

## Pecking and Respiration Rhythms of Pigeons (*Columba livia*)

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The production and coordination of rhythmic activities in birds is seldom investigated. Here we describe the pecking and breathing rhythms of pigeons under different conditions. When feeding from a heap of small grains, hungry pigeons pecked at regular intervals of about 0.3 s. The pecking rhythm was slightly slower in the afternoon. The pecking rhythm induced by the dopaminergic drug apomorphine was somewhat faster but some overt pecks were skipped. The mean respiratory cycle during a nonpecking baseline condition lasted about 2.5 s. Breathing was slightly faster in the afternoon. During bouts of grain pecking, the breathing cycle shortened to about 1.7 s but returned to baseline soon afterwards. Under the influence of apomorphine, the respiration cycle duration was reduced to about 0.8 s. There was a relative interaction between the pecking and breathing rhythms, the pecks tending to occur at particular points of the inspiration and expiration phases. This partial entrainment was less pronounced during apomorphine-induced than grain-induced pecking. The mechanisms and functions that might be involved are discussed.

Pecking    Feeding    Apomorphine    Respiration    Rhythms    Coupling    Pigeons

The pecking response of pigeons has attracted much research attention over the last decades. As a relatively simple action produced by a relatively small brain, it appeared to be appropriate for a thorough behavioral and physiological analysis of grasping movement. The spatio-temporal course of individual pecks has accordingly been described in some detail. Originally considered to be a rather invariant fixed action pattern, recent studies show pecking to be a much more flexible behavior pattern than expected. Its precise temporo-spatial dynamics have been shown to be influenced by a host of different factors (see, e.g., Hörster, Krumm, Mohr, & Delius, 2002; Ploog & Zeigler, 1995; Schall & Delius, 1991; Siemann & Delius, 1992a;

Zeigler, Jäger & Palacios, 1993; Zweers, 1982). Nevertheless, when hungry pigeons feed from a heap of small grains, when they search for few grains among a heap of grit, when they peck on a key for occasional food rewards, or when they are treated with apomorphine, they tend to produce repetitive, stereotyped pecks at high rates for continuous bouts that can last from many minutes (grain, grit) up to a few hours (key, apomorphine) (Delius, 1985; Palya & Zacny, 1980). Apomorphine, a direct agonist of the neurotransmitter dopamine, is well known to elicit protracted spells of continuous pecking in birds. It has been suspected to activate a hypothetical central pecking pacemaker substrate. Apomorphine-induced pecks,

although highly similar to feeding pecks in terms of their movement kinematics and facilitated by food deprivation, are usually not directed at grains (the drug having an anorectic side effect) but at other small, salient, and usually inedible stimuli. If grains are pecked they are mostly not swallowed (Brunelli, Magni, Moruzzi, & Musumeci, 1975; Keller, Delius, & Acerbo, 2002; Siemann & Delius, 1992b). The rhythmicity underlying these cases of serial pecking has not received much attention and relatively little is known about the factors that influence it. An earlier study of ours showed that there tended to be timing linkages between the pecking and cardiac rhythms of pigeons (Delius, Lindenblatt, & Lombardi, 1986). This partial coupling occurred even though the heart activity seemed functionally unrelated to pecking.

Here we present data characterizing the serial pecking of pigeons and describing the coordination of such repetitive pecking with the breathing rhythm. This latter rhythm is generally assumed to be driven by a neuromedullar pacemaker assembly (Fortin, Champagnat, & Lumsden, 1994; Michal, Ballam, & Kunz, 1981). Breathing can be expected to be closely linked to pecking because both activities involve a competitive engagement of the oral cavity when swallowing occurs (Grabatin & Abs, 1986; McFarland & Lund, 1993). This study also supplements other studies that have shown several different rhythmic activities in birds exhibit coordinative linkages (Banzett, Nations, Wang, Butler, & Lehr, 1992; Berger, Roy, & Hart, 1970; Funk, Milsom, & Steeves, 1992; Hohtola & Johansen, 1987; Wohlschläger, Jäger, & Delius, 1993). The frequent occurrence of various kinds of coupling among rhythmic behaviors was first noticed a long time ago (Coleman, 1921).

