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#### INTRODUCTION

In the normal environment of an animal one and the same object can yield very different patterns of retinal activation depending on the particular lighting conditions and on the relative orientation and distance the object has with respect to the animal's eyes. It is nevertheless imperative for the sake of evolutionary fitness that animals positively recognize at least a range of objects in spite of this apparent variability. Furthermore it is equally important that different objects be recognized by some abstract criteria as belonging to one of several classes of objects. To these classes the animal can then respond with relatively unitary sets of responses in spite of the individual diversity of the member objects. We humans of course make constant use of such capabilities in the course of daily life with respect to scores of objects. Psychologists give the collective names of perceptual invariance and perceptual concepts to the phenomena underlying these competences. Engineers have recently made efforts to provide robots with comparable performances. While their implementation is feasible in principle it has been found that they require an inordinate amount of computing power. Small-brained animals such as birds are necessarily short of information processing capacity and may thus have to forgo some perceptual invariance and concept capabilities. But the impression of field students of avian behaviour is that, if anything, the visual performance of most birds outclasses their own. For some basic functions this impression has indeed been supported by formal research. Pigeons (*Columba livia*) for example have colour vision that is more sophisticated than ours in being at least tetrachromatic with a spectral sensitivity extending into the near-ultraviolet and an additional ability to detect the polarization plane of light (Emmert, Delius, 1980; Delius et al., 1976).

#### ROTATION INVARIANCE

We have recently begun to examine experimentally the extent of pigeons' visual invariance abilities. With Valerie Hollard (Auckland, New Zealand) we studied their performance in a situation that demands the visual identification of specific forms when these appear at various angular orientations. This requires a mechanism that ensures a rotational invariance of pattern recognition. More specifically, the birds had to repeatedly recognize a predetermined target out of pairs of mirror-image shapes when these were displayed at angular orientations coinciding or not coinciding with the target's alignment. To get the pigeons to perform the task we employed an operant discrimination learning paradigm known as matching-to-sample (Carter, Werner, 1978). The food-deprived birds were placed in a three-key Skinner-box. An automatic slide projector displayed shapes on the back of the translucent keys. The opening of a shutter first allowed the pigeons to view the target or sample shape projected on the middle key. The birds were required to acknowledge this stimulus by pecking the key a number of times. This caused the two side-key shutters to open, exposing the two comparison patterns on them. One of these

patterns was geometrically identical to the sample pattern. The other pattern was its mirror image. The pigeons of one group had then to peck the key wearing the identical, matching, those of another group of birds, the odd, non-matching shape. If they did so correctly they were rewarded with brief access to food, if they chose the wrong shape they were punished with a brief period of darkness. The next trial began with the presentation of the next sample and so forth. The daily sessions consisted of 40 such trials. After training for some 40 sessions with sets where the orientation of sample and comparison stimuli were the same, series of 10 sessions were conducted with sets of stimuli that systematically explored the effect of angular disparities between samples and comparison shapes. The order in which the various stimulus sets occurred was randomized, as was of course the sequence in which the correct and incorrect stimuli appeared on the left and the right response keys. The whole procedure was controlled by a suitably programmed microcomputer which also recorded all the pertinent data, in particular the correct or incorrect nature of the response in each trial as well the latency or reaction time corresponding to each response. This is the time interval between the onset of the comparison stimuli and the peck to one of them for each trial (Hollard, Delius, 1982).

It was found that pigeons could master the task quite efficiently. Error rates could be as low as 10% and the reaction times as fast as 0.7 sec. The most important result however was that the error rates and the reaction times were nearly constant, that is neither varied significantly as a function of the degree of orientation disparity between the samples and the comparison patterns. In other words the pigeons found it equally easy to identify the matching (or non-matching) comparison patterns, regardless of whether these were oriented the same way as the sample (0 degrees) or tilted by 45, 90, 135 or even 180 degrees clockwise. This was so irrelevantly of whether the pigeons were dealing with patterns and their mirror images with which they had had extensive previous experience or with totally new patterns. Essentially the same results were also obtained if the comparison stimuli were always shown in the standard orientation but the samples were presented in varying angular positions between 0 and 180 degrees (Fig. 1).

