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An Attempt to Confirm Magnetic Sensitivity in the Pigeon, Columba livia

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Summary. An attempt was made to test the sensitivity of homing pigeons to weak magnetic variations of the order of the ones naturally occurring on earth. Pigeons were first subjected to a cardiac orienting reflex test to 50 magnetic stimuli and to 50 control stimuli presented alone and randomly interdigitated. They were then subjected to a differential nociceptive conditioning procedure using the same magnetic and control stimuli for 100 trials under each stimulus condition. Cardiac activity was used as an index of reactivity throughout the study. The tests were performed in uniform magnetic fields using 1 to diameter Helmholtz coils. Results indicate that the magnetic stimuli presentations did not evoke a cardiac orienting reflex when compared to the cardiac orienting response of control pigeons to a neutral luminous stimulus. Moreover, results from the conditioning tests indicate that the magnetic stimuli were not used by the pigeons as a cue presaging the forthcoming shock. It is concluded that, in the present experimental situation, homing pigeons did not respond to small changes in the ambient magnetic field with changes in autonomic functioning. Results are discussed in the context of the inappropriateness of the stimuli and tests used to show magnetic sensitivity in birds.

Introduction

There is a growing literature suggesting that the earth's magnetic field might be a source of directional information for some migrants and homing pigeons (Wiltschko and Wiltschko, 1972; Southern, 1972; Keeton, 1974x, 1974b; Walcott and Green, 1974). Evidence of this influence is mainly derived from research on the European Robin (Erithacus rubecula) and two species of European warblers (Sylvia communis and Sylvia borin) (Wiltschko, 1972, 1974; Wiltschko and Wiltschko, 1972, 1975x, 1975b) and on the Ring-Billed Gull (Larus delawarensis) (Southern, 1970, 1972). The results of research on the homing pigeon appear contradictory. Yeagley (1947) had reported one test release in which homing pigeons carrying magnets were disoriented when compared to a brass-carrying group. Subsequent attempts to repeat this experiment failed to confirm these preliminary results (Yeagley, 1951; Matthews, 1951; Bochenski et al., 1960). On the other hand. Keeton (1974a, 1974b) has shown that pigeons carrying bar magnets were disoriented at unfamiliar test sites when released under total overcast than under clear sky. Supportive evidence also comes from Walcott and Green (1974) who found that pigeons wearing a small Helmholtz coil around the head tended to fly in a direction opposite from home, when the artificial field produced had its axial inclination reversed (North up). Although magnetic sensitivity and its use by some invertebrates and lower vertebrates is known (Brown, 1962; Schneider, 1963; Barnothy, 1964; Ratner and Jennings, 1968; Martin and Lindauer, 1973) laboratory experiments using conditioning techniques have failed to show the existence of such a sensitivity in the pigeon (Orgel and Smith, 1954; Meyer and Lambe, 1966). One exception is the report of Reille (1968) on pigeons responding by heart rate accelerations to variations of an experimentally manipulated local magnetic field. However, responding level is low when compared to what is usually obtained in similar conditions using visual or auditory stimuli, leaving open the question of the biological significance of this form of sensitivity in the behavioural repertoire of the pigeon.

Our own results using cardiac orienting and conditioned responses are reported in the present paper. They are in complete agreement with Kreithen and Keeton (1974) who failed to replicate Reille's (1968) findings and they do not provide support to the existence in the pigeon of a magnetic sensitivity to static magnetic fields.

Methods

Subjects. The subjects were 38 (male and female) homing pigeons (*Columba livia*) ranging in age from 4 to 36 months. These birds were either originals (N=11) or descendants (N=27) of a stock given by the Federation Royale Colombophile de Belgique and raised under similar conditions in the laboratory. The past homing or racing experience *of* the I1 original subjects used was uncontrolled. All birds were free to fly around the loft and to reproduce but had had no homing experience during the previous year. The day before the start of the experiment and on the following three days of experimentation, each pigeon was isolated in a small cage adjacent to the experimental room.

