Effects of Magnets on Pigeon Homing

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ALTHOUGH THE POSSIBILITY THAT magnetic cues might be used in avian orientation has been suggested numerous times (refs. 1 to 13), it has never gained wide support. Yeagley (ref. 10) reported one test release in which homing pigeons carrying magnets were disoriented whereas controls carrying brasses were not; but neither he (ref. 11) nor other investigators (refs. 14 to 18) attempting to repeat his experiment ever obtained such results again. Moreover, several workers (refs. 19 to 28) who attempted to detect a sensitivity of birds to magnetic stimuli or to condition birds to respond behaviorally to such stimuli were unsuccessful.

Recently, however, Merkel and his colleagues (refs. 29 to 33) have claimed that European robins can orient in the absence of visual cues, and that predictable deviations in the robins' orientation can be produced by alteration of the magnetic field surrounding their cages; Perdeck (ref. 34) has attempted unsuccessfully to repeat these experiments. Southern (ref. 35) has reported a correlation between the accuracy of ring-billed gulls' orientation and fluctuations in the strength of the Earth's magnetic field. Graue (ref. 36) has mentioned that pigeons released near magnetic anomalies (total intensity) show more scatter in vanishing bearings than do similar pigeons released at sites with a normal magnetic field. Talkington (ref. 37) has claimed that pigeons tracked by helicopter exhibit a strong tendency to skirt around or head between magnetic anomalies. Several Russian workers (refs. 38 to 40) have reported a general increase in locomotor activity when birds are placed in artificial magnetic fields, and Reille (ref. 41) has reported success in conditioning pigeons to respond by heart rate changes to changes in the strength of an artificial magnetic field only slightly stronger than the Earth's.

In addition to these reports that birds respond to magnetic stimuli, there have been numerous claims that a variety of invertebrates exhibit orientational responses to artificial magnetic fields (refs. 42 to 52). Of particular interest is the recent demonstration by Lindauer and Martin (ref. 53) that terrestrial magnetism affects the orientation of the waggle dance of honeybees.

In view of these recent reports, and our own (ref. 54) demonstration that there is redundancy of cues in the pigeon orientational system, we reopened the question of whether magnets mounted on pigeons can affect the birds' homing behavior. Our early results are now available (ref. 65). This paper reviews those results, reports on some more recent tests, and discusses possible implications of our findings.

METHODS

Each of our tests consisted of alternately releasing individual pigeons from two treatment groups. The birds for the two treatments were chosen randomly from a flock housed in a single pen, where they had experienced identical feeding, exercise, and training; in this way differences due to age, motivation, or physical condition were minimized. The birds of the experimental group wore a magnet bar glued, just prior to release, to the back at the base of the neck; the birds of the control group wore a brass bar of the same size, weight, and placement. In the early tests, the bars were approximately 2.5 × 0.64 × 0.25 cm and weighed between 2.7 and 3.2 grams; the field strength of the magnets at their poles averaged about 255 G (the field strength at 8 cm, at the bird's head, was about 0.45 G). In some of the later tests, bars measuring approximately 2.5 × 0.64 × 0.32 and weighing between 4.5 and 4.8 grams were used; the field strength of these magnets at their poles averaged about 600 G (1.1 G at 8 cm away). Neither of the two sizes of bars appeared to cause the pigeons any discomfort, and there were no detectable differences between the two sizes in their effects on homing behavior.

The birds were carried to the release sites in closed vehicles. They were tossed from the hand, the directions of toss being randomized. The release sites were carefully chosen to give clear visibility for a long distance in all directions. The observers watched each bird with 10 × 50 binoculars until it vanished from sight, and a compass bearing for the vanishing point was recorded to the nearest five degrees. The vanishing interval, i.e., the interval between toss and vanishing, was timed with a stopwatch. The time of arrival of each bird at the home loft was recorded, so that homing speeds could be calculated.

The circular mean for each group of vanishing bearings was calculated by vector analysis (ref. 55). The V test (ref. 56) was used to determine whether the bearings were significantly homeward oriented. The vanishing intervals and homing speeds of brass- and magnet-laden birds in each test were compared by means of the matched-pairs signed-ranks test (ref. 57).

For each series of tests, the bearings from the separate releases were also pooled, with the home directions all set to 0°. The pooled bearings were then tested for homeward orientation using the V test. When appropriate, the extents of scatter of the pooled bearings for the two treatments were compared by means of an F test proposed by Watson and explained in simple terms by Emlen and Penney (ref. 58).

TEST RELEASES

As far as one can tell from the literature, previous test releases of birds carrying magnets were all conducted on clear days. Since our experiments (ref. 54) had indicated that the orientation process used by pigeons on sunny days differs in some respects from that used on overcast days, we were particularly interested in finding out what would happen if birds carrying magnets were released under total overcast, when the Sun compass would be unavailable to them.

First, however, we conducted a series of tests (our series I) under Sun to determine whether we would get results like those already published by others. In all our releases of experienced birds from both familiar and unfamiliar sites at distances of 27 to 50 km (from north, east, and south), both the control birds and the experimentals were well-oriented homeward, and in no case was there a significant difference between the two treatments in homing speeds. Figure 1 shows the pooled bearings from the six tests in this series; both the experimental and control birds are homeward oriented at $P<0.00001$. Thus these results agreed with those of other authors (refs. 14 to 18).

We now proceeded to conduct a series of similar tests (our series III) under total overcast, using experienced birds at sites where they had never previously been released; again the distances were 27 to 50 km. In five of seven tests the brass-laden birds were homeward oriented whereas the magnet-laden birds were not. Thus these five tests yielded results strikingly different from those obtained in the Sun releases. However, the other two releases in this series confused the picture somewhat—in one release both groups of birds were homeward oriented, and in one neither group was oriented. Figure 2 shows the pooled bearings for the seven releases in this series. The birds carrying brasses are homeward oriented at $P<0.00001$; the very large value of N for the birds carrying magnets has permitted detection of homeward orientation at $P = 0.02$ (Rayleigh test, $P = 0.06$). However, the bearings of the magnet-bearing birds are significantly more scattered than those of the brass-bearing birds ($P<0.005$).