This result is remarkable because previous experiments (Cooper, Sheppard, 1978) as well as our own using students instead of pigeons (Hollard, Delius, 1982), have shown that the performance of humans in this kind of task is markedly dependent on the degree of rotation of the comparison patterns. Particularly the reaction times are a monotonically increasing function of the disparity angle. Overall, humans were also much slower in responding than the pigeons. The interpretation supported by introspective accounts is that humans have to rotate a memory representation of the sample stepwise, each time comparing it for coincidence with the comparison stimuli. This sequential procedure, known as mental rotation, has all the characteristics of thinking or, as psychologists prefer to say nowadays, of a cognitive process. Pigeons obviously solve the problem in a different, more immediate, automatic way that in earlier times might have been labelled as reflexive or even instinctive. Parallel rather than sequential information processing seems to be brought into play by their visual system.

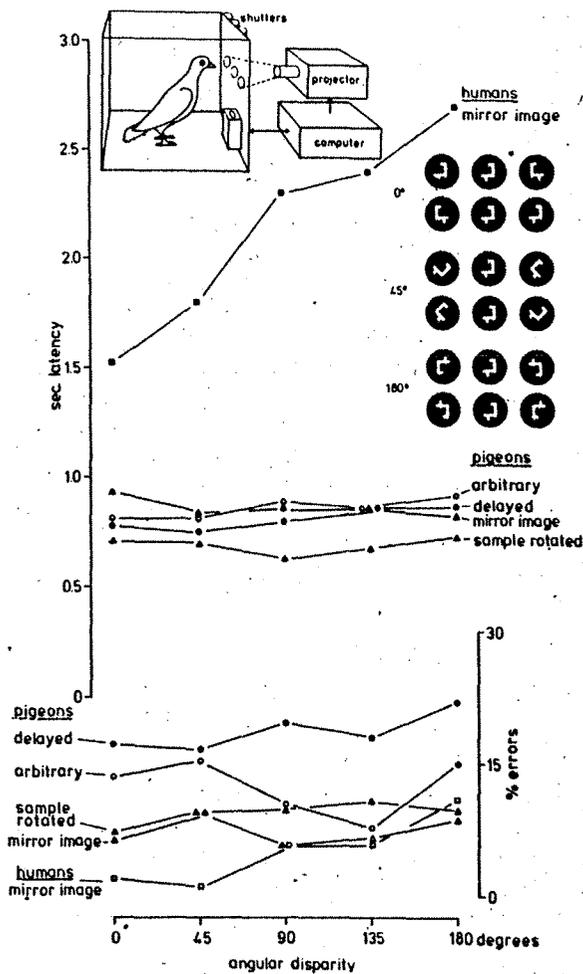


Fig. 1. Latencies and error rates of pigeons and humans during rotational invariance tasks with visual patterns. The insets illustrate the apparatus employed and give examples of the matching-to-sample tasks (see text for further details)

Most of the studies on mental rotation in humans, although not ours, were done with a procedure that required the subjects to refer to the sample or target as an engram, that is as information stored in memory. We considered that perhaps this might be an important factor. Experiments with pigeons in which the sample pattern was shut off 5 sec before the comparison stimuli came on, a delayed matching-to-sample procedure, led to some deterioration of performance but there was still no evidence of any dependence on the orientation disparity of the forms (Fig. 1).

Now, humans yield a performance similar to that of our pigeons in an other kind of rotational invariance task where instead of mirror images the

odd patterns are arbitrarily different shapes (White, 1980). Just in case, we have tested pigeons with an analogous task and found that their performance was the same as when they dealt with mirror-image pairs of shapes. There is considerable evidence that for humans mirror-image shapes are peculiarly difficult to distinguish (Corballis, Beale, 1976). It seems possible that for pigeons this is not so and preliminary experiments of ours suggest that they may indeed find them easy to discriminate.

