, 2009; Miller & Cohen, 2001; Dosenbach, et al., 2008), whereby especially its dorsolateral parts initiate performance adjustments (Ridderinkhof, et al., 2004). Successful inhibition of automatic approach-avoidance tendencies requires the control of the impulsive system by the reflective system or, in terms of the neuroscientific explanation, the inhibition of subcortical bottom-up activity by prefrontal cortical top-down regulation (Ernst & Fudge, 2009; Bechara, 2005; Ernst, et al., 2006).

The investigation of automatic approach-avoidance tendencies and their regulation requires the use of implicit measures (Wiers, et al., 2007; De Houwer, et al., 2001), since

impulsive processes occur mainly out of awareness and cannot be assessed by participants' explicit reports. One frequently used task is the Approach-Avoidance Task (AAT; De Houwer, et al., 2001) with the advantage of simulating approach-avoidance behaviour and, thereby, directly assessing the behavioural components of impulses. In the current study, we used a joystick version of the AAT (cf. Rinck & Becker, 2007): Participants move a joystick for either approaching or avoiding pictures presented on a computer screen. Approach and avoidance behaviour are simulated by increasing picture size when pulling the joystick towards the own body and, respectively, by decreasing picture size when pushing the joystick forward. The instructed behaviour either matches implicit reaction tendencies (compatible conditions: e.g. approaching positive pictures and avoiding negative ones) or requires their regulation for performing an alternative reaction (incompatible conditions: e.g. avoiding positive pictures or approaching negative ones). Therefore, incompatible reactions elicit longer reaction times than compatible ones, an effect also known as stimulus response compatibility effect (SRC effect; Krieglmeyer & Deutsch, 2010; Eder & Rothermund, 2008a). In healthy subjects, such SRC effects have been shown for positive and negative stimuli (Eder & Rothermund, 2008a; Krieglmeyer & Deutsch, 2010; Krieglmeyer, et al., 2010).

In clinical research, SRC effects for anxiety-relevant stimuli were found in individuals with enhanced levels of anxiety and anxiety disorders reflecting their pathologically enhanced avoidance tendencies (e.g. Heuer, et al., 2007). Most important for our focus of interest, in addicted patients, the AAT yielded SRC effects in terms of facilitated approach and hindered avoidance behaviour for addiction-related stimuli. This was shown for hazardous drinkers (Field, et al., 2008; Wiers, et al., 2009), tobacco smokers (e.g. Bradley, et al., 2004) and regular cannabis users (Field, et al., 2006).

Mechanisms underlying SRC effects (i.e. differences between compatible and incompatible reactions) are described as follows by the two perspectives introduced above. Dual-process models of cognitive-emotional psychology assume the impulsive system to be organized like an associative network, wherein the representation of a stimulus is directly and tightly linked with its emotional evaluation and frequently co-occurring behavioural reactions (e.g. Strack & Deutsch, 2004). Hence, SRC effects depict the difference between – on the one hand – the faster activation of usually evoked behavioural schemata via the impulsive system in compatible situations and – on the other hand – the slower process of their inhibition and the initiation of an alternative reaction by the reflective system in incompatible situations. Following the results of previous neurobiological studies, SRC

effects might arise from the difference between a faster activation of striatum and amygdala during automatic approach-avoidance tendencies in compatible situations compared to the slower top-down PFC control, which is required to inhibit this bottom-up activity to allow for an alternative reaction in incompatible situations (cf. Bechara, 2005; Ernst & Fudge, 2009; Miller & Cohen, 2001).

These two perspectives also explain the altered SRC effects in addiction. Due to prior experience, addiction-related stimuli and approach behaviour are closely linked to each other within the impulsive system of addicted individuals (Bechara, 2005; Everitt, et al., 1999). Since, at the same time, their reflective system is dysfunctional, inhibition processes do not occur sufficiently and the automatically triggered approach tendencies can prevail, resulting in continued substance consumption and relapse. Pathological alterations shown at the neuronal level match these theoretical considerations. The general approach system overlaps with brain structures known to be highly relevant in addiction (Ernst, et al., 2006; Ernst & Fudge, 2009). In the progressive course of addiction, the amygdala, where stimuli are linked to their affective attributes, is assumed to dysfunctionally communicate with the ventral striatum (Bechara, 2005; Everitt, et al., 1999), which in turn becomes sensitized for incentive values of addiction-related stimuli (e.g. Robinson & Berridge, 2003; Montague & Berns, 2002; Vollstadt-Klein, et al., 2010). Besides this abnormal activity in the amygdalaventral striatum system, the PFC was as well shown to be dysfunctional in addicted individuals in situations requiring behavioural regulation (Li, et al., 2009; Bechara & Martin, 2004). Following these former results, the neuronal processes underlying the extensive approach behaviour in addicted individuals might be best described as an imbalance of heightened striatal and decreased PFC activity (Bechara, 2005).

In the present pilot study, we combined the introduced hypotheses and methods from cognitive-emotional psychology and neurosciences for the first time. Directly during the AAT, we assessed prefrontal cortical activity by means of functional near-infrared spectroscopy (fNIRS), an optical imaging method (see e.g. Obrig & Villringer, 2003). Similar to functional magnetic resonance imaging (fMRI), it is a haemodynamic-based technique that has been shown to measure cortical activation in a valid (Plichta, et al., 2007a) and reliable manner (Plichta, et al., 2006; Plichta, et al., 2007b; Schecklmann, et al., 2008). Due to limitations in depth resolution, fNIRS cannot depict subcortical activation in striatum and amygdala arising from automatic approach-avoidance tendencies. However, for the following advantages, we prefered fNIRS as imaging method: First, the joystick version of the AAT requires arm

movements. In this experimental design, it is very difficult for participants to not move the rest of their body, what might cause movement artefacts. Due to the relatively flexible arrangement of the optodes to the head, fNIRS is less sensitive to movement artefacts than e.g. fMRI, magnetoencephalography (MEG) or positron emission tomography (PET), where the head must remain in a totally fixed position. Second, fNIRS allows participants to remain in a sitting position, i.e., it enables measurements in an ecologically more valid situation than fMRI or PET. Sitting upright compared to lying is the more typical setting for human approach-avoidance reactions. Third, the silent working mode of fNIRS and the non-claustrophobic measurement situation prevent disturbance and stress (cf. Pripfl, et al., 2006), which might interfere with emotional processing. Furthermore, the spatial resolution of fNIRS is higher than in MEG and, in comparison to PET, no radioactive substances are used during the measurement.

For the present study, we exploratively tested the combination of AAT and fNIRS in a sample of 15 young adults with two different picture sets, in order to assess the cortical aspect of the above-described model. In experiment 1, we presented positive and negative pictures from the International Affective Picture System (IAPS; Lang, et al., 2005). Since these stimuli are of general emotional relevance, they should elicit automatic approach, respectively avoidance tendencies, whereby incompatible reactions should require regulation by dorsolateral PFC (DLPFC). In experiment 2, participants reacted to pictures of alcohol and non-alcohol products. Due to the non-pathological sample characteristics, we expected the relevance of this picture set not to be as universal as for the IAPS pictures, but to depend on participants' individual appraisal of alcohol consumption. As in former studies (Field, et al., 2008; Wiers, et al., 2009), we expected already small differences in this relevance to modulate participants' behavioural and also brain reactions. Investigating such differences in healthy participants, whose brains do not show any severe alterations as e.g. atrophy or alterations due to co-morbid psychiatric disorders, might allow to relate the altered reactions to specific alterations in brain functions, respectively, in this pilot study, to alterations in prefrontal functions. Besides the DLPFC, the orbitofrontal cortex (OFC) was in our focus of interest. Its anterior lateral part is the only by fNIRS measurable structure of the general reward system (e.g. Peters & Buchel, 2010) and of a circuitry underlying the anticipation of positive drug effects at later stages of addiction (Koob & Volkow, 2010). This part of the OFC is a phylogenetically recent structure processing secondary rewards (i.e. reinforcers whose values have been learnt before; Sescousse, et al., 2010; Kringelbach & Rolls, 2004). In this context, we interpret its activation to reflect affective appraisal of the required reactions.

Knowledge about reactions of the healthy brain could help to detect specific alterations in addiction and improve experimental parameters for future studies.

In summary, the present study aimed at investigating the neuronal basis of behavioural SRC effects during the AAT by means of fNIRS. In experiment 1, we hypothesized behavioural SRC effects and regulation processes during incompatible reactions to be reflected in enhanced activation of the DLPFC. In experiment 2, we expected reactions to be modulated by the relevance of the alcohol pictures as reflected in participants' individual consumption pattern. Amount of drinking and positive validation of alcohol as indicated by subjective measures should be negatively correlated with reaction times (RTs) for approaching alcohol pictures and positively correlated with RTs for avoiding alcohol pictures, respectively. With regard to fNIRS, we focussed on DLPFC and anterior lateral OFC, where we expected regulatory (DLPFC) and evaluative activity (OFC) to be positively correlated with these characteristics of alcohol consumption.

#### 4.3 Methods

## 4.3.1 Participants

Fifteen young adults were recruited from the experimenters' acquaintances (seven males; mean age  $23.4 \pm 2.5$  years, range: 21 - 29 years). All participants were right-handed (Edinburgh Handedness Inventory; Oldfield, 1971). For excluding a history of psychiatric, neurological or severe internistic disorders, all participants filled in a screening questionnaire based on the structured clinical interview for DSM-IV (SKID; Wittchen, et al., 1997). Furthermore, we screened participants for ensuring no current intake of any psychotropic medication or illicit drugs. After detailed explanation of the procedure, written informed consent was obtained from all participants. The study was approved by the local Ethics Committee of the University of Wuerzburg and all procedures were in accordance with the Declaration of Helsinki in its latest version from 2008.

#### 4.3.2 Materials

## 4.3.2.1 Self-report measures and picture rating

The state version of the Positive Affect Negative Affect Schedule (PANAS; Krohne, et al., 1996) was used to assess the current mood status. Trait anxiety was assessed with the trait scale from the State-Trait-Anxiety-Inventory (STAI-X2; Laux, et al., 1981). Furthermore, participants reported their amount of alcohol consumption within the last month. These specifications were transformed into the unit gram of absolute alcohol via the formula "amount [in ml] x volume per cent [in Vol-%] x 0.79 [density of alcohol in kg/l]". Following the standards of the German Centre for Addiction Issues (Raiser & Bartsch, 2010), the parameter volume per cent for the different beverages was taken from Bühringer (1999). Additionally, participants filled in the German version of the Brief Alcohol-Expectancy Questionnaire (Brief AEQ-G; Demmel & Hagen, 2003), which assesses expectancies of positive alcohol effects. The items can be assigned to the two factors social motives (internal consistency r = .90 (Cronbachs alpha), retest reliability r = .88) and reduction of tension and emotional regulation (internal consistency r = .70 (Cronbachs alpha), retest reliability r = .79). Furthermore, participants rated the alcohol and non-alcohol picture stimuli with regard to valence, arousal and ease of recognition. Valence and arousal ratings were assessed by means of the Self Assessment Manikin (Lang, et al., 2005), a scale ranging from unpleasant (-4) to pleasant (+4) and from not arousing (0) to very arousing (9), respectively. Ease of recognition was assessed by means of a 5-point-Likert scale ranging from 1 (easy to recognize) to 5 (difficult to recognize).

#### 4.3.2.2 Picture material

We used two picture sets containing two different picture categories each. The resulting four picture categories consisted of ten different pictures each. In experiment 1, positive and negative IAPS pictures (Lang, et al., 2005; negative pictures: 1040, 1080, 1200, 1201, 1220, 1230, 1301, 1302, 1930, 1931; positive pictures: 1419, 1440, 1601, 1602, 1604, 1750, 8031, 8120, 8465, 8470) were presented. Except for six pictures, these stimuli have already been used in a previous AAT investigation (Wiers, et al., 2009). The negative and positive pictures differed significantly in valence (t(18) = 5.5, p < .001) but not with regard to arousal (t(18) = 1.8, n.s.). Concerning emotional categories, these pictures are examples for negative emotions as fear or disgust, respectively positive emotions as excitement or mixtures of amusement, awe, contentment and excitement (Mikels, et al., 2005).

In experiment 2, participants reacted to pictures of well-known alcohol and non-alcohol products. These pictures were created in our laboratory and, prior to this study, tested for suitability by means of subjective ratings in another sample (see supplementary material for examples of the picture set). We used beverage bottles of brands which are commonly used by German young adults as e.g. *Becks*, *Baileys* or *Wodka Gorbatschow*. In so doing, we tried to cover the diversity of beverages and preferences by composing the pictures of examples of beer, wine, hard liquor (e.g. vodka) and mixed drinks (alcohol mixed with non-alcohol, ready for sale; in Germany known as "alco-pops"). For the non-alcohol pictures we also chose common brands, e.g. *Bionade*, *Steigerwald Mineralwasser* or *Hitchcock Orangensaft*. These pictures were matched in pairs to the alcohol pictures according to their visual similarity (shape of bottle, colour, colour and arrangement of eye-catching details).

## 4.3.2.3 Approach Avoidance Task (AAT)

Participants were seated in a viewing distance of approximately 50 cm to the computer screen and reacted via a standard computer joystick (Logitech Attack 3). Stimulus presentation and behavioural data collection was realized with the software "Presentation" (Neurobehavioral Systems, CA, USA). As soon as a picture appeared on the computer screen, participants had to either push or pull the joystick as fast as possible with their dominant hand (all participants were right-handed). Both experiments consisted of two AAT runs (cf. Field, et al., 2008). The respective instruction was given prior to each run by specifying which picture category had to be approached (i.e. pulled) and which one had be avoided (i.e. pushed). This procedure resulted in the following four conditions. Experiment 1 consisted of one run with the two compatible conditions approaching positive pictures and avoiding negative pictures and of one run with the two incompatible conditions approaching negative pictures and avoiding positive pictures. In experiment 2, participants had to approach alcohol pictures and avoid non-alcohol pictures in the first run and vice versa in the second. Within each run, the ten different pictures of each category were presented three times in randomized order. Therefore, one run consisted of 60 trials (10 pictures x 2 categories x 3 presentations).

Each trial started with one of the pictures being presented in medium size in the centre of the screen (resolution 400 x 300 pixels, size 8 x 10.5 cm). The zooming effect was generated by changing the picture size in relation to the position of the joystick in six inclination steps of

4° in each direction (cf. Rinck & Becker, 2007): Pulling the joystick by approximately 7° replaced the picture by the same picture enlarged by the factor 1.2. Further pulling led to a further enlargement of the picture size (by the factor 1.3 of the original picture size at 11°, 1.4 at 15°,1.55 at 19°,1.7 at 23°, 1.85 at 27°). In contrast to that, pushing the joystick led to a reduction of the picture size (by the factor .75 of the original picture size at -7°, .65 at -11°, .55 at -15°, .44 at -19°, .33 at -23°, .17 at -27°). Irrespective of whether the joystick was moved in the correct or wrong direction, the picture disappeared as soon as the angle of the joystick was 30° and -30°, respectively. Motions to the left and right side had no effects. Subsequently, a fixation cross appeared with a remark to let the joystick slide back into the middle (default position). The length of this inter-trial interval was randomly jittered between 3000 msec and 8500 msec followed by an empty screen for 500 msec. One run lasted for about 7 minutes in total.

#### 4.3.2.4 Procedure and order of AAT runs

Having signed informed consent forms, participants filled in the questionnaires and practised the arm movements required during the AAT (pulling and pushing the joystick). Afterwards, participants were shown the pictures of the alcohol and non-alcohol products and were asked to name them aloud. In so doing, we ensured that participants were familiar with all products. While the order of experiment 1 and 2 was kept constant for all participants, the order of the two runs in each experiment was pseudorandomized across subjects. Having completed both experiments, participants rated the alcohol and non-alcohol pictures as described above (see 4.3.2.1).

### 4.3.3 Data recording and analysis

Participants showed low error rates. In experiment 1, error rates did not differ between compatible conditions (mean number of errors  $1.3 \pm 1.4$ ) and incompatible conditions (mean number of errors  $1.1 \pm 1.3$ ; t(14) < 1). In experiment 2, error rates did not differ between the four conditions (F(1.6,14) = 2.05, n.s. (Greenhouse-Geisser corrected); mean number of errors over all conditions  $2.7 \pm 2.2$ ). These error trials were excluded from further analyses of behavioural as well as of fNIRS data.

#### 4.3.3.1 Behavioural data

RTs were defined as the time-interval between picture onset and the joystick's end position. For every participant, median RTs were calculated for each of the eight combinations of picture category and response direction (experiment 1: approach positive, avoid negative, avoid positive, approach negative; experiment 2: approach alcohol, avoid non-alcohol, avoid alcohol, approach non-alcohol). Median RTs are less sensitive to outliers than arithmetic means and are usually used in the analyses of the AAT (see e.g. Heuer, et al., 2007).

## 4.3.3.2 Functional Near-Infrared Spectroscopy (fNIRS)

FNIRS measurements were conducted with a continuous wave system (ETG-4000, Hitachi Medical Co., Japan) using two different wavelengths (695 ± 20 and 830 ± 20 nm) at a temporal resolution of 10 Hz. We used a 52-channels array consisting of 17 light emitters and 16 photo-detectors arranged in 3 rows with 11 optodes each (see figure 7). A channel (i.e. a measuring point of activation) is defined as the region between one emitter and one neighbouring detector. The inter-optode distance of 30 mm resulted in a spatial resolution of approx. 30 mm and a measuring depth up to approx. 15 mm beneath the scalp. Changes of absorbed near-infrared light were transformed into relative concentration changes of oxygenated (O<sub>2</sub>Hb) and deoxygenated haemoglobin (HHb) by means of a modified Beer-Lambert law. Local increases of O<sub>2</sub>Hb as well as decreases of HHb are indicators of cortical activity (Strangman, et al., 2002; Obrig & Villringer, 2003). Thereby, O<sub>2</sub>Hb is known to be the parameter with the higher power, while HHb is more sensitive for local haemodynamic changes (Hoshi, et al., 2001; Plichta, et al., 2006; Plichta, et al., 2007b). The probe set was placed over prefrontal regions covering an area of approx. 6 x 30 cm. According to Okamoto et al. (2004), standard EEG positions (International 10/20-System; Jasper, 1958) were used for its orientation: The centre optode in the lowest row was fixed over Fpz, while both ends of the probe set were located symmetrically towards T3 and T4. Cortical regions lying below the different channels were determined according to the co-registration of fNIRS-channels to MNI space (Okamoto, et al., 2009).

FNIRS data were analysed with MATLAB (version 7.9.0; MathWorks, MA, USA). Raw data were pre-processed by applying a moving average filter (time window: 5 sec) and a seven-element discrete cosine transform basis set to remove slow baseline drifts and the

high frequency portion of the data. Additionally, for correction of movement artefacts, trials at the beginning and the end of measurements were removed if their z-transformed data showed abrupt signal changes resulting in O<sub>2</sub>Hb or HHb concentrations more than two standard deviations above or beneath the mean. The pre-processed fNIRS time series were analyzed in an event-related way with a model-based approach applying the general linear model (GLM), i.e. haemodynamic response functions were convolved with the event sequence (Plichta, et al., 2007a; Plichta, et al., 2007b). In more detail, the pre-processed data were analyzed according to the two-stage ordinary least squares (OLS) estimation methodology (e.g. Bullmore, et al., 1996; Marchini & Smith, 2003). We used Gaussian haemodynamic response functions (HRF) with a peak time of 6.5 sec as predictors for the O<sub>2</sub>Hb and HHb time series. A delta function indicating the onset of picture presentations was convolved with the predictors and the first-stage OLS estimation was performed. Resulting residuals were inspected for model conformity. The analyses were corrected for serial correlated errors by fitting a first-order autoregressive process to the error term by the Cochrane-Orcutt procedure (Cochrane & Orcutt, 1949). At the second stage, beta weights, which represent the amplitudes of the haemodynamic response, were re-estimated (single subject level). For the group analyses, we used a random-effects model with beta-weights of each subject as the dataset. On this second level, statistical inferences were done conducting the ANOVAs as described in 4.3.4.1.

#### 4.3.4 Statistical analysis

SPSS for Windows (version 17.0; SPSS Inc., IL, USA) was used for statistical analyses.

#### 4.3.4.1 Repeated measures ANOVAs

RTs, O<sub>2</sub>Hb and HHb data were subjected to 2x2 repeated-measures analyses of variance (rmANOVA). In both experiments, direction of movement (avoid vs. approach) was one of the two within-subject factors. The second within-subject factor was valence (positive vs. negative pictures) and drink (alcohol vs. non-alcohol pictures), respectively. RmANOVAs of O<sub>2</sub>Hb and HHb data were conducted channel-wise (cf. Ehlis, et al., 2009). Since this procedure resulted in 52 tests performed for each of the two fNIRS parameters, we applied a multiple testing correction of the significance threshold (Dubey-Armitage-Parmar correction; see Sankoh, et al., 1997). This modified Bonferroni adjustment takes into account the high

spatial correlations of the fNIRS data. Mean Pearson correlation coefficients between the fNIRS channels were averaged separately for  $O_2Hb$  and HHb across the two runs of each experiment, resulting in adjusted significance thresholds (see  $\alpha_{corr}$  as specified for the respective results).

Due to the particularly exploratory character of experiment 2 (minor relevance of the picture set due to the non-pathological sample characteristics), we additionally report effects at uncorrected level of significance ( $\alpha$ =.05) in DLPFC (right: channel 2, 3, 13, 14; left: channel 8, 9, 18, 19) and anterior lateral OFC (right: channel 44, 45; left: channel 50, 51) as our regions of interest (ROIs) for these data. Post-hoc tests of significant interactions were performed by means of two-tailed paired samples *t*-tests for analyzing the effects of movement direction depending on valence (avoid positive vs. avoid negative, approach positive vs. approach negative) and on drink (avoid alcohol vs. avoid non-alcohol, approach alcohol vs. approach non-alcohol), respectively. RTs were tested for normal distribution (Kolmogorov-Smirnov Z test). If this requirement for ANOVAs was not met, significant results were confirmed by non-parametric Wilcoxon Z tests.

Additionally, compatibility effect scores, i.e. SRC effects were determined for each participant and measure (RTs,  $O_2$ Hb and HHb data). As derived from previous studies (e.g. Heuer, et al., 2007), these scores were calculated as the value for the incompatible condition minus the value for the compatible condition, e.g.  $O_2$ Hb data for avoiding positive pictures minus approaching them. The advantage of these scores is to reflect the relative direction and strength of SRC effects because stimulus valence is kept constant. Higher values indicate stronger effort in the incompatible conditions. These compatibility effect scores were tested for statistical significance by means of two-tailed one sample *t*-tests. With regard to significant interactions in the rmANOVA, the analysis of such compatibility effect scores was also used as post-hoc analysis of valence and drink effects depending on movement direction. Effect sizes were calculated as partial Eta squared  $\eta_p^2$  and Cohen's *d* for significant results of the ANOVA and the *t*-tests, respectively.

#### 4.3.4.2 Correlational analyses

Effects in fNIRS data were further analyzed by means of Pearson correlations for investigating relations between significantly activated channels and self-report data as well

as the respective RTs. Taking into account the problem of multiple testing, *p*-values were Bonferroni adjusted by the number of correlations performed with the same data (see respective results for details). Before calculating these correlations, box-and-whisker plots were applied to detect outliers in the self-report data and in the RTs per condition. Since outliers can significantly distort results especially in small samples, participants identified as outliers (beneath 5% quartile or above 95% quartile) or extreme outliers (beneath 1% quartile or above 99% quartile) were excluded from correlational analyses with the respective measure. With regard to current mood (PANAS), one participant was identified as an outlier for the positive affect scale. Considering the level of trait anxiety (STAI-X2), there was one outlier. More precisely, the PANAS outlier was excluded for all correlations between the PANAS and RTs, respectively fNIRS data. In the same way, the STAI-X2 outlier was excluded for all correlations, effect sizes were calculated as the explained variance *r*<sup>2</sup>.

#### 4.4 Results

#### 4.4.1 Experiment 1: IAPS pictures

## 4.4.1.1 Reaction Times (RTs)

Average RTs and compatibility effect scores are listed in table 2. Descriptively, RTs revealed the expected SRC effects, however, the interaction between valence and movement direction did not reach significance (F(1,14) < 1). There also was no main effect of direction (F(1,14) = 1.48, n.s), but a highly significant main effect of valence (F(1,14) = 9.05, p = .009,  $\eta_p^2 = .39$ ; Z = 2.39, p = .017). RTs were shorter for negative IAPS pictures than for positive ones. Due to the non-significant interaction and main effect of direction, neither the compatibility effect score for the positive nor for the negative pictures differed from zero (t(14) = 1.25, n.s. and t(14) = 1.06, n.s., respectively).

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Table 2: Mean reaction times of individual median RTs in msec (mean, standard deviation)

		movemen	compatibility		
		avoid	approach	effect score <sup>a</sup>	
Experiment 1: IAPS pictures	positive	916.07 (157.94)	866.63 (84)	49.43 (153.37)	
	negative	839.17 (109.62)	877.9 (144.37)	-38.73 (141.97)	
Experiment 2: beverage pictures	alcohol	984.7 (105.06)	946.03 (131.8)	38.67 (113.01)	
	non-alcohol	1007.53 (128.04)	975.37 (116.01)	32.17 (113.21)	

<sup>&</sup>lt;sup>a</sup> difference of RTs\_avoid minus RTs\_approach

#### 4.4.1.2 Functional data

## 4.4.1.2.1 Oxygenated haemoglobin (O₂Hb)

While the main effect direction did not reach significance in any of the channels ( $\alpha_{corr}$ =.02), rmANOVAs yielded a significant main effect for valence in dorsal frontomedian cortex (DFMC) in channels #6 (F(1,14) = 6.86, p = .02,  $\eta^2$  = .33), #15 (F(1,14) = 10.36, p = .006,  $\eta^2$  = .43), #16 (F(1,14) = 7.42, p = .016,  $\eta^2$  = .35), #27 (F(1,14) = 7.41, p = .017,  $\eta^2$  = .35) and, by trend, in channel #5 (F(1,14) = 5.33, p = .037,  $\eta^2$  = .28): Positive pictures elicited stronger activation than negative pictures (see figure 7).

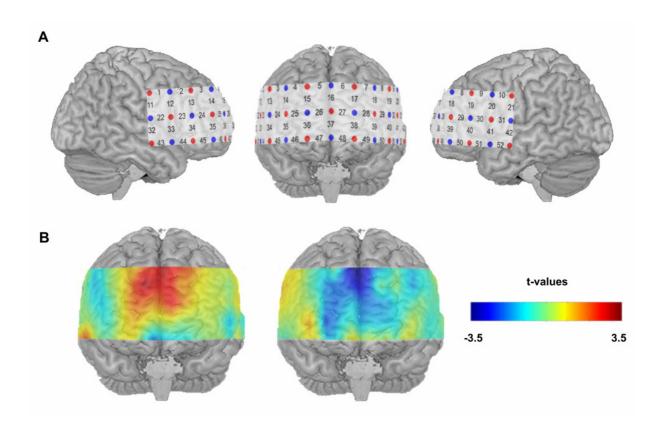


Figure 7: A: Arrangement of the 52 fNIRS channels superimposed on a standard brain surface

B: Statistical maps for oxygenated haemoglobin ( $O_2$ Hb, left panel) and for deoxygenated haemoglobin (HHb, right panel) for the main effect valence in experiment 1: positive pictures caused stronger oxygenation and a stronger decrease of HHb in dorsal frontomedian cortex (DFMC) than negative pictures.

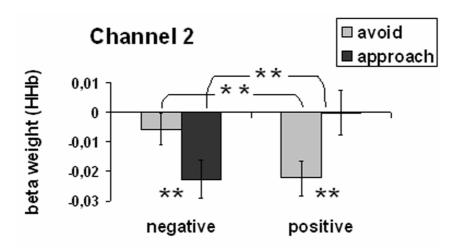


Figure 8: Interaction of stimulus valence (positive vs. negative pictures) and movement direction (avoid vs. approach) in deoxygenated haemoglobin (HHb) in channel 2 (right DLPFC) for N=15 participants (F (1,14) = 17.52, p = .001,  $\eta^2$  = .56). Incompatible reactions (avoid positive, approach negative) compared to compatible reactions (approach positive, avoid negative) caused a stronger decrease of HHb (i.e. stronger cortical activation) of the right DLPFC. Error bars indicate  $\pm$  1 standard error of the mean. \*\* p < .01

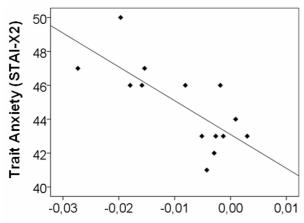
## 4.4.1.2.2 Deoxygenated haemoglobin (HHb)

A significant interaction of valence x direction could be found in right DLPFC in channel #2 ( $\alpha_{corr}$ =.004; F(1,14) = 17.52, p = .001,  $\eta^2$  = .56; see figure 8). Post-hoc tests showed incompatible conditions to cause a stronger decrease of HHb than compatible conditions. Avoiding positive pictures led to a significantly stronger decrease of HHb than avoiding negative pictures (t(14) = 3.18, p = .007, d = .82), while approaching negative pictures caused a significantly stronger decrease of HHb than approaching positive pictures (t(14) = 2.99, p = .01, d = .77). Furthermore, avoiding positive pictures led to a significantly stronger decrease of HHb than approaching positive pictures (t(14) = 3.48, p = .004, d = .9). Finally, approaching negative pictures led to a significantly larger decrease of HHb than avoiding negative pictures (t(1,14) = 3.06, p = .008, d = .79).

In left DLPFC, there was a significant main effect of direction in channel #8  $(F(1,14) = 13.97, p = .002, \eta^2 = .5)$ : Pulling pictures caused a stronger decrease of HHb than pushing pictures. Furthermore, rmANOVAs showed a significant main effect of valence in DFMC in channel #5  $(F(1,14) = 11.85, p = .004, \eta^2 = .46)$  and, by trend, in channel #16  $(F(1,14) = 9.5, p = .008, \eta^2 = .4)$ : Positive pictures led to a stronger decrease of HHb than negative pictures (see figure 7).

## 4.4.1.3 Correlational analyses

RTs did neither correlate with self-report data nor with changes in  $O_2Hb$  (n = 15). There were also no correlations between  $O_2Hb$  and self-report data, while changes in HHb concentration for the main effect direction in left DLPFC in channel #8 ("approach" minus "avoid") were significantly negatively correlated with level of trait anxiety (STAI-X2; n = 14 (one participant excluded as outlier), r = -.74, p = .002,  $r^2 = .55$ ; see figure 9): The more anxious participants were in general, the stronger was the decrease of HHb during pulling pictures compared to pushing pictures. In contrast, changes in HHb concentration were neither correlated with current negative feelings (negative affect scale of PANAS; n = 15, r = .02, n.s.) nor current positive feelings (positive affect scale of PANAS; n = 14 (one participant excluded as outlier), r = -.29, n.s.). To correct for multiple testing,  $\alpha$  was set to  $\alpha = .017$  (due to three performed correlations).



HHb: approach (pull) minus avoid (push)

Figure 9: Correlation between participants' level of trait anxiety (STAI-X2) and deoxygenated haemoglobin (HHb) for the main effect direction

(approach minus avoid) in channel 8 (left DLPFC; n = 14 (one participant excluded as outlier), r = -.74, p = .002,  $r^2 = .55$ )

The more anxious participants were in general, the stronger was their decrease of HHb (i.e. cortical activation) in left DLPFC during approach compared to avoidance movements.

### 4.4.2 Experiment 2: Alcohol and non-alcohol pictures

### 4.4.2.1 Subjective specifications

Participants reported to have drunk  $30.4 \pm 16.5$  gram of absolute alcohol within the last month. Thereby, their drinking amount was far below the critical values set by the BZGA (alcohol consumption at risk: more than 12 and 24 grams per day for women and men, respectively). Participants rated alcohol pictures as more negative than non-alcohol pictures (t(14) = 3.71, p = .002, d = .96), without any difference in arousal level (t(14) = 1.39, n.s.). Furthermore, alcohol and non-alcohol pictures did not differ with regard to ease of recognition (t(14) = 1.37, n.s.).

# 4.4.2.2 Reaction Times (RTs)

Average RTs and compatibility effect scores are listed in table 2. There was no interaction between drink and movement direction (F(1,14) < 1). The main effects of direction and drink reached significance: RTs were shorter for approaching than for avoiding pictures (F(1,14) = 6.92, p = .02,  $\eta_p^2 = .33$ ; Z = 2.47, p = .013) and for alcohol compared to non-alcohol pictures (F(1,14) = 9.77, p = .007,  $\eta_p^2 = .41$ ; Z = 2.3, p = .021). Neither the compatibility effect score for the alcohol nor for the non-alcohol pictures differed from zero (t(14) = 1.33, n.s.; Z = 1.82, p = .069 and t(14) = 1.1, n.s.; Z < 1, n.s., respectively).

### 4.4.2.3 Functional data

# 4.4.2.3.1 Oxygenated haemoglobin (O₂Hb)

By trend, rmANOVAs revealed a significant main effect for drink in DFMC in channel #15 ( $\alpha_{corr}$ =.015; F(1,14) = 5.5, p = .03,  $\eta^2$  = .28; see figure 7): Alcohol pictures resulted in stronger activation than non-alcohol pictures. Using an uncorrected level of significance for channels located in the ROIs ( $\alpha$ =.05), there were no effects in DLPFC, but a significant interaction drink x direction in OFC in channel #51 (F(1,14) = 4.51, p = .05,  $\eta^2$  = .24; see figure 10A). Approaching alcohol pictures led to stronger activation than approaching non-alcohol pictures by trend (t(14) = 2.02, p = .063, d = .52), while there was no difference for avoiding pictures (t(14) = 1.75, n.s.). Furthermore, approaching alcohol pictures led to a significantly stronger activation than avoiding alcohol pictures (t(14) = 2.48, p = .026, d = .64), while there were no effects of movement direction on the processing of non-alcohol pictures (t(1,14) < 1).

# 4.4.2.3.2 Deoxygenated haemoglobin (HHb)

The analysis of HHb yielded no significant effects ( $\alpha_{corr}$ =.004).

# 4.4.2.4 Correlational analyses

RTs neither correlated with self-report data nor with the subjective ratings of the pictures (n = 15). Functional data also neither correlated with participants' amount of drinking nor with subjective ratings of the pictures (n = 15). With regard to the interaction of drink x direction in channel #51, changes in  $O_2$ Hb concentration for the difference between approaching minus avoiding alcohol pictures were significantly positively correlated with positive expectancies of alcohol effects in terms of *reduction of tension and emotional regulation* (AEQ; n = 15, r = .601, p = .018,  $r^2 = .36$ ; see figure 10B). No such correlation could be found between  $O_2$ Hb concentration and participants' expectation of alcohol to facilitate social contacts (AEQ-factor *social motives*; n = 15, r = .37, n.s.). To correct for multiple testing, p-values were set to p = .025 (due to two performed correlations).

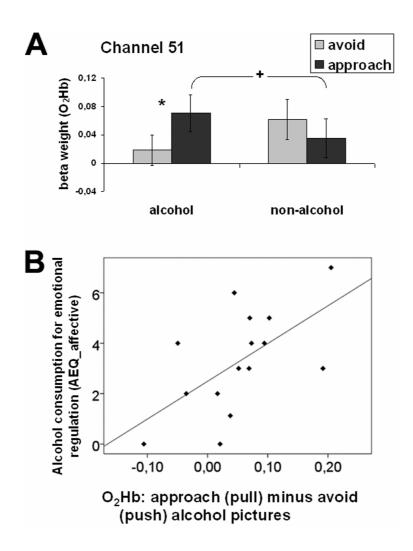


Figure 10: A: Interaction of drink (alcohol vs. non-alcohol pictures) and movement direction (avoid vs. approach) in oxygenated haemoglobin ( $O_2Hb$ )

in channel 51 (left anterior lateral OFC) for N=15 participants (F(1,14) = 4.51, p = .05,  $n^2 = .24$ ).

Approaching compared to avoiding alcohol pictures caused a stronger increase of  $O_2Hb$  (i.e. stronger cortical activation) within the left anterior lateral OFC, which processes secondary rewards. Error bars indicate  $\pm$  1 standard error of the mean.

B: Correlation between alcohol consumption due to positive expectancies of alcohol effects with regard to emotional regulation (AEQ affective scale) and oxygenated haemoglobin ( $O_2Hb$ ) for approaching minus avoiding alcohol pictures in channel 51 (left OFC; n = 15, r = .601, p = .018,  $r^2 = .36$ )

The more participants expected alcohol to have positive effects in terms of emotional regulation, the more pleasant they perceived approaching compared to avoiding alcohol pictures as indicated in their OFC activity.

<sup>\*</sup> p < .05, + p < .1

### 4.5 Discussion

### 4.5.1 Experiment 1

In line with our hypothesis, right DLPFC showed stronger activation in terms of a decrease of HHb during incompatible compared to compatible reactions. Approaching negative and avoiding positive pictures required regulatory activity at this neuronal level. Prior studies investigating regulation and inhibition of inappropriate motor responses also found PFC activity mainly in right hemisphere (Aron, et al., 2004; Knoch & Fehr, 2007; Coxon, et al., 2008). Since HHb compared to O<sub>2</sub>Hb is regarded as the fNIRS parameter with higher local sensitivity (cf. Hoshi, et al., 2001; Plichta, et al., 2006), this result supports the DLPFC as part of the suggested neuronal model underlying processes during the AAT.

Behavioural data revealed the expected SRC effects in terms of increased RTs for incompatible conditions only numerically, but not statistically significantly. RTs were generally shorter for negative compared to positive pictures. Since negative stimuli are known to induce basic motor preparation for enabling fast responses to threat (Flykt, 2006), participants might have reacted generally faster to them irrespective of movement direction. Furthermore, we assume the negative IAPS pictures to have been of greater emotional relevance. While the negative pictures displayed dangerous animals (e.g. snarling dogs) and thereby common signals for avoidance behaviour, the positive pictures, in contrast, rather comprised stimuli which were not typical for human approach tendencies (e.g. butterflies). In this context, enhanced RTs for the positive IAPS pictures might also reflect a more laborious classification process. In addition, the used instruction informed participants prior to each block, whether they would have to accomplish compatible or incompatible reactions. This knowledge might have served as a cognitive preparation thereby reducing the effects of incompatibility on RTs as the common final parameter of several distinct neuronal processes. Future studies should therefore use positive pictures displaying stimuli more typical for actual human approach tendencies (e.g. delicious food) and a non-explicit instruction that does not prepare participants for subsequent compatibility effects (e.g. Wiers, et al., 2010).

The assumption of positive pictures inducing a more laborious classification is supported by our fNIRS data. Channels located over DFMC showed a larger increase of O<sub>2</sub>Hb and a larger decrease of HHb after positive compared to negative pictures. This area is crucial for self-control (Brass & Haggard, 2007) and rule application under uncertainty (Volz, et al.,

2003), i.e. for internally guided behavioural control. Correct responses required participants to classify pictures according to their valence and to remember the direction assigned beforehand. Since the stronger activation occurred independently from the instructed direction, it might reflect enhanced cognitive effort for recognizing the valence of positive pictures.

With regard to left DLPFC, we found an effect of movement direction: Approach movements caused a larger decrease of HHb than avoidance movements. This finding is in line with prior studies revealing more left hemispheric frontal activity during approaching stimuli irrespective of their valence (Berkman & Lieberman, 2010) and with Davidson's theory of hemispheric asymmetry, where the left hemisphere is postulated to be specialized for approach behaviour (Davidson, et al., 1990; Sutton & Davidson, 1997). An interpretation of this finding in terms of Davidson's theory is also supported by the correlation of HHb with participants' level of trait anxiety: The more anxious participants were in general, the stronger the decrease of HHb was during approaching than avoiding pictures. We assume this result to reflect participants' sensitivity of the prefrontal approach system as postulated by Davidson. With increasing trait anxiety, the consequences of approaching stimuli become more relevant than those of avoiding stimuli (cf. Cunningham, et al., 2010). Since no such correlation existed with state measures (cf. Sutton & Davidson, 1997), we take these findings as a first hint that cortical activation patterns during the AAT depict relatively stable characteristics.

# 4.5.2 Experiment 2

At the corrected level of significance, alcohol compared to non-alcohol pictures elicited a tendency for a larger increase of O<sub>2</sub>Hb in DFMC. As in experiment 1, we interpret this activation to depict internally guided behavioural control (Brass & Haggard, 2007; Volz, et al., 2003). For a more detailed interpretation of this finding, we took into consideration participants' RTs as well as explicit subjective specifications. RTs were shorter for alcohol compared to non-alcohol pictures. As already described above, we consider shorter RTs as indicators of greater relevance. In this pre-study for future research on alcohol dependence, participants might have perceived the alcohol pictures as more important stimuli due to their knowledge of the aim of the present study. In this context, the activation of DFMC might depict the participants recognizing the pictures' content and remembering the instruction

while – at the same time – bearing in mind the higher relevance of the alcohol pictures and thereby accelerating their behavioural reactions. Furthermore, participants rated alcohol pictures as less pleasant than non-alcohol pictures, while they indicated no differences with regard to arousal and ease of recognition. This might be caused by social desirability effects due to acquaintanceship with the experimenter since alcohol pictures are directly addiction-related stimuli.

Exploring our ROIs at an uncorrected level of significance, fNIRS revealed no effects in DLPFC, but increased oxygenation in left anterior lateral OFC (orbital part of inferior frontal gyrus) during approaching compared to avoiding alcohol pictures. We interpret the OFC activation to reflect affective appraisal of the required reactions (Sescousse, et al., 2010): Participants experienced approaching alcohol pictures as more pleasant than avoiding them. Due to the low amount and frequency of alcohol consumption, we did not expect our sample to show such an effect. However, this result is consistent with studies considering O2Hb to constitute the fNIRS parameter with the higher global power, i.e., the possibility to detect even small effects (cf. Hoshi, et al., 2001; Plichta, et al., 2006). The above described difference was the larger the more participants expected alcohol to have positive effects in terms of emotional regulation. This finding is in line with our assumption that the relevance of the picture set depends on participants' individual appraisal of alcohol consumption. For this non-pathological sample, motivation for drinking alcohol was the pivotal criterion, while amount of drinking had no influence. While fNIRS showed such details, behavioural data only revealed faster RTs for alcohol than non-alcohol pictures as already described above and for approaching pictures compared to avoiding them. We interpret this latter effect as general appetence of our sample for approaching beverage pictures.

#### 4.5.3 General Discussion

For the first time, we combined hypotheses from cognitive-emotional psychology and neurosciences with regard to automatic and regulated approach-avoidance behaviour. We investigated cortical processes during the AAT by means of fNIRS in a sample of healthy participants.

In Experiment 1, we presented positive and negative IAPS pictures as typical stimuli for eliciting human approach and avoidance tendencies. We hypothesized SRC effects in terms of longer RTs as well as stronger activation of DLPFC in incompatible compared to compatible conditions depicting the necessary regulatory activity. Data analyses revealed RTs to be confounded by experimental conditions. Since we could only show statistically non significant behavioural SRC effects, we cannot make any direct conclusions on their neuronal correlates. However, in accordance with suggested neuronal models of approachavoidance behaviour, right DLPFC showed more regulatory activity in terms of decrease of HHb during incompatible (i.e. regulated) compared to compatible (i.e. automatic) reactions. Furthermore, left DLPFC showed increased activation in terms of stronger decreases in HHb concentration during approach than avoidance movements irrespective of stimulus valence. This activation pattern in left DLPFC became increasingly pronounced with increasing trait anxiety, which is in line with Davidson's theory of hemispheric asymmetry. Taken together, fNIRS allowed to differentiate between automatic and regulated reactions with regard to regulatory activity in right DLPFC, while such effects were not significantly observable in RTs. Furthermore, cortical activation patterns seem to be modulated by stable personality characteristics. This result might indicate the AAT as a helpful tool for measuring interindividual differences in the functional organisation of neuronal structures suggested to underlie behavioural approach-avoidance impulses and their control.

In experiment 2, we explored the reactions of healthy participants to alcohol and non-alcohol pictures. As hypothesized, processing of reactions to alcohol pictures depended on participants' individual positive appraisal of alcohol consumption. Participants' knowledge of the study aim might have biased RTs resulting in no influences of movement direction for alcohol pictures. Nevertheless, fNIRS data revealed stronger activation for approaching compared to avoiding alcohol pictures in left anterior lateral OFC (orbital part of inferior frontal gyrus) at an uncorrected level of significance. This activation difference was more pronounced the more participants expected alcohol to enable emotional regulation. While the OFC – as part of the general reward system processing secondary reinforcers – was sensitive for such small interindividual valuation differences, there were no effects in DLPFC as our second ROI. This might indicate that participants differed with regard to their appraisal of approaching alcohol. However, they did not yet show any tighter connections between this valuation and the behavioural pattern of approaching, that would turn the condition "avoid alcohol" into an incompatible condition and require regulatory activity in DLPFC. Nevertheless, we found a divergence between this implicit measure and participants' explicit

picture ratings. Therefore, functional measurements during the AAT might offer the possibility to assess evaluation of alcohol stimuli without distortion by social desirability in future studies on alcohol addiction.

In summary, fNIRS extended behavioural results by revealing insight into cortical subprocesses such as regulation and affective stimulus evaluation, which constitute approachavoidance reactions. Although our results are limited due to the small sample size and the pilot character of the study, they are a first support of the suggested neuronal correlates of behavioural approach-avoidance impulses and their control (cf. Ernst & Fudge, 2009; Bechara, 2005). Importantly, cortical processes were modulated differently than RTs as the entire result of different sub-processes. This is in line with other findings from the neuroimaging literature where measured activation patterns are suggested to be modified by not assessed compensational effects in other brain regions resulting in different modulation at the neuronal and the behavioural level (e.g. Gron, et al., 2003). Therefore, measurements of brain activity during the AAT might offer the possibility to identify contributions of each subprocess to the behavioural outcome and to understand factors modulating specific subprocesses. Thereby, future studies following our pilot study should investigate larger samples for ensuring the general validity of these results. Another limitation of our results might have been the six repetitions of each picture during the entire experiment: Participants' apperception of the pictures' emotionality might have decreased with increasing number of presentations. Since this decrease might depend on subject specific characteristics as e.g. personality traits, the six repetitions might have caused additional intra- and inter-subject variability. Future studies should try to enhance the number of presented pictures thereby still ensuring the necessary number of trials. Furthermore, fNIRS studies need to be complemented by fMRI studies which allow for depicting activity in subcortical structures, i.e. for investigating the entire neuronal basis of dual-process models of behavioural impulses and their control. Besides knowledge about the basic behavioural principles of approachavoidance in general, the combination of the AAT and fNIRS/fMRI might also be appropriate for detecting specifically altered sub-processes of approach impulses and their regulation in addiction disorders.

# 4.6 Supplementary material

Examples of alcohol and non-alcohol pictures used in experiment 2.

The full set is available upon request: lena.ernst@med.uni-tuebingen.de

Pictures were matched with regard to visual similarity (shape of bottle, colour, colour and arrangement of eye-catching details).

















# 5 Study A2: MAOA-uVNTR as neurobiological moderator

The contents of this chapter are published in:

Ernst, LH, Lutz, E, Ehlis, A-C, Fallgatter, AJ, Reif, A, & Plichta, MM (2013): Genetic variation in *MAOA* modulates prefrontal cortical regulation of approach-avoidance reactions. *Neuropsychobiology*, *67*(3), 168-180.

See 17.1 (organizational remarks) with regard to the formatting of the text (use of abbreviations, headings, etc.) and the rights for publications.

#### 5.1 Abstract

Regulation of automatic approach and avoidance behaviour requires affective and cognitive control, which are both influenced by a genetic variation in the gene encoding Monoamine Oxidase A (termed *MAOA*-uVNTR). The current study investigated *MAOA* genotype as moderator of prefrontal cortical activation measured with functional near-infrared spectroscopy (fNIRS) in 37 healthy young adults during performance of the approach-avoidance task (AAT) with positive and negative pictures.