Our results at this point seemed to indicate that magnets do not disorient experienced birds when the Sun is visible, but that they often do cause disorientation at unfamiliar release sites when the Sun is not visible. This could mean that the birds can use Sun cues and magnetic cues interchangeably, but that both together are seldom needed.

We had previously demonstrated that experienced pigeons can orient homeward under total overcast at unfamiliar release sites (ref. 54) but that first-flight birds cannot (ref. 59). The results discussed above now suggested that the experienced birds might be orienting under overcast by using magnetic cues as a substitute for Sun cues. But if this were true, why could not the first-flight birds do the same thing? We thought it possible that early training under sunny conditions is necessary to make pigeons responsive to magnetic cues, even though they can use Sun cues without prior training. To test this possibility, we put magnets or brasses on a large number of young birds when they first began to fly, and left these on throughout early training that consisted of a number of flock releases at distances of 1.6 to 16 km from all four cardinal directions. Some of the training flights were under overcast. Our earlier experience had shown that this was sufficient training to enable normal birds to orient under total overcast at distant unfamiliar release sites.

When the training was complete, these birds were used in a series of three test releases (our series V) under total overcast at a site 49.4 km south of the loft. Just before each bird was released, its magnet or brass was removed. Our thought was that the birds carrying brasses might have learned to use normal magnetic cues during their training, whereas the birds carrying magnets might not have been able to learn to do this. If this were so, then on their first single-toss flight under total overcast without magnets or brasses the birds that had until now worn brasses should be able to orient but the birds that had worn magnets should not. However, in each of the three test releases both groups were homeward oriented. Figure 3 shows the pooled bearings for the three releases in this series; both the experimental and the control birds are homeward oriented at $P < 0.00001$, and there is no significant difference in scatter between them. However, in

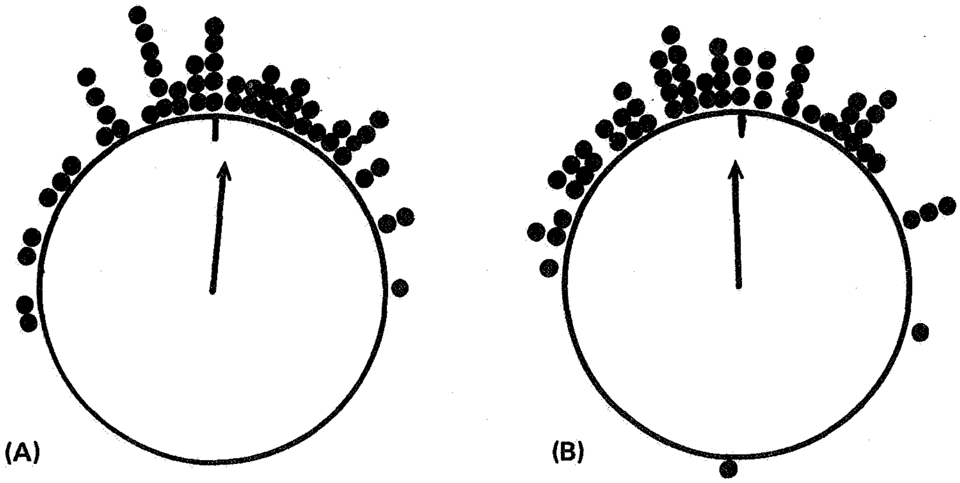

FIGURE 1. Pooled bearings from series I releases; experienced pigeons released under sunny conditions from distances of 27 to 50 km. Releases were from North, East, and South; home bearings have been adjusted to 0° (indicated by short line at the top of circle). The mean vectors are shown as arrows, with the maximum possible length of a mean vector (i.e., $r = 1$) represented by the radius of the circle. (A) Birds carrying brass bars, mean bearing 3°, $r = 0.738$ (homeward oriented $P < 0.00001$). (B) Birds carrying magnets, mean bearing 357°, $r = 0.727$ (homeward oriented, $P < 0.00001$).

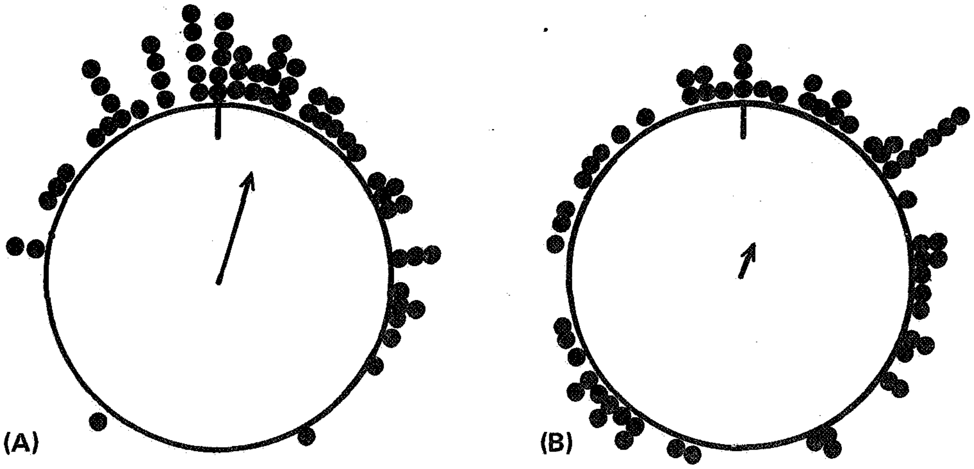

FIGURE 2. Pooled bearings from series III releases; experienced pigeons released under total overcast from distances of 27 to 50 km. Releases were from North and South; home bearings adjusted to 0°. (A) Birds carrying brass bars, mean bearing 17°, $r = 0.625$ (homeward oriented, $P < 0.00001$). (B) Birds carrying magnets, mean bearing 23°, $r = 0.211$ (homeward oriented, $P = 0.02$).