#### Method

##### Subjects

Six adult domestic pigeons (*Columba livia*) of a local homing stock were employed. They were housed in individual cages (40 × 45 × 35 cm) located in a well-ventilated and brightly illuminated animal room. Lights were on from 0600 to 2000 h. For the duration of the experiments the birds were kept food deprived to 90% of their ad libitum feeding weight. All treatments conformed with the rules and regulations of the German animal welfare law.

##### Apparatus

A plastic tube (10 mm long, 1.5 mm diameter) was chronically fixed on the top of the beak of each pigeon with tissue adhesive (Histoacryl). Before each experimental session the leads of a thermotransducer were wedged into this tube so that its sensing tip (0.6 mm diameter) came to rest just within one of the bird's nostrils (Fig. 1). The transducer was connected through a flexible twin wire (1.2 mm diameter) to an amplifier (Neurolog) that fed into one channel of an analog-to-digital converter (Keithley) linked to a personal computer (Compaq). Inspired air was at ambient temperature (about 20°C) and expired air at pigeon body temperature (about 40°C). The system responded to breath temperature changes with a resolution of about 0.1°C and with a delay (phase shift) of about 65 ms due to the thermal capacitance of the transducer. Pecking movements had no detectable influence on the nostril temperature records (Fig. 1).

For recording pecks at grains, the pigeons were introduced into a cage placed on a heavy table. They

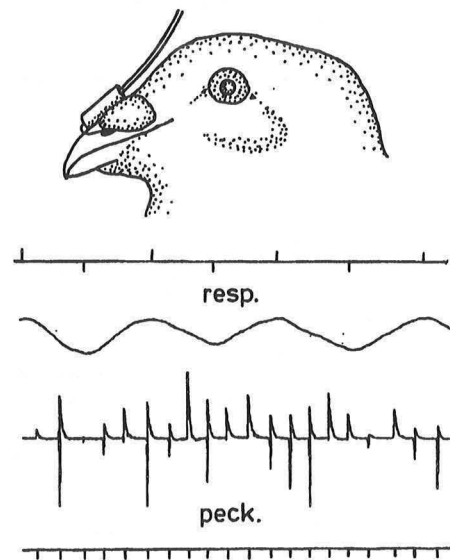


Figure 1. Thermotransducer placement and examples of respiration and pecking records together with standardized breathing and pecking traces. The peck marks (bottom trace) are about 0.3 s apart.

were offered about 250 millet seeds (about 2 mm diameter) in a light dish (50 mm diameter) cemented onto a piezoceramic disc (Valvo, 25 mm diameter) glued onto an iron slab resting on the tabletop. The output of this transducer was fed through a separate amplifier and into a second channel of the converter. The system recorded individual beak impacts within the dish with a negligible delay. Occasionally it also responded to the impact of grains that were sometimes rejected by the birds (see below).

Because, as explained earlier, apomorphine-induced pecks were not directed at grains, but instead at small features of the cage walls, a different arrangement had to be used. The cage walls were mounted on four piezoceramic discs mounted upon four iron slabs. The cage floor rested separately on the tabletop without touching the walls. No food bowl was present. The transducers were connected in parallel to the amplifier/converter system and yielded signals upon all wall pecks except for some very soft pecks. The system did not respond to any other activities except occasionally to wing or tail contacts with the walls (see below).

During all recording periods the pigeons were also videotaped along with an online monitor display of the peck and breath recordings. The synchronization signal of the camera fed into one channel of the a/d converter. The display included subject and period identification symbols and a video frame counter.