Apparatus. The immobilized animal was placed in a small aluminium cage (30 x 25 x 25 cm) situated in between two pairs of Helmholtz-Gaussian coils that are needed to produce the artificial magnetic fields. A restraint was imposed by wrapping the bird in an elastic bandage that permitted movements of the head and neck only. The bird was placed on a plexiglass hammock and further restricted by placing several turns of bandage around both the animal and the hammock. The unconditional stimulus (UCS) was a 0.2-0.5 s of a 1 to 2 mA footshock (90 V. DC.) dry cell delivered between a needle electrode inserted in the footpad and a metal ring fastened around the metatarsal region of the opposite leg. Shock levels were adjusted empirically in order to maintain shock intensity and duration at the minimum level required to produce a leg flexion and marked tachycardia. Heart beats were constantly monitored by means of three electrodes, one inserted in the base of each wing and one on the more ventral part of the breast. The cardiac signal was amplified and fed to a R-peak detector which triggered at each QRS wave of the electrocardiogram (Tobin et al., 1970)

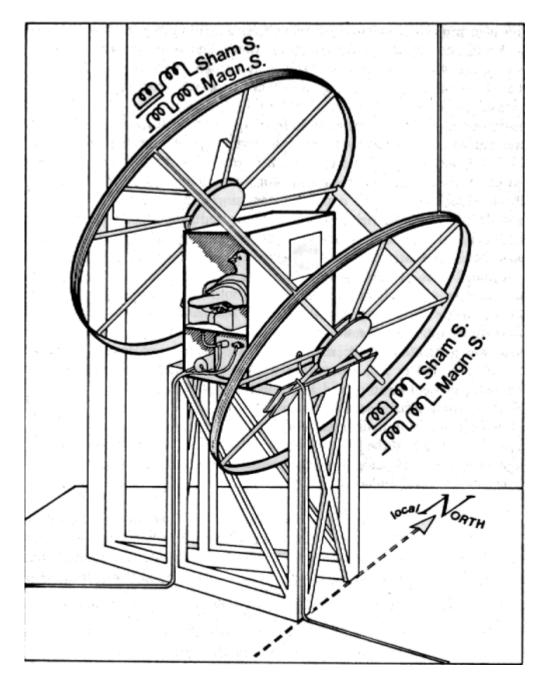


Fig. 1. Pigeon in experimental situation. The animal is restrained and placed between the four coils of 24 turns needed to produce the magnetic and control stimuli. Cardiac activity is monitored and treated in an adjacent room. The cardiac amplifier and the shocker are placed under the subject. The axis of the coils makes a 90° angle with the horizontal projection of the local field declination and presents an angle of 40° relative to gravity. Magnetic and sham stimuli arrangements are shown.

Stimuli. Five conditional stimuli (CSs) were used. Two were magnetic stimuli, 2 were sham magnetic stimuli and one was a luminous stimulus. The magnetic CSs were produced by 2 pairs of Helmholtz Gaussian coils mounted in series. These coils were placed on 2 parallel aluminium cylinder (diameter: 1 m) 50 cm from each other. The 2 cylinders were fastened on a wooden frame (Fig. 1). Each pair of coils consisted of 4 turns of a flat ribbon containing 12 copper conductors. Odd and even conductors were soldered together in order to form two coils of 24 turns. The coils could be activated independently of each other or in unison. The 4 coils were connected in series and in such a way that their axis made a 90° angle with the horizontal (H) component of the local magnetic field (declination of the axis: due West) and presented an inclination (I) of 40° relative to gravity. The North of the generated artificial field was up. Artificial static magnetic

