

HOMING OF MAGNETIZED AND DEMAGNETIZED PIGEONS

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Accepted 15 July 1987

SUMMARY

Homing pigeons appear to use the earth's magnetic field as a compass and perhaps as part of their position-finding system or 'map'. The sensory system they use to detect magnetic fields is unknown, but two current possibilities are some mode of response by the pineal organ or by the visual system, or it may be based on the magnetite crystals found in their heads. Three series of experiments to test the involvement of magnetite are reported here. The alignment of the permanent magnetic domains in the birds heads was altered by (a) demagnetizing the birds, (b) magnetizing them with a strong magnetic field and (c) exposing the birds to a strong magnetic gradient. None of these treatments had a marked effect on the pigeon's orientation or homing under sunny skies, but a few results obtained under overcast skies suggest that demagnetizing the birds may have increased the scatter of their vanishing bearings. Perhaps pigeons use one magnetic sensor for their magnetic compass and another for some component of the map.

INTRODUCTION

A variety of evidence now indicates that homing pigeons may use a magnetic compass to determine directions when celestial cues are unavailable. For example, magnets (Keeton, 1971, 1972) or paired coils (Walcott & Green, 1974; Visalberghi & Alleva, 1979) attached to the heads or backs of homing pigeons disrupt their ability to orient on overcast days. On sunny days, neither magnets nor coils have much effect (Keeton, 1972; Walcott, 1977). Two experiments suggest that the magnetic compass of birds may be bipolar and cannot distinguish north from south except on the basis of the inclination of the field lines. The north-seeking pole of a compass needle free to rotate in three dimensions will point north and down in the northern hemisphere, while the south-seeking end will point south and up. When Wiltshko & Wiltshko (1972) and Wiltshko (1972) reversed the north-south polarity of the earth's field (so that the south-seeking pole of a compass pointed north and down), the orientation of

Key words: pigeon, homing, magnetism, navigation.

robins in a test cage was unaffected. When, however, they rotated the field so that the field lines pointed down towards the east rather than the north, then the robins were reoriented by an equivalent amount, regardless of the polarity of the field. Similarly, Walcott & Green (1974) and Visalberghi & Alleva (1979) found that when pigeons were fitted with paired coils which generated fields whose magnetic north pointed down, the birds were correctly oriented towards home under overcast skies. If the south pole of the induced field pointed down, the birds flew away from home. Vector addition of the earth and coil fields (Walcott & Green, 1974) indicates that in the first case the direction of the dip angle ought to have been to the north while in the second case it should have been to the south.

In addition to the relatively clear effects of strong (roughly earth strength) magnetic fields on the direction-finding abilities of pigeons under overcast skies, an increasing body of correlations suggests that small (0.1–1%) changes in the earth's magnetic field strength affect initial orientation, homing speed and bird navigation in general (Keeton, Larkin & Windsor, 1974; Yeagley, 1951; Schreiber & Rossi, 1976, 1978; Southern, 1971, 1972; Moore, 1977; Larkin & Sutherland, 1977; Carr, Switzer & Hollander, 1982). For example, pigeons seem to home more slowly and more pigeons are lost on days when there have been a large number of sun spots. Furthermore, magnetic storms ranging from 0.1 to 5% of the earth's total magnetic field strength alter the orientation of both ring-billed gulls and homing pigeons. Keeton *et al.* (1974) repeatedly released a group of experienced homing pigeons at the same site and found that the average vanishing bearing of these birds shifted counterclockwise with increasing magnetic variability.

Pigeons released at magnetic anomalies (places where the earth's magnetic field strength varies irregularly) show an increase in the scatter of their vanishing bearings that is correlated with the amount of variability in the magnetic field (Walcott, 1978, 1982). Kiepenheuer (1982, 1986) has recently also found that pigeons released at a strong and irregular anomaly in the Rhine Valley were disoriented, whereas control birds released outside the anomaly were well-oriented towards home. Wagner (1976), Frei & Wagner (1976) and Frei (1982), working with an anomaly in Switzerland, report that deflections of the pigeons' vanishing bearings from the direction of home were related to the magnetic topography around the release site. But these Swiss anomalies were quite weak (of the order of 200 γ) and not particularly irregular. At strong anomalies (3000 γ or about 6% of the earth field) pigeons seem totally disoriented, although homing speed and success are normal. Although there is no direct proof that the pigeons' disorientation is due to the distorted magnetic field, such a suggestion is supported by the correlation between the degree of magnetic variability at the anomaly and the amount of scatter of the pigeons' vanishing bearings.

These effects of magnetic anomalies are evident on clear days when the sun compass is available and, from clock-shift data (e.g. Schmidt-Koenig, 1961), takes precedence. Moreover, the small magnetic fluctuations at anomalies and from magnetic storms should have little effect upon a magnetic compass system. It is tempting to suppose that storms and anomalies disrupt the pigeons' ability to sense

where they are relative to their home, and that the 'map' (Kramer, 1953) or 'type III navigation' (Griffin, 1955) depends in part upon the small, systematic changes in magnetic field strength over the surface of the earth (Gould, 1980, 1982, 1985; Lednor, 1982; Moore, 1980; Walcott, 1980, 1982; for a review see Presti, 1985; Wallraff, 1983; Wiltschko, Nohr, Fuller & Wiltschko, 1986).

Whether the effects of magnetic storms occur during transport to the release site, at the release point, or both, is not clear. Larkin & Keeton (1976) found that bar magnets applied just before release on sunny days mimicked the effects of a maximal magnetic storm. The effects of localized magnetic anomalies appear to result from a distortion of site-specific information. Walcott (1977) found that paired coils with an earth-strength field activated just before release deflected the pigeons' vanishing bearings even on sunny days. At the same time, Kiepenheuer (1978), Wiltschko, Wiltschko & Keeton (1978), Papi *et al.* (1978) and Benvenuti, Baldaccini & Ioale (1982) all found that altering the magnetic field on the trip to the release point had a significant effect on the pigeons' vanishing bearings.