Carriers of the low- compared to the high-expressing genetic variant (*MAOA-L* vs. *MAOA-H*) showed increasing regulatory activity in right dorsolateral prefrontal cortex (DLPFC) during incompatible conditions (approach negative, avoid positive). This might have been a compensatory mechanism for stronger emotional reactions as shown in previous studies and might have prevented any influence of incompatibility on behaviour. In contrast, fewer errors but also lower activity in right DLPFC during processing of negative compared to positive stimuli indicated *MAOA-H* carriers to have used other regulatory areas. This resulted in slower reaction times in incompatible conditions, but – in line with the known better cognitive regulation efficiency – allowed to perform incompatible reactions without activating DLPFC as the highest control instance. Carriers of one low- and one high-expressing allele lay as intermediate group between the reactions of the low- and high-expressing groups.

The relatively small sample size and restriction of fNIRS to assessment of cortical activity limit our findings. Nevertheless, these first results suggest monoaminergic mechanisms to

contribute to interindividual differences in the two basic behavioural principles of approach and avoidance and their neuronal correlates.

### 5.2 Introduction

Approach and avoidance constitute two basic principles of behavioural reactions to positive respectively negative stimuli (cf. Carver, 2006). Thereby, automatically triggered, unconscious reactions guarantee current survival, while consciously controlled reactions are crucial for flexible behaviour.

Neuroscientific models associate mainly the striatum with automatic approach reactions towards positive stimuli and the amygdala with automatic avoidance reactions towards negative stimuli, respectively (e.g. Ernst & Fudge, 2009). Controlled reactions are assumed to be mediated by the prefrontal cortex (PFC; Ernst & Fudge, 2009; Miller & Cohen, 2001); in particular, the dorsolateral PFC (DLPFC) is known to initiate performance adjustments (Ridderinkhof, et al., 2004).

The Approach-Avoidance Task (AAT; De Houwer, et al., 2001) directly assesses behavioural approach-avoidance impulses and their deliberative regulation. In compatible conditions, the instructed behaviour matches implicit reaction tendencies (approaching positive stimuli or avoiding negative ones), while such tendencies have to be inhibited for performing an alternative reaction in incompatible conditions (avoiding positive stimuli or approaching negative ones). Stimulus response compatibility effects (SRC effects) describe the phenomenon of longer reaction times in incompatible compared to compatible conditions (cf. Krieglmeyer & Deutsch, 2010).

So far, a study with functional near-infrared spectroscopy (fNIRS) has revealed neuronal SRC effects in right DLPFC in terms of stronger activation in incompatible compared to compatible conditions (Ernst, et al., 2013c; cf. Ernst, et al., in press). The current study aims to extend these first findings by investigating whether regulation of automatic approach-avoidance reactions is modulated by genetic factors influencing the activity of involved brain regions. Due to the emotional stimulus content, managing the conflict in incompatible AAT

conditions depends not only on cognitive control, but also on the affective response. Variations in the gene encoding Monoamine Oxidase A (*MAOA*-uVNTR; see methods for details) significantly determine both processes.

In humans, *MAOA* genotypes have been investigated with regard to personality traits, where carriers of the low-expressing genetic variant (*MAOA-L*) repeatedly, but not always (Haberstick, et al., 2005) showed enhanced trait impulsivity (Huang, et al., 2004; Foley, et al., 2004) and even aggressive, criminal behaviour (Nilsson, et al., 2006). On the other hand, female carriers of high-expressing alleles (*MAOA-H*) are more prone to develop panic disorder (Reif, et al., 2012). Moreover, imaging genetic studies tested *MAOA* genotypes as moderator of brain activation during both affective and cognitive paradigms. Comparisons of *MAOA-L* carriers to *MAOA-H* carriers revealed stronger activation of emotionally relevant areas and lower activation of cognitively relevant areas.

In detail, during a face matching task known to activate emotional circuits, Meyer-Lindenberg et al. (2006) showed increased activity in left amygdala and decreased response of ventral cingulate cortex, left orbitofrontal cortex (OFC) and left insular cortex in *MAOA-L* carriers compared to *MAOA-H* carriers. These effects were independent of gender. In an emotional memory task, only male *MAOA-L* carriers displayed increased activation in left amygdala and hippocampal formation during retrieval of aversive events (Meyer-Lindenberg, et al., 2006). Also testing both genders, in *MAOA-L* compared to *MAOA-H* carriers, Eisenberger et al. (2007) found greater activity in dorsal anterior cingulate cortex (dACC) during a task simulating social exclusion, indicating socioemotional hypersensitivity.

With regard to cognitive paradigms, male *MAOA-L* carriers showed deficient activation in dACC during response inhibition in a flanker task (Meyer-Lindenberg, et al., 2006). Four other cognitive studies tested only male participants: In an attention network test, Fan et al. (2003) found *MAOA-L* carriers to respond slower by trend. In another smaller sample, which was also tested with functional magnetic resonance imaging (fMRI), behavioural differences were not detected, however, *MAOA-H* carriers, but not *MAOA-L* carriers, showed the common pattern of more activation for incongruent than for congruent conditions in dACC. In an n-back task, Cerasa et al. (2008) showed *MAOA-L* compared to *MAOA-H* carriers to display longer reaction times (RTs) and lower activation in right ventrolateral PFC (VLPFC). Also in an n-back task, Enge et al. (Carter, et al., 2000) found inferior performance of *MAOA-*

L compared to MAOA-H carriers in terms of enhanced RTs and slower processing speed as indicated by longer latencies of the P3b event-related potential (ERP). Passamonti et al. (2006) found MAOA-L carriers to display – by trend – slower RTs than MAOA-H carriers in a GoNoGo task. Moreover, MAOA-L carriers showed generally stronger activity in right superior parietal cortex and lower activity in right VLPFC. Again, only in MAOA-H carriers, there was the common increase in prefrontal activation during the high load condition.

Not only functional but also structural changes were observed: Voxel based morphometry (VBM) analyses revealed comparatively lower volume of cingulate gyrus, bilateral amygdalae, insula and hypothalamus; with the maximum of volume differences in anterior cingulate cortex in both male and female *MAOA-L* carriers (Meyer-Lindenberg, et al., 2006). Importantly, these structural differences are unlikely to explain the above reported functional differences, since both increased and decreased reactivity was observed in the these regions.

While most studies concentrated on *MAOA-L* and *MAOA-H* groups (i.e., participants homozygous (female)/hemizygous (male) for the 3- and 4-copies-repeat, respectively; see methods for detailed explanation), Eisenberger et al. (2007) and Meyer-Lindenberg et al. (2006) also investigated heterozygous *MAOA-LH* carriers (a repetition pattern of one 3- and one 4-repeat allele, which only exists in women due to the X-chromosomal localization of the gene). These analyses revealed evidence for a gene-dosage-effect: The functional responses of *MAOA-LH* carriers were intermediate between the homozygous groups, i.e. lay between *MAOA-L* and *MAOA-H* carriers' responses. During presentation of negative affective facial stimuli, Lee and Ham (2008) found similar group differences in left amygdala for sad faces and in right ACC and hippocampus for angry faces.

Therefore, the current study investigated the influences of *MAOA* genotype as moderator on regulation of automatic approach-avoidance reactions by comparing groups of *MAOA-L* carriers (female 3/3 and male 3/- carriers, respectively), *MAOA-LH* carriers (female 3/4 carriers) and *MAOA-H* carriers (female 4/4 and male 4/- carriers, respectively). Due to the above reported results and since, so far, no behavioural study on the AAT has revealed gender differences, we investigate both male and female participants.

Following the neuroscientific models introduced above (Ernst & Fudge, 2009) and the result of our previous study (Ernst, et al., 2013c), we concentrated on prefrontal cortex as important control instance by assessing its activity with functional near-infrared spectroscopy (fNIRS). This optical imaging method (see e.g. Obrig & Villringer, 2003) is - similar to fMRI a haemodynamic-based technique. FNIRS measures cortical activity in a valid (Plichta, et al., 2007a) and reliable manner (Plichta, et al., 2006; Plichta, et al., 2007b; Schecklmann, et al., 2008). Activation in subcortical structures as the striatum and amygdala cannot be depicted due to limitations in depth resolution. However, fNIRS has several advantages for application during the AAT: First, we used the joystick version of the AAT, in which participants had to push a joystick away from the own body (avoidance) or to pull it towards the own body (approach). Since optodes are relatively flexible arranged to the head, fNIRS is less sensitive to movement artefacts than methods requiring participants' head to remain in a totally fixed position, e.g. fMRI, magnetoencephalography (MEG) or positron emission tomography (PET). Second, sitting upright as during fNIRS measurements is a more typical setting for human approach-avoidance reactions than lying in an fMRI- or PET-scanner, i.e. fNIRS guarantees an ecologically more valid situation. Third, there is no machine noise or claustrophobic measurement situation causing disturbance and stress which might interfere with emotional processing (cf. Pripfl, et al., 2006).

Following the above reported results and interpretations, we expected *MAOA-L* carriers compared to *MAOA-H* carriers to be more influenced by their automatic reaction tendencies due to emotionally stronger reactions and decreased regulatory activation in DLPFC. In other words, we hypothesized *MAOA-L* carriers compared to *MAOA-H* carriers to show stronger behavioural SRC effects and decreased SRC effects in DLPFC. Moreover, we expected *MAOA-LH* carriers to be intermediate between *MAOA-L* and *MAOA-H* carriers with regard to both their behavioural and neuronal reactions.

#### 5.3 Material and Methods

### 5.3.1 Participants

40 healthy young adults currently not taking any psychotropic medication or illicit drugs participated in this study (17 males; mean age = 22.24, SD = 1.61, age range: 20 - 26 years; see also table 3). For excluding psychiatric, neurological or severe internistic disorders,

participants filled in a screening questionnaire based on the structured clinical interview for DSM-IV (SKID; Wittchen, et al., 1997). Three participants had to be excluded due to problems in extracting genetic information. Thus, the data of 37 subjects were analyzed. The study was approved by the local Ethics Committee of the University of Wuerzburg and all procedures were in accordance with the Declaration of Helsinki in its version from 2008.

### 5.3.2 Allelic distribution

Monoamine oxidase (*MAO*) is a mitochondrial enzyme primarily responsible for serotonin (5-HT) degradation (cf. Shih, et al., 1999). The *MAOA* isoform shows greater affinity to the 5-HT substrate than the other isoform *MAOB*. A variable number of tandem repeats (VNTR) polymorphism in the promoter region of the *MAOA* gene, which is localized on the X-chromosome (Xp11.4-Xp11.3), influences gene expression and consequently enzymatic activity (Sabol, et al., 1998): While carriers of 2, 3 or 5 copies of a 30-bp repeat element show relatively low enzyme expression, it is relatively higher for carriers of 3.5 and 4 copies. Low enzyme expression results in greater 5-HT availability.

Due to the X-linked gene localization, we analyzed three categories: 1) The *MAOA-L* group (hemizygous male 3/- carriers and homozygous female 3/3 carriers; n=7), 2) the *MAOA-LH* group (heterozygous female 3/4 carriers; n=8) and 3) the *MAOA-H* group (hemizygous male 4/- carriers and homozygous female 4/4 carriers; n=22; see table 3 for more details and comparisons of groups). Such an allelic distribution of 18.9% for *MAOA-L* carriers, 21.6% for *MAOA-LH* carriers and 59.5% for *MAOA-H* carriers is comparable to previous studies (Cerasa, et al., 2008; Passamonti, et al., 2006; Reif, et al., 2008).

### 5.3.3 Genotyping

Deoxyribonucleic acid (DNA) of 3 participants was extracted via saliva samples due to problems during taking the blood sample. Otherwise, venous blood was drawn and DNA was extracted using a standard de-salting method. *MAOA*-uVNTR was genotyped using a previously published protocol. Briefly, PCR fragments were amplified using the primers 5'-AGCCTGACCGTGGAGAAGG and 5'-GGACCTGGGCAGTTGTGC flanking the polymorphic region located approximately 1.1 kb upstream the ATG codon. The PCR reaction mixture contained 50 ng of genomic DNA, 10 pmol of each primer, 2.5mM of each dNTP, 25mM

MgCl2, 75mM Tris-HCl, 20mM (NH<sub>4</sub>)<sub>2</sub>SO<sub>4</sub>, 0.01% Tween-20, and 0.5U of Taq DNA polymerase. Cycling conditions were 40 s at 94 °C, 40 s at 63 °C, 60 s at 72 °C for 35 cycles. PCR products were separated by electrophoresis and visualized by ethidium bromide staining.

# 5.3.4 Approach-Avoidance Task (AAT)

We used a joystick version of the AAT with the same task arrangement as in a previous study (see Ernst, et al., 2013c). Here, we only report the keypoints. Participants reacted with their dominant hand to negative pictures from the International Affective Picture System (IAPS; numbers 1052, 1200, 1205, 1280, 1525, 1930, 6244, 6250.1, 6370, 6510) and to positive IAPS pictures (numbers 4626, 4660, 4689, 7330, 7450, 8080, 8200, 8370, 8490, 8501; Lang, et al., 2005). The two categories differed significantly in valence (t(18) = 5.5,p < .001), but not in arousal (t(18) = 1.8, n.s.). The study comprised two blocks of the AAT (cf. Field, et al., 2008): During one block, participants were instructed to pull positive pictures towards themselves and to push negative pictures away (compatible conditions); during the other block, participants were instructed to push positive pictures away and to pull negative pictures towards themselves (incompatible conditions). Across subjects, the order of these two blocks was pseudorandomized. 10 different pictures of each valence category were presented three times in randomized order within each block. Therefore, one block consisted of 60 trials (10 pictures x 2 categories x 3 presentations). Changing the picture size according to the position of the joystick in 6 inclination steps of 4° in each direction created the zooming effect (cf. Rinck & Becker, 2007): Pulling and pushing the joystick replaced the picture by the same picture enlarged and reduced, respectively. Inter-trial intervals were randomly jittered between 3500 msec and 9000 msec. In total, one block lasted for about 7 minutes.

## 5.3.5 Procedure

After detailed explanation of the study, written informed consent was obtained from all participants. Pull- and push-movements were practised with example stimuli not used in the following experiment. Handedness and current mood status were assessed with the Edinburgh Handedness Inventory (Oldfield, 1971) and the Positive Affect Negative Affect Schedule (PANAS; Krohne, et al., 1996), respectively. After the AAT, a trail-making test for assessing participants' general speed of processing was applied (Zahlen-Verbindungs-Test

(ZVT); Oswald & Roth, 1987; numbers from 1 to 90 positioned randomly on a sheet of paper have to be sequentially connected by drawing lines). With regard to stable personality traits, reactivity of the behavioural inhibition system (BIS) and of the behavioural activation system (BAS) were assessed via the German version of Carver and White's (1994) BIS/BAS scales (Strobel, et al., 2001) with the scales BIS, BAS-drive, BAS-funseeking and BAS-reward-responsiveness. At the end, the blood and saliva samples were taken, respectively.

### 5.3.6 Data recording and analysis

Independent of group and condition, participants made few errors (see table 4 and analyses in result section). As in previous AAT studies (cf. Rinck & Becker, 2007), these few error trials were excluded from further analyses of the reaction times as well as of the fNIRS data. For each participant, at least 26 correct trials per condition (avoid negative, approach negative, avoid positive, approach positive) were valid.

#### 5.3.6.1 Behavioural data

Median reaction times (RTs) were calculated for each of the four conditions. Median RTs are usually used in the analyses of the AAT, since they are less sensitive to outliers than arithmetic means (see e.g. De Houwer, et al., 2001; Heuer, et al., 2007).

# 5.3.6.2 Functional near-infrared spectroscopy (fNIRS)

Again, since the technical arrangement was identical to a previous study (see Ernst, et al., 2013c), we only give a brief description. We used a continuous wave system (ETG-4000, Hitachi Medical Co., Japan) working with two different wavelengths ( $695 \pm 20$  and  $830 \pm 20$  nm) and a temporal resolution of 10 Hz. The 52-channels array (see figure 11*A*) allowing for a spatial resolution of ~30 mm and a measuring depth up to ~15 mm beneath the scalp was placed over prefrontal regions. Local increases of oxygenated haemoglobin ( $O_2$ Hb) as well as decreases of deoxygenated haemoglobin (HHb) indicate cortical activity (Strangman, et al., 2002; Obrig & Villringer, 2003). The probe set was placed over prefrontal regions according to standard EEG positions (International 10/20-System; Jasper, 1958) as suggested by Okamoto et al. (2004). The co-registration of fNIRS-channels to MNI space as described by Okamoto et al. (2009) was used to determine cortical regions underlying the different channels. The software MATLAB (version 7.9.0) was applied to analyze fNIRS time

series in an event-related way with a model-based approach applying the general linear model (GLM), i.e. Gaussian hemodynamic response functions with a peak time of 6.5 sec were convolved with the event sequence (Plichta, et al., 2007a; Plichta, et al., 2007b).

## 5.3.7 Statistical analysis

For statistical analyses, SPSS for Windows (version 19.0) was used.

RTs, O<sub>2</sub>Hb and HHb data were subjected to three-way mixed design analyses of variance (ANOVAs) with two within-subject factors (valence (positive vs. negative) and direction of movement (avoid vs. approach)) and the between-subject factor group (*MAOA-L* vs. *MAOA-LH* vs. *MAOA-H* carriers). Post-hoc tests of significant three-way and two-way interactions were performed by means of two-way ANOVAs and two-tailed paired sample t-tests/two-sample t-tests, respectively. In case of significant three-way interactions, we also tested for group differences with regard to valence-specific SRC effects by applying univariate ANOVAs for analyzing SRC effects in each of the two valence categories separately.

Number of errors and RTs were tested for normal distribution (Kolmogorov-Smirnov Z test). If this requirement for ANOVAs was not met, significant results were confirmed by non-parametric Friedman two-way ANOVA, Kruskal–Wallis one-way ANOVA by ranks, Wilcoxon-Z tests or Wilcoxon-W tests.

ANOVAs of  $O_2$ Hb and HHb data were conducted channel-wise (cf. Ehlis, et al., 2009; Ernst, et al., 2013c), resulting in 52 tests performed for each of the two fNIRS parameters. Therefore, we applied a multiple testing correction of the significance threshold (Dubey-Armitage-Parmar correction; see Sankoh, et al., 1997), which is a modified Bonferroni adjustment and takes into account the high spatial correlations of the fNIRS data. Mean Pearson correlation coefficients between the fNIRS channels were averaged separately for  $O_2$ Hb and HHb across the two runs of each experiment, resulting in adjusted significance thresholds (see  $\alpha_{corr}$  as specified for the respective results).

### 5.4 Results

### **5.4.1 Descriptives**

Differences between groups were tested by means of one-way ANOVAs and – in case of not normally distributed variables – also by means of Kruskal–Wallis one-way ANOVA by ranks. Categorical variables were tested by means of Freeman-Halton tests. There were no group differences with regard to age, gender, handedness, general speed of processing (ZVT), sequence of runs, smoking status, current mood status (PANAS questionnaire) and stable personality traits as assessed via the BIS/BAS questionnaire (see table 3 for details).

### Legend for table 3 (see next page):

Since only female individuals can be MAOA-LH carriers, we additionally compared exclusively MAOA-L to MAOA-H carriers. This test revealed no differences in distribution of gender ( $\chi^2(1)$ =.62, p=.67).

PANAS scales from PANAS questionnaire (Krohne, et al., 1996), BIS and BAS scales from BIS/BAS questionnaire (Carver & White, 1994), ZVT = Zahlenverbindungstest (Oswald & Roth, 1987)

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Table 3: Comparisons of group characteristics

variable	MAOA-L carriers (n=7)	MAOA-LH carriers (n=8)	MAOA-H carriers (n=22)	test for difference
age	m=22.29, SD=1.8	m=21.38, SD=1.19	m=22.55, SD=1.63	F(2,34)=1.62, $\chi^2(2)=3.12$
gender (m / f)	5/2	- / 8	12 / 10	p=.007 <sup>++</sup>
handedness (right / left / ambidext)	6/0/1	6/1/1	20 / 0 / 2	p=.52
general speed of processing (ZVT; in sec)	m=57.14, SD=6.44	m=61.81, SD=6.19	m=60.95, SD=10.83	F(2,34)=.55
sequence of runs: first run (approach positive – avoid negative – approach negative)	5/2	3 / 5	10 / 12	p=.44
smoking (no / yes)	5/1	7 / 1	17 / 5	p=.87
PANAS: negative affect	mean=13.29, SD=2.06	mean=13.13, SD=2.23	mean=11.91, SD=1.97	F(2,34)=1.79, $\chi^2(2)=3.94$
PANAS: positive affect	mean=31.57, SD=4.96	mean=31.63, SD=6.89	mean=30.41, SD=4.73	F(2,34)=.23, $\chi^2(2)$ =.77
BIS	mean=18.29, SD=3.55	mean=18.88, SD=2.75	mean=19.73, SD=3.18	F(2,34)=.63, $\chi^2(2)=1.93$
BAS-drive	mean=12.29, SD=1.5	mean=11.75, SD=2.05	mean=12.14, SD=1.67	F(2,34)=.21, $\chi^2(2)$ =.13
BAS-funseeking	mean=12.29, SD=2.21	mean=11.25, SD=1.67	mean=11.82, SD=1.5	F(2,34)=.72, $\chi^2(2)=2.02$
BAS-reward- sensitivity	mean=16.86, SD=1.86	mean=16.63, SD=2	mean=16.45, SD=2.86	F(2,34)=.07, $\chi^2(2)$ =.04

#### 5.4.2 Behavioural data

## 5.4.2.1 Reaction Times (RTs)

The three-way ANOVA revealed a significant interaction of group x valence x direction  $(F(2,34) = 3.58, p = .039, \eta_p^2 = .17)$ . When further analyzing each of the three groups separately, ANOVA revealed a main effect of valence in both MAOA-L carriers  $(F(1,6) = 10.52, p = .018, \eta_p^2 = .64; see also figure 11) and MAOA-LH carriers$  $(F(1,7) = 21.71, p = .002, \eta_p^2 = .76)$ : Both groups were faster in reacting to negative than positive pictures. In MAOA-H carriers, the interaction of valence x direction and the main effect of valence were significant  $(F(1,21) = 13.36, p = .001, \eta_0^2 = .39, respectively)$ F(1,21) = 19.69, p < .001,  $\eta_p^2 = .48$ ). MAOA-H carriers also reacted faster to negative than positive pictures in general. Post-hoc t-tests showed the interaction to be in the expected direction: MAOA-H carriers showed SRC effects for both negative and positive pictures. They were faster during the compatible than the incompatible conditions: avoid negative was faster than approach negative (t(21) = 2.13, p = .045, d = 0.46), respectively approach positive was faster than avoid positive (t(21) = 2.92, p = .008, d = 0.62). Furthermore, the compatible condition avoid negative was faster than avoid positive (t(21) = 6.45, p < .001, d = 1.37), while the difference between approaching negative and positive pictures did not reach significance (t(21) = .26, n.s.). For comparisons between groups, we tested SRC scores by means of one-way ANOVAs. Groups did neither differ with regard to negative nor positive pictures (F(2,34) = 1.35, n.s. and F(2,34) = 1.96, n.s., respectively).

#### 5.4.2.2 Errors

Errors for each of the four conditions (avoid negative, approach negative, avoid positive, approach positive) were compared between groups by means of Kruskal–Wallis one-way ANOVA by ranks. There was no difference between groups in any of the conditions (see table 4). The four conditions were also compared within each group by means of Friedman two-way ANOVA by ranks. There were no differences between conditions in MAOA-L carriers and MAOA-LH carriers ( $X^2(2) = 3.96$ , n.s. and  $X^2(2) = 1.8$ , n.s., respectively). In MAOA-H carriers, the interaction valence x direction reached significance ( $X^2(2) = 17.13$ , p = .001). Post-hoc Wilcoxon-Z tests revealed MAOA-H carriers to make more errors when reacting to positive than to negative pictures, in particular during *avoiding* (avoid: Z = 3.09, p = .002; approach: Z = 2.36, p = .018).

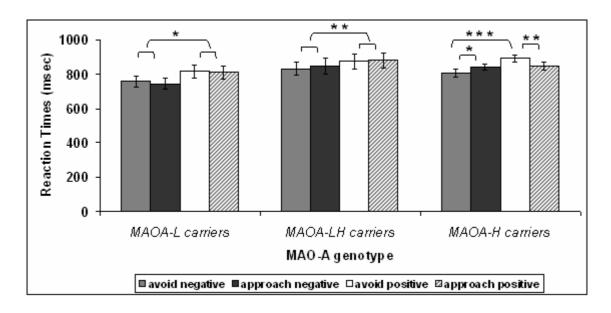


Figure 11: Reaction Times (RTs) per condition and group (mean, SEM)

The significant interaction group x valence x direction comprised no significant differences between groups. Further analyses within each group revealed generally faster RTs for negative than positive pictures in *MAOA-L* and *MAOA-LH* carriers. In *MAOA-H* carriers, the significant interaction valence x direction comprised SRC effects for both positive and negative pictures, i.e. the compatible conditions *avoid negative* and *approach positive* were faster than the incompatible conditions *approach negative* and *avoid positive*, respectively. \* p<.05, \*\* p<.01, \*\*\* p<.001

Table 4: Number of errors per condition and group

Comparisons of groups by means of Kruskal–Wallis one-way ANOVA by ranks revealed no significant differences.

	mean (SD)			
	<i>MAOA-L</i> carriers	MAOA-LH carriers	MAOA-H carriers	test for difference
avoid negative	1.00 (1.29) 0-3	.13 (.35) 0-1	.18 (.40) 0-1	X <sup>2</sup> (2)=3.66
approach negative	.29 (.49) 0-1	.50 (.93) 0-2	.23 (.53) 0-2	X <sup>2</sup> (2)=.48
avoid positive	.71 (.49) 0-1	.75 (1.17) 0-3	1.09 (1.1) 0-4	X <sup>2</sup> (2)=1.33
approach positive	1.00 (.58) 0-2	.50 (.76) 0-2	.86 (1.32) 0-5	X <sup>2</sup> (2)=2.39

### 5.4.3 Functional data

### 5.4.3.1 Oxygenated haemoglobin (O<sub>2</sub>Hb)

The three-way ANOVA revealed a significant interaction of group x valence x direction in right DLPFC in channel #14 ( $\alpha_{corr}$  = .0052; F(2,34) = 7.1, p = .003,  $\eta_p^2$  = .295), #24 (F(2,34) = 9.04, p = .001,  $\eta_p^2$  = .356) and #25 (F(2,34) = 6.47, p = .004,  $\eta_p^2$  = .276) and in left DLPFC in channel #29 (F(2,34) = 6.45, p = .004,  $\eta_p^2$  = .275). For further analyses,  $\alpha$  was set to .05 and we pooled the significant channels #14, #24, #25 to one analysis region over right DLPFC.

When further analyzing each of the three groups separately, in MAOA-L carriers, ANOVA revealed a significant interaction of valence x direction in right DLPFC (F(1,6) = 7.1, p = .037,  $\eta_p^2 = .542$ ) and – by trend – in left DLPFC (#29; (F(1,6) = 4.1, p = .09,  $\eta_p^2 = .404$ ). Although data were normally distributed in each of the four conditions, we additionally applied Wilcoxon-Z tests in the post-hoc analysis due to the small sample size. These post-hoc tests showed SRC effects, i.e. stronger activation during valence-specific incompatible than compatible conditions, for both positive pictures (t(6) = 2.94, p = .026, d = 1.11; Z = 2.03, p = .043) as well as negative pictures (t(6) = 2.17, p = .073, d = 0.82; Z = 2.03, p = .043): There was stronger oxygenation during avoiding compared to approaching positive pictures, respectively during approaching compared to avoiding negative pictures. Also, avoiding positive pictures caused more activation than avoiding negative pictures (t(6) = 2.54, p = .044, d = 0.96; Z = 2.03, p = .043) and approaching negative pictures caused more activation than approaching positive pictures (t(6) = 2.2, p = .069, d = 0.84; Z = 2.2, p = .028). In MAOA-LH carriers, the interaction of valence x direction reached significance in left, but not right DLPFC by trend (#29; F(1,7) = 4.34, p = .076,  $\eta_p^2$  = .383): MAOA-LH carriers also showed more activation during incompatible than compatible conditions. In MAOA-H carriers, ANOVA revealed a main effect of valence in right DLPFC (F(1,21) = 8.12, p = .01,  $\eta_{\rm p}^2$  = .28): Positive pictures caused stronger activation than negative ones.

Between-group comparisons of SRC scores in right DLPFC by means of one-way ANOVAs and Kruskal–Wallis one-way ANOVA by ranks revealed a linear decrease from *MAOA-L* to *MAOA-LH* to *MAOA-H* carriers for negative (F(1,34) = 13.68, p = .001,  $\eta_p^2$  = .287;  $\chi^2(2)$  = 8.54, p = .01) and positive pictures (F(1,34) = 9.77, p = .004,  $\eta_p^2$  = .232;  $\chi^2(2)$  = 6.19, p = .04; see also figures 12 and 13). With regard to negative pictures, post-hoc two-tailed t-

tests and Wilcoxon-W tests revealed MAOA-L carriers to show stronger SRC effects than MAOA-H carriers (t(7.06) = 2.59, p = .036, d = 1.28; Z = 2.65, p = .008), while they did not differ from MAOA-LH carriers (t(13) = 1.21, n.s.; Z = 1.16, n.s.). Moreover, MAOA-LH carriers showed stronger SRC effects than MAOA-H carriers (t(28) = 2.17, p = .039, d = 0.84; Z = 1.74, p = .08). For positive pictures, MAOA-L carriers also showed stronger SRC effects than MAOA-LH carriers by trend (t(13) = 1.88, p = .083, d = 0.96; Z = 1.85, p = .064) and than MAOA-LH carriers (t(27) = 3.06, p = .005, d = 1.26; Z = 2.29, p = .02). MAOA-LH carriers did not differ from MAOA-H carriers (t(28) = 1.04, n.s.; Z = .94, n.s.). As for the within analysis, we additionally applied the reported non-parametric tests due to the small sample size, although SRC scores were normally distributed in each of the three MAOA groups.

# 5.4.3.2 Deoxygenated haemoglobin (HHb)

The analysis of HHb revealed no influence of *MAOA* group or direction, but a main effect of valence in channels #33 ( $\alpha_{corr}$  = .003; F(1,34) = 12.08, p = .001,  $\eta_p^2$  = .26), #44 (F(1,34) = 17.08, p = .000,  $\eta_p^2$  = .33), #50 (F(1,34) = 16.23, p = .000,  $\eta_p^2$  = .32) and #51 (F(1,34) = 11.16, p = .002,  $\eta_p^2$  = .25): Participants showed a stronger decrease in HHb for positive than negative pictures in left (#50, #51) and right (#33, #44) anterior lateral OFC (inferior frontal gyrus).

### 5.4.4 Tests for influence of gender

MAOA-L and MAOA-H carriers did not differ with regard to numbers of male and female participants. Furthermore, we repeated the analyses of RTs, errors and functional data with gender as second between-subject factor, i.e. as covariate: There were no significant influences of gender (all p > .05). However, due to the low number of MAOA-L carriers, this testing might not be valid and – therefore – final conclusions cannot be drawn from the current sample.

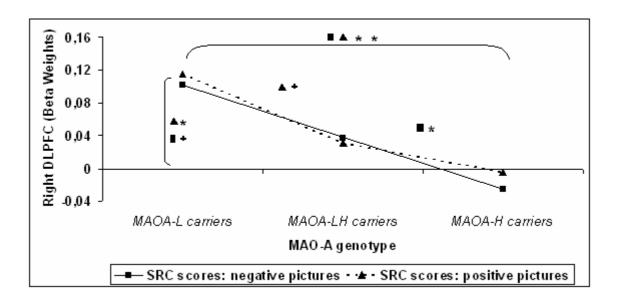


Figure 12: SRC scores in right DLPFC (means per group)

For both positive (**A**) and negative (**I**) pictures, between-group comparisons revealed a linear decrease in SRC scores from *MAOA-L* to *MAOA-LH* to *MAOA-H* carriers comprising significantly stronger SRC effects for *MAOA-L* compared to *MAOA-H* carriers. Furthermore, *MAOA-L* carriers showed – by trend – stronger SRC effects than *MAOA-LH* carriers for positive pictures and *MAOA-LH* carriers showed stronger SRC effects than *MAOA-H* carriers for negative pictures. Vertical signs of significance indicate *MAOA-L* carriers to show significant SRC effects, i.e. stronger activation during valence-specific incompatible than compatible conditions for both positive and negative pictures: They showed stronger oxygenation during avoiding compared to approaching positive pictures, respectively during approaching compared to avoiding negative pictures.

<sup>+</sup> p<.1, \* p<.05, \*\* p<.01

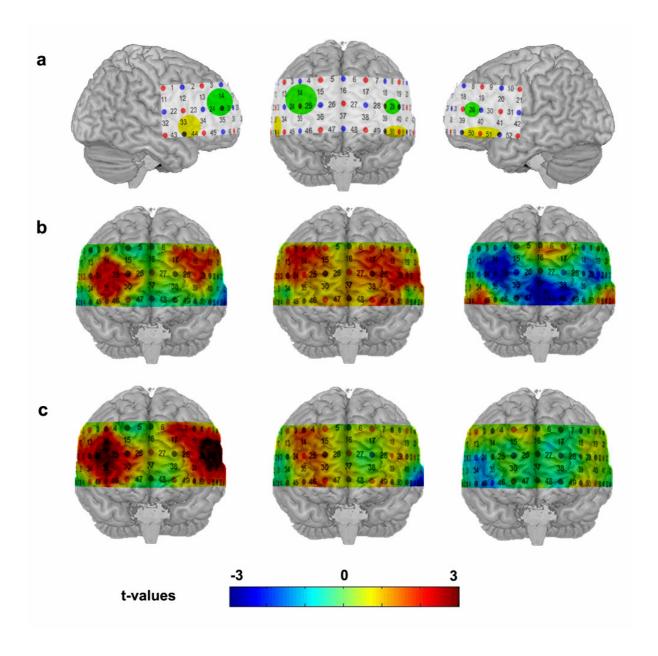


Figure 13: a: Arrangement of the 52 fNIRS channels superimposed on a standard brain surface Significant channels in DLPFC (green circles) and OFC (yellow circles) are marked.

b & c: Statistical maps of SRC scores in oxygenated haemoglobin ( $O_2$ Hb) for MAOA-L carriers (n=7; left panel), MAOA-LH carriers (n=8; middle) and MAOA-H carriers (n=22; right panel) with regard to negative pictures (difference between approaching and avoiding, b) and positive pictures (difference between avoiding and approaching, c)

#### 5.5 Discussion

The current study showed *MAOA* genotype to be a moderator of PFC activity during regulating automatic approach-avoidance reactions. Thereby, between-group-comparisons of SRC effects in DLPFC revealed a linear decrease from *MAOA-L* to *MAOA-LH* to *MAOA-H* carriers for both positive and negative pictures: *MAOA-L* carriers were characterized by stronger regulation than *MAOA-LH* and *MAOA-H* carriers. At the behavioural level, there were no significant group differences, what might be due to a closer relation of genetic influences to neuronal than behavioural reactions (Hariri & Weinberger, 2003).

These functional data are opposite to our hypothesis of *MAOA-L* carriers to display lower prefrontal regulation. However, when also taking into account the known heightened affective reactivity of *MAOA-L* carriers (Meyer-Lindenberg, et al., 2006; Lee & Ham, 2008), enhanced prefrontal regulatory activity might have been necessary to perform the required reactions in incompatible AAT-conditions. In line with this assumption, Buckholtz et al. (2008) found enhanced amygdala activation during a face matching task in male *MAOA-L* carriers to be accompanied by increased functional connectivity between amygdala and ventromedial PFC (vmPFC). This was interpreted as compensatory response to a primary regulatory deficiency in the loop between amygdala and rostral cingulate cortex in terms of vmPFC acting as a secondary control mechanism. Similarly, Meyer-Lindenberg et al. (2006) showed reduced amygdala-orbitofrontal connectivity during a face matching task and, at the same time, increased bilateral OFC volumes in male *MAOA-L* carriers. Since the OFC is crucially implicated in regulation of the amygdala, the increased volume might also represent a compensatory mechanism.

Following these findings, we interpret the enhanced activity in DLPFC in *MAOA-L* carriers as a higher order compensatory mechanism regulating the assumed heightened emotional reaction and finally determining the behavioural response. Furthermore, specifically right DLPFC is suggested to constitute the highest control centre in the human brain (Ridderinkhof, et al., 2004) and the SRC effect in our previous AAT study as well as previous cognition related differences between *MAOA* genotypes were right-lateralized (Ernst, et al., 2013c; Passamonti, et al., 2006).

The linear decreases between groups with regard to SRC effects in right DLPFC fit the results of Meyer-Lindenberg (2006) suggesting a gene-dosage effect: *MAOA-LH* carriers lay as an intermediate group between the homo-/hemizygous subjects.

When regarding analysis results within each group, *MAOA-L* carriers showed clear regulation effects in right and – by trend – left DLPFC. In right DLPFC, there were SRC effects for both negative and positive pictures, i.e. stronger activation during incompatible than compatible conditions. This compensatory prefrontal activation might have resulted in very efficient regulation of behaviour, since there were no RTs SRC effects. *MAOA-L* carriers showed solely generally faster RTs for negative than positive pictures. Such a behavioural effect is in line with previous studies showing negative stimuli – probably due to their higher impact for survival – to be preferentially processed and to elicit basic motor preparation for enabling fast responses (Flykt, 2006; Ohman, et al., 2001). Similar response patterns were found in *MAOA-LH* carriers.

Importantly, these valence specific behavioural reactions are not allegeable to less intense mood induction by positive pictures: Irrespective of group, participants showed stronger activation for positive than negative pictures in both left and right anterior lateral OFC (inferior frontal gyrus), a brain region belonging to the general reward system indicating positive evaluation (cf. Kringelbach & Rolls, 2004; Peters & Buchel, 2010; Sescousse, et al., 2010).

In contrast to *MAOA-L* and *MAOA-LH* carriers, *MAOA-H* carriers displayed no regulation in DLPFC, but generally more activation for positive than negative pictures. At behavioural level, they showed longer RTs for incompatible compared to compatible conditions comprising clear SRC effects for both positive and negative pictures. These results are in line with studies showing emotional information to cause deactivation of prefrontal regulation areas, whereby negatively valenced material specifically deactivated right DLPFC (Dolcos & McCarthy, 2006; De Raedt, et al., 2010). Such a mechanism might have reduced activity in right DLPFC for negative compared to positive pictures and might have lowered cognitive regulation resulting in SRC effects at behavioural level, i.e. in dominance of automatic reaction tendencies.

However, even with such lowered PFC control, *MAOA-H* carriers could perform the required AAT-reactions. Therefore, we assume *MAOA-H* carriers to have regulated their affective reactions via another area, as e.g. the dACC, where previous studies showed deficits in *MAOA-L* carriers (Fan, et al., 2003; Buckholtz, et al., 2008). Such a pre-regulation might have allowed to perform the required incompatible reactions without the necessity of activating the DLPFC as highest control region, while, yet, resulting in behavioural SRC effects. Thereby, *MAOA-H* carriers made even fewer errors when reacting to the – evolutionary – more important negative stimuli, while there were no such differences in *MAOA-L* and *MAOA-LH* carriers. This finding indicates *MAOA-H* carriers to have been more responsive for the different effects of negative and positive stimuli. Future studies in fMRI are necessary to clarify, if such a stronger differentiation might also be visible in terms of stronger pre-regulation activity for reactions to negative stimuli.

In summary, although MAOA-H carriers' reactions were also affected by incompatibility of the AAT-conditions, the enhanced prefrontal activity indicated the regulation of automatic approach-avoidance reactions to pose a more difficult challenge for MAOA-L carriers. With regard to the underlying molecular and neuronal mechanisms of such differences, the general role of 5-HT in cognition and emotion has to be taken into account. The MAOA enzyme inactivates 5-HT by oxidative deamination inside the neuron (Tokunaga & Ishikawa, 1992). Acute tryptophan depletion (ATD) in humans and destruction of serotonergic projections in animals revealed reduced whole-brain 5-HT levels to differently affect cognitive domains, whereby some findings were controversial (Park, et al., 1994; Clarke, et al., 2004). Functions such as reversal learning depending on the ventral PFC were shown to be impaired (Park, et al., 1994). Working memory processes were worsened in animals (Hritcu, et al., 2007), but were not altered in humans, although the related prefrontal activity was altered (Allen, et al., 2006). Further findings such as impaired memory consolidation, but improved focussed attention (Schmitt, et al., 2000) are in line with the idea that 5-HT regulates specific local microcircuits inside the PFC (cf. Passamonti, et al., 2008a). The ventral PFC is an end region of ascending projections from serotonergic neurons in the raphe nuclei (Preece, et al., 2004; Hritcu, et al., 2007). The above reported functional and structural changes in the cingulate cortex as region with the highest density of 5-HT receptors within the human cortex are also in accordance with this consideration (Varnas, et al., 2004). Furthermore, application of the 5-HT agonist fenfluramine showed reduced serotonergic responsivity in MAOA-H carriers (Manuck, et al., 2000). In this context, our finding of enhanced activity in DLPFC in MAOA-L carriers might also be interpreted in an

alternative manner: Cerasa et al. (Cerasa, et al., 2008) and Passamonti et al. (Passamonti, et al., 2006) suggested the high-expressing genetic variant (MAOA-H carriers) to be accompanied by increased prefrontal activation to compensate for reduced cortical efficiency due to reduced 5-HT function. In the n-back study of Enge et al. (Enge, et al., 2011), the amplitude of the N2 ERP as indicator of withholding inadequate, prepotent reactions was generally enhanced in MAOA-L compared to MAOA-H carriers. With regard to the present study, we took the possibility of superior inhibitory control in MAOA-L carriers into account by additionally comparing RTs in incompatible and compatible conditions (irrespective of valence) between MAOA-L and MAOA-H carriers. There were no differences in compatible conditions (t(27) = -1.04, n.s.), but a trend for faster reactions of MAOA-L carriers in incompatible conditions (t(27) = -1.99, p = .06). However, this alternative interpretation needs clarification in future studies, since it is not supported by the behavioural results of the other studies on executive functions and MAOA (Cerasa, et al., 2008; Passamonti, et al., 2006; Enge, et al., 2011) and the low-expressing genetic variant has repeatedly been linked to impulsive behaviour, which - in turn - is often accompanied by diminished inhibitory control (cf. Brower & Price, 2001; Morgan & Lilienfeld, 2000).

Activity of the serotonergic system was also associated with the personality dimensions neuroticism and harm avoidance (Carver & Miller, 2006; Cloninger, et al., 1993). The short allele of the 5-HT transporter (5-HTTLPR) resulting in reduced serotonergic function was even shown to be a risk factor for depression (Caspi, et al., 2003). Furthermore, the serotonergic system was suggested to mediate the fine-tuning of other neurotransmitter systems such as dopamine (DA), norepinephrine (NE) and acetylcholine, which - in turn affect executive control processes and emotional processes (Robbins, 1997; Hurley, et al., 2004). During brain development, MAOA is the major enzyme for 5-HT and NE (Shih, et al., 1999) and 5-HT is strongly involved into neuronal proliferation, migration, differentiation and synaptogenesis (Buznikov, et al., 2001). Buckholtz et al. (Buckholtz, et al., 2008) suggested that elevated 5-HT and NE levels during brain development as a result of low MAOA activity in MAOA-L carriers go along with changes in the maturation of key nodes within circuits for emotional arousal and regulation (cf. Gross & Hen, 2004). This, in turn, might facilitate stabilization of stimulus-response biases as is in line with our interpretation of the current findings. However, MAOA was suggested to be a "plasticity gene" rather than a "vulnerability gene" (Belsky, et al., 2009), probably by balancing impulsive fight versus anxious flight reactions especially in interaction with environmental influences. Such possible geneenvironment interactions might account to some extent for associations of MAOA variants

with different mental disorders (e.g., violent behaviours Caspi, et al., 2002). As reported above, male *MAOA-L* carriers were at higher risk for aggression and violence (Nilsson, et al., 2006), while a recent study found higher risk for panic disorder in female *MAO-H* carriers (Reif, et al., 2012). Enhanced amygdala activation during retrieval of aversive events was not only found in male *MAO-L* carriers, but also on the other hand in female *MAO-H* carriers (Meyer-Lindenberg, et al., 2006). Thus, with regard to the AAT as comprising emotional aspects, future studies should concentrate on such possible gender differences.

Our results are limited due to several reasons. First, our sample sizes for *MAOA-L* and *MAOA-LH* carriers were small, since we did not have the opportunity to work with stratified samples. While our sample sizes are comparable to some of the previous studies (*MAOA-L* vs. *MAOA-H* carriers: Fan, et al., 2003: n=8 each; Cerasa, et al., 2008: n=14 vs. n=16; Passamonti, et al., 2006: n=12 each; Eisenberger, et al., 2007: *MAOA-L* n=13, *MAOA-LH* n=10, *MAOA-H* n=9) and the application of adequate non-parametric tests accounted for this circumstance, future studies with larger, stratified samples are necessary for generalizing our results.

Second, with regard to all dependent variables, we tested for three-way interactions as derived from our hypotheses. In case of significance of this omnibus test, the found effect was further characterized by the applied post-hoc tests. Thereby, we took the common approach of applying a significance level of p < .05 for not increasing the risk of type II errors as would be the case in applying a conservative Bonferroni adjustment to these post-hoc tests. However, future studies concentrating on replicating our effects in larger samples should apply planned Scheffé post-hoc tests for limiting the risk of type I errors.

Third, due to the limited depth resolution of fNIRS and the chosen prefrontal measurement arrangement, we cannot make conclusions on activation of subcortical or other cortical regions. Future fMRI studies might allow to answer questions on the assumed alternative regulatory activity in *MAOA-H* carriers.

Fourth, while *MAOA* is primarily responsible for 5-HT degradation, to a lesser extent, it also catabolizes NE and DA (Shih, et al., 1999). Moreover, other genetic polymorphisms have been reported to significantly influence affective or cognitive processing. Specifically, a

genetic variation in the serotonin transporter (*5-HTTLPR*) has been shown to focally affect amygdala function (e.g. Pezawas, et al., 2005), while the *COMT val158met* polymorphism is known to degrade cortical DA and determine cognitive processing efficiency (e.g. Egan, et al., 2001). Similar to Buckholtz et al. (2008), we, therefore, ruled out systematic differences in distribution of these genotypes between the three *MAOA* groups. In line with the results of Buckholtz et al. (2008), we neither found significant influences of *5-HTTLPR*- nor *COMT*-genotype on behavioural and brain reactions (see supplementary material for details). However, Passamonti et al. (2008a) reported an allele-allele interaction of *MAOA* and *5-HTTLPR* polymorphisms in the ACC. While we cannot test for such an interaction due to the small sample size, future studies should consider this aspect in stratifying their samples. Thereby, further investigations on possible epistatic effects of the *MAOA* polymorphism and a polymorphism in the promoter region of the NE transporter gene (*NET-3081*; cf. Enge, et al., 2011) might also be of interest for the AAT as depicting different aspects of executive functions.

Fifth, with regard to potentially influencing variables, our groups did not differ in age, handedness, general speed of processing, status of smoking, current mood and reactivity of BIS or BAS (cf. Ernst, et al., 2012). Importantly, taking into account previously found gender-by-gene interactions (Meyer-Lindenberg, et al., 2006; Buckholtz, et al., 2008), current results did not reveal significant influences of gender, as, so far, have also not been reported in any AAT study. However, the small sample size of especially *MAOA-L* carriers (5 male, 2 female) does not allow for final conclusions. Future studies in larger samples are necessary to test specifically for gender differences.

Summing up, MAOA genotype significantly influenced regulation of automatic approach-avoidance reactions. MAOA-L carriers compared to MAOA-H carriers showed stronger regulation in right DLPFC for both negative and positive pictures. Furthermore, MAOA-LH carriers represented an intermediate group between MAOA-L and MAOA-H carriers, supporting a gene-dosage-effect as suggested by Meyer-Lindenberg et al. (2006). Withingroup analyses indicated MAOA-L carriers to compensate probably stronger emotional reactions by stronger regulatory activity in right DLPFC resulting in no behavioural SRC effects. In contrast, fewer errors but also lower activity in right DLPFC during processing of negative compared to positive stimuli indicated MAOA-H carriers to have used other regulatory areas, as e.g. the dACC. This might have resulted in the observed behavioural SRC effects, but allowed to perform incompatible AAT-reactions without activating DLPFC. In

other words, lower enzymatic activity of *MAOA* resulting in higher monoaminergic levels and probably pronounced affective reactions in terms of stronger stimulus-response biases was associated with the necessity to activate right DLPFC as highest control instance for regulating automatic approach-avoidance reactions during the AAT. Future studies prolonging this finding will contribute to a better understanding of how monoaminergic mechanisms underlie interindividual differences in the basic behavioural principles of approach and avoidance and their neuronal correlates.