fields were produced by the application of a rapidly growing (1 ma of leading edge) current of either 450 mA in the case of the North-West field or 850 mA for the West field. The magnetic CSs were the resultant of one of these fields and the local magnetic field in the room (Force=48,394 gammas (γ); H=21.465 γ ; D=4°12'; I=63°40'). At a current of 450 mA, the CS produced was almost North-West (D=-48°40') with an intensity (F=) of 35.631 γ (H=32,924.7 γ ; Z=13.621.4 γ) and an inclination of 22°28'. North down. At 850 mA, the resultant was a more West field (D=-66°15') having an intensity and inclination of respectively 63.373 d, and of -13°54', the North being up (H=51,&IO y; Z=-12.823.7 y). Control procedures for responses to heat and vibrations generated by the magnetic felds were provided by the use of opposed coils producing sham fields. Opposed coils were first used by Reille (1968) in order to control a posteriori for artifacts. However the tests were done with new coils added to the original ones and by reducing the current flowing through them to 2~f of the original intensity. In the present experiment the sham fields were produced by having the same coils mounted in series m such a way that the current circulated in opposite direction in the 2coils of each pair. The same heat and vibrations were thus produced as in the artificial magnetic stimuli but the magnetic component was non-existent (no variation was thus introduced in the local magnetic field). The magnetic characteristics of the coils were measured empirically in situ with the use of a magnetometer and it was also verified that no magnetic component was generated by the sham field. The 2 sham felds were produced respectively by the application of a 450 or 850 mA current to the coils. The luminous CS used was produced by a 24 V DC incandescent lamp placed 10 cm in front of the animal. A trial consisted of 60 consecutive heart beats electronically counted. The CS onset coincided with the R peak of the 30th beat and was maintained for the following 30 beats; the 60th beat terminated the CS and facultatively triggered the footshock at its offset. The first 30 beats preceding the CS presentation served as a baseline. The heart beats were recorded on an audio tape recorder (Sony, TC252W. stereo) to be fed, processed and analysed by a PDP-12 computer (Digital Equipment Co.).

The sequence of stimuli and the random temporal distribution of trials was controlled by means of a magnetic tape recorder (Uher 2400, stereophonic) on which pulses had been previously recorded. These pulses when detected by the control apparatus triggered a trial presentation and selected the appropriate stimulus. In order to eliminate all possible cues coming from the control and recording apparatus, the experimental room was constantly flooded by a white noise (Grason Stadler Noise Generator, Model 90113) fed through a 12 cm diameter speaker distant of 2m from the animal. A decibel metre (Realistic. Model 33-1028) situated in place off the animal and directed toward the noise source gave a reading of approximately 80 db. this being an average overall level. The control apparatus was placed in rooms adjacent to the experimental room and the power supply required for driving the coils as well as the electromagnetic relays used to select the appropriate stimuli were placed in a room at least 20 m from the animal. To an added precaution, the electromagnetic relays were buried in a container of sand.

Procedures. Four randomly assigned groups were created. Each group name designates the CS+ (always reinforced by a

footshock) that was used throughout the differential conditioning procedure far the group. The first group (North-West, N=10) received the North-West field as CS- and the corresponding sham-North-West stimulus as CS-. The second experimental group (West, N=10) received the West field as CS+ and the sham-West stimulus as CS-. The third group (Sham, N=8) was used to control for the neutrality of the differential conditioning stimuli: half of the subjects received the sham-North-West stimulus as CS+ and the corresponding North-West field as CS-. Finally, a fourth group (Lumt, N=10) served as an absolute comparison group for stimulus detection and received as CS + a light accompanied by either a West field (N=5) or a North-West field (N=5). The corresponding sham stimuli served as CS-. The experiment itself was divided into a cardiac orienting response phase (one day) and a conditioning phase (two consecutive days). The first phase consisted in presenting to the subject 50 CSs+ and 50 CSs- in a random order, systematically omitting to give the footshock as CS + offset. This phase was made in order to study the cardiac orienting reflex to the various stimuli as well as its evolution through repeated evocation. The procedure used in the conditioning phase was one of differential conditioning: the CS + was always followed by a nociceptive footshock delivered at CS t offset, and the CS-was never reinforced. In this phase distributed over two consecutive daily sessions, 100 CSs+ and 100 CSs- were presented in a random order, at a regimen of 50 presentations of each CS per day. In both phases, the mean inter-trial interval was 101 s (range 70 120). Each experimental session lasted approximately 3 h, beginning with a 15 min settling period. The inter-stimulus interval during conditioning as well as the duration of all stimuli used as CSs were variable and relative to the momentary heart rate of the subject (=30 beats). In both phases, the random order of presentation of the CSs as well as the inter-trial intervals were counterbalanced over each group by interchanging for half of the subjects the stimulus that was triggered by a given channel of the magnetic tape programmer.

