

THE INITIAL ORIENTATION OF HOMING PIGEONS AT THE MAGNETIC EQUATOR: COMPASS MECHANISMS AND THE EFFECT OF APPLIED MAGNETS

BY RONALD RANVAUD¹, KLAUS SCHMIDT-KOENIG^{2,3},
JÖRG U. GANZHORN^{2,*}, JAKOB KIEPENHEUER^{2,†},
ODIVAL C. GASPAROTTO¹ AND LUIZ R. G. BRITTO¹

¹*Instituto de Ciências Biomédicas, USP, Sao Paulo, SP, Brasil,*

²*Beim Kupferhammer 8, 7400 Tübingen, Federal Republic of Germany and*

³*Department of Zoology, Duke University, Durham, NC 27706, USA*

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Summary

Homing pigeons are thought to use the earth's magnetic field for direction finding. Though the sensory system and the characteristics of the magnetic field used are unknown, it can be hypothesized that pigeons have an inclination compass, as do some migratory birds. When released at the magnetic equator, this inclination compass ought to be suspended. In addition, releasing pigeons when the sun is at or very close to the zenith renders the sun compass inoperational. However, released under these conditions, homing pigeons are not disorientated. Though they vanish on average in a different direction from pigeons released when the sun compass is available, they still show a directional preference close to magnetic north. This directional preference could be disrupted in some years by the application of magnets to the pigeons' back. In other years this treatment as well as another magnetic treatment did not produce any difference between experimental pigeons and controls. These results confirm once more that, if magnetic effects exist, they are of a rather discrete nature.

Introduction

Studies of homing pigeon orientation in the last half century have produced a number of concepts, hypotheses and controversies, without providing, however, a universally accepted outline of the essential physiological mechanisms at play. The map-and-compass idea of Kramer (1953) has survived to this day, almost exclusively because of the predictable and consistent results obtained with clock-shift experiments, which unequivocally demonstrate the use of the sun compass,

*To whom reprint requests should be sent.

†Present address: MPI Verhaltensphysiologie, 8130 Seewiesen, Federal Republic of Germany.

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when available, as the most basic known participant in the homing process (Schmidt-Koenig, 1990; Schmidt-Koenig *et al.* 1991). The successful orientation of pigeons under total overcast conditions has been explained in terms of a backup compass mechanism, which requires the detection of the geomagnetic field by the bird, and not in terms of a hypothesis that might compete with the map-and-compass idea. This seemed natural since empirical evidence for a magnetic compass in the orientation of migratory passerines had been gathered in several years' work by Merkel and Fromme (1958) and Wiltschko (e.g. Wiltschko, 1968, 1973; Wiltschko and Wiltschko, 1972, 1988, 1990), and its applicability to the case of pigeons was suggested by the results of Walcott and Green (1974), by and large confirmed by Visalberghi and Alleva (1979). A very curious feature of the magnetic compass mechanism, as described in the literature, is the observation that the biophysics and/or the neural circuitry responsible for transduction and decoding of magnetic stimuli lead to no change in orientation behaviour when the polarity of the magnetic field is inverted. An inversion in the choice of the direction of orientation occurs when the *inclination* of the magnetic field is inverted, an effect obtained by inverting either the horizontal or the vertical component of the field, but not both. No physiological receptor adapted to magnetic field detection is known in birds, even if much speculation has appeared in the literature, especially in connection with reports some years ago of magnetic particles in the head of pigeons (Walcott *et al.* 1979; Walcott *et al.* 1988). Furthermore, conditioning of pigeons and other birds to magnetic stimuli in the laboratory has been unsuccessful until now (see papers headed by Griffin, 1987). Only recent positive results obtained with unconditioned responses by Quentmeier (1989) appear to be a promising means of establishing and studying the physiological relevance of magnetic fields in the laboratory in a non-migratory, non-homing context.

The map conceived by Kramer has been the subject of much speculation. Olfactory cues and their gradients, associated with wind directions, have been proposed as the physiological substrate for the map (Papi *et al.* 1972, 1973; Wallraff, 1980). Other proposals have involved geomagnetic variables (Lednor and Walcott, 1988) and infrasound (Kreithen and Quine, 1981). One difficulty with these hypotheses is that, where the empirical experimental evidence appears perhaps more compelling (e.g. olfaction compared to infrasound), it is difficult to demonstrate that the geophysical substrate possesses the structure necessary for the purpose of composing a map. Where there is no doubt that the ambient variable has the properties required to provide map information (geomagnetic field), the experimental evidence in its favour is lacking.

With all this in mind we designed a series of experiments in which, through the choice of geographic location, time of year and hour of day we could test several of the ideas discussed above under conditions not previously investigated.