Since pigeons appear able to sense not only the direction of the earth's field but also minute changes in field strength, it seems likely that they must have a specialized magnetic detector system. An intriguing candidate for this sense organ is the magnetite reported by Walcott, Gould & Kirschvink (1979) and Presti & Pettigrew (1980) in the head or neck of pigeons and by Beason & Nichols (1984), Beason & Brennan (1986) in bobolinks. These magnetite crystals act like permanent magnets; about 40% of the pigeons examined showed a net magnetic remanence. In the other 60%, magnetic remanence could be induced by a strong magnetic field. In a subsequent study, over 80 pigeons were examined by Walcott & Walcott (1982). Although the same techniques as previously were used, no consistent intrinsic or inducible remanence was found. However, serially sectioned pigeon heads, stained with an iron stain and examined under the light microscope, revealed three sites where intracellular positively staining granules were abundant: in the Harderian glands, at the base of the beak just posterior to the cere, and in cells lying close to a bony ledge just ventral to the olfactory nerves and olfactory lobes. While the histological results clearly demonstrate the presence of intracellular iron-containing granules, the difference in results obtained using magnetometry are puzzling. It is possible, as Gould, Kirschvink & Deffeyes (1978) and Gould (1980) suggest for honeybees, that magnetic detection could be based on superparamagnetic magnetite crystals, which are found in large numbers in bees and are too small to have a permanent remanence at physiological temperatures. Gould (1980) and Kirschvink & Gould (1981) describe how superparamagnetic detectors might work and calculate their sensitivity. In such a case, permanent-domain magnetite might not be necessary.

It is also conceivable that pigeons might make use of a magnetic field detection system associated with the retina (Leask, 1977). Semm (1983), Semm, Nohr, Demaine & Wiltschko (1984) and Semm & Demaine (1986) have recorded electrical responses in cells of the nucleus of the basal optic root and the optic tectum to earth-strength magnetic field stimulation.

If pigeon heads are not always measurably magnetic it might seem that permanent-domain magnetite cannot form the basis of a magnetic detector. Calculations made by Kirschvink & Gould (1981), however, suggest that this is not the case. A few hundred or thousand permanent-domain magnetite grains would be sufficient for a sensitive magnetic compass (though not for a magnetic map system) yet could not be detected by the SQUID magnetometers used to measure the magnetization of pigeon heads. The sensitivity of these magnetometers is about 10^{-8} e.m.u. and the moment of a relatively small number of permanent-domain magnetite grains would be well below this (10^{-9} e.m.u. for 103 single domains).

The behavioural, magnetic and histological evidence suggest to us four alternative hypotheses. (1) The total properties of a permanent-domain magnetite array are important in orientation. (2) The collective magnetic arrangement of permanent-domain magnetite particles is not important; rather it is the individual particles themselves that are responsible for the detection of magnetic information. (3) Magnetic sensitivity is based on superparamagnetic domains. (4) The magnetite grains have nothing to do with the pigeons' sensitivity to magnetic fields.

In an effort to test the first hypothesis – that the magnetic properties of the total array of magnetite grains might be important – we demagnetized homing pigeons in a strong alternating magnetic field. This process reverses the polarity of half the grains, thereby disabling a detector which depends on the total alignment of the grains. We tested the effect of this procedure by releasing the pigeons at normal sites on both sunny and overcast days and by releasing them also at magnetically anomalous sites on sunny days. We also tried to align the permanent-domain magnetic grains in a strong magnetic field. Finally, we examined the effect on the pigeons' orientation of exposing the birds to a strong magnetic gradient that exerted a translational force on the permanent-domain magnetite grains.

MATERIALS AND METHODS

Experienced, adult pigeons from our loft in Lincoln, MA, were trained as a flock along a line SSE of the loft to a distance of 50 miles (80 km). They were then each given a series of single tosses along this line until they were returning promptly from 80 km. One single toss from 48 to 80 km West of the loft completed their training.

The relative alignment of the moments of the permanent-domain magnetite grains was altered by putting the birds in the centre of a 0.21 T 60 Hz a.c. Coil described by Gould, Kirschvink, Deffeyes & Brines (1980) and fabricated by the Princeton Plasma Physics Laboratory Coil Shop. This coil was itself located inside a 10-coil system (McElhinny, Luck & Edwards, 1971) which was used to cancel the earth's field to within about 0.02% of normal.

From other data (Walcott *et al.* 1979; Kirschvink & Gould, 1981) we know that the field adequate to reverse the polarity of the pigeons' permanent magnetic domains is about 0.07 T applied along the long axis of each grain. Each pigeon was held in the centre of the coil as a 10-A current was applied and then gradually reduced to zero.

This procedure was followed three times with each pigeon so that the head was demagnetized once in each of three mutually orthogonal orientations. As a result every magnetite domain, regardless of its alignment in the pigeon, felt a minimum demagnetization field of 0.15 T. (0.15 T is the maximum theoretical unblocking field required to reverse a permanent magnetite domain.) The strong alternating field served to flip the magnetic moments back and forth until the slowly declining current reduced the field below the strength just necessary to flip the moment. At this point, the last polarity strong enough to effect reversal is retained indefinitely. Exactly when a particular grain drops out is a function of its size, shape and orientation, so that its ultimate polarity is determined by chance. Hence for elongate grains, half the moments will be reversed. We call this procedure 'deGaussing'. The null field around the a.c. solenoid was maintained in order to avoid a 0.5×10^{-4} T bias on the moments of the grains which would tend to align them with the earth's field. Gould *et al.* (1980) have demonstrated that this arrangement works on crystals roughly twice as magnetically 'hard' as those of pigeons.