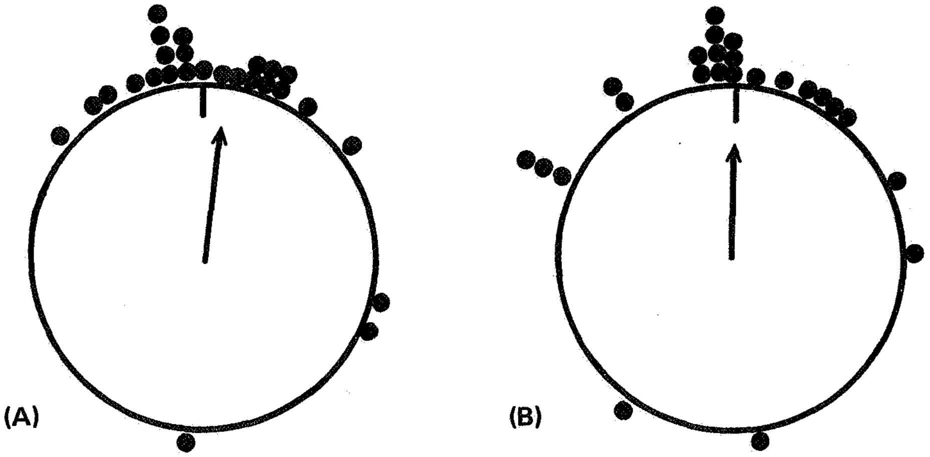

FIGURE 3. **Pooled bearings from series V releases; from 49.4 km South under total overcast; home bearing adjusted to 0°. (A) Birds that formerly wore bars, mean bearing 6°, r = 0.761 (homeward oriented, $P < 0.00001$). (B) Birds that formerly wore magnets, mean bearing 0°, r = 0.657 (homeward oriented, $P \leqq 0.00001$).**

each of the releases the former magnet-laden birds took significantly longer to vanish. Thus, contrary to our expectations, the magnet-laden birds had apparently learned, during training, whatever is necessary to enable them to orient homeward under total overcast at an unfamiliar release site, but apparently the experience of wearing the magnets had made them slower in choosing their bearings.

We now had to reconsider our earlier ideas about the effects of training. Accordingly, we decided to look closer at the orientation behavior of first-flight pigeons. First we conducted a series of test releases (our series VI) under Sun, using first-flight youngsters only about three months old. In all three tests of this series (conducted from 26.7 km north), the magnet-laden birds vanished randomly whereas the brass birds were oriented homeward. Figure 4 shows the pooled bearings for the three releases in this series; the birds carrying brasses are homeward oriented at $P<0.00001$, whereas the birds carrying magnets are random, $P = 0.40$ (Rayleigh test, $P = 0.77$). The difference in scatter is significant at $P < 0.005$.

Since we had already shown that first-flight pigeons require the Sun for orientation whereas experienced birds do not (ref. 59), and the results of the series VI tests seemed to indicate that first-flight pigeons also require magnetic cues whereas experienced birds do not (see series I above), it seemed to us that perhaps training has the effect of making pigeons sufficiently adept at homing so that they can orient with less information than they need on their first flight.

However, this formulation soon proved to be much too simple. A series of six test releases (our series VII) under Sun using older first-flight birds (8 to 9 mo old) yielded mixed results. In three of these tests, the birds carrying brasses were oriented homeward whereas the birds carrying magnets were not, thus agreeing with the results of series VI. But in two tests both groups were homeward oriented, and in one test both groups were random. Thus it appeared that in some cases first-flight birds are not both-

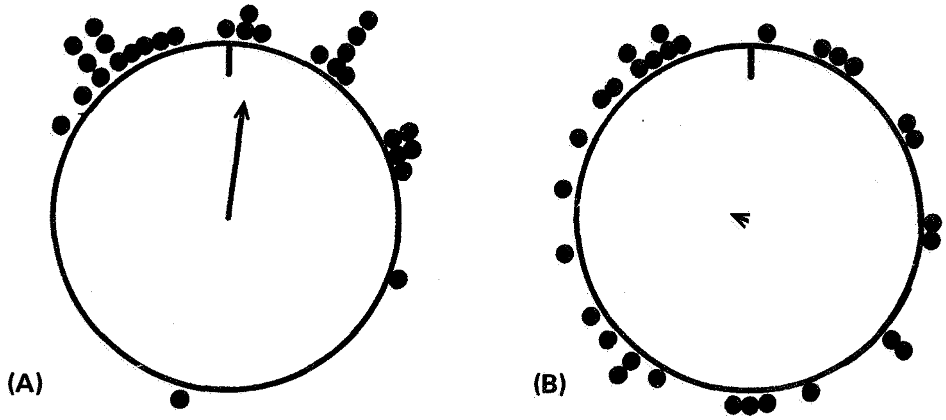

FIGURE 4. **Pooled bearings from series VI release; very young first-flight pigeons released under sunny conditions from 26.7 km North; home bearing adjusted to 0°; (A) Birds carrying brass bars, mean bearing 7°, r = 0.669 (homeward oriented $P < 0.00001$). (B) Birds carrying magnets, mean bearing 290°, r = 0.094 (not homeward oriented, $P = 0.40$).**

ered by magnets. Perhaps the greater maturity of the birds used in these tests is the reason, or perhaps it is the experience of more exercise flights at the loft.

