

## Sensory Mechanisms Related to Homing in Pigeons

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### Abstract

Besides having a well-developed vestibular system, pigeons possess a gravity and inertia sensitive system mediated by displacement of the viscera, presumed to stimulate mesenteric mechanoreceptors. Classical conditioning experiments confirm a sensitivity to atmospheric pressure changes. Failure to demonstrate a magnetic field orientation sensitivity in an instrumental conditioning situation is reported. Behavioral and physiological experiments establishing the pigeon's ability to detect and orient itself with respect to an overhead polarized light are referred to. Failure to demonstrate discrimination of such a plane orientation on other experiments suggests that mechanisms connected with the upper field of vision are specialized for polarization plane detection. Evidence that pigeons can perceive and discriminate ultraviolet light is mentioned. Finally reference is made to the widespread forebrain projections of olfactory input.

Accurate information about position or position changes with reference to gravity and inertia must be an important prerequisite for navigation. The vestibular sense organs of pigeons are accordingly well developed. The cerebellum, the main processing projection of this sensory complex in vertebrates, is comparatively large in birds. The vestibular projections to the thalamus of pigeons also seem to be relatively more extensive than those found in mammals (Vollrath and Delius, 1976). Moreover some of the units seem to be engaged in performing a compensating function that must be postulated if vestibular information is to be used for spatial orientation of the body in an animal with a neck as mobile as that of birds. Neck mechanoreceptor afferences and labyrinthine input are integrated by these units in a way that is qualitatively compatible with a compensation of head movements relative to the body (Mittelstaedt, 1964). Birds do not seem to rely on this mechanism alone. It has been known for some time that wing, tail and leg righting-reflexes persist in pigeons whose spinal cord has been transected at thoracic levels (Biederman-Thorson and Thorson, 1973). Recording from the sacral dorsal root fibers of such pigeons we found that a proportion of the units responded to pitch, roll, and yaw even after we had transected the somatic branches of the dorsal roots. Mechanical movement of the viscera with an implanted balloon or lever suggests that this activity was due to the stimulation of mesenteric mechanoreceptors whose axons reach the dorsal roots through the rami communicantes. The viscera thus function in a manner analogous to otoliths (Delius and Vollrath, 1973).

Even though pigeons seem unusually well oriented with respect to gravity, they still have some striking difficulties in certain situations in which we might expect these orientation abilities to be used. We have found that they have considerable difficulty in learning to discriminate an oblique cross (x) from a vertical/horizontal one (+)

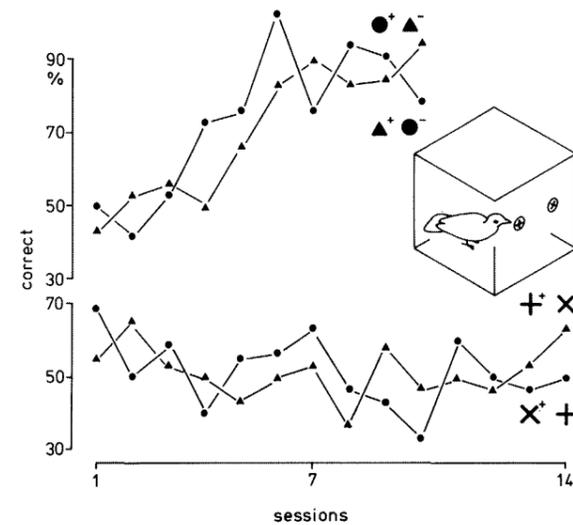


Fig. 1. Learning curves of the same two pigeons discriminating an *upright* and an *oblique cross* and a *triangle* and *circle* in separate experiments. Each session consisted of 30 trials

projected on the pecking keys of a Skinner box (Fig. 1). Reports suggesting that pigeons have some difficulty in recognizing varying orientations of other visual patterns displayed on Skinner box keys can also be found in the literature (Corballis and Beale, 1976). The error seems to arise from the fact that when observing the figures the pigeon seems to align its head along the vertical or oblique axis of the figures and obviously does not compensate this alignment with vestibularly available information about the true vertical. It remains to be established whether this difficulty is restricted to the pigeon's binocular frontal field of vision, served by the red field of the retina, that appears somewhat specialized for food gathering (Galifret, 1968, Catania, 1964, Romeskie and Yager, 1976 but see Friedman, 1975). An inability to learn to discriminate grains by their orientation seems affordable, perhaps even desirable, for a pigeon, if it can spontaneously align its head to enable a good bill grip on them.