Considering the characteristics of the magnetic compass proposed by Wiltschko, it is clear that, if the ambient geomagnetic field is horizontal, the mechanism should fail, at least in part, and the birds would not have a functioning magnetic

backup in case the sun compass were to be removed. Such a horizontal ambient field occurs on the magnetic equator, and our choice of release sites fell on this region, in the northeast of Brazil. There, because of the proximity of the geographic equator, the sun culminates in or very near the zenith twice each year, around the equinoxes. When this occurs near midday the sun compass is temporarily suspended. It is then possible to observe, in the course of a single day, the orientation of pigeons deprived or not of the sun compass, by releasing the birds around noon or at other times of day, respectively. An additional feature of the proximity of the geographic equator is that the wind pattern in the region is rather special. The direction of the wind is almost perfectly constant throughout the year and wind speeds are on average rather high (trade wind phenomenon). This means that wind-borne information of an olfactory nature, potentially useful in constructing a map, could in all probability only be transmitted in one direction, towards the west-northwest, and concomitant gradients could develop, by wind transport, also exclusively in a restricted range of directions. Though this could furnish one rather stable grid component of the map, it should severely restrict the map mechanisms associated with atmospheric odours. The exact consequences of the trade winds cannot be quantified at present because of the lack of realistic models or accurate descriptions of the olfactory mechanisms purportedly involved. Nevertheless, the constancy of the wind direction provides an ambient cue that would certainly be available, in principle, for compass purposes. These, as well as effects associated with magnetic fields, are considered in the present paper.

In previous reports of data gathered in 1982, 1983 and 1984 (Ranvaud *et al.* 1983, 1986, 1988), the orientation of birds released in the morning and in the afternoon was described and contrasted with the behaviour of the birds at midday. Untreated controls in the morning and in the afternoon consistently showed a strong deviation to the left of home (about 80°), a finding that also occurred in the following years (1986 and 1988). According to the map-and-compass hypothesis if at noon the birds were deprived of all compass mechanisms, they would be predicted to depart randomly. Under the experimental conditions, both known compass mechanisms are inactivated at midday, but, contrary to expectation, birds released with the sun near the zenith were highly directed. Their mean vanishing bearings, however, were very close to magnetic north, a full 135° to the left of home, or about 55° to the left of that of morning or afternoon birds (Watson U^2 -test: $P < 0.001$; Ranvaud *et al.* 1988). Again this result held true every year in which experiments were performed. The implication of this result is that, when the sun is only a few degrees from the zenith, there is, at the magnetic equator, indeed no backup mechanism that allows the birds to orient the way they do in the presence of the sun compass. This is consistent with the supposition that no viable compass mechanism exists in the experimental region, beside the well-known two. The direction from which the wind is blowing, at noon as at all other times, in spite of being practically constant, is not apparently useful for maintaining the initial orientation of the pigeons in the absence of the sun compass. Otherwise pigeons should be able to maintain similar directions when the sun is at or close to the

zenith as they do when their sun compass is operational. Something, however, is providing a directional reference to the noon pigeons, since their orientation is highly non-random and they are not passively drifting downwind. Since more than one release site was used, with almost identical results, this orienting factor was not a restricted site-specific variable. Either the noon pigeons follow, for some reason, a broad regional cue unrelated to the home direction, or they are misled in their estimate of the home direction by some backup cue, different from the sun or the magnetic inclination compass. This hypothetical backup cue might not be a compass at all, or it could be a compass that is miscalibrated by about 55° .

To determine if some kind of magnetic cue might be involved in the orientation of our pigeons, in spite of the horizontal ambient magnetic field, magnets were applied to the birds. In 1983 strong magnets were applied to the head of experimental animals, and in 1984 and 1986 to their back, always just prior to release (following Keeton, 1971, 1972). This was done in the hope of masking ambient magnetic cues, thus altering the behaviour of the birds, if indeed orientation was based on magnetism at all. As previously reported, the pooled data of 1983 and 1984, with different magnets, showed a statistically significant effect (Watson U^2 -test: $P < 0.01$) on the noon pigeons in two out of three release sites, and a much smaller, non-significant ($P > 0.05$) effect on pigeons that had a functioning sun compass at their disposal (Ranvaud *et al.* 1988). So it seemed that again some geomagnetic cue was at work in orienting the pigeons, but now at release sites on the magnetic equator. If this could be confirmed, it would lend strength to the supposition that geomagnetic information participates in something other than a dip compass type mechanism, as suggested by Keeton (1974). Later data (1986), however, did not confirm these findings, and pooled 1983, 1984 and 1986 data no longer show statistical significance for effects associated with the application of strong magnets for pigeons released at any time of day, even though experimental pigeons show somewhat more scatter than controls.

In 1988 the magnetic treatment was quite different. Rather than using magnets to attempt to disrupt the northward flight of the pigeons released around noon, the experimental design was aimed, on the contrary, at providing the birds with a functioning inclination compass such as that described by Wiltschko. The basic idea was to reproduce chronically the geometrical configuration of Walcott and Green (1974), by applying weak circular magnets to the head of the pigeons. These magnets produced a field of earth strength at a distance of 1 cm along the axis, so that a purely vertical artificial component would be added to the earth's horizontal field; the resultant field through the head of the pigeon would then have an inclination of about 45° and would be similar to the geomagnetic situation prevalent in temperate latitudes. The magnets were applied to the birds approximately 2 weeks prior to transportation to the release site, during which time they had free flight around the loft, so as to become accustomed to the magnets and to the inclined magnetic field through their heads. At the loft, about 300 km away from the release sites, the geomagnetic field had an inclination of about -8° in 1988 (magnetic southern hemisphere). Because of the small value of the

inclination, the pigeons wearing magnets at the loft would be exposed, perhaps for the first time in their life, to conditions that permit the use of an inclination Wiltschko-type compass, and would have the opportunity to incorporate it into their loft-based navigational data bank. In order better to discriminate effects that these weak magnets might have, in half of the experimental pigeons the magnets were left unchanged at the release site, but in the other half the magnets were reversed just prior to release, so as to invert the estimated north direction by 180° . Thus, if the experimental manipulation were effective in providing the birds with an inclination magnetic compass, those animals whose magnet had been unaltered should show an orientation under the midday sun similar to that of the morning or afternoon birds, whereas the others, whose magnet had been turned upside-down just prior to release, should vanish close to the opposite direction. If for any reason the experimental procedure failed to provide the pigeons with a viable magnetic inclination compass, the magnets would, in any case, modify magnetic cues available to the birds, so that some nonspecific perturbing effect might be expected in their orientation, as with strong magnets.

