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ORIENTATION-DISTURBING MAGNETIC TREATMENT AFFECTS THE PIGEON OPIOID SYSTEM

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Summary

Keeping homing pigeons in an oscillating magnetic field of low intensity is known to increase the scattering of initial bearings and/or their deflection towards a specific direction. To determine whether these effects on orientation are the outcome of direct interference with the birds' navigational mechanism or are the side-effect of problems in another biological system, experiments were performed to test whether the same effects could be induced by non-magnetic treatments. The initial orientation of pigeons treated with the prototypic opiate antagonist naloxone (1 mg kg^{-1}) displayed similar disturbances to those observed in magnetically treated birds. In both cases, the orientation was significantly different from that of control birds.

The concentration and affinity of the brain's μ-opiate receptors were then assessed in magnetically treated birds by using [^{3}H]dihydromorphine as a ligand. The concentration of μ-opiate receptors fell significantly in these birds, whereas the affinity of the receptors was unaffected.

We conclude that it appears improbable that the navigational mechanism of pigeons is directly influenced by magnetic treatments. What these do seem to produce is a lack of compensation for the stress experienced by pigeons subjected to a test release.

Introduction

It has often been reported that an alteration of the magnetic field around a bird

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produces a modification of its orientation behaviour (see Wiltschko and Wiltschko, 1988, for references). Even if it is often difficult to replicate the results and the recorded effects are very small (Griffin, 1987, 1990; Able and Bingman, 1987), these findings are usually taken as support for the concept that birds use the earth's magnetic field to determine directions in space ('compass sense') or even to calculate their position with respect to a specific goal ('map sense').

The findings can be divided into two groups. In the first, consisting of a small number of experiments, birds kept in a magnetic field that is similar to, but deflected from, the natural one show a corresponding deflection of their body axis (e.g. Wiltschko, 1968). Here the evidence that they rely on a magnetic compass is fairly direct and plausible. Conversely, in the second group, the effects are either different from those expected or totally unpredictable as they are obtained with wholly unnatural fields (e.g. Papi *et al.* 1983). In these cases one can argue that the observed effect may not be the consequence of interference with the animal's navigational mechanism, but the side-effect of a disturbance in another biological system. This possibility, among other things, is suggested by the results of Kavaliers and Ossenkopp (1986, 1988) and Kavaliers *et al.* (1985), who showed that keeping the animals for 30 min in a rotating magnetic field produces effects similar to those of naloxone injections (e.g. in mice, a reduction of both locomotory activity and analgesia). This allowed the authors to assume that magnetic fields interfere with the endogenous opioid system.

In homing pigeons, which are favourite objects of biomagnetic experimentation, only one method was successful in bending flight bearings towards a specific direction. This was achieved under overcast skies, by releasing birds that had had a pair of small coils fixed around their head; the coils induced a field with the north magnetic pole up (Walcott and Green, 1974; Visalberghi and Alleva, 1979). Attempts to communicate meaningful magnetic information during the outward journey failed (Kiepenheuer, 1978; Wiltschko *et al.* 1978); like the treatments with unnatural fields (Papi *et al.* 1983), they only led to a greater increase of scattering and/or a certain degree of deflection of the mean bearing. Homing success and speed were never consistently affected, even when a device generating an artificial field was carried by birds during their homing flight (Lednor and Walcott, 1983; Papi and Ioalè, 1987).

All this strengthens the suspicion that magnetic treatments may disturb pigeon orientation in a nonspecific, indirect way. We have tested the concept that the endogenous opioid system may be affected by magnetic treatments that have been found to disturb initial orientation. To do this, we first compared the effects on orientation of magnetic treatment with those of naloxone injection. This substance was choosen as it is a prototypic opiate antagonist and birds are known to have a functional opioid system implicated in several behavioural responses (see Kavaliers, 1991, for references). We then determined the concentration and affinity of the brain's μ-opiate receptors in pigeons after they had been given magnetic treatment.

Materials and methods

Test releases

All the experiments were performed with naive, 1-year-old pigeons which belonged to the Arnino loft, near Pisa.