##### Procedure

The birds were first familiarized with the apparatus and procedure in five preliminary, daily sessions. Then each bird underwent three daily recording sessions. They lasted for about 60 min each and took place at three different times of day in random sequences balanced across subjects. The morning sessions were run between 0900 and 1000 h, the noon sessions between 1200 and 1300 h, and the afternoon sessions between 1500 and 1600 h. Fifteen minutes before any recording began, the breath transducer was attached to the bird's beak, followed by a 90-s baseline recording period during which no grain was offered. During this period the pigeons did not peck and mostly stood still. After a 10-min pause there was a second 90-s recording period during which grain was offered, and the pigeons consumed it. After a further pause of 10 min this latter condi-

tion was repeated. After an additional interval of 10 min the baseline no-grain condition was repeated. If the pigeons, as they sometimes did, displayed any intruding activity such as preening or walking during the recording periods, these periods were discarded, and additional recording commenced until periods free of such interfering behavior were obtained.

Pecking induced by apomorphine and its relation to respiration was examined during additional sessions in three randomly selected pigeons. A dose of 0.5 mg apomorphine (Teclapharm) per kg body weight was injected into the pectoral muscle a few minutes before each session. The first two sessions served to sensitize the pigeons to the drug (i.e., to increase the response to the dose used, Keller et al., 2002). Pecking and breathing were recorded during four 90-s periods separated by 10-min intervals during two final sessions when the pigeons showed virtually continuous pecking throughout the sessions.

##### Record Processing

The onset of each inspiration and expiration phase present in the raw breathing records was converted by a maxima/minima-detecting algorithm into standardized upward and downward marks on a separate trace. The time intervals between pairs of successive upward marks defined complete breathing cycles (Fig. 1). The raw pecking impact records were similarly converted into a separate trace with standardized pecking marks. The videotapes were later examined in slow motion and, when required, in single frames, to manually remove from the record traces rare artifactual peck marks due to dropped grains (dish) or body contacts (walls) and to insert missing marks due to occasional soft pecks. These corrections involved less than 1% of the peck marks evaluated. The traces of a few recording periods could not be corrected in this manner because the pigeons had partially pecked out of the camera's view. Pecking that occurred during these periods was not included in the data analysis but the breathing data that they provided were used. The breathing records were all checked for regularity during the above editing.

##### Data Analysis

The time interval between two peck trace marks corresponded to the duration of a complete peck

cycle. Rare (less than 1%) peck cycles longer than 500 ms (mainly due to occasional swallowing hiccups recognizable as head-nodding movements or alarm responses recognizable as head raising and scanning movements) were disregarded. Mean peck interval durations ( $\pm$ SD) are expressed in milliseconds. Pecking frequencies are given as pecks per second. The time interval between two upward, inspiration marks defined the duration of a respiration cycle. For brevity the durations of breathing cycles and phases are all expressed in centiseconds (cs) rather than milliseconds. Rare (less than 0.5%) breathing cycles longer than 400 cs (arrests due to occasional alarm responses) were disregarded before computing mean breathing phase and cycle durations ( $\pm$ SD). Breathing frequencies are indicated in breaths per minute. The 6.5-cs response lag of the breathing records with respect to the pecking records mentioned earlier was compensated with a correspondingly computed correction when the interactions between pecking and breathing rhythms were analyzed.

### Results

First, we describe pecking rhythms elicited by grains and induced by apomorphine. Next, we consider the pigeons' breathing rhythm while awake but inactive, while pecking for grains, and while pecking under the influence of apomorphine. Lastly, we examine the extent to which grain-elicited pecks and apomorphine-induced pecks were keyed to the ongoing respiratory rhythm.

#### Grain-Elicited Pecking

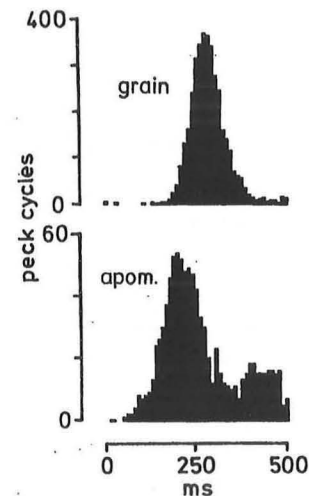
All pigeons began to peck immediately when the millet grains were poured into the feeding bowl.

