

Evidence that pigeons orient to geomagnetic intensity during homing

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The influence of the Earth's magnetic field on locomotory orientation has been studied in many taxa but is best understood for homing pigeons (*Columba livia*). Effects of experimentally induced and naturally occurring perturbations in the geomagnetic field suggest that pigeons are sensitive to changes in geomagnetic parameters. However, whether pigeons use the Earth's magnetic field for position determination remains unknown. Here we report an apparent orientation to the *intensity* gradient of the geomagnetic field observed in pigeons homing from sites in and around a magnetic anomaly. From flight trajectories recorded by GPS-based tracking devices, we noted that many pigeons released at unfamiliar sites initially flew, in some cases up to several kilometres, in directions parallel and/or perpendicular to the bearing of the local intensity field. This behaviour occurred irrespective of the homeward direction and significantly more often than what was expected by random chance. Our study describes a novel behaviour which provides strong evidence that pigeons when homing detect and respond to spatial variation in the Earth's magnetic field—information of potential use for navigation.

Keywords: homing pigeon; orientation behaviour; global positioning device

1. INTRODUCTION

Organisms of a wide variety of taxonomic groups, ranging from bacteria to insects and representatives of all major classes of vertebrates, are known to orient their bodies, parts of their bodies, objects they construct (e.g. nests) or their movement trajectories in relation to the Earth's magnetic field (for comprehensive reviews, see Wiltschko & Wiltschko 1995, 2005). For some species, such behaviour may facilitate return to preferred environments (Blakemore 1975; Frankel *et al.* 1979; Kirschvink 1980) or assist in building activities (Becker 1976); for others, ample evidence clearly indicates that orientation to or based on attributes of the geomagnetic field is undertaken specifically for purposes of direction finding and navigation.

Geomagnetic parameters, such as *intensity* and *inclination*, are distributed systematically over the Earth in such a way that they can provide useful and reliable information to animals about location (Skiles 1985). These factors, either individually or in combination with others, have been proposed for various species to be one or more axes of a navigational map which indicates position relative to a goal (e.g. Walker 1998; Phillips *et al.* 2002; Boles & Lohmann 2003; Lohmann *et al.* 2004). Geomagnetic features also may serve as landmarks (Kirschvink *et al.* 1986; Klinowska 1988; Klimley 1993) or as 'triggers' for location-dependent behaviours, such as changes in course direction or in physiological condition during migration (Beck & Wiltschko 1988; Fransson *et al.* 2001; Lohmann *et al.* 2001). Whether magnetic cues are components of the navigational maps of animals, however, is a question which continues to be debated.

Evidence of response to spatial and temporal variations in geomagnetic parameters by animals during homing or migration is strongest for racing pigeons. The effects of

induced magnetic fields (Walcott & Green 1974; Lednor & Walcott 1983) and the influence of magnetic anomalies (Walcott 1978; Kiepenheuer 1982) and storms (Keeton *et al.* 1974) on initial orientation behaviour have led to suggestions that pigeons can detect changes in the intensity gradient of the Earth's magnetic field and use this information for position determination (Viguier 1882; Moore 1980; Gould 1982; Walker 1998). However, persistent questions about the (i) sensitivity of the presumed magnetoreceptors, (ii) inconsistency of effects, (iii) interpretation of cues from areas where the Earth's magnetic field is not systematically distributed, and (iv) difficulty of manipulating the geomagnetic field in such a way that it provides incorrect information about location for experimental purposes make it difficult to determine whether pigeons (or other animals) navigate using geomagnetic cues (Walraff 1983; Gould 1985; Walcott 1991).

Here we describe an unusual behaviour observed in pigeons homing from sites in and around a natural magnetic anomaly. The anomaly, an area where the Earth's magnetic field is spatially distorted, presents opportunities to assess how the homing behaviour of pigeons is affected by spatial variation of geomagnetic parameters. If intensity does play a role in their navigational map, then behaviour undertaken by pigeons to determine their locations relative to goals may be influenced by the orientation of the intensity field (Walker 1998). To test this idea, we sought to determine whether the initial flight trajectories of pigeons released at sites around the anomaly were associated with the local orientation of the intensity field.

2. MATERIAL AND METHODS

(a) *Characterization of magnetic field*

Release sites were located in or around the Auckland Junction Magnetic Anomaly (JMA). The source of the JMA is a

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deep-seated structural dislocation approximately 1.6 km below the Earth's surface and is not correlated with surface topography. The magnetic map used in this study was produced from point data ($n=5671$) collected during an aerial survey (mean altitude, approx. 330 m) of the study area using a proton procession magnetometer. We used universal kriging, incorporating second-order polynomial and anisotropic trends (which corrected for global irregularities in magnetic intensity and the path of the aerial survey, respectively) to construct a gradient surface of total magnetic intensity. Using a digital map of the magnetic field and a geographical information system (ESRI ARCMAP v. 9.0), we then determined the compass bearing of the intensity field at the location of each position fix within each pigeon's flight trajectory. The grid-cell size of the slope and aspect surfaces of the intensity field was 25 m.