Figure 5 shows the pooled bearings for the six releases in series VII. The birds carrying brasses are homeward oriented at $P <$ 0.00001, whereas the birds carrying magnets are not, $P = 0.14$ (Rayleigh test, $P =$ 0.24). One may question, however, whether the V test or Rayleigh test can legitimately be applied to the pooled bearings of the magnet birds, inasmuch as their distribution appears, on visual inspection, to be bimodal. The contrast between this distribution and that of the very young first-flight birds carrying magnets in the similar releases of series VI (fig. 4B) is striking, and raises the possibility that greater maturity has resulted in increased ability to detect the proper vector but that the magnets interfere with the choice of polarity.

Not only did the picture concerning first-flight birds become somewhat cloudy, but so did the picture concerning experienced birds released under Sun. The releases of series I had all been conducted at relatively short distances (27 to 50 km). When we conducted tests under Sun at greater distances, the results were different. One series of such tests (our series II) consisted of three releases from 84.5 km south, using experienced birds new to the site. In the first of these tests the magnet birds vanished randomly whereas the brass birds were homeward oriented (fig. 6A); the magnet birds also had significantly slower homing speeds. Although both groups of birds were homeward oriented in the second and third tests of this series (figs. 6B, 6C), the magnet-laden birds of both tests had significantly longer vanishing intervals, and the magnet-laden birds of the second test had significantly slower homing speeds.

In an attempt to determine whether magnets would cause a decrement in orientational or homing performance under Sun at comparable distances from directions other than south, we conducted two releases (our series VIII) from 73.5 km north, again using experienced birds, new to the site. In the first of these releases (fig. 7A), the brass-laden birds were homeward oriented ($P = 0.002$) whereas the magnet-laden birds were not ($P = 0.077$). In the second test (fig. 7B), both groups were homeward oriented ($P < 0.0001$ for each). In neither release was there a significant difference in vanishing intervals or homing speeds.

If we look at the releases of series II and VIII combined, we find that in four of the five tests the birds carrying magnets exhibited a poorer performance than the birds carrying brasses, in at least one of the three variables measured (orientation, vanishing interval, homing speed). This seems to suggest that at longer distances magnets can affect the behavior of experienced pigeons released under Sun, just as magnets often affect the performance of first-flight birds under Sun at shorter distances (see series VI and VII). This conclusion appears to be valid only for birds new to the release site, however, because in a series of eleven tests (our series IX) under Sun from the same release site used in series VIII (73.5 km north), magnets had no detectable effect on birds with prior experience at the site (fig. 8), i.e. in none of these tests was there a significant difference between controls and experimentals in orientation, vanishing intervals, or homing speed. We plan soon to conduct test releases at distances of 160 to 320 km to check on the general applicability of these generalizations concerning the effects of magnets and of prior experience at the release site.

Having found that magnets often affect the performance of first-flight birds under Sun, even at short distances, and having learned that magnets sometimes affect experienced birds under Sun at longer distances, we decided to perform a series of releases (our series X) under Sun using young birds prepared the same way as in series V (i.e., trained in flocks up to 16 km in all directions, while wearing permanently mounted magnets

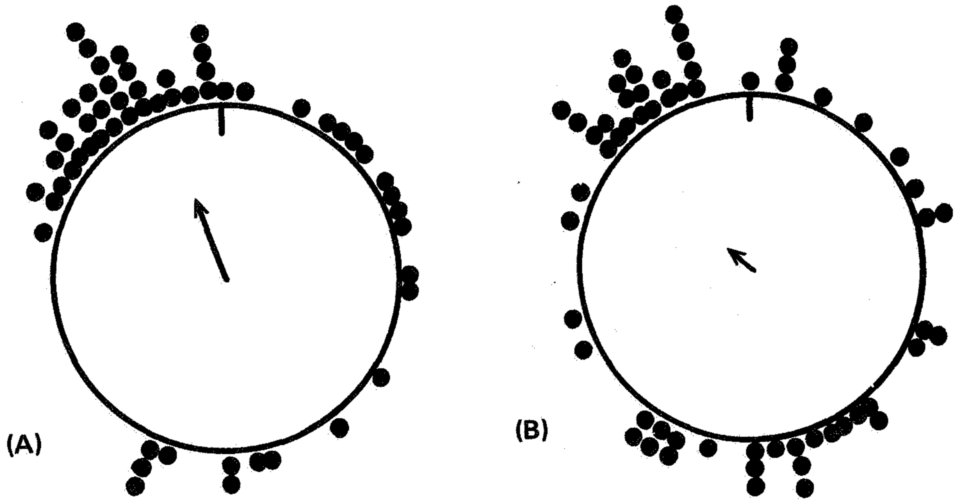

FIGURE 5. Pooled bearings from series VII releases; mature first-flight pigeons released under sunny conditions from distances of 27 to 50 km. Releases were from North and South; home bearings adjusted to 0°. (A) Birds carrying brass bars, mean bearing 340°, $r = 0.475$ (homeward oriented, $P < 0.00001$). (B) Birds carrying magnets, mean bearing 310°, $r = 0.155$ (not homeward oriented, $P = 0.14$).