We have established that pigeons know up from down. It would be useful for them to have information about how far up or down they were. This can be provided by barometric sensitivity, i.e., by a sense organ responsive to atmospheric pressure levels (see however Bilge, 1973). Such a sensitivity was demonstrated by Kreithen and Keeton (1974a). We just wish briefly to report experiments that were begun independently (Watson, 1974) and that fully support their findings. They were initiated by an incidental observation that pigeons performing steadily in certain behavioral experiments were disturbed by the opening and closing of remote laboratory doors even when it was highly unlikely that they could have heard anything. We used an aversive classical heart rate conditioning technique similar to that used by Delius and Tarpay (1974). Pigeons equipped with chronically implanted electrocardiogram and shock electrodes were placed in a through-ventilated pressure chamber and, at random intervals, experienced 10-s pressure increases (or decreases) preceding the administration of a 50-Hz 0.8 mA 0.1-s shock. Heart beats were counted during pairs of 10-s periods that were quasirandomly alternated and separated by an approximately 2-min variable interval. During half of these pairs (control), chamber pressure remained equal to atmospheric pressure. In the remaining pairs (experimental), atmospheric pressure was again used in the first 10-s

period but during the second period a pressure change, followed by shock, was instituted.

From these 25 control and 25 experimental pairs of periods we derived separate signed mean changes in heart beats per 10-s where the control yielded an estimate of the baseline heart-rate trend over the session (usually a slight downward trend) and the experimental pairs gave an estimate of the conditioned heart-rate increases superimposed on this trend. The signed difference between the two means gave the net conditioned heart-rate increases occurring in the presence of the pressure wave.

For two pigeons the conditioned stimulus was a pressure increase, for one it was a pressure decrease. During the initial sessions with each animal the 10-s pressure pulses had an amplitude of 10 cm H<sub>2</sub>O. Then each animal had two sessions with 2 cm H<sub>2</sub>O pulses and finally they had three control sessions incorporating shocks but without pressure changes.

Since the results for the subjects receiving pressure increases and decreases did not differ, they were lumped together for Figure 2, which presents the mean net conditioned responses for all sessions in the form of histograms. It is clear that pigeons can detect pressure changes and that their threshold lies below 2 cm H<sub>2</sub>O. This means that they should be able to detect altitude changes of at least 20 m. Yodlowski et al. (1977) showed that the pressure sensitivity can be considered as an extension of the hearing capabilities into the very low frequency range and speculated on whether they might be able to extract navigational cues from naturally occurring ultra-low frequency sound phenomena. It is, however, unclear whether pigeons can detect steady pressure levels.

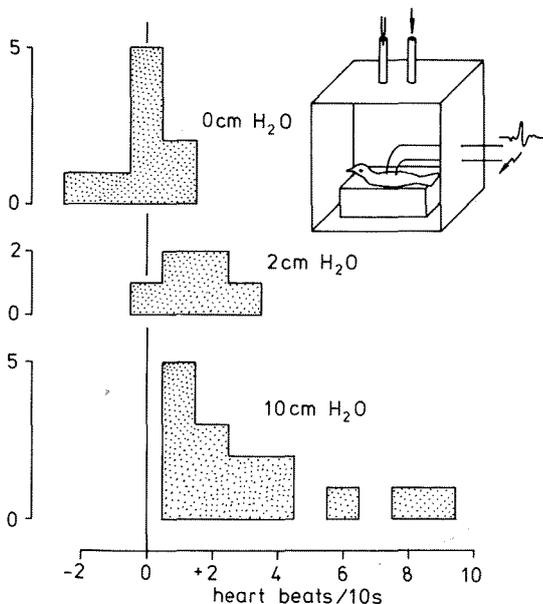


Fig. 2. Distribution of mean conditioned heart-rate changes for 3 subjects tested with pressure changes of 10 cm H<sub>2</sub>O (5 sessions), 2 cm H<sub>2</sub>O (2 sessions) and in control sessions (0 cm H<sub>2</sub>O, 3 sessions)

Our present effort is directed at identifying the sensory organ responsible for this pressure sensitivity, a likely candidate being Vitali's organ, a closed, hair-cell lined vesicle located just below the middle ear lining (Benjamins, 1926), but so far we have not been able to produce definitive evidence because surgical access to the vesicle is difficult.