In an effort to align all the permanent magnetic moments, at least roughly, we placed each pigeon's head between the pole pieces of a gap magnet (Edmund Scientific no. 71 501). The gap was set at 2.4 or 2.8 cm corresponding to fields of 0.145 and 0.115 T, respectively. This field should be sufficient to align roughly 68 or 64 % of the permanent domains. As a result, roughly one-third of the moments should be flipped as compared to one-half in the deGaussing procedure. For most experiments the pigeon was oriented so that the field lines passed transversely through its head in a horizontal plane – that is, so that its eyes faced the pole pieces of the magnet. The bird's head was slowly put between the pole pieces, held there momentarily, and then slowly withdrawn. The 'Gaussing' was performed at the release site immediately before the pigeon was released.

To expose pigeons to a strong magnetic gradient, they were taken to the Francis Bitter National Magnet Laboratory at the Massachusetts Institute of Technology in Cambridge, MA. Here they were placed slightly off centre in a 12 T solenoid. This arrangement exposed the pigeon's head and neck to a maximum gradient of about 8 T cm^{-1} . With the pigeon firmly fixed in place, the current in the solenoid was gradually and smoothly increased to its maximum value over a period of 45 s. It was then gradually decreased to zero. Control birds were placed in the magnet for an equal time, with the cooling water running, but without any current. In a second series, the same procedure and same peak current was used, but the current was ramped smoothly up to maximum over 2 min, held there for 1 min and then decreased to zero over 2 min. According to calculations in Kirschvink & Gould (1981), the first procedure would move a 1000 Å domain approximately 1 mm in a solution 10 times as viscous as water, while the second would move such a domain 3.8 mm.

Pigeons were transported from the loft to the release point either in the back of a station wagon or in the front compartment of a Volkswagen estate. The release points used and the direction and distance to home were: Worcester Airport, 086° , 50 km; Carver, 310° , 71 km; Hancock, 152° , 84 km; Lynnfield, 248° , 25 km; Providence,

27°, 61 km. For some experiments the gap magnet was carried in a mu-metal box which served to isolate the birds from the field of the magnet. At the release point each pigeon was equipped with a small radio beacon (Cochran, 1967) and tracked for 15 min or until it vanished from radio range. The bearings of birds whose signals vanished in less than 3 min were excluded from analysis. The direction to the pigeon at 15 min or when it vanished was recorded and is given in the diagrams. Mean bearings were computed with the Rayleigh test and tested for non-uniformity with the *V*-test. Distributions of bearings were compared with the Watson U^2 test (Batschelet, 1981) and differences in the amount of scatter were assessed with a non-parametric test proposed by Wallraff (1979) and described in Batschelet (1981). Vanishing intervals and homing speeds were compared with the Mann–Whitney *U*-test (Zar, 1974).

RESULTS

If the magnetic sensitivity of homing pigeons were dependent on an array of permanent magnetite domains of ordered polarity, then deGaussing a pigeon might cause it to become disoriented. If deGaussing caused an effect on sunny days when pigeons are presumably relying on their sun compasses, this would suggest that an ordered polarity detector might be involved in the map system. If, however, deGaussing only had an effect on overcast days when the sun was not visible, it would suggest that this same sort of detector was involved in the magnetic compass system.

To test these ideas, pigeons were taken from their lofts and deGaussed. Along with control birds they were taken to a magnetically normal release site, released and tracked. As Fig. 1A,B shows, birds released at two sites under sunny conditions showed no significant deficit in their ability to orient towards home. Both controls and experimentals are well-oriented with the customary release point biases in each case. The experimental birds have somewhat greater scatter than the controls at Worcester, and somewhat less at Carver. In neither case are the differences significant. In both cases the deGaussed birds departed on an average bearing 11–12° clockwise of the controls. There was no significant difference in time to vanish from the release point, homing speed or the number of birds that returned. Data for this and all other tests reported here are summarized in Table 1.

To see whether deGaussing might be more effective if it were carried out at the release site, we moved the coils to Hancock, NH and conducted a series of tests there. Half the birds were deGaussed immediately before release under sunny skies. As Fig. 1C indicates, this made no difference to the results; the performance of both control and experimental birds was essentially identical. Apparently deGaussing has little effect on either vanishing bearings or homing performance on sunny days.

The effects of releasing deGaussed pigeons under overcast skies, when they are probably relying on magnetic compass information, are shown in Fig. 1D. The vanishing bearings of deGaussed birds were more scattered than those of the controls and the mean vanishing bearing was again rotated clockwise. Unfortunately, since

the number of days with solid overcast skies during the summer was small, too few birds were released to make these differences statistically significant. The best that can be said is that the control birds, although random under the Rayleigh test ($P = 0.09$) were significantly oriented by the V -test ($P = < 0.05$). The orientation of the deGaussed birds was random by both tests. Time to vanish from the release point, homing speed and the number of birds that returned were the same for both groups. Thus, if one can believe the results from the few birds released under