Birds were treated in three different ways. Magnetically treated (M) birds were transported to the release site inside a small cage set at the centre of three pairs of Helmholtz coils, which produced a continuous, irregular change in the induced magnetic flux between +0.70 and −0.20 G (1 G=10^{-4} T). Further details on the features of the flux appeared in a previous paper (Ioalè and Guidarini, 1985). M-birds were transported in a different van from the others; the magnetic treatment was applied during the journey to the release site and continued there for a total of 3 h. The minimum time elapsing between the end of the treatment and the release of single birds was a few minutes, and the maximum was several hours.

Birds to be treated with naloxone (N) were injected at the release site 50–120 min before release. They received 1 mg kg^{-1} of naloxone hydrochloride intraperitoneally in 1 ml of isotonic solution. Control birds (C) were injected intraperitoneally with 1 ml of isotonic saline solution.

In five of the nine experiments, all three pigeon groups were released; in the other four, only C- and N-birds were tested.

The birds were released singly, alternating an equal number of birds belonging to different groups. Each pigeon was observed with binoculars (10×40) and its bearing recorded 1 min after release and when the bird vanished. All the releases were performed in sunny conditions, with little or no wind. Standard methods of circular statistics were applied (Batschelet, 1981). The homeward component (**h**) was calculated as $\mathbf{h}=\mathbf{a}\cos(\alpha-H)$, where **a** is the length of the mean vector and H is the home direction.

All the experiments reported here were performed in 1988 and 1990; additional data on the 1988 experiments have been reported in a table in a previous paper (Papi and Luschi, 1990).

Study of μ-opiate receptors

Two experiments to study opiate receptors were performed in 1990. To reduce individual variability, only male birds were used. In the first experiment, five experimental, 1-year-old birds (M) were kept in the van for magnetic treatment close to the loft and subjected to the same treatment as the M-birds used in release tests. Five control birds of the same age were kept in a similar cage in another van parked nearby. Birds were taken out of the cage singly and killed by breaking the spinal cord near the neck. The skull was immediately opened and the brain put in liquid nitrogen. The birds were kept in the van for between 2 h 05 min and 3 h 56 min. In the second experiment, the birds were three and half months old. Ten magnetically treated and nine control birds were killed after being kept in the van for between 3 h 30 min and 6 h 15 min. In this experiment the birds were put in

the vans at the loft and then transported to the laboratory in Pisa. Treatment took place partly *en route* (8 km) and partly while the vans were parked. Other procedures were as in the first experiment.

For the receptor assay, the brains were individually homogenized (glass–Teflon homogenizer) in 10 volumes of 0.32 mol l^{-1} sucrose. Homogenates were centrifuged at 1400 *g* for 10 min; the resulting supernatants were incubated at 37°C for 30 min in order to dissociate endogenous ligands which might interfere with the assay of opioid receptors. At the end of the incubation the material was centrifuged again at 48 000 *g* for 30 min. The pellets obtained (plasma membranes) were resuspended and homogenized in the assay buffer (50 mmol l^{-1} Tris–HCl, pH 7.4). The protein content of each plasma membrane preparation was determined according to the method of Bradford (1976).

μ-Opioid receptor assay was performed using dihydromorphine (DHM) as a ligand, since this drug mostly binds to μ receptors (Lord *et al.* 1977). Although it is known that dihydromorphine can bind to both μ and δ receptors, it is also well known that it binds to μ receptors with high affinity and to δ receptors with low affinity (Lord *et al.* 1977; Pasternak and Wood, 1986). In our receptor assay, binding parameters (i.e. hot and cold ligand concentrations) have been selected so that only [^{3}H]DHM site with high affinity can be detected. This is confirmed by the statistical analysis of the data. The analysis of the data from binding experiments with the LIGAND program (see below) reveals the presence of only one class of high-affinity [^{3}H]DHM binding site.

Cold dihydromorphine was generously provided by Dr L. Terenius, Uppsala, Sweden. [^{3}H]DHM was purchased from Amersham International, Buckinghamshire, England. The binding assay was performed as previously described (Piva *et al.* 1987), with a few modifications.

The binding characteristics of μ-opioid receptors (K_d=dissociation constant and B_{max}=maximal binding capacity) were determined by means of displacement curves (five dose points per curve) performed on plasma membranes derived from each brain. [^{3}H]DHM (0.22 nmol l^{-1}) was incubated in the presence of increasing concentrations of unlabelled DHM (0.1 nmol l^{-1}–1 μmol l^{-1}) and 200 μl of brain plasma membranes (approximately 150–200 μg of protein). Incubations were carried out at 25°C for 30 min. Tubes were then rapidly filtered through Whatman GF/B filters; each filter was washed twice with 5 ml of ice-cold buffer and counted in a 7 ml Instagel scintillation cocktail (Packard Instruments, Milan). In order to minimize the interassay variations, all displacement curves were performed in the same assay.