# 5.6 Supplementary material

#### Further analyses of genetic influences

The allelic distributions of the serotonin transporter (5-HTTLPR) and the COMT val158met polymorphism did not differ between the three MAOA groups (see table 5).

Additional analyses revealed neither in behavioural nor in functional data any significant differences between the three genotypes of *5-HTTLPR* and *COMT*, respectively (all p > .05).

Table 5: Allelic distributions of 5-HTTLPR- and COMT-genotypes in MAOA groups

Comparisons of groups by means of Freeman-Halton tests revealed no significant differences.

I = long allele, s = short allele

genotype	MAOA-L carriers (n=7)	MAOA-LH carriers (n=8)	MAOA-H carriers (n=22)	test for difference
5-HTTLPR (I/I / s/I / s/s)	4/2/1	5/2/1	8/9/4	p=.85
COMT (Met/Met / Val/Met / Val/Val)	3/3/1	2/3/3	4 / 13 / 5	p=.59

# 6 Study A3: GoNoGo AAT and whole brain activity

The contents of this chapter are submitted for publication:

Ernst, LH, Plichta, MM, Hahn, T, Hösl, F, Bender, B, Wildgruber, D, Ehlis, A-C, Fallgatter, AJ, Erb, M (submitted): Approaching the negative is worse than avoiding the positive: A GoNoGo version of the Approach-Avoidance Task in fMRI

See 17.1 (organizational remarks) with regard to the formatting of the text (use of abbreviations, headings, etc.) and the rights for publications.

#### 6.1 Abstract

Approaching positive and avoiding negative stimuli are fundamental principles of behaviour. The current study investigated the regulation of these automatic, compatible reactions for initializing incompatible reactions (*approach negative*, *avoid positive*) with functional magnetic resonance imaging during a cued GoNoGo version of the Approach-Avoidance Task: The cue event indicates participants to prepare a response, while the move event signals to realize it (Go trials) or to inhibit it (NoGo trials).

For negative pictures, strong neuronal response preparation at the cue event in the anterior cingulum, insula, thalamus, frontal and parietal cortices was followed by even faster incompatible than compatible reactions. The more negative and arousing participants rated the pictures, the stronger they showed response initiation processes at the move event in the right midbrain and – thereby – the stronger the observed reversed behavioural effects were. In NoGo conditions, the inhibition of automatically elicited compatible response tendencies required more regulation via the superior parietal lobule than the inhibition of prepared incompatible reactions.

In contrast, for positive pictures, incompatible reactions were mainly regulated at the move event (frontal and parietal cortices) and resulted in prolonged reactions. Missing neuronal regulation effects in the NoGo conditions further indicated positive pictures to elicit only weak compatible approach tendencies.

These results revealed a higher conflict potential for the incompatible reactions *approach* negative than for avoid positive. This might indicate avoidance reactions to negative stimuli

to be more important than approach reactions to positive stimuli. Future studies have to show the ecological validity of these findings.

### 6.2 Introduction

Approaching positive and avoiding negative stimuli are fundamental principles of behaviour (Carver, 2006). Automatically triggered reactions are essential for survival, while conscious, controlled reactions guarantee behavioural flexibility. The Approach-Avoidance Task (AAT) allows for the investigation of both automatic approach-avoidance tendencies and their regulation: A picture is presented in the middle of a computer screen with a little manikin on its right or left side (cf. De Houwer, et al., 2001). According to the frame of the picture (landscape or portrait format), participants either have to move the manikin towards the picture or away from it by pressing a button. These instructed reaction either matches implicit response tendencies (compatible conditions: approaching positive pictures and avoiding negative ones) or requires their regulation for performing an alternative response (incompatible conditions: avoiding positive pictures or approaching negative ones). Thereby, incompatible responses elicit longer reaction times than compatible ones (stimulus response compatibility effects; SRC effects).

Their neuronal correlates were investigated by means of functional near-infrared spectroscopy (fNIRS): We showed regulatory neuronal SRC effects in the right dorsolateral prefrontal cortex (PFC) in terms of enhanced activity during incompatible compared to compatible conditions (Ernst, et al., 2013c; cf. also Ernst, et al., in press). In studies on social emotional behaviour using facial expressions, functional magnetic resonance imaging (fMRI) revealed regulatory activity in ventrolateral PFC, frontal pole, supramarginal gyrus and inferior parietal lobule (Roelofs, et al., 2009; Volman, et al., 2011b). The present study aimed at the further investigation of such neuronal SRC effects. We used a new version of the AAT in terms of a GoNoGo task. In short, one trial consists of two events: The cue event indicates the participant to prepare a response, while the move event signals to realize it (Go trials) or to inhibit it (NoGo trials).

We expected the cue event to elicit regulatory neuronal SRC effects, since there is a mismatch between the mental representations of the instructed direction and the response

tendency automatically elicited by the stimulus valence in incompatible conditions. At the move event, neuronal regulatory SRC effects in the Go trials should depict the acquisition of regulatory capacities for actually performing incompatible responses. In contrast, in the NoGo conditions, we expected reversed SRC effects, i.e., a shift in the concept of compatibility: Inhibiting compatible reactions should be an incompatible situation, while not performing an incompatible reaction should be a compatible situation.

In the present fMRI study, a sample of 34 healthy young adults reacted to pictures from the International Affective Pictures System (IAPS; Lang, et al., 2005) as stimuli of general emotional relevance. Regions of interest were the anterior and middle cingulate gyrus, insula, thalamus, frontal and parietal cortices, which are essential for the regulation of cognitive and affective conflicts (see methods for details). Moreover, our previous results indicated negative compared to positive stimuli to elicit stronger SRC effects (Ernst, et al., 2012; Ernst, et al., 2013a). Therefore, we concentrated on differences between processing the AAT with positive and negative stimuli.

### 6.3 Methods

### 6.3.1 Participants

34 students were recruited via the official mailing list of the University of Tuebingen (18 males; mean age  $24.6 \pm 3.5$  years). All participants had normal or corrected to normal vision (contact lenses or the scanner glasses with adequate strength). Three participants were left-handed (Edinburgh Handedness Inventory; Oldfield, 1971). They had no psychiatric, neurological or severe internistic disorders as verified via a screening questionnaire based on the structured clinical interview for DSM-IV (SKID; Wittchen, et al., 1997). We also screened participants for ensuring no current intake of any psychotropic medication or illicit drugs. After detailed explanation of the procedure, written informed consent was obtained from all participants. The study was approved by the local Ethics Committee of the University of Tuebingen and all procedures were in accordance with the Declaration of Helsinki in its version from 2008.

## 6.3.2 Stimuli and apparatus

We used ten negative, neutral and positive pictures, respectively, from the International Affective Picture System (IAPS; Lang, et al., 2005; negative pictures: 1052, 1200, 1205, 1280, 1525, 1930, 6244, 6250.1, 6370, 6510; neutral pictures: 7002, 7004, 7009, 7010, 7080, 7090, 7150, 7175, 7233, 7950; positive pictures: 4626, 4660, 4689, 7330, 7450, 8080, 8200, 8370, 8490, 8501).

Participants reacted via pressing the right or left button on a fiber optic response system (Photon Control, Burnaby, Canada) with their right and left index fingers, respectively. The software "Presentation" (Neurobehavioral Systems, CA, USA) was used to present stimuli and to collect behavioural data. A video projector outside the scanner room projected the stimuli on a translucent screen at the end of the scanner table. Participants could see the stimuli via a mirror above the head coil.

# 6.3.3 Approach-Avoidance Task (AAT)

Each trial contained two events (see figure 14): The cue event consisted of a picture presented in the centre of the screen surrounded by a black frame (duration: 750 ms). Also, a little black manikin was presented on either right or left side of the picture outside the frame. Then, a black fixation cross on white ground appeared for 2250 ms (inter-stimulus interval, ISI). Afterwards, during the move event, the combination of picture, frame and position of the manikin was repeated. However, the colour of the manikin now was either red or green. A red manikin indicated a NoGo-trial (50% of trials), participants should not react. A green manikin indicated a Go-trial. This move event was presented for a maximum of 750 ms or ended by the key press, whereby the rest time was added to the inter-trial interval (ITI). Participants were instructed to react according to the shape of the frame: Half of them should move the manikin towards the picture (approach), when the frame was given in a lengthwise format, and away from the picture (avoidance) in case of a crosswise format. The other half of the sample was instructed to react vice versa. Pressing the right and left button caused the manikin to move to the right and left side, respectively. Thereby, it disappeared for 50 ms and reappeared at the new position for 200 ms. The distance covered by the manikin was always approximately 17 % of the width of the screen. The ITI (black fixation cross on white ground) was randomly jittered (3000 ms, 3500 ms, 4000 ms, 4500 ms, 5000 ms). Additionally, stimulus onsets of the cue events were randomly shifted relative to scan onset (500 ms, 1000 ms, 1500 ms), resulting in a total ITI duration of at least 3500 ms and 6500 ms at maximum.

Each of the five runs consisted of 72 trials and lasted for about 10 minutes. One run contained 36 approach (frame in portrait format) and 36 avoidance trials (frame in landscape format or vice versa). Thereby, in half of the trials each, the manikin was on the left side. Within each of these four combinations of frame format and manikin position, the three valence categories (negative, neutral, positive) were presented six times each, resulting in two or three presentations of each picture during one run. Each of these combinations was repeated three following times at a maximum. In total, over the five runs, there were 60 trials for each of the six cue conditions (approach negative / approach neutral / approach positive / avoid negative / avoid neutral / avoid positive) and 30 trials for each of the 12 move conditions (each of the cue combinations as Go or NoGo condition).

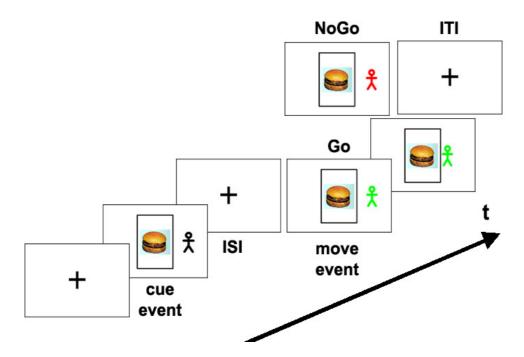


Figure 14: Trialcourse of the cued GoNoGo version of the AAT

Each trial contained two events: The cue event (duration: 750 ms) indicated response preparation. At the move event, participants had to react (Go condition, green manikin) or to inhibit the prepared response (NoGo condition, red manikin, 750 ms). ISI = inter-stimulus interval: 2250 ms / ITI = inter-trial interval: randomly jittered [3000 ms, 3500 ms, 4000 ms, 4500 ms, 5000 ms] / stimulus onsets of the cue events were randomly shifted relative to scan onset [500 ms, 1000 ms, 1500 ms] / t = time

The example depicts an approach reaction to a positive stimuli; the NoGo condition is only shown for illustration reasons.

#### 6.3.4 Procedure

For ensuring a sufficient number of correct trials, participants practiced the task outside the scanner until they achieved 95% or more correct reactions. Furthermore, at the end of each run, participants received a short visual information on their performance, i.e., on the percentage of correct and incorrect reactions. During the practice trials, we used coloured boxes instead of IAPS pictures for minimizing familiarity effects. However, for ensuring that the pictures' content was unambiguous, participants were shown the pictures and were asked to name them aloud. After the five AAT runs inside the scanner, participants rated the IAPS pictures by means of the Self Assessment Manikin (Lang, et al., 2005) with regard to valence (scale ranging from unpleasant (-4) to pleasant (+4)) and arousal (not arousing (1) to very arousing (9)).

# 6.3.5 Functional magnetic resonance image data acquisition and preprocessing

Data were collected on a Siemens Magnetom Sonata Maestro Class 1.5 T scanner (Erlangen, Germany) using an 8-channel phased array head coil for reception and the body coil for transmission. The scanning session started with a high resolution, sagittal T1-weighted anatomical scan (3D-MPRAGE (magnetization-prepared rapid gradient-echo sequence), TR/TI/TE = 1300/660/3.19 ms, flip angle [FA]  $15^{\circ}$ , field of view [FOV] =  $256 \times 256$  mm², matrix =  $256 \times 256$ , 176 slices, voxel size =  $1 \times 1 \times 1$  mm³). Next, the five runs of functional data were acquired by echo-planar imaging (EPI) sequences covering the whole brain (TR = 2000 ms, TE = 40 ms, FOV = 192 mm², matrix =  $64 \times 64$ , voxel size =  $3 \times 3 \times 3.5$  mm³, gap = 10%, 29 interleaved slices). One run consisted of 305 acquisitions, of which the first five images were discarded in order to reach equilibrium of magnetization.

Data were analyzed using Statistical Parametric Mapping (SPM8; Wellcome Trust Centre for Imaging Neuroscience; http://www.fil.ion.ucl.ac.uk/spm/). All images were realigned using the first image as a reference, unwarped using a static field map (Andersson, et al., 2001) and corrected for slice timing and motion-susceptibility interaction. The anatomical image was normalized using the unified segmentation tool to estimate the nonlinear transformation to the Montreal Neurological Institute (MNI) atlas space (tissue probability maps; Collins, et al., 1994). For the mean EPI image, the nonlinear transformation to the EPI template (MNI)

space) was estimated with the standard normalization tool. The resulting images were coregistered to the anatomical reference image and smoothed with an isotropic Gaussian kernel of 8 mm full-width at half maximum (FWHM).

# 6.3.6 Functional magnetic resonance imaging: First and second level analyses

First, single-subject analyses were performed based on the general linear model (Friston, et al., 1994): Using a stick function convolved with the canonical hemodynamic response function, a separate regressor was defined for each of the events, which were time-locked to stimulus onset. The time series of each subject were filtered with a highpass filter (cutoff frequency 1/128 Hz) for removing low frequency components. The error term was modelled as an autoregressive process to account for serial autocorrelation within the data (Friston, et al., 2002).

For each subject, individual activation maps were calculated using t-contrasts of  $\beta$ -weights for each condition relative to the respective neutral condition (approach negative vs. approach neutral, avoid negative vs. avoid neutral, equally for positive stimuli; Go approach negative vs. Go approach neutral, NoGo approach negative vs. NoGo approach neutral, etc.). We used this relativasation for separating effects due to the respective valence from effects due to the mere presentation of stimuli. Furthermore, errors were modelled as one additional regressor.

The length of 2.25 s of our ISI was in accordance with previous research revealing a minimum length of 2 s to result in linear overlaps of activations, i.e., to allow for data interpretations. Nevertheless, to eliminate any distortion of the activity at the cue event by the overlap with the activation patterns of the move event, we orthogonalized the  $\beta$ -weights of the cue events to the  $\beta$ -weights of the respective move events. A second level random-effects analysis was used for the statistical evaluation of group data. We used the GLM Flex toolbox for SPM (http://nmr.mgh.harvard.edu/harvardagingbrain/People/AaronSchultz/GLM\_Flex.html) for setting up a flexible factorial design with the factors direction (approach, avoid) and valence (negative (vs. neutral), positive (vs. neutral)) for the cue event and with the additional factor

Go-NoGo (Go, NoGo) for the move event.

Results are reported for our regions of interest (ROIs), whereby the search volume was restricted to the respective mask volume and corrections for multiple comparisons were performed by applying a small volume correction (Worsley, et al., 1996). Local maxima had to be separated for at least 8 mm and the threshold of cluster size was set to 50 voxels. The bi-hemispheric ROIs were defined using the WFU pickatlas (Maldjian, et al., 2003). As mentioned in the introduction section, we expected regulatory SRC effects in regions important for the solution of affective and cognitive response conflicts. The anterior cingulate cortex (ACC) is a monitoring system essential for detecting conflicts (van Veen & Carter, 2002) and modulating other brain areas for initiating performance adjustments (Carter, et al., 2000; Crottaz-Herbette & Menon, 2006; WFU: anterior and middle cingulum). The PFC is a main instance for the implementation of response control (cf. Ernst & Fudge, 2009): Prefrontal regions are involved in the initiation of performance adjustments (MacDonald, et al., 2000), in spatial working memory (WM), as well as in inhibition and action selection processes (Nee, et al., 2013; WFU: precentral, superior, middle, medial, inferior frontal and rectal gyrus, supplementary motor area, rolandic operculum). The parietal cortex is important for spatial orientation, WM and attention processes (Dosenbach, et al., 2008; Nee, et al., 2013; WFU: inferior and superior parietal lobule, supramarginal, postcentral and angular gyrus, precuneus, paracentral lobule). The insula is activated during monitoring processes and emotional arousal (Dosenbach, et al., 2008; Cole & Schneider, 2007). The thalamus is essential for the alerting aspect of attention (Fan, et al., 2005).

## 6.3.7 Statistical analysis of ratings and behavioural data

For further statistical analyses, SPSS for Windows (version 19.0; SPSS, Inc., Chicago, IL, USA) was used. Valence and arousal ratings for the three valence categories were compared by means of univariate analyses of variance (ANOVAs). In case of significance, the valence conditions were further compared by means of two-tailed paired sample t-tests.<sup>24</sup>

RTs of correct trials were measured as time from picture onset of the move event until the button press. For making behavioural SRC effects less vulnerable to biases due to outliers

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<sup>&</sup>lt;sup>24</sup> Here, we did not analyze the values for negative and positive pictures relative to the neutral pictures, since we were interested in all three valence categories for ensuring the hypothesized valence evaluations. Thereby, it should be noted that the comparison between negative and positive evaluations is the same as when the relative values would be used, since subtracting the neutral ratings equals a linear transformation.

and differences in average response time, we calculated so-called D-scores (cf. Ernst, et al., in press): The difference between the mean RTs is divided by the personalized standard deviation of the response latencies of the two included conditions, i.e. (*mean avoid positive* minus *mean approach positive*)/((*standard deviation avoid positive* plus *standard deviation approach positive*)/2) and (*mean approach negative* minus *mean avoid negative*)/((*standard deviation approach negative*) plus *standard deviation avoid negative*)/2; cf. Greenwald, et al., 2003). For getting RTs relative to the neutral stimuli, we subtracted D-scores for the neutral pictures built as for the positive pictures from D-scores for the positive pictures and D-scores for the neutral pictures built as for the negative pictures from D-scores for the negative pictures. Positive values of the resulting D-scores reflect the hypothesized compatibility and incompatibility of the respective conditions. The resulting D-scores for positive and negative pictures were compared by means of two-tailed paired sample t-tests and were each tested for significance by means of two-tailed one sample t-tests. Effect sizes were calculated as partial Eta squared  $\eta_p^2$  and Cohen's d for the results of the ANOVA and the t-tests, respectively.

Errors were analyzed as usually in a GoNoGo task: Omission errors indicating missing reactions and commission errors indicating false alarms and – furthermore – the frequency of falsely directed Go-reactions. Thereby, we analyzed error rates of negative and positive pictures minus the respective neutral condition by means of non-parametric Wilcoxon-Z tests.

## 6.4 Results

### 6.4.1 Picture ratings

With regard to the valence ratings, the ANOVA showed significant differences  $(F(1.76,57.92)=295.59,\ p<.001,\ \eta^2=.9)$ . Post-hoc t-tests revealed pictures to be rated as expected: Negative pictures were perceived to be more negative than neutral  $(t(33)=-14.53,\ p<.001;\ d=2.49)$  and positive pictures  $(t(33)=-20.75,\ p<.001,\ d=3.56)$ , while positive pictures were rated as more positive than neutral ones  $(t(33)=12.24,\ p<.001,\ d=2.1)$ . Thereby, the intensity of valence (i.e., the relative amount of valence ratings) did not differ between negative and positive pictures  $(t(33)=.97,\ p=.34,\ d=.17)$ .

Furthermore, the ANOVA revealed significant effects in the arousal ratings  $(F(2,66) = 124.3, p < .001, \eta^2 = .79)$ . As expected, post-hoc t-tests revealed no differences between negative and positive pictures (t(33) = 1.56, p = .13, d = .2), while neutral pictures were less arousing than negative (t(33) = 13.28, p < .001, d = 2.28) and positive pictures (t(33) = 13.32, p < .001, d = 2.6).

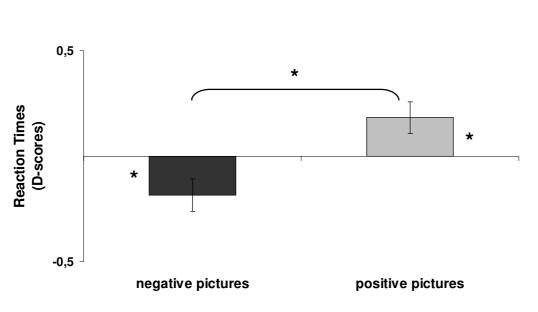
#### 6.4.2 Behavioural data

#### 6.4.2.1 Error rates

Participants showed low error rates leaving a minimum of 23 valid trials for every participant in each condition. With regard to omission and commission errors as well as falsely conducted Go reactions, there were neither SRC effects, i.e. significant differences between approaching and avoiding, nor differences between SRC scores for negative and positive pictures (all p > .05).

# 6.4.2.2 Reaction Times (RTs)

The significant D-scores for positive pictures (t(33) = 2.4, p = .02, d = .41) were stronger than for negative pictures (t(33) = 2.56, p = .02, d = .44), whereby the negative pictures elicited significant reversed D-scores (t(33) = -2.41, p = .02, d = .41).



Times (Dscores) for negative and positive stimuli. SRC effects were significant for positive pictures, but for negative pictures, reversed SRC effects were found. \* p < .05

Figure 15: Reaction

#### 6.4.3 Functional data

#### 6.4.3.1 Cue event: SRC scores

SRC scores were calculated as the difference between the incompatible and the compatible condition, i.e., as *approach negative* minus *avoid negative* and as *avoid positive* minus *approach positive*. As described in the methods section, these values already comprised the difference to the respective neutral condition, e.g., *approach negative* minus *approach neutral*, etc. Significantly positive values indicate stronger activation in incompatible compared to compatible conditions.

At a threshold of p < .05 (SVC corrected), there were significant SRC effects in all investigated ROIs (see table 6 and figure 16). For positive pictures, SRC effects were only found in the left middle frontal gyrus (MFG) and inferior frontal gyrus (IFG; see table 6).

Table 6: SRC effects for negative (approach vs. avoid) and positive pictures (avoid vs. approach) at the cue event

in the ROIs at a significance level of p < .05 (SVC corrected).

Labelling of brain regions according to Anatomical Automatic Labeling (AAL) atlas, cluster size in number of voxels, MNI coordinates of local maxima.

	cluster	MNI coordinates			
brain regions	size	t		1	1
			Х	у	Z
negative pictures					
cingulum					
R middle cingulate gyrus	271	3.86	9	23	34
L middle cingulate gyrus		3.5	-7	17	35
L middle cingulate gyrus		3.25	-12	-22	43
L middle cingulate gyrus		3.14	-9	-22	34
L middle cingulate gyrus		2.54	-9	2	37
L middle cingulate gyrus		2.34	-9	-10	49
L supplementary motor area		2.19	-3	2	46
insula					
R insula	216	4.21	36	20	13
R insula		3.74	45	8	4
R insula		3.28	39	-1	10
R insula		2.72	33	29	7

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R superior frontal gyrus   2.28   18   -1   49   49   434   49   49   49   49   4							
R postcentral gyrus   2.27   43.5   -23.5   64   R inferior frontal gyrus, opercular part   2.27   48   8   28   28   39   -13   37   37   37   37   38   38   38   3							
R inferior frontal gyrus, opercular part R precentral gyrus R superior frontal gyrus L middle frontal gyrus R superior medial frontal gyrus R superior medial frontal gyrus R superior medial frontal gyrus R middle frontal gyrus R middle frontal gyrus R middle frontal gyrus R middle frontal gyrus R inferior frontal gyrus, opercular part R inferior frontal gyrus, opercular part R inferior frontal gyrus, opercular part R rolandic operculum R inferior frontal gyrus, opercular part L insula L insula							
R precentral gyrus R superior frontal gyrus L middle frontal gyrus R middle frontal gyrus R superior medial frontal gyrus R superior medial frontal gyrus R middle frontal gyrus R inferior frontal gyrus, opercular part R inferior frontal gyrus, opercular part R rolandic operculum R inferior frontal gyrus, opercular part L insula L insula		, ,,					
R superior frontal gyrus       2.16       30       50       10         L middle frontal gyrus       2.13       -45       23       43         R middle frontal gyrus       2.08       48       32       22         R superior medial frontal gyrus       2.00       44       34         R middle frontal gyrus       2.0       39       44       34         R middle frontal gyrus       1.97       39       53       19         R inferior frontal gyrus, opercular part       3.373       45       11       4         R inferior frontal gyrus, opercular part       3.33       39       17       7         R rolandic operculum       2.85       39       -4       10         R inferior frontal gyrus, opercular part       2.2       57       11       8.5         L insula       59       3.22       -33       17       10         L insula       2.72       -42       11       1							
L middle frontal gyrus R middle frontal gyrus R superior medial frontal gyrus R middle frontal gyrus R inferior frontal gyrus, opercular part R inferior frontal gyrus, triangular part R rolandic operculum R inferior frontal gyrus, opercular part L insula L insula  2.13 2.08 48 32 22 2.02 6 29 37 1.97 39 53 19 133 3.73 45 11 4 3.39 36 23 13 3.33 39 17 7 2.85 39 -4 10 2.2 57 11 8.5 10 2.72 -42 11 1							
R middle frontal gyrus       2.08       48       32       22         R superior medial frontal gyrus       2.02       6       29       37         R middle frontal gyrus       2.0       39       44       34         R middle frontal gyrus       1.97       39       53       19         R inferior frontal gyrus, opercular part       3.39       36       23       13         R inferior frontal gyrus, opercular part       3.33       39       17       7         R rolandic operculum       2.85       39       -4       10         R inferior frontal gyrus, opercular part       2.2       57       11       8.5         L insula       59       3.22       -33       17       10         L insula       2.72       -42       11       1							
R superior medial frontal gyrus       2.02       6       29       37         R middle frontal gyrus       2.0       39       44       34         R middle frontal gyrus       1.97       39       53       19         R inferior frontal gyrus, opercular part       3.39       36       23       13         R inferior frontal gyrus, opercular part       3.33       39       17       7         R rolandic operculum       2.85       39       -4       10         R inferior frontal gyrus, opercular part       2.2       57       11       8.5         L insula       59       3.22       -33       17       10         L insula       2.72       -42       11       1		<b>0</b> ,					
R middle frontal gyrus       2.0       39       44       34         R middle frontal gyrus       1.97       39       53       19         R inferior frontal gyrus, opercular part       133       3.73       45       11       4         R inferior frontal gyrus, opercular part       3.39       36       23       13         R rolandic operculum       2.85       39       -4       10         R inferior frontal gyrus, opercular part       2.2       57       11       8.5         L insula       59       3.22       -33       17       10         L insula       2.72       -42       11       1		<b>.</b>					
R middle frontal gyrus       1.97       39       53       19         R inferior frontal gyrus, opercular part       133       3.73       45       11       4         R inferior frontal gyrus, opercular part       3.39       36       23       13         R rolandic operculum       2.85       39       -4       10         R inferior frontal gyrus, opercular part       2.2       57       11       8.5         L insula       59       3.22       -33       17       10         L insula       2.72       -42       11       1							
R inferior frontal gyrus, opercular part R inferior frontal gyrus, triangular part R inferior frontal gyrus, opercular part R rolandic operculum R inferior frontal gyrus, opercular part L insula L insula  133  3.73  45  3.39  36  23  13  7  2.85  39  -4  10  2.2  57  11  8.5  2.7  2.7  -42  11  1		<b>.</b>					
R inferior frontal gyrus, triangular part R inferior frontal gyrus, opercular part R rolandic operculum R inferior frontal gyrus, opercular part L insula L insula  8 3.39 36 23 17 7 2.85 39 -4 10 2.2 57 11 8.5 3.32 -33 17 10 2.72 -42 11 1		<b>.</b>	133				
R inferior frontal gyrus, opercular part R rolandic operculum R inferior frontal gyrus, opercular part L insula L insula  8 3.33 39 -4 10 2.85 39 -4 10 3.59 3.22 57 11 8.5 3.22 -33 17 10 2.72 -42 11 1							13
R rolandic operculum       2.85       39       -4       10         R inferior frontal gyrus, opercular part L insula       59       2.2       57       11       8.5         L insula       3.22       -33       17       10         2.72       -42       11       1				3.33	39	17	7
L insula 59 3.22 -33 17 10 L insula 2.72 -42 11 1		R rolandic operculum			39		10
L insula 2.72 -42 11 1		• • • • • • • • • • • • • • • • • • • •					
			59				
L insula     2.66   -36   23   1							
		L Insula		2.66	-36	23	1

L insula		2.57	-30	29	4
L precentral gyrus L superior parietal lobule L superior parietal lobule R superior parietal lobule R inferior parietal lobule R precuneus R precuneus L supplementary motor area R angular gyrus L precentral gyrus L paracentral lobule L precentral gyrus R superior parietal lobule L postcentral gyrus R supramarginal gyrus L postcentral gyrus R postcentral gyrus L precentral gyrus L postcentral gyrus L postcentral gyrus L precentral gyrus L precentral gyrus L precentral gyrus L precentral gyrus L paracentral lobule R supramarginal gyrus L inferior parietal lobule L precentral gyrus R supramarginal gyrus L postcentral gyrus L postcentral gyrus R postcentral gyrus R postcentral gyrus R postcentral gyrus R supramarginal gyrus L postcentral gyrus R postcentral gyrus R supramarginal gyrus L precuneus L postcentral gyrus R supramarginal gyrus L precuneus L postcentral gyrus	2618	5.9 5.38 5.25 4.89 4.44 4.27 4.24 4.23 4.13 3.98 3.77 3.76 3.51 3.02 2.97 2.54 2.52 2.43 2.41 2.38 2.37 2.34 2.34 2.32 2.31 2.29 2.29 2.29 2.29 2.21 2.17 2.00 1.91	-46.5 -21 -27 27 33 18 12 -9 27 -51 -18 -48 -36 42 -36 30 -39 -3 -42 48 -57 -12 -48 42 -15 42 -9 -48	-5.5 -70 -58 -61 -55 -64 -73 -10 -61 -4 -22 -7 -64 -31 -28 -37 -19 -25 -25 -28 -10 -22 -43 -19 -55 -25 -40 -31 -43 -46 -34	34 55 49 55 49 43 55 77.5 43 25 76 52 64 55 34 79 25 37 43 64 22 46 70 58 58 79 49 31 76 52
postive pictures					
frontal cortex L middle frontal gyrus L middle frontal gyrus L inferior frontal gyrus, triangular part L middle frontal gyrus	94	2.87 2.67 2.52 2.23	-45 -42 -39 -30	35 35 29 32	31 22 13 13

#### 6.4.3.2 Move event: Interaction GoNoGo with SRC scores

For Go conditions, SRC scores were calculated as for the cue event, while, for NoGo conditions, reversed SRC scores were calculated the other way round (compatible minus incompatible condition). For each ROI, the interaction GoNoGo x (reversed) SRC scores was used as a mask (t-test, p < .05, SVC corrected), wherein we applied post-hoc t-tests for SRC effects in the Go conditions and reversed SRC effects in the NoGo conditions.

For negative pictures, there were no significant SRC effects in the Go conditions.<sup>25</sup> Reversed SRC effects in the NoGo conditions were observed in the right superior parietal lobule (SPL). For positive pictures, we found SRC effects in the Go conditions in the frontal and parietal cortex (see table 7 and figure 16), while there were no significant reversed SRC effects in the NoGo conditions.<sup>26</sup>

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<sup>&</sup>lt;sup>25</sup> Only when lowering the minimal size of significant clusters to 5 voxels, there were SRC effects in the right middle cingulate gyrus (6 voxels, t = 2.14, x/y/z = 15/-16/46) and the left angular gyrus (5 voxels, t = 2.03, x/y/z = -42/-52/22).

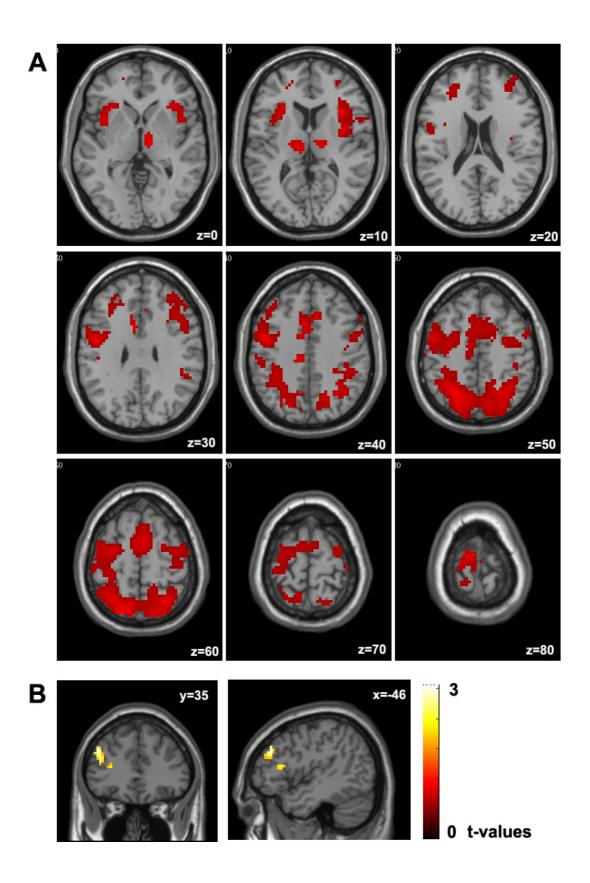
<sup>&</sup>lt;sup>26</sup> Only when lowering the minimal size of significant clusters to 5 voxels, there were reversed SRC effects in the right MFG (6 voxels, t = 2.27, x/y/z = 33/50/10), right superior orbital gyrus (5 voxels, t = 2.16, x/y/z = 21/59/-5), right superior frontal gyrus (9 voxels, t = 2.14, x/y/z = 16.5/24.5/40) and right postcentral gyrus (5 voxels, t = 2.78, x/y/z = 39/-43/70).

Table 7: SRC effects in Go conditions (negative pictures: approach vs. avoid; positive pictures: avoid vs. approach) and reversed SRC effects (revSRC) in NoGo conditions (negative pictures: avoid vs. approach; positive pictures: approach vs. avoid) at the move event

in the ROIs (interaction GoNoGo x (reversed) SRC scores as mask (t-test, p < .05, SVC corrected) for post-hoc t-tests).

Labelling of brain regions according to Anatomical Automatic Labeling (AAL) atlas, cluster size in number of voxels, MNI coordinates of local maxima.

brain regions	cluster	t	MNI coordin		nates
	size		X	у	Z
negative pictures					
parietal cortex Go SRC NoGo revSRC R superior parietal lobule	61	- 4.66	- 45	- -46	- 61
positive pictures					
frontal cortex Go SRC L precentral gyrus L precentral gyrus R precentral gyrus R superior frontal gyrus R middle frontal gyrus R inferior frontal gyrus, opercular part R inferior frontal gyrus, triangular part R precentral gyrus R middle frontal gyrus R middle frontal gyrus L middle frontal gyrus L middle orbital gyrus L middle frontal gyrus L middle frontal gyrus L middle frontal gyrus NoGo revSRC parietal cortex Go SRC	52 176 72	4.07 2.95 3.7 3.22 2.5 3.22 2.84 2.63 2.57 2.55 2.88 2.76 2.49	-30 -30 27 30 42 54 54 52.5 46.5 40.5 -30 -36 -27	-31 -10 -25 -10 -1 23 32 6.5 32 38 51.5 56	58 64 64 67 64 34 22 43 32.5 31 -2 19
L postcentral gyrus L inferior parietal lobule L precentral gyrus L superior parietal lobule L postcentral gyrus R precuneus L superior parietal lobule L supramarginal gyrus L postcentral gyrus L postcentral gyrus NoGo revSRC	212 51	4.8 4.27 4.07 3.6 2.65 2.43 1.96 3.55 3.54 3.47	-30 -39 -30 -18 -39 3 -18 -63 -60	-34 -46 -31 -40 -37 -43 -58 -22 -13 -13	46 46 58 61 64 58 64 28 43 31



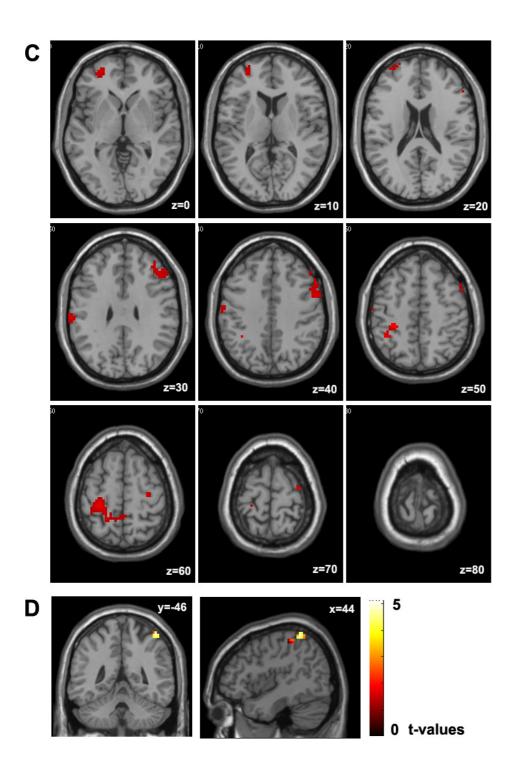


Figure 16: Neuronal activity at the cue event (A, B) and the move event (C, D)

- A) Neuronal pattern of SRC effects for **negative** stimuli at the cue event. For the respective t-values see table 6.
- B) SRC effects in left middle frontal gyrus (MFG) for **positive** stimuli at the cue event.
- C) Neuronal pattern of SRC effects for **positive** stimuli at the move event in Go conditions. For the respective t-values see table 7.
- D) Reversed SRC effects in right superior parietal lobule (SPL) for **negative** stimuli at the move event in NoGo conditions.

### 6.5 Discussion

The current study investigated the regulation of automatic approach-avoidance reactions by means of fMRI in healthy participants during a cued GoNoGo version of the AAT. Regulating the compatible reaction tendency avoid negative for conducting the incompatible reaction approach negative constituted a pronounced conflict, while realizing the incompatible reaction avoid positive instead of the compatible reaction approach positive merely elicited modest regulatory activity.

Regarding the involved regions in more detail revealed insight into the respective regulatory sub-processes: At the cue event (preparation phase) and in Go conditions at the move event (reaction phase), in incompatible conditions, compatible reaction tendencies elicited by the picture valence had to be inhibited for performing the incompatible reaction instructed by the picture frame. The broadest neuronal SRC effects, i.e., stronger activity in the incompatible than compatible condition, were found for negative pictures at the cue event: The middle cingulate gyrus (dorsal part of the ACC) is essential for conflict monitoring (van Veen & Carter, 2002) and conflict solution (Weissman, et al., 2005; Bush, et al., 2000). It is also involved in translating intentions into actions (Paus, 2001). The adjacent precentral gyrus (preCG) and supplementary motor area (SMA) indicated response preparation (Cole & Schneider, 2007) and distractor resistance (Nee, et al., 2013).

SRC effects were also observable in the anterior insula, a main instance for relating motivational states to subjective feelings and goal settings (Wager & Feldman Barrett, 2004). Moreover, it is part of a system responsible for conflict monitoring (Dosenbach, et al., 2008) and contributes to the inhibition of reactions (Huster, et al., 2011). Furthermore, the adjacent frontal opercular regions, specifically the right IFG, are involved in inhibition and top-down control processes with regard to movements (Aron, et al., 2004) and memories (Anderson, et al., 2004). The thalamus is associated with the alerting function of attention (Fan, et al., 2005) and the transmission of sensory information about the body's physiological state to the cortex, i.e., to consciousness (Craig, 2002).

Furthermore, the MFG is responsible for the maintenance and manipulation of spatial contents in WM (D'Esposito, et al., 1999; cf. Nee, et al., 2013), for distractor resistance (Sakai, et al., 2002), action monitoring (cf. Petrides, 2000) and action selection (Rowe, et al.,

2000). The superior (medial) frontal gyrus reflects controlled attention allocation (Corbetta & Shulman, 2002), executive processes of spatial WM (Nee, et al., 2013) and self-referential evaluation processes (Gusnard, et al., 2001).

SRC effects were also found in the SPL, which is involved in visual WM capacity (Todd & Marois, 2004), spatial WM in general (Nee, et al., 2013) and top-down control of visual attention (Kastner & Ungerleider, 2000; Friedman-Hill, et al., 2003). Furthermore, the precuneus is responsible for taking first-person perspective and for spatial imagination (Cavanna & Trimble, 2006). Together with the thalamic activity, it might reflect participants' identification with the manikin and its situation. The inferior parietal lobule (IPL) was suggested to be involved in attentional processes in terms of foregrounding contents in WM by means of activating semantic and conceptual details of this item (Nee, et al., 2013; cf. Dosenbach, et al., 2008), while the supramarginal gyrus (SMG) guarantees controlled attention allocation (Corbetta & Shulman, 2002). SRC effects in the postcentral gyrus (postCG) are in line with previously reported activity of this somatosensory region during not only motor performance (e.g. Huster, et al., 2011), but also motor imagery (e.g. Porro, et al., 1996).

In contrast, at the move event, when actually realizing the incompatible reactions (Go condition), there was no pronounced significant activity in any of these ROIs for negative pictures. For positive pictures, preparatory SRC effects at the cue event were restricted to left MFG and IFG, i.e., to action selection and response inhibition processes. At the move event, in Go conditions, SRC effects comprised frontal (preCG, right IFG, MFG) and parietal (left postCG, SPL, IPL, precuneus, SMG) response mechanisms.

Moreover, in NoGo conditions at the move event, we hypothesized reversed SRC effects: The inhibition of automatically elicited compatible response tendencies is incompatible, while not performing the prepared incompatible reaction becomes a compatible situation. For negative pictures, the right SPL showed this effect. Previously, this region was suggested to control the switching between different response rules as necessary at the move event (Chiu & Yantis, 2009). Such a shift in the concept of compatibility and the allocation of regulatory resources was not observed for positive pictures.

With regard to the behavioural data, positive pictures caused SRC effects: RTs were longer for incompatible than compatible conditions. For negative pictures, SRC effects were reversed than expected: Incompatible reactions were faster than compatible ones. However, the explicit valence ratings revealed participants to have perceived the valence categories as expected. Importantly, there were neither any differences with regard to the arousal ratings nor the absolute valence ratings. Rather, the reversed behavioural SRC effects for negative pictures are in line with the strong neuronal preparation effect at the cue event. Moreover, in Go conditions, activity in the right midbrain as an area responsible for response initiation (Gruber & Gould, 2010) mediated the relation between participants' behaviour and their sensitivity for the pictures' negativity: The more negative and arousing participants rated the pictures, the stronger they showed SRC effects in the right midbrain and – thereby – the stronger the reversed behavioural SRC effects were (see supplements for details).

In sum, these findings are in line with an evolutionary based perspective, which assumes negative stimuli to be more important for participants' survival (cf. Rozin & Royzman, 2001). We suggest an extension of this concept to the behavioural level, since our results indicate a stronger elicitation of avoidance tendencies by negative stimuli than of approach tendencies by positive stimuli (cf. Cacioppo, et al., 1997).

For negative pictures, strong response preparation was observed as soon as the conflict was given (cue event). This extensive pre-regulation was followed by even reversed behavioural SRC effects. Furthermore, the more negative participants perceived the pictures, the stronger they showed response initiation processes, when realizing the reaction, and – thereby – the stronger the observed reversed behavioural SRC effects were. Importantly, this individual subcortical response regulation and the missing cortical group effect are in accordance with models suggesting reactions to negative stimuli to rely on subcortical structures for guaranteeing their fast realization (LeDoux, 1994). In NoGo conditions, neuronal reversed SRC effects indicated the inhibition of automatically elicited compatible response tendencies to require more regulation than the inhibition of prepared incompatible reactions.

In contrast, positive pictures were associated with only weak automatic approach tendencies: Early response preparation at the cue event was restricted; rather, regulatory SRC effects emerged mainly at the actual reaction (move event) resulting in the usual behavioural SRC effects. Importantly, there was no pronounced contribution of the thalamus, ACC and insula, what indicated an only marginal conflict situation not eliciting attentional alerting and conflict monitoring processes. The missing neuronal reversed SRC effects in the NoGo conditions further indicated positive pictures to elicit only weak compatible approach tendencies.

Taken together, these findings indicate the conflict in incompatible conditions to represent different situations for negative and positive stimuli: The stronger elicitation of avoidance reactions by negative stimuli might reflect the higher necessity for fast reactions in dangerous situations than for fast reactions in pleasant situations for guaranteeing an organisms' survival. Therefore, inhibiting such avoidance tendencies in incompatible AAT conditions constituted an enormous conflict, while inhibiting positive approach tendencies was merely an unpleasant situation.

The current results are limited with regard to the following aspects: First, the used pictorial material represents theoretical scenes. Future studies should investigate the ecological validity of these findings by relating parameters of the AAT to participants' behaviour for real stimuli (cf. Krieglmeyer & Deutsch, 2010). Second, we used participants' explicit valence ratings as specification of the pictures' effectiveness. However, these measures might be distorted, since participants had to explicitly think of evaluations, which usually happen outside the awareness. Measures from an implicit evaluation task might evade this issue.

Nevertheless, this first AAT investigation explicitly separating positive and negative stimuli in the data analysis, revealed evidence that the evolutionary based assumption of negative stimuli being more important than positive stimuli might extend to the behavioural level: Our results indicate avoidance reactions to negative stimuli to be more important than approach reactions to positive stimuli. This resulted in higher conflict potential for the incompatible reactions approach negative and than for avoid positive. Future studies are necessary to determine the ecological validity of these findings.

# 6.6 Supplementary material

#### **Mediation model**

Taking into account the high relevance of negative stimuli and the reversed behavioural SRC effects, one might expect regulatory SRC effects at the move event in Go conditions despite the preparatory SRC effects at the cue event. For further exploring this aspect, we used a more individually orientated approach and correlated the Dscores with the neuronal activity in the Go conditions. At a level of p < .001 uncorrected, there was a significant negative correlation between Dscores and neuronal SRC scores in the right midbrain including the red nucleus (8 voxel, t = 3.37, x/y/z = 9/-25/-5), i.e., in an area responsible for the initiation of movements (Gruber & Gould, 2010): The stronger participants activated this area in incompatible compared to compatible conditions, the stronger they showed reversed behavioural SRC effects.

Furthermore, we investigated the relation of this correlation to participants' evaluation of the pictures. We tested a mediation model with the interaction of participants' valence x arousal ratings as independent variable (X), Dscores as dependent variable (Y) and beta weights of the SRC scores for the above described midbrain region as mediator (M; cf. Ernst, et al., 2012). The interaction of the ratings was calculated as the valence ratings multiplied with the arousal ratings, whereby both were relativised at the respective ratings for neutral stimuli. The analysis was conducted via standard path-analytic approaches by Hayes (PROCESS tool for SPSS; Hayes, 2012; http://www.afhayes.com/spss-sas-and-mplus-macros-and-code.html; cf. Preacher & Hayes, 2004; Preacher & Hayes, 2008; Hayes, 2009). The following equations were estimated to derive the total, direct, and indirect effects of the predictor on the criterion variable through the mediator:

- (1) criterion variable = constant + c\*(predictor) + error
- (2) mediator = constant + a\*(predictor) + error
- (3) criterion variable = constant + c'\*(predictor) + b\*(mediator) + error

All coefficients were estimated using ordinary least-squares (OLS) regression. Thereby, the criterion for statistical significance was p = .05.