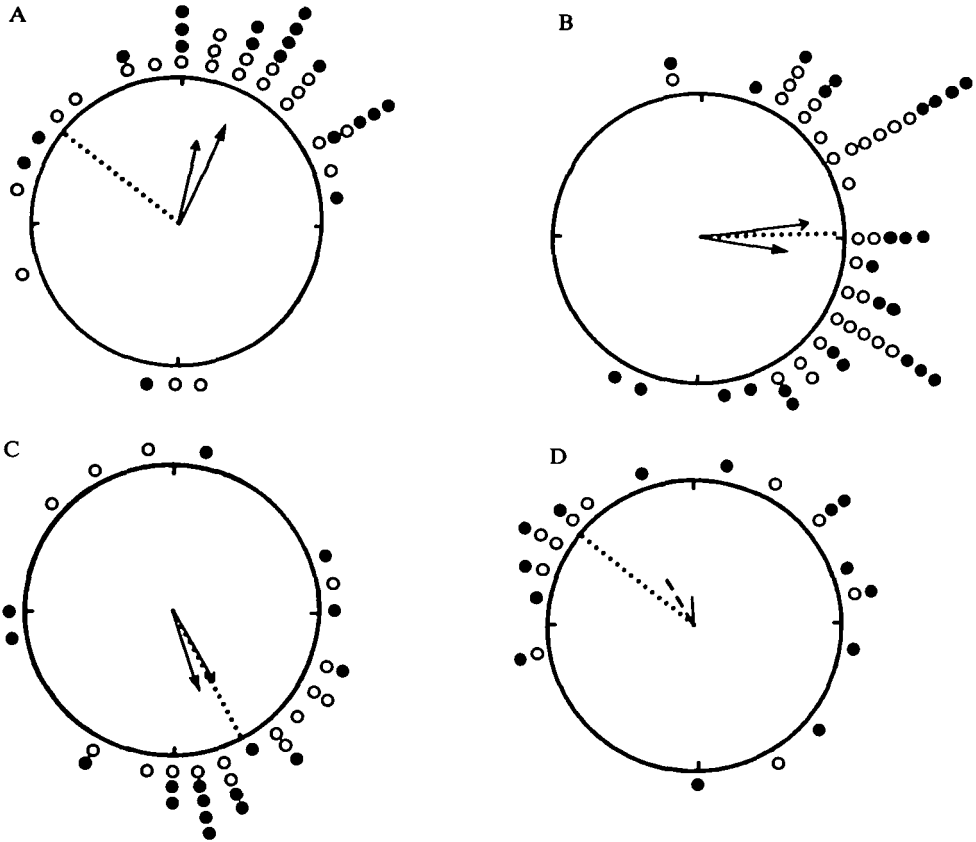


Fig. 1. Bearings of control pigeons and of pigeons deGaussed at the loft and released at Carver, MA (A) or Worcester, Airport, MA (B). In C birds were taken to Hancock, NH and deGaussed there. All birds were released under sunny skies, except the birds shown in D, which were released at Carver, MA under totally overcast skies. In this and all the following diagrams, each dot on the periphery of the circle represents the radio bearing of a single pigeon. The open circles are the bearings of control pigeons, the solid dots, experimental pigeons. The dotted line inside each circle indicates home direction, each diagram being plotted with magnetic North towards the top of the page. The arrow originating at the centre of each diagram represents the mean vector calculated by the Rayleigh test. It is drawn to scale, with the radius of the circle set to a vector length of 1. An arrowhead indicates the test was significant ($P < 0.05$) under the Rayleigh test. An open arrowhead or dashed line indicates control birds, a solid arrowhead or solid line, experimental pigeons. Further details of text results are given in Table 1.

Table 1. Summary of data on initial orientation and homing performance

Site	Treatment	Sun O/C	Con	MVB(N)	τ	P	MVI	N15	MHS	Homing success		
										No. on day	No. late	No. lost
Worcester Airport	DeGauss at loft	S	C	82 (28)	0.766	0.0000	10.5 (12)	16	11.7 (18)	18	7	3
			E	99 (26)	0.617	0.0000	9.7 (10)	16	11.2 (22)	22	3	2
Carver	DeGauss at loft	S	C	18 (22)	0.507	0.0027	9.3 (7)	15	15.1 (17)	17	5	0
			E	24 (19)	0.691	0.0000	9.8 (9)	10	16.0 (11)	11	7	1
Hancock	DeGauss at site	S	C	150 (16)	0.572	0.0039	11.9 (8)	8	9.7 (5)	5	12	7
			E	161 (17)	0.583	0.0021	11.0 (4)	13	13.6 (5)	5	13	5
Carver	DeGauss at loft	O	C	327 (10)	0.411	0.1880	12.6 (5)	5	12.1 (6)	6	4	0
			E	352 (13)	0.213	0.5626	9.0 (2)	11	10.4 (7)	7	3	3
Lynnfield anomaly	DeGauss at loft	S	C	128 (33)	0.163	0.4212	10.5 (10)	23	6.5 (22)	22	11	0
			E	72 (22)	0.228	0.3210	8.1 (9)	13	7.2 (18)	18	8	0
Hancock	Gauss	S	C	147 (16)	0.764	0.0000	12.4 (7)	9	14.6 (5)	5	10	3
			E	147 (16)	0.929	0.0000	8.9 (7)	9	16.9 (9)	10	6	0
Worcester Airport	Gauss	S	C	111 (22)	0.469	0.0066	7.2 (10)	12	12.4 (10)	10	13	2
			E	132 (21)	0.703	0.0000	7.5 (10)	11	10.9 (12)	12	13	0
Hancock	Gauss (magnet transported separately)	S	C	162 (16)	0.699	0.0001	9.3 (7)	11	16.9 (8)	8	11	1
			E	149 (18)	0.738	0.0000	11.1 (9)	9	21.3 (10)	10	5	4
Hancock	Gauss (vertical)	S	C	160 (15)	0.787	0.0000	11.0 (9)	6	16.4 (8)	8	5	4
			E	166L (14)	0.840	0.0000	11.3 (6)	8	13.7 (4)	4	11	3
Providence	Gradient test 1980	S	C	311 (24)	0.739	0.0000	15.5 (19)	5	15.6 (18)	18	7	0
			E	319 (27)	0.349	0.0354	14.6 (14)	13	16.4 (13)	13	10	0
Providence	Gradient test 1981	S	C	325 (19)	0.323	0.1376	16.0 (15)	4	10.7 (16)	18	3	1
			E	316 (17)	0.654	0.0003	14.1 (14)	3	12.9 (13)	14	3	2

Sun O/C, tests were conducted under sun (S) or overcast (O) skies.

Con, C, control treatment; E, experimental treatment.

MVB(N), the mean vanishing bearing; the number of bearings obtained is shown in parenthesis.

τ , the mean vector length.

P, the probability that the distribution of bearings is uniform under the Rayleigh test.

MVI, the mean vanishing interval of birds vanishing in less than 15 min; the sample size is shown in parentheses.

N15, the number of birds remaining in radio range 15 min after release.

MHS, the mean homing speed (in miles per hour) of birds returning on day 1, the day of the test; the sample size is shown in parentheses.

Homing success, No. on day is the number of birds that returned on the day of release; No. late is the number that returned after the day of release; and No. lost is the number of birds that never returned.