The data obtained from the displacement curves for each group of animals (C- or M-birds) were fitted together and analysed by means of the LIGAND computerized curve-fitting program of Munson and Rodbard (1980), supplied by the Biomedical Computing Technology Center (Nashville, Tennessee). This fitting of the data allows the determination of the K_d and B_{max} values for each experimental group (C- or M-birds). B_{max} values are expressed in terms of fmol mg^{-1} protein. The values of the binding parameters (K_d and B_{max}) obtained

for the two groups of animals were also statistically compared (M- *vs* C-birds) by the program.

The reproducibility and accuracy of the binding assay are demonstrated by the percentage coefficients of variation of the binding parameters: K_d=12–20 %, B_{max}=7–15 %, non-specific binding=2–6 %.

Results

Test releases

Initial orientation in the nine releases is shown in Fig. 1 and Table 1. In all the releases the C-birds turned out to be better oriented than N- and M-birds, the value of the homeward component always being higher. According to the U^2-test, the difference between C-birds and experimental groups reaches significance in 11 cases out of 14. The difference between C- and N-birds is not significant in experiments 4, 5 and 7. The initial orientation of N- and M-birds is significantly different in one case out of five.

Comparing the pooled distributions of all C- and N-bearings, one finds a significant difference (U=1.37, P<0.001). The comparisons between C- and M- and between N- and M-birds were performed taking into account only the tests in which all three groups took part. The difference between C- and M-bird bearings is significant (U=0.96, P<0.001); that between M- and N-bird bearings is not (U=0.17, P>0.05).

The behaviour of N- and M-birds was very similar in four of the five tests performed with both these groups, as they either deflected in the same direction with respect to the C-group (releases 2, 3, 9) or showed a high degree of scattering (release 7). In release 8, in contrast, N-bird bearings deflected and M-bird bearings were randomly distributed. The variability in orientation observed in N-birds is not attributable to the differences in time elapsed between naloxone injection and release (50–120 min). The comparisons between birds released early or late after injection revealed no significant differences in any releases (Watson U^2-test, P>0.05 in all cases).

Considering the bearings recorded 1 min after release (Table 1), we found that C-birds differed significantly from experimental birds in only three cases. The difference between this result and that obtained by comparing the bearings at the moment of vanishing is due to the fact that at 1 min the mean bearing of C-birds was less divergent from those of the other groups than when they disappeared from sight. At 1 min, N-birds differed from M-birds in only one case.

The difference between vanishing times was only significant in release 8, with the C-birds vanishing faster than both experimental groups. In releases 2 and 7, N-birds vanished faster than M-birds.

Homing times were recorded in five releases. C-birds performed better than N-birds in release 5 and better than M-birds in release 7. When all the data on homing performance were pooled, no significant differences were found.