This test revealed the presumptions for mediation to be fulfilled ( $R^2 = .45$ , F(2,31) = 8.34, p = .001). The midbrain activity was a mediator, i.e., a mechanism, in the relation between participants' ratings and their behaviour: The more negative and arousing participants rated

the negative pictures, the stronger they showed SRC effects in the right midbrain, when realizing the Go reactions, and – thereby – by trend, the stronger they showed reversed behavioural SRC effects (path c in figure 17; equation 1;  $\beta_c = .31$ , SE = .01, t = 1.85, p = .073).

In detail, the interaction of valence x arousal ratings was negatively associated with SRC effects in the right midbrain (path a in figure 17; equation 2;  $\beta_a$  = -.06, SE = .02, t = -2.52, p = .02): The more negative and arousing participants rated the negative pictures, the larger their neuronal SRC effects were, i.e., the stronger their neuronal activity was in the incompatible condition *approach negative (Go)* compared to the compatible condition *avoid negative (Go)*. The direct effect of the interaction valence x arousal ratings on behavioural Dscores was not significant (path c' in figure 17; equation 3;  $\beta_{c'}$  = .002, SE = .008, t = .3, p = .76). The indirect effect of the interaction valence x arousal ratings on behavioural Dscores was quantified as the product of the OLS regression coefficient estimating neuronal SRC effects from the ratings (path a in figure 17) and the OLS regression coefficient estimating behavioural Dscores from the neuronal SRC effects (path b in figure 17;  $\beta_b$  = -.31, SE = .08, t = -4.02, p = .0003).

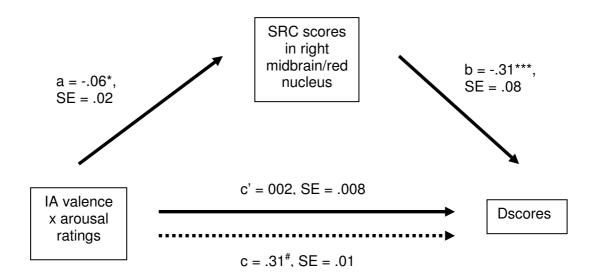


Figure 17: Mediator model with path coefficients

The dotted line indicates the effect of the ratings on behaviour when neuronal activity is not included as a mediator. a, b, c and c' are unstandardized OLS regression coefficients.  $^{\#}$  < .1,  $^{*}$  p<.05,  $^{***}$  p<.001

# 6.7 Additional analyses: Habituation effects

The following analyses are not contained in the publication due to its limited scope. However, they complement the above reported findings for important aspects. Additionally, we tested for habituation effects and increases in activity over the five runs. Thereby, we concentrated on the comparison of the first and last run (run a vs. run e; run e vs. run a). D-scores were compared by means of two-tailed paired sample t-tests. Neither for negative, nor for positive stimuli, there was a significant difference between the two runs (t(33) = -.81, p = .42; t(33) = .07, p = .94).

At the neuronal level, for each ROI, the interaction run x SRC scores was used as a mask (F-test, p < .05, SVC corrected; for NoGo conditions: run x reversed SRC scores), wherein decreases (run a > e) and increases of activity (run e > a) were tested via post-hoc t-tests (cluster size of at least 50 voxels).

With regard to the cue event (preparation phase), there were no increases in activity for negative pictures. Rather, activity was reduced in run e compared to run a in frontal regions responsible for response preparation (preCG, SMA), spatial working memory and self-referential evaluation processes (superior (medial) frontal gyrus; for details see table 8). However, parietal areas responsible for spatial working memory components showed no reduction. Parietal decrease was restricted to the precuneus as responsible for taking first-person perspective. Activity also decreased in the thalamus and in the anterior insula. This might indicate a reduction of the induced emotional arousal and alerting aspect by the incompatible condition *approach negative*. However, the ACC as main instance for conflict monitoring and solution did not show such habituation effects. In other words, the importance of solving the AAT conflict with negative stimuli already at the cue event remained stable, while the induced emotional arousal and the necessity to directly prepare the reactions decreased.

With regard to the move event, neuronal SRC effects in the Go conditions decreased in the rostral part of the ACC, what might indicate a decrease in emotional reactivity to the affective aspects of the AAT conflict (Bush, et al., 2000). With regard to frontal and parietal areas, we found both increases and decreases in SRC effects (for details see table 9). Thereby, in frontal areas, the number of decreasing voxels exceeded the number of

increasing voxels, while the reversed pattern was found for parietal areas. This might indicate a shift of reaction control from frontal to parietal areas. Following models of cognitive control, which assume the prefrontal cortex to constitute the highest regulation instance in the human brain (e.g. Miller & Cohen, 2001), this shift might indicate practice effects in realizing the required reactions according to the given combination of picture frame and manikin position. In the NoGo conditions, we found a general decrease of reversed SRC effects in frontal and parietal regions from run a to run, while there were no increases (for details see table 10). Together with the decreasing response preparation effects at the cue event, this might indicate a reduction in the strength of automatic avoidance reactions elicited by negative stimuli. Importantly, these decreases did not comprise the superior parietal lobule, i.e., the higher response control mechanisms guaranteeing the switching between different response rules as necessary at the move event. Taken together, for negative stimuli, the elicitation of automatic avoidance reactions decreased over the time to some extent, while the necessity of solving the conflict in incompatible conditions already at the cue event (ACC) and of activating higher response control mechanisms in the NoGo conditions (SPL) remained stable.

In contrast, for positive pictures, the alterations in activity were different. At the cue event, there was an increase in activity in the right precuneus, indicating an increase in participants' identification with the manikin's situation (for details see table 11). However, at the move event, in Go conditions, activity related to response regulation decreased in frontal and parietal areas (SMA, preCG, postCG; for details see table 12). This might indicate a shift of activity related to conflict solution from the move event to the cue event. In NoGo conditions, there were no changes, what supports the low conflict potential of not realizing approach reactions to positive stimuli (for details see table 13).

Taken together, for positive stimuli, the response conflict seemed to become more personal over the time as indicated in an increase in participants' identification with the situation (right precuneus). However, at the same time, regulatory activity directly related to response realization decreased. This might indicate a decrease in the elicitation of automatic approach reactions. Therefore, the increase of activity at the cue event might reflect a practice effect with regard to regulation preparation, while – at the same time – behavioural impulses and the necessity for regulation decreased.

#### Table 8: Negative stimuli, cue event

Decreases (run a > e) and increases (run e > a) in SRC effects for negative pictures (approach vs. avoid) at the cue event in the ROIs (interaction run x SRC scores as mask (Ftest, p < .05, SVC corrected)). Labeling of brain regions according to Anatomical Automatic Labeling (AAL) atlas, cluster size in number of voxels, MNI coordinates of local maxima.

brain regions	cluster	1 T 1			nates
biani regions	size		х	у	z
insula					
run a > e					
L insula	59	3.6	-36	17	-2
run e > a	-	-	-	-	-
thalamus					
run a > e	404	4 74		00	_
L thalamus	124	4.74	-6	-22	1
L thalamus		3.97	-6	-25	10
L thalamus		3.71	-15	-22	-2
R thalamus		3.6	9	-22	-2
R thalamus		3.51	9	-13	1
run e > a	-	-	-	-	-
frontal cortex					
run a > e	80	5.08	-15	-13	70
L precentral gyrus L supplementary motor area	00	4.03	-12	-13   -4	70
R precentral gyrus	144	4.19	21	- <del>1</del>	70
R supplementary motor area	144	4.19	9	-13	70
R precentral gyrus		3.39	36	-16	64
R superior frontal gyrus		3.29	15	-10	58
R precentral gyrus		2.99	33	-13	52
R precentral gyrus		2.66	27	-7	49
R supplementary motor area	187	3.88	12	23	46
R superior frontal gyrus	107	3.84	21	35	37
R superior medial frontal gyrus		3.72	12	38	43
L superior medial frontal gyrus		3.02	-6	23	37
L superior medial frontal gyrus		2.84	0	29	40
R precentral gyrus	53	3.85	42	2	31
R inferior frontal gyrus, opercular part		3.42	45	8	25
L superior frontal gyrus	87	3.84	-27	44	43
L superior frontal gyrus		2.81	-21	26	43
L superior frontal gyrus		2.74	-15	44	37
L precentral gyrus	115	3.67	-33	9.5	41.5
L middle frontal gyrus		2.88	-45	20	40
L precentral gyrus		2.45	-42	-4	43
L inferior orbital gyrus	101	3.35	-42	32	-5
L insula		3.11	-39	20	-5
L inferior orbital gyrus		3.03	-48	35	-14
L inferior frontal gyrus, triangular part		2.96	-30	32	4
run e > a	-	-	-	-	-
parietal cortex					

run a > e					
R calcarine fissure	62	5.07	15	-49	7
R precuneus		4.03	21	-49	1
run e > a	-	-	-	-	-

Table 9: Negative stimuli, move event, Go conditions

Decreases (run a > e) and increases (run e > a) in SRC effects for negative pictures (approach vs. avoid) at the move event in Go conditions in the ROIs (interaction run x Go SRC scores as mask (F-test, p < .05, SVC corrected)). Labeling of brain regions according to Anatomical Automatic Labeling (AAL) atlas, cluster size in number of voxels, MNI coordinates of local maxima.

			MNI coordinates					
brain regions	cluster size	t	MNI	coordii	nates			
	Size		x	у	Z			
cingulum								
run a > e								
L anterior cingulate gyrus	190	3.95	-15	44	10			
R anterior cingulate gyrus		3.9	13.5	39.5	16			
R anterior cingulate gyrus		3.47	18	44	1			
R anterior cingulate gyrus		2.75	3	41	13			
L superior medial frontal gyrus		2.17	-3	54.5	1			
R anterior cingulate gyrus run e > a		2.08	6	35	-2			
frontal cortex	_	_	_	_	_			
run a > e								
R middle orbital gyrus	50	3.57	15	44	-2			
R middle orbital gyrus		2.63	6	41	-14			
L superior medial frontal gyrus	56	2.76	-15	47	13			
L superior medial frontal gyrus		2.41	-3	59	4			
L anterior cingulate gyrus		1.93	-6	47	4			
run e > a								
L superior frontal gyrus	54	3.54	-24	-4	61			
L middle frontal gyrus		2.76	-36	5_	64			
L precentral gyrus		2.43	-33	-7	55			
parietal cortex								
run a > e R paracentral lobule	128	3.26	6	-31	73			
R supplementary motor area	120	2.71	9	-19	73 79			
L paracentral lobule		2.61	-9	-28	70			
L precuneus		2.26	-6	-40	67			
run e > a		2.20		'	0,			
R postcentral gyrus	197	4.65	42	-28	40			
R supramarginal gyrus		4.42	63	-28	49			
R postcentral gyrus		2.91	45	-25	55			
R postcentral gyrus		2.53	54	-16	58			
R postcentral gyrus		2.44	30	-34	40			

L supramarginal gyrus	119	3.06	-60	-28	43
L postcentral gyrus		2.95	-51	-34	50.5
L inferior parietal lobule		2.81	-39	-40	49
L postcentral gyrus		2.27	-42	-25	43

Table 10: Negative stimuli, move event, NoGo conditions

Decreases (run a > e) and increases (run e > a) in reversed SRC effects for negative pictures (avoid vs. approach) at the move event in NoGo conditions in the ROIs (interaction run x NoGo revSRC scores as mask (F-test, p < .05, SVC corrected)). Labeling of brain regions according to Anatomical Automatic Labeling (AAL) atlas, cluster size in number of voxels, MNI coordinates of local maxima.

brain regions	cluster	t	MNI coord		nates
3 - 3	size		X	у	z
frontal cortex					
run a > e					
L supplementary motor area	337	4.44	-12	-10	67
L precentral gyrus		3.74	-21	-19	67
L superior frontal gyrus		3.61	-21	2	64
L supplementary motor area		3.51	-6	-4	73
R supplementary motor area		3.25	6	-7	73
L supplementary motor area		2.99	-3	-13	58
L middle frontal gyrus		2.67	-27	-10	50.5
R precentral gyrus	85	3.89	58.5	-1	46
R inferior frontal gyrus, opercular part		3.18	60	14	31
R precentral gyrus		2.91	45	-10	43
R precentral gyrus	90	3.05	33	-16	64
R precentral gyrus		2.97	33	-10	50.5
R superior frontal gyrus	0.4	2.78	22.5	-7	67
L inferior frontal gyrus, opercular part	61	2.83	-54	11	7
L rolandic operculum		2.77	-57	-1	7
L precentral gyrus		2.63	-54	2	16
run e > a	-	-	-	-	-
parietal cortex					
run a > e	077	4.04	45	0.4	F0
R postcentral gyrus	377	4.61	45	-31	52
R supramarginal gyrus		4.33	60	-40	25
R supramarginal gyrus		3.85	66	-28	34
R supramarginal gyrus		3.11	61.5	-25	46
R postcentral gyrus	EC	2.57	48	-25	64
L supramarginal gyrus	56	3.76	-60	-46 -34	31 52
L postcentral gyrus	108	3.63 2.87	-33 -54	-34 -34	52 49
L inferior parietal lobule		2.07	-54	-34	49
run e > a	-	<u> </u>	<u> </u>	<u> </u>	<u> </u>

STUDY A3: FMRI

#### Table 11: Positive stimuli, cue event

Decreases (run a > e) and increases (run e > a) in SRC effects for positive pictures (avoid vs. approach) at the cue event in the ROIs (interaction run x SRC scores as mask (F-test, p < .05, SVC corrected)). Labeling of brain regions according to Anatomical Automatic Labeling (AAL) atlas, cluster size in number of voxels, MNI coordinates of local maxima.

brain regions	cluster size	t	MNI coordinates			
			x	у	z	
parietal cortex						
run a > e	-	-	-	-	-	
run e > a						
R precuneus	58	2.99	15	-46	7	
R precuneus		2.92	3	-55	11.5	

Table 12: Positive stimuli, move event, Go conditions

Decreases (run a > e) and increases (run e > a) in SRC effects for positive pictures (avoid vs. approach) at the move event in Go conditions in the ROIs (interaction run x Go SRC scores as mask (F-test, p < .05, SVC corrected)). Labeling of brain regions according to Anatomical Automatic Labeling (AAL) atlas, cluster size in number of voxels, MNI coordinates of local maxima.

brain regions	cluster	t	MNI coordinates			
•	size		x	у	z	
frontal cortex						
run a > e						
R supplementary motor area	77	4.11	9	-4	58	
R supplementary motor area		4.02	9	-13	55	
R postcentral gyrus	56	3.61	52.5	-14.5	55	
R precentral gyrus		2.71	39	-22	56.5	
run e > a	-	-	-	-	-	
parietal cortex						
run a > e						
R postcentral gyrus	69	3.67	52.5	-16	55	
R postcentral gyrus		3.05	45	-22	52	
R supramarginal gyrus		2.36	63	-25	49	
L postcentral gyrus	98	3.57	-43.5	-20.5	37	
L rolandic operculum		1.9	-48	-13	22	
run e > a	-	-	-	-		

# 7 Study A4: Learned stimulus response compatibility

The contents of this chapter are published in:

Ernst LH, Plichta MM, Lutz E, Zesewitz AK, Tupak SV, Dresler T, Ehlis A-C, Fallgatter AJ (2013): Prefrontal activation patterns of automatic and regulated approach-avoidance reactions – A functional near-infrared spectroscopy (fNIRS) study. *Cortex*, 49 (1), 131-142.

See 17.1 (organizational remarks) with regard to the formatting of the text (use of abbreviations, headings, etc.) and the rights for publications.

Study A4 was already contained in the above cited publication (see chapter 4). There, study A4 is denominated *study 2*, since the original publication also contains study A1 (referred to as *study 1*).

# 8 Study B1: SRC effects in ERPs

The contents of this chapter are published in:

Ernst, LH, Ehlis, A-C, Dresler, T, Tupak, SV, Weidner, A, Fallgatter, AJ (2013): N1 and N2 ERPs reflect the regulation of automatic approach tendencies to positive stimuli. *Neuroscience Research*, 75(3), 239-249.

See 17.1 (organizational remarks) with regard to the formatting of the text (use of abbreviations, headings, etc.) and the rights for publications.

### 8.1 Abstract

The Approach-Avoidance Task (AAT) measures automatic approach-avoidance tendencies and their regulation: Compatible reactions (approach positive, avoid negative) are faster than incompatible ones (approach negative, avoid positive). The present study assessed event-related potentials (ERPs) in 15 healthy persons for depicting neuropsychological sub-processes of such stimulus-response compatibility (SRC) effects.

Early attention allocation preparing efficient stimulus classification (N1 ERP) and response inhibition on the level of response representations (N2 ERP) were found to underlie the solution of the AAT-conflict. For positive stimuli, these processes were enhanced during the incompatible condition *avoid positive* compared to the compatible condition *approach positive*. Source localization analysis revealed activity in right occipital areas (N1 ERP), and in left DLPFC and insula (N2 ERP) to be neuronal generators of these electrophysiological SRC effects. This neuronal regulation resulted in no influence of incompatibility at the behavioural level. For negative pictures, we found the reversed pattern: There were no electrophysiological SRC effects, but clear behavioural SRC effects in both RTs and error frequency, i.e. participants were faster and made fewer errors during avoiding than approaching negative pictures. These valence-specific differences are in line with previous studies indicating negative stimuli – probably due to higher importance for survival – to more strongly influence behaviour.

# 8.2 Introduction

Approach and avoidance reactions are basic behavioural principles which allow for regulating the organism's needs (Davidson, et al., 1990; Carver, 2006). A large part of these reactions are triggered automatically by stimuli which are highly relevant for the organism (Hofmann, et al., 2009). Quickly grabbing delicious food or running away from a dangerous animal are examples for such reactions which are essential for surviving and achieving hedonic fulfilment in the short term. According to several psychological theories, the automatic quality of these reactions is due to a direct link between emotions evoked by stimulus evaluation and behaviour (Neumann, et al., 2003; Lang & Bradley, 2008). In this context, emotions are defined as action dispositions facilitating appropriate reactions towards emotionally significant stimuli. However, human beings often have to restrain those immediate impulses by means of self-control for achieving goals, which are essential in the long-term. Dual-system models of impulse and self-control assume two semi-independent systems to underlie these processes (Strack & Deutsch, 2004; Hofmann, et al., 2009): While an impulsive system steers automatic reactions, a reflective system is responsible for their inhibition and the initiation of alternative reactions.

Due to the implicit nature of impulsive processes, approach-avoidance tendencies cannot be reported explicitly by the participants, but must be quantified by means of implicit measures (Wiers, et al., 2007; De Houwer, et al., 2009a). The Approach-Avoidance Task (AAT) is especially appropriate because it assesses the behavioural components of impulses by means of simulating approach and avoidance behaviour. In the current study, we used a joystick version of the AAT (cf. Rinck & Becker, 2007). According to the given instruction, participants either have to approach or to avoid pictures presented on a computer screen by moving a joystick. Pulling the joystick towards one's own body produces an increase in picture size (approach), whereas pushing the joystick forward leads to a decrease (avoidance). In the compatible task conditions, the instructed behaviour is in line with implicit reaction tendencies (approaching positive pictures and avoiding negative ones). However, in the incompatible conditions, the automatic tendencies have to be regulated in order to initiate a contrary response (avoiding positive pictures or approaching negative ones). Therefore, individuals show longer reaction times in incompatible than in compatible conditions, socalled stimulus-response compatibility effects (SRC effects; Krieglmeyer & Deutsch, 2010). Such SRC effects have been shown for positive and negative stimuli in healthy subjects (Eder & Rothermund, 2008a). Furthermore, the AAT has also been used successfully to

detect SRC effects for addiction-related stimuli in addicted individuals (Field, et al., 2008; Bradley, et al., 2004; Wiers, et al., 2006) and for phobia-relevant stimuli in phobic persons (Heuer, et al., 2007; Rinck & Becker, 2007; Lange, et al., 2008), in whom approach and avoidance tendencies, respectively, are pathologically enhanced.

With regard to neuronal correlates of such SRC effects, imaging studies in general showed activity in the striatum and amygdala to be associated with automatic approach and avoidance reactions, respectively (Ernst & Fudge, 2009). Furthermore, models of top-down regulation assume the prefrontal cortex (PFC) as a main control instance of the brain, which allows for an adaptive inhibition of this subcortical bottom-up activity (Hariri, et al., 2000; Ernst & Fudge, 2009). In a functional near-infrared spectroscopy (fNIRS) study, we could show neuronal SRC effects in the right dorsolateral prefrontal cortex (DLPFC) in terms of enhanced activity during incompatible compared to compatible conditions (approach vs. avoid negative, avoid vs. approach positive; Ernst, et al., 2013c).

In studies on social emotional behaviour using functional magnetic resonance imaging during an AAT with facial expressions, regulatory activity was observed in left lateral orbitofrontal cortex and ventrolateral PFC (VLPFC; Roelofs, et al., 2009) and in bilateral VLPFC and frontal pole (also in fusiform gyrus, left supramarginal and inferior parietal gyrus; Volman, et al., 2011b). Furthermore, inhibition of left anterior PFC (aPFC) by means of transcranial magnetic stimulation was associated with decreased perfusion in bilateral aPFC and posterior parietal cortex and with increased perfusion in amygdalae and left fusiform face area (continuous arterial spin labelling; Volman, et al., 2011a).

In the current study, we concentrated on the neuropsychological basis of SRC effects by combining the AAT with electroencephalography (EEG). Although EEG is limited in terms of spatial resolution, its temporal resolution in the range of milliseconds is optimally suited to display different subcomponents of regulating approach-avoidance impulses in terms of event-related potentials (ERPs). SRC effects might result from a conflict at the response-selection stage, when the intuitive response competes with the instructed response (see also dual-route models of SRC effects in general, e.g. Kornblum, et al., 1990).

On the one hand, this consideration suggests modulations of the fronto-central N2 ERP as indicator of early response inhibition on the level of response representations prior to response selection, when – as in the AAT – two response tendencies are simultaneously activated (van Boxtel, et al., 2001; Van 't Ent, 2002; Bartholow, et al., 2005; for a review see Folstein & Van Petten, 2008). The N2 ERP is evoked during a multitude of different response conflict inducing paradigms, such as auditory and spatial Simon tasks (e.g. Bockler, et al., 2011; Spape, et al., 2011), GoNoGo tasks (e.g. Falkenstein, et al., 1999), Eriksen Flanker tasks (e.g. Bartholow, et al., 2005), Stop Signal tasks (e.g. van Boxtel, et al., 2001) or Stroop tasks (e.g. West & Alain, 1999). Thereby, higher amplitudes are known to index cognitive control adjustments, which are reflected in subsequent improvement of behavioural performance (Gajewski, et al., 2008; Clayson & Larson, 2011a). With regard to the processing of emotional stimuli, the N2 ERP was interpreted as passage between automatic and controlled phases of the orienting response, i.e., as depicting the final steps of automatic attention allocation (cf. Daffner, et al., 2000).

On the other hand, this specification of the AAT-conflict also indicates attentional mechanisms ensuring a different weighting of relevant and irrelevant task features. Following previous studies, there are three attention-related components of interest. First, incompatible AAT-conditions correspond to uncommon, emotionally relevant situations, which are known to capture automatic attention as reflected in enhanced amplitudes of the P1 ERP (Smith, et al., 2003; Delplanque, et al., 2004; Olofsson, et al., 2008). Second, the N1 ERP is known to reflect early attention allocation facilitating further perceptual processing and classification of stimuli, i.e. to constitute a gating mechanism preparing efficient conflict processing (Vogel & Luck, 2000; Luck, et al., 2000; Griffin, et al., 2002; Naatanen & Michie, 1979). Third, the P3 ERP indicates the allocation of capacity-limited attentional resources toward relevant situations (Nieuwenhuis, et al., 2005; Hajcak, et al., 2009; Linden, 2005). Thereby, it was interpreted to reflect a process mediating between perceptual stimulus analysis and response initiation (Verleger, et al., 2005) updating response representations (Donchin & Coles, 1988).

With regard to direct evidence, until now, there are three studies assessing ERPs during the AAT: In high, but not low trait avoidant participants, van Peer et al. (2007) showed cortisol administration (i.e. stress induction) to elicit behavioural SRC effects for angry faces (faster avoidance than approach reactions) by increasing reaction times in the critical, affect-incongruent condition *approach angry faces*. Comparable to the relation between behaviour

and the N2 ERP as reported above, this worsening of performance was accompanied by an enhancement of N2 and P3 ERP amplitudes in the non-critical, affect-congruent condition avoid angry faces compared to the affect-incongruent condition avoid happy faces. When testing patients with social anxiety disorder, van Peer et al. (2009) found no effects in the P3 ERP. However, in patients with high levels of social anxiety, the amplitudes of a component specific for the processing of facial expressions (P150 ERP) were enhanced after cortisol administration during avoidance compared to approach of both happy and angry faces. In a sample of healthy young adults, we found the P3 ERP to be strongly modulated by individual levels of a personality trait reflecting the willingness for active behavioural regulation (goal-oriented pursuit; Ernst, et al., 2012): For negative pictures, the neuropsychological mechanism of controlled attention allocation mediated the relation between personality and behaviour. Stronger goal-oriented pursuit was associated with higher controlled attention allocation to the incompatible compared to the compatible condition and – thereby – with less automatic avoidance tendencies.

While these studies concentrated on the influence of specific personality traits, in the present study, we aimed to investigate the neuropsychological correlates of regulating automatic approach-avoidance impulses in a more general manner. We tested a sample of healthy young adults with positive and negative pictures from the International Affective Picture System (IAPS; Lang, et al., 2005). These pictures depict different stimuli and situations of general emotional relevance and, therefore, should elicit automatic approach and avoidance tendencies, respectively. Following the above introduced characteristics of the AAT-conflict, we concentrated on response inhibition (N2 ERP) and attention-related processes (P1, N1 and P3 ERP) as possible subcomponents of this regulation process: Besides SRC effects at the behavioural level, we expected electrophysiological SRC effects in the N2 ERP: Higher amplitudes during incompatible compared to compatible conditions should reflect the necessary response inhibition. We further tested for SRC effects in attention-related ERPs: Compared to compatible AAT-conditions, the incompatible AATconditions might evoke enhanced automatic attention allocation (P1 ERP) as well as attention processes preceding efficient stimulus classification (N1 ERP) and linking perceptual stimulus analysis to response initiation (P3 ERP). For the first time, we conducted a source localization analysis to identify the brain areas generating these electrophysiological effects. This knowledge might further contribute to our understanding of approach-avoidance behaviour including the exact functional processes involved (through ERPs) and brain structures underlying behavioural SRC effects.

# 8.3 Materials and methods

## 8.3.1 Participants

Sixteen healthy young adults participated in this study. All participants were currently not taking any psychotropic medication or illicit drugs. Additionally, a screening questionnaire based on the structured clinical interview for DSM-IV disorders (SCID; Wittchen, et al., 1997) was applied to exclude a history of psychiatric, neurological or severe internal disorders. One participant had to be excluded due to technical problems during the measurement. Thus, the data of fifteen subjects (three men; mean age  $24.2 \pm 2.5$  years) were analyzed. After detailed explanation of the study, written informed consent was obtained from all participants. The study was approved by the local Ethics Committee of the University of Wuerzburg and all procedures were in accordance with the Declaration of Helsinki in its version from 2008.

# 8.3.2 Approach-Avoidance Task (AAT)

Having filled in the questionnaires, participants were seated approximately 50 cm away from the computer screen. A standard computer joystick (Logitech Attack 3) was located on a table in front of them. The software "Presentation" (Neurobehavioral Systems, California, USA) was used to present positive and negative IAPS pictures (Lang, et al., 2005; negative pictures: 1040, 1080, 1200, 1201, 1220, 1230, 1301, 1302, 1419, 1930; positive pictures: 1440, 1601, 1602, 1604, 1750, 1931, 8031, 8120, 8465, 8470; cf. Wiers, et al., 2009). The negative and positive pictures differed significantly in valence (t(18) = 5.5, p < .001) but not with regard to arousal (t(18) = 1.8, n.s.). As soon as a picture appeared on the computer screen, participants had to either push or pull the joystick towards or away from themselves as fast as possible with their dominant hand (2 participants were left-handed). Before the experiment, participants practised these movements with other pictures. Participants performed the AAT twice (cf. Field, et al., 2008): During one block, they were instructed to pull positive pictures towards themselves and to push negative pictures away (compatible conditions); for the other block, they had to push positive pictures away and pull negative pictures towards themselves (incompatible conditions). The order of these two blocks was pseudorandomized across subjects. Within each block, 10 different pictures of each category (positive and negative IAPS pictures) were presented three times each in randomized order. Therefore, one block consisted of 60 trials (10 pictures x 2 categories x 3 presentations).

Each trial started with one of the pictures presented in medium size in the centre of the screen (resolution 400 x 300 pixels, size 8 x 10.5 cm). The zooming effect was created by changing the picture size according to the position of the joystick in 6 inclination steps of 4° in each direction (cf. Rinck & Becker, 2007): Pulling the joystick by approximately 7° replaced the picture by the same picture enlarged by the factor 1.2. Further pulling led to a further enlargement of the picture size (by the factor 1.3 of the original picture size at 11°, 1.4 at 15°,1.55 at 19°,1.7 at 23°, 1.85 at 27°). In contrast to that, pushing the joystick led to a reduction of the picture size (by the factor 0.75 of the original picture size at -7°, 0.65 at -11°, 0.55 at -15°, 0.44 at -19°, 0.33 at -23°, 0.17 at -27°). Irrespective of whether the joystick was moved in the correct or wrong direction, the picture disappeared as soon as the angle of the joystick was 30° or -30°. Motions to the left and right side caused no effects. Afterwards, a fixation cross appeared with a remark to let the joystick slide back into the middle (default position). The length of this intertrial interval was jittered randomly between 1500 ms and 3000 ms. An empty screen of 500 ms followed before the next trial. Thus, one block lasted for about 4 minutes.

# 8.3.3 Data recording and analysis

Participants showed low error rates (false reactions and attempts to correct false reactions; see table 13 and results section for analysis). For each participant, more than 20 correct trials per condition were valid. Error trials were excluded from further analyses of the ERP data.

# 8.3.3.1 Statistical analysis and stimulus-response compatibility scores (SRC scores)

Statistical analyses were performed with SPSS for Windows (version 19.0). We conducted repeated-measures analyses of variance (rmANOVAs) with sequence of the two AAT runs (incompatible conditions first vs. compatible conditions first) as between-subject factor and direction of movement (approach vs. avoid) and valence (positive vs. negative pictures) as within-subject factors. Sequence of the two runs was included to rule out familiarity effects with regard to the processing of the pictures. For non-normally distributed variables (Kolmogorov-Smirnov Z test, p < .2), we tested main effects and the 3-way interaction sequence x direction x valence by means of the non-parametric Wald-Type

Statistic (WTS) as provided in the nparLD package for R (version 2.15.1, The R Foundation for Statistical Computing; Noguchi, et al., 2012).

Furthermore, we concentrated on SRC effects as our main hypotheses. SRC scores were determined for each participant for errors, RTs and amplitudes of the ERPs. These scores were calculated by subtracting the value of the compatible condition from that of the incompatible condition, i.e. as *approach negative minus avoid negative* and *avoid positive minus approach positive*. These SRC scores were tested for statistical significance by means of two-tailed one sample t-tests. The magnitudes of SRC scores for negative and positive pictures were compared by means of two-tailed paired samples t-tests. Since, so far, there are not many closely related results, we conducted the current study as a pilot study and – thereby – decided to apply significance level of p < .05. For non-normally distributed variables (Kolmogorov-Smirnov Z test, p < .2), we tested by means of non-parametric Wilcoxon-Z-tests. Effect sizes were calculated as partial Eta squared  $\eta_p^2$  and Cohen's d for the results of the ANOVA and the t-tests/Wilcoxon-Z-tests, respectively.

#### 8.3.3.2 Behavioural data

Reaction times (RTs) were measured from picture onset until the joystick was moved into one of the two end positions. For avoiding systematic distortions of RTs due to the found differences in error frequency between the four conditions (see results section), we applied – as already reported by Barkby et al. (2012) – penalties for errors by recoding RTs on error trials as the mean RTs plus 2 standard deviations of the respective condition for each participant. Next, the so supplemented means of all trials were calculated for each of the four conditions. Additionally, we report the analysis of median RTs without penalties (see 8.4.2.2).

## 8.3.3.3 Electroencephalography

EEG was recorded with a 64-channel DC-amplifier and the software "Vision Recorder" (Brain Products, Munich, Germany). 21 scalp electrodes (Fp1, Fpz, Fp2, F7, F3, Fz, F4, F8, T3, C3, Cz, C4, T4, T5, P3, Pz, P4, T6, O1, Oz, O2) and the mastoids were placed according to the International 10/20-System (Jasper, 1958); all sites were referenced to FCz. Eye movements were registered by means of three electrodes at the epicanthus of each eye and at the infra-orbital position of the right eye. Electrode impedances were kept below  $5 \, k\Omega$ .

Sampling rate was 1000 Hz and bandpass was set to 0.1 – 70 Hz. EEG data were analyzed by "Vision Analyzer" software (Brain Products, Munich, Germany). They were re-referenced to the average reference. After an eye movement artefact correction (Gratton, et al., 1992), data were first segmented into epochs of 900 ms starting 200 ms before the onset of the picture stimulus (cf. e.g. Leutgeb, et al., 2009). An artefact rejection excluded all segments with amplitudes exceeding ± 70 μV or voltage-steps of more than 70 μV per sampling point. Afterwards, a baseline correction was applied using the first 200 ms as reference and epochs were averaged separately for each of the four combinations of picture type and response direction for correct trials. Sufficient numbers of artefact-free segments (> 20) remained for all participants in each combination after the artefact rejection (avoid negative: 27.73 ± 2.89; approach negative: 27.6 ± 2.35; approach positive: 29.07 ± 1.44; avoid positive: 28.27 ± 1.51).<sup>27</sup> Based on the stimulus-locked grand average curves and on the theoretical considerations described above, the P1, N1, N2 and P3 ERPs were quantified at electrode sites selected on the basis of the topographical maps, the amplitude maps and previous studies. We analyzed the P1 ERP within 90 - 130 ms at the positions O1, O2 and Oz (cf. Clark, et al., 1995; Luck, et al., 1990; Doherty, et al., 2005), the N1 ERP within 130 - 180 ms at O1, O2 and Oz (cf. Vogel & Luck, 2000; Doherty, et al., 2005) and within 100 – 160 ms at Fz and Cz (cf. Mulert, et al., 2005), the N2 ERP within 250 - 320 ms at Fz and Cz (cf. Clayson & Larson, 2011a; Folstein & Van Petten, 2008), the P3 ERP within 350 - 410 ms at Cz and Pz (early part of the P3 ERP) and within 450 – 570 ms at Pz (late part of the P3 ERP; cf. van Peer, et al., 2007; Gajewski, et al., 2008). Peaks were individually defined in the respective average data. Values were determined as difference from peak to trough (negative components) and vice versa (positive components).

# 8.3.3.4 sLORETA Source Localization Analyses

Source localization analysis was conducted for the significant effects (see results section: N1 and N2 ERPs) by means of standardized low-resolution brain electromagnetic tomography (sLORETA; Fuchs, et al., 2002; Pascual-Marqui, 2002; Jurcak, et al., 2007). sLORETA computes statistical maps from scalp potentials of EEG data by applying a weighted minimum norm inverse solution. Thereby, locating neuronal sources underlying the scalp potentials is possible with small error. In more detail, sLORETA calculates the standardized current density at 6239 gray matter voxels in the cortex, ACC and hippocampus

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<sup>&</sup>lt;sup>27</sup> Thereby, there were no differences between the four conditions: Non-parametric Wilcoxon-Z-tests revealed neither SRC effects for negative (Z = -.28, p = .78, d = .05), nor for positive pictures (Z = -.38, p = .7 d = .1). Furthermore, SRC scores for negative pictures did not differ from SRC scores for positive pictures (Z = -.03, p = .97, d = .03).

of the Montreal neurological institute (MNI) reference brain. Neuronal sources are estimated under the assumption that neighbouring voxels should have a maximally similar electrical activity. For the present study, this inverse solution was computed separately per condition and subject for ERPs revealing significant effects in their amplitudes (P1 / N1 and N2 ERPs; see results section). Raw data were normalized in a subject-wise manner. For each voxel, the critical task conditions (negative vs. positive pictures / SRC scores for negative and positive pictures (i.e., approach vs. avoid negative and avoid vs. approach positive, respectively); SRC scores for negative vs. positive pictures) were tested using the nonparametric method implemented in the software. Also implemented is a correction for multiple comparisons by performing randomization (5,000 permutations; Pascual-Marqui, 2002). These comparisons of voxel-based sLORETA images were conducted by means of ttests with a 5% level of significance for the mean activity in time windows corresponding to the N1 ERP and N2 ERP. For taking into account individual variability, we chose broad time windows when searching for individual peaks of the ERP amplitudes (see above). For the sLORETA analyses, in which data of the entire time window are taken into account, we restricted the time windows to those ranges in which the entire group showed the highest probability for the respective ERP peak (P1 ERP: 90-109 ms / N1 ERP: 155-180 ms and N2 ERP: 250-275 ms).

#### 8.4 Results

With regard to all behavioural and electrophysiological variables, there were no significant interactions  $sequence \times direction \times valence$  or significant main effects of sequence (all p > .05): The sequence of the two AAT runs did not significantly influence the effects reported below.

With regard to the main effects of *direction* and *valence*, there were significant main effects of *valence* for the median RTs and for the P1 ERP at O2 (see below; all other p > .05).

## **8.4.1 Errors**

Non-parametric Wilcoxon-Z-tests revealed significant SRC effects for negative (Z = 2.4, p = .016, d = .62), but not for positive pictures (Z = .61, p = .54, d = .12): Participants made more errors in the incompatible condition *approach negative* than in the compatible condition *avoid negative*, while incompatibility did not influence error frequency for positive pictures. Furthermore, SRC effects for negative pictures were stronger than for positive pictures (Z = 1.97, p = .048, d = .56; see also table 13).

## 8.4.2 Reaction Times

# 8.4.2.1 Penalty corrected SRC scores

There were significant SRC effects for negative ( $66.6 \pm 116.1 \text{ ms}$ ; t(14) = 2.22, p = .043, d = .57), but not for positive pictures ( $-15.7 \pm 111.3 \text{ ms}$ ; Z = -.45, p = .65, d = .14): RTs were faster for the compatible condition *avoid negative* than for the incompatible condition *approach negative*, while incompatibility did not influence RTs for positive pictures. Comparison of the two picture types revealed SRC effects to be stronger for negative than for positive pictures (Z = -2.22, p = .03, d = .72).

# 8.4.2.2 Median SRC scores (without penalty correction)

There were neither significant SRC effects for negative  $(20.1 \pm 86.0 \text{ ms}; t(14) = .91, p = .38, d = .23)$ , nor for positive pictures  $(-15.5 \pm 91.2 \text{ ms}; t(14) = -.66, p = .52, d = .17)$ . Comparison of the two picture types revealed no difference (t(14) = 1.32, p = .21, d = .34). The rmANOVA revealed a significant main effect of *valence*  $(F(1,14)=6.94, p = .02, \eta_p^2 = .33)$ : Participants reacted faster to negative than positive pictures (see also table 1).

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<sup>&</sup>lt;sup>28</sup> Though, these error rates were low, they significantly differently affected the number of remaining correct reactions per condition. Non-parametric Wilcoxon-Z-tests revealed significant reversed SRC effects for negative pictures (Z = -2.4, p = .02, d = .62): On average, there were more correct reactions for the compatible condition *avoid negative* than the incompatible condition *approach negative*. For positive pictures, SRC effects were also reversed, but not significant (Z = -.61, p = .54, p = .12). Furthermore, the reversed SRC scores for the negative pictures were significantly stronger than for the positive pictures (Z = -1.97, p = .048, d = .56).

Table 13: Error frequency and average reaction times in ms (mean, standard deviation)

		error frequency		reaction times	
		avoid	approach	avoid	approach
IAPS pictures	positive	.67 (.9)	.53 (.64)	835.5 (122.6)	851.1 (79.4)
	negative	.4 (.63)	1.6 (1.96)	795.4 (116.8)	815.5 (112.2)

#### 8.4.3 ERP data

At the following electrode positions, analyses revealed significant results (cf. also figure 20). With regard to the P3 ERP, there were no significant results.

#### 8.4.3.1 P1 ERP

Electrode position O2: The rmANOVA revealed a significant main effect of valence  $(WTS(1) = 12.45, p < .001^{29})$ : Negative pictures caused higher amplitudes than positive ones.

# 8.4.3.2 N1 ERP

Electrode position O2: While there were no SRC effects for negative pictures (Z = -1.08, p = .28, d = .29), SRC scores for positive pictures differed significantly from zero (Z = -2.61, p = .009, d = .93), i.e. amplitudes were higher for the incompatible condition *avoid positive* than for the compatible condition *approach positive*. There were no significant differences between SRC scores when comparing both picture types (Z = -1.65, p = .1, d = .5; see also figure 20D and 18B).

Electrode position Oz: While there were no SRC effects for negative pictures (Z = -.8, p = .43, d = .21), SRC scores for positive pictures differed significantly from zero (Z = -2.39, p = .017, d = .74), i.e. amplitudes were higher for the incompatible condition *avoid positive* than for the compatible condition *approach positive*. Thereby, SRC scores for positive

<sup>&</sup>lt;sup>29</sup> The parametric ANOVA revealed the following effect size: F(1,13)=9.99, p=.008,  $\eta_0^2=.44$ .

pictures were significantly stronger than for negative pictures (Z = -2.16, p = .031, d = .84; see also figure 18).

#### 8.4.3.3 N2 ERP

Electrode position Cz: SRC effects for positive pictures were significant (t(14) = -2.37, p = .033, d = .61): Amplitudes were higher for the incompatible condition *avoid positive* than for the compatible condition *approach positive*. There were no SRC effects for negative pictures (t(14) = .40, p = .69, d = .1). Comparison of the two picture types revealed SRC effects to not differ significantly between positive and negative pictures (t(14) = 1.89, p = .079; d = .49; see also figure 19).

# 8.4.4 sLORETA analyses

#### 8.4.4.1 P1 ERP

sLORETA analysis showed no significant neuronal activity corresponding to the main effect of *valence* ( $t_{crit} = 2.56$ ).

# 8.4.4.2 N1 ERP

sLORETA analysis showed SRC effects for positive pictures to be accompanied by significant activity in the cuneus and lingual gyrus in the right occipital lobe (BA19, BA18;  $t_{\text{crit}}$  = 4.07; see also figure 18D). In line with the scalp ERP data, no significant activation occurred for SRC scores to negative pictures or for the comparison of SRC scores for positive and negative pictures.

#### 8.4.4.3 N2 ERP

Significant neuronal activity corresponding to the SRC effect for positive pictures in the N2 ERP was localized in the insula (BA13;  $t_{crit} = 3.97$ ), in the middle frontal gyrus (BA46, BA9, corresponding to the DLPFC) and in the adjacent inferior frontal gyrus (BA45; see also figure 19D). There was no significant activity for scalp SRC-scores for negative pictures. The

sLORETA comparison of positive and negative pictures revealed – by trend – significant differences in neuronal activity in the middle frontal gyrus (BA46;  $t_{crit}$  = 3.53). These effects were all left lateralized.

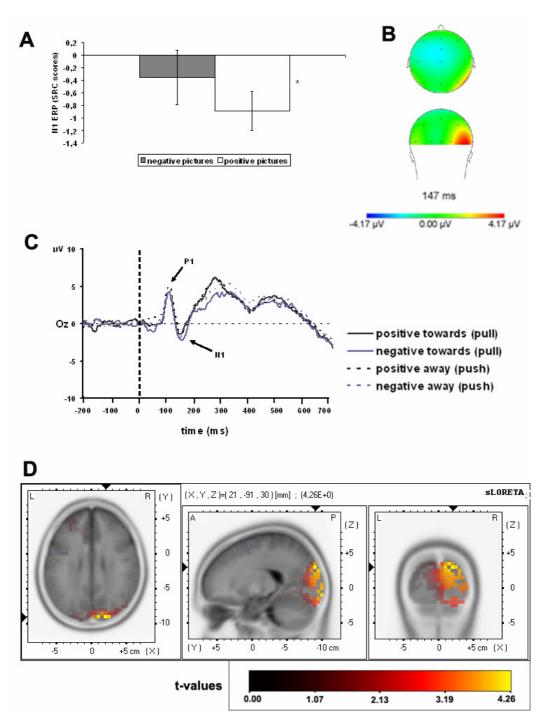


Figure 18: SRC effects in the N1 ERP

A: SRC scores (approach minus avoid negative, avoid minus approach positive) for the amplitudes of the N1 ERP (means, SEM).

B: Topographical map of the N1 ERP

C: Grand average curves of the N1 ERP at Oz during approaching positive (black line) and negative (gray line) IAPS pictures, avoiding positive (black dashed line) and negative (gray dashed line) IAPS pictures.

D: Results of source localization analysis (sLORETA) for SRC scores for positive pictures (avoid minus approach positive).

<sup>\*</sup> p < .05

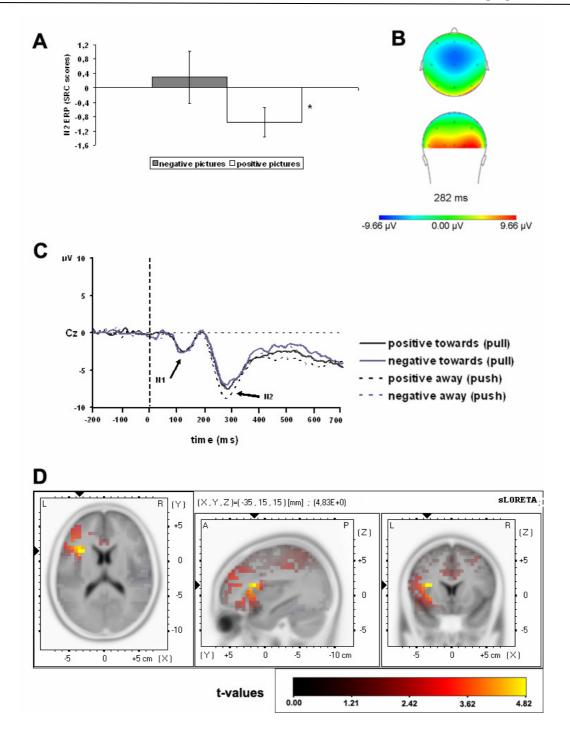


Figure 19: SRC effects in the N2 ERP

A: SRC scores (approach minus avoid negative, avoid minus approach positive) for the amplitudes of the N2 ERP (means, SEM).

- B: Topographical map of the N2 ERP
- C: Grand average curves of the N2 ERP at Cz during approaching positive (black line) and negative (gray line) IAPS pictures, avoiding positive (black dashed line) and negative (gray dashed line) IAPS pictures.
- D: Results of source localization analysis (sLORETA) for SRC scores for positive pictures (avoid minus approach positive).

<sup>\*</sup> p < .05

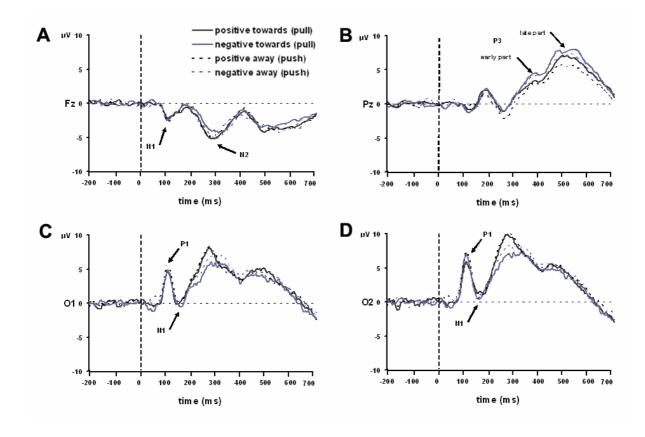


Figure 20: Grand average curves at the positions Fz (A), Pz (B), O1 (C) and O2 (D)
Approaching positive (black line) and negative (gray line) IAPS pictures, avoiding positive (black dashed line) and negative (gray dashed line) IAPS pictures

# 8.5 Discussion

The current study aimed at investigating the neuropsychological correlates of regulating automatic approach-avoidance impulses. Thereby, we concentrated on response inhibition (N2 ERP) and attention-related processes (P1, N1 and P3 ERP) as possible subcomponents of this regulation process. For positive pictures, the expected electrophysiological SRC effects emerged in the N1 and N2 ERP in terms of higher amplitudes during the incompatible condition *avoid positive* compared to the compatible condition *approach positive*. These electrophysiological SRC effects indicate efficient regulation of the AAT-conflict in response to positive pictures, which seems to have prevented any influence of incompatibility on behaviour since there were no behavioural SRC effects.