**Table 1.** Durations in Milliseconds of Grain-Elicited and Apomorphine-Induced Peck Cycles

Bird	Grain Pecks		Apomorphine Pecks	
	<i>n</i>	Mean (SD)	<i>n</i>	Mean (SD)
I	1235	287 (51)	340	296 (104)
II	1318	298 (49)	294	258 (99)
III	1179	297 (51)	296	247 (87)
IV	1474	337 (53)		
V	583	321 (67)		
VI	964	302 (45)		
Sums/averages	6753	307 (17)	930	267 (21)

Pecking was rapid and continuous. A total of 6753 pecks were evaluated across all pigeons during corresponding recording periods. The peck cycle durations (i.e., the time elapsed between consecutive peck marks) are shown in Table 1. The average duration of all peck cycles recorded under the grain pecking condition was 307 ms. The mean pecking rate ranged from 3.5 pecks/s (pigeon I) to 3.0 pecks/s (pigeon IV). The average of 3.2 pecks/s conforms well with rates that have been reported previously for such serial pecking (Hörster et al., 2002). Figure 2 (upper panel) shows that when hungry pigeons fed from a heap of freely available small grains, pecking was highly repetitive and clearly rhythmic. The distribution of duration of peck cycles was approximately normal, narrowly spread, and only slightly skewed. The histograms corresponding to the individual pigeons all showed the same characteristics.

Though not separately shown in Table 1, average peck cycle durations decreased slightly from morning ( $319 \pm 21$  ms) through noon ( $316 \pm 20$  ms) to afternoon ( $301 \pm 25$  ms). The difference between morning and afternoon was statistically significant (Wilcoxon test,  $T = 0$ ,  $p < 0.05$ ).



**Figure 2.** Frequency of different peck cycle durations for grain-elicited and apomorphine-induced pecking. Pooled data of pigeons I, II, and III.

#### Apomorphine-Induced Pecking

Table 1 shows that the mean cycle duration of apomorphine-induced pecks decreased in two birds but not in the third one. On average, the mean peck cycle duration was somewhat shorter, but not significantly, than that of grain-induced pecks (267 ms compared with 307 ms). This shortening was accompanied by an increase in intraindividual variance. The mean pecking rate under apomorphine was 3.7 pecks/s and ranged from 4.0 pecks/s (pigeon III) to 3.3 pecks/s (pigeon I). The interindividual variation of grain-induced and apomorphine-induced pecking was comparable. However, a comparison of the histograms depicted in Figure 2 shows that the main cycle duration peak corresponding to the apomorphine-induced pecks (median about 220 ms) was shorter than the peak corresponding to the grain-induced pecks (median about 290 ms). The histogram of the apomorphine-induced pecks displayed a secondary smaller peak at about a double interval duration (median about 440 ms). This suggests that the apomorphine-induced pecking was driven by a faster underlying rhythm but that about 20% of the programmed pecks were not overtly expressed. There was no indication of any time-of-day modulation in the duration of pecking cycles induced by apomorphine.

#### Breathing While Behaviorally Inactive

The breathing recorded during the baseline periods in which the birds were awake and attentive but inactive both with respect to pecking and other behaviors, such as preening and walking, is described first. This set of data serves as a baseline for later

comparisons. We distinguished between baseline data acquired before and after the pigeons had been pecking grain. Table 2 shows the data concerning breathing during the periods 10 min before the pigeons had pecked at grain. Rather marked individual differences were apparent. The slowest and fastest mean breathing rates were exhibited by pigeon II (28.6 breath/min) and pigeon V (18.7 breath/min), respectively. The overall average of 23.8 breath/min coincides with resting respiration frequencies reported previously (Powell, 2000). The individual inspiration to expiration duration ratios also showed an appreciable variation. The breathing cycle durations were modulated by the time of day insofar as the cycles were somewhat longer in the morning ( $319 \pm 48$  cs) than at noon ( $221 \pm 23$  cs) and in the afternoon ( $238 \pm 31$  cs; data not shown in Table 2). The differences between morning and both noon and afternoon were significant (Wilcoxon tests,  $T = 0$ ,  $p < 0.05$ ).