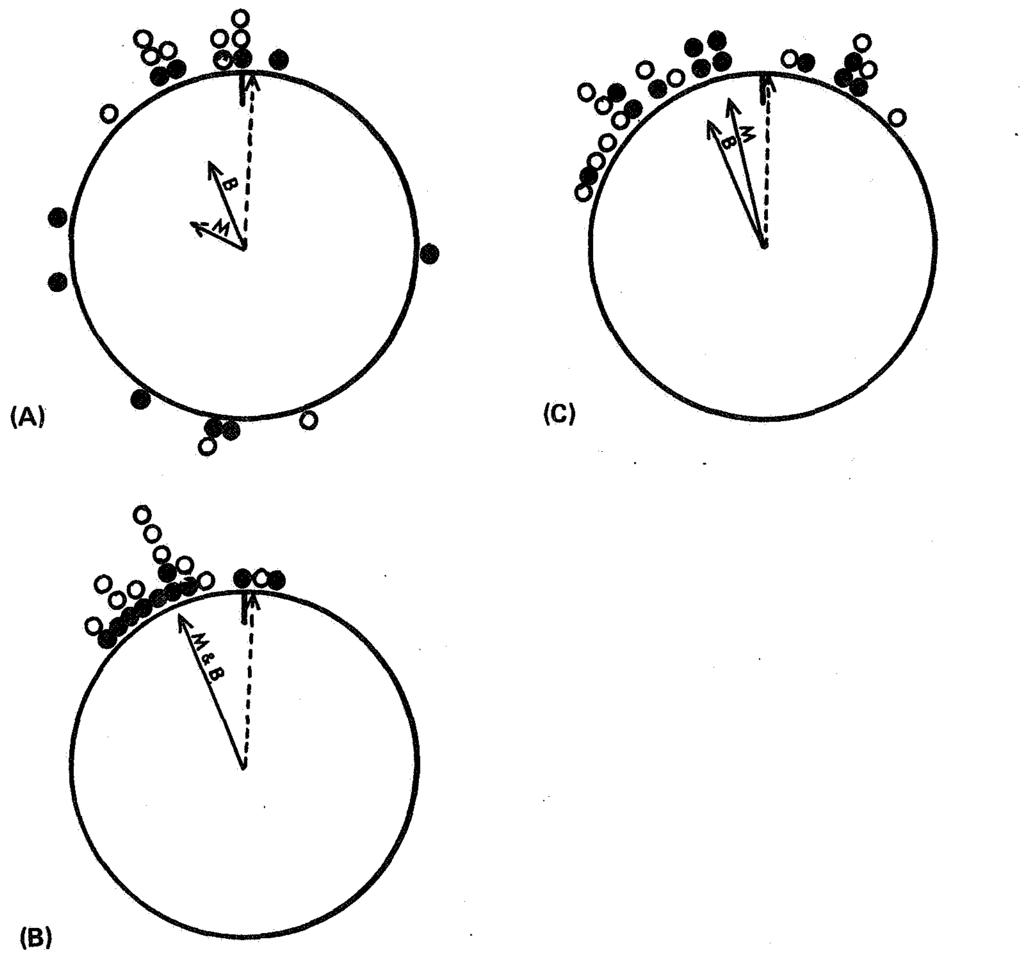

FIGURE 6. Series II releases; experienced pigeons, new to the site, released under sunny conditions from 84.5 km South. Home bearing (dashed arrow) is 3°; true North is indicated by short line at inner margin of top of circle. In figures 6 to 9, black symbols represent bearings of birds carrying magnets and open symbols represent bearings of birds carrying brass bars. (A) Release of May 20, 1970; mean bearing (B) of birds carrying brass bars, 341°, $r = 0.584$ (homeward oriented, $P = 0.009$); mean bearing (M) of birds carrying magnets, 291°, $r = 0.231$ (not homeward oriented, $P = 0.34$). (B) Release of May 21, 1970; mean bearing of brass birds, 337°, $r = 0.972$ (homeward oriented, $P < 0.0001$); mean bearing of magnet birds, 338°, $r = 0.960$ (homeward oriented, $P < 0.0001$). (C) Release of July 8, 1970; mean bearing of brass birds, 337°, $r = 0.780$ (homeward oriented, $P = 0.0005$); mean bearing of magnet birds, 350°, $r = 0.865$ (homeward oriented, $P < 0.0001$).

or brasses). All the tests in this series are being conducted from 73.5 km north. In some of these tests the magnets or brasses are taken off just before the birds are released, and in other tests the magnets and brasses are left on. In all tests performed so far, both

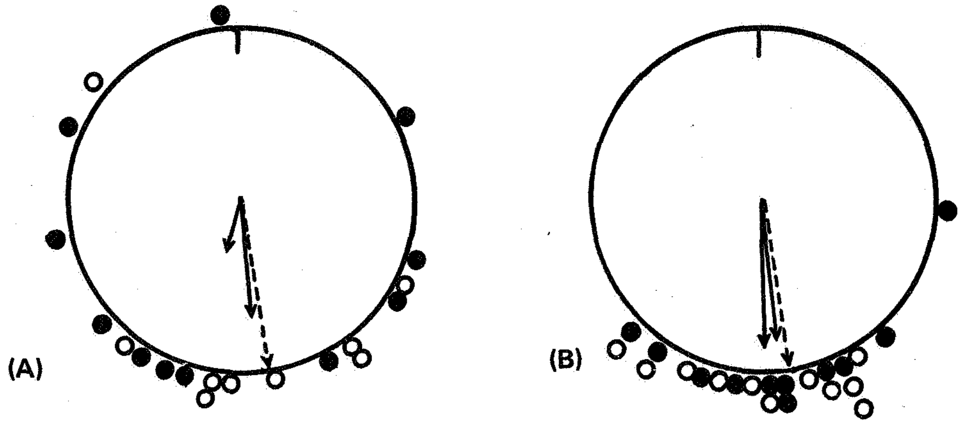

FIGURE 7. Series VIII releases; experienced pigeons, new to the site, released under sunny conditions from 73.5 km North. Home bearing (dashed arrow) is 173°. (A) Release of August 20, 1970; mean bearing of birds carrying brass bars, 177°, r = 0.691 (homeward oriented, $P = 0.002$); mean bearing of birds carrying magnets. 196°, r = 0.327 (not homeward oriented, $P = 0.08$). (B) Release of August 22, 1970; mean bearing of brass birds (longer arrow), 180°, r = 0.907 (homeward oriented, $P < 0.0001$); mean bearing of magnet birds (shorter arrow), 175°, r = 0.834 (homeward oriented, $P < 0.0001$).