In more detail, in line with our hypothesis, the AAT-conflict in incompatible conditions was accompanied by enhanced early attention allocation as indicated by the occipital N1 ERP (cf. Griffin, et al., 2002; Doherty, et al., 2005). This is in line with previous studies showing high-conflict conditions to evoke higher amplitudes of the N1 ERP (e.g. Kirmizi-Alsan, et al., 2006). This component was found to reflect a discrimination process facilitating further perceptual processing of stimuli (Jepma, et al., 2009). In several conflict-related studies, such a prefered processing – which is supposed to be a gating mechanism preparing efficient stimulus classification and conflict processing (Vogel & Luck, 2000; Luck, et al., 2000; Naatanen & Michie, 1979) – was shown to precede the N2 ERP (e.g. Van 't Ent, 2002; Melara, et al., 2008; Doucet & Stelmack, 2000; West & Alain, 1999).

Also in line with our hypothesis, for positive pictures, response inhibition as indicated by the fronto-central N2 ERP was clearly more pronounced during incompatible than during compatible conditions. This is in accordance with previous findings on conflict processing in general (Forster, et al., 2011; Clayson & Larson, 2011a; Gajewski, et al., 2008; Yeung & Cohen, 2006) revealing enhanced N2 amplitudes to be associated with better behavioural regulation and vice versa. Furthermore, this modulation of the N2 ERP implies successful solution of the AAT-conflict for positive pictures, i.e. inhibition of the intuitive response for performing the simultaneously activated instructed response, to involve processes on the level of response representations prior to response selection (cf. Bartholow, et al., 2005; Bockler, et al., 2011; Folstein & Van Petten, 2008).

The reversed pattern was found for negative pictures: While there were no electrophysiological SRC effects, results showed clear behavioural SRC effects in RTs and error frequency, i.e. participants were faster and made fewer errors during avoiding compared to approaching negative pictures (for a discussion of the RTs finding see also below the limitation section). Such valence-specific differences revealing behavioural SRC effects for the negative but not significantly for the positive pictures are in line with a previous AAT-study (Ernst, et al., 2012). These findings might be understood in the light of evolutionary based considerations (Flykt, 2006; Ohman, et al., 2001), which assume negative stimuli to be of generally higher importance for survival. For positive pictures, the incompatible AAT-condition is merely unpleasant, while, for negative pictures, it might represent a dangerous situation resulting in more pronounced behavioural effects (cf. Ekman, 1992; Ohman, et al., 2001). In the current study, especially the heightened error frequency during *approach negative*, i.e. the heightened number of conducting the

compatible response avoid negative instead of approach negative, supports this interpretation. Furthermore, at the position O2, we found generally enhanced P1 ERP amplitudes, i.e. enhanced automatic attention allocation, for negative compared to positive pictures. Also, when not applying penalties for errors, RTs were faster for negative than positive stimuli.

At first glance, our finding of no SRC effect in the N2 ERP for the negative stimuli is not in accordance with such an assumption: The AAT-conflict should be especially pronounced for the negative stimuli. However, it is known from previous studies on the processing of emotional stimuli, in which the N2 ERP was described as depicting the final steps of automatic attention allocation (Carretie, et al., 2004), that unpleasant stimuli lead to reduced N2 amplitudes. Thus, it can not be excluded that the negative valence might have cancelled out SRC effects in the N2 ERP for the negative pictures. Moreover, van Peer et al. (2007) did neither find SRC effects for happy nor angry faces in the N2 ERP. They suggest this to be due to the nature of the AAT-conflict: The intuitive response competes with the instructed response, while in paradigms eliciting clear N2 effects – as e.g. Eriksen Flanker tasks (e.g. Bartholow, et al., 2005), Stop Signal tasks (e.g. van Boxtel, et al., 2001) or Stroop tasks (e.g. West & Alain, 1999) – the conflict results from two response tendencies elicited simultaneously by the stimulus. Therefore, at least in some situations, the AAT-conflict might be represented at another level than the conflicts in the paradigms mentioned above.

This might also explain the finding of no SRC effects in the N1 ERP for negative pictures. As reported in our prior study (Ernst, et al., 2012), the processing of negative pictures was more efficient, the higher individuals' levels of *goal-oriented pursuit* were, a personality trait reflecting the willingness for active behavioural regulation. This indicates the efficient processing of the AAT-conflict for negative pictures to strongly depend on active, conscious regulation, while it might not be closely related to early perceptual processes.

With regard to the P1 and P3 ERP, there were no significant SRC effects. In the AAT-study of van Peer et al. (2007), the above described modulations of the P3 ERP were found in persons with extreme expressions of anxiety-related personality characteristics after stress induction via cortisol administration. This discrepancy in findings might be due to specifically pronounced alterations in attention processes as known with regard to anxiety-related phenomena (cf. Beck & Clark, 1997; Bar-Haim, 2011) as well as the pharmacological

manipulation that was not included in the present study design. Moreover, when looking at the entire group, in our prior study, there were also no significant SRC effects in the P1 and P3 ERPs (Ernst, et al., 2012). Instead, we found the mediator model as reported above, whereby the P3 ERP clearly depended on individual levels of the personality trait *goal-oriented pursuit*. The attentional sub-processes reflected by the P1 and P3 ERPs might be more informative in anxiety-related contexts and with regard to the investigation of interindividual differences.

With regard to neuronal generators of the electrophysiological SRC effects, source localization analysis revealed activity in the cuneus and lingual gyrus of the right occipital lobe to underlie the SRC effect in the N1 ERP and activity in left insula and DLPFC to accompany the N2 ERP SRC effect. This localization of the N1 ERP effect is in line with previous studies showing the involvement of occipito-parietal and -temporal areas (e.g. Clark, et al., 1995). The contribution of DLPFC activity to the N2 SRC effect fits our previous findings with fNIRS (Ernst, et al., 2013c), where the DLPFC – a frontal lobe area crucially involved in initiating alternative behavioural responses – was also more strongly activated in incompatible AAT-conditions. However, while the fNIRS SRC effect emerged in the right hemisphere, the neuronal generators of the N2 SRC effects were in the left hemisphere. Future fMRI studies are necessary to clarify, if this difference is due to the different methods and samples or if there are possible lateralization effects.

Moreover, while previous studies (cf. van Veen & Carter, 2002; Folstein & Van Petten, 2008) showed N2 ERP effects to originate from the anterior cingulate cortex as an important neuronal instance for conflict monitoring, the present data showed effects in the left insula. The insular cortex is known to be involved in conscious emotional experiences (e.g. Craig, 2009), but is also part of a general salience system responsible for monitoring the environment and selecting appropriate responses (Taylor, et al., 2009; Huster, et al., 2011). The finding of insular activity might be due to the affective characteristic of the AAT-conflict when inhibiting the intuitive response evoked by the stimulus valence.

While the current study revealed important information on neuropsychological processes underlying the AAT-conflict, our results are limited due the small sample size. Specifically with regard to the behavioural results, in the current study, SRC effects for negative pictures were significant, while our fNIRS sample reacting to the same picture set did not show

significant SRC effects (Ernst, et al., 2013c). SRC effects might represent a general phenomenon, however, they are also significantly affected by interindividual variability due to personality traits (cf. Ernst, et al., 2012). Interindividual differences might counterbalance each other in a large sample, while, in smaller samples such as the current one or the fNIRS-sample, the distribution of personality expressions might not be broad enough to cancel out such individual impact on group level. As a result, SRC effects as general behavioural patterns might not be clearly observable at group level. Future studies in larger samples are required to show the general validity of our results.

Similarly, while we did not find significant influences of the sequence of the two runs, experimental designs allowing for the analysis of trial-by-trial variability are necessary for finally determining the impact of familiarity effects due to repetition of the stimuli. Thereby, it might be helpful to follow the design of Volman et al. (2011b) and to also use neutral pictures for subtracting effects to such stimuli from reactions to emotional stimuli, i.e., to separate emotional from directional effects.

Moreover, while the "directions" of SRC effects were the same for the analysis of penalty corrected and not corrected RTs (negative: approach > avoid; positive: reversed: approach vs. avoid), the SRC effect for negative pictures was only significant, when penalties were applied. So far, this analysis method was only reported once (Barkby, et al., 2012). We used it for avoiding systematic distortions of RTs due to the found differences in error frequency, namely the above reported SRC effects for negative pictures and the significant difference in SRC effects between negative and positive pictures. Although error rates were low, the corresponding differences between conditions with regard to the number of remaining correct reactions were also found to be significant. Technical studies are necessary to test the adequacy of such a correction, since for other conflict paradigms such as e.g. flanker or GoNoGo tasks, in which generally higher error rates for the incompatible conditions are a common finding, the usage of penalties is not established. However, in our case, the found enhancement of error frequency was valence specific and the AAT has no comparable research tradition. Methods for the RT analysis are still in a developmental process; recently, also, an attempt to reduce distorting influences of excessive intra-individual variability in clinical samples has been adopted from technical studies on another implicit task, the implicit association task (IAT; Wiers, et al., 2011; Ernst, et al., 2013c; cf. Greenwald, et al., 2003).

Additionally, future studies should also clarify the level, which the AAT-conflict is represented at, and differences in the processing of positive and negative stimuli. Thereby, specifically studies with functional magnetic resonance imaging (fMRI) depicting the entire brain might allow to disentangle the contributions of different brain structures when reacting to positive and negative stimuli. Following the above introduced assumption that negative stimuli are more relevant for behaviour, solving the AAT-conflict with negative stimuli might, for example, depend less on prefrontal control. Our finding, that the N2 ERP was not enhanced in the incompatible condition approach negative and that the related source localization analysis did not reveal prefrontal contributions to this aspect of the reactions to negative stimuli might be seen as a first hint to such different, valence specific representation levels of the AAT-conflict. While our fNIRS study (Ernst, et al., 2013c) found the involvement of the DLPFC as structure essential for the initiation of performance adjustments (cf. Ridderinkhof, et al., 2004), the N2 ERP is interpreted to mainly reflect the cognitive aspects of conflict processing (cf. Enriquez-Geppert, et al., 2012). However, as mentioned above, the N2 ERP is also known to be reduced by negative valence (Carretie, et al., 2004). Therefore, future studies investigating possible valence specific differences in representation levels should clearly exclude such alternative explanations simply due to technical or conceptual restrictions.

Summing up, we found early attention allocation in terms of a gating mechanism preparing efficient stimulus classification and conflict processing (N1 ERP) and response inhibition on the level of response representations prior to response selection (N2 ERP) to constitute neuropsychological sub-processes underlying the AAT-conflict, i.e. the inhibition of automatic behavioural impulses and the initiation of an alternative response. For positive stimuli, these processes were enhanced during the incompatible condition *avoid positive* compared to the compatible condition *approach positive*. Source localization analysis revealed activity in right occipital areas (N1 ERP), and in left DLPFC and insula (N2 ERP) to be neuronal generators of these electrophysiological SRC effects. This neuronal regulation resulted in no influence of incompatibility at the behavioural level. For negative pictures, we found the reversed pattern: There were no electrophysiological SRC effects, but clear behavioural SRC effects in both RTs and error frequency, probably due to higher importance of negative stimuli for behaviour.

Future studies broadening these first findings might contribute to a better understanding of the regulation of approach-avoidance impulses by revealing information on the link

between stimulus evaluation and approach-avoidance reactions as general behavioural principles. Furthermore, as already initiated by van Peer et al. (2007; 2009), the combination of the AAT with the assessment of ERPs might be useful for investigating which neuropsychological sub-processes are specifically altered in addiction and anxiety disorders, where pathological approach-avoidance reactions have been found (cf. Ernst, et al., in press). Thereby, accompanying methodological studies should clarify the possibilities and restrictions of this experimental combination.

# 9 Study B2: Controlled attention allocation as neuropsychological mediator

The contents of this chapter are published in:

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See 17.1 (organizational remarks) with regard to the formatting of the text (use of abbreviations, headings, etc.) and the rights for publications.

#### 9.1 Abstract

Approach and avoidance are two basic behavioural principles. The current study investigated neuropsychological mechanisms underlying the influence of the personality characteristic *goal-oriented pursuit* on the efficiency of regulating such approach-avoidance reactions.

Therefore, the P3 event-related potential (ERP) reflecting controlled attention allocation was assessed during the Approach-Avoidance Task (AAT) with positive and negative pictures in 36 healthy participants.

For negative pictures, analyses revealed the neuropsychological mechanism of controlled attention allocation to mediate the relation between personality and behaviour: Stronger goal-oriented pursuit was associated with higher controlled attention allocation to the incompatible compared to the compatible condition and – thereby – with less automatic avoidance tendencies in response to negative pictures, i.e., with higher efficiency of regulation.

Results are discussed in terms of their implications for future studies on mechanisms determining the influence of personality traits, situational factors and their interaction on approach-avoidance behaviour.

## 9.2 Introduction

Approach and avoidance are two basic principles of behavioural tendencies caused by positive and negative stimuli, respectively (cf. Carver, 2006). Automatically triggered, unconscious reactions constitute the basis of current survival. In contrast, consciously controlled reactions guarantee flexibility in our daily lives. The current study aimed at investigating the underlying neuropsychological mechanisms of interindividual differences in the efficiency of these regulation processes.

Thereby, we refer to models offered by cognitive-emotional psychology and neurosciences. In cognitive-emotional psychology, dual-process models of impulse and self-control describe two semi-independent systems: an impulsive system producing automatic reactions and a reflective system responsible for controlled reactions (e.g. Strack & Deutsch, 2004). Neuroscientific models associate mainly the striatum and amygdala with automatic approach reactions towards positive stimuli and avoidance reactions towards negative stimuli, respectively (Ernst & Fudge, 2009; Tomer, et al., 2008; O'Doherty, et al., 2004; Cunningham, et al., 2010; Schlund & Cataldo, 2010). The prefrontal cortex (PFC) as a main neuronal control instance is assumed to steer controlled reactions (Ernst & Fudge, 2009; Miller & Cohen, 2001; Dosenbach, et al., 2008); in particular, the dorsolateral PFC (DLPFC) initiates performance adjustments (Ridderinkhof, et al., 2004).

A frequently used implicit task for assessing both automatic and regulated approach-avoidance behaviour is the Approach-Avoidance Task (AAT; De Houwer, et al., 2001). We used the joystick version (cf. Rinck & Becker, 2007): Pulling a joystick towards the own body increases the size of a picture presented on a computer screen, thereby simulating approach. In parallel, pushing a joystick forward decreases the picture size, i.e., simulates avoidance. In compatible conditions, the instructed behaviour matches implicit reaction tendencies (approaching positive pictures or avoiding negative ones), while incompatible conditions require the inhibition of such tendencies for performing an alternative reaction (avoiding positive pictures or approaching negative ones). Longer reaction times in incompatible compared to compatible situations are known as stimulus response compatibility effect (SRC effect; Krieglmeyer & Deutsch, 2010; Eder & Rothermund, 2008b; Krieglmeyer, et al., 2010).

Following the two models described above, such SRC effects result because incompatible reactions require the regulation of approach-avoidance impulses in terms of the reflective system controlling the impulsive system or, with regard to the neuroscientific explanation, in terms of prefrontal cortical top-down regulation inhibiting subcortical bottom-up activity (Ernst & Fudge, 2009; Bechara, 2005; Ernst, et al., 2006). So far, we could show neuronal SRC effects in the right dorsolateral prefrontal cortex (DLPFC): Activity as assessed with functional near-infrared spectroscopy (fNIRS) was enhanced during incompatible compared to compatible conditions (approach vs. avoid negative, avoid vs. approach positive; Ernst, et al., 2013c).

In the present study, we aimed at investigating interindividual differences in the efficiency of these regulation processes and their related neuropsychological mechanisms. Previous studies revealed that personality characteristics related to cognitive control significantly influence these processes: Automatic attitudes towards erotic, food and alcohol stimuli exerted a stronger influence on behaviour when levels of working memory (WM) capacity and trait self-control, respectively, were low (Hofmann, et al., 2008; Friese, et al., 2008). In the present study, a control-related personality trait specifically determining approachavoidance reactions was in our focus of interest: Goal-oriented pursuit significantly influences the efficiency of active behavioural regulation as required in incompatible AAT-conditions (Carver & White, 1994; Berkman, et al., 2009). This personality trait is part of Gray's Reinforcement Sensitivity Theory (RST). Gray (1981, 1982, 1994, 1990a; cf. Fowles, 1980; for the revised RST (rRST) see Gray & McNaughton, 2000) describes two motivational systems, whose reactivity determines behaviour and experience of emotions: An approach system described as the Behavioural Activation System (BAS) and an avoidance system consisting of the Behavioural Inhibition System (BIS) and the Fight/Flight/Freeze System (FFFS). The BAS facilitates approach behaviour to positive reaction outcomes and is responsible for goal-directed efforts and active approach of security with the aim of preserving an organism's homeostasis. Thereby, the BAS is involved in the experience of positive emotions such as hope (pre goal attainment affect) and happiness (post goal attainment affect).

According to Carver and White (Carver & White, 1994), the BAS consists of three sub-dimensions: (a) responsiveness to reward (BAS-reward-responsiveness), (b) the tendency to seek out potentially rewarding situations (BAS-funseeking) and (c) strong goal-oriented pursuit (BAS-drive). The first two dimensions assess sensitivity for enjoyment and should not

be closely related to AAT-reactions, since the AAT is not a classical reward task with explicit gains and losses. The latter dimension, however, is of interest for the current study: It reflects goal-oriented pursuit in terms of motivated cognitive performance and control of subcortical responses to emotional stimuli by the prefrontal cortex (Carver & White, 1994; cf. Passamonti, et al., 2008b; Putman, et al., 2010). In other words, this trait depicts the willingness for active behavioural regulation in order to achieve a desired, positive outcome. Such regulation is necessary in incompatible AAT-conditions, when participants have to inhibit an automatic reaction and instead execute an alternative, incompatible reaction. Thereby, such a correct response ends the incompatible, unpleasant situation and turns it into a positive outcome, i.e., the solution of the AAT-conflict equals a situation of negative reinforcement.

BAS-drive is assumed to be positively associated with improved behavioural responses leading to a desired outcome, i.e., with better behavioural regulation (Carver & White, 1994; cf. Scheres & Sanfey, 2006). This also held true, when participants reacted to a stimulus which was hedonically aversive (Berkman, et al., 2009). Such a reaction equals the ending of the incompatible AAT-condition with negative stimuli. Therefore, we expected higher BAS-drive scores to be accompanied by less behavioural SRC effects, i.e., better behavioural regulation, in response to both positive and negative stimuli.

Moreover, we were interested in the neuropsychological mechanisms underlying such interindividual differences. Thereby, we concentrated on the parietal P3 ERP<sup>30</sup>, which indicates the allocation of capacity-limited attentional resources towards relevant situations (Nieuwenhuis, et al., 2005; Hajcak, et al., 2010; Linden, 2005). It has been interpreted to reflect a process mediating between perceptual stimulus analysis and response initiation (Verleger, et al., 2005), updating response representations and short-term memory after uncertainty induced by conflict (Donchin & Coles, 1988). With regard to paradigms including cognitive conflicts, the amplitude of the P3 ERP was also associated with response inhibition processes (e.g. Clayson & Larson, 2011a; Randall & Smith, 2011; Fruhholz, et al., 2011).

The neuronal basis of the P3 ERP was described as phasic activity of the neuromodulatory locus coeruleus-norepinephrine (LC-NE) system to the outcome of internal

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<sup>&</sup>lt;sup>30</sup> In the current study, we are not interested in the so-called novelty P3, a variant of the P3, which emerges as orienting response to distracter stimuli earlier at fronto-central sites in classical oddball paradigms (Polich & Criado, 2006).

decision-making processes and the resulting effects of noradrenergic potentiation of information processing (Nieuwenhuis, et al., 2005). Thereby, its functional role was subsumed as processes initiating cognitive regulation as necessary for conflict resolution. In the current paper, when referring to the functional role of the P3 ERP, we use the expression "controlled attention allocation" for taking into account both the recruitment of capacity-limited attention repeatedly associated with the P3 ERP and the initial steps of conscious cognitive regulation.

Previous studies showed enhanced P3 ERP amplitudes in different conflict situations (e.g. Fruhholz, et al., 2011; Clayson & Larson, 2011a; Moser, et al., 2008; Hillman, et al., 2009a; Hillman, et al., 2009b; Randall & Smith, 2011). Thereby, higher P3 ERP amplitudes were associated with better behavioural performance (e.g. Clayson & Larson, 2011b). With regard to the AAT, we expect the regulation process in incompatible conditions to require enhanced allocation of controlled attentional resources for inhibiting the automatic response and initiating the correct, incompatible response. Therefore, we expected SRC effects in the P3 ERP in terms of enhanced amplitudes during correct incompatible compared to compatible approach-avoidance reactions. Furthermore, we expected stronger P3 SRC effects to be accompanied by less pronounced SRC effects at the behavioural level.

Finally, we connected the three components of personality, neuropsychological mechanism and behaviour in terms of a mediator model: We tested whether the influence of interindividual differences in goal-oriented pursuit on behaviour is mediated by controlled attention allocation, i.e., whether the amount of controlled attention allocation is a mechanism underlying the impact of this personality trait on behaviour.

With regard to the specificity of our mediator model, we took into account two other factors. First, we also analyzed a second ERP: Besides requiring controlled attention allocation, incompatible AAT-conditions equate to uncommon, emotionally relevant situations, which are known to capture automatic attention as indicated by the P1 ERP (Olofsson & Polich, 2007; Smith, et al., 2003). Therefore, the P1 ERP might be heightened for incompatible compared to compatible reactions, i.e., reveal SRC effects. We also tested our mediator model with the amplitudes of the P1 ERP. However, since automatic attention allocation is not a process directly related to the successful solution of the AAT-conflict, we

expected the suggested mediator model to only hold true for the relations between BAS-drive scores, the P3 ERP and behaviour.

Second, we also tested for influences of the second system described by Gray (1982, 1994; for the rRST see Gray & McNaughton, 2000), the avoidance system. The FFFS reflects sensitivity to punishment and is therefore not of interest for the current study. Also, it is not explicitly assessed via Carver and White's questionnaire. The other part of the avoidance system, however, the BIS, might be related to the AAT. It is described as a conflict detection system, responsible for passively approaching security by inhibiting ongoing behaviour, i.e., it contributes to the solution of conflicts by facilitating defensive behaviour. With regard to the AAT, one previous study has revealed high expressions of the BIS, i.e., high trait avoidance scores to worsen behavioural performance under specific circumstances: In high, but not low trait avoidant participants, van Peer et al. (2007) showed cortisol administration (i.e., stress induction) to elicit behavioural SRC effects for angry faces (faster avoidance than approach reactions) by increasing reaction times in the critical, affectincongruent condition approach angry faces. This worsening of performance was accompanied by an enhancement of P3 ERP amplitudes in the non-critical, affect-congruent condition avoid angry faces compared to the affect-incongruent condition avoid happy faces, while amplitudes did not increase in the critical condition approach angry faces. This result supports our assumption that an increase of P3 ERP amplitudes, i.e., of controlled attention allocation, is related to successful, efficient processing of incompatible AAT-conditions. Although, the results of van Peer et al. (van Peer, et al., 2007) might only be valid for the specific circumstance of high-trait avoidant participants after stress-induction, we tested if higher BIS scores fit into a mediator model showing reduced P3 SRC effects to underlie stronger behavioural SRC effects.

To sum up, the current study investigated the neuropsychological mechanisms underlying the influence of a control-related personality characteristic on the regulation of approach-avoidance behaviour in a situation of general validity for the first time: Healthy persons reacted to positive and negative pictures from the International Affective Picture System (IAPS) as stimuli of general emotional relevance in a common laboratory setting, i.e., in a stress-free situation.

Thereby, we extent the studies described above, which concentrated on the investigation of potential moderators (i.e., on variables which define categorical subgroups with different qualities; van Peer, et al., 2007; Hofmann, et al., 2008; Friese, et al., 2008). We tested a mediator model with the neuropsychological mechanism of controlled attention allocation as a mechanism potentially mediating the influence of personality on behaviour. More precisely, we expected stronger goal-oriented pursuit (as indicated by higher BAS-drive scores) to be associated with better behavioural regulation (as indicated by less pronounced behavioural SRC effects), with higher controlled attention allocation (as indicated by more pronounced P3 ERP SRC effects) as a mediating factor of this relation.

#### 9.3 Material and methods

# 9.3.1 Participants

Participants were 40 healthy young adults (18 males; mean age = 24.44, SD = 1.86, age range: 21-28 years) currently not taking any psychotropic medication or illicit drugs. For excluding psychiatric, neurological or severe internistic disorders, participants filled in a screening questionnaire based on the structured clinical interview for DSM-IV (SCID; Wittchen, et al., 1997). Due to technical problems, four participants had to be excluded. Thus, the data of 36 subjects were analyzed. Three participants (2 males) were left-handed (Edinburgh Handedness Inventory; Oldfield, 1971). The study was approved by the local Ethics Committee of the University of Wuerzburg and all procedures were in accordance with the Declaration of Helsinki (version from 2008).

#### 9.3.2 Materials

# 9.3.2.1 Self-report measures

The Positive Affect Negative Affect Schedule (PANAS; Krohne, et al., 1996) was used to assess current mood status. For measuring reactivity of the BIS and BAS, we used the German version of Carver and White's (Carver & White, 1994) BIS/BAS scales (Strobel, et al., 2001) with the scales BIS, BAS-drive, BAS-funseeking and BAS-reward-responsiveness.

# 9.3.2.2 Approach-Avoidance Task (AAT)

As in previous studies, we used a joystick version of the AAT. The technical details of this arrangement can be found in Ernst et al. (2013c). Here, we only report the most crucial details and the few differences.

Numbers of the used IAPS pictures were 1052, 1200, 1205, 1280, 1525, 1930, 6244, 6250.1, 6370, 6510 (negative pictures) and 4626, 4660, 4689, 7330, 7450, 8080, 8200, 8370, 8490, 8501 (positive pictures; Lang, et al., 2005). The two categories differed significantly in valence (t(18) = 5.5, p < .001), but not in arousal (t(18) = 1.8, n.s.). Participants performed two blocks of the AAT (cf. Field, et al., 2008): During one block, they were instructed to pull positive pictures towards themselves and to push negative pictures away (compatible conditions); during the other block, they had to push positive pictures away and to pull negative pictures towards themselves (incompatible conditions). The order of these two blocks was pseudorandomized across subjects. Within each block, 10 different pictures of each valence category were presented three times in randomized order. Therefore, one block consisted of 60 trials (10 pictures x 2 categories x 3 presentations).

The zooming effect was created by changing the picture size according to the position of the joystick in 6 inclination steps of 4° in each direction (cf. Rinck & Becker, 2007): Pulling the joystick replaced the picture by the same picture enlarged, while pushing the joystick led to a reduction of the picture size. The length of the intertrial interval was jittered randomly between 2000 ms and 3500 ms. Therefore, one block lasted for about 4 minutes.

#### 9.3.2.3 Procedure

After detailed explanation of the study, written informed consent was obtained from all participants. Furthermore, they practised the pull- and push-movements with example stimuli not used in the following experiment. During arrangement of the EEG electrodes, participants filled in questionnaires. After the AAT, participants' general speed of processing was tested with a trail-making test, in which numbers from 1 to 90 positioned randomly on a sheet of paper have to be sequentially connected by drawing lines (Zahlen-Verbindungs-Test (ZVT); Oswald & Roth, 1987).

# 9.3.2.4 Data recording and analysis

Error rates did not differ between compatible conditions (mean error rate = 2.1, SD = 1.8, range 0-6) and incompatible conditions (mean error rate = 1.9, SD = 1.8, range 0-7; t(35) = .47, n.s.; Wilcoxon Z = .85, n.s.). These few error trials were excluded from further analyses of the behavioural as well as of the ERP data.

#### 9.3.2.4.1 Behavioural data

Median reaction times (RTs) were calculated for each of the four combinations of picture type and response direction (positive towards, negative away, positive away, negative towards). Median RTs are usually used in the analyses of the AAT, since they are less sensitive to outliers than arithmetic means (see e.g. De Houwer, et al., 2001; Rinck & Becker, 2007; Heuer, et al., 2007).

# 9.3.2.4.2 Electroencephalography (EEG)

EEG was recorded with a 64-channel DC-amplifier and the software "Vision Recorder" (Brain Products, Munich, Germany). 21 scalp electrodes and the mastoids were placed according to the International 10/20-System (Jasper, 1958); all sites were referenced to FCz. Eye movements were registered by means of three electrodes at the epicanthus of each eye and at the infra-orbital position of the right eye. Electrode impedances were kept below 5 k $\Omega$ . Sampling rate was 1000 Hz and bandpass was set to 0.1 – 70 Hz. EEG data were analyzed by "Vision Analyzer" software (Brain Products, Munich, Germany). They were re-referenced to the average reference. After an eye movement artefact correction (Gratton, et al., 1983), data were first segmented into epochs of 900 ms starting 200 ms before the onset of the picture stimulus. An artefact rejection excluded all segments with amplitudes exceeding  $\pm$  70  $\mu V$  or voltage-steps of more than 70  $\mu V$  per sampling point. Afterwards, a baseline correction was applied using the first 200 ms as reference and epochs were averaged separately for each of the four combinations of picture type and response direction. Sufficient numbers of artefact-free segments (> 20) remained for all 36 participants in each combination after the artefact rejection. The P1 and P3 ERPs were quantified at electrode sites selected on the basis of the topographical maps and previous studies. We analyzed the P1 component within 90 - 170 ms at O1 and O2 (cf. Clark & Hillyard, 1996) and the P3 component within 310 - 440 ms at Pz (cf. Leutgeb, et al., 2009; Fruhholz, et al., 2011). Peak values were determined as difference from trough to peak.

# 9.3.2.5 Statistical analysis

Statistical analyses were performed with SPSS for Windows (version 19.0).

# 9.3.2.5.1 Repeated-measures Analyses of Variance (RmANOVAs)

RTs and amplitudes of the ERPs were subjected to repeated-measures analyses of variance (rmANOVAs), with direction of movement (away (avoid) vs. towards (approach)) and valence (negative vs. positive pictures) as within-subject factors. Post-hoc tests of significant interactions were performed by means of two-tailed paired samples t-tests. RTs and ERPs were tested for normal distribution (Kolmogorov-Smirnov Z test). If this requirement for ANOVAs was not met, significant results were confirmed by non-parametric Wilcoxon Z tests. Additionally, compatibility effect scores indicating the relative strength of SRC effects were determined for each participant and measure (RTs and amplitudes of the ERPs; cf. e.g. Heuer, et al., 2007). In the present study, these scores were calculated as the value for the incompatible minus the value for the compatible condition, e.g. the magnitude of P3 amplitudes for pulling minus the amplitudes for pushing negative pictures. Effect sizes were calculated as partial Eta squared  $\eta_p^2$  and Cohen's d for the results of the ANOVA and the t-tests, respectively.

## 9.3.2.5.2 Mediation analysis

We conducted the mediation analyses by using standard path-analytic approaches as developed by Hayes (PROCESS procedure for SPSS; Hayes, 2012; http://www.afhayes.com/spss-sas-and-mplus-macros-and-code.html; cf. Preacher & Hayes, 2004; Preacher & Hayes, 2008; Hayes, 2009). We tested the mediator models as described in the introduction (see also results section): The personality characteristic (BAS-drive or BIS scores) was entered as predictor, the neuropsychological mechanism (SRC effects in P3 or P1 ERP amplitudes) was the tested mediator and behavioural SRC effects constituted the criterion variable. For each of these mediation analyses, the following equations were estimated to derive the total, direct, and indirect effects of the respective predictor on the criterion variable through the respective mediator:

(1) criterion variable = constant + c(predictor) + error

- (2) mediator = constant + a(predictor) + error
- (3) criterion variable = constant + c'(predictor) + b(mediator) + error

All coefficients were estimated using ordinary least-squares (OLS) regression. Thereby, the criterion for statistical significance was p = .05. See results section and figure 3 for further details.

#### 9.4 Results

# 9.4.1 Descriptives

Participants covered a wide range of possible BAS-drive scores (0-16): range 6-16, m = 12.64, SD = 3.63, Kolmogorov Smirnov Z test for normal distribution (K-S Z) = .154, p = .03 (see table 14 of supplementary material for details of the distribution). These scores are comparable to norms (Carver & White, 1994) and to previously published ranges in student samples (e.g. Beaver, et al., 2008). The other scales revealed similar results: BAS-funseeking, range 7-16 (possible: 0-16), m = 11.97, SD = 2.16, K-S Z = .255, p < .001; BAS-reward-responsiveness, range 10-20 (possible: 0-20), m = 16.31, SD = 2.08, K-S Z = .142, p = .065; BIS, range 12-28 (possible: 0-28), m = 20.17, SD = 3.63, K-S Z = .131, p = .12.

# 9.4.2 Reaction Times (RTs)

The 2x2 ANOVA showed a significant interaction between valence x direction  $(F(1,35) = 4.88, p = .034, \eta^2 = .122)$  and a significant main effect of valence  $(F(1,35) = 36.59, p < .001, \eta^2 = .511)$ : RTs to negative pictures were faster than to positive ones.

Post-hoc t-tests revealed a significant SRC effect for negative pictures (t(35) = 2.81, p = .008, d = 0.47; Z = 2.47, p = .013): Participants reacted faster in the compatible condition avoid negative pictures than in the incompatible condition approach negative pictures (see also figure 21A). The SRC effect for positive pictures was not significant (t(35) = 1.22, n.s.; Z = 0.85, n.s.). Furthermore, avoiding negative pictures was faster than avoiding positive ones (t(35) = 4.73, p < .001, d = 0.79; Z = 4.07, p < .001).

#### 9.4.3 P3 ERP

The 2x2 ANOVA showed a significant main effect of valence (F(1,35) = 8.11, p = .007,  $\eta^2$  = .188): Amplitudes of the P3 ERP were generally larger for negative than for positive pictures. SRC effects were neither significant for negative (t(35) = -.98, n.s.) nor for positive pictures (t(35) = -1.65, n.s.; see also figure 21B and figure 22A).

# 9.4.4 P1 ERP

A 2 x 2 x 2 rmANOVA revealed neither the interaction between the within-factors electrode position (O1 vs. O2), valence (positive vs. negative) and direction (approach vs. avoid) nor the main effect of position to be significant (F(1,35) = .91, n.s. and F(1,35) = 2.94, n.s.). Therefore, for the further analyses, we averaged the amplitudes of the P1 ERP at O1 and O2. The 2x2 ANOVA with the factors valence and direction showed a significant main effect of valence (F(1,35) = 21.29, p < .001,  $\eta^2$  = .378): Amplitudes of the P1 ERP were larger for negative than for positive pictures. SRC effects were neither significant for negative (t(35) = -1.89, n.s.), nor for positive pictures (t(35) = .46, n.s.; see also figure 21C and figures 22B and 22C).

# 9.4.5 Mediation analyses

We tested if potential covariates such as current mood (PANAS), age, gender, handedness, general speed of processing (ZVT), smoking status, measurement time and sequence of the two runs were related to the variables of the mediator models by means of correlations (Pearsons r, respectively Eta squared; see table S2B of supplementary material for details). There were only correlations between the negative affect scale of the PANAS and RTs SRC scores for negative pictures (r = .383, p = .021) and the BIS scale (r = .333, p = .047), respectively. However, these correlations were caused by one extreme outlier on the negative affect scale of the PANAS, who was more than 3 standard deviations above the mean (score=31, m = 12.67, SD = 3.62). When repeating the correlations without this participant, both were no longer existent (r = .202 and r = .197, respectively, both n.s.; see figure 24 of supplementary material for details). Except for these pseudo-correlations, there were no other significant correlations between the control variables and components of the mediator model. Therefore, we did not include any of the control variables as covariate into the mediation analyses.

Additionally, we tested all variables for gender differences (see table 15 of supplementary material for details). Solely with regard to the BIS scale, female participants had slightly higher scores than male participants (t(34) = 2.12, p = .04, Z = 2.4, p = .02). However, gender was not a significant covariate in the mediation analyses with BIS as predictor (see also below). Since there were no further differences between female and male participants with regard to the above mentioned potentially influencing variables as well as the variables of the mediation models, we did not include gender as a covariate into further analyses.

The mediation analyses revealed the following results: When entering BAS-drive as predictor, P3 ERP SRC scores as mediator and RTs SRC scores as criterion into the model, the presumptions for mediation were not fulfilled with regard to positive pictures ( $R^2 = .03$ , F(2,33) = .49, p = .62), but were fulfilled with regard to negative pictures ( $R^2 = .28$ , F(2,33) = 6.25, p = .005; see also figure 23 and figure 25 of supplementary material).

In detail, as expected, the higher individuals scored on the BAS-drive scale, the lower their RTs SRC scores were for negative stimuli, i.e., the less slowly participants reacted in the incompatible than in the compatible condition or – in other words – the less automatic avoidance tendencies dominated their reactions to negative pictures (path c in figure 23; equation 1;  $\beta_c$  = -49.4, SE = 21.16, t = -2.33, p = .026). Also in line with our presumptions, goal-oriented pursuit was positively associated with controlled attention allocation (path a in figure 23; equation 2;  $\beta_a$  = .68, SE = .15, t = 4.62, p = .0001): The higher individuals scored on the BAS-drive scale, the larger their P3 ERP SRC scores were for negative stimuli, i.e., the larger their P3 ERP amplitudes were in the incompatible condition *approach negative* compared to the compatible condition *avoid negative*. The direct effect of goal-oriented pursuit (BAS\_drive) on RTs SRC scores for negative pictures was not significant (path c' in figure 23; equation 3;  $\beta_{c'}$  = -2.61, SE = 6.29, t = -.41, p = .68).

The indirect effect of BAS\_drive on RTs SRC scores for negative pictures was tested for significance via a bias-corrected bootstrap-confidence interval (CI). Using the PROCESS procedure with 1,000 bootstrap samples revealed a significant negative indirect effect of BAS\_drive on RTs SRC scores for negative pictures through controlled attention allocation (point estimate = -9.74, 95% percentile CI = -19.09 to -2.15). This indirect effect was quantified as the product of the OLS regression coefficient estimating controlled attention

allocation from BAS\_drive (path a in figure 23) and the OLS regression coefficient estimating RTs SRC scores for negative pictures from controlled attention allocation controlling for BAS\_drive (path b in figure 23;  $\beta_b = -14.28$ , SE = 5.73, t = -2.49, p = .018).

As described in the introduction, we tested the specificity of this model by also analyzing the following mediation models. However, none of these models was significant. We tested a model with BAS-drive as predictor, P1 ERP SRC scores as mediator and RTs SRC scores as criterion (positive pictures:  $R^2 = .04$ , F(2,33) = .75, p = .48; negative pictures:  $R^2 = .14$ , F(2,33) = 2.65, p = .09). We also tested a model with BIS as predictor, P3 ERP SRC scores as mediator and RTs SRC scores as criterion (positive pictures:  $R^2 = .01$ , F(2,33) = .21, p = .82; negative pictures:  $R^2 = .07$ , F(2,33) = 1.62, p = .21). Finally, we tested a model with BIS as predictor, P1 ERP SRC scores as mediator and RTs SRC scores as criterion (positive pictures:  $R^2 = .02$ , F(2,33) = .31, p = .74; negative pictures:  $R^2 = .07$ , F(2,33) = 1.18, p = .32).

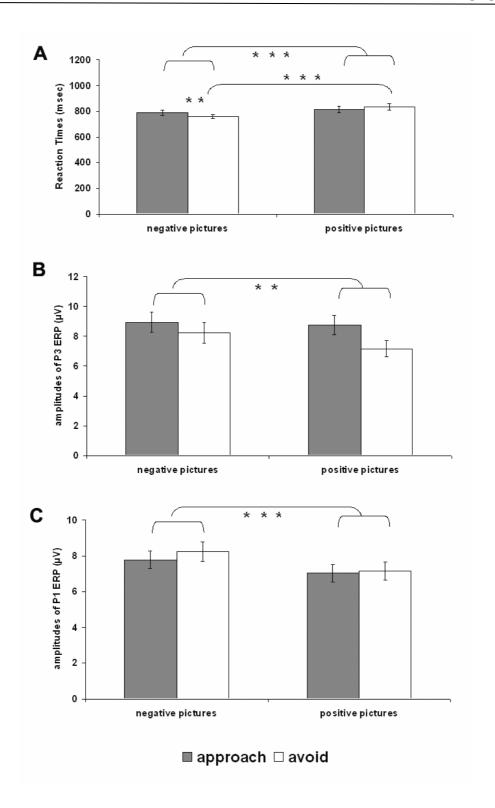


Figure 21: Mean values and standard errors of the mean for

A) Reaction times averaged at O1 and O2

B) P3 ERP amplitudes at Pz

C) P1 ERP amplitudes

\*\* p<.01, \*\*\* p<.001

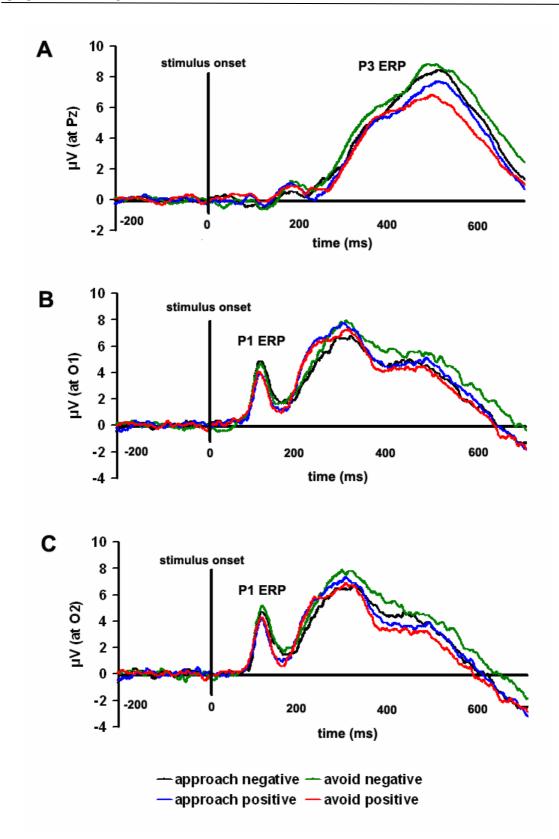


Figure 22: Grand average curves for the P1 and P3 ERPs

approach negative pictures (black line), avoid negative pictures (green line), approach positive pictures (blue line), avoid positive pictures (red line)

A) P3 ERP at Pz

B) P1 ERP at O1

C) P1 ERP at O2

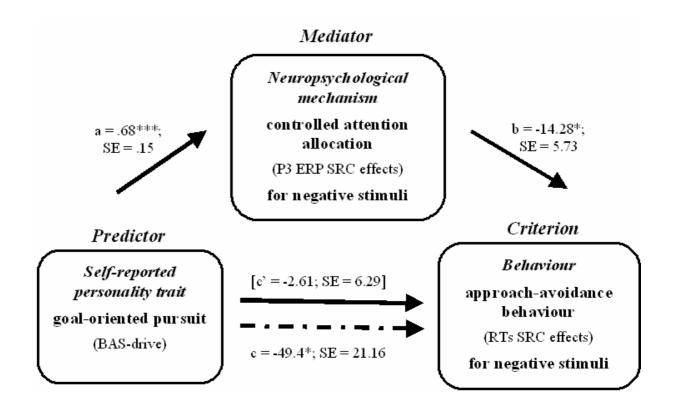


Figure 23: Mediator model with path coefficients for reactions to negative stimuli

Mediation analyses revealed controlled attention allocation to constitute a mediator in the relation between goal-oriented pursuit and dominance of automatic avoidance tendencies to negative stimuli: The higher individuals rated their goal-oriented pursuit, the more they allocated controlled attention to the incompatible condition *approach negative* compared to the compatible condition *avoid negative* and, thereby, the less slowly they reacted in the incompatible than in the compatible condition.

The dotted line indicates the effect of goal-oriented pursuit on behaviour when controlled attention allocation is not included as a mediator.

a, b, c and c' are unstandardized OLS regression coefficients

BAS-drive scale from BIS/BAS questionnaire (Carver & White, 1994), RTs = Reaction Times, P3 ERP = P3 event-related potential, SRC scores= stimulus response compatibility scores \* p<.05, \*\*\* p<.001

#### 9.5 Discussion

The current study investigated the neuropsychological processes underlying interindividual differences in the regulation of approach-avoidance reactions during the AAT. Thereby, we concentrated on the influence of goal-oriented pursuit as relevant personality trait: We tested a mediator model with P3 ERP SRC effects, i.e., controlled attention allocation, as mechanism mediating the influence of this personality trait on behaviour.

In line with our hypotheses, with more pronounced goal-oriented pursuit in terms of higher BAS-drive scores, larger P3 ERP SRC effects were observed for negative pictures, i.e., participants allocated an increasing amount of controlled attention to incompatible compared to compatible conditions. Also, stronger goal-oriented pursuit was associated with fewer behavioural SRC effects for negative pictures, i.e., less prolonged RTs in the incompatible condition *approach negative* compared to the compatible condition *avoid negative*. As expected, thereby, P3 ERP SRC effects were a mediator in the relation between goal-oriented pursuit and behavioural SRC effects, i.e., controlled attention allocation was a mechanism underlying the impact of this personality trait on behaviour in response to negative stimuli. Potential covariates such as gender, current mood or general speed of processing did not influence this mediation.

With regard to dual-process models from cognitive-emotional psychology, this result indicates the interaction between the reflective and the impulsive system (as necessary during incompatible trials), first, to be an individually highly different process depending on characteristics such as goal-oriented pursuit and, second, to involve the neuropsychological mechanism of controlled attention allocation. For interpreting the processes reflected by the P3 ERP (= P300), we take into consideration that "although, most theorizing about the P300 has focused on top-down manipulations of attention, even early data suggested that intrinsic motivational properties of visual stimuli can modulate the P300" (Hajcak, et al., 2010; p.133). Therefore, the P3 ERP might represent processes mainly related to the reflective, but also the impulsive system.

The analyses testing the specificity of this mediation model support our interpretation by revealing automatic attention allocation (P1 ERP SRC effects) to not constitute such a mediator: As hypothesized, automatic attention allocation was not associated with the relation between interindividual differences in goal-oriented pursuit and behavioural regulation. With regard to dual-process models from cognitive-emotional psychology, the P1 ERP might reflect bottom-up activity of the impulsive system, but not top-down mechanisms from the reflective system as necessary for successful behavioural regulation in incompatible trials.

Furthermore, we found only goal-oriented pursuit (BAS-drive), i.e., a personality trait reflecting active regulation, to constitute a predictor in the mediator model, while passive avoidance (BIS) did not. This missing relation differs from the results of van Peer et al. (2007), which might be due to differences in the sample and situation characteristics: Van Peer et al. (2007) found worse behavioural regulation only in the special situation of high trait avoidant participants after cortisol administration (i.e., after stress induction). Moreover, this missing relation also differs from the results of Berkman et al. (2009), who found higher BISscores to be associated with faster responses to conflict than non-conflict trials in an incentive task. Berkman et al. (2009) interpreted their result as reflecting a reaction advantage due to higher sensitivity for detecting conflicts. The current study and the study by van Peer et al. (2007), used versions of the AAT, in which compatible and incompatible trials were grouped into two separate runs. Although this fact was not explicitly explained to the participants, the given instruction might have informed them and - thereby - substantially reduced the influence of conflict sensitivity (BIS-scores) on incompatible AAT-reactions. Another reason for these differences between the AAT-results and the findings obtained by Berkman et al. (2009) might be found in the construction of the BIS-scale. Recently, it has been suggested that more than half of the BIS-scale items are more closely related to the FFFS, i.e., to sensitivity of punishment, than to the BIS (see Smillie, et al., 2006; Heym, et al., 2008). However, since the AAT does not include explicit punishments, this also might have reduced a possible relation between the BIS-scale and the AAT.