Materials and methods

Pigeons *Columba livia* L. raised and trained around Fortaleza, Ceará, Brazil ($\lambda=38^\circ30'W$, $\phi=3^\circ52'S$), were individually released from three sites at the magnetic equator close to Granja, near the northern coast of Brazil ($\lambda=40^\circ51'W$, $\phi=3^\circ00'S$). Home is about 300 km from the release sites at about 115° east of geographic north. Owing to logistical constraints, pigeons were housed for up to about 1 week at Camocim (26 km north of Granja) prior to release. The experimental procedure upon release has been described (Ranvaud *et al.* 1983, 1986, 1988). Statistical analyses were performed according to Batschelet (1981).

The experiments reported here were carried out between 1983 and 1988 from 22 September to 10 October, always in the period during which sun culmination occurs within 3.5° of the zenith. Pigeons were released under clear skies. A steady wind was blowing at $2-7\text{ m s}^{-1}$ from the east, shifting to north-east owing to an on-shore wind building up during the day. Pigeons were released in the morning (09:30–10:00 h local time; local time is GMT -3 h), around noon (11:15–11:45 h) or in the afternoon (13:00–13:30 h). In the morning and in the afternoon, sun elevations were about $60-67.5^\circ$. Under these conditions the pigeons used their sun compass for direction finding (Ranvaud *et al.* 1988; Schmidt-Koenig *et al.* 1991). These two groups have been combined for the present analysis and termed the non-noon (NN) group. Pigeons released around noon (sun altitude $>84^\circ$; sun culmination occurred at about 11:30 h local time) were assumed not to have a sun compass available. This group is called the high-noon (HN) group.

The geomagnetic field was strictly horizontal only for the first year (1983). Though actual measurements at the release sites are lacking, the inclination was of the order of 3° in 1988 (Peddie, 1982). Since there seems to be no difference between the behaviour of control pigeons as the years go by, it appears that we can

set a lower limit of at least 3° in the inclination necessary for geomagnetic equator conditions to hold in our experimental set-up.

Strong magnets

In 1983 small round magnets (diameter 5 mm; height 2 mm; mass 0.4 g) were attached to the head of experimental pigeons. At 1 cm distance these magnets produced an artificial field that is about twenty times as strong as the earth's magnetic field. At 2 cm distance their strength amounts to about twice the strength of the geomagnetic field.

In 1984 and 1986 we glued bar magnets (diameter 2 mm; length 25 mm; mass 1.5 g) to the back of the pigeons, following the procedure outlined by Keeton (1971). These bar magnets glued to the back produced an artificial field of about the strength of the earth's magnetic field at the head of the pigeon (Ranvaud *et al.* 1986). Magnets were provided by Permag GmbH, Planegg, FRG.

Weak magnets

For reasons outlined in the Introduction, we attached disks (diameter 20 mm) of weak magnetic foil with Velcro on the head of the experimental pigeons in 1988. The magnetic foil was glued between two layers of Velcro and produced a field of about local geomagnetic strength at a distance of 1 cm. This allowed reversal of the magnets prior to release. With the head in a resting position, the applied magnets were as nearly horizontal as could be achieved by eye. The weak magnets did not provide a homogeneous field across the head of the pigeon. They should, however, have added a nearly pure vertical component to the existing horizontal magnetic field of the earth, resulting in a total field inclined at about 45° . This treatment was meant to provide the pigeons with the possibility of acquiring and using a Wiltschko-type inclination compass. In half of these pigeons, the weak magnets were inverted just prior to release [group I (=inverted)]. They would then be in a situation similar to Walcott's SUP birds, with the 'poleward direction' towards magnetic north. In the other half, the magnets stayed as they had been applied some weeks before at the loft [group D (=direct)], in an NUP configuration, with the 'poleward direction' towards magnetic south. If the birds at the loft were sensitive to the 8° inclination of the local geomagnetic field, the 'poleward direction' for them would be magnetic south also.

Controls

Controls in 1988 had, like those in 1983, cardboard or copper weights glued to their head so as to subject the birds to as many of the manipulations applied to experimental pigeons as possible without, however, introducing any magnetic perturbation. Controls in 1984 and in 1986 were untreated, not carrying any sharp magnets.