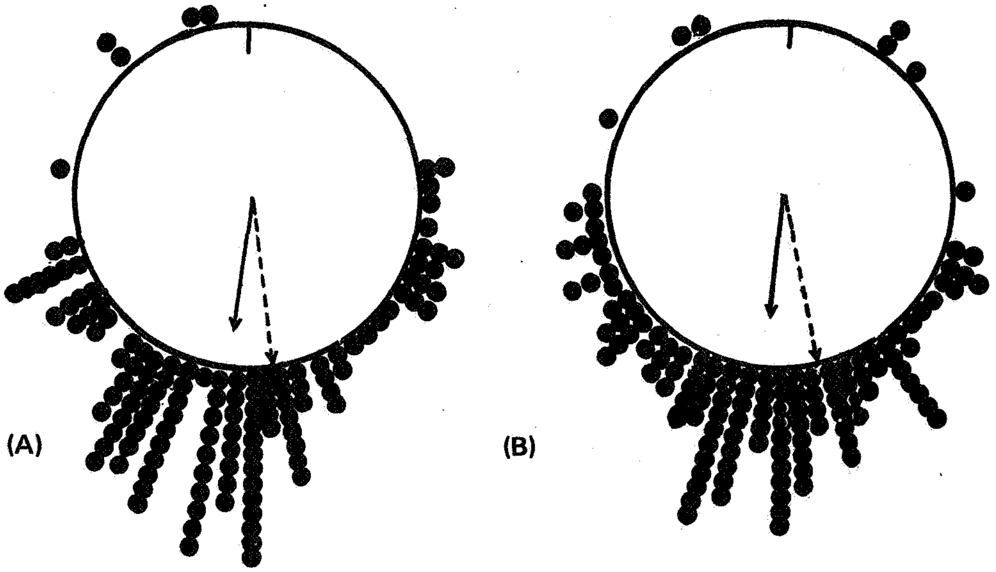

FIGURE 8. Pooled bearings from series IX releases; experienced pigeons, with prior experience at the site, released under sunny conditions from 73.5 km North. Home bearing (dashed arrow) is 173°. (A) Birds carrying brass bars, mean bearing 188°, r = 0.737 (homeward oriented, $P < 0.00001$). (B) Birds carrying magnets, mean bearing 191°, r = 0.721 (homeward oriented, $P < 0.00001$).

groups of birds have been homeward oriented, and in no case has there been a significant difference in vanishing intervals or homing speeds. Thus the apparent lengthening of vanishing intervals under overcast as a result of prior wearing of magnets, seen in series V, has not been found under Sun. Furthermore, the extensive experience of wearing magnets during short training flights may actually have made the birds better able to orient accurately while wearing magnets at distant unfamiliar sites; more tests, which we plan to conduct soon, should establish whether or not this tentative conclusion is true. Detailed data for this series will be published when all the tests have been completed.

Two other series of tests, recently begun, may be mentioned briefly. In the first of these, small circular magnets (1 cm diameter, 0.2 cm thick, 1 gram weight, field strength approximately 220 G) are glued to the top of the birds' heads; control birds wear brasses of the same size, shape, and weight. Figure 9 shows the bearings obtained in the first release in this series; the birds carrying brasses were homeward oriented ($P = 0.0002$), whereas the birds carrying magnets were not ($P = 0.12$).

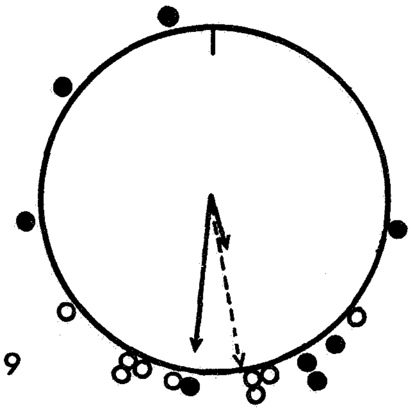

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FIGURE 9. Bearings from test using magnets glued to birds' heads. Experienced birds, new to the site, released under sunny conditions, September 6, 1970. Home bearing (dashed arrow), 173°; distance, 73.5 km. Mean bearing of birds carrying brass bars (longer solid arrow), 184°, r = 0.879 (homeward oriented, $P = 0.0002$). Mean bearing of birds carrying magnets (shorter solid arrow), 168°, r = 0.294 (not homeward oriented, $P = 0.12$).

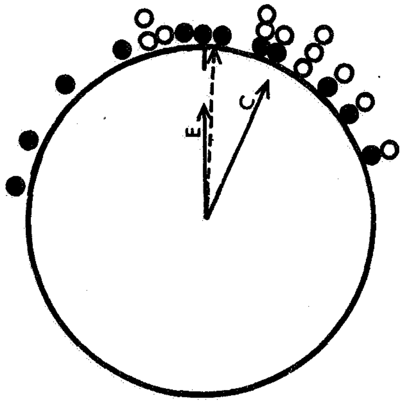

FIGURE 10. Bearings from test using birds wearing Walcott-type electromagnets. Experienced birds, new to the site, released under sunny conditions, August 20, 1970. Home bearing (dashed arrow), 3°; distance 84.5 km. Bearings of control birds wearing nonfunctioning electromagnets are represented by open symbols, bearings of experimental birds wearing functioning electromagnets by black symbols. Mean bearing (C) of control birds, 25°, r = 0.901 (homeward oriented, $P < 0.0001$). Mean bearing (E) of experimental birds, 1°, r = 0.723 (homeward oriented, $P = 0.0003$).