The breathing recorded 10 min after the last bouts of grain pecking (averages shown in Table 2) differed only slightly. The pigeons thus returned to a baseline respiratory activity soon after the two 90-s periods of repetitive pecking had ended. However, the postpecking breathing only showed a nonsignificant trend relative to daytime (data not shown).

#### Breathing While Grain Pecking

We now examine the extent to which breathing is modified by pecking, focusing first on the effects of grain-induced pecking. The breathing cycles (Table 3) were significantly shorter than those shown during the baseline condition (Table 2; Wilcoxon test,  $T = 0$ ,  $p < 0.05$ ), resulting in a mean breathing rate

**Table 2.** Baseline Breathing Cycle, Inspiration Phase, Expiration Phase Durations in Centiseconds and Inspiration/Expiration Ratios

Bird	<i>n</i>	Cycle Duration	Inspiration	Expiration	Ratio
I	104	241 (80)	78 (18)	164 (72)	0.47
II	124	210 (35)	73 (9)	136 (30)	0.54
III	104	252 (55)	90 (8)	162 (52)	0.56
IV	123	274 (52)	99 (19)	175 (41)	0.57
V	77	329 (78)	125 (35)	203 (63)	0.61
VI	97	244 (59)	76 (25)	168 (46)	0.45
Sum/average	629	258 (37)	90 (18)	168 (20)	0.54
After pecking	657	251 (32)	90 (14)	162 (23)	0.55

Note: The last line shows recovery data recorded 10 min after the last grain-pecking period (the individual data are omitted).

**Table 3.** Breathing Cycle, Inspiration Phase, Expiration Phase Durations in Centiseconds and Inspiration/Expiration Ratios During Grain Pecking and Apomorphine Pecking

Bird	Breathing While Grain Pecking					Breathing While Apomorphine Pecking				
	n	Cycle	Inspiration	Expiration	Ratio	n	Cycle	Inspiration	Expiration	Ratio
I	317	163 (40)	67 (17)	96 (29)	0.70	775	88 (27)	45 (17)	42 (17)	1.07
II	279	168 (33)	73 (17)	95 (26)	0.77	665	110 (31)	50 (11)	61 (24)	0.82
III	253	180 (31)	87 (15)	94 (23)	0.92	786	58 (19)	31 (12)	27 (11)	1.15
IV	485	140 (26)	66 (16)	74 (18)	0.89					
V	165	196 (49)	93 (31)	103 (38)	0.90					
VI	205	162 (46)	62 (15)	100 (41)	0.62					
Sum/average	1704	168 (17)	74 (11)	93 (9)	0.76	2226	85 (21)	42 (79)	44 (14)	0.95

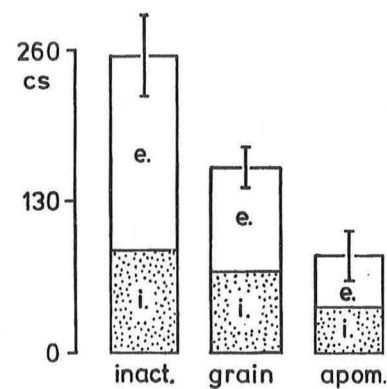
of 35.7 cycles/min. This nevertheless represents a very minor increase in breathing frequency, because, for example, when flying pigeons breath at rates above 400 cycles/min (Powell, 2000). The interindividual differences were of a similar order to those during the baseline condition, ranging from 30.6 cycle/min (pigeon IV) to 42.8 cycles/min (pigeon V). The shortening of the cycles was due to a marked reduction of the expiration phase (on average by nearly half) and a lesser reduction of the inspiration phase (Fig. 3). The average inspiration/expiration ratio accordingly increased appreciably, from an average 0.54 during the baseline condition to an average 0.76 during the grain-pecking condition. The reduction of the breathing cycle duration from the baseline condition to the grain-pecking condition was larger in the afternoon than in the morning or at noon. Consequently, the breathing cycle durations while grain pecking were no longer significantly influenced by the time of day (morning  $168 \pm 26$ ; noon  $167 \pm 19$ ; afternoon  $179 \pm 32$ ).