Results

Control groups

Fig. 1A,B shows the bearings of control pigeons released in 1983, 1984 and 1986, either with (NN group) or without (HN group) the sun compass at their disposal. The data of 1983 involve a small number of pigeons and are distinguished from those of 1984 and 1986 because the experimental treatment was different in 1983 (small disk magnets on the head rather than bar magnets on the back). Also, one of the two release sites of 1983 could not be used in following years, because of the growth of vegetation that completely hid the horizon, and was substituted by another with much better visibility. The data obtained with control pigeons in 1986, not previously reported, were consistent with the results of previous years. The differences between corresponding groups in different years do not appear to be significant when comparisons are made using the Watson U^2 -test ($P > 0.50$). The coincidence of the mean direction of HN birds with magnetic north, previously reported, is still present in the sense that magnetic north is included in the confidence interval of the data at a 95 % level ($C_{95\%}$) in all years ($C_{95\%} = \pm 40^\circ$, $\pm 35^\circ$ and $\pm 38^\circ$, *versus* deviations of 23° , 4° and 38° , all to the left of magnetic north, for the years 1983, 1984 and 1986, respectively). When data from all three years are pooled, the deviation left of magnetic north of HN pigeons is 18° and $C_{95\%} = \pm 25^\circ$. The difference between the HN and NN groups is highly significant (Watson U^2 -test: $P < 0.001$), and results for both groups are far from random (Rayleigh test: $P < 0.001$).

The results for control groups of 1988 are shown in Fig. 2A,B. Again there is compatibility of behaviour of these controls with controls of previous years. No difference can be detected between the vanishing bearings of Fig. 1A,B and corresponding ones of Fig. 2A,B by applying the Watson U^2 -test ($P > 0.50$). The HN birds carrying sham magnets show a mean vanishing bearing 3° to the right of magnetic north, 50° to the left of NN birds, and both sets of results are non-random (Rayleigh test: $P < 0.01$). The 1988 NN and HN mean directions correspond closely with values of previous years (14° and 21° , respectively, to the right of pooled data from 1983, 1984 and 1986), but the difference between NN and HN groups in 1988 is not significant (Watson U^2 -test: $P = 0.17$), probably because of the relatively small sample sizes.

Experimental groups

Strong magnets: overall results

The vanishing bearings of pigeons carrying strong magnets either on their head (1983 data) or on their back (1984 and 1986) are shown in Fig. 1C,D. Results for both NN and HN data, pooling the 3 years, are significantly non-random (Rayleigh test: $P = 0.001$ and $P = 0.002$, respectively) and significantly different from each other (Watson U^2 -test: $P = 0.025$). Visual comparison of these circular diagrams with the equivalent controls (Fig. 1A,B) shows a larger scatter, but little if any difference in mean vanishing directions. Pooling data for the three years and