Needless to say, like many others, we have also attempted to condition pigeons to magnetic field changes. While there can be no doubt that pigeons, among other birds, are sensitive to magnetic forces (e.g., Larkin and Keeton, 1976; Walcott and Green, 1974; Wiltschko and Wiltschko, 1972), it has proved difficult to demonstrate this in the laboratory (Kreithen and Keeton, 1974c; Beaugrand, 1976, 1977; but see Bookman, 1977), a prerequisite for attempting to identify the sensory process by which they are able to do so. We can only report a further failure (Freeman, 1974). We surrounded an octagonal Skinner box bearing a pecking key on every alternate wall with three pairs of orthogonally collocated Helmholtz coils. Automatic programming controlled the sequence of events in each session and recorded the subjects' responses. In particular it activated the Helmholtz coil pairs in a manner adequate to produce the desired net magnetic fields, cancelling where necessary natural earth magnetic field components.

Two animals were presented with alternative 0.20 Oe magnetic fields devoid of a vertical component and at right angles to each other. One subject was rewarded for choosing either of the pair of keys lined up with the relevant magnetic field. The other subject had to choose the keys at right angles to the momentary field orientation. A third pigeon had the same task as the first one but the fields had a downward vertical component of 0.40 Oe (corresponding to the normal local vertical component). None of the animals showed any sign of discriminating between the alternative fields during 17 sessions. In a similar situation described below, but involving polarized light, discrimination was observed after one to seven sessions. This also applied to two of the above pigeons that were subsequently used in that experiment. Eight to 11 further sessions, in which the horizontal component intensities were doubled (0.40 Oe), with only two pecking keys available, and in which a response was demanded to the key coinciding with the magnetic north (first and third subjects) or west (second subject), did not yield discrimination either (Fig. 3). Five to eight additional sessions, with only two keys, in which the horizontal fields were twice the strength as before (0.40 Oe), all without a vertical component and with reversed polarity at a rate of 0.5 Hz (first two subjects) or 10 Hz (last subject), were similarly ineffectual.

The fact that pigeons are capable of orienting by the sun compass method, much as bees do, suggested that they might use the sun-coupled polarization pattern of skylight to supplement this capability. This presupposes that they can detect the polarization plane of light. Kreithen and Keeton (1974b) showed that pigeons could differentiate between a light source with a stationary and rotating plane of polarization. Independently we found (Delius et al., 1976) that pigeons placed in a Skinner box similar to that described earlier for the magnetism experiment, could learn to choose keys aligned in specified ways with the randomly rotated polarization plane of an overhead light source. In additional experiments we found that the time course of the bioelectric response of the pigeon's eye to a light flash varied with the orientation of its polarization plane. The effect was maximal when the light fell on the lower retina. This would agree with the results of two other behavioral experiments that yielded weak or no evidence of discrimination of polarization plane orientation in pigeons. Montgomery and Heinemann (1952) could not get pigeons to perform such dis-

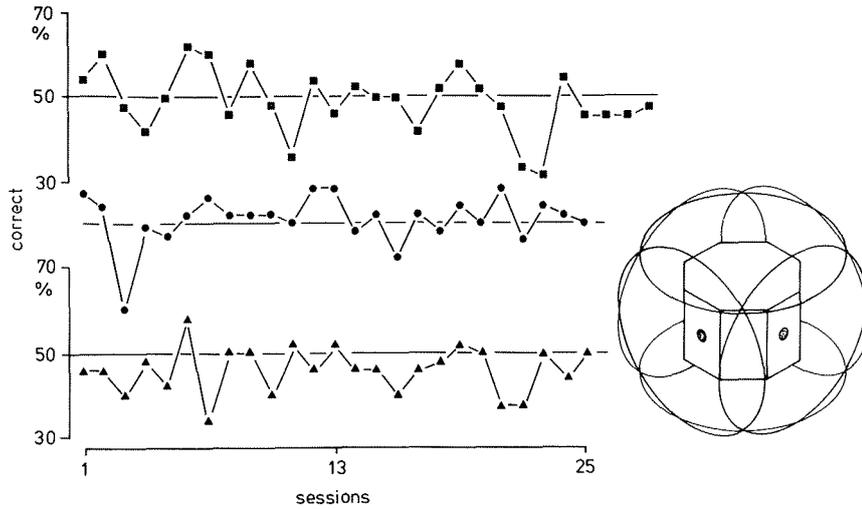


Fig. 3. Discrimination performance of three birds tested under various static magnetic field intensity conditions (see text). Four response keys were used during the first 17 sessions; only 2 keys were available during subsequent sessions