The second of these recently begun series is an attempt to repeat the tests using electromagnets reported in this volume by Walcott. Unfortunately, in the one such test we have performed so far (fig. 10), our results differed from those of Walcott; both the experimentals and the controls were homeward oriented and there was no significant difference in vanishing intervals or homing success. We plan much more tests as soon as we have redesigned the apparatus so as to cause less discomfort to the birds.

DISCUSSION OF RESULTS

Our test releases provide evidence that under certain conditions magnets can cause confusion to homing pigeons. If we consider only those tests in which the birds of one group were homeward oriented and the birds of the other group were not, we find that in all 13 such cases it was the brass-laden birds that were oriented and the magnet-laden birds that were not. The binomial probability (one-tailed) of getting such results by chance alone is only 0.0001. Similarly, in all five tests where there was a significant difference in homing speeds, it was the magnet-laden birds that were slower; the chance probability of this is 0.031. In all eight tests in which there was a significant difference in vanishing intervals, it was the magnet-laden birds that took longer; chance probability, 0.004. Or if we examine the results in another way, and consider all releases in which there was a significant difference between the two treatments in at least one of the three variables measured, we find 21 such releases, and in all cases it was the magnet-laden birds that exhibited the poorer performance; the chance probability of such results is considerably less than one in a million.

It seems unlikely that these results are due simply to some general disturbing effect of the magnets, since the effects of the magnets differ depending upon weather conditions, the previous training of the birds, and whether or not the birds have had prior experience at the release site. I think it more likely that the magnets have a direct effect on the orientational mechanisms used by the pigeons. It is important to point out, however, that our results do not provide direct proof that pigeons can use magnetic cues in homing, though that is of course one possible implication. Another possibility is that some component or components of the orientation system, important under certain conditions but not under others, fails to function properly in the presence of a magnetic field as strong as that imposed on the birds by the magnets we used. We hope soon to be able to evaluate these alternative possibilities.

For the sake of argument, the rest of this discussion will assume that the first of the two above-mentioned interpretations of our data is correct, i.e. that pigeons are capable of using magnetic cues as one component of their orientation system.

A first question that comes to mind is what might be the mechanism whereby a pigeon could detect magnetic cues. Unfortunately, no convincing answer is yet available. Both Yeagley (ref. 10) and Talkington (refs. 12 and 13) have hypothesized that a bird's movement through the Earth's magnetic field might result in an induced electromotive force, which might then be detected. However, even if one assumes an optimal situation (e.g. flight at 64 km per hr, with the cross-sectional area of the bird cutting the lines of magnetic force exactly at the perpendicular), the most optimistic estimate of the induced emf is on the order of 1 mV per cm; an estimate on the order of 1 μV per cm is probably more realistic for the required sensitivity of the bird's sensory apparatus if directional information is to be obtained. Not only is this an extremely small value, but its calculation disregards the point made by several authors (refs. 60 to 62) that the electric fields resulting from motion through a magnetic field cannot be distinguished from uniform static fields; since the electrostatic field of the Earth's atmosphere is on the order of 1 V per cm, but quite variable, it follows that it is exceedingly unlikely that a pigeon could detect, against this background, the minute superimposed voltage resulting from its movement through the Earth's magnetic field.

Another possibility was suggested by

Stewart in 1957 (ref. 63), but has been largely ignored (a hypothesis nearly identical to that of Stewart was suggested to me in February 1970, by Robert R. Capranica of Cornell University; at that time, neither Capranica nor I was aware of Stewart's paper). As a bird flies through the atmospheric electric field, an electrostatic field will build up on its surface, just as it does on an airplane. This makes the bird, in effect, a moving electric charge. Now, such a moving charge will be surrounded by its own magnetic field. The Earth's magnetic field and the magnetic field around the bird should then interact to produce a torque on the bird, which the bird might detect. However, even under the most optimistic assumptions, calculations indicate that the torque would be on the order of only 1 dyne.

It is therefore understandable that Stewart's hypothesis has been dismissed, since at first glance it would seem unlikely that a flying pigeon could distinguish so small a torque against a background of the numerous other torques it must be experiencing from wind and atmospheric turbulence. But there are at least two reasons why Stewart's hypothesis should receive some consideration here. First, it has recently been shown that feathers exhibit piezoelectric properties, twisting when exposed to electric stress, with the degree of twist proportional to the strength of the electrical excitation (ref. 64). Receptors in the feather sockets might measure this twist, thus enabling the bird to measure, indirectly, both the electrostatic field on its feathers and the surrounding magnetic field. Given this information, the potential for deriving information concerning the Earth's magnetic field from the torque experienced by the bird is considerably enhanced. Second, sensory physiology provides numerous examples to substantiate the generalization that organisms have evolved remarkable abilities to separate signals from noise whenever the signals have been really important to them. Therefore we should not be too hasty in dismissing hypotheses based on birds' detection of very weak signals.

Having given reasons for reconsidering Stewart's hypothesis, however, I must now say that, if birds can detect weak magnetic stimuli, it seems to me likely that the detection is based on some direct effect of the magnetic field on the sensory apparatus of the organism, rather than on an induced emf or the sort of indirect process discussed in the preceding paragraph. One possibility would be actual mechanical displacement of some structure, in the way that gravity causes displacement of the otoliths or vibrations cause displacement of the cilia of hair cells in the cochlea. In this regard, it is pointed out that the displacement necessary to result in a generator potential need not be great; in the cochlea, for example, movement of the cilium of a hair cell through a distance less than the diameter of a hydrogen atom is sufficient to initiate impulses in the auditory nerve fiber. However, mechanical displacement is not the only possible way in which magnetic fields might have a direct effect on some sensory apparatus; another possibility would be the alteration of molecules or atoms in sensory cells. This might be a molecular change similar to that produced by light in photoreceptors, or perhaps (to be even more daring) a nuclear magnetic resonance effect.