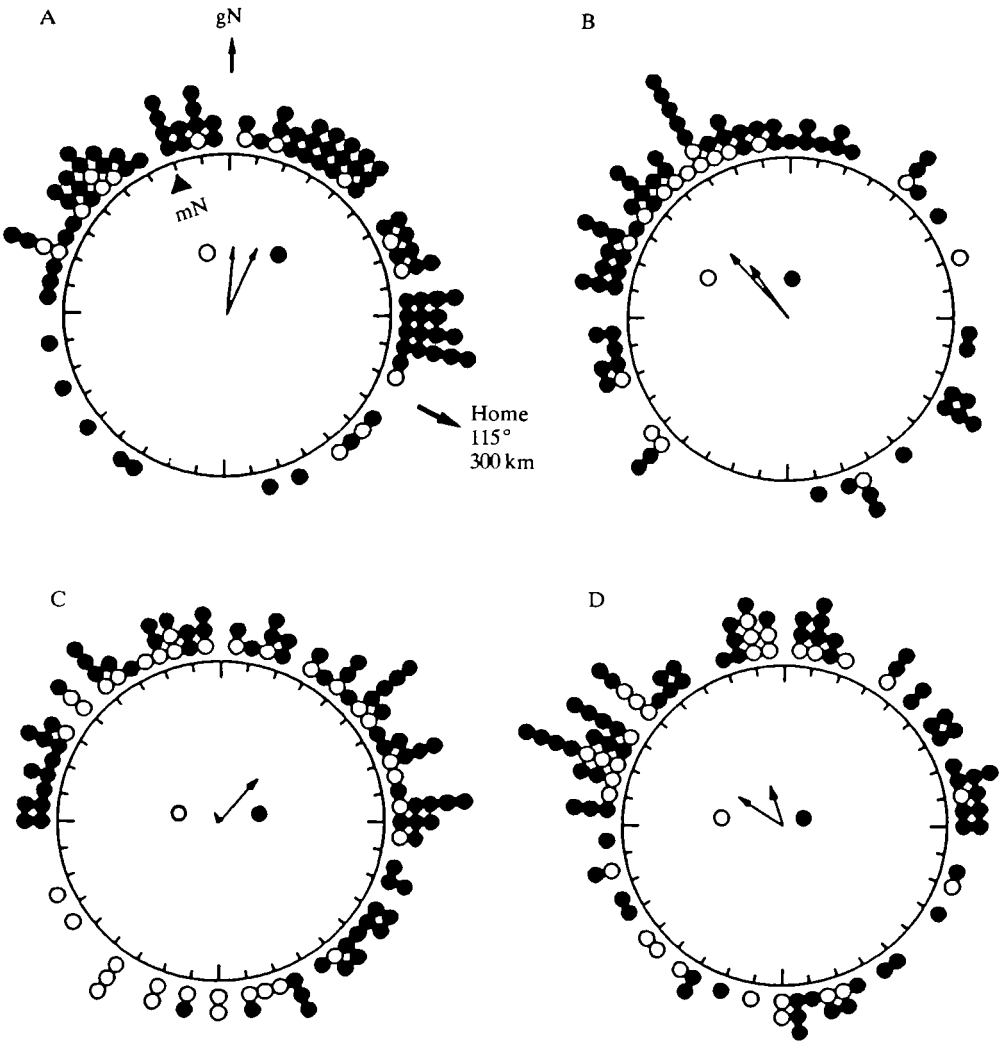


Fig. 1. Initial orientation of control pigeons (A,B) and pigeons carrying strong magnets (C,D). Geographic north (gN) is up, magnetic north (mN) is 20° to the left of geographic north. a , α , N are length, direction and sample size, respectively, of the mean vector of vanishing bearings pooled with respect to geographic north. (A) Non-noon (NN) controls. Data of 1983 (○), $\alpha=3^\circ$, $a=0.41$, $N=15$; data of 1984+1986 (●), $\alpha=22^\circ$, $a=0.44$, $N=83$; pooled data, $\alpha=19^\circ$, $a=0.43$, $N=98$. (B) High-noon (HN) controls. Data of 1983 (○), $\alpha=317^\circ$, $a=0.55$, $N=16$; data of 1984 and 1986 (●), $\alpha=323^\circ$, $a=0.41$, $N=63$; pooled data, $\alpha=322^\circ$, $a=0.44$, $N=79$. (C) NN experimentals, carrying strong magnets. Data of 1983 (○), $\alpha=330^\circ$, $a=0.05$, $N=34$; data of 1984 and 1986 (●), $\alpha=42^\circ$, $a=0.35$, $N=73$; pooled data, $\alpha=39^\circ$, $a=0.24$, $N=107$. (D) HN experimentals, carrying strong magnets. Data of 1983 (○), $\alpha=302^\circ$, $a=0.33$, $N=29$; data of 1984 and 1986 (●), $\alpha=342^\circ$, $a=0.25$, $N=71$; pooled data, $\alpha=328^\circ$, $a=0.26$, $N=100$.