Data Quantification. Tape recording of cardiac activity failed to function properly on three occasions and two subjects developed marked arrhythmia during conditioning and were thus omitted from the data analyses. In the interest of maintaining equal number of subjects in each group, 5 other subjects were randomly discarded. The final data analyses were done on 28 of the 38 subjects, with 7 subjects per group. In order to analyse cardiac reactivity to stimulation, a PDP-12 computer reduced cardiac recordings for each trial to 59 cardiac periods, with an accuracy of 1 ms (1,000 Hz oscillator). Ten trials were analysed for each subject under each phase and stimulus condition. The first appearance of each CS+ and CS- as well as 9 other pairs of CS+ and CS-, sequentially and evenly spaced in the subsequent recording, were retained for analysis. Trials presenting missing beats, artefacts or marked responses during the basal level sampling were automatically discarded and *the next* occurrence of the same stimulus retained.

The cardiac periods were converted into difference scores in order to minimize the effects of individual differences in basal levels. The 4 periods immediately preceding any given CS were used as basal level by taking a mean across the 4 periods. The corresponding basal level was then substracted from each dam point and the digit 200 was added to the difference. All analyses of variance were run on the difference scores using the CARDIVAR program, (Wilson, 1974).

Results

Cardiac response curves for the four groups are constituted of units in ms of difference of time intervals between successive beats and basal level. Acceleration responses are presented by a downward curve. Figure 2 illustrates the cardiac orienting phase and Figures 3 and 4 the cardiac conditioning phase. These figures represent means for period changes during stimulus presentation for the 10 trial blocks retained for analysis.

Cardiac Orienting Responses. It is evident from an inspection of Figure 2 that none of the three groups of pigeons receiving magnetic stimuli (groups North-West, West and Sham) shows any reliable response to magnetic fields presentations. This was confirmed by several Anova's on individual groups comparing responses to magnetic stimuli versus sham-control stimuli [largest 17(1/6)=0.62, p > 1] as well as from an Anova on the pooled data of the three groups [17(1/20)=0.04. p > 1]. Individual Anova's do not confirm the existence of any differences between successive cardiac periods either for the magnetic stimuli [largest F(14/84)=1.166, p > 1] or the sham presentations [largest 17(14/84)=1.02, p > 1].

In contrast with the lack of cardiac responding to magnetic stimuli, presentations of luminous stimuli to group Lumi evoked a marked cardio-accelerative response significantly different from that of the control sham stimuli [17(1/6)=8.72,p<0.001, for stimuli; 17(28/168)=8.1905.p<0.001 for the interaction between stimuli and cardiac periods] as well as from all other responses emitted by the other groups [smallest 17(1/12)=6.21, p<0.05, for stimuli; smallest F(28/336)=5.40, p<0.0001, for the interaction between groups and stimuli]. The reliability of this response to lights is further confirmed by successive cardiac

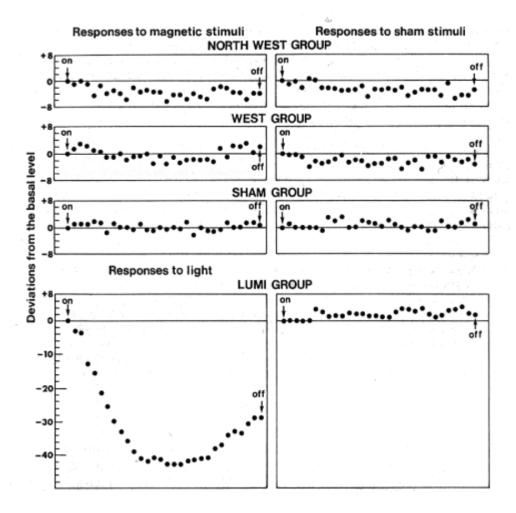


Fig. 2. Phase I: Cardiac orienting reflex. Cardiac responses for each group averaged over 10 trials for each stimulus presented. Units are ms of difference of time interval between successive beats and the basal level (first point). An accelerative response is presented by a downward curve. The stimulus lasts 29 cardiac periods

periods reaching level of significance [F(14/84)=7.10, p<0.001]. This response to a light is resistant to habituation (repeated presentation of light stimuli) as confirmed by the fact that the interaction between successive trials and cardiac periods is not significant [F(126/756)=1.008, p>1]. Linear and quadratic trends of the response are both significant [F(1/24)=7.966, p<0.01 and 14.067, p<0.001], supporting previous reports on the cardiac orienting response in the pigeon (Cohen and MacDonald, 1971; Cohen and Pitts, 1968).