This suggests that the sequential, mental rotation process might only be brought into play when the shapes to be distinguished are very difficult to discriminate. For humans there is an indication that indeed mental rotation results are obtained with non-mirror-image odd shapes only when the shapes are highly complex. Perhaps pigeons would also yield such a performance if one would select shapes that are especially hard for them to discriminate. Visual pattern discriminations as compared with colour and brightness discriminations are more difficult for pigeons than they are for humans, thus the experiment involving non-mirror images might have already fulfilled this condition but this issue needs further experimentation. Alternatively one can hypothesize that pigeons store information about shapes in an orientation-free mode. They thus should have difficulty with tasks demanding the discrimination of one and the same shape at different orientations. We have found that pigeons indeed have considerable difficulty in learning to discriminate an upright cross + from a tilted cross x (Delius, Emmerton, 1978). This could have to do with the fact that pigeons operate visually predominantly on the horizontal plane where the orientation of objects is largely arbitrary relative to the position of the observer. Humans view predominantly the vertical plane where both observer and objects tend to have an orientation determined by the effects of gravity. Pigeons have however been shown capable of discriminating very small angular orientations disparities of line stimuli (Klipec et al., 1979) and thus this explanation can be only a partial one.

We have further wondered whether the rotational invariance performance of pigeons might be due to the fact that they have a visual system predominantly based on the midbrain optic tectum as compared with the mammals that have a mainly endbrain, striate cortex based system. As a first step we examined the performance of our pigeons after they had been surgically deprived of their telencephalic Wulst, a brain area that contains the avian homologue of the mammalian visual cortex. Their invariance performance was completely unaffected. Thus the information processing required for it clearly does not take place there. This contrasts with the consequences of visual cortex ablations in primates who are then very nearly blind and certainly incapable of mental rotation (Milner, 1970).

#### VISUAL CONCEPTS

In the research summarized above we made the assumption that pigeons are capable of detecting the identity or conversely the oddity of sample and comparison shapes in a generalized, concept-like fashion. However there has been controversy as to whether pigeons really can achieve this (Carter, Werner, 1978). Since our pigeons' matching-to-sample performance in the rotational invariance tests was maintained even when they had to deal with shapes completely new to them (Hollard, Delius, 1982) we have no doubt that they can. If

previous experimenters had some difficulty with demonstrating a conceptualization of identity/oddity by pigeons then we believe that this has been due to the employment of too few training stimuli, inviting the pigeons to use simpler strategies, and to the use of designs that allowed the strong novelty aversion that characterizes these animals to come into play.

There is another way in which the issue of whether pigeons can conceptualize is relevant here. We mentioned earlier that it is possible that pigeons in contrast to humans distinguish between mirror-images shapes just as well as between any arbitrarily different shapes. This suggests that the birds may not be able to recognize the special equivalence of mirror-image shapes. That could imply that pigeons may not recognize bilaterally symmetric shapes as a particular class of forms consisting of two fused mirror-image halves. Morgan et al. (1976) have mentioned evidence that supported this view but Delius and Habers (1978) found that pigeons seemed to be able to discriminate bilaterally symmetric from asymmetric shapes in a generalizing manner.

With Brigitte Nowak we have investigated this issue more thoroughly. Pigeons were trained to discriminate 26 bilaterally symmetric shapes from an equal number of asymmetric shapes using a free operant successive discrimination procedure (Delius, Nowak, 1983). The shapes were back-projected onto the single key of a Skinner-box in a randomized sequence. Each shape was shown for a standard 30 sec. One group of pigeons was required to peck the symmetric pattern for occasional food reward and not to peck the alternative patterns to avoid extensions of the presentation time of the non-rewarded stimulus. Performance was measured by the percentage of responses to the correct stimuli out of all responses during the standard 30 sec presentations. The daily sessions involved the displaying of 40 shapes. All pigeons learned to perform at a level of 80% or more responses correct within 25 sessions. In interspersed trials they were then exposed to test shapes with which they had no previous experience with under extinction conditions, that is where responses had no consequences. The birds classified these stimuli with high accuracy, that is they responded with high frequency to the novel stimuli that belonged to the same class as those training stimuli that had yielded reward and much less to those that were of the same type as those training stimuli that had resulted in punishment. This was so even when the geometrical style of the test figures differed markedly from the training shapes (Fig. 2).

There can be no doubt that the pigeons recognized the bilateral symmetry, or else the asymmetry, of the figures in a concept-like, generalized fashion. They did so regardless of the fact that in one test series the asymmetric stimuli were repeated shapes especially designed to have a redundancy at least as high as that characterizing symmetric forms and that in another series the test figures were presented with varied symmetry axis orientations, differently from the training stimuli which always had a vertical axis. The pigeons' symmetry recognition was not impaired when they had to perform with one eye covered by an eye-patch. The competence for symmetry recognition can not thus be somehow ascribed to the bilateral symmetry of the nervous system. The mechanisms with which pigeons recognize symmetry do not seem to correspond with any that have been proposed to explain symmetry identification by humans (Corballis, Beale, 1976). Rather we have put forward an alternative theory of our own.