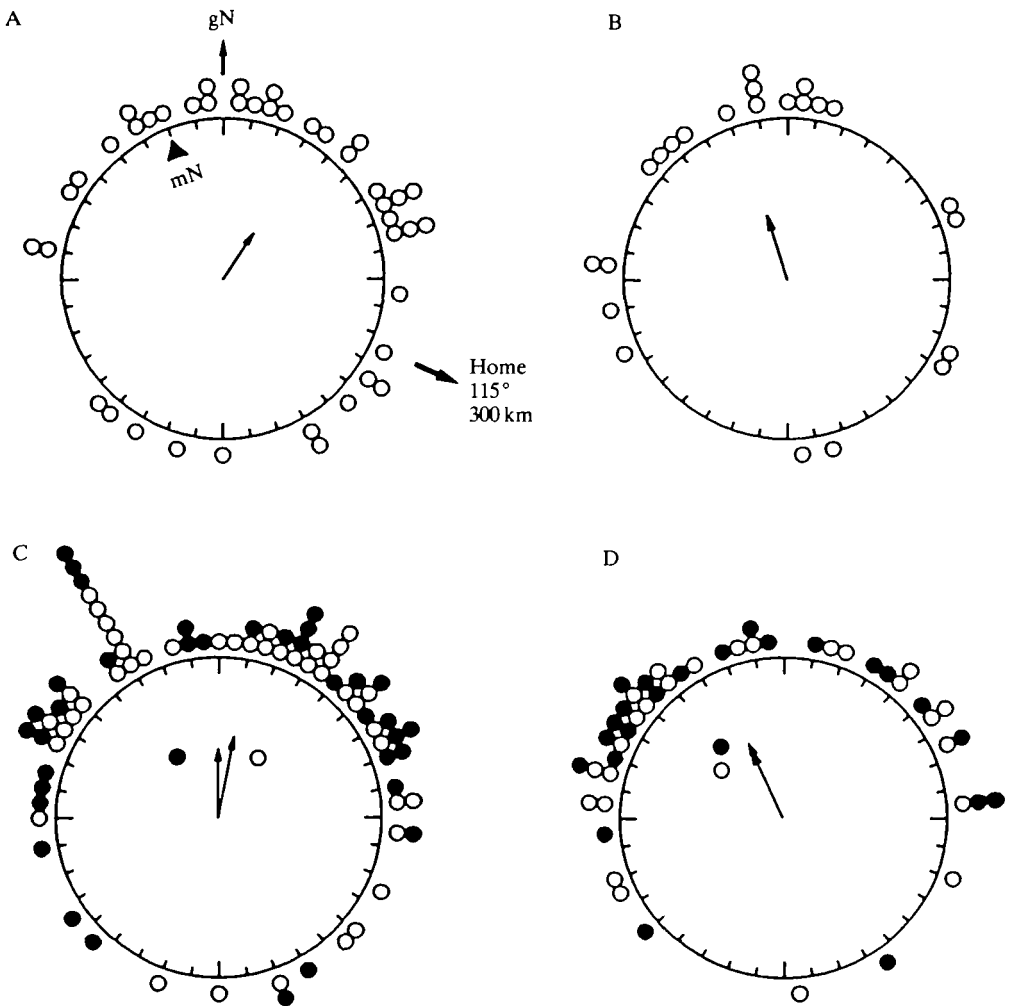


Fig. 2. Initial orientation of control pigeons (A,B) and pigeons carrying large weak magnets (C,D). For further explanation see Fig. 1. (A) NN controls, $\alpha=33^\circ$, $a=0.34$, $N=42$; (B) HN controls, $\alpha=343^\circ$, $a=0.42$, $N=23$; (C) NN experimentals, carrying weak magnets. Group D ('direct' magnets) (○), $\alpha=11^\circ$, $a=0.50$, $N=43$; group I ('inverted' magnets) (●), $\alpha=360^\circ$, $a=0.43$, $N=36$; D+I, $\alpha=6^\circ$, $a=0.47$, $N=79$. (D) HN experimentals, carrying weak magnets. Group D ('direct' magnets) (○), $\alpha=335^\circ$, $a=0.45$, $N=25$; group I ('inverted' magnets) (●), $\alpha=335^\circ$, $a=0.52$, $N=23$; D+I, $\alpha=335^\circ$, $a=0.48$, $N=48$.

applying the Watson U^2 -test, a significance level of only $P=0.095$ is observed comparing HN controls with HN experimentals, and $P=0.17$ for NN birds. Addition of the 1986 data to the results of previous years, presented in Ranvaud *et al.* (1988), decreases the statistical difference between HN controls and experimentals, as measured by the Watson U^2 -test, from a highly significant level ($P<0.006$) to an unacceptable one ($P=0.095$). The difference between experimen-

tals and controls is also decreased in the case of NN birds ($P=0.07$ to $P=0.17$). The 1986 data thus do not confirm the indications of previous years that magnetic cues might be involved in the orientation of pigeons under the experimental conditions described above. If magnetic effects exist, they do not manifest themselves on a reproducible basis.

Strong magnets: details

It is important to note that on some occasions the application of magnets produced an apparently large effect. The 1983 non-noon data in Fig. 1C show a very small mean vector. This result, however, is a consequence of an inexplicably anomalous behaviour at one of the release sites, where NN bearings are inverted relative to the mean direction at the same site the previous year and at both other sites for all years. In fact the 1983 data of Fig. 1C are bimodal. Fig. 3A–D shows the results of 1984, in which it is seen that the magnets have a strong scattering effect on high-noon birds (Rayleigh test applied to controls and experimentals: $P=0.002$ and 0.48 , respectively; Watson U^2 -test: $P=0.055$). In comparison, NN pigeons are almost unaffected (Rayleigh test: $P=0.001$ and 0.011 , respectively), both of these effects being present at both release sites.

Weak magnets

The data obtained by releasing pigeons with the large weak magnets glued to their head so as to provide them with conditions for an inclination-type compass mechanism, such as that described by Wiltschko, are shown in Fig. 2C,D. The most striking characteristic of these data is that there is no difference in the mean vanishing directions of HN (Fig. 2D) birds released with the magnet untouched (D group) and those whose magnet was inverted (I group) just prior to release. Both vanished highly non-randomly (Rayleigh test: $P=0.002$ for both) 5° and 8° to the left of magnetic north and of controls, respectively. Neither of these two experimental groups is different from controls (Watson U^2 -test: $P=0.50$). There is also no significant effect of the experimental treatment on the NN pigeons released with a functioning sun compass (Fig. 2C). D and I groups differ by 11° in their mean direction, but the Watson U^2 -test ascribes a level of significance above $P=0.05$ to differences between them as well as in relation to controls. Pooled experimentals are deflected about 27° to the left of controls but application of the Watson U^2 -test fails to demonstrate any difference between controls and pigeons carrying magnets of either type ($P>0.05$). There is thus no evidence of any effect on the orientation of our pigeons due to the application of the weak large magnets either with inversion or not, at any time of day.

Discussion

The data obtained with control pigeons in five separate series of releases between 1982 and 1988 are all consistent and indicate that control pigeons released on the magnetic equator, at three sites in the region between Camocim and