Cardiac Conditioned Responses. The response curves for the second phase are presented at Figures 3 and 4. Both conditioning days were analysed independently. The results are essentially the same as in the previous phase. Although magnetic stimuli were systematically reinforced for 100 trials by a noxious footshock, no cardiac response ever developed to magnetic presentations. This is confirmed by several Anova's on individual groups comparing cardiac responses to both magnetic and sham stimuli over the 10 presentations [largest F(1/6)=2.45, p > 1] as well as Anova's on the pooled data of the groups Northwest and West [largest F(1/13)=0.072, p > 1 for stimuli]. On the other hand, group Lumi showed a systematic cardio-accelerative response to lights which differs significantly from its response to sham-stimulus presentations [smallest F(1/6)=16.86, p < 0.0001, for stimuli; smallest F(28/168)=3.1835, p < 0.001 for the interaction between cardiac periods and stimuli] as well as from all other responses emitted by the other 3 groups [smallest F(1/12)=21.91, p < 0.001 for groups (treatments); smallest F(28/336)=5.1812, p < 0.001 for the interaction between groups and cardiac periods]. Linear and quadratic trends of the response curves are both significant [smallest F(1/24)=16.852, p < 0.001 for linearity and F(1/24)=5.467, p < 0.05 for quadraticity] confirming previous reports (Cohen and MacDonald, 1971; Cohen and Pitts, 1968) on the conditioned response to lights in the pigeon.

Figures 2-4 might suggest that the curves describing cardiac activity to magnetic or sham stimuli systematically lie either above ox below basal level. Since there has been a tendency in the literature on the influence of magnetic fields on birds to rely on effects having a very small magnitude but achieving statistical significance by second order analysis on pooled means, additional analyses were thus performed to test this trend in the data.

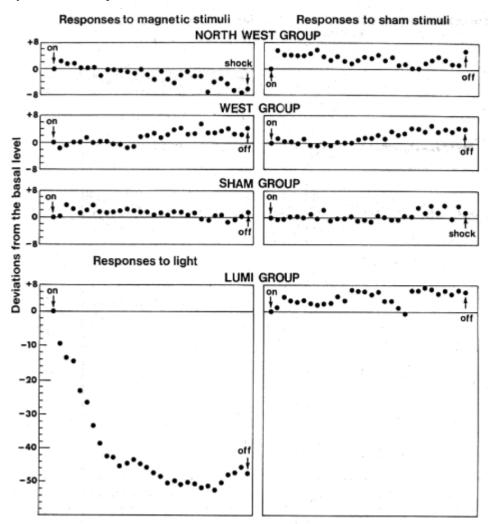


Fig. 3. Phase I: Conditioning 1. Conditioned cardiac responses averaged over 10 trials for each stimulus. The shock onset coindices with the offset of the magnetic or luminous stimuli (Groups North-west, West and Lumi) and with the sham stimulus offset for group Sham

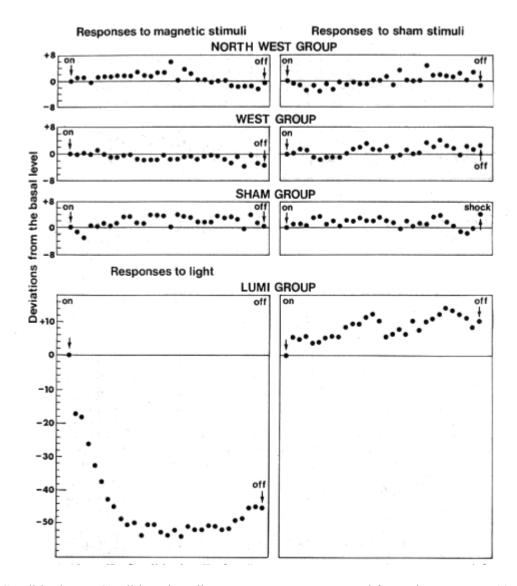


Fig. 4. Phase II: Conditioning II. Conditioned cardiac response curves averaged for each group over 10 trials far both magnetic-light and control stimuli. Same as in Figure 3