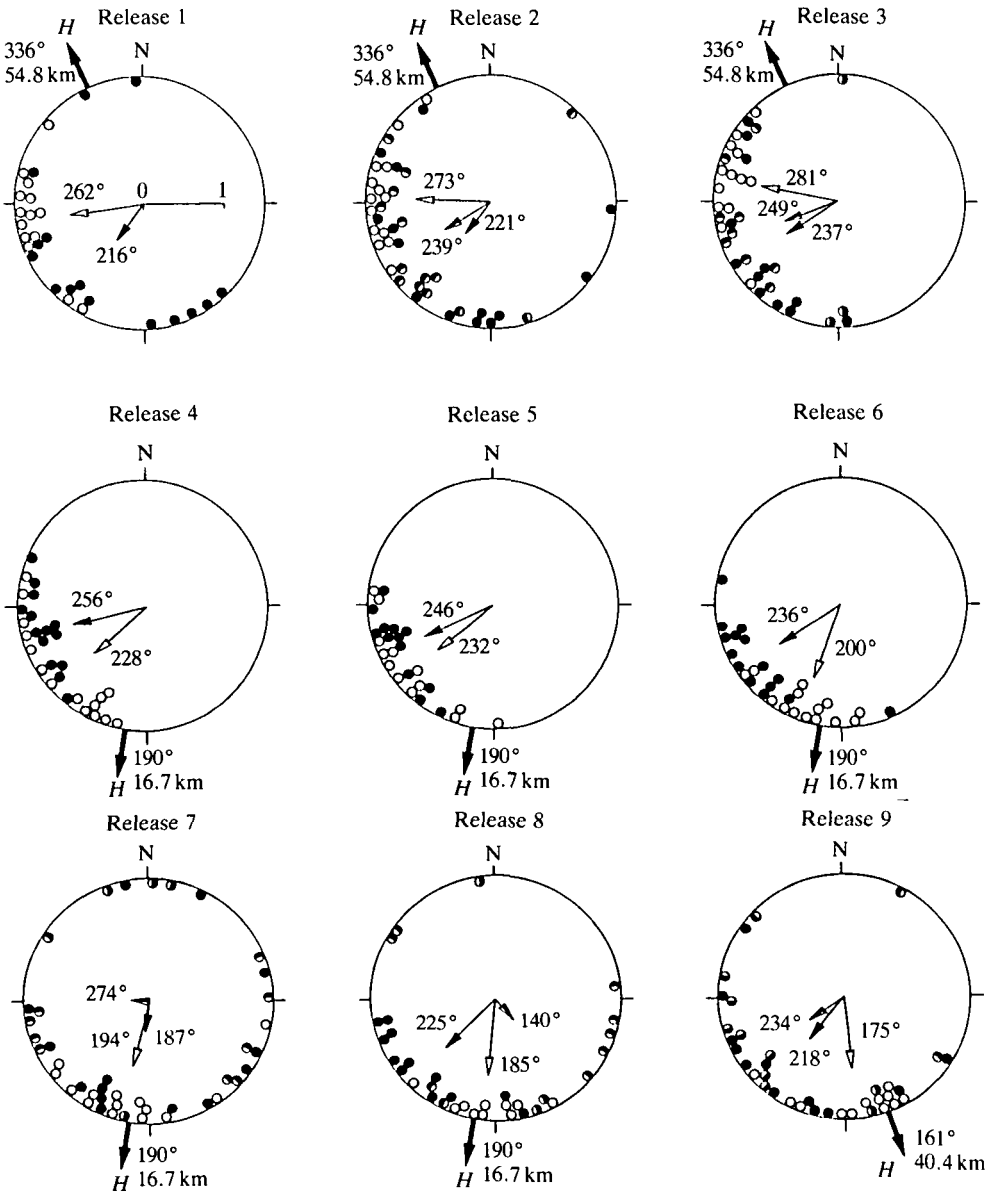

Fig. 1. Initial orientation in the nine releases. Each dot at the periphery indicates the vanishing bearing of a pigeon; open symbols refer to C-, filled symbols to N- and half-filled symbols to M-birds. The inner arrows represent the mean vectors; vector length can be read from the scale in the diagram for release 1. Outer arrows indicate home direction (*H*). The distance from home is also given. N, magnetic north.