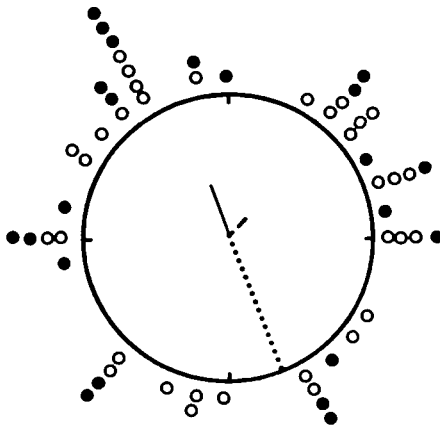


Fig. 2. Initial orientation of pigeons deGaussed at the loft and control pigeons released at the magnetic anomaly at Lynnfield, MA. For conventions see Fig. 1.

overcast skies, deGaussing seems to have had a greater effect than it did when the sun was visible.

That deGaussing had no effect on sunny days does not necessarily mean that it did not affect a magnetic map. It could be that the pigeons simply switched to some back-up system; that the map as well as the compass is redundant. To test this idea we released deGaussed pigeons at a magnetic anomaly. If deGaussing had destroyed their ability to detect the irregular field of the anomaly and they were using a non-magnetic back-up system, we would predict that the birds might be well-oriented. As Fig. 2 shows, however, deGaussed pigeons released at the magnetic anomaly at Lynnfield, MA were just about as disoriented as the controls. It appears that even if deGaussing disrupts a magnetic compass system, it has little or no effect upon the map.

Of the pigeons examined by Walcott *et al.* (1979) in a magnetometer, only about 40% had a natural magnetic remanence. It seemed possible that increasing the alignment of the permanent magnetite grains by Gaussing the pigeon would have more of an effect than deGaussing. We transported birds to the release point in a carrying cage next to which there was a gap magnet enclosed in a mu-metal box. One group of pigeons had their heads placed between the pole pieces of the magnet with their eyes facing the poles. The controls were simply released and tracked. Under sunny skies at Worcester, MA and Hancock, NH, the experimental birds were, if anything, better oriented than the controls (Fig. 3A,B). The differences were not significant, and there was no significant difference in any measure of homing performance.

Since the gap magnet in the mu-metal box was carried next to the pigeons on their outward journey, it seemed possible that the magnetic field around the pigeons might have been distorted by this procedure. To test this we carried the pigeons and the magnet in separate vehicles. As Fig. 3C,D shows, there was essentially no difference

between Gaussed and control pigeons. We also tried another head orientation during Gaussing such that the magnetic field lines passed vertically through the pigeon's head. As Fig. 3B,D illustrates, there was no difference between birds Gaussed horizontally and those Gaussed vertically. It appears that Gaussing has remarkably little effect upon birds released under sunny conditions.

The evidence so far suggests that neither Gaussing nor deGaussing has much effect upon the pigeons' orientation under sunny conditions. But if pigeons are using particles of permanent-domain magnetite as part of a sensory system to detect the earth's magnetic field, applying a sufficiently strong magnetic gradient might cause the particles to shift and interfere with their functioning. We applied a magnetic field gradient of 8 T cm^{-1} to the pigeons' heads and then released and tracked the birds

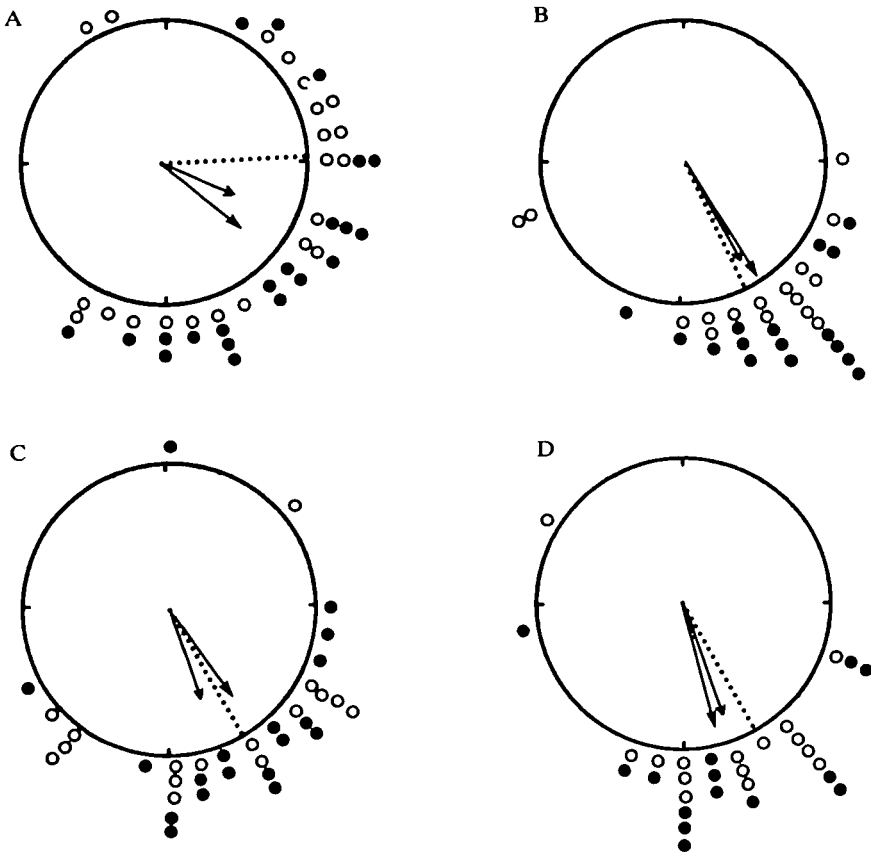


Fig. 3. Orientation of birds Gaussed immediately prior to release under sunny skies. (A) Results at Worcester, MA; (B) results of Gaussed birds at Hancock, NH. At both sites both groups of birds were carried close to a mu-metal box containing the gap magnet. Experimental birds were Gaussed horizontally at both sites. (C) Control birds transported to the site in a separate vehicle from that carrying the gap magnet, and then Gaussed at Hancock; (D) birds Gaussed vertically and released at Hancock. Conventions as in Fig. 1.