For positive stimuli, we did not find a mediation model with BAS-drive scores and P3 ERP SRC effects. In other words, goal-oriented pursuit and controlled attention allocation were more tightly linked to solving the AAT-conflict with negative than positive stimuli. This result might be due to different characteristics of the AAT-conflict when involving negative versus positive stimuli: Executing an incompatible reaction with positive stimuli, i.e., avoiding positive stimuli, might just constitute an unpleasant situation, while – following evolutionary-based suggestions (cf. Ohman, et al., 2001; Flykt, 2006) – approaching negative stimuli might be perceived as a more dangerous situation. Therefore, the reduction of negativity when ending an incompatible trial by a correct response, i.e., the amount of negative reinforcement, might be more pronounced when participants have to react to negative stimuli. Regarding the ending of such a negative conflict situation as a more desired outcome might explain why the willingness to actively regulate behavioural responses, i.e., goal-oriented pursuit, and controlled attention allocation were more closely related to differences between incompatible and compatible negative trials. The finding by Scheres and Sanfey

(2006) support this interpretation: They showed higher BAS-drives scores to be positively associated with the strategy to maximize the likelihood of being rewarded in an economic game.

Furthermore, this interpretation is in line with the revised version of the RST (rRST; Gray & McNaughton, 2000). Earlier versions of the RST assumed each of the two systems to be responsible for only one hedonic tone, namely the BAS for positive affect and the BIS for negative affect. In contrast, later developments suggest both systems to be involved in both hedonic tones (cf. Carver, 2004), since positive and negative affect are assumed to derive from achieving or not achieving a desired goal, respectively. In other words, not the hedonic quality of the stimulus is the relevant feature, but the hedonic quality of the response outcome: Achieving a goal via the activation of one of the two systems causes positive affect. In the AAT, a negative incompatible trial is an extremely unpleasant situation; however, its ending via activation of BAS-related aspects as assessed with the BAS-drive scale is a highly pleasant situation, re-establishing the organisms' homeostasis. In an explorative manner, we also tested the mediation model with the two other BAS-scales. However, in line with our expectations, neither BAS-funseeking nor BAS-reward-responsiveness fit into our mediation model (p > .05). As already mentioned above, these two BAS-scales are not related to active behavioural regulation as necessary for solving the AAT-conflict, since they depict only sensitivity for enjoyment.

Besides these mediation analyses that were focussed on our aim to investigate interindividual differences in the efficiency of such regulation processes, we also analyzed the data at group analysis level. We found a stronger dominance of automatic reactions to negative than to positive stimuli in terms of behavioural SRC effects emerging only for negative pictures. Also, at group analysis level, there were no significant SRC effects in ERPs; instead, negative compared to positive pictures caught more attention in general. This finding matches our mediation-finding and previous research indicating negative pictures to capture more attention (e.g. Ohman, et al., 2001) and to have a greater impact on information processing (e.g. Pratto & John, 1991; Ito, et al., 1998). The non-significance of electrophysiological SRC-effects at the group level might be due to summing-up the neuronal responses when looking at the entire group. When regarded as an entity, our sample was clearly influenced by the incompatibility resulting in the significant SRC effect at the behavioural level. The hypothesized and found negative relation between the amount of SRC effects in behaviour and in the P3 ERP amplitudes at the individual level might explain why

summing-up the neuronal responses resulted in a non-significant effect at the group level. In other words, when regarding the entire sample, the significant behavioural SRC-effect might also be interpreted as an only partially efficient solution of the AAT-conflict being associated with the respective neuronal result – namely only partially efficient neuronal regulation resulting in non-significant neuronal effects.

This finding indicates that for understanding the relation between brain and behaviour, it might be useful to complement group results by conducting analyses at the individual level also in future studies, especially when groups are not completely homogeneous with regard to important characteristics (as e.g. personality traits).

Although our findings reveal this important information on neuropsychological processes underlying controlled approach-avoidance reactions, they might be limited due to several reasons. First, we measured behaviour and personality at different levels: While we used the AAT as implicit measure for both automatic and regulated behaviour, we assessed the personality characteristic by means of a self-report questionnaire. Such questionnaires require participants to explicitly think of and report mental tendencies usually influencing their behaviour outside awareness. This might have distorted the reported personality trait to some extent.

Second, we concentrated on goal-oriented pursuit (BAS-drive) and controlled attention allocation, which only fit into a mediator model for negative pictures. As already indicated above, this might be due to the AAT-conflict with positive pictures being less problematic. Besides assuming such crucial differences between negative and positive AAT-conflicts, mood induction by the positive pictures used in this study also might have been not intense enough to cause the incompatible condition *avoid positive* to be experienced as sufficiently "negative" and its solution to constitute a real negative reinforcement. However, this might only hold true for persons with average scores on reward sensitivity (such as our participants), since Wiers et al. (2009) showed young adults with genetic risk factors for alcohol dependency, i.e., with enhanced reward sensitivity for alcohol cues, to depict generalized approach biases for appetitive stimuli in the AAT, inter alia for positive IAPS pictures.

Third, ecological validity of our results might be limited since everyday situations are frequently characterized by much higher stress levels and emotional distraction than test situations in the laboratory. High stress levels and emotional distraction are known to crucially lower available WM and self-regulation resources (Muraven & Baumeister, 2000; Dolcos & McCarthy, 2006), as well as to alter the influence of personality traits on behaviour (e.g. Verona, et al., 2009). Friese et al. (2008; cf. also Field & Quigley, 2009) showed that systematic experimental diminution of WM or self-regulation capacity enhances the impact of impulses on behaviour. In a similar way, as already mentioned earlier, stress induction via cortisol administration enhanced avoidance biases for angry faces in high trait avoidant persons (van Peer, et al., 2007), i.e., it strengthened the influence of automatic tendencies on behaviour depending on personality characteristics. On the other hand, Gullo and Stieger (2011) showed hazardous drinkers, i.e., persons with probably high levels of reward sensitivity, to show better behavioural performance in the lowa Gambling Task after stress induction. Following these findings, the stress level seems to be a powerful situational determiner of approach-avoidance behaviour. Future studies should take this into account by testing the relations between personality, brain and behaviour under various stress levels, thereby allowing to disentangle the contributions of personality traits and situational factors to approach-avoidance behaviour.

Fourth, our sample covered a wide range of the possible scores of BIS and BAS scales. However, future studies using larger samples covering this range in a tighter way are necessary to show the generalizability of our findings. Thereby, it might be of specific interest, whether persons with extreme BAS-drive scores show the same pattern as found here. While behavioural regulation was shown to improve with increasing BAS-drive scores (cf. Berkman, et al., 2009), previous studies also revealed one exception: When confronted with pictures of angry faces as task-irrelevant, distracting stimuli, increasing BAS-drive scores were associated with heightened behavioural interference effects and reduced neuronal regulation (Putman, et al., 2010; Passamonti, et al., 2008b). Importantly, this effect was not found for emotional or negative facial expressions in general (Beaver, et al., 2008). Due to high positive correlations between BAS-drive and trait anger scores, the angry faces were assumed to have functioned as a social challenge. While there are no items directly referring to aggression or anger in the BAS-drive scale, both goal-oriented pursuit (BAS-drive) and trait anger relate to active, dominant behaviour. Thereby, the cognitive disturbances might reflect distraction due to an automatic tendency for aggressive, active

reactions to angry faces. In other words, in this exceptional situation, the advantage of willingness to react turned into a disadvantage.

Taken together, we found the neuropsychological mechanism of controlled attention allocation to constitute a mediator in the relation between personality and behaviour to negative stimuli: More pronounced goal-oriented pursuit was associated with higher controlled attention allocation and – thereby –faster RTs in incompatible compared to compatible conditions. Besides contributing to a better comprehension of approach-avoidance as two basic principles of behaviour, such mediation analyses might also allow to identify neuropsychological mechanisms underlying specific contributions of personality traits and situational factors. Furthermore, they might help to better understand the dynamics of the interaction between personality and a given situation as well as the resulting influence on behaviour. Such results might also be interesting for applications of the AAT to clinical issues as e.g. addiction disorders, where the co-action of personality traits such as impulsivity or self-control and situational factors such as emotional stress or cue-induced craving determines relapses to happen or not (cf. Koob & Volkow, 2010).

# 9.6 Supplementary material

Table 14: Distributions of BIS/BAS scores: Scores, frequencies, i.e. number of participants per score, and percentage of participants per score for BIS, BAS-drive, BAS-funseeking and BAS-reward-responsiveness scales

BIS score	fre- quency (n)	percen- tage (%)	BAS- drive score	fre- quency (n)	percen- tage (%)	BAS- funsee- king score	fre- quenc y (n)	percen- tage (%)	BAS-reward- responsive- ness score	fre- quency (n)	percen- tage (%)
12	1	2,8	6	1	2,8	7	2	5,6	10	1	2,8
15	3	8,3	9	1	2,8	8	1	2,8	13	1	2,8
17	4	11,1	10	2	5,6	9	2	5,6	14	3	8,3
18	3	8,3	11	5	13,9	10	2	5,6	15	8	22,2
19	6	16,7	12	6	16,7	11	2	5,6	16	8	22,2
20	4	11,1	13	8	22,2	12	16	44,4	17	4	11,1
21	5	13,9	14	8	22,2	13	3	8,3	18	4	11,1
22	1	2,8	15	3	8,3	14	4	11,1	19	6	16,7
23	2	5,6	16	2	5,6	15	2	5,6	20	1	2,8
24	2	5,6				16	2	5,6			
25	1	2,8									
26	2	5,6									
27	1	2,8									
28	1	2,8									

Table 15: Tests for gender differences in variables of the mediator model (A) and in potential covariates (B) by means of t-tests and – if variables were not normally distributed – by non-parametric Wilcoxon Z tests

Categorical variables were tested by means of Chi-squared tests, respectively *time of measurement* by means of the Freeman-Halton test.

RTs = Reaction Times, SRC scores = stimulus response compatibility scores, PANAS scales from Positive Affect Negative Affect Schedule (PANAS; Krohne, et al., 1996), ZVT = Zahlen-Verbindungs-Test (Oswald & Roth, 1987)

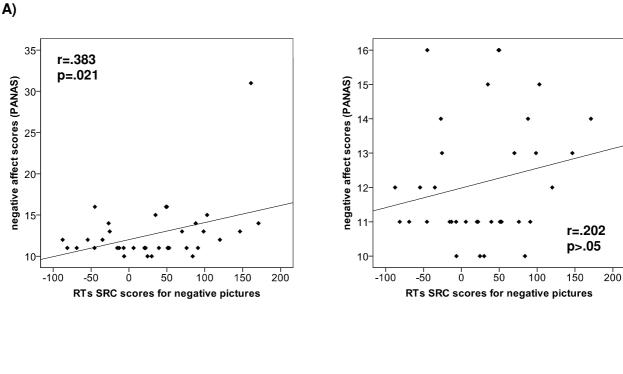
#### A)

iabla	male part	icipants	female pa	articipants	test for difference	
variable	mean	SD	mean	SD		
BAS-drive scores	12.28	2.44	13.0	1.46	t(34)=1.08, Z=.482	
BIS scores	18.94	4.08	21.39	2.7	t(34)=2.12*, Z=2.4*	
P3 ERP SRC scores: negative pictures	-1.06	2.43	.34	1.78	t(34)=1.97	
P3 ERP SRC scores: positive pictures	-1.03	2.56	18	1.73	t(34)=1.17, Z=1.11	
P1 ERP SRC scores: negative pictures	37	1.07	58	1.87	t(34)=.42	
P1 ERP SRC scores: positive pictures	.20	1.63	.05	1.68	t(34)=.28	
Difference between P3 ERP and P1 ERP SRC scores: negative pictures	69	2.81	.92	2.99	t(34)=1.67	
Difference between P3 ERP and P1 ERP SRC scores: positive pictures	-1.23	3.31	23	2.95	t(34)=.96, Z=.87	
RTs SRC scores: negative pictures	32.69	69.35	30.0	66.55	t(34)=.12	
RTs SRC scores: positive pictures	32.03	60.81	8.83	129.83	t(34)=.69	

<sup>\*</sup> p < .05

# B)

variable	male participants	female participants	test for difference	
PANAS negative affect scores	mean=12.28, SD=1.81	mean=13.06, SD=4.83	t(34)=.40, Z=.17	
PANAS positive affect scores	mean=28.11, SD=5.25	mean=27.39, SD=5.48	t(34)=.64	
age	mean=24.5, SD=1.65	mean=24.39, SD=2.09	t(34)=.18, Z=.16	
general speed of processing (ZVT; in sec)	mean=57.17, SD=6.75	mean=55.9, SD=11.63	t(34)=.40	
handedness (left / right)	2 / 16	1 / 17	χ <sup>2</sup> =.36	
smoking (no / yes)	13 / 5	14 / 4	χ <sup>2</sup> =.15	
time of measurement (8-12 am/ 12am-5pm / 5-9pm)	5/6/6	7/8/3	p=0.53	
sequence of runs: first run (approach positive – avoid negative / avoid positive – approach negative)	10 / 8	9/9	χ <sup>2</sup> =.11	



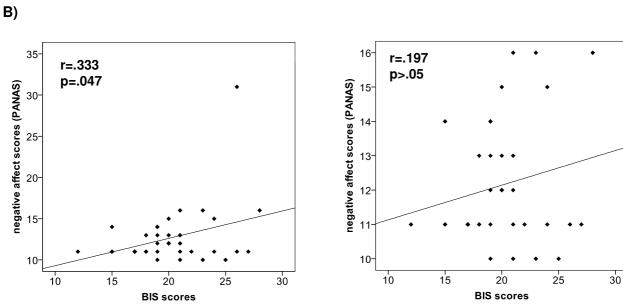
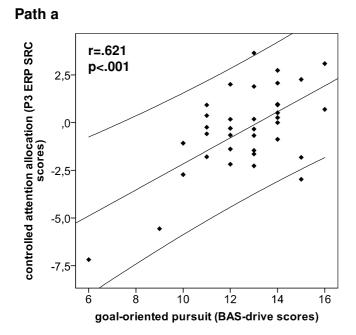
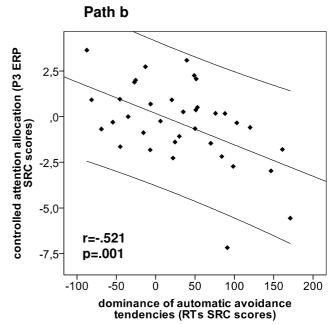


Figure 24: Scatter-plots of correlations between negative affect scale of the PANAS questionnaire and RTs SRC scores for negative pictures (A), respectively BIS scores (B) for all participants (left panels) and after excluding the extreme outlier (right panels).

RTs = Reaction Times, SRC scores = stimulus response compatibility scores





#### Path c

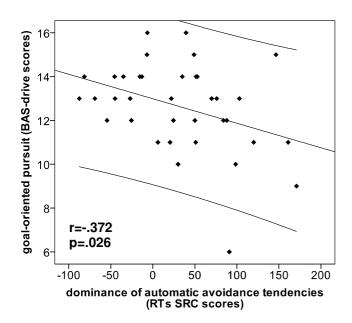


Figure 25: For illustrating the relations of the significant mediation model and for showing their validity, we present scatter-plots of the correlations (95% confidence intervals):

Path a: Correlation between goal-oriented pursuit (BAS-drive scores) and controlled attention allocation (P3 ERP SRC scores).  $R^2 = .386$ , Durbin-Watson statistic = 1.755 (i.e. homoscedasticity of residuals)

Path b: Correlation between controlled attention allocation (P3 ERP SRC scores) and dominance of automatic avoidance tendencies (RTs SRC scores).  $R^2 = .275$ , Durbin-Watson statistic = 1.755 (i.e. homoscedasticity of residuals)

Path c: Correlation between goal-oriented pursuit (BAS-drive scores) and dominance of automatic avoidance tendencies (RTs SRC scores).  $R^2 = .138$ , Durbin-Watson statistic = 1.897 (i.e. homoscedasticity of residuals)

RTs = Reaction Times, SRC scores = stimulus response compatibility scores

Furthermore, while P3 ERP SRC scores and RTs SRC scores for negative pictures were normally distributed, BAS-drive scores were not (K-S Z=.15, p=.03). Visual inspection of BAS-drive scores via boxplots identified one participant as outlier (score = 6, i.e. more than 3 standard deviations (SD = 2.02) beneath the mean (m = 12.64)). When exploratively excluding this participant, there were no more outliers and BAS-drive scores were normally distributed. Repetition of the mediation analyses without this participant revealed the same results as with all 36 participants:

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R<sup>2</sup> = .29, F(2,33) = 6.52, p = .004 path a: β = .52, SE = .17, t = 2.99, p = .005 path b: β = -16.23, SE = 5.91, t = -2.74, p = .01 path c: β = -13.92, SE = 6.49, t = -2.15, p = .039 path c': β = -5.47, SE = 6.68, t = -.82, p = .42 indirect effect of BAS_drive on RTs SRC scores for negative pictures: point estimate = -8.46, 95% percentile CI = -19.98 to -1.81
```

#### 10 General Discussion

The studies of the current thesis aimed at investigating the neuronal and neuropsychological correlates of behavioural SRC effects in the AAT, i.e., of longer RTs in incompatible than compatible conditions. Thereby, explanations for SRC effects were deduced from cognitive-emotional psychology, neuronal and neuropsychological models, i.e., from all three perspectives, which were taken as theoretical framework.

Each of the six studies concentrated on a unique question, revealed unique findings and had its own limitations. These aspects were discussed in the respective chapters in detail (see chapters 4-9). Here, I discuss findings, which are common to the six studies, and the issues, which can only be answered by regarding all studies together. Furthermore, the results of the current thesis are discussed with regard to general theories of affective evaluation and their relation to behaviour as described in the General Introduction (see spec. 1.1.3).

# 10.1 Neuronal insights

In studies A1 and A2, I investigated neuronal correlates of SRC effects. As outlined in 1.2.2, several neuronal models suggest the PFC to exert substantial top-down control. Specifically the model of Ernst and Fudge (2009), which was taken as theoretical framework, suggests the PFC to be the main structure for regulating automatic approach-avoidance tendencies. The latter ones are assumed to arise from activation of the striatum and the amygdala, respectively.

### 10.1.1 Studies A1 and A2: FNIRS and activity in DLPFC

Therefore, I concentrated on cortical activity in the frontal lobe: FNIRS was used to assess the contributions of prefrontal areas, specifically of the DLPFC as main control instance and structure mainly responsible for initiating performance adjustments (Miller & Cohen, 2001). Both studies, A1 and A2, support the assumption of the DLPFC to essentially contribute to regulation processes in incompatible AAT conditions. Study A1 showed neuronal SRC effects in right DLPFC: As expected, incompatible, regulated reactions (avoid

positive, approach negative) compared to compatible, automatic reactions (approach positive, avoid negative) caused stronger activation in terms of a decrease of HHb.

In study A2, interindividual differences in RTs as linked to genetic variations in the MAOA coding gene (MAOA-uVNTR) were also associated with regulatory activity in right and - less clearly - in left DLPFC. There were no differences between the groups in behavioural SRC effects. However, there was a linear decrease from MAOA-L to MAOA-LH to MAOA-H carriers in DLPFC activity for both positive and negative pictures: MAOA-L carriers showed stronger SRC effects, i.e., stronger regulation than MAOA-LH and MAOA-H carriers. MAOA-L carriers are known to show more extensive affective reactions (Meyer-Lindenberg, et al., 2006). Therefore, these participants might have needed to more strongly activate their PFC in incompatible AAT-conditions, i.e., to use a higher order compensatory regulation mechanism. Analyses within the group of MAOA-L carriers supported this interpretation. They revealed SRC effects in O<sub>2</sub>Hb<sup>31</sup> for both negative and positive pictures in right DLPFC, while - probably due to this efficient regulation of behaviour - there were no significant behavioural SRC effects. In contrast, the MAOA-H genotype, which had been associated with better cognitive regulatory abilities (Passamonti, et al., 2006), showed no SRC effects in DLPFC, but behavioural SRC effects for both positive and negative pictures. Pre-regulation via other brain areas might have allowed them to perform incompatible reactions without the DLPFC as highest control region. Specifically, regulatory activity in the dACC was also shown to be better in MAOA-H than in MAOA-L carriers (Buckholtz, et al., 2008). In other words, results of study A2 revealed hints on the contribution of other regulatory brain areas than the DLPFC.

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 $<sup>^{31}</sup>$  The differences in the results with regard to the fNIRS parameters HHb and  $O_2$ Hb might be due to the different sample sizes and characteristics of these parameters: HHb is the fNIRS parameter with the higher local sensitivity (cf. Hoshi, et al., 2001; Plichta, et al., 2006a), what might complicate homogeneous and – thereby – at group level significant activation patterns in larger samples with more interindividual variability. In contrast,  $O_2$ Hb is considered to constitute the fNIRS parameter with the higher global power, i.e., the higher possibility to detect even small effects (cf. the findings of study A4).

#### 10.1.2 Study A3: FMRI and activity in whole brain

In study A3, the usage of fMRI allowed for depicting activity in the entire brain and – thereby – revealed evidence for an essential contribution of other brain areas to incompatible AAT reactions. As the fNIRS studies, study A3 also aimed at regulatory neuronal SRC effects in terms of enhanced activity in incompatible compared to compatible conditions. Thereby, I concentrated on the ACC, the insula, the thalamus as well as on frontal and parietal cortices. These ROIs were previously shown to be responsible for regulatory subprocesses as necessary for solving affective and cognitive response conflicts, i.e., as presumably necessary for solving the AAT conflict.

In short, in these ROIs, the used cued GoNoGo version of the AAT clearly elicited the expected regulatory SRC effects for negative pictures at the cue event (preparation phase), while, for positive pictures, such SRC effects were restricted to frontal areas. With regard to the move event (reaction phase), the Go condition elicited regulatory SRC effects in frontal and parietal regions for positive stimuli, while there were no significant effects for negative stimuli. In the NoGo conditions, we found the expected reversed SRC effects, i.e., enhanced regulatory activity in compatible compared to incompatible conditions in the right superior parietal lobule (SPL) for negative stimuli, while there were no significant effects for positive stimuli.

In more detail, the cue event with negative pictures elicited SRC effects in middle cingulate gyrus, i.e., in the dorsal part of the ACC. This is in line with the general description of ACC functions as conflict monitoring system (van Veen & Carter, 2002), what implies stronger activity in incompatible conditions as conflict situations. Furthermore, activity in this area was previously associated with conflict solution in terms of focussing attention to relevant stimuli (Weissman, et al., 2005; for a review see also Bush, et al., 2000). The ACC was also shown to be involved in attention allocation in terms of top-down modulation of primary sensory cortices (Crottaz-Herbette & Menon, 2006). In our case, SRC effects might indicate participants to have focussed their attention on the picture frame indicating the correct response, while the irrelevant stimulus feature *picture valence*, which presumably automatically attracted participants' attention, had to be ignored (cf. Nee, et al., 2013). Furthermore, Paus (2001) defined the ACC as essential brain region for translating intentions into actions, since it is involved in motor control, cognitive control and the regulation of arousal states. SRC effects were also observable in the adjacent precentral gyrus (preCG)

and supplementary motor area (SMA). These areas are associated with response preparation during delay periods in conflict paradigms (e.g. Cole & Schneider, 2007), with the linkage of cognition to action (Nachev, et al., 2008) and with distractor resistance (Nee, et al., 2013). The found SRC effects are in line with the assumption, that these processes are necessary for conducting correct incompatible reactions in the AAT.

With regard to the insula, its anterior parts also showed SRC effects. The anterior insula was suggested to be a main instance for motivational states and their relation to subjective feelings and goal settings (Wager & Feldman Barrett, 2004). It is involved in the sustainment of emotional arousal during delay periods (Cole & Schneider, 2007). Together with the ACC, it is responsible for the integration of emotionally salient interoceptive information as necessary for forming a subjective representation of one's body (Taylor, et al., 2009). In the context of the manikin version of the AAT, this activity pattern might reflect participants' identification with the manikin in terms of creating a representation of their body at the position of the manikin. Moreover, the anterior insula is also part of a system responsible for conflict monitoring (Dosenbach, et al., 2008; see also 10.2.4) and was previously shown to underlie – together with the basalganglia, the cingulate cortex and the SMA – the inhibition of reactions in a stop signal task (Huster, et al., 2011).

The adjacent frontal opercular regions, specifically the right inferior frontal gyrus (IFG), are involved in inhibition and top-down control processes with regard to movements (basalganglia/nucleus subthalamicus; Aron, et al., 2004) and memories (hippocampus; Anderson, et al., 2004). In the present study, these SRC effects might reflect intrusion resistance in incompatible conditions, i.e., might indicate the necessity to inhibit irrelevant valence-movements (S-R) memories as automatically induced by the stimulus valence. Furthermore, – together with the right preCG – the right IFG was suggested to underlie subvocal rehearsal of verbal WM content (Smith & Jonides, 1998). This is of interest for the AAT, since participants might have rehearsed the given instruction rules for conducting correct responses.

SRC effects as indicators of regulatory activity were also observed in the thalamus, which is known to be involved in the alerting function of attention (Fan, et al., 2005), in set-maintenance processes of cognitive control (Dosenbach, et al., 2008) and in the transmission of sensory information about the body's physiological state to the cortex, i.e., to

consciousness (Craig, 2002). Conducting incompatible reactions with negative stimuli represents an enormous conflict (see 10.3), what might have resulted in a strong alerting reaction and the feedback from the body, that the person is in danger. Therefore, the thalamic activity might also reflect participants' identification with the manikin and its situation.

Besides the above mentioned frontal contributions to response preparation and inhibition, the middle frontal gyrus (MFG) also showed SRC effects. This area is known to be responsible for the maintenance (midVLPFC) and manipulation (midDLPFC) of spatial contents in WM (D'Esposito, et al., 1999; cf. also Nee, et al., 2013). In the current study, participants had to combine the instruction rules associated with the frame format and the manikin position to conduct a correct response. Furthermore, the MFG was shown to be involved in distractor resistance (Sakai, et al., 2002), action monitoring (cf. Petrides, 2000) and action selection (Rowe, et al., 2000). The superior (medial) frontal gyrus is involved in executive processes of spatial WM (Nee, et al., 2013; caudal superior frontal sulcus) and in self-referential evaluation processes (Gusnard, et al., 2001). This latter aspect might be of specific interest for the current study, since the concept of the manikin AAT assumes participants to identify themselves with the manikin, i.e., to create a meaning of its position for themselves.

With regard to parietal areas, SRC effects were found in the SPL, which is involved in visual WM capacity (Todd & Marois, 2004), spatial WM in general (Nee, et al., 2013) and top-down control of visual attention (Kastner & Ungerleider, 2000; Friedman-Hill, et al., 2003). In the current study, activity in this region might be necessary for preparing the correct response, since the position of the manikin and – thereby – the required movement are already given at the cue event and have to be maintained until the Go or NoGo signal at the move event. The SPL is also involved in controlled attention allocation (Corbetta & Shulman, 2002) and in distractor resistance (Nee, et al., 2013). Furthermore, Chiu and Yantis (2009) suggested the SPL to constitute an instance for cognitive control comprising the shifting between different cognitive control functions such as shifting spatial attention and switching categorization rules. Furthermore, the precuneus was shown to be responsible for taking first-person perspective, i.e., for taking the perspective of an acting and self-observing person and for spatial imagination (Cavanna & Trimble, 2006). As suggested with regard to the above described SRC effects in the thalamus and SFG, this activity might reflect participants's identification with the manikin and its situation, i.e., it might reflect the efficiency

of the manikin version of the AAT. The inferior parietal lobule (IPL) was suggested to be involved in attentional processes in terms of foregrounding contents in WM by means of activating semantic and conceptual details of this item (Nee, et al., 2013; cf. also Dosenbach, et al., 2008), while the supramarginal gyrus (SMG) guarantees controlled attention allocation (Corbetta & Shulman, 2002); in the current study, the instructed response had to be more preferably processed than the automatic reaction tendencies. SRC effects in the postcentral gyrus (postCG) are in line with previously reported activity of this somatosensory region during not only actual motor performance (Huster, et al., 2011), but also motor imagery (Porro, et al., 1996). This activity pattern further supports the assumption of pronounced response preparation for negative stimuli for incompatible reactions at the cue event.

In contrast, for positive pictures, SRC effects at the cue event were less distinctive. Here, only left MFG and IFG showed SRC effects, what might indicate response preparation and inhibition processes.

At the move event, the expected shift of compatibility, which was tested as the interaction between the factor GoNoGo and (reversed) SRC effects, was asymmetric, since it was carried by the NoGo conditions for the negative pictures and by the Go conditions for the positive pictures. Reversed SRC effects in NoGo conditions at the move event were hypothesized, since the inhibition of automatically elicited compatible response tendencies should be incompatible and the inhibition of the prepared incompatible reaction should become a compatible situation. For negative pictures, the strong and broad SRC effects at the cue event were followed by a restriction of SRC effects in the Go conditions to the right middle cingulate gyrus and left angular gyrus. However, these effects were only observable, when lowering the minimal size of significant clusters to 5 voxels. This indicates further conflict solution and - more importantly - the involvement of spatial orientation in terms of a left-right distinction (angular gyrus; Hirnstein, et al., 2011), what might be seen as the neuronal correlate of realizing the prepared responses. In contrast, frontal regions as highest control instances were not activated. In NoGo conditions, the right SPL showed the hypothesized reversed SRC effects. As mentioned above, the SPL was suggested to control the switching between different response rules (Chiu & Yantis, 2009). At the move event, participants had to switch between realizing the respone as indicated by the green Go signal and inhibiting the response as signaled by the red NoGo manikin.

For positive pictures, SRC effects in Go conditions at the move event emerged in frontal and parietal regions: The preCG indicated response preparation, the right IFG showed the involvement of response inhibition and the MFG indicated the contribution of general action selection and WM processes. Furthermore, there were SRC effects in the left postCG and SPL as regions for somatosensory feedback processing, spatial WM and attention processes. With regard to the only weak SRC effects at the cue event, this might indicate the main solution of the AAT conflict to happen at the same time point as the response and to not need strong preparation. In the NoGo conditions, there were no pronounced reversed SRC effects. Only when lowering the minimal size of significant clusters to 5 voxels, there were reversed SRC effects in the right MFG, right superior orbital gyrus, right SFG and right postCG.

At the behavioural level, positive pictures caused the expected SRC effects, but the processing of negative pictures resulted in reversed SRC effects, i.e., in faster RTs for incompatible than compatible conditions. A more detailed interpretation of these behavioural differences and of relations between the neuronal and behavioural level is given in 10.3.3.

### 10.1.3 Comparison with previous AAT studies in fMRI

Previous fMRI investigations on the AAT showed regulatory activity in left lateral OFC and VLPFC (BA 47/12, BA 45) during incompatible trials (approach angry faces, avoid happy faces; Roelofs, et al., 2009; for an outline see also 1.3.4). Thereby, the stronger participants' OFC was activated during *approach angry*, the longer their RTs were. The authors interpreted this pattern as reflecting the stronger recruitement of orbitofrontal resources when RT costs in this incompatible condition increased. In another study also using facial expressions, bilateral VLPFC and frontal pole (BA 10, BA 47/12) were stronger activated during incompatible than compatible conditions (Volman, et al., 2011b). This pattern was also observable in bilateral fusiform gyrus (BA 37) and left SMG (BA 40/48) and IPL (BA 40). As for the RTs, this pattern was only significant, when participants explicitly reacted to the valence of the shown facial expression, i.e., when they consciously processed the stimulus valence, but not when they reacted to the gender of the facial expressions.<sup>32</sup>

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<sup>&</sup>lt;sup>32</sup> With regard to the behavioural analysis of this study, it should be noted that Volman et al. (2011b) used the same instruction and task design as did Roelofs et al. (2009). However, they did not find the

Furthermore, Volman et al. (2011b) showed behavioural and neuronal reactions to be modulated by male participants' endogenous testosterone level: Low testosterone levels were associated with less slowing of RTs in incongruent trials, stronger VLPFC activity in incongruent compared to congruent trials and less coupling between left VLPFC and right amygdala in incongruent trials. This might reflect persons with low emotional reactivity to show less distraction by affective faces and better prefrontal regulation, what seemed to have resulted in a reduction of the necessity to inhibit amygdalar activity.

Volman et al. (2011a) applied inhibitory TMS (continuous theta burst stimulation, cTBS) to the left aPFC. After control TMS, error rates were non-significantly enhanced in incompatible compared to compatible conditions, a pattern, which turned significant after cTBS. This worsening of performance was not observable in RTs (both groups showed the expected SRC effects, incompatible > compatible). However, the measurements with ASL showed a decrease of perfusion in bilateral aPFC (BA 10) and rostral ACC (BA 24/32) as well as in right posterior parietal cortex (BA 7) and posterior intraparietal sulcus. While the contribution of these regulatory areas was weakened, bilateral amygdalae (BA 34) and left FFA (BA 37) as emotionally sensitive regions showed enhanced perfusion.

Taken together, these results also showed frontal and parietal areas as well as the ACC to be of importance for regulating the response conflicts in the AAT. However, compared to the present thesis, the findings for the ACC were restricted to perfusion differences as revealed via ASL (Volman, et al., 2011a). These studies aimed at the investigation of social approach-avoidance processes and — therefore — used facial stimuli. Nevertheless, contributions of the ACC as general conflict monitoring instance would be expected, since social interactions are highly important situations. However, the used task design resulted in two blocks, one with compatible conditions and one with incompatible conditions. To my opinion, this might have reduced the necessity for conflict monitoring, since the probability of conflicts to occur was not existent (0%) and always present (100%), respectively.

same results, namely significant SRC effects for the valence instruction and no SRC effects for the alternative instruction. Only when analyzing RTs of both instruction versions together, SRC effects reached significance. Moreover, when excluding the additionally used pictures of neutral faces from the analysis, Volman et al. (2011b) could repeat the findings of Roelofs et al. (2009).

With regard to contributions of the PFC, the areas involved in the studies of Roelofs et al. (2009) and Volman et al. (2011b) lay more ventral than the activity in DLPFC as found in the fNIRS studies of the current thesis. Future studies have to clarify, first, if such differences are due to the used stimulus material (faces vs. IAPS pictures) and, second, if the reliability of functional imaging measures is adequate. Moreover, in the current fMRI study, activity in the MFG might be seen as the correspondent to the DLPFC activity. However, it should be noted that the studies of the current thesis did not only use different methods for assessing neuronal activity (fMRI vs. fNIRS), but also different version of the AAT: In the fNIRS studies, participants had to directly conduct the reactions, when the stimulus was presented. Therefore, the found activity in DLPFC is in accordance with the suggestion of the model of D'Esposito (1999, see also above 10.1.2), that the midDLPFC as part of the MFG is responsible for the manipulation aspects of spatial contents in WM. Similarly, Rowe et al. (2000) associated the DLPFC (BA 46) with response selection processes, but not with the maintenance of WM contents. In contrast, in the GoNoGo version of the AAT as used in the fMRI study, the cued task design resulted in delayed realizations of responses, i.e., required the maintenance of visual contents in WM. This might explain, why activity was not restricted to the DLPFC/MFG, but also involved other frontal and parietal areas. Moreover, while the DLPFC is often suggested to constitute the highest control instance in the human brain (e.g. Miller & Cohen, 2001), its definition often refers to BA 46 and BA 9, but is not always identical and unambiguous (for a summary see Nee, et al., 2013). Moreover, this definition concentrates on the surface of the cortex. For the fNIRS studies, such a restriction is adequate, because this measurement technique cannot reach deeper regions. However, in fMRI, deeper cortical layers are also assessed, i.e., definitions of regions according to e.g., the automatic anatomical labelling (AAL) atlas, which takes into account the entire gyri, might be more adequate for labeling the found neuronal clusters.

#### 10.1.4 Revised model

Following the findings of the current thesis, I suggest an extension of the model suggested by Ernst and Fudge (2009) with regard to its application to the AAT: The results of study A3 (fMRI) revealed the conflict in incompatible AAT conditions for negative stimuli to be solved via contributions of the ACC. This is in line with theories suggesting the ACC to be the most important monitoring instance in the human brain (van Veen & Carter, 2002). This finding further confirms my interpretation of the results for the *MAOA-H* genotype in study A2:

The missing SRC effects in DLPFC might be due to the significant contributions of other brain areas, such as e.g. the ACC (for details see also 5.5). Furthermore, SRC effects at the cue event for negative stimuli were also found in the anterior insula. This region was shown to be important for monitoring and conscious emotional experience (Dosenbach, et al., 2008; Wager & Feldman Barrett, 2004). Moreover, in study B1, for positive pictures, the conducted source analysis revealed the N2 ERP as indicator of conflict processing to emerge from the left insula and DLPFC (for details see 8.4.4). The strong parietal contributions found in study A3 further question the status of the PFC as unique regulation instance. However, it is important to keep in mind, that the used GoNoGo version might have elicited additional control processes such as e.g., the maintenance of contents in WM. In comparison, in the AAT version used in the fNIRS studies, the reactions had to be directly conducted. Future studies in fMRI should clarify the contributions of the ACC, the insula and parietal areas in usual AAT versions. The PFC might constitute the highest control instance, however, the strong linkage of its activity to cingular, insular and parietal processes as shown in network analyses (Corbetta & Shulman, 2002; Dosenbach, et al., 2008) emphasizes the distribution of cognitive control capacities to several instances (for details see 10.2.4). The results of study A3 indicate this principle to also be valid for the AAT.

Interestingly, the assumption of such important other contributions to the regulation might also be extended to the subcortical level: The mediation analysis of study A3 revealed participants' valence and arousal ratings to determine, how strongly Go reactions to negative stimuli at the move event (i.e. the actual realization of responses) depended on enhanced activity in incompatible compared to compatible conditions in the right midbrain, including the red nucleus: The more negative and arousing participants' rated the negative pictures, the stronger SRC effects in the right midbrain were and - thereby - the more pronounced the reversed behavioural SRC effects were (see also 10.3.3). In contrast, the group analysis did not reveal pronounced SRC effects in frontal cortices or any of the other above mentioned regulation and conflict monitoring instances. The red nucleus is an area responsible for the initiation of movements (Gruber & Gould, 2010; cf. Dypvik & Bland, 2004). Following the model of LeDoux (1994), such SRC effects in the midbrain/red nucleus might be interpreted as subcortical regulation not requiring the contribution of cortical areas (see however the discussion of the importance of cortical SRC effects at the cue event in 10.5.3): LeDoux (1994) suggested his low road for fast avoidance reactions to guarantee the survival in dangerous situations (see 1.2.3). Similarly, conducting incompatible reactions for negative stimuli in the cued GoNoGo AAT might rely mainly on subcortical structures, since these

responses have been prepared at the cue event and might be realized without any further detailed, cortical analysis for guaranteeing the speed of the reactions. In 10.5.3, this mediation result is further related to the theoretical background from cognitive-emotional psychology.

The model of Ernst and Fudge (2009) suggests the amygdala and the striatum to be responsible for the realization of the compatible reactions avoid negative and approach positive, respectively. However, in general, the amygdala is described to reflect the emotional arousal elicited by stimuli irrespective of their valence (Hamann & Mao, 2002; cf. also Cunningham, et al., 2010; Hamann & Mao, 2002; Schlund & Cataldo, 2010). The above described result of the connectivity analysis between the VLPFC and the amygdala also used both incompatible conditions approach angry and avoid happy (Volman, et al., 2011b), which - presumably - elicit stronger arousal than compatible conditions. Even in patients with major depression, who are especially sensitive for negative stimuli, Derntl et al. (2011) only found a trend for reduced amygdalar activation in comparison to healthy controls, but did not report significant differences within the patient group for approach-avoidance reactions to happy compared to angry faces. Similarly, the striatum was suggested to be involved in movement initiations processes in general, not only in approach reactions (Carretie, et al., 2009; O'Doherty, et al., 2004; Tomer, et al., 2008). Therefore, in the current fMRI analysis (study A3), I concentrated on neuronal SRC effects, i.e., on the regulation of incompatible reactions. Future studies should also analyze compatible AAT reactions, whereby the search volume might also comprise other structures important for movement initialization such as the SMA and the basalganglia. Since the investigation of this question would require for several additional ROIs, to my opinion, it should be addressed in a separated study for avoiding an inflation of the probability of type I errors.

## 10.1.5 Study A4: Learned stimulus response compatibility

In study A4, I investigated participants' reactions to pictures of alcohol and non-alcohol stimuli. During approaching compared to avoiding alcohol pictures, there was enhanced activity in terms of stronger oxygenation (O<sub>2</sub>Hb) in left anterior lateral OFC (orbital part of the IFG). Following previous findings (Sescousse, et al., 2010), participants seemed to have experienced approaching alcohol pictures as more pleasant than avoiding them. However, this effect was only found, when applying an uncorrected threshold of significance, what

might be due to the pilot character of this study and the related low amount and frequency of alcohol consumption of the sample. As expected, this effect was the stronger, the more positive participants' expectation about beneficial effects of alcohol in terms of emotional regulation were (cf. the results of van Gucht et al. (2008), who investigated conditioned approach tendencies to chocolate stimuli).

This finding is in line with suggestions by Bechara (2005; cf. also Deutsch & Strack, 2006), that addiction-relevant stimuli are associated with approach tendencies due to prior positive learning experiences as reflected in the OFC, the only structure of the general reward circuitries that is measurable with fNIRS (Koob & Volkow, 2010). Importantly, when participants reacted to positive and negative IAPS pictures, the OFC did not reveal differences between compatible and incompatible AAT conditions. This might be explainable by the content of IAPS pictures: They depict emotional scenes of general emotional value, which does not have to be learned. In contrast, the OFC depicts the value of secondary reinforcers such as addiction related cues (Sescousse, et al., 2010).

Furthermore, I expected enhanced DLPFC activity during the so-defined incompatible condition *avoid alcohol* compared to the compatible condition *approach alcohol*. However, there were no differences between the two conditions indicating contributions of the DLPFC as highest control instance to not be necessary. This might be due to the characteristics of the sample: Participants were not addicted or at risk for alcohol addiction and did not show behavioural approach biases. Obviously, their neuronal processing of alcohol stimuli was not yet critically altered, but – presumably – could be regulated by other brain areas, what, finally, did not result in behavioural SRC effects.

These results hint to the possibility, that approach-avoidance reactions to specific classes of stimuli activate additional or other neuronal areas than did the reactions to IAPS pictures as stimuli of general emotional relevance (cf. also above the discussion of the findings for facial stimuli).

### 10.2 Neuropsychological insights

Studies B1 and B2 concentrated on the neuropsychological processes underlying SRC effects. In 1.2.3, the potential of ERPs for assessing different attentional sub-components and response inhibition was outlined. More details on the specific ERPs were given in the introduction sections of study B1 (8.2) and B2 (9.2).

#### 10.2.1 N1, P1 and P3 ERPs and attentional processes

In study B1, the occipital N1 ERP, which reflects early attention allocation preparing efficient stimulus classification (Vogel & Luck, 2000), was enhanced during the incompatible condition *avoid positive* compared to the compatible condition *approach positive*. At the behavioural level, this regulation in terms of electrophysiological SRC effects resulted in no differences between compatible and incompatible conditions. In line with previous studies (e.g. Clark, et al., 1995), activity in the cuneus and lingual gyrus of the right occipital lobe underlay the SRC effect in the N1 ERP. In contrast, for negative pictures, the reversed pattern was found: There were no SRC effects in the N1 ERP, but in RTs and error frequency, i.e., participants were slower and made more errors during the incompatible condition *approach negative* than during the compatible condition *avoid negative*. These results are in line with previous findings indicating negative stimuli to be more important for survival (e.g. Flykt, 2006). This might explain their stronger influence on behaviour. For a more detailed discussion of this aspect see 10.3.

While there were no effects in the other two investigated ERPs indicating attentional processes (P1 and P3 ERP), study B2 revealed important contributions of the P3 ERP to the solution of the AAT conflict. The investigated mediator model could explain the data for negative pictures: The higher participants rated their expressions of goal-oriented pursuit (BAS-drive scores), the more pronounced P3 ERP SRC effects were, i.e., the higher participants' controlled attention allocation was in the incompatible condition *approach negative* compared to the compatible condition *avoid negative*. Furthermore, the higher the goal-oriented pursuit ratings were, the less pronounced the behavioural SRC effects were, i.e., the less prolonged RTs were in incompatible compared to compatible conditions. Thereby, P3 ERP SRC effects mediated the relation between goal-oriented pursuit and behavioural SRC effects, i.e., controlled attention allocation constituted a mechanism, how this personality trait influenced behaviour to negative stimuli. These relationships were not

found for positive pictures, what is in line with the assumption of positive stimuli being less relevant than negative stimuli (see 10.3).

As described in 2.1, I took the RIM as a dual-process model from cognitive-emotional psychology as theoretical background for these investigations on the electrophysiological correlates of SRC effects. For solving the conflict in incompatible trials, the reflective system has to inhibit the impulsive system, what – at the neuropsychological level – should be accompanied by enhanced controlled attention allocation as necessary in conflict situations. The P3 ERP was shown to reflect such controlled attention allocation (Nieuwenhuis, et al., 2005). Importantly, however, the P3 ERP was also shown to be modulated by earlier attentional phenomena such as automatic attentional allocation to eye-catching visual stimuli (Hajcak, et al., 2010). In this context, the P3 ERP should not be interpreted to reflect exclusively processes related to the reflective system, but rather to also reflect impulsive processes and the inhibitory interaction between the two systems. Also, in the context of the RIM, the P1 ERP might reflect processes solely related to the impulsive system. In line with the assumption, that such processes are not sufficient for solving the response conflict in incompatible conditions, the P1 ERP did not constitute a mediator in the above described model.

With regard to the initial hypothesis of the N1 ERP and the P1 ERP to depict automatic attention allocation to stimuli eliciting automatic approach-avoidance tendencies, there were only supporting findings for the N1 ERP in study B1. However, van Peer et al. (2007; 2009) showed modulations in the P150 ERP and P3 ERP (see 1.3.4), when investigating anxiety-related phenomena. Therefore, one might assume, that these attentional sub-processes are closely linked to anxiety-related phenomena and not sufficiently sensitive or informative in healthy individuals reacting to stimuli of general emotional relevance. Moreover, interindividual differences, such as found in study B2, result in variability of responses and – thereby – possibly in a masking of significant group effects. As discussed in 8.5, in large samples, the distribution of such interindividual difference might counterbalance each other and might cancel out such individual impacts on group level, a requisite not fulfilled in study B1 with a sample size of only 15 participants.

Furthermore, the impact of such individual influences might have been facilitated, because the used instruction might have prepared participants for the incompatibility of the

conditions *approach negative* and *avoid positive* as presented in one task block. This preparation effect might have reduced the impact of automatic attention allocation processes to incompatible trials as natural reaction ensuring an efficient conflict solution in a first step (Huang & Luo, 2006; see 10.3.4 for details). Rather, as suggested by Krieglmeyer and Deutsch (2010), such an instruction might lead to a general enhancement of cognitive control in the incompatible task block and – thereby – to a masking of bottom-up influences from automatic processes.

#### 10.2.2 N2 ERP and response inhibition

In study B1, I found significant SRC effects in the N2 ERP only for positive stimuli. As explained in detail below (see 10.3.1), negative stimuli seem to have been more important than positive stimuli. Therefore, the AAT conflict and the related SRC effects should be especially pronounced for negative stimuli. However, previous studies, which investigated the processing of emotional stimuli and – thereby – described the N2 ERP as reflecting the final steps of automatic attention allocation (Carretie, et al., 2004), showed unpleasant stimuli to be associated with reduced N2 amplitudes. In other words, negatively valenced stimulus material might have canceled out SRC effects in study B1. For this and the following reasons, I did not analyze the N2 ERP in study B2.

For a valid analysis of the N2 ERP, there might also be difficulties in the characteristics of the AAT conflict. With regard to the manikin version of the AAT, De Houwer et al. (2001) defined SRC effects as affective Simon effects<sup>33</sup>. First, a relevant characteristic, the given instruction, determines the correct response. Second, an irrelevant characteristic, the stimulus valence, must be ignored. Third, the required responses meaningfully relate to the irrelevant, but not to the relevant characteristic, since both the behavioural response and the irrelevant stimulus valence have affective properties. This equalisation by De Houwer et al. (2001) implies the AAT conflict to constitute more an R-R conflict than an S-R conflict. Thereby, it also indicates the N2 ERP to not be the most suitable component for investigating

<sup>&</sup>lt;sup>33</sup> In a classical Simon task, participants are instructed to respond to the colour of a presented stimulus by pressing either a left or right button. Although, the stimulus location is irrelevant, it influences the reactions: Reactions are faster, when the locations of the stimulus and the button correspond, i.e., when a stimulus, whose colour is associated with a left button press, is presented on the left side of the computer screen and vice versa. This is, because the behavioural response and the irrelevant stimulus location share the spatial dimension as a common dimension (De Houwer, et al., 2001).

the AAT conflict, since this component mainly reflects S-R conflicts. This explanation was also suggested by van Peer et al. (2007), who found only partly significant modulations of the N2 ERP, but no significant SRC effects (for details see 1.3.4). It remains unclear, if this argumentation is also valid for the joystick AAT as used in study B1.

Moreover, Stroop tasks reliably elicit N2 ERPs (Folstein & Van Petten, 2008). In Stroop tasks, participants react to the colour of a word while ignoring its meaning, which denotes a colour. In contrast to Simon tasks and the AAT, the relevant feature colour is also related to the response in a meaningful way (cf. De Houwer, et al., 2001). This constellation also represents an R-R conflict: The conflict results from two intuitive reaction tendencies competeting with each other, namely, the reaction related to the to-be-ignored meaning and the reaction related to the colour (cf. van Peer, et al., 2007). Rather, a systematic review of studies on the N2 ERP concluded this component to be elicited by the necessity to correct incorrectly prepared reactions (Folstein & Van Petten, 2008). This conclusion is in line with the fact, that several other conflict paradigms also reliably elicit N2 ERPs (Folstein & Van Petten, 2008). In Eriksen Flanker tasks, a central letter is flanked on the left and right side by other, identical letters. The central letter can be the same as the flanker letters (congruent conditions) or different from them (incongruent conditions). It determines the response which has to be conducted. In other words, two intuitive reaction tendencies compete with each other, namely the reaction related to the to-be-ignored flankers and the reaction related to the central stimulus (cf. van Peer, et al., 2007; Folstein & Van Petten, 2008). In GoNoGo paradigms - in cued task versions - a first stimulus indicates the participant to prepare the response. It is followed by a second stimulus either signaling to realize the response (Go condition) or to inhibit it (NoGo condition). Stop signal paradigms might be seen as a further development of GoNoGo tasks. Here, the inhibition of responses (stop condition) is signaled shortly after a Go signal, i.e., refers to an already initiated response. Both paradigms elicited N2 ERPs in a variety of studies (Folstein & Van Petten, 2008). Future studies have to clarify the relation of the definition by Folstein and van Petten (2008) to the AAT conflict. Thereby, task variants might be used for eliciting stronger response preparation effects than did the joystick AAT. A cued GoNoGo version (cf. study A3) or an instruction, which is not orientated at the valence and - thereby - does not result in a separate task block for all incompatible conditions, might allow for further investigating the N2 ERP and the related processes during the AAT.

#### 10.2.3 Hemispheric asymmetry

Study B2 also investigated the influence of interindividual differences in the personality trait goal-oriented pursuit as measured by the BAS-drive scale (Carver & White, 1994; see chapter 9 and 10.2.1). The BIS and BAS of Gray's (1994) RST were described in 1.1.2, together with possible relations to another influential theory of neuronal correlates of approach-avoidance reactions: Davidson's (1990) theory of hemispheric asymmetry assumes the processing of approach behaviour to be left-lateralized and of avoidance-behaviour to be right-lateralized. With regard to the findings of the current thesis, study A1 revealed approach compared to avoidance reactions to be associated with enhanced activation of left DLPFC (stronger decrease of HHb; for details see 4.5.1; cf. Berkman & Lieberman, 2010).

In the other fNIRS and fMRI studies, the analyses concentrated on SRC effects, i.e., on regulation processes, and did not explicitly test for effects solely due to the movement direction. In study A1, SRC effects were found in the right DLPFC and study A2 revealed different groups of the MAOA genotype to differ in neuronal SRC effects in the right DLPFC. Such a right-lateralized pattern is in line with other studies also revealing the regulation of inappropriate motor responses to cause mainly right-hemispheric PFC activity (Aron, et al., 2004; Knoch & Fehr, 2007). However, in study B1, source localization analysis revealed activity in right occipital areas to underlie SRC effects in the N1 ERP and activity in the left DLPFC and insula to underlie SRC effects in the N2 ERP. In study A3, the activity patterns in fMRI also comprising subcortical and parietal cortical areas were bilateral except for the few explicitly mentioned findings (see 10.1.2). These lateralizations were in line with previously suggested hemispheric differences with regard to specific regulatory sub-processes such as e.g., intrusion resistance (right superior frontal sulcus, Nee, et al., 2013). Future studies in fMRI should use adequate statistical analysis, such as e.g., the laterality index (LI) for conducting systematic comparisons of right and left hemispheric neuronal patterns (for a discussion of different analysis methods see Seghier, 2008; cf. also the meta-analysis of Wager et al. (2003) as described in 1.1.2). In this way, it might be possible to differentiate laterality effects due to approach-avoidance processes from laterality effects due to a specialization of regulatory sub-processes.

With regard to the above introduced aspect of a relation between Davidson's (1990) theory of hemispheric asymmetry and Gray's (1994) RST, Harmon-Jones and Allen (1997) –

as already mentioned in 1.1.2 – showed higher BAS scores to be accompanied by relatively stronger left than right hemispheric frontal activity (reduced alpha band activity). However, when further investigating this aspect, Hewig et al. (2006) showed higher BAS scores to be associated with greater bilateral activity in PFC (resting EEG, alpha power). The authors attributed this finding to the fact, that behavioural activation as assessed via the BAS scales can involve both, approach and avoidance reaction tendencies (see also 11.2; cf. Carver, 2006): Behavioural activation aims at the preservation of an advantageous state, whereby the adequacy of approach or avoidance reactions might depend on situational circumstances. This conclusion is in line with the mediation result of study B2, in which a sub-component of behavioural activation (goal-oriented pursuit, BAS-drive) determined the efficiency of ending the AAT conflict for negative stimuli by conducting a fast, correct incompatible reaction (approach negative, for a more detailed discussion see also 10.4.1). In future fMRI studies, neuronal patterns in the AAT should be related to participants' BAS scores, as done in study B2 for the P3 ERP: It should be clarified, if goal-oriented pursuit or the other two BAS-subscales (see 9.2) relate to laterality effects due to regulation (approach negative, avoid positive; Hewig, et al., 2006 and study B2) and/or due to action motivation (approach, avoid; Berkman & Lieberman, 2010).

#### 10.2.4 Neuronal networks in fMRI

In study A3, regulatory SRC effects for both positive and negative stimuli as indicators of cognitive control comprised activity in several areas. This is in line with previous assumptions of neuronal networks underlying cognitive control mechanisms: With regard to attentional processes, in their review, Corbetta and Shulman (2002) suggest a bilateral dorsal frontoparietal network, comprising the superior frontal cortex and the intraparietal cortex, to be responsible for top-down controlled attention allocation (see also 1.2.3). In our results, structures of this network were activated during the solution of the respone conflict in incompatible conditions (SFG, MFG, parietal cortices; see 10.1.2). As the P3 ERP in study B2 (see however the critical comment on the P3 ERP in 10.2.1), this finding might indicate the expected enhanced controlled attention allocation in incompatible conditions.

While many theories assume the PFC (specifically the DLPFC; e.g. Miller, 2000) and the dACC (MacDonald, et al., 2000; see also 1.2.2) to constitute the main control centres of the brain, Dosenbach et al. (2008) emphasized a repeated finding in the organization of complex

biological systems: Important control functions are usually distributed to several instances for ensuring the functionality of the system in case of the impairment of one instance. In line with this suggestion, data from resting state-functional connectivity MRI (rs-fcMRI; analyzed with graph theory and hierarchical clustering) revealed two distinct top-down control networks: A fronto-parietal network, comprising the DLPFC, IPL, dorsal frontal cortex, intraparietal sulcus, precuneus and middle cingulate cortex, was shown to be responsible for the initiation and adjustment of control on a trial-to-trial basis. Since its structures overlap with the dorsal frontoparietal network by Corbetta and Shulman (2002), Dosenbach et al. (2008) suggested it to be responsible for both the initiation of attentional control and the processing of feedback to rapidly adjust control settings. Furthermore, this network is also responsible for sustained activity between cues and following targets. With regard to the findings of study A3, structures of this network showed SRC effects at the cue event for negative pictures (see 10.1.2 for details), what indicates a specifically strong sustainment of control during the ISI in this condition.

In contrast, a cingulo-opercular network – comprising the aPFC, anterior insula/frontal operculum, dACC/medial superior frontal cortex and thalamus – was shown to provide stable set-maintenance over the entire task epoch (Dosenbach, et al., 2008). In study A3, such a set maintenance might be seen in keeping the instruction rules in mind and activate them specifically in incompatible conditions. Again, most distinctively, the neuronal SRC effects for negative pictures at the cue event matched this network. This confirms the interpretation, that negative incompatible reactions need a high amount of cognitive control, what might also include the foregrounding of the incompatible instruction rules in WM (Nee, et al., 2013).

A third instance might be seen in the cerebellum, which was suggested to be interposed between the other two networks (Dosenbach, et al., 2008). It was shown to be involved in the processing of errors and to be connected to the DLPFC, IPL and thalamus. Therefore, an interchange of error information with the other two networks is likely, contributing to the optimization of performance. In study A3, the cerebellum was not completely assessed, since current fMRI protocols do not allow for the measurement of the entire distance from the top to the bottom of the brain without substantially worsening the temporal solution. Future AAT studies in fMRI might concentrate solely on the cerebellum for showing its meaning in automatic approach-avoidance reactions and their regulation.

While the present findings revealed first insights into neuronal processes underlying the regulation of automatic approach-avoidance tendencies, future studies have to clarify the cooperation of these single instances. Connectivity and network analyses of activity assessed during the AAT (cf. 11.3) constitute an essential development to attribute neuropsychological functions such as attentional processes to simultaneously activated regions.

### 10.3 Valence specificity:

## Approaching the negative is not avoiding the positive

This chapter refers to differences in the processing of negative and positive stimuli at group level. Thereby, the results reported above (10.1 and 10.2) are reconsidered with a focus on valence specific findings. The following chapter (10.4) discusses those findings of the current thesis, which showed such differences to also comprise individual variations.

#### 10.3.1 Studies A1 and B1

As mentioned in the General Introduction (2.1), the current thesis separately analyzed the processing of positive and negative stimuli. In study A1, both valence categories elicited neuronal regulatory SRC effects in right DLPFC. However, with regard to the behavioural level, the expected SRC effects in terms of increased RTs for incompatible compared to compatible conditions emerged only numerically, but not statistically significantly. Rather, RTs were generally shorter for negative compared to positive pictures.

In study B1, for positive pictures, electrophysiological SRC effects were observed for the N1 and N2 ERP in terms of higher amplitudes during the incompatible condition *avoid positive* compared to the compatible condition *approach positive*. In other words, for positive pictures, the AAT conflict was efficiently regulated and – thereby – the influence of incompatibility on behaviour reduced as reflected in no behavioural SRC effects. In contrast, for negative pictures, there were no electrophysiological SRC effects, but behavioural SRC effects: Participants made fewer errors and reacted faster during *avoid negative* compared to *approach negative*.

These findings might be understood in the context of evolutionary based considerations (Flykt, 2006; Ohman, et al., 2001): There, negative stimuli are suggested to be generally more important for survival than positive stimuli. This argumentation might explain the faster RTs for negative stimuli in study A1. Moreover, the incompatible AAT condition for positive pictures might be merely unpleasant, while, for negative pictures, it might represent a dangerous situation. This might have resulted in the more pronounced behavioural SRC effects in study B1 (see 10.3.4 for a more detailed argumentation). However, from such a perspective, one would also expect differences in SRC effects at the neuronal level. In

general, negative stimuli should be associated with stronger regulatory effects. However, the sample sizes of only 15 participants each might have been too small for reliably detecting all differences. Furthermore, such differences might be more pronounced in other brain regions than assessed with fNIRS. Another reason for the found differences might have been the typicality of the used pictures for the two valence categories positive and negative.

### 10.3.2 Typicality of pictures

The IAPS picture set for studies A1 and B1 was orientated at one of the other two AAT studies using IAPS pictures (Wiers, et al., 2009; see also 2.1). There, in contrast to Lavender and Hommel (2007b), the two valence categories did not differ with regard to arousal. However, a closer inspection revealed six of the positive pictures - to my opinion - to not depict typical positive scenes. Furthermore, in study A1, analysis revealed stronger activation (larger increase of O₂Hb and larger decrease of HHb) in dorsal frontomedian cortex (DFMC) for positive pictures in general. This might indicate positive pictures to have been more difficult to categorize as being positive than negative pictures as being negative: The DFMC is involved in self-control (Brass & Haggard, 2007) and rule application under uncertainty (Volz, et al., 2003), i.e., in internally guided behaviour. In the used joystick version of the AAT, participants had to classify pictures according to their valence and had to remember the instructed direction. The stronger activation was observed independently from the instructed direction. Therefore, it might indicate enhanced cognitive effort for recognizing the valence of the positive pictures. This laborious classification process might also be reflected in the enhanced RTs for positive pictures. Furthermore, non-typical positive pictures (e.g. butterflies) might have elicited only weak approach tendencies.

Previous studies already addressed this problem: Lavender and Hommel (2007b) used participants' explicit valence ratings for dividing the picture stimuli into moderately vs. extremely positive and negative stimuli (see appendix of this study). The so assessed valence strength did not moderate the results, when participants consciously evaluated the picture valence (this question was only tested for this affective instruction condition, see p. 1288 of Lavender & Hommel, 2007b). However, the positive and negative stimuli were not matched for arousal prior to their selection and the authors did not report arousal ratings of their participants. Chen and Bargh (1999) followed considerations on the moderating effect of attitude strength on phenomena such as the affective priming effect (see 1.1.1) and included

the factor attitude strength into their analyses. They categorized the attitude strength of the used word stimuli as weak or strong according to participants' categorization speed (goodbad). These data were taken from a prior study, which also contained pre-studies aiming at the collection of normative evaluation data of these stimuli (Bargh, et al., 1992, appendix). When participants consciously categorized the valence of the words (Chen & Bargh, 1999, exp. 1, positive – pull, negative – push), there was no interaction with congruency (i.e., with SRC effects), but solely a significant main effect of attitude strength indicating generally faster reactions for strong attitude objects (see footnote 1, p. 223 of Chen & Bargh, 1999). When participants unconsciously processed the valence (Chen & Bargh, 1999, exp. 2, always push or pull, see description in 1.3.1.2), this main effect was not replicated, what the authors interpreted to be "[...] consistent with the interpretation that the two sets of stimuli differ in terms of how quickly they are consciously evaluated but not how quickly they are responded to in general." (Chen & Bargh, 1999, footnote 2, p. 223, line 9-12). This conclusion is in line with Bargh's (1992) assumption on the independence of automatic attitude activation from attitude strength (cf. 1.1.1). However, the main effect of attitude strength in case of the explicit valence instruction is similar to the assumed influence of minor typicality for the positive pictures in study A1.

While the argument of negative stimuli being more important still might have been valid, I assumed such difficulties caused by the content of the positive pictures to also have influenced the results. Therefore, for the following studies, I chose more typical stimuli for human approach and avoidance tendencies: Positive pictures depicted delicious food, erotic scenes and funny leisure time scenes, while negative pictures contained dangerous animals and criminal scenes. Again, the arousal level of positive and negative pictures was matched according to the indications of the original rating sample of Lang et al. (2005). This final picture set was used in studies A2, A3 and B2 (see figures 4-6). Applying that picture set revealed clear behavioural SRC effects for both positive and negative stimuli at group level (see chapters 5, 6 and 9; see 10.4 for a discussion of the influences of interindividual differences).

#### 10.3.3 Study A3

In study A3, the used GoNoGo version of the AAT allowed not only for investigating the regulation of automatic approach-avoidance reactions for conducting an alternative,

incompatible reaction, but also for investigating their regulation when just inhibiting compatible reactions in NoGo conditions. The detailed neuronal results were already reported above (see 10.1.2). With regard to the behavioural level, positive pictures caused the expected SRC effects: RTs were longer for incompatible than compatible conditions. For negative pictures, SRC effects were reversed than expected: Incompatible reactions were faster than compatible ones. However, the explicit valence ratings revealed participants to have perceived the three valence categories negative, neutral and positive as expected. Importantly, there was neither any difference between the three categories with regard to the arousal ratings nor between negative and positive stimuli for the absolute valence ratings.

Regarding the neuronal and behavioural results of study A3 together, they support the assumption of negative stimuli being more important than positive stimuli. Here, I suggest an extension of this argumentation to the behavioural level. Specifically the findings of study A3 indicate a stronger elicitation of avoidance tendencies by negative stimuli than of approach tendencies by positive stimuli: For negative pictures, the cue event elicited strong response preparation effects. This pre-regulation, which emerged as soon as the conflict was given, resulted in reversed behavioural SRC effects. At the move event, the mediation analysis showed activity in the right midbrain including the red nucleus, i.e., an area responsible for the initiation of responses (Gruber & Gould, 2010), to mediate the relation between participants' behaviour and their valence and arousal ratings: The more negative and arousing participants perceived the pictures, the stronger they showed response initiation processes, when realizing the reaction, and - thereby - the stronger the observed reversed behavioural SRC effects were. In other words, the reversed behavioural SRC effects might be due to the task variant, which comprises the possibility to prepare reactions. Thereby, as outlined in more detail in 10.5.3, this preparation might have resulted in extremely fast reactions in incompatible conditions via subcortical pathways including the red nucleus. In NoGo conditions, negative stimuli were associated with neuronal reversed SRC effects in the right SPL. This activity pattern indicates the inhibition of automatically elicited compatible response tendencies to need more regulatory resources than the inhibition of prepared incompatible reactions.

In contrast, positive stimuli seem to have elicited relatively weak automatic approach tendencies: Neuronal activity at the cue event indicating a pre-regulation of the required responses was only found in frontal areas. At the move event, i.e., at the time point of the actual reaction, broader SRC effects emerged in frontal and parietal areas. However, the

thalamus, the ACC and the insula did not show such neuronal SRC effects. This might be seen as reflecting the AAT conflict with positive stimuli to constitute an only marginal conflict situation, which did not elicit attentional alerting and conflict monitoring processes. In the NoGo conditions, there were no reversed SRC effects, what further supported the interpretation, that positive pictures elicited only weak compatible approach tendencies: These weak tendencies did not require strong inhibition in the NoGo conditions.

This interpretation is further supported by the findings of habituation effects in important regulatory areas only for positive, but not for negative pictures: Differences between the two valence categories were also found with regard to habituation effects over the five runs: For negative pictures, the necessity of solving the conflict in incompatible conditions already at the cue event (ACC) and of activating higher response control mechanisms in the NoGo conditions (SPL) remained stable. In contrast, for positive pictures, activity decreased in frontal and parietal preparatory areas in Go conditions (SMA, preCG, postCG) indicating this conflict to weaken over the time.

With regard to previous studies, Roelofs et al. (2009) conducted a conjunction analysis as test for commonly activated areas of processing the AAT with angry and happy faces. This analysis revealed the above reported activity in left VLPFC and OFC to be caused by both angry and happy faces (see 10.1.3). In study A3, it was not adequate to conduct such a conjunction analysis, since the cued GoNoGo version with each trial comprising both a cue and a move event caused the above reported differences in the time point of conflict processing: Regulatory activity for positive stimuli mainly occurred at the move event, while SRC effects for negative stimuli were concentrated on the cue event. Therefore, a conjunction analysis would have required the comparison of contrasts from different time points. This, however, would also include a comparison of different processes, since preparing reactions at the cue event are not completely identical with performing the reactions at the move event.

In sum, the behavioural and neuronal findings of study A3 as well as their relation (mediation analysis) revealed clear differences between the AAT conflict for negative and positive stimuli. While negative stimuli elicited strong avoidance reactions, positive stimuli elicited only weak approach tendencies. This difference is in line with the assumption that fast avoidance reactions in dangerous situations are more important for guaranteeing an

organisms' survival than fast approach reactions in pleasant situations. As a result, the inhibition of avoidance tendencies in incompatible AAT conditions with negative stimuli comprised an enormous conflict potential, while the inhibition of approach tendencies towards positive stimuli equalled merely an unpleasant situation.

#### 10.3.4 Theoretical and experimental background: Negativity bias

Negative stimuli seem to have been more important in the current studies. The above suggested extension of this concept to the behavioural level is derived from previous statements in the classical literature: Miller (1944) summarized results on conflicts involving approach-avoidance reactions in rats and humans. His 3<sup>rd</sup> postulate says that "The strength of avoidance increases more rapidly with nearness than does that of approach. In other words, it may be said that the avoidance gradient is *steeper* than the approach gradient." (Miller, 1944, p. 433, line 41-44).

The postulate of Miller (1944) fits later experimental findings on prefered processing of negatively valenced stimuli. In general, the term *negativity bias* refers to a greater sensitivity for negative than positive information (Rozin & Royzman, 2001). In their review, Rozin and Royzman (2001) subsumed the negativity bias to work via four principles: First, the principle of negative potency means that negative events are more potent and of higher salience than objectively equal positive events. A related phenomenon is *loss aversion*, i.e., the subjective experience of a higher intensity of negative feelings in case of loosing an object than of positive feelings in case of gaining an object (Kahnemann & Tversky, 1984). Second, the principle of steeper negative gradients implies that – compared to the positivity of positive stimuli – the negativity of negative stimuli increases more rapidly when spatially or temporally approaching them. Third, the principle of negativity dominance means that the holistic perception of an entity comprising both negative and positive elements is more strongly influenced by the negative values. Fourth, the principle of greater negative differentiation means that – compared to positive stimuli – the conceptual representations of negative stimuli and the related response patterns are more elaborated and fine-tuned.

With regard to the generalizability of the negativity bias, Taylor (1991) concluded that negative compared to positive events mobilize an organism stronger with regard to

physiological arousal as well as cognitive and emotional reactions (cf. below 10.5.3). A more recent review further subsumed the pronounced impact of the negativity bias on cultural, social and everyday phenomena (Baumeister, et al., 2001). As Rozin and Royzman (2001), it also reviewed experimental research showing the negativity bias to significantly influence a huge variety of psychological areas such as perception, attention, learning, mood, memory and impression formation.

Most interesting for the current thesis is the question, at which stage of information processing the negativity bias happens. ERP studies addressed these detailed mechanisms. Ito et al. (Ito, et al., 1998) showed negative compared to positive stimuli to elicit larger amplitudes of the late positive potential (LPP), i.e., stronger emotional reactions. Thereby, the two valence categories were matched with regard to frequency, absolute valence value and arousal. This result revealed the negativity bias to operate at the level of evaluative categorization processes, which are assumed to happen automatically (see 1.1.1). However, Huang and Luo (2006; P2 ERP; cf. also Huang & Luo, 2007) and Smith et al. (2003; P1 ERP) showed early attentional processes to already reflect the negativity bias in terms of higher attention allocation to negative than positive stimuli (cf. the results of study B1 on the N1 ERP). In a Stroop task, Pratto and John (1991) showed negatively compared to positively valenced personality traits to attract more attention resulting in prolonged RTs. They suggested this result to reflect an automatic vigilance mechanism in terms of negative stimuli automatically attracting more attention than positive stimuli. While Pratto and John (1991) draw this conclusion on problems induced by negativity, Öhman et al. (2001) and Flykt (2006) saw the original function of such a vigilance bias in the faster detection of negative stimuli and - thereby - in the guarantee for fast, advantageous responses. In sum, these findings showed the negativity bias to not happen at the response output stage, but earlier at information processing stages. Ito et al. (1998) saw the advantage of such an early mechanism in the effortless re-direction of attention to threatening events.

The computational model of evaluative space by Cacioppo et al. (1997; see also Cacioppo & Berntson, 1994) represents a theoretical framework for relying the negativity bias to its behavioural output. Cacioppo et al. (1997) emphasized, that positive and negative evaluative processes and the related formation of attitudes are not equivalent and interchangeable. Thereby, the specific characteristic of the negative motivational system is the negativity bias, while the positive motivational system is characterized by the positivity offset. Cacioppo et al. (1997) defined the negativity bias as a higher reactivity of the negative

compared to the positive motivational system: Comparable amounts of input result in a stronger activation: "With each unit of activation, the change in negative motivational output is larger than the change in positive motivational output." (Cacioppo, et al., 1997, p. 13, line 27-29, left text column). This principle results in the steeper gradient of the activation function of negativity in the evaluative space (see figure 26) and explains the more pronounced influence of negativity than positivity on the psychological domains reported above. With regard to behaviour, it matches the postulate by Miller (1944), that the gradient of avoidance reactions is steeper than this of approach reactions. The positivity offset is relevant at low levels of motivational activation. Cacioppo et al. (1997) stated that "[...] the positivity offset is the tendency for there to be a weak positive (approach) motivational output at zero input [...]" (p. 12, line 8-10, right text column). In other words, the necessary level of input for activating the positive motivational system is lower than for the negative motivational system. At such low levels of input, the intercept of the positivity function is steeper than of the negativity function, what results in more positive evaluations (cf. the mere exposure effect, see 1.1.3.1).

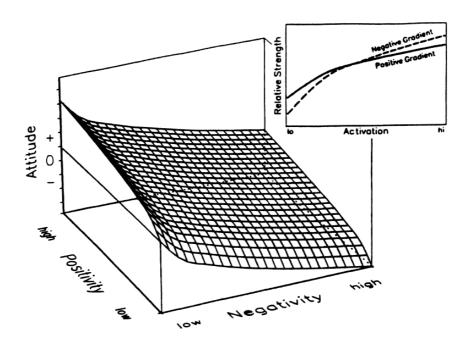


Figure 26: The bivariate evaluation space and its attitudinal surface.

This surface reflects the attitude (in relative units) of a person toward (+) or away from (-) a specific stimulus.

The smaller graph on the right side relates the strength of positive and negative forces to activation or movement in the same way as suggested by Miller (1944).

Modified according to Cacioppo and Berntson (1994) and Cacioppo et al. (1997).

Explanations for the existence of the negativity bias assume it to be both innate and acquired via experience. The review by Rozin and Royzman (2001) distinguishes three perspectives. According to evolutionary orientated approaches, the negativity bias emerges, because it results in adaptive advantages: Fast reactions to negative stimuli as dangerous and more likely perilous situations contribute more to an organisms' survival than fast reactions to positive stimuli, which are associated with only harmless consequences. Developmental theories extend this argumentation to a description of the negativity bias as built-in predisposition, since learning opportunities might be rare. Mechanistic theories argue via psychological laws: The lower frequency of negative events in everyday life makes them more informative. Also, negative events are more contagious, since they encroach upon neighbouring domains more easily and are more resistant to elimination attempts. With regard to influence on society, the negativity bias might also be supported by the pursuit of purity and perfection as principles of many religious and moral concepts: Perfect standards are easier to fail than to achieve.

However, the negativity bias is also associated with costs (cf. the above reported results of Pratto & John, 1991). Lang (1995) reported the free viewing time for negative IAPS pictures to be longer than for positive IAPS pictures. Such an attachment of attention might account for longer RTs for negative than positive stimuli in some AAT studies using words: They might have equalled lexical decision tasks (van Dantzig, et al., 2008; cf. Wentura, et al., 2000), from which similar distorting influences of enhanced free viewing times are known (e.g. Meier & Robinson, 2004). These results are reversed than my results in study A1 (shorter RTs for negative than positive pictures; see 10.3.1; cf. Lavender & Hommel, 2007b), but clearly indicate the necessity to control for such distortions. Here, for future studies, the joystick version of the AAT is advantageous, since it allows for dividing RTs into initiation times and movement times (Solarz, 1960; cf. van Peer, et al., 2007). The former parameter might be more strongly influenced by such problems.

### 10.3.5 The usage of neutral stimuli

In study A3, I relativised participants' reactions to positive and negative stimuli at their reactions to neutral stimuli. Thereby, I aimed at a separation of effects caused by the valence from effects caused by the mere presentation of stimuli. Therefore, the above reported results of study A3 are corrected for such distorting influences. With regard to the two

different time points of main regulatory activity (negative stimuli: cue event vs. positive stimuli: move event), which did not allow for a direct statistical comparison of positive and negative stimuli (see 10.1.3), this extraction of the mere valence effects equalled a standardization to a zero-point and upvalued the descriptive comparison of positive and negative stimuli.

Until now, several previous studies also used neutral stimuli: Wentura et al. (2000, exp. 3) showed no differences between the RTs for approach and avoidance reactions with neutral adjectives. Van Dantzig et al. (2008, words) and Volman et al. (2011b, facial expressions; cf. also the footnote in 6.1.3) used neutral stimuli, but did not further analyze the related reactions.

It should be noted, however, that the used neutral pictures might have represented another class of pictures than the affective pictures, since they depicted single objects of utility and not complex scenes. Future studies aiming at the investigation of approach-avoidance processes directly related to neutral stimuli might use e.g., abstract patterns for guaranteeing the same level of complexity.

#### 10.3.6 Interindividual differences

Besides problems with regard to the picture material (see 10.3.2), I suggest another factor to influence the finding of significant SRC effects at group level. Interindividual differences in the processing of conflicts or emotion regulation might also be relevant for the processing of the AAT conflict (cf. the results of study A3). This aspect was the main research topic of studies A2 and B2. These results are discussed in the next chapter. In sum, they also revealed evidence for a higher importance of negative stimuli. This is in line with the 4<sup>th</sup> postulate of Miller (1944), which says that "[...] The strength of the tendencies to approach or to avoid varies with the strength of the drive upon which they are based. Thus, an increased drive may be said to raise the *height* of the entire gradient." (p. 434, line 1-4; cf. the general postulate on the negativity bias, 10.3.4).

#### 10.4 Interindividual differences

The current thesis followed previous assumptions that automatic approach-avoidance reactions are universal reaction tendencies to positive and negative stimuli, respectively (Carver, 2006). As mentioned above (2.2.1), so far, the influence of interindividual differences on these processes in healthy participants reacting to stimuli of general emotional relevance has only been investigated by Puca et al. (2006): High expressions of avoidance motives as assessed via the MMG were associated with higher peak force for avoidance than approach movements. The reversed pattern was found for low expressions of avoidance. Nevertheless, there are several other results and interpretations emphasizing the possibility of relevant influences of interindividual differences with regard to the strength of automatic approach-avoidance tendencies and the efficiency of the related regulation processes.

Krieglmeyer and Deutsch (2010) suggested a theoretical framework for such influences as already cited in 2.2.1. They used this framework for investigating the strength of avoidance tendencies for spider pictures in individuals with various levels of spider phobia: The stronger participants rated their fear of spiders, the more strongly they showed a behavioural tendency for avoiding spider pictures (see 1.3.3 for details). Similarly, study A4 showed a significant correlation between individuals' appraisal of alcohol consumption and activity of left OFC: The more participants expected alcohol to have positive effects in terms of emotional regulation, the stronger activated their left lateral OFC was during approaching compared to avoiding alcohol pictures. In other words, interindividual differences in the appraisal of alcohol consumption defined the valence of the combination of an alcohol picture and a movement direction.

## 10.4.1 Study B2: Goal-oriented pursuit as mediator

While these studies concentrated on the processing of specific stimuli in specific subgroups, I was also interested in interindividual differences among healthy participants reacting to stimuli of general emotional relevance. Thereby, trait personality characteristics were in the focus of interest. Both, the investigated approach-avoidance reactions and personality traits reflect long-lasting individual patterns of stimuli evaluations and reactions

(cf. Buckholtz, et al., 2008). In contrast, state personality characteristics refer to only temporary influences of affective experiences and thoughts on emotion and behaviour.