The ten trials for each individual subject under one stimulus condition were first averaged. This set of 29 data points was considered as being above basal level when at least 50% of its points (15) lied above its average basal level. Table IA summarizes the frequency counts for the mean subject trials satisfying the criterion. No difference in this table reaches significance (largest $Chi^2=0.033$, p<0.85; smallest Mann-Whitney U=3, p=0.35).

Second, the same computational procedure was applied to the average group condition trials presented at Figures 2-4. At a criterion of 50 %, it comes out that 5 magnetic and 6 sham curves (out of 9) lie above basal level (Table 1B). This difference is evidently not significant (although not tested for). Even if the criterion is gradually reduced from 50% of the points to 10%, no difference reaches significance whatsoever, indicating no systematic effect playing for one stimulus condition and not for the other.

Table 1. Frequency count of data points above the basal-level. A Based on the m individual trial (29 points). OR, Orienting Response phase; CR1, conditioning phase, day 1; CR2, conditioning phase, day 2. NS, number of subjects for which at least 50% of their data points exceeded the basal-level (N=7 per cell). FP, number of points exceeding the basal-level, summed across the 7 subjects in the group-condition (maximum of points=7 x 29). B Based on the mean group-trial of 29 points. :\'P, number of points in the mean group-condition trial exceeding the basal level value

	Group	Phase	Stimulus Magnetic		Control	
			NS	NP	NS	NP
	N-West	OR	3	80 (39.4%)	2	70 (34.48%)
		CR1	2	84 (41.3%)	6	147 (72.4%)
		CR2	- 5	107 (52.7%)	2	84 (41.38%)
	West	OR.	3	92 (45.32%)	2	74 (36.45%
		CR1	5	128 (63.05%)	5	130 (64.04%
		CR2	3	86 (42.36%)	4	111 (54.67%
	Sham	OR	- 6	138 (67.9%)	6	133 (65.5%)
		CR1	6	125 (61.5%)	5	120 (59.1%)
		CR2	6	150 (73.89%)	5	126 (62.07%
	Total	OR	12	310 (59.9%)	10:	277 (45.48%
		CR1	13	337 (55.33%)	16	397 (65.18%
		CR2	14	343 56.32%)	11	321 (52.71%
	Grand total		39	990 (54.18%)	- 37	995 (54.46%
	N-West	OR		1 (3.44%)		2 (6.89%)
		CR1		6 (20.68%)		29 (100%)
		CR2		21 (72.4%)		15 (51.0%)
	West	OR		13 (44.8%)		0 (0.0%)
		CR1		23 (79.3%)		24 (82.76%)
		CR2		2 (6.89%)		21 (72.41%)
	Sham	OR		19 (65.5%)		25 (86.2%)
		CR1		25 (86.2%)		16 (55.2%)
		CR2		26 (89.65%)		25 (86.2%)
	Total	OR :		33 (37.9%)		27 (31.03%)
		CR1		55 (62.06%)		69 (79.31%)
		CR2		49 (56.32%)		61 (70.11%)
	Grand total			136 (52.10%)		157 (60.15%)

In summary, no cardiac response was evoked by repeated magnetic or sham stimuli presented alone as compared to luminous stimuli presentations. Furthermore, the magnetic and sham-control stimuli were not used by the birds as a warning for a forthcoming shock. It is concluded that, in the present experimental situation, magnetic fields were not a sufficient or adequate cue 1) to evoke a cardiac orienting reflex, 2) to permit homing pigeons to demonstrate differential cardiac activity to the impending shock-