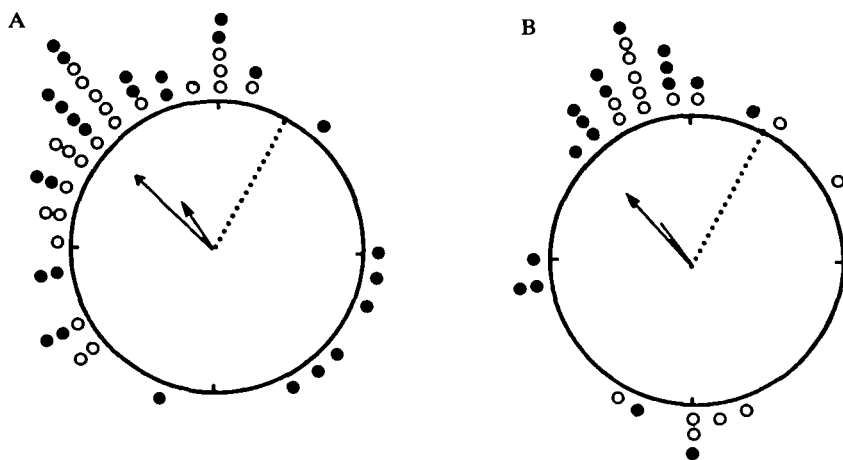


Fig. 4. Results of exposing pigeons to a powerful (0.8 T cm^{-1}) gradient. (A) Tests done in 1980; (B) results obtained in 1981. Conventions as in Fig. 1.

under sunny conditions. As Fig. 4A shows, the experimental birds were less accurately oriented than the controls, but the difference in scatter is not significant. Vanishing time was greater and homing speed was slower for the experimental birds but the differences were not significant (Mann–Whitney U -test, $P > 0.05$). In the second series (Fig. 4B), the opposite results were obtained; the control birds were more scattered than the experimental group. The two groups did not differ significantly in their initial orientation, time to vanish or homing speed. Unfortunately, no experiments were done under overcast skies.

DISCUSSION

The results of the Gaussing and deGaussing experiments clearly rule out the possibility that, under sunny conditions, pigeons rely on a magnetic detector in which the polarity of permanent-domain magnetite crystals is critical. Any receptor based on an orderly alignment of single permanent domains should be disrupted if the moments of half the domains are reversed by deGaussing. Under overcast skies there is a hint that the vanishing bearings of deGaussed pigeons were more scattered than those of controls. It is unfortunate that there are so few data under overcast skies, because if pigeons were using an ordered magnetite array for their compass one might expect little or no effect of deGaussing under sunny skies, when old and experienced pigeons would be using their sun compass, but would only see the effect under overcast skies when they were using a magnetic compass.

Kiepenheuer, Ranvaud & Maret (1986) report that exposing pigeons to a homogeneous magnetic field of 10 T (100 000 G) for 1 min caused both a significant bias in the direction as well as an increased scatter in their vanishing bearings. This effect persisted for at least 6 weeks after exposure. The field to which our pigeons were exposed was about the same strength and the length of the exposure was about

the same, but we arranged for the pigeons to experience a substantial magnetic gradient. A single magnet in the uniform field will attempt to align itself with the applied field but will not be subject to a translational force. In a gradient, however, the magnet will not only tend to align itself with the field but also there will be a net force on the magnet. The familiar example is the effect of one bar magnet on another as they are brought together; if they are free to rotate, they align with one another so that they attract. It is surprising that our treatment had so little effect; it was altogether more drastic than Kiepenheuer's. It is possible that Kiepenheuer *et al.* (1986) were using young pigeons who might be relying more on the magnetic compass than the old experienced pigeons we were using. It is also possible that the gradient so disrupted the receptor that the pigeons failed to use it. Although it seems improbable that any permanent-domain magnetite-based receptor could survive the disruptive force of the gradient, a superparamagnetic system would be far less affected.

If the apparent sensitivity of pigeons to earth-strength magnetic fields (suitable for compass information) and to small-magnetic field changes (used in some way in the map) is based on magnetite, then unless the pigeon's map is fully redundant with respect to magnetic cues, we can draw two main conclusions from these experiments. First, any magnetic map system, if it depends on magnetite at all, must depend on superparamagnetic crystals since (a) many pigeons lack detectable permanent-domain magnetite and (b) Gaussing and deGaussing had no effect on sunny days. Second, the magnetic compass system could depend on permanent-domain magnetite since (a) so little is needed that it could fall below the threshold of the detector and (b) the small amount of data obtained under overcast skies indicated that deGaussed pigeons were more affected under overcast than under sunny skies. Finally, the results we obtained in these experiments are also consistent with the idea that pigeons can detect a magnetic field in some part of their visual system. If that were the case, none of the treatments we gave the pigeons would be expected to have any effect.

We are grateful to Richard B. Frankel and his colleagues for their hospitality at the Francis Bitter National Magnet Laboratory at the Massachusetts Institute of Technology. We also thank all the students for their help with the experiments and the NSF grant no. BNS-7810518 for financial support.

REFERENCES

- BATSCHLET, E. (1981). *Circular Statistics in Biology*. London, New York, Toronto: Academic Press.
- BEASON, R. C. (1986). Magnetic orientation and magnetically sensitive in migratory birds. In *Biophysical Effects of Steady Magnetic Fields* (ed. G. Maret, N. Broccara & J. Kiepenheuer), pp. 167–172. Berlin, New York: Springer-Verlag.
- BEASON, R. C. & BRENNAN, W. J. (1986). Natural and induced magnetization in the bobolink, *Dolichonyx oryzivorus* (Aves: Icteridea). *J. exp. Biol.* **125**, 49–56.
- BEASON, R. C. & NICHOLS, J. E. (1984). Magnetic orientation and magnetically sensitive material in the Bobolink (*Dolichonyx oryzivorus*), a transequatorial migrant. *Nature, Lond.* **309**, 151–153.