As described earlier, soon after grain pecking, breathing returned to near baseline (Table 2). The repetitive pecking had a considerable, but only transient, influence on the breathing cycles. If the increase in respiratory rate during pecking had been due to physical exertion during pecking, the breathing rate would be expected to gradually increase after the onset of a pecking bout. However, the mean duration of the first three breathing cycles of each of the pecking periods ( $170 \pm 26$  cs,  $n = 57$ ) was virtually identical to the mean of all the cycles of the same periods ( $173 \pm 29$  cs,  $n = 758$ ) and already much shorter than the  $251 \pm 32$  cs ( $n = 629$ ) cycle duration operating during the preceding inactive baseline condition. This suggests that the accelerated respiration during pecking was not a conse-

quence of muscular exertion but due to other causes to be considered later.

#### Breathing During Apomorphine Pecking

Apomorphine administration induced fast pecking and breathing (Table 3). Compared to the average 35 breath/min shown by the same birds during grain pecking, the average breathing rate increased twofold to 70 breath/min, ranging from 54.5 breath/min (pigeon II) to 103 breath/min (pigeon III). Confidence interval computations indicated that this increase was significant ( $p < 0.01$ ). The frequency increment is nevertheless still quite minor relative to the rate of over 600 breath/min at which pigeons pant in fully strenuous situations (Powell, 2000). The



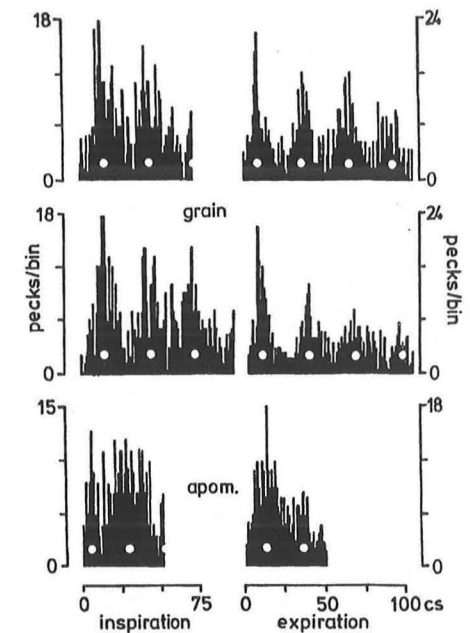
**Figure 3.** Mean respiration cycle durations ( $\pm$ SD) in centiseconds during the baseline inactive condition, during grain pecking, and during apomorphine pecking. The lower part of each column represents the mean inspiration phase, the upper part the mean expiration phase duration.

time of day had no significant influence on the breathing cycle durations under apomorphine. The average inspiration/expiration ratio of 0.95 was appreciably higher than the 0.79 ratio of the same birds while pecking at grain. This reflects a further marked shortening of the expiration phase and a lesser one of the inspiration phase (Fig. 3).

#### Interactions Between Pecking and Breathing

To assess the timing relations between breathing and grain pecking, we computed graphs analogous to the poststimulus firing histograms routinely used in neurophysiological research (e.g., Zigmond, Bloom, Landis, Roberts, & Squire, 1999). The histograms plotted the cumulated occurrence of pecks within successive 1-cs-wide time bins across the duration of a larger number of inspiration and expiration phases, all synchronized with respect to their onset (0 cs). Figure 4 (upper and middle panels) shows these postinspiration and postexpiration pecking histograms for pigeons I (based on 185 breath cycles) and pigeon III (based on 198 breath cycles). The histograms are shown truncated at roughly the corresponding mean inspiration and expiration phase durations with one additional SD taken from Table 2. The histograms of the other four birds revealed a very similar pattern. They all showed that the grain pecks were not evenly distributed across the respiration cycles but tended to occur at particular instants of the inspiration and expiration phases. Initial peak densities of pecking were apparent in all pigeons at about 10–20 cs after the onset of the inspiration phases and 10–15 cs after the onset of the expiration phases. Further, progressively decreasing pecking peaks were invariably present at successive intervals corresponding to the individuals' mean peck cycle durations listed in Table 1 (open circles in Fig. 4). These results indicate that there was an appreciable temporal link between the grain pecking and breathing rhythms.