(b) Global positioning devices

We constructed miniature global positioning devices (GPDs) to record the flight trajectories of the pigeons as they homed from release sites (for technical details, see Steiner *et al.* 2000; von Hünenbein *et al.* 2000; Biro *et al.* 2002). The devices were attached to the backs of the pigeons with harnesses and were configured to operate continuously, recording one position fix per second with an accuracy of approximately 4 m CEP in the horizontal plane (circular error of probability, the distance from the benchmark location which encompasses 50% of the calculated position fixes).

(c) Experimental animals and releases

All test birds belonged to a local pigeon racer and had training and racing experience (from locations south of the loft) over distances of up to several hundred kilometres. Test birds were all adults (equal proportion of males and females), most were between 2 and 3 years of age; a few individuals ranged up to 8 years. Prior to their release, the birds were trained for several weeks to carry the harness and weight of the tracking devices. To determine whether flight behaviour varied in relation to geomagnetic intensity, we released pigeons at 15 sites in and around the moderately strong magnetic anomaly (approx. 400 nT above the regional main-field intensity). At each site, only one bird was released per day and each bird was released only once at each site. All flight occurred on days when the orb of the Sun was visible and when wind speeds were less than 15 km h⁻¹.

(d) Data analysis

Upon recovery of the GPDs, we observed that not all trajectories were oriented in the general homeward direction until some birds had flown at least 4 km from their release sites. This result is incongruous with those of other studies in which pigeons typically were homeward oriented within 2 km of the release site (Wiltschko 1992). Therefore, in order to focus on initial position determination behaviour, which we assumed had occurred when a pigeon's flight trajectory was first consistently oriented in the homeward direction, we excluded from subsequent analysis all fixes greater than 4 km from their respective release sites (the mean number of remaining position fixes per individual trajectory was $n=497 \pm 53$ 95% CI). In order to compare our results with those of other studies, we repeated the analysis on a second dataset which comprised only the first 2 km of the pigeons' flight trajectories.

We used a randomization test to quantify the association of the pigeons' flight trajectories with the orientation of the intensity field. In comparison with more standard statistical methods, randomization tests have two main advantages: they are valid even without random samples, and it is relatively easy to take into account the peculiarities of the situation of interest and use non-standard test statistics (Manly 1997). A randomization method was chosen because it allowed us to specifically test whether the extent of both parallel and perpendicular alignment of each pigeon's flight path with the direction of the underlying intensity contours was greater than what is expected to occur by chance alone. For such an analysis, the circular statistics regularly used in orientation studies and standard correlative techniques are unsuitable.

Our test used as the basic unit of analysis the difference between the bearing of each segment of a flight trajectory (the closed interval between two adjacent position fixes) and the bearing (*aspect*) of the intensity field at the same location (henceforth represented as ΔFI). The test algorithm first counted the number of segments in a trajectory in which ΔFI was less than a prescribed critical threshold value, the 'alignment parameter', A_C . A_C represented the maximum value of ΔFI in which the bearings of a trajectory segment and the intensity field were considered to be closely aligned. The test algorithm determined the total number of segments in a trajectory, S , in which ΔFI was less than A_C . A test distribution was generated by iteratively calculating 4999 values of S using randomly oriented bearings of the intensity field.

The extent of alignment of each flight trajectory was determined by ascertaining where in the distribution of all values of S (randomized and non-randomized) the value of S calculated using the real (non-randomized) data fell. Independent tests were performed to evaluate the significance of parallel, perpendicular and right-angle (both parallel and perpendicular) alignments over a range of values of A_C and on both the first 2 and 4 km of a flight trajectory. The procedure was repeated for all flight trajectories, using a significance level for S of $\alpha=0.05$. The computational algorithm was written and executed in MATLAB v. 6.5.0.

(e) Association of geomagnetic intensity with other potential cues

The geomagnetic field at some locations on Earth is correlated with other potential navigational cues, such as gravity (Dornfeldt 1991), surface topography (Arnould-Taylor & Malewski 1955; Matthews 1963) or other landscape features (Braithwaite & Guilford 1991; Holland 2003; Biro *et al.* 2004; Lipp *et al.* 2004) known to influence the homing behaviour of pigeons. This being the case, we examined how the spatial distribution of intensity at our study site varied in relation to other environmental factors which might have affected the pigeons' flight trajectories. We used spatial cross-correlation (Goodchild 1986) to assess the strength of association between geomagnetic intensity and other potential navigational cues which vary continuously in space. The area of assessment for this analysis was that which encompassed the position fixes of all flight trajectories with a minimum convex polygon plus a surrounding buffer area 2 km in width. The buffer was included to account for the possibility that the pigeons' flight trajectories were influenced by landscape features other than those immediately below them. Spatial cross-correlation was calculated using the CORRELATION function in the GRID module of ESRI ARCMAP v. 9.0. Each surface was modelled with the same parameter values using ordinary kriging

(using the named procedure ARCMAP v. 9.0 Geostatistical Analyst). More detailed results of these analyses are available upon request.