- BENVENUTI, S., BALDACCINI, N. E. & IOALE, P. (1982). Pigeon homing: effect of altered magnetic field during displacement on initial orientation. In *Avian Navigation* (ed. F. Papi & H. G. Wallraff), pp. 140–148. Berlin: Springer-Verlag.
- CARR, P. H., SWITZER, W. P. & HOLLANDER, W. F. (1982). Evidence for interference with navigation of homing pigeons by a magnetic storm. *Iowa State J. Res.* **56**, 327–340.
- COCHRAN, W. (1967). 145–160 mHz beacon tag transmitter for small animals. *BIAC Information Module M-15*. AIBS Washington, DC.
- FREI, U. (1982). Homing pigeons' behaviour in the irregular magnetic field of Western Switzerland. In *Avian Navigation* (ed. F. Papi & H. G. Wallraff), pp. 129–139. Berlin: Springer-Verlag.
- FREI, U. & WAGNER, G. (1976). Die Anfangsorientierung von Brieftauben im erdmagnetisch gestörten Gebiet des Mont Jorat. *Rev. suisse Zool.* **83**, 891–897.
- GOULD, J. L. (1980). The case for magnetic sensitivity in birds and bees (such as it is). *Am. Scient.* **68**, 256–267.
- GOULD, J. L. (1982). The map sense of pigeons. *Nature, Lond.* **296**, 205–211.
- GOULD, J. L. (1985). Are animal maps magnetic? In *Magnetite Biomineralization and Magnetoreception in Organisms* (ed. J. L. Kirschvink, D. S. Jones & B. J. MacFadden), pp. 257–268. New York, London: Plenum Press.
- GOULD, J. L., KIRSCHVINK, J. L. & DEFFEYES, K. S. (1978). Bees have magnetic remanence. *Science* **202**, 1026–1028.
- GOULD, J. L., KIRSCHVINK, J. L., DEFFEYES, K. S. & BRINES, M. L. (1980). Orientation of demagnetized bees. *J. exp. Biol.* **86**, 1–8.
- GRIFFIN, D. R. (1955). Bird Navigation. In *Recent Studies in Avian Biology* (ed. A. Wolfson), pp. 154–197. Urbana: University of Illinois Press.
- KEETON, W. T. (1971). Magnets interfere with pigeon homing. *Proc. natn. Acad. Sci. U.S.A.* **68**, 102–106.
- KEETON, W. T. (1972). Effects of magnets on pigeon homing. In *Animal Orientation and Navigation* (ed. S. R. Galler, K. Schmidt-Koenig, G. J. Jacobs & R. E. Belleville), pp. 579–593. NASA SP-262.
- KEETON, W. T., LARKIN, T. S. & WINDSOR, D. M. (1974). Normal fluctuations in the earth's magnetic field influence pigeon orientation. *J. comp. Physiol.* **95**, 95–103.
- KIEPENHEUER, J. (1978). Inversion of the magnetic field during transport: Its influence on the homing behavior of pigeons. In *Animal Migration, Navigation and Homing* (ed. K. Schmidt-Koenig & W. T. Keeton), pp. 131–151. Heidelberg: Springer-Verlag.
- KIEPENHEUER, J. (1982). The effect of magnetic anomalies on the homing behavior of pigeons: an attempt to analyze the possible factors involved. In *Avian Navigation* (ed. F. Papi & H. G. Wallraff), pp. 120–128. Berlin: Springer-Verlag.
- KIEPENHEUER, J. (1986). A further analysis of the orientation behavior of pigeons released within magnetic anomalies. In *Biophysical Effects of Steady Magnetic Fields* (ed. G. Maret, N. Broccara & J. Kiepenheuer), pp. 148–153. Berlin, New York: Springer-Verlag.
- KIEPENHEUER, J., RANVAUD, R. & MARET, G. (1986). The effect of ultrahigh magnetic fields on the initial orientation of homing pigeons. In *Biophysical Effects of Steady Magnetic Fields* (ed. G. Maret, N. Broccara & J. Kiepenheuer), pp. 189–193. Berlin, New York: Springer-Verlag.
- KIRSCHVINK, J. L. & GOULD, J. L. (1981). Biogenic magnetite as a basis for magnetic field detection in animals. *Biosystems* **13**, 181–201.
- KRAMER, G. (1953). Die Sonnenorientierung der Vogel. *Verh. dt. Zool. Ges.* **1952**, 72–84.
- LARKIN, R. P. & SUTHERLAND, P. J. (1977). Migrating birds react to Project Seafarer's electromagnetic field. *Science* **195**, 777–779.
- LARKIN, T. S. & KEETON, W. T. (1976). Bar magnets mask the effect of normal magnetic disturbances on pigeon orientation. *J. comp. Physiol.* **110**, 227–231.
- LEASK, M. J. M. (1977). A physiochemical mechanism for magnetic field detection by migrating birds and homing pigeons. *Nature, Lond.* **267**, 144–145.
- LEDNOR, A. J. (1982). Magnetic navigation in pigeons: possibilities and problems. In *Avian Navigation* (ed. F. Papi & H. G. Wallraff), pp. 109–119. Berlin: Springer-Verlag.
- MC ELHINNEY, M. W., LUCK, G. R. & EDWARDS, D. (1971). A large volume magnetic free space. *Pure appl. Geophys.* **90**, 126–130.
- MOORE, B. R. (1980). Is the homing pigeon's map geomagnetic? *Nature, Lond.* **285**, 69–70.