Discussion

The data presented here show that the homing pigeon did not respond with changes in cardiac activity to the experimental presentation of magnetic variations of the order of the ones occurring in nature. Magnetic stimuli neither evoked a cardiac orienting reflex nor were used as a warning signal for the forthcoming footshock. These results agree with previous reports of failure to show any magnetic sensitivity in birds using operant and respondent conditioning (Orgel and Smith, 1954; Meyer and Lambe, 1966; Emlen, 1970). Reille's (1968) suggestion of sensitivity in the pigeon using cardiac conditioning was the single exception and must be considered doubtful. Pigeons can easily be conditioned to weak auditive or vibrational stimuli and such stimuli, usually well correlated with experimental presentations could have contaminated the data of Reille (1968). Although homing experiments (Keeton, 1974a; Walcott and Green, 1974) as well as experiments involving spontaneous orienting behaviour in arenas or octogonal cages (Southern, 1972; Wiltschko and Wiltschko, 1975a, 1975b) show that magnetic fields modify orienting behaviour, research on birds gives no indication on how detection is made possible and up to now no experiment has demonstrated clearly that there was in fact detection. In these experiments, it cannot be excluded that the magnetic field has an indirect effect on other levels of functioning. For example, the magnetic field could desynchronise or introduce a bias into a biological clock, that could in turn provoke a misinterpretation of astronomical, topographical or other hitherto unsuspected cues. This could explain the persistent failure of laboratory experiments to develop a magnetic sensitivity model using conditioning. However, it is doubtful that the magnetic field would only have a general effect since magnetic effects have been shown to be dependent on variables such as the experience or age of the subjects (Keeton, 1974b), weather conditions (Keeton, 1972) and release site (Keeton, 1974b).

On the other hand, Southern's (1972), Wiltschko and Wiltschko's (1972, 1975 a, 1975b) birds were tested under static magnetic fields; since their limited movements in the cages were probably insufficient to induce an electromotive force and plumage polarization, a sensitivity mechanism under static conditions must be postulated. Kreithen and Keeton (1974) and Keeton (1974b) have stressed to the fact that biomagnetic effects were found in experiments involving a locomotor activity and slowly adapting response patterns and/or long duration stimuli. All laboratory experiments, including this one, using stationary animals and/or stimuli of short duration have failed. It is possible that this special case of sensitivity requires the integration of the signal over a relatively extended time basis or interval. A similar integrative process is suspected for the pineal gland's reception mechanism of luminous stimuli in birds (Menaker and Oksche, 1974). Such an integrative mechanism might explain the inertia or "Hysteresis" effects to magnetism reported for bees (Martin and Lindauer, 1973), snails (Brown, 1971) and birds (Eldarov, 1964; Shumakov, 1967; Wiltschko and Merkel, 1971; Wiltschko, 1972).

The failure of laboratory experiments to demonstrate a magnetic sensitivity may in part be attributable to biological constraints not satisfied by the test situation (Shettleworth, 1972). Magnetic detection and utilisation could be restricted to a particular situation, having no motor or autonomic correlates other than to be specifically integrated into orienting adjustments of the bird while actively flying home or migrating. This use would also be conditional upon internal, Immoral, motivational states and on the capacity of the physical environment to trigger and regulate behaviour. Moreover, the possibility that the tests used were inadequate cannot be excluded completely since the range of stimuli that can come to control an animal's behaviour is not only limited by what its sensory systems can respond to differentially but also to their access to higher mechanisms such as learning. A particular example of this biological limitation is provided by studies of discrimination learning in the octopus (Wells, 1964). The octopus responds readily to the weights of objects by adjusting its tentacles appropriately to support an object lowered into its tank. However, even after intensive training, the animal cannot discriminate between objects of different weights although it can readily learn shape discrimination in a similar task. Other evidences suggest that this discriminative limit is due to the fact that the information concerning the position of parts of the animal's body is not available centrally (Shettleworth, 1972). In resume, while it is difficult to interpret negative results, the repeated failure of laboratory experiments to develop an experimental model of magnetic detection suggests that the pertinence of the classical conception and methodology used to study magnetic sensitivity is questionable. A laboratory model presenting greater external validity must be sought and new experiments must be conducted taking into account the notion of the biological limits of the organism under study. Finally, many more negative results must be gathered before it is concluded that birds are insensitive to magnetic fields.

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