Table 1. *Results of the test releases*

Release number	Date	Home direction (degrees)	Home distance (km)	Treatment	Number of birds released	Bearings recorded	Mean bearing	Mean vector length	Homeward component
1	25 May 1988	336	54.8	C	15	14 (15)	262° (207°)	0.911*** (0.636**)	+0.251 (−0.396)
				N	15	15 (15)	216° (180°)	0.534* (0.619**)	−0.265 (−0.556)
2	21 June 1988	336	54.8	C	14	14 (14)	273° (233°)	0.912*** (0.514*)	+0.413 (−0.115)
				N	14	14 (13)	221° (216°)	0.528* (0.435*)	−0.225 (−0.219)
				M	14	14 (14)	239° (239°)	0.671*** (0.665***)	−0.081 (−0.076)
3	18 August 1988	336	54.8	C	13	13 (13)	281° (253°)	0.927*** (0.792***)	+0.527 (+0.095)
				N	13	12 (11)	237° (219°)	0.752*** (0.785***)	−0.117 (−0.359)
				M	13	12 (12)	249° (266°)	0.687** (0.783***)	+0.033 (+0.266)
4	3 June 1988	190	16.7	C	15	15 (15)	228° (212°)	0.880*** (0.852***)	+0.689 (+0.788)
				N	15	14 (15)	256° (237°)	0.941*** (0.333)	+0.389 (+0.227)
5	24 June 1988	190	16.7	C	14	13 (12)	232° (230°)	0.891*** (0.865***)	+0.657 (+0.747)
				N	14	13 (14)	246° (221°)	0.940*** (0.876***)	+0.529 (+0.748)
6	5 August 1988	190	16.7	C	15	14 (14)	200° (173°)	0.951*** (0.857***)	+0.937 (+0.821)
				N	15	15 (15)	236° (213°)	0.891*** (0.678***)	+0.622 (+0.626)
7	28 June 1990	190	16.7	C	14	14 (13)	194° (169°)	0.846*** (0.554*)	+0.845 (+0.028)
				N	14	14 (14)	187° (165°)	0.405 (0.607**)	+0.404 (+0.552)
				M	15	14 (15)	274° (106°)	0.054 (0.251)	+0.006 (+0.028)
8	5 July 1990	190	16.7	C	11	10 (10)	185° (185°)	0.948*** (0.879***)	+0.945 (+0.875)
				N	12	12 (12)	225° (188°)	0.874*** (0.649**)	+0.714 (+0.649)
				M	12	12 (12)	140° (179°)	0.132 (0.565*)	+0.207 (+0.555)
9	11 August 1988	161	40.4	C	13	12 (11)	175° (206°)	0.923*** (0.325)	+0.894 (+0.231)
				N	14	12 (12)	218° (166°)	0.698*** (0.530*)	+0.383 (+0.528)
				M	14	12 (12)	234° (193°)	0.502* (0.493)	+0.144 (+0.416)

C, control birds; N, birds treated with naloxone; M, magnetically treated birds.
Values in parentheses refer to data obtained 1 min after release.
Significance was assessed using the Rayleigh test (mean vector length) and is indicated by asterisks: * $P<0.05$; ** $P<0.01$; *** $P<0.001$.

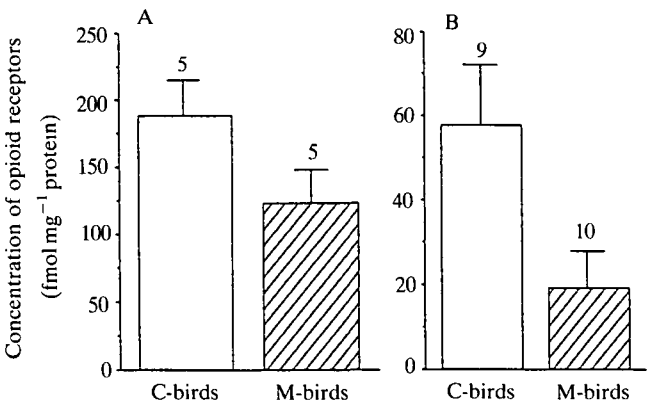

Fig. 2. Results of the μ receptor studies. (A) First experiment; (B) second experiment. C-birds: control birds; M-birds: magnetically treated birds. Bars indicate 1 standard error of the mean. Numbers of birds are shown above the columns.

μ-Opiate receptors

The binding characteristics of μ-opiate receptors in the whole of the brain were assessed in two experiments (Fig. 2). In the first, the concentration of opioid receptors binding DHM in M-birds (123.30 fmol mg^{-1} protein) was lower than that observed in C-animals (188.35 fmol mg^{-1} protein). This result was indicative, but not significant. In the second experiment, however, the difference turned out to be significant ($P<0.05$). In this case, the mean values for the concentration of opioid receptors were 57.62 and 19.17 fmol mg^{-1} protein for C- and M-birds, respectively. It appears from the data that the concentration of brain μ-opioid receptors observed in the second experiment is lower than that reported in the first experiment, both in C- and in M-birds. This difference is possibly explained by the fact that male pigeons of different ages have been used in the two studies (1-year-old *vs* 3.5-month-old animals). It has actually been demonstrated, at least in mammals (Piva *et al.* 1987; Landymore and Wilkinson, 1990; Limonta *et al.* 1991), that brain opioid receptors undergo significant variations with progressing age.