Study A1 and B2 showed only trait personality characteristics to influence the assessed approach-avoidance reactions. In study A1, there was a significant negative correlation between the level of trait anxiety (STAI-X2) and the activity in left DLPFC: The higher participants indicated their levels of trait anxiety, the stronger their decrease of HHb (i.e., the stronger their cortical activation) was in left DLPFC during approach compared to avoidance movements. For a further interpretation of this result see the discussion of study A1 (4.5.1). In study B2, I concentrated on a personality trait, which should be important for the AAT conflict. As described in the General Introduction (see 2.2.1) and 9.2, solving the AAT conflict comprises active behavioural and cognitive regulation of approach-avoidance behaviour. The personality trait goal-oriented pursuit as derived from Gray's (1994) RST significantly influences such processes (Carver & White, 1994; Passamonti, et al., 2008b). Furthermore, I chose a mediator approach for investigating such influences on neuronal and behavioural processes. Neuronal activity was assessed in terms of the P3 ERP as a component reflecting controlled attention allocation (Nieuwenhuis, et al., 2005). For negative pictures, the neuropsychological mechanism of controlled attention allocation mediated the relation between personality and behaviour: Stronger goal-oriented pursuit was associated with higher controlled attention allocation to the incompatible than the compatible condition and thereby - with higher efficiency of behavioural regulation in terms of less automatic avoidance tendencies in response to negative pictures. For positive pictures, no such relations emerged. These results are in line with the above described differences between the processing of positive and negative pictures (see 10.3): The incompatible condition approach negative constitutes a greater conflict situation than avoid positive due to a stronger elicitation of avoidance tendencies to negative than approach tendencies to positive stimuli. In accordance with this interpretation, in study B2, controlled attention allocation, i.e., a neuropsychological regulation mechanism, and goal-oriented pursuit, i.e., the willingness to actively regulate behavioural responses, were more closely related to the AAT conflict with negative than with positive stimuli.

Importantly, such a mediation model was not fulfilled for the state characteristics assessed via the PANAS. However, the PANAS might not be the best questionnaire for this issue, since it assesses the current affective state and not the amount of the current willingness to achieve goals. Furthermore, future studies should also investigate the role of

impulsivity (cf. Friese, et al., 2008). While study B2 concentrated on personality characteristics related to the regulation process, impulsivity and emotional reactivity might be very influencable with regard to automatic reaction tendencies.

## 10.4.2 Study A2: MAO-A genotype as moderator

With regard to moderator designs, i.e., the influence of a variable defining categorical subgroups with different qualities (cf. Hayes, 2012), Volman et al. (2011b) investigated the influence of the salivary level of endogenous testosterone in male participants on approach-avoidance reactions to facial stimuli. Both, behavioural and neuronal reactions were modulated as described in 10.1.3. Van Peer et al. (2007, 2009) concentrated on the interaction of social phobic personality traits and cortisol administration as described in detail in 2.2.1.

In study A2, my moderator variable was the variation in the gene encoding *MAOA* (*MAOA*-uVNTR), which influences both emotional reactivity and cognitive regulation (Passamonti, et al., 2006; Buckholtz, et al., 2008). These results were already reported in detail in 10.1.1. With regard to differences between the processing of negative and positive stimuli, solely *MAOA-H* carriers seemed to have been responsive for different effect of the two valence categories: Their presumed pre-regulation of the AAT conflict via other brain areas than the DLPFC, such as e.g. the dACC, was accompanied by a lower error frequency for reactions to negative than positive stimuli. In other words, in this sub-group, which was previously associated with higher cognitive control capacities than the other genotype groups (cf. Enge, et al., 2011), at least one behavioural parameter revealed the AAT with negative stimuli to be more efficiently processed. However, the reliability of these findings has to be shown in larger, stratified samples.

## 10.4.3 Influence of sample size and different analysis options of RTs

The results of study B2 and A2 revealed variables, which are closely related to emotional reactivity and cognitive regulation capacity, to contribute to the processing of the AAT conflict and to the final strengths of the responses. Krieglmeyer and Deutsch (2010) assumed "[...]

that individual differences in approach-avoidance reactions towards normatively positive and negative words are small." (p. 826, line 34-36, left text column). I also assume SRC effects to represent a general phenomenon, however, the present results clearly vote for a significant influence of interindividual differences during the processing of stimuli of general emotional relevance. This interpretation is further supported by the fact, that I followed the warning of Krieglmeyer and Deutsch (2010; see 2.1) and unambiguously defined pull movements as approach and push movements as avoidance responses. Therefore, distortions of the results due to this aspect can be excluded.

Rather, the current results hint to another important aspect, namely the sample size. Studies A1 and B1 used the same picture material, however, behavioural SRC effects for negative pictures were only significant in study B1, but not in study A1 (both n=15). As shown in study B2, SRC effects can be significantly affected by interindividual differences in personality traits. In this larger sample (n=34), SRC effects were also significant at group level. Therefore, I conclude, that in larger samples interindividual differences might counterbalance each other, while, however, in smaller samples, the distribution of personality expressions might not be broad enough to cancel out such individual impact on group level. As a result, in smaller samples, SRC effects as general behavioural patterns might not be clearly observable at group level. Such an effect might also account for the differences in the processing of positive pictures. In study A1, there were non-significant reversed SRC effects, while in study B1, there were significant SRC effects. Moreover, in study B1, significant behavioural SRC effects for negative pictures were only obtained, when applying a penalty correction for too many errors in the condition approach negative. Otherwise, study B1 revealed the same behavioural results as study A1: RTs were generally faster for negative than positive pictures. This confirms my conclusion, that distortions of reaction time patterns are more likely and influential on smaller samples.

For reducing distortions of group results due to intraindividual reaction variability, previous research on the AAT used different methods. Very early AAT studies used mean reaction times for analyzing RTs, then, several outlier criteria such as e.g., ± 3 standard deviations (SD) were applied. Finally, median RTs were used, since, there, the influence of outliers on individual medium RTs is reduced. The work by Krieglmeyer and Deutsch (2010) is the only systematic comparison of several analysis methods for different AAT versions. It revealed the magnitude of SRC effects to be sensitive to intraindividual variability and, therefore, to depend on the analysis method. Recent AAT studies tried to implement a further

correction method as used in other implicit tasks. With regard to distorting influences of excessive intraindividual variability as given e.g., in RTs of patients samples, so called D-scores were reported: The difference between the mean RTs of two conditions is divided by the personalized standard deviation of the response latencies of the two included conditions (see Wiers, et al., 2011). This procedure was adopted from technical studies on such influences on the implicit association task (IAT; Greenwald, et al., 2003), while similar technical studies directly on the AAT are still missing.

In short, there are several considerations in previous studies, that SRC effects can be masked by non-systematic intravariability influences and systematic interindividual differences. Barkby et al. (2012) were the first to take into account the possibility of similar effects by systematic differences in error rates, i.e., in the frequency of "avoided" reactions. While they applied a penalty correction in a sample of alcohol addicted patients reacting to addiction related stimuli, in study B1, I was confronted with systematic differences in error rates in a sample of healthy controls: Although the overall error rates were small, there was a significant difference between the incompatible and compatible condition, but only for negative pictures. So, the finding of enhanced error rates was valence specific. Moreover, these low error rates also significantly differently affected the number of remaining correct reactions per condition (see added analysis in the footnote in 8.4): Corresponding to the error analysis, there were significant reversed SRC effects for the negative pictures, i.e., more remaining correct reactions for the compatible condition avoid negative than for the incompatible condition approach negative. SRC effects for positive pictures were also reversed, but not significant. The reversed SRC effect for the negative pictures was significantly stronger than for the positive pictures. To my opinion, the distortion of RTs by such a systematic "avoidance" of the high-conflict reactions approach negative has to be taken into account. Moreover, the directions of SRC scores for RTs were the same for both analyses with regard to negative and positive pictures (for negative pictures: as expected, incompatible > compatible; for positive pictures: reversed to the hypothesis, compatible > incompatible). However, as discussed in the discussion section of study B1 (8.5), these results are preliminary and the analysis of the AAT has to be further developed with regard to such issues.

#### 10.4.4 Influence of gender

With regard to modulating influences of gender, the small sample size of n=15 in the basic studies A1 and B1 did not allow for such a testing. In study B2, I compared female and male participants with regard to all assessed variables (see 9.4 for details). There were no differences, except for the BIS scale: Female participants reached higher scores than male participants. This difference, however, did not influence the reported mediation results.

In study A2, especially the small sample size of the *MAOA-L* subgroup complicated testing for gender differences (n=7; 5 male, 2 female participants). Actually, one might doubt the validity of any testing with only five or two members in one subgroup. However, in an explorative manner, I analyzed the data for gender influences, since results of the *MAOA-H* carriers (n=22; 12 male, 10 female participants) might allow for the generation of subsequent research questions. The following analyses are only reported here, but were not reported in the publication of study A2.

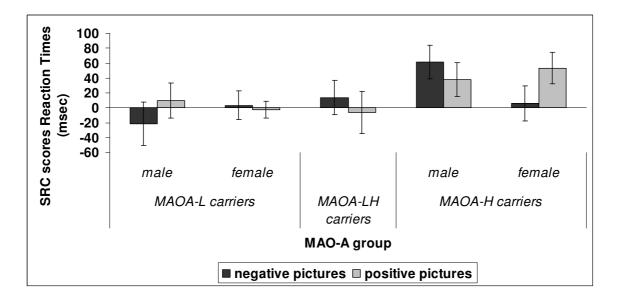
Since only female individuals can be MAOA-LH carriers, in addition to the reported comparisons of all three subgroups, I compared exclusively MAOA-L to MAOA-H carriers. This test revealed no differences in the distribution of gender ( $\chi^2(1)=.62$ , p=.67, Fisher's exact test for 2 x 2 contingency tables). Furthermore, I repeated the analyses of RTs, errors and functional data with gender as second between-subject factor, i.e., as a covariate: There were no significant influences of gender (all p > .05). In a further analysis, I separately tested MAOA-L and MAOA-H carriers: Neither in MAOA-L nor in MAOA-H carriers, there were gender differences in any variable (see below for details, table S16). Only by trend, female compared to male MAOA-H carriers made fewer errors during avoiding positive pictures (Z = 1.75, p = .08).

Table 16: Comparisons of male and female participants

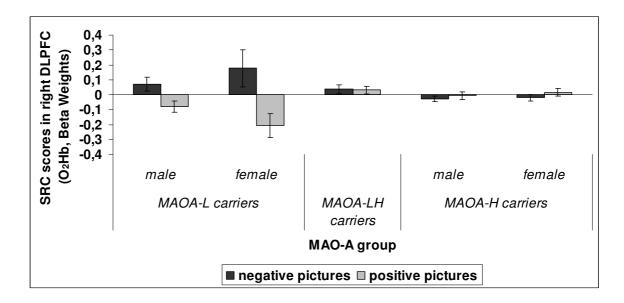
	MAOA-L carriers (5 male, 2 female participants)	<i>MAOA-H</i> carriers (12 male, 10 female participants)
RTs SRC scores: negative pictures	t(5)=.5, Z<.001	t(20)=1.71, Z=1.32
RTs SRC scores: positive pictures	t(5)=.3, Z=.39	t(20)=.51, Z=.53
O <sub>2</sub> Hb SRC scores in right DLPFC: negative pictures	t(5)=1.02, Z=1.16	t(20)=.27, Z=.46
O₂Hb SRC scores in right DLPFC: positive pictures	t(5)=1.67, Z=.78	t(20)=.55, Z=.46
Errors: avoid negative	Z<.001	Z=.1
Errors: aproach negative	Z=.98	Z=1.28
Errors: avoid positive	Z=.98	Z=1.75 (p=.08)
Errors: aproach positive	Z<.001	Z=1.29

Comparisons by means of t-tests and non-parametric Wilcoxon-W tests revealed no significant differences.

A)



B)



C)

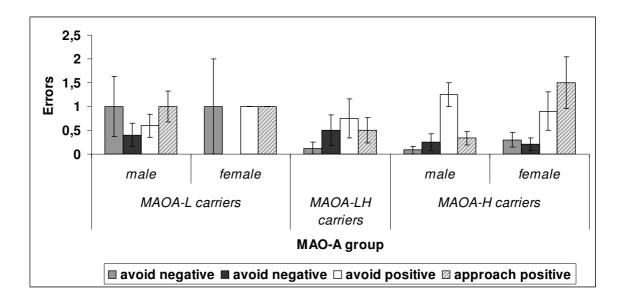


Figure 27: Comparisons of male and female participants (mean, SEM)

Comparisons revealed no significant differences with regard to A) RTs SRC scores, B) O<sub>2</sub>Hb SRC scores in right DLPFC and C) errors. See table 16 for statistical details.

As mentioned in the discussion of study A2 (see 5.5), *MAOA* can be seen as a "vulnerability gene", whereby gender seems to influence the risk for pathologies differently in the genetic subgroups. Future studies should test such an interaction between genotype and gender in a stratified sample.

The first AAT study by Solarz (1960) showed the valence x movement interaction as reported in 1.3.1 to be stronger in female than male participants. In subsequent AAT studies, possible gender effects were controlled by investigating only women (Rotteveel & Phaf, 2004) or men (Cretenet & Dru, 2004). Moreover, Seidel et al. (2010b; cf. Seidel, et al., 2010a) analyzed the influence of both the gender of participants and the gender of the presented emotional face on approach-avoidance reactions in a joystick AAT. Only the gender of the emotional face significantly interacted with the emotional expression: Participants reacted generally faster to angry and disgusted male than female faces.

With regard to these only marginal gender differences, but the significant mediation results of study B2, I suggest approach-avoidance reactions to be influenced by personality traits defining cognitive regulation capacities or emotional reactivity, but not directly by participants' gender. Therefore, I decided against the testing for gender differences in study A3. However, further analyses in larger, stratified samples are necessary for finally clarifying the influence of participants' gender on approach-avoidance reactions, since the factor gender significantly influences important sub-processes such as e.g., emotional reactivity to different stimulus types (Bradley, et al., 2001).

## 10.5 Integration of neuronal findings and psychological models

As described above (1.3.2), SRC effects result from automatic reaction tendencies competing with the instructed regulated processes. Both, the motivational view and the evaluative coding view/TEC offer explanations with regard to the underlying mechanisms (see 1.3.2). At the beginning, this section takes a closer look at these specifications and the differences between the two perspectives. Then, I discuss their relation to the results of the current thesis. Thereby, I derive an explanation alternative to the RIM as discussed above (10.1.4) for integrating the neuronal and psychological aspects, specifically with regard to the found differences between the processing of positive and negative stimuli.

# 10.5.1 Common assumptions of the motivational view and the evaluative coding view

As described in 1.3.2, the motivational view assumes SRC effects to result from the following sequence (Krieglmeyer & Deutsch, 2010): The valence of a stimulus is automatically processed and activates the motivational approach system in case of positive valence or the avoidance system in case of negative valence. Thereby, the behavioural schemata associated with these systems are also activated, namely approach tendencies or avoidance tendencies. Consequently, reactions, which are in line with these pre-activated reaction tendencies, are facilitated, while incompatible reactions are slower. The alternative explanation by the evaluative coding view refers to SRC effects as affective-mapping effects (Lavender & Hommel, 2007b; see also 1.1.3.6 and 1.3.2). The cognitive representations of approach and avoidance reactions are assumed to comprise affective feature codes, since they are usually associated with positive and negative action results, respectively. If the affective feature code assigned to a stimulus overlaps with the affective feature code of approach-avoidance reactions in the common coding system, RTs are faster, since one part of the representation of the reaction is already activated. Thereby, both, the motivational view and the evaluative coding view assume the AAT conflict to be located at a cognitive, representational level and not at the motor level.

In exp. 1 and 2, Eder and Rothermund (2008a) showed the intentional labeling of joystick movements and not the movements themselves to be the essential aspect for the generation of SRC effects. In exp. 1, pulling the joystick towards the body and pushing it away from the

body were instructed as *toward* vs. *away* and as *down* vs. *up*, respectively. For the first instruction, SRC effects were as expected, i.e., congruent movements (positive-toward/pull, negative-away/push) were faster than incongruent ones. For the second instruction, the response label and not the movement direction determined the compatibility of the conditions: Positive-up/push and negative-down/pull were faster than positive-down/pull and negative-up/push. This result is in accordance with the rating study of Eder and Rothermund (2008a), which showed the response label *up* to be rated as positive and the label *down* as negative. Reversed results were gained in exp. 2, when the response labels did not refer to the participants' body, but to the monitor. In other words, SRC effects and – thereby – the compatibility between the stimulus valence and the response labels depended upon the reference point of the movements.

Although, response labels, i.e., the cognitive representations of responses, are more essential than the movement per se, the mere symbolic processing of evaluative response labels without motor enactment was not sufficient to produce SRC effects. In exp. 5 by Eder and Rothermund (2008a), the valence of adjectives determined the direction of the to be conducted responses. Thereby, the adjectives were presented before the words toward or away, which served as Go signals indicating the prepared responses to be executed (a string of consonants signaled NoGo conditions). Participants, who pulled the joystick as toward movement and pushed it away as away movement, showed SRC effects. However, when toward meant pushing to the right side and away pushing to the left side, there were no significant SRC effects. This result is different from the findings of another experiment, in which left-right movements labeled as towards-away movements produced SRC effects: In exp. 3, Eder and Rothermund (2008a) defined joystick movements to the right and left side as toward vs. away and up vs. down, respectively. For these horizontal movements, participants showed SRC effects as for the ususal sagittal movements in exp. 2 (see above): Congruent stimulus-response pairings were faster reacted to. The critical difference in exp. 5 was, that the response labels toward and away were dissociated from the motor representations, which were activated with the adjective. According to the evaluative-coding view, the adjective activated affective feature codes of the word valence and the motor representation of the associated reaction inclusive its affective feature code; the Go signal activated the motor representation of the actually conducted movement including its affective feature code. Thereby, the correspondence between the affective feature code of the adjective and of the instructed response activated by it and by the Go-signal was not sufficient to elicit SRC effects. Rather, a further correspondence with the affective feature code of the actually realized motor representation was necessary.<sup>34</sup>

The results of Eder and Klauer (2009) further support the relevance of motor aspects for the induction of SRC effects. Eder and Klauer (2009) emphasized the dynamic nature of the TEC: In a first stage, feature codes of an event are activated (activation stage); in a second stage, feature codes belonging together are bound to a coherent event code (integration stage). While the first step results in higher accessibility of the activated feature codes, this latter step results in lower accessibility of all bound feature codes. Eder and Klauer (2009) used this temporal dependency for showing the inadequacy of the explanations of the motivational account: According to the motivational view, congruent S-R combinations should always produce reaction benefits. The evaluative coding view, however, assumes congruency during the activation stage to be beneficial due to the higher accessibility of the activated feature codes, but to produce costs during the integration stage due to the lower accessibility of the activated feature codes. Eder and Klauer (2009) used a dual-task setup, in which participants, first, had to push (avoidance) or to pull (approach) a joystick and, second, had to identify the valence of a masked word (positive-negative). When this word was presented before a tone signal, which indicated the required direction of the joystick movement, congruency between the valence of the word and the valence of the movement was associated with better identification performance (exp. 3). However, when the word was presented after this tone signal, i.e., when the movement planning was finished and the activated response feature codes including the affective feature codes were already integrated into one event, congruency was associated with worse identification performance (cf. also exp. 1 and 2), an effect known as action-valence blindness. Eder and Klauer (2009) conclude that this action-valence blindness effects are due to motor induced difficulties (cf. the results of exp. 5 of Eder & Rothermund, 2008a).

While these results revealed short-comings of the motivational view, they support an assumption shared by the motivational view and the evaluative coding view, namely, that SRC effects emerge at the response selection stage (cf. the discussion on the suitability of the N2 ERP in 10.2.2, see also 10.5.2). At the same time, however, the results of exp. 3 and

<sup>&</sup>lt;sup>34</sup> In this context, Cacioppo et al. (1993) showed that knowledge about the motor reaction was not sufficient to produce evaluative effects: When conducting the movements by themselves, participants associated arm flexion with approach and arm extension with avoidance (exp. 4). In contrast, observing another person to conduct the muscle contractions did not produce such significant association patterns (exp. 5).

5 by Eder and Rothermund (2008a) show that distance-regulation is not a necessary aspect for eliciting SRC effects, since reactions to the left and right do not regulate any distance to the participant. Similarly, as mentioned in 1.3.1.1 and 1.3.1.2, Rotteveel and Phaf (2004, exp. 1) found SRC effects in an AAT version with three perpendicular buttons, in which arm flexion and extension were not associated with distance regulation.

A further common aspect of both explanations is the assumption of two processes or routes contributing to the generation of SRC effects. At one side, automatic reaction tendencies in compatible conditions are realized via a system functioning automatically and outside of awareness. At the other side, controlled, regulated reactions in incompatible conditions are conducted via another system working via cognitive control and consciousness. The motivational view is closely linked to the RIM, i.e., to a representative of dual-process models from cognitive-emotional psychology (see 1.3.2; Strack & Deutsch, 2004): The impulsive system activates usual behavioural schemata very fast in compatible situations, while the reflective system needs more time for inhibiting such automatic reaction tendencies and for initiating an alternative reaction according to the given instruction in incompatible conditions. Thereby, the functioning of the impulsive system might be seen as the correlate of the motivational orientation (cf. also 1.2.1, thesis 8 of the RIM): Its network structure and the related activation spreads guarantee for fast activations of all representational nodes belonging to one behavioural schemata. Complementing the above described assumptions of the evaluative coding view, Eder and Rothermund (2008a) suggest the overlapping of feature codes in the common representational space to also work via two routes of response selection. With regard to the automatic route, the overlap of conceptually related stimulus features and features of the response representation can automatically activate the response. The other route underlies the intentional translation of stimulus features into response features, i.e., it realizes the instructed response. Thereby, "[...] this route takes the stimulus valence as a parameter, proceeds with a search of the appropriate valence-movement mapping rule, and then activates the required motor movement." (Eder & Rothermund, 2008a, p. 277, line 10-13, left text column). In compatible conditions, the responses activated by the two routes are identical, while, in incompatible conditions, the divergent response representations result in a conflict (cf. the discussion on the N2 ERP in 10.2.2).

## 10.5.2 Differences between the motivational view and the evaluative coding view

The dual-route structure of the evalutative coding view differs, however, from the motivational view and RIM with regard to the following aspects: First, it includes the assumption of a direct relation between the stimulus and the response: The mediating mechanism of valence compatibility is possible due to the common respresentational space of stimuli and responses, while the motivational view suggests an indirect relation between stimuli and reactions via the motivational systems (see 1.3.2; cf. also thesis 8 of the RIM in 1.2.1). Second, the motivational view assumes the link between stimulus valence and behaviour to be outside intentional control settings. The evaluative coding view, however, suggests direct response activations, i.e., the automatic route, to depend on the intentional context: The task instruction functions as a top-down specification of available response codes, since it determines which feature codes are actually activated and how strongly they are weighted. In case of the AAT, an evaluative task instruction, i.e., the instruction to react according to the stimulus' valence, ensures a higher availability and stronger weighting of affective feature codes (see also below for more details). Third, the motivational view assumes automatically activated responses to be functionally related to the stimulus. In contrast, the explanations from the evaluative coding view are valid for any motor behaviour that includes affective response codes. Thereby, the evaluative coding view does not presume long-term associations between stimuli and response features.

In exp. 4, Eder and Rothermund (2008a) systematically tested the assumptions of the motivational vs. the evaluative coding view. In a joystick AAT, participants were instructed to classify positive and negative words either in a congruent way (positive-pull, negative-push) or in an incongruent way (positive-push, negative-pull). The background colour of the computer screen (orange vs. blue) signaled the compatibility or incompatibility of the current trial. Thereby, the colour either changed 1.3 seconds before the adjective's presentation (long preparation phase) or simultaneously with the adjective's presentation (no preparation phase). In both preparation conditions, the size of SRC effects was comparable, while RTs were generally shorter for the long preparation phase. In other words, SRC effects were not mediated by the retrieval of S-R mapping rules from memory as assumed by the motivational view. There, the stimulus valence is expected to function as a prime facilitating the retrieval of response representations with the same valence (see also 1.1.3.2). This facilitation effect should be weaker after the long preparation phase, i.e., compatible reactions should be less facilitated and – thereby – SRC effects should be diminished: Since the possible S-R

combinations are reduced from four to two, one part of the rule-specification process is already completed before the stimulus valence can be influential. The comparability of the SRC effects support the explanation for SRC effects from the evaluative coding view, which relies on the direct activation of emotional response codes in the common coding space by the stimulus valence and not on memory retrieval of S-R mapping rules.

Krieglmeyer and Deutsch (2010) conducted a more detailed analysis of these findings and conclusions. They used a manikin version of the AAT with a centered word stimulus and a manikin either above or below it. Participants were instructed to move the manikin upward or downward, depending on the valence of the presented word. The starting position of the manikin defined, whether *upward* and *downward* equaled towards or away from the stimulus. However, this correspondence was not explicitly mentioned. Thereby, motivation-compatible conditions were conditions, in which the manikin was moved towards positive words and away from negative words. In contrast, evaluation-compatible conditions were conditions, in which the manikin was moved upward, when a positive word was shown, and downward, when a negative word was presented. In sum, there were four possible combinations, which allowed for separately testing motivational- and evaluative-compatibility effects (see figure 1 of Krieglmeyer, et al., 2010). As in exp. 2 of Eder and Rothermund (2008a), evaluationcompatible reactions were faster. Furthermore, solely when reactions were evaluationcompatible, motivational compatibility effects were also observed, although participants were not instructed to label their reactions as approach and avoidance movements (exp. 1). This effect might be due to a general enhancement of cognitive control in the evaluationincompatible task block masking bottom-up modulations, i.e., it might reflect the dependency of SRC effects upon evaluation intentions (cf. 1.3.1.2 and the statement of context dependency by the evaluative-coding view discussed in this section). Therefore, in exp. 2, Krieglmeyer and Deutsch (2010) used an intermixed task design and instructed participants to respond according to the grammatical category of the words. Now, both, when participants moved a manikin on a computer screen via button presses (manikin version, exp. 2a) and when participants moved a pen on a writing table (exp. 2b), motivational compatibility effects were found independently of evaluation-compatibility and evaluation compatibility effects were no longer observed.

Krieglmeyer and Deutsch (2010) interpreted their findings as support for the motivational view, but not for the evaluative coding view. However, I suggest an alternative interpretation in terms of the specifications of the evaluative coding view. As introduced above, the

automaticity of the automatic route is assumed to depend on the current top-down specification of evaluative response codings. Eder and Rothermund (2008a) also suggest this aspect as alternative explanation for non-significant SRC effects, when participants did not explicitly process the stimulus valence, but categorized the presented stimuli according to another feature such as e.g. the gender of the faces. For example, in the study of Rotteveel and Phaf (2004, exp. 2), SRC effects were non-significant. See 1.3.1.2 for a detailed description of these findings and the alternative argumentation of Krieglmeyer and Deutsch (2010), that a clear definition of the movements as approach and avoidance is the essential aspect. According to the argumentation of Eder and Rothermund (2008a), the given instruction strongly influences the weighting of available response codes. In experiments, in which participants have to react according to the stimulus valence, the evaluative decision instruction might have weighted the affective response features more strongly than in an instruction condition, in which the valence is processed unintentionally. In the latter conditions, affective SRC effects might not happen because affective feature codes are not available for the automatic route.

Following these argumentations, the results of exp. 1 of Krieglmeyer and Deutsch (2010) fit the assumption of the automatic route to depend on the context, as was also partly discussed by Krieglmeyer and Deutsch (2010) themselves: The instruction determines the availability of possible feature codes; in this case, the evaluative instruction enhances the availability of affective feature codes. This might have resulted in the overall presence of evaluation-compatible effects, which depend upon the compatibility of the stimulus valence and the valence of the instructed response codes (upward, downward; cf. the rating study of Eder & Rothermund, 2008a). The non-mentioned response labels towards and away and their affective feature codes might have been less available and - thereby - less influential on participants' reactions. In an analoguous manner, in exp. 2 of Krieglmeyer and Deutsch (2010), the non-evaluative instruction might have made affective feature codes less available in general. Yet, affective feature codes of towards and away movements might have been more available than affective feature codes of upward and downward movements, since the former movements equal approach and avoidance movements with regard to the word stimulus as clearly defined target of the task. Moreover, the cognitive representations of approach and avoidance movements might more tightly contain affective feature codes than the representations of upward and downward movements, because in their natural occurrence, they are more frequently associated with positive and negative consequences.

However, it should be kept in mind that the evaluative coding view does not necessarily presume such a functional or long-term relation between stimuli and responses. The results of Rotteveel and Phaf (2004, exp. 1; AAT version with three perpendicular buttons; see above, 1.3.1.1 and 1.3.1.2) and of exp. 3 of Eder and Rothermund (2008a; left-right movements; see also above) clearly showed SRC effects, although S-R associations were neither functionally in terms of distance regulation nor build in a long-term process.

#### 10.5.3 Relevance of this debate for the present findings

The results of this systematic testing of the evaluative coding view vs. the motivational view support the evaluative coding view stronger than the motivational view. Moreover, the evaluative coding view also offers the possibility to integrate a relevant part of the motivational explanation: Eder and Klauer (2009) emphasize that the TEC cannot explain, where the evaluative meaning of behaviour is originally derived from. Rather, they suggest the motivational context to determine the formation of motor representations and their evaluative contents. Importantly, however, as already mentioned above in 10.5.3 and 10.5.4, the integration of context-dependent affective feature codes into motor representations is not assumed to be based on long-term associations between stimuli and response features. This statement is supported by the above reported results of Eder and Rothermund (2008a), which showed the given task instruction, i.e., a short-term induced context, to be sufficient for altering S-R mapping rules.

I follow this argumentation and integration, when suggesting a possible explanation for the found differences between the processing of negative and positive stimuli: The automatic route in the dual-route model might be more important for reactions to negative stimuli. As explained above, Eder and Klauer (2009) suggest the availability of affective feature codes to depend on the induction of an evaluative processing context. This consideration can be applied to my findings of severe differences between the processing of positive and negative stimuli: The more dangerous nature of negative stimuli might make it easier to create a motivational context (cf. 10.3.4), which activates the affective feature codes of the related avoidance reactions. This might result in the stronger activation of automatic avoidance tendencies to negative stimuli compared to the activation of automatic approach tendencies to positive stimuli. The findings of the current thesis, specifically the different time points in the processing of the AAT conflict for negative (cue event) and positive stimuli (move event)

in study A3, might be explained by such a mechanism. As described in details above (10.1.4), the pronounced SRC effects at the cue event might be seen as reflecting a very strong activation of automatic avoidance reactions to negative stimuli or – in terms of the evaluative coding view – as reflecting a very *easy* activation of compatible reactions via the automatic route: For negative stimuli, it was necessary to already show strong regulatory activity at the cue event, i.e., at the time point of conflict presentation, although, this was not the time point of the actual reaction. Similarly, at the move event, in NoGo conditions, the reversed neuronal SRC effects indicated the inhibition of automatic avoidance tendencies to require more regulatory activity than the inhibition of prepared incompatible reactions. In contrast, with regard to positive stimuli, the AAT conflict was mainly solved at the move event, i.e., at the time point of the actual reaction, what indicates automatic approach tendencies to not have been strongly elicited at the cue event. Additionally, the inhibition of automatic approach tendencies in the NoGo conditions was not associated with extensive regulation.

Such an easier accessibility of the automatic route for negative stimuli might be the result of more pronounced connections between stimuli features and affective response features due to the higher importance of avoidance reactions to negative, dangerous stimuli for the organisms' survival (cf. 10.3.4; Rozin & Royzman, 2001). Although – as mentioned above – the evaluative coding view does not presume such long-term S-R associations, connections between negative stimuli and avoidance reactions might have faster emerged and tighter built and renewed in a long-term association process due to the more severe consequences.

Moreover, the evaluative coding view assumes the strength of the respective motivation, i.e., of the context dependency, to be also defined by characteristics of the individual (Eder & Rothermund, 2008a). In line with this statement, I found such interindividual influences (for details see 10.4). Most importantly, in study A3, participants' valence and arousal ratings of negative stimuli were significantly linked to their neuronal and behavioural reactions at the move event (see 10.1.4): The more negative and arousing participants rated the negative pictures, the stronger SRC effects in the right midbrain (including the red nucleus) were and – thereby – the more pronounced the reversed behavioural SRC effects were. As suggested in 10.1.4, the contribution of these subcortical areas as responsible for the initiation of movements (Gruber & Gould, 2010) might reflect subcortical regulation (cf. LeDoux, 1994). While this result might indicate the reflective system of the RIM or the intentional route of the evaluative coding view to partly rely on subcortical activity, it might also reflect the automatic

route to exert regulatory activity. Thereby, it is of interest, that dual-process frameworks also exist with regard to emotion regulation: Gyurak et al. (2011) described an integration of implicit and explicit forms of emotional regulation, whereby explicit regulation is defined as conscious, effortful and implicit as automatic, unconscious. Such implicit emotion regulation comprises the habitual, unconscious application of frequently used regulatory strategies or the automatization of regulatory intentions for achieving specific goals. These mechanisms allow for a fast, effortless regulation of emotions (cf. Koole & Rothermund, 2011).

The latter mechanism might have happened during the AAT: Participants had to apply the same task instruction as learned prior to the fMRI session during the five runs in the scanner. Thereby, realizing incompatible reactions was a conflict situation, but – at the same time – a correct response comprised the ending of the respective conflict. As outlined above (10.3.3 and 10.3.4.), the condition *approach negative* might be a more problematic situation than the condition *avoid positive*. Therefore, realizing a correct incompatible reaction *approach negative* means the ending of enormous incompatibility and – thereby – equals emotional regulation. These reactions might have induced a stronger experience of negative reinforcement than ending the incompatible condition *avoid positive* via a correct response (cf. Carver, 2006; Higgins, 1997).

This might have resulted in a stronger automatization of the intention to end the condition approach negative via a correct response (cf. Eder (2011) as discussed in 10.6.3), what might be depicted in the subcortical regulatory activity. Importantly, however, this automatization might have been only possible due to the preparation of incompatible responses at the cue event (cf. the strong SRC effects for negative stimuli at the cue event): The investment of cognitive control capacities just at the beginning of the conflict might have restricted the necessary processes at the move event to the initation of the prepared movements. Furthermore, this consultation of controlled, reflective processes at only one time point and the further more automatic processing might also reflect ecological efficiency with regard to the allocation of limited control ressources. With regard to study A3, this "division of labour" between the intentional and automatic route obviously was effective, since the sample showed even reversed SRC effects, i.e., faster RTs in incompatible compared to compatible conditions. At the individual level, this relation was influenced by participants' sensitivity of the pictures' negativity as reported above, whereby the automatization in terms of the subcortical regulation was the stronger, the more negative and arousing participants perceived the pictures. The assumption of such an automatization and

improvement of regulatory efficiency further is in line with the mobilization – minimization hypothesis of Taylor (1991): "Negative (adverse or threatening) events evoke strong and rapid physiological, cognitive, emotional, and social responses. This mobilization of the organism is followed by physiological, cognitive, and behavioral responses that damp down, minimize, and even erase the impact of that event." (p. 67, abstract, line 1-3). It remains to investigate in future studies, if such implicit, automatic response regulation can also emerge in AAT variants without a cue event, i.e., without the possibility of controlled response preparation.

The results of study B2 complement these interpretations. There, the mediation model was only found for negative, but not for positive stimuli (see also 10.4.1). For negative pictures, the neuropsychological mechanism of controlled attention allocation mediated the relation between personality and behaviour: Stronger goal-oriented pursuit was associated with higher controlled attention allocation to the incompatible compared to the compatible condition and – thereby – with less automatic avoidance tendencies in response to negative pictures, i.e., with higher efficiency of regulation. In other words, controlled attention allocation and the personality trait goal-oriented pursuit as depicting the willingness to actively regulate behavioural responses were more closely related to the ending of the AAT conflict with negative than with positive stimuli. This valence difference supports the assumption of higher conflict potential in the incompatible condition approach negative compared to avoid positive and – thereby – the necessity to invest more cognitive control capacities.

Following the suggestions of the evaluative coding view/TEC, the automatization of ending the conflict *approach negative* via a (fast) correct response would be based on the formation of a new automatic route between negative stimuli and approach reactions, i.e., on a new feature overlap in the common coding space: In the context of the AAT, the cognitive representations of negative stimuli might acquire the feature of positive affect, when they are combined with correct approach reactions, that allow for ending this enormous conflict.

With regard to the systematic comparison of the motivational view and the evaluative coding view at the beginning of this chapter, such a newly built connection between a stimulus and a response is only possible according to the perspective of the evaluative

coding view. There, short-term connections are possible and the context dependency of S-R translations is emphasized.

#### 10.5.4 Integration of neuronal and psychological theories

With regard to the nature of the common coding space assumed by the evaluative coding view, Eder and Klauer (2009) suggest it to be located in the semantic space. However, to my opinion, this assumption presumes the processing of stimuli on a conscious and semantic level. In case of the AAT, this assumption might be appropriate for studies using word stimuli. However, with regard to other AAT studies using pictorial stimuli and/or instructions not explicitly referring to the pictures' valence, this assumption cannot be valid. Moreover, to my opinion, the suggested characteristics of the automatic route speak against a conscious, semantic construction (cf. below the comparison of deep vs. shallow processing modes in embodiment theories).

The perspective of embodiment theories might be useful for this issue: As the motivational view and the evaluative coding view, explanations derived from embodiment theories also describe the AAT conflict to be located at a cognitive, representational level and not at the motor level (see 1.1.3.4). As described in detail in 1.1.3.4, embodiment theories assume knowledge to be embodied: Reacting to the environment creates a repertoire of specific activation patterns in the modality specific systems of the brain (Barsalou, 1999), i.e., in the sensory systems (perception), in the motor systems (action) and in the introspective systems (conscious experiences; Niedenthal, et al., 2005b). In other words, such neuronal activation patterns are assumed to constitute the integration basis of all information processing (Niedenthal, et al., 2005b). For example, the PSS theory (Barsalou, 1999) refers to the CZ theory, in which Damasio (1989) proposed simultaneous multiregional neuronal activation to underlie memory and cognition. According to the PSS theory, these stored modality-specific patterns can be re-enacted by simply activating mental representations of a stimulus.

In other words, the relation between these stored patterns of neuronal activity (representing the sensory consequences of an action) and the respective action is bidirectional. This concept is shared by the *ideo-motor principle* (James, 1890b), which

postulates, that motor reactions can be triggered by these representations of their effects. Importantly, this principle also underlies the TEC as mother theory of the evaluative coding view. As mentioned in 1.1.3.6, the TEC does not specify the neuronal basis of the common coding space of perception and action. However, in the affectively enriched version of the TEC (for details see 1.1.3.6), Lavender and Hommel (2007b) explicitly referred to Damasio's somatic marker hypothesis (Damasio, 1994a; for details see 1.1.3.3 and 1.2.2): To their opinion, Damasio's somatic marker hypothesis as representative of embodiment theories equals an affective extension of James' *ideo-motor principle* (James, 1890b), since it attributes to affective codes the same function as the *ideo-motor principle* attributes to perceptual representations of action effects in general: They serve as retrieval cues for actions ensuring the selection of the most appropriate response.

Following these considerations, I suggest the assumptions of embodiment theories in general to be suitable as neuronal basis for the common coding space of the evaluative coding view/TEC: With regard to the AAT, both, the affective response and the motor reaction might be described as embodied knowledge, i.e., as modality-specific neuronal patterns, sharing some feature codes. Thereby, embodiment theories assume re-enactments of motor tendencies to not require consciousness (Barsalou, et al., 2003). This assumption is in line with the findings of study A3, in which – although participants unconsciously processed the picture valence – negative stimuli elicited strong avoidance tendencies as soon as the response conflict was given at the cue event and the realization of the response at the move event was mediated via the right midbrain, i.e., via subcortical structures.

Furthermore, embodiment theories assume such re-enactments to be context dependent, modality-specific neuronal patterns specific since the also contain situation conceptualizations for ensuring the preparation of adequate actions (Barsalou, et al., 2003). This mode of cognition is referred to as deep processing (Barsalou, et al., 2003). In contrast, shallow processing means the use of superficial representations at word-level (Barsalou, 1999). This latter processing style might match the assumption of Eder and Klauer (2009), that the common coding space is located in semantic space. In the context of the deep processing mode, i.e., in the context of situation specific conceptualizations, it remains to clarify, under which conditions short-term S-R associations can be built and re-enacted. In principle, embodiment theories assume rather high frequent S-R pairings to underlie the creation of embodied knowledge (Barsalou, 1999). However, my interpretation of the subcortical regulation in study A3 for negative stimuli is in accordance with the classical test of the somatic marker hypothesis by Damasio et al. (1991; 1996). Healthy controls developed a feeling for the right decision option (card deck) early during the course of the task. Under specific circumstances such as e.g., dangerous, negative situations, it might be possible and useful for an organism to develop bidirectional S-R associations without extensive repetitions (cf. the beginning of chapter 1 and chapter 12). Here, it should be mentioned, that the first AAT study by Solarz (1960) aimed to investigate, if compatible S-R relations are learned more rapidly than incompatible S-R relations. In other words, Solarz (1960) did not assume the AAT to depict long-term S-R relations, but rather short-terms characteristics: The classification of words as used in this task design was seen as a behavioural pattern usually not associated with positive and negative stimuli.

In general, future neuroimaging studies have to clarify, how exactly such a common coding space at the neuronal level might be built up. Damasio (1989) assumed CZ to be constituted by sensory and motor association cortices, limbic structures (entorhinal cortex, hippocampus, amygdala, cingulate cortices) and the cerebellum (see .1.1.3.3 and 1.1.3.4). The fMRI study by Melcher et al. (2008) revealed the passive perception of tones, which previously had been associated with specific actions, to elicit related activity in the cerebellum, SMA, premotor and somatosensory cortices. This might be interpreted as depicting the anticipation of these actions in terms of their modality-specific neuronal patterns. However, to my opinion, the theoretical statements on the neuronal basis of embodied knowledge require for another level of investigation: Methods from computational neuroscience (see 1.2.3) might be better suitable for investigating the temporal binding and integration of modality-specific patterns to complex stimulus representations.

## 10.6 General strengths and limitations

This section refers to strengths and limitations common to several or all of the six studies included in the current thesis. Aspects, which only refer to one specific investigation, are dealt with in the discussion section of the respective study.

## 10.6.1 Functional imaging measures supplement behavioural measures

Approach and avoidance motivation are powerful determiners of human behaviour. However, they do not necessarily result in observable behaviour (cf. Elliot & Covington, 2001). Moreover, behaviour is the end-parameter of several different sub-processes and does not allow for conclusions on single processes, since they might be differently modulated. The measurement of neuronal activity via functional imaging measures represents a means for investigating the neuronal correlates of such sub-processes and their relation to the final end-parameter behaviour. It also allows for depicting dissimilar modulations of these sub-processes and behaviour (cf. Gron, et al., 2003; Bockler, et al., 2011). The studies of the current thesis showed this advantage of combining behavioural measurements with neuroimaging methods: As reported in detail above (10.1 and 10.2), non-significant behavioural results could not be equalled with a non-efficiency of the AAT. Rather, in studies A1, A2 and B1, neuronal and neuropsychological measures clearly indicated participants to have processed the AAT conflict very efficiently, what resulted in no effect of the conflict up to the behavioural level.

In classical experiments from cognitive-emotional psychology, measurements are restricted to the behavioural level. This usually results in no publication of non-significant results, since it cannot be excluded, that the missing findings are due to difficulties in the task design. I did not explicitly check on such a publication bias by creating a funnel plot of the published studies. However, to my knowledge, the results of Barkby et al. (2012; alcohol dependency) are the only published non-significant results of studies restricted to the behavioural level. A significant influence of technical problems on behavioural data can – of course – also not be excluded in neuroimaging studies. However, the present findings show that non-significant behavioural data should not be solely attributed to such problems and – thereby – ignored. Such a publication bias might result in the description of SRC effects as more universal and generally elicited than it actually is the case.

#### 10.6.2 Generalizability of the current findings

The samples of all six studies consisted of healthy young adults (students). They reacted to IAPS pictures as stimuli of general emotional relevance (Lang, et al., 2005). Thereby, approach-avoidance reactions are assumed to be basic behavioural dimensions (Carver, 2006). Nevertheless, the generalizability of these findings has to be shown in future studies (see 11.1), since there remain several critical aspects. First, specifically when analyzing the influence of interindividual differences such as e.g. personality traits, the distribution of the different expressions in the sample has to be sufficient for allowing for a correlational analysis (cf. the additional analysis in the supplementary material of study B2).

Second, it might be interesting to clarify, if there are any differences between emotional categories in the elicitation of the valence-response patterns *negative-avoid* and *positive-approach* (cf. the results of Seidel, et al., 2010b). While the IAPS picture set is orientated at the dimensional approach to classify emotions (Lang, et al., 2005; see also 1.1.1), Mikels et al. (2005) suggested a classification of negative IAPS pictures into the four emotional categories *anger*, *disgust*, *fear* and *sadness* as basic negative emotions in categorical accounts (cf. Ekman, 1993). According to Lang et al. (1993), these categories adequately describe the discrete emotions comprised by the IAPS pictures. Furthermore, participants also grouped positive IAPS pictures into the categories *amusement*, *awe*, *contentment* and *excitement*. Pictures which could not be clearly assigned to one or several specific categories were identified as *undifferentiated*. However, this categorization attempt does not contain all IAPS pictures used in the current thesis, therefore, it remains an aspect for future studies to also take into account the categorical affiliation of the emotional stimuli. With regard to the special case of the emotion *anger*, the reader is relegated to the next passage.

Third, the AAT assesses very simple approach-avoidance reactions. Their comparability to real-life situations might be limited due to the following reasons: Many studies realized approach reactions to positive stimuli as bending the arm and avoidance reactions to negative stimuli as extending the arm (for an overview and discussion of the influence of the reference point of movements see 1.3). Besides the technical issues discussed in 1.3, in principle, bending extremities, i.e., activity of the flexor, can also result from a negative affective state as in the withdrawal reflex (Clarke & Harris, 2004). Analoguous, extending extremities can also follow the processing of a positively valenced situation as hugging someone in situations associated with pity or nurturance (Lang, 1995). Similarly, anger as

negative affect can be associated with approach behaviour for an organisms' defense (see 1.1.2; cf. however Seidel, et al., 2010b for the AAT); sad facial expressions were suggested to constitute a request for help, i.e., to elicit approach tendencies (Horstmann, 2003).

Almost all studies realized approach and avoidance via arm movements or similar contributions of the finger or arms, i.e., of the upper extremities (see 1.3 for details on different task versions). When testing similar reactions with the legs, i.e., with the lower extremities, the expected interaction valence x direction was not found (unpublished exp. cited in Cacioppo, et al., 1993). However, this might partly be due to the task design, since this study asked participants to activate the motivational approach and avoidance system by pressing their heels against a desk and their toes against another object, respectively. Future studies might test for SRC effects in the lower extremities by using more typical, distance regulating approach-avoidance movements.

As described in 1.1.1, approach tendencies are also associated with activity of the zygomaticus muscle as responsible for smiling, while avoidance tendencies are associtated with activity of the corrugator muscle as responsible for frowning (cf. Lang, et al., 1993). Recently, Neumann et al. (in press) showed the relation between affective evaluations and manual reactions to depend on the cognitive coding of these responses. In contrast, the relation between affective evaluations and facial reactions was not influenced by experimental manipulations of the response label, i.e., it seems to be less flexible. This findings fits the assumption that manual approach-avoidance have to be flexible for being adaptive (cf. the discussion of the reference point in 1.3). With regard to the neuronal level, it would be interesting to combine such an experiment with neuroimaging measures for investigating, if there are also related differences in the inhibition of compatible reactions.

Moreover, the AAT was also used to investigate social attitudes (cf. also 11.1): In exp. 2 of Seibt et al. (2008), students showed facilitated approach behaviour to pictures of young persons, but facilitated avoidance behaviour to pictures of older persons. This pattern is in line with previously shown implicit negative evaluations of elderly persons (Dasgupta & Greenwald, 2001). Similarly, Neumann et al. (2004) showed pictures depicting persons with acquired immunodeficiency syndrome (AIDS) to elicit avoidance tendencies in persons with negative attitudes towards this illness.

#### 10.6.3 Restrictions of the implicity of the AAT

De Houwer et al. (2009a) presented a theoretical frame for defining the suitability of implicit measures. Thereby, they emphasized the necessity of experimental manipulations proving the causal relation between attributes or other implicit processes and behavioural outcomes (cf. also 1.2 and 1.3.3). In general, with regard to the reliability and validity of implicit measures, it is discussed that – possibly – a certain amount of the stimulus feature, which is assumed to be implicitly processed, has to be conscious or pre-activated (cf. the assumptions of the TEC on the context dependency of the automatic route): Reliability of implicit measures was enhanced, when participants had to consciously process parts of the respective stimulus feature (e.g. Olson & Fazio, 2003).

Moreover, Eder (2011) questioned the level of implicity of the processes assessed via the AAT: Participants had to classify positive and negative IAPS pictures as depicting animals or humans. Thereby, participants showed the usual SRC effects, when they were also instructed to watch out for pictures with a red border and to classify them according to the rule "approach (pull) positive and avoid (push) negative". However, when participants were instructed to keep the reversed intention in mind (avoid positive, approach negative), i.e., when control intentions were implemented by the task instruction, SRC effects were reversed (cf. the results of study A3). This regulation of automatic response tendencies shows, that – at least in some situations – implicit processes might be under conscious control and – therefore – the validity of implicit measures is not guaranteed.

As mentioned above, the results of studies B2 and A3 are restricted with regard to the assessment of the personality trait goal-oriented pursuit and valence evaluations, respectively. Both studies used explicit measures, while participants' behaviour was assessed via the implicit AAT; the neuronal level also might be seen as an implicit, not influencable measure. Such explicit measures can be distorted, since participants report processes usually happening outside awareness (cf. the results of Lange, et al., 2008). Moreover, social desirability or similar effects can produce evaluations not reflecting participants' true attitudes: As did studies B2 and A3, Barkby et al. (2012) reported significant correlations between SRC effects for alcohol stimuli and patients' answers in a questionnaire assessing drinking reasons. In contrast, Neumann et al. (2004) found significant relations of participants' SRC effects with implicit attitudes as assessed via the IAT, but not with explicitly

reported attitudes. However, this study investigated attitudes with regard to AIDS, i.e., a topic highly prone to effects of social desirability.

## 11 Future Directions

Future research has to concentrate on important aspects, which – so far – have not been sufficiently taken into account. While the discussion sections of the different studies and the General Discussion until now pointed to more focal issues, here, I present more universal suggestions.

## 11.1 Criterion validity and approach-avoidance index

With regard to the criterion validity of the AAT, until now, there are only a few studies taking into account this aspect. Krieglmeyer and Deutsch (2010) draw conclusions on different versions of the AAT with regard to spider phobic reactions by correlating AAT reactions with participants' specifications in questionnaires (see 1.3.3; cf. the results of Barkby, et al., 2012 with regard to alcohol dependency; cf. the results of studies B2, A3 and A4). Neumann et al. (2004) related AAT reactions to attitudes as assessed via the IAT (see 10.6.3). Solely the studies of Wiers et al. (2010, 2011) related AAT reactions to other behavioural measures: A retraining of the approach bias towards alcohol stimuli via the AAT reduced alcohol intake and the frequency of relapses in students and patients, respectively (cf. Spruyt, et al., 2013). With regard to healthy participants reacting to positive and negative stimuli of general emotional relevance, solid evidence for the criterion validity of the AAT in terms of a real-life behavioural test is still missing.

Moreover, there are other techniques in previous studies, which might be combined with the AAT and real-life tests of approach-avoidance behaviour to develop a stable index of individual approach-avoidance tendencies. Derntl et al. (2011) asked participants to look at facial expressions and to indicate via a button press, if they would approach, avoid or not react to this person in vivo. Kim et al. (2010) asked participants to self-regulate the viewing time of three picture types (attractive faces, food stimuli, IAPS pictures). An enhancement of the time was interpreted as approach tendency and a reduction as avoidance tendency. Participants showed interindividually different, but intraindividually – across the three stimulus types – stable, law-like patterns of approach-avoidance choices (trade-off between approach-avoidance tendencies, saturation function for preference). Moreover, other implicit measures, such as e.g., the IAT might allow for acquiring variance in participants' affective evaluations, which is not explained by the AAT (cf. Thush, et al., 2007). The results from these different perspectives might be combined to one approach-avoidance index, according

to the principle, that the strengths of one measure might compensate the limitations of another measure.

#### 11.2 Situational influence

Another aspect, which, so far, has been neglected, is the investigation of situational dependency of approach-avoidance reactions. Although, the behaviour assessed in the AAT might be of general validity, the investigations with regard to interindividual differences revealed significant influences (see studies B2 and A3). Similarly, intraindividual differences might determine the degree to which approach-avoidance reactions are elicited.

First of all, for the used IAPS pictures, Lang et al. (2005) gave evaluations not only for the dimensions *valence* and *arousal*, but also for a third dimension *dominance* (dominated – in control). This dimension assesses the feeling of participants' superiority with regard to the depicted scene (feeling of being able to deal with the situation). The study of Wentura et al. (2000, exp. 3) is the only AAT investigation, in which the authors took into account, that the concepts *positive* and *negative* might depend on the perspective of the evaluator (see also 1.3.1.1). Following a distinction from investigations on social situations, Wentura et al. (2000) used adjectives describing personality traits, that were either possessor-relevant or other-relevant. The authors – thereby – defined *possesor-relevant* as expressing an unconditionally adaptive or maladaptive trait of the participant and *other-relevant* as (mal)adaptive trait of another person. SRC effects were only found for the processing of other-relevant words, i.e., the affective evaluation of a given stimulus was not only determined by its objective valence, but more significantly by its relation to the evaluator: Reactions to another person seem to depend on the "valence" assigned to this person and the anticipated consequences for the evaluator.

Such dependencies should be further taken into account in future AAT studies, since they might be extremely important in everyday life. The feeling of control might be essential for initiating a movement, i.e., for altering the distance to a stimulus, or for deciding on the means how to regulate this distance (cf. Krieglmeyer & Deutsch, 2010 and Elliot & Covington, 2001). Here, it should be noted, that humans can regulate the distance to a situation not only in a spatial way, but also in terms of altering the temporal or psychological relation (cf. Seibt, et al., 2008). Similarly, the initiation of regulatory, but also of compatible

reactions might depend on the interaction between participants' expectancies with regard to the probability of a success and the assigned value (expectancy-value theory of achievement motivation, Wigfield & Eccles, 2000; cf. Ajzen, 1985).

Moreover, the studies of van Peer et al. (2007, 2009) revealed stress induction via cortisol administration to significantly influence social phobic behaviour (see 1.3.4). Similarly, in healthy controls, the stress level might be an important factor in defining the strengths and speed of approach-avoidance reactions. Future investigations should experimentally manipulate participants' stress level and/or WM capacity for getting insight into their relation to both the elicitation and regulation of automatic response tendencies. Previous studies showed impulses to dominate behaviour in case of exhausted cognitive control capacities (Friese, et al., 2008).

## 11.3 Advanced analyses

Until now, the analyses applied to behavioural and neuroimaging data from AAT studies mainly concentrated on classical variance and group analyses. Moreover, technically orientated investigations were neglected. However, as for other conflict paradigms, there might be task specific effects and problems (see 10.2.2 for the discussion on the problem of the N2 ERP). Future studies should concentrate on the identification of such systematic variance due to technical aspects (cf. the development of D-scores as derived from the IAT). This variance could mask effects and should be separated from the actually interesting variance due to intra- or interindividual differences.

First, effects from following on preceding trials or trial-by-trial variability should be taken into account (cf. the analyses of Kim, et al., 2010). For example, the Gratton effect (sequential congruency effect) was frequently reported in different conflict paradigms: Conflict effects are larger in trials, which follow congruent trials, than in trials, which follow incongruent trials (Gratton, et al., 1992; Mayr & Awh, 2009; Schmidt & De Houwer, 2011). Future AAT studies should balance the sequence of events with regard to the frequency of compatible and incompatible trials preceding incompatible trials.

Second, with regard to the meaning of differences between conditions in the frequency of errors (see 10.4.3), previous attempts to include errors into the analysis of RTs should be

further developed. Lavender and Hommel (2007b) and van Dantzig et al. (2008) tested for speed-accuracy trade-off effects by correlating the speed of reactions with the respective error rates: Participants might voluntarily slow the speed of their responses for avoiding errors.

Third, with regard to the above discussed advantages of neuroimaging methods compared to investigations solely assessing behavioural parameters (see 10.6.1), measurements via EMG might allow for assessing reaction tendencies even in the absence of observable behaviour. Thereby, it might be specifically interesting, if subliminally presented stimuli also elicit approach or avoidance tendencies. Similarly, in EEG, the lateralized readiness potential (LRP) is highly suitable for depicting response preparation effects (see e.g. the results of Eder et al. (2012) in a sequential affective priming paradigm). However, with regard to the ERP investigations of the current thesis, the used joystick version restricted the manual reactions to only one hand, i.e., here, LRPs would not have been informative.

Last, while the GoNoGo version developed for study A3 allowed for separating preparatory effects from direct response realization and also allowed for the investigation of response inhibition processes, further variants of the task might allow for also separating other sub-processes. Moreover, more advanced analyses of the neuroimaging data are necessary, such as e.g., network or connectivity analysis (see 1.2.3; cf. Cole & Schneider, 2007), for coming up to the complexity of cooperations between different brain areas. Specifically with regard to the negativity bias and the subcortical regulation route as discussed above (see 10.3.3 and 10.5.3), this approach might be useful: Interestingly, a recent rs-fcMRI investigation in humans differentiated a rubral (related to the red nucleus) from a nigral (related to the substantia nigra) network (Nioche, et al., 2009): The red nucleus showed connectivity to structures constituting a network for salience and executive control, but this network did merely overlap with structures connected to the substantia nigra. This finding might represent the neuronal correlate of a differentiation between a motor network responsible for fast, more unconscious reactions (rubral network) and a motor network responsible for more voluntarily controlled reactions (nigral network; cf. Dypvik & Bland, 2004; cf. LeDoux, 1994). Disentangling such connectivity patterns during AAT reactions might reveal further insight into the neuronal and neuropsychological processes underlying behavioural SRC effects.

## 12 Conclusions

The thesis at hand revealed general insight into neuronal and neuropsychological processes underlying automatic approach-avoidance tendencies and their regulation. Moreover, as the title "Approaching the negative is not avoiding the positive [...]" already indicates, the results showed significant differences between processes related to positive and negative stimuli. In short, specifically the findings of studies B2 and A3 indicated automatic avoidance reactions to negative stimuli to be stronger elicited than automatic approach reactions to positive stimuli. As a consequence, the conflict potential of the incompatible, regulated condition approach negative was higher than for avoid positive.

In study B2, the willingness to actively regulate behavioural responses (goal-oriented pursuit) defined the amount of controlled attention allocation and – thereby – the effectiveness of behavioural regulation of avoidance tendencies for negative stimuli. Similar relations were not found for positive stimuli. This difference indicates a higher necessity of allocating regulatory resources to negative than positive AAT conflicts.

In study A3, for positive pictures, incompatible reactions mainly elicited regulatory activity at the move event. This finding was associated with usual behavioural SRC effects. In contrast, negative stimuli elicited very strong neuronal SRC effects at the cue event indicating pronounced response preparation. Moreover, the more negative participants rated the pictures, the stronger they showed response initiation processes at the move event in the right midbrain (including the red nucleus) and the stronger they showed reversed behavioural SRC effects. Thereby, the brain activity constituted a mediator in the relation between the ratings and the behaviour. This subcortical regulatory activity might have been possible due to the prior conflict solution at the cue event. It might indicate efficient two-stage behavioural control, whereby limited cortical control capacities were applied only once. Then, the prepared responses were realized without a further detailed, cortical analysis, but via subcortical routes. This implicit conflict regulation mechanism (see 10.5.3) might be closely related to the efficient maintenance of the organisms' homeostasis (see the beginning of chapter 1): Detecting deviations from a balanced state via feelings allows for the fast initiation of corrective reactions (Damasio & Carvalho, 2013). The findings of study A3 might be seen as depicting the neuronal correlates of such a balancing reaction.

#### 13 References

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# 14 List of Abbreviations

abbreviation	meaning
AAL	anatomical automatic labeling
AAT	approach avoidance task
ACC	anterior cingulate cortex
ACh	acetylcholine
aPFC	anterior prefrontal cortex
ASL	continuous arterial spin labeling
BA	Brodmann area
BAS	Behavioural Approach System
BIS	Behavioural Inhibition System
BOLD (contrast)	blood oxygenation level dependent (contrast)
CNS	central nervous system
cTBS	continuous theta burst stimulation
DA	dopamine
dACC	dorsal anterior cingulate cortex
DCM	dynamic causal modelling
DFMC	dorsal frontomedian cortex
DLPFC	dorsolateral prefrontal cortex
DLPFK	dorsolateraler präfrontaler Kortex
EEG	electroencephalographie/-gramm
EKP	ereigniskorreliertes Potential
EMG	electromyographie/-gramm
ERN	error-related negativity
ERP(s)	event-related potential(s)
exp.	experiment
FFA	fusiform face area
FFFS	Fight/Flight/Freeze System
fMRI	functional magnetic resonance imaging
fMRT	funktionelle Magnetresonanztomographie
fNIRS	functional near infrared spectroscopy
GABA	gamma aminobutyric acid
GCM	Granger causality mapping
HHb	deoxygenated haemoglobin
HIT	Hard Interface Theory
IAT	implicit association task
IFG	inferior frontal gyrus
IPL	inferior parietal lobule
ISI	interstimulus interval
ITC	inferior temporal cortex
LC	locus coeruleus
LI	laterality index
LPP	late positive potential
LRP	lateralized readiness potential
MAOA	Monoamin Oxidase A
<i>MAOA</i> -uVNTR	gene encoding MAOA
MAOA-L carriers	carriers of the low-expressing genetic variant

IVNTR
one low-expressing and one high-
allel of MAOA-uVNTR
the high-expressing genetic
<i>MAOA</i> -uVNTR
ntal gyrus
e grid
and Opportunity as DEterminants
nrine
al cortex
d haemoglobin
nission tomography
cortex
gyrus
campal place area
gyrus
mpulsive model
nterest
te-functional connectivity MRI
einforcement sensitivity theory
nes
zeiten
y attentional system
eviation
equation modelling
ontal gyrus
campal system
itary motor area
inal gyrus
arietal lobule
sponse compatibility effects
Reaktions-Kompatibilitäts Effekte
Event Coding
al magnetic stimulation
al PFC
ial prefrontal cortex
emory
,
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## 17 Organizational Remarks

The present thesis comprises one submitted and four published publications. Following the guidelines of the respective publishers, these original texts can be contained in a doctoral thesis not published in another commercial way. Details on the author's rights of publication can be checked with the author (lena.ernst@med.uni-tuebingen.de).

#### 17.1 Formatting

The formatting of the published studies must not be changed. Therefore, **each study is** handled as a unique entity with regard to the use of abbreviations and details in the text layout. Solely the numeration of the headings, the tables and the figures, as well as the references in the text to them are altered in such a way, that all chapters build a coherent sequence. The references for the literature in press are updated.

#### 17.2 Contributions of the author

For all included studies, the author was the "man in charge", i.e., essentially involved with regard to the development of the research questions, the programming of the paradigms, the collection, analyses and interpretation of the data as well as the final publication. The co-authors supported single processes, such as the collection or the analyses of the data.

### 17.3 Eidesstattliche Erklärung

Ich erkläre hiermit, dass ich die zur Promotion eingereichte Arbeit mit dem Titel: Approaching the negative is not avoiding the positive: FNIRS, ERP and fMRI studies on the Approach-Avoidance Task selbständig verfasst, nur die angegebenen Quellen und Hilfsmittel benutzt und wörtlich oder inhaltlich übernommene Stellen als solche gekennzeichnet habe. Ich erkläre, dass die Richtlinien zur Sicherung guter wissenschaftlicher Praxis der Universität Tübingen (Beschluss des Senats vom 25.5.2000) beachtet wurden. Ich versichere an Eides statt, dass diese Angaben wahr sind und dass ich nichts verschwiegen habe. Mir ist bekannt, dass die falsche Abgabe einer Versicherung an Eides statt mit Freiheitsstrafe bis zu drei Jahren oder mit Geldstrafe bestraft wird.

Lena Ernst

Tübingen, im August 2013

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