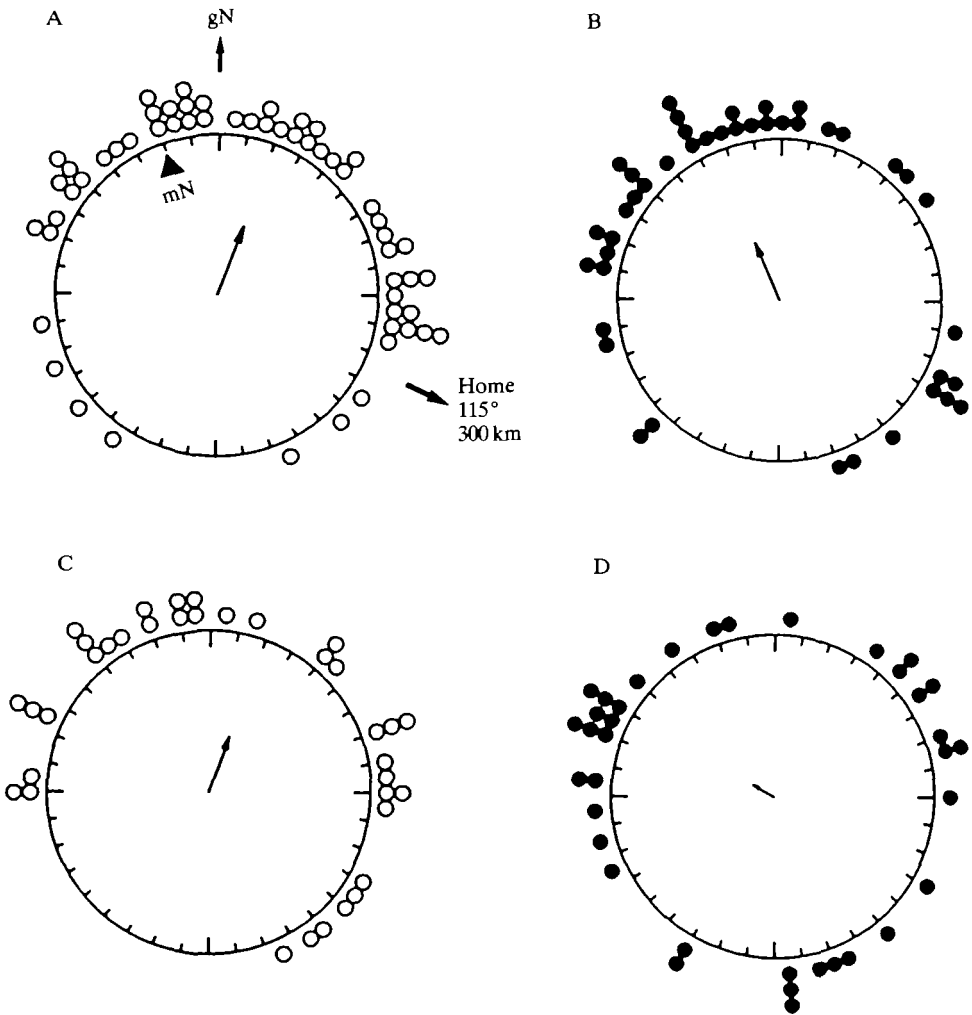


Fig. 3. Indication of an effect (Watson U^2 -test: $P=0.055$) of strong magnets observed sporadically under high-noon conditions; initial orientation of control pigeons (A,B) and pigeons carrying strong magnets (C,D) in 1984. For further explanation see Fig. 1. (A) NN controls, $\alpha=21^\circ$, $a=0.46$, $N=57$; (B) HN controls, $\alpha=336^\circ$, $a=0.39$, $N=43$; (C) NN experimentals, $\alpha=19^\circ$, $a=0.36$, $N=36$; (D) HN experimentals, $\alpha=299^\circ$, $a=0.14$, $N=37$.

Granja, 300 km west-northwest of their lofts in Fortaleza (Ceará, Brazil), orient about 70° – 90° to the left of home when the sun compass is available, but vanish in a direction close to magnetic north, a further 60° to the left, when the sun provides no directional cues during its zenith passage. The bias to the left of home shown by control birds, released when the sun compass is available, is no larger than that often observed in the initial orientation of pigeons, and has no satisfactory explanation.

Concerning the tendency of control pigeons released with the sun near the zenith to fly towards magnetic north, it is difficult to argue against the supposition that it is due to local characteristics or to some other non-specific effect. Until this can be demonstrated, however, it is interesting to speculate on alternative mechanisms that might explain more constructively the behaviour observed. In terms of the map-and-compass model it could be thought that some form of compass is available to the noon birds, but biased 60° to the left of the conventional sun compass. Only three compass mechanisms have been described in the literature, and all three should be unavailable to the noon birds. The magnetic inclination compass reported to guide the *Zugunruhe* of migratory birds fails in a horizontal magnetic field (Wiltschko and Wiltschko, 1972, Fig. 1e). The random orientation observed by Wiltschko in laboratory magnetic equator conditions, however, might be a bimodal distribution with a rather large scatter. According to present evidence, the magnetic inclination compass mechanism at the magnetic equator might indicate to the birds the north-south axis without telling them which is south and which is north, since the angle of inclination is equal (and zero) both for a northward and for a southward path. Under such circumstances, it might be expected that the noon birds would show a bimodal distribution, with an axis not very different from the mean directions of non-noon birds. If the north-south axis indicated by the magnetic compass were in disagreement with the indication of north provided by the sun compass, a bimodal distribution with an axis different from the mean direction of non-noon birds should be apparent; or the result might be randomness. But the essentially unimodal orientation observed cannot be explained by any reasonable modification of the Wiltschko mechanism.

The sun compass might be completely eliminated only for birds released in the middle of the noon release window when the sun is within some small angle of the zenith, but it is not clear how this would result in the observed behaviour. What might be reasonably expected is that noon birds would show a much larger scatter than NN birds, but the orientation direction should remain approximately the same. Neither prediction is verified. The third compass mechanism described in the literature depends on the visibility of stars and can hardly be thought to give rise to the northward tendency of our noon birds.

Some undescribed compass mechanism might be at work in our experimental conditions. The direction from which the wind blows, for example, is certainly available to the birds day and night as an indication of a fixed cardinal direction which could, in principle, be used for compass purposes. From an evolutionary point of view, this ambient condition is sufficiently rare to allow speculation about the existence of such an 'Aeolic compass' only for species that evolved in the trade-wind or similar regions of the world. Nonetheless, much has been said about the importance of wind-borne odours and the association by the pigeon of such odours with the directions from which the winds that bring them blow. It is permissible to speculate that the birds bred in Fortaleza would associate the wind direction with constant cardinal direction. This mechanism could guide the pigeons well under

noon conditions, but would lead them 60° to the left of non-noon birds only if there were an error (to the left) of 60° in their estimate of wind direction with respect to the sun compass. No evidence could be found that this could be the case, except if such an error were postulated to be the cause of the leftward bias of non-noon birds relative to the home direction. The noon birds would then be using a leftward-biased compass on a leftward-distorted map. This is a rather far-fetched speculation, however, and the only clear statement that can be made is that in the present experiments noon birds show a deflection of 60° to the left of non-noon controls. Deflections observed with some other experimental treatments, except clock-shifts, also lack a satisfactory explanation (e.g. Wallraff, 1966, 1979; Baldaccini *et al.* 1975; Ioalé and Benvenuti, 1983; Schmidt-Koenig, 1987).