criminations when the stimuli were shown on pecking keys. In another of our experiments (Delius and Emmerton, in press), using an automated Y maze with stimuli displayed on the end walls, we found at best weak evidence of discrimination even after using various procedures designed to aid the animals in this discrimination task (Fig. 4). In both cases

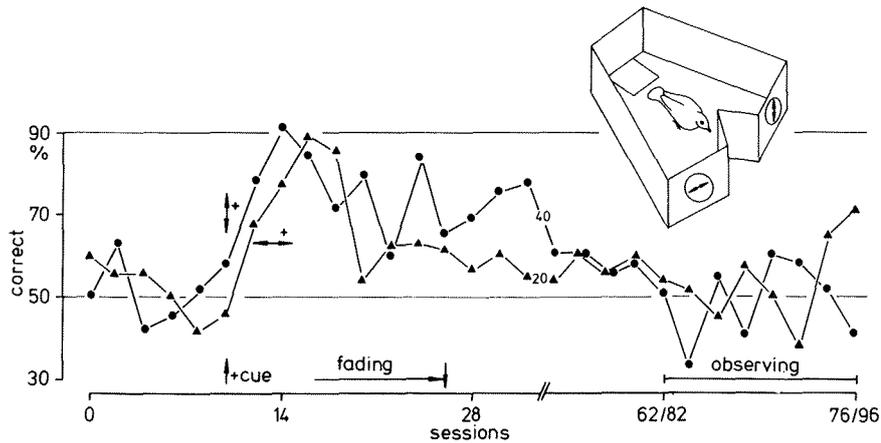


Fig. 4. Learning curves of two pigeons discriminating the polarization plane orientation of a pair of stimuli in a Y maze. In an effort to aid the discrimination task a correction procedure was used throughout; a temporary light cue, subsequently faded off, marked the correct stimulus; later, subjects had to fulfil a 5-s stimulus observing period prior to making a choice. Means of pairs of sessions are plotted. For simplification 20 (40) sessions have been omitted

the pigeons can be expected not to have viewed stimuli with their upper field of vision. We have referred before to possible functional differences between the various parts of the pigeon's visual space that are reflected, to some extent at least, in differentiation of various areas of the retina (Galifret, 1968). The results of another experiment using the same tall octagonal Skinner box, but a bright light bar as an orientational cue instead of the polarization plane, suggest that the upper field of vision might not be as adept at the utilisation of brightness patterns for orientation (Delius and Emmerton, in press).

Although we know that pigeons, unlike bees, can detect the polarization plane orientation of nonultraviolet light, the fact that the polarization of skylight is maximal in the ultraviolet range raises the question of whether pigeons can see this short-wavelength light. Wright (1972) produced good evidence that they can by showing that nonexclusion of ultraviolet cues can contaminate the discrimination of longer wavelength light. One of us has shown electroretinographically that the eye's sensitivity extends at least to 360 nm, where sensitivity is, however, still increasing (Emmerton, 1975, Delius and Emmerton, in press; see also Kreithen, this volume). In a behavioral experiment it was also shown that pigeons can discriminate well between ultraviolet stimuli of different wavelengths. This experiment also suggested that their color vision within the human visible range is more complex than ours. In view of the pigeon's wavelength detection and discrimination abilities, we are at present examining the wavelength-dependent responses to polarized light, being particularly interested to see if polarization sensitivity is enhanced when ultraviolet stimuli are used.

Olfaction is said to provide cues for homing (Papi et al., 1972; Benvenuti et al., 1973), which would seem to be contrary to the general belief that birds have a poorly developed sense of smell. This generalization has been found to need correction in several instances (Wenzel, 1973). As far as pigeons are concerned, we can report from some current electrophysiological work (Delius and Middler, in prep.; see also Wenzel and Rieke, 1975) that the plurality and complexity of olfactory projections found in the pigeon's forebrain is surprising, suggesting that this bird cannot be an olfactory slouch!

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