Figure 4 (bottom panels) shows the same kind of histograms for apomorphine pecking based on 131 breathing cycles by pigeon I. Data obtained from the other two pigeons were similar. Apomorphine-induced pecks were somewhat more evenly distributed over the markedly shortened breathing cycles than grain-elicited pecks. Nevertheless, the occurrence of apomorphine pecks was never totally random with respect to the inspiration and expiration



**Figure 4.** Postinspiration onset histograms and postexpiration onset histograms of pecks cumulated in successive centisecond-wide bins. (Top and Middle) Grain pecking of pigeon I and pigeon III. (Bottom) Apomorphine pecking of pigeon I. The open circle marks are spaced according to the corresponding mean peck intervals given in Table 1.

phases. The histograms exhibit a narrow peak in peck density at about 6 cs after the onset of inspiration and a broader peak about 14 cs after the onset of expiration. Less well-defined secondary peaks are apparent after about a further 25 cs, corresponding to this bird's modal apomorphine pecking cycle duration. Thus, even under apomorphine there was some degree of coordination between the pecking and breathing rhythms.

#### Discussion

Pecking of millet grains shown by the pigeons was of a highly rhythmic nature. The peck cycle durations varied by less than 10% between different pigeons and between different times of day. Moreover, although not shown, the mean cycle duration of the individual pigeons remained highly constant

across the replicated measurement periods. This invariance is somewhat surprising, inasmuch as most of the recent evidence has tended to stress the variability of pecking movements (Hörster, 1997; Siemann & Delius, 1992a). However, these studies focused on the effect of different conditions, whereas we kept the feeding conditions constant. The use of small grains facilitated grasping and swallowing. Nevertheless, even such undisturbed pecking involves the timed activation of dozens of neck muscle pairs, each of these muscles innervated by separate groups of motoneurons (Hörster, Franchini, & Daniel, 1990; Van den Berge, 1979). This might lead one to expect more pronounced timing variances. The relative regularity of pecking cannot be explained by the argument that the peck movements are performed as fast as mechanically possible, because pigeons significantly shorten the interpeck intervals as they are increasingly food deprived (Siemann & Delius, 1992a). Moreover, they are able to shorten their peck cycle durations by about half when operantly conditioned to do so (Hörster et al., 2002). However, the natural resonance frequency of the head-and-neck mechanics probably influences the rhythmicity of pecking. Additional loads attached to the head have been found to lengthen the duration of peck cycles (Siemann & Delius, 1992a). Still, it seems possible that a central oscillatory neural network might drive the rhythmic pecking of pigeons. Electrograms recorded from the frontal telencephalon indicate that as pigeons prepare to initiate a grain-pecking bout, they already exhibit recurrent potential peaks at the rate of about 3/s to which the subsequent pecks are then synchronized. Upon cessation of overt pecking, these rhythmic potentials often persist for a few cycles. Comparable electrogram rhythms were also observed in conjunction with apomorphine-induced pecking (Delius, unpublished data; see also Boyko & Bures, 1975; Dubbleadam, 1998).

Apomorphine might activate and accelerate this hypothetical central peck generator. Indeed, the distribution of peck cycle durations shown in Figure 2 suggests that as the accelerated rhythm persisted, occasional overt pecks were skipped without disturbing the underlying cyclicity. We cannot dismiss the possibility that the shortening of pecking cycles under apomorphine was due to the fact that they did not involve any grain swallowing. However, the orolingual transport of small grains such as the millet

used here is known to be accomplished with a so-called "glue-and-slide" action, which does not interfere with the initiation of a subsequent peck (Siemann & Delius, 1992a; Zweers, 1982). Also, it is not certain whether apomorphine pecking might not include laryngeal closures, due to the swallowing of saliva. This would make the drug-induced pecks even more similar to the millet-elicited pecks.