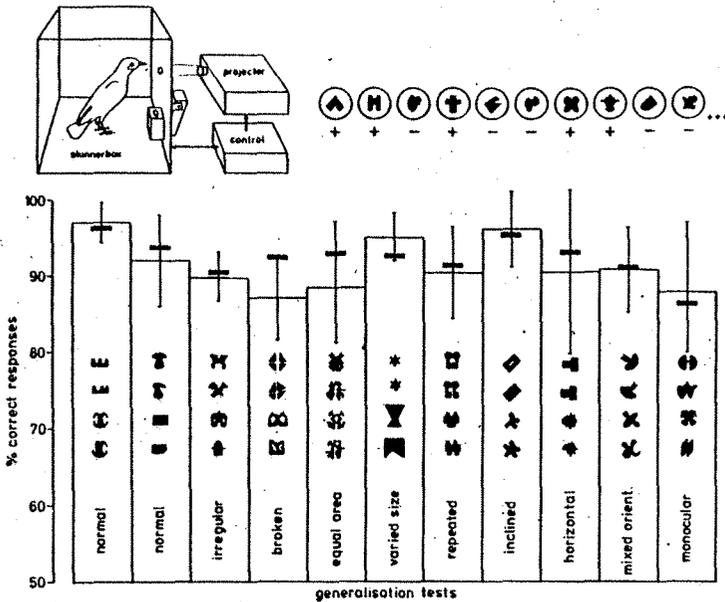


Fig. 2. Mean correct response scores (columns) of pigeons generalizing a symmetry/asymmetry discrimination to various sets of novel visual patterns (examples shown). The concurrent performance on the training stimuli is indicated by bars. The insets illustrate the apparatus employed and the successive discrimination conditioning with examples of the training stimuli.

It is known that the visual system of both birds and mammals performs a kind of spatial Fourier analysis (De Valois, De Valois, 1980; Jassik-Gerschenfeld, Hardy, 1981). If symmetric and asymmetric shapes are examined from this point of view one finds that at the symmetry axis the Fourier components have a special phase relationship being all in-phase (0 degrees) and/or anti-phase (180 degrees) to each other whereas such conjunction does not occur anywhere in an asymmetric pattern. There is evidence that these phase relationships have a special status for humans (Atkinson, Campbell, 1974) and there are reasons to expect that the same is true in birds. This has to do with the fact that both visual systems have to deal with an information surface, the retinal image. This can only be done with neuronal networks that have a multiply symmetrical microstructure.

If such neural filters are the basis of symmetry recognition it seems unlikely that our pigeons developed them during training. Rather it must be suspected that they only learned to apply pre-existing ones to the task in hand. Additional experiments suggest that naive adult pigeons have a slight but consistent spontaneous preference for asymmetric patterns and that they can bring a symmetry/asymmetry recognition to bear at a very early stage of discrimination learning. We assume, admittedly so far without proof, that, as it is apparently the case in humans (Bornstein et al., 1981), the relevant networks are laid down very early in neurogenesis and predominantly

under genetic control. If that is so one may doubt whether it is appropriate to talk about a symmetry concept. That is a matter of definition but pigeons have of course been shown able to truly learn a variety of other perceptual concepts such as people, person, tree, oak leaf, pigeon, fish, and so forth (Herrenstein, de Villiers, 1980).

Returning to symmetry recognition one may ask about its adaptive value. Referring to insectivorous birds Curio (1976) suggested that it may aid them to break the camouflage of some of their prey. For pigeons and as a matter of fact humans it is more difficult to make such a case. Rather, as already indicated above, we believe that visual symmetry is really a by-product of structures selected to fulfil other more general visual information processing functions.

#### CONCLUSION

In spite of their relative microcephaly, implying limitations in information processing capacities pigeons and presumably other birds perform at least some perceptual invariance and conceptualization functions which are known to be highly demanding on computing power. In at least one instance the pigeon's performance was found to be superior to that of the macrocephalic human species.

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