My intent here is not to espouse any one particular hypothesis for detection of magnetic fields, but simply to emphasize that if organisms can detect magnetic stimuli (and the paper by Lindauer in this symposium appears to add greatly to the probability that honeybees, at least, can do this), then the detection mechanisms for which we must seek may well involve processes different from those most frequently suggested in the past.

Magnetic stimuli differ considerably from most of the kinds of stimuli we normally think about; for example, there is no reason to assume that the receptors will be on or even near the surface of the body, since magnetic fields pass through the body. Thus the receptors could be anywhere inside the animal, for example in the brain itself.

However, even if future research conclusively demonstrates that pigeons use magnetic cues in orientation, it is my conviction that we will still be far from a complete understanding of the pigeon navigation system. It seems likely that magnetic cues, like the Sun compass and, perhaps, landmarks, constitute only one element in an exceedingly complex and redundant system. Witness the disturbing variability found in the results of the tests reported in this paper—until we can explain why magnets caused disorientation in some tests but not in others, even when weather conditions, prior experience of the birds, and all other readily apparent variables were held constant, we have a long way to go. Take, for example, the two releases shown in figures 6A and 6B. The field observers reported a strong subjective impression that the birds in the figure 6A test showed two quite different behavioral patterns—only two of the 10 brass-laden birds ever entered the southern half of the sky, whereas all of the 10 magnet-laden birds spent a major portion of their circling time in the southern sky. By contrast, in the test of figure 6B, the same observers had the impression that all the birds belonged to one behavioral group—no bird from either treatment entered the southern half of the sky, and most flew off toward home with no circling. Yet the birds used in these two tests were drawn at random from the same pen, were of the same age and breeding, and had had identical training. Furthermore, the two tests were conducted on consecutive days under what appeared to be nearly identical wind and weather conditions. Why, then, did the two tests yield such different results? I am led to the conclusion that in addition to Sun, landmarks, and perhaps magnetism there remain other important cues that we must discover before we can put the pieces together to produce a satisfying description of the pigeon navigation system.

As a further example of the sort of evidence that leads me to this conviction, let me mention briefly a clock-shift test (six hours fast) that we recently performed under sunny conditions. This release was from a site 33.5 km east of the loft, a site from which we had made more than 50 previous releases, with the mean bearings of normal birds always being well oriented homeward. Furthermore, we had conducted many previous clock-shift tests at this site under sunny conditions and had always obtained a homeward-directed mean vector for the control birds and a southward-directed mean vector for birds clock shifted six hours fast. Yet on this particular day the control birds vanished nonrandomly northward (353°) and the shifted birds westward (266°). In other words, the mean bearings of the two treatments differed by roughly 90° (actually 87°), as expected, but both means were rotated nearly 90° clockwise from the predicted directions. We could detect no odd conditions of wind or weather, and the *K* values reported by the government indicated no unusual magnetic activity that day. Yet something appeared to have rotated the navigational grid of our birds, affecting both treatments in the same manner so that they maintained the expected relationship to each other.

Though we do not yet know all the cues used by a navigating pigeon, we can begin to say something about the relative importance of the cues we do know. Numerous workers, among them my own group (ref. 54), have shown that clock-shifted pigeons released under Sun vanish at roughly the predicted angle relative to the controls even when released at sites from which they have flown many times before. Thus it seems established that the Sun compass is at a higher level in the hierarchy of cues than landmarks. Since our tests indicate that magnets have no effect (short distances) or only a small effect (long distances) on experienced pigeons released under Sun at unfamiliar sites, we can probably safely conclude that the Sun compass also ranks higher in the hierarchy of cues than magnetism. When the Sun-compass information and familiar landmarks are both available and are in agreement, magnets appear to have no disturbing effect on experienced birds even at long distances (fig. 8); in other words, Sun and landmark cues together can completely eliminate any effects of magnetic cues. We have so far conducted only a few tests using experienced pigeons carrying magnets released under total overcast at familiar sites, and cannot therefore make any final statement about the relative importance of familiar landmarks and magnetic cues; however, our tentative impression is that magnetic cues rank higher than familiar landmarks, at least at distances of 32 kilometers or more.

All of the above speculations about the hierarchy of cues in the pigeon navigation system apply only to experienced birds. The tests discussed in this paper, and others (not involving magnets) to be published elsewhere, suggest that the various cues interact in quite different ways in first-flight pigeons. Perhaps detailed comparisons of the orientational behavior of first-flight and experienced pigeons will help us discover additional cues or cue interactions, and will permit us someday to begin to see at least the outlines of a unifying theory to explain the intriguing mystery of pigeon homing.

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DISCUSSION

GALLER: Have you tried (1) comparing brass-laden birds with brass-laden birds and (2) using bar magnets on one set of birds and degaussed steel on the other set?

KEETON: (1) We have done brass versus brass, and also brass versus birds wearing nothing; there is no difference. In other words, the weight of the bars doesn't appear to cause any difficulties. In all the tests shown in the figures, the controls were wearing brass bars equivalent to the magnet bars in size and weight. However, our tests indicate that we could do just as well with control birds wearing nothing. (2) We have considered it, but have not yet done it. The use of the Helmholtz-coil technique (mentioned by Walcott) gives a more uniform field than just bar magnets. On the other hand, the coils introduce a great deal more abnormal behavior on the part of the bird, because the birds decidedly dislike the apparatus. We are trying to build coils that can be controlled from the ground by radio, so that we shall be able to turn them on or off or vary the field strength at will.

GRIFFIN: All of this recent evidence on magnetic effects is very impressive. But I am not sure about your last point, that new and not yet identified sensory channels must be involved. This appears to me a situation where the variables are not yet all controlled. But an uncontrolled variable does not necessarily mean a wholly new sensory modality.

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