- MOORE, F. R. (1977). Geomagnetic disturbance and the orientation of nocturnally migrating birds. *Science* **196**, 682–684.
- PAPI, F., IOALE, P., FIASCHI, V., BENVENUTI, S. & BALDACCINI, N. E. (1978). Pigeon homing: Cues detected during the outward journey influence initial orientation. In *Animal Migration, Navigation and Homing* (ed. K. Schmidt-Koenig & W. T. Keeton), pp. 65–77. Heidelberg: Springer-Verlag.
- PRESTI, D. E. (1985). Avian navigation, geomagnetic field sensitivity and biogenic magnetite. In *Magnetite Biomineralization and Magnetoreception in Organisms* (ed. J. L. Kirschvink, D. S. Jones & B. J. MacFadden), pp. 455–482. New York, London: Plenum Press.
- PRESTI, D. & PETTIGREW, J. D. (1980). Ferromagnetic coupling to muscle receptors as a basis for geomagnetic field sensitivity in animals. *Nature, Lond.* **285**, 99–101.
- SCHMIDT-KOENIG, K. (1961). Die Sonne als Kompass im Heim-Orientierungssystem der Brieftauben. *Z. Tierpsychol.* **18**, 221–244.
- SCHREIBER, B. & ROSSI, O. (1976). Correlation between race arrivals of homing pigeons and solar activity. *Boll. Zool.* **43**, 317–320.
- SCHREIBER, B. & ROSSI, O. (1978). Correlation between magnetic storms due to solar spots and pigeon homing performances. *IEEE Trans. Magn.* **14**, 961–963.
- SEMM, P. (1983). Neurobiological investigations on the magnetic sensitivity of the pineal gland in rodents and pigeons. *Comp. Biochem. Physiol.* **76A**, 683–689.
- SEMM, P. & DEMAINE, C. (1986). Neurophysiological properties of magnetic cells in the pigeon's visual system. *J. comp. Physiol. A* **159**, 619–625.
- SEMM, P., NOHR, D., DEMAINE, C. & WILTSCHKO, W. (1984). Neural basis of the magnetic compass: interactions of visual, magnetic and vestibular inputs to the pigeon brain. *J. comp. Physiol. A* **155**, 283–288.
- SOUTHERN, W. E. (1971). Gull orientation by magnetic cues: a hypothesis revisited. *Ann. N. Y. Acad. Sci.* **188**, 295–311.
- SOUTHERN, W. E. (1972). Influence of disturbances in the earth's magnetic field on ring-billed bull orientation. *Condor* **74**, 102–105.
- VISALBERGHI, E. & ALLEVA, E. (1979). Magnetic influences on pigeon homing. *Biol. Bull. mar. biol. Lab., Woods Hole* **156**, 246–256.
- WAGNER, G. (1976). Das Orientierungsverhalten von Brieftauben im erdmagnetisch gestorten Gebiete des Chasseral. *Rev. suisse Zool.* **83**, 883–890.
- WALCOTT, C. (1977). Magnetic fields and the orientation of homing pigeons under sun. *J. exp. Biol.* **70**, 105–123.
- WALCOTT, C. (1978). Anomalies in the earth's magnetic field increase the scatter of pigeon's vanishing bearings. In *Animal Migration, Navigation and Homing* (ed. K. Schmidt-Koenig & W. T. Keeton), pp. 143–151. Berlin, Heidelberg, New York: Springer-Verlag.
- WALCOTT, C. (1980). Effects of magnetic fields on pigeon orientation. In *Acta XVII Congressus Internationalis Ornithologici* (ed. R. Nohring), pp. 588–592. Berlin: Deutsche Ornithologen-Gesellschaft.
- WALCOTT, C. (1982). Is there evidence for a magnetic map in pigeons? In *Avian Navigation* (ed. F. Papi & H. G. Wallraff), pp. 99–108. Berlin: Springer-Verlag.
- WALCOTT, C., GOULD, J. L. & KIRSCHVINK, J. L. (1979). Pigeons have magnets. *Science* **205**, 1027–1029.
- WALCOTT, C. & GREEN, R. (1974). Orientation of homing pigeons altered by a change in the direction of an applied magnetic field. *Science* **184**, 180–182.
- WALCOTT, C. & WALCOTT, B. (1982). A search for magnetic field receptors in animals. In *Avian Navigation* (ed. F. Papi & H. G. Wallraff), pp. 338–343. Berlin: Springer-Verlag.
- WALLRAFF, H. G. (1979). Goal-oriented and compass-oriented movements of displaced homing pigeons after confinement in differentially shielded aviaries. *Behav. Ecol. Sociobiol.* **5**, 201–225.
- WALLRAFF, H. G. (1983). Relevance of atmospheric odors and geomagnetic field to pigeon navigation: What is the "map" basis? *Comp. Biochem. Physiol.* **76A**, 643–663.
- WILTSCHKO, R., WILTSCHKO, W. & KEETON, W. T. (1978). Effect of outward journey in an altered magnetic field on the orientation of young pigeons. In *Animal Migration, Navigation and Homing* (ed. K. Schmidt-Koenig & W. T. Keeton), pp. 152–161. Heidelberg: Springer-Verlag.

- WILTSCHKO, W. (1972). The influence of magnetic total intensity and inclination on directions preferred by migrating robins (*Erithacus rubecula*). In *Animal Orientation and Navigation* (ed. S. R. Galler, K. Schmidt-Koenig, G. J. Jacobs, & R. E. Belleville), pp. 569–578. NASA SP-262.
- WILTSCHKO, W., NOHR, D., FULLER, E. & WILTSCHKO, R. (1986). Pigeon homing: The use of magnetic information in position finding. In *Biophysical Effects of Steady Magnetic Fields* (ed. G. Maret, N. Broccara & J. Kiepenheuer), pp. 154–162. Berlin, New York: Springer-Verlag.
- WILTSCHKO, W. & WILTSCHKO, R. (1972). Magnetic compass of european robins. *Science* **176**, 62–64.
- YEAGLEY, H. L. (1951). A preliminary study of the physical basis of bird navigation II. *J. appl. Physics* **22**, 746–760.
- ZAR, J. H. (1974). *Biostatistical Analysis*. Englewood Cliffs, NJ: Prentice-Hall, Inc.