The observation that the difference between C- and M-birds reached significance only in the second experiment seems to be due to the difference in age between the birds used rather than to the higher number of animals tested. The comparison between the data for five C- and five M-pigeons, which had been randomly chosen from those used in the second experiment, does, in fact, reach significance ($P<0.05$).

The fall in the number of opioid receptors was not accompanied by any significant change in the K_d values in either experiment (first experiment: C-birds 8.63×10^{-9} mol l^{-1}, M-birds 7.17×10^{-9} mol l^{-1}; second experiment: C-birds 5.41×10^{-9} mol l^{-1}, M-birds 2.68×10^{-9} mol^{-1}).

Discussion

Some conclusions can be drawn from the present experiments. First, the

comparison of the orientational behaviour of the three groups shows that N- and M-birds behave differently from C-birds, so that their orientation can be considered to have been altered. Both in N- and in M-pigeons, the treatment increases the scattering of bearings and/or deflects them, often towards the so-called 'preferred compass direction' (PCD, Wallraff, 1978), which is loft-specific (in our birds roughly southwest). The bearing distribution of the N-birds is not significantly different from that of the M-birds in four cases out of five, and the pooled distributions of the two groups are both different from random and do not differ from each other. Therefore, the effects of naloxone treatment on orientation are, on the whole, similar to those of magnetic treatment.

Second, magnetic treatment interferes with the opioid system, as shown by the falls in the μ receptor concentrations observed after treatment. The difference in the concentrations between our two experiments appears to be due to the difference in age of the pigeons used in the two cases.

In the present experiments only one type of opioid receptor has been evaluated, namely the μ receptor. One topic calling for attention in future studies is the effect of magnetic fields on the other classes of opioid receptors. It must also be stressed that the evaluation of opioid receptors has been performed in the 'total' brain of the treated animals and their controls; the evaluation of these receptors in specific areas might provide more clear-cut results. It may well be that evaluation of the whole brain has had some sort of dilution effect.

The orientation behaviour of the N-birds clearly shows that a considerable disturbance of the initial orientation can also be obtained with a treatment which, like the injection of naloxone, is unlikely to interfere directly with the navigational system of the animals. Rather, the disturbance of orientation shown by N-birds seems to be dependent on the antagonistic activity exerted by naloxone towards the opioids, which are prevented from compensating for the stress resulting from transport and handling during the test. This is in accordance with the observation that many wild birds, which are easily stressed by captivity and handling, when released from their cages either escape in any direction or fly away in a specific bearing unrelated to that of home. The latter behaviour was called 'nonsense orientation' by Matthews (1961), who was the first to describe it. In pigeons, the tendency to scatter in all directions or to fly towards a loft-specific bearing (PCD) is usually balanced by the tendency to fly home. We cannot see any objection to considering scattering and the tendency to choose the PCD as induced by stress. Scattering and the PCD-tendency often decrease with experience (Wallraff, 1986), while fear also decreases in pigeons that are used to being handled and released far from home.

Thus, it is now possible to try to give an answer to the question that was raised in the Introduction. Is the disturbance in orientation produced by magnetic treatment really due to a direct interference with the navigational mechanism of the animals or is it just a side-effect of the alteration of the opioid system, which prevents pigeons from compensating for the stress experienced?

Several findings support the second hypothesis: (a) the similarity of the

disturbance in orientation produced by magnetic and naloxone treatment; (b) the absence of an effect of magnetic treatments on the homing performances, both in our experiments and in those of others (Benvenuti *et al.* 1982; Ioalè and Guidarini, 1985; Ioalè and Teyssèdre, 1989; Papi *et al.* 1983; Teyssèdre, 1986); and (c) the fact that magnetic treatments are more effective in disturbing orientation in very young pigeons than in older ones (Wiltschko and Wiltschko, 1978), which are probably less sensitive to stressing factors.

Thus, we believe it is probable that the behavioural effects recorded in M- and N-birds are attributable to the same cause, i.e. to the alteration of the opioid system induced by the treatment in both groups. The present experiments, therefore, suggest that greater caution is needed in planning new experiments and in evaluating the nature of the effects that magnetic or other stress-inducing treatments have been reported to have produced on bird orientation.

The project for the present experiments originated during stimulating discussions with Dr Enrico Alleva (Rome) and Professor Luciano Martini (Milan). The authors wish to thank Professor P. Ioalè for his help in the experiments.

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