The rhythmical respiration of birds, despite the peculiarities of their air sac breathing (Brackenbury, 1981; Powell, 2000), appears to be primarily determined, as in mammals, by the activity of a rhombencephalic neural pacemaker network (Fortin et al., 1994; Michal et al., 1981; Von Saalfeld, 1937). The oscillatory activity of this neuronal network is naturally subject to considerable extrinsic modulation. Among other things, it is quite obviously affected by obstructions of the airways and by the level of muscular exertion. In the present study the respiration rate increased markedly while the pigeons pecked for grain and even more while they pecked under the influence of apomorphine. It is unlikely that the brief laryngeal closures connected with millet grain swallowing were somehow responsible for the breathing accelerations during grain pecking because the even larger breathing acceleration observed under apomorphine occurred when laryngeal closures were minor or absent. Indeed, even though the limited high-frequency response of the recording system might have obscured them, our records did not reveal any traces of breathing arrests associated with swallowing (Fig. 1). The cumulating oxygen debts and carbon dioxide loads arising from muscular activity are also unlikely to have been responsible for the respiratory rate acceleration connected with pecking bouts because we found that the breathing rate increase began immediately after the onset of grain pecking. It is known that, at least in mammals, signals arising from the mere activation of muscles can increase respiration in an immediate feed-forward manner through various mechanisms (Cohen & Obrist, 1975; Miyamura, Ishida, & Yasuda, 1992). Birds are indeed also known to immediately adjust their breathing to ambient temperature changes in such a feed-forward way (Nichelmann, 1985). Whether the very marked acceleration of the breathing rhythm induced by apomorphine can be wholly explained by this kind of anticipatory mechanism seems doubtful, because the breathing rate increased disproportionately to the

pecking rate. It is true that, besides inducing accelerated pecking, apomorphine can also increase the locomotory activity of pigeons. It is, of course, known that longer term muscular activity leads to mounting gas debts that affect respiratory intensity in a feedback manner (Brackenbury, 1991; Scheidt & Piiper, 1986). But the activity increase shown by our pigeons seemed too mild to explain the appreciable breathing increase that we observed. We suspect instead that apomorphine may have also acted directly on the central breathing pacemaker. Because systemically administered apomorphine invariably elicits pecking, it is unfortunately not possible to examine its effect on the respiration rhythmicity alone.

It is well established that the locomotor activity in pigeons is subject to a circadian rhythm. The hormone melatonin secreted by the pineal and the eyes has been implicated (Chabot & Menaker, 1992a; Oshima, Yamada, Goto, & Ebihara, 1989). A diurnal rhythm is also apparent in the pigeon's food intake, in which there is a small peak in the morning, a trough at noon, and a major maximum in the afternoon (Zeigler, Green, & Lehrer, 1971; see also Chabot & Menaker, 1992b). Here we have shown that the time of day also modulates grain-pecking and breathing rhythms by slowing and accelerating them, respectively, in the afternoon, but that the circadian effect on breathing was overridden when grain or apomorphine activated pecking.

We have further shown that although the rhythmicities of pecking and breathing were of quite different frequencies (about 2–4 pecks/s and about 0.3–1.2 breath/s), they nevertheless interacted in that pecking preferentially occurred at certain points of the breathing cycle. This obviously does not involve any absolute locking between the two rhythms. We suppose that the pecking rhythm transiently corresponds with the breathing rhythm, although there may also be a reverse effect. Von Holst (1939) introduced the notion of relative coordination for this kind of phenomena. He coined the term "magnet-effect" for the capacity of one rhythm to draw another rhythm into transient synchronies. It seems that weak neural linkages rather than any mechanical coupling are usually responsible for such relative coordination phenomena (Glass, 2001). Whether the neural linkages between rhythm-generating networks have evolved rather incidentally, or whether they have evolved because they serve some functional purpose

such as energy saving or neuronal economy, has often been disputed (Banzett et al., 1992; Berger & Hart, 1974; Rassler, Waurick, & Ebert, 1990). Regardless, we have now shown that the rhythmic pecking of pigeons is partially coupled not only to the heartbeat rhythm (Delius et al., 1986) but also to the breathing rhythm.

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