Given the rather large scatter in the bearings observed, it is unclear whether too much importance might be attached to the observation that the orientation of HN pigeons is towards magnetic north, with a detectable, but statistically difficult to treat, small percentage of the population flying towards magnetic south. It is rather striking, however, that departures along a magnetic north-south axis are predicted by the Kiepenheuer magnetoclinic route model, originally proposed in connection with bird migration (Kiepenheuer, 1984). A very important characteristic of this model is that it departs completely from the map-and-compass scheme and provides an example of an alternative means of orientation. Except in the very special case in which the birds' detector is horizontal (which would lead to random departures), the magnetoclinic route is always magnetic north-south in a horizontal ambient field, regardless of the angle at which the birds' detector is set.

On several occasions speculations have been advanced that geomagnetic cues are involved in the map (Gould, 1982) or in some navigational function other than the dip compass (Walcott, 1982; Lednor, 1982; Walcott *et al.* 1988). The evidence in favour of such speculation is general non-specific effects of various magnetic perturbations not directly tied with the inclination compass mechanism, mostly under sunny conditions. Often these effects are sporadic, being present on some occasions and absent on others (Kiepenheuer *et al.* 1986; Walcott *et al.* 1988). In the experiments reported here, the effects of various kinds of magnets are visible on only one occasion, in the orientation of HN birds in 1984. The fact that the 1984 result was not reproduced under conditions that were meant to be as close as possible in 1986 is puzzling, but by no means unique in orientation research. Three interpretations are possible. The first is that no matter how unlikely on a statistical basis, the effects observed in 1984 are indeed fortuitous, and of no biological significance. The second is that the directional information the pigeons glean from the magnetic field is functional only on some occasions and not on others, in spite of the fact that the situations are designed to be identical. However, it is difficult to understand what uncontrolled variables might at some times substitute or overshadow the magnetic information used for navigation. The third interpretation is that, to be biologically significant, an effect need not be so overwhelming as to be always observable in the face of a multitude of distracting inputs always present in the environment and in the motivational and physiological state of the

animal. The variability of orientation experiments might then be a characteristic to be expected in this kind of behaviour. This possibility is certainly the most interesting one, but it requires quantitative proof, perhaps through the formulation and improvement of realistic quantitative models of the homing process.

There are other explanations of why no reliable effects of magnets were observed in the experiments reported here. The 1988 experiments are those that, in principle, would have the best chance of demonstrating an effect, since the perturbation applied best fits what is known about the physiological characteristics of the magnetic detector. If the orientation of the D group (magnet unchanged upon release) had been no different from that of NN birds and that of I birds inverted 180° , the result would have been a rather spectacular demonstration of the magnetic inclination compass. First, however, it could well be that the 2-week period that the pigeons spent at the loft with the large weak magnets on their heads was too short for them to establish this newly acquired dip compass as a useful means of navigation. Second, it may be that there is a critical age at which the mechanism is learned and incorporated in the pigeons' orientation behaviour so that, in the present case, the magnetic compass cue was simply ignored by the birds. Finally, it could also be that visibility of the sun blocks the use of the magnetic compass (but not necessarily all other magnetic cues) even when the sun, near the zenith, does not provide directional information. This last supposition is consistent with unpublished data of I. O. C. Gasparotto who found that, in contrast to controls, pigeons released with the sun near the zenith at a latitude of 23°S depart randomly, in spite of the fact that the region possesses a geomagnetic field with a sizeable dip, which should favour the existence of a magnetic dip compass.

In conclusion, at present it is unfortunately impossible to argue convincingly in favour of any of the speculations raised in the Discussion. The tendency of pigeons to fly towards magnetic north when the sun compass is not available under our experimental conditions was observed consistently over several years, and is very unlikely to be a random result. Investigation of this question has revealed once more the variable nature of magnetic effects in pigeon orientation, if indeed any such effects are present. Our results suggest that there is no mechanism to substitute adequately for the sun compass at the magnetic equator when the sun is in the zenith.

Until such time as the physiological sensitivity of pigeons to magnetic stimuli can be unambiguously established and accurately characterized in the laboratory as to its dependence on field strength, variation, polarity, inclination etc., it is very difficult to advance our understanding of how such stimuli might participate in the orientation behaviour of these birds. At the same time, considerable progress might be achieved by developing more realistic models of orientation behaviour with a view to establishing with greater confidence the limits of biological significance of various effects. The present statistical methods are probably very limited in this respect, not for lack of mathematical rigour, but in their adequacy for addressing the underlying biological problem. With the evidence as it stands, our results at the magnetic equator are not proof against the participation of

magnetic stimuli in pigeon orientation, but they once more confirm that, if magnetic effects exist, they are of a rather discrete nature.

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