3. RESULTS

In total, we obtained 92 complete flight trajectories of pigeons from the point of release to the location of the loft. Inspection of the trajectories from sites where the birds exhibited substantial homeward error showed that near-linear (at least three position fixes) sections, which varied in length from several hundred to well over a thousand metres, were often oriented parallel or perpendicular to the direction of regional isodynamics (figure 1*a–c*). In a number of trajectories, ‘box-like’ patterns, with the sides of the ‘boxes’ oriented parallel and perpendicular to orientation of the intensity field, were also evident (figure 1*d–f*). Irrespective of whether we used the 2 or 4 km dataset, or the size of the alignment parameter, A_C , the flight directions of a large proportion of the pigeons were found to be significantly oriented with respect to the direction of the intensity field. For example, using a 13.5° alignment parameter (15% of the total possible difference between the direction of flight and the intensity field) with the 4 km dataset, we found that 59 out of the 92 (64.1%) trajectories exhibited significant alignment: 29 trajectories (31.5%) were aligned parallel to the field, 33 (35.7%) were aligned perpendicular to the field and 42 (45.7%) were aligned both parallel and perpendicular to the field (some individuals exhibited more than one type of response). The probabilities of observing these numbers of significantly aligned trajectories by chance (calculated using the binomial theorem) were 5.22×10^{-16} , 5.83×10^{-20} and 5.09×10^{-30} , respectively. The results of the randomization test using other values for the alignment parameter on both the 2 and 4 km datasets were similar, indicating that the analytical procedure was robust to variation in test parameters (table 1).

At our study site, geomagnetic intensity is not strongly correlated with surface topography (i.e. elevation) or slope ($r < 0.09$ for both factors), but is moderately correlated with gravity ($r = 0.62$). Spatial association of intensity and gravity is not surprising given that variations in the composition of the crustal rocks which produce magnetic anomalies also alter the gravity field. It is important to note that environmental factors which vary continuously can be correlated in magnitude but not be similarly oriented in space. Surfaces which differ strongly in *aspect* are not oriented in the same direction, thus the movement trajectories of animals following the isopleths of one surface will not be coincident with the isopleths of a second surface which differs markedly in *aspect*. The cross-correlations of the *aspect* of geomagnetic intensity with the *aspects* of surface elevation and gravity at our study site are $r = 0.09$ and $r = 0.002$, respectively. Such low values indicate that these factors are not directionally coincident with magnetic intensity. Visual examination of other environmental cues which may affect homing behaviour but vary in space discretely (thereby preventing analysis using spatial cross-correlation), such as land cover, soil type, vegetation, roads, railways, rivers or hedgerows, indicated no strong or regular associations with geomagnetic intensity (lack of space prohibits inclusion of graphical depictions of these factors). These results show that geomagnetic intensity at our study is not strongly associated with the other

navigational cues we evaluated which could provide an alternative explanation for the alignment behaviour.

4. DISCUSSION

Why pigeons initially fly after release in directions with respect to that of the local intensity field begs explanation. To date, the principal functions proposed for the use of the magnetic sense in animals are orientation and navigation (see the comprehensive reviews in Wiltschko & Wiltschko 1995, 2005). Some animals are known to directly sense changes in magnetic intensity, an ability which may contribute to the development of their navigational map (Semm & Beason 1990; Beason & Semm 1996; Lohmann & Lohmann 1996). Sustained flight oriented to the direction of the intensity field can only be achieved if pigeons are capable of detecting spatial variations in the field’s magnitude. Observations that pigeons can discriminate spatial differences in geomagnetic intensity (although made when changes in intensity were several orders of magnitude greater than that provided by the anomaly in this study) during conditioning experiments (Mora *et al.* 2004), as well as those suggesting that pigeons are sensitive to small intensity changes (Keeton *et al.* 1974; Walcott 1978; this study) provide evidence that information about spatial differences in intensity is ‘available’ to pigeons for use in position determination. It may be that the alignment behaviour represents a sampling strategy undertaken by the pigeons in order to determine the local intensity value, information they may use in their navigational map (see Kramer 1953; Moore 1980; Gould 1982; Walker 1998).

Alignment of flight direction to that of the geomagnetic field provides possible explanations for several previously reported observations of the homing behaviour of pigeons. The initial flight trajectories of pigeons released at other magnetic anomalies were found to be related to the slopes of the local intensity gradients (Frei & Wagner 1976; Wagner 1983), behaviour similar to the perpendicular alignments described in this study. The ‘release site bias’, a commonly observed, systematic and persistent deviation from the homeward direction particular to specific locations (Keeton 1973; Windsor 1975), may at some sites result from the tendency of pigeons to align their flight in directions relative to the geomagnetic field (as in figure 1*a–d*). Conversely, alignment at sites where the intensity field has the same bearing as the homeward direction would be expected to produce little or no release bias.

Alignment behaviour may also explain how magnetic anomalies and storms disrupt the initial orientation of pigeons homing from unfamiliar release sites. If the behaviour is undertaken to determine local values of geomagnetic intensity for position determination, then irregular spatial and temporal variations of the intensity field should make assessment of field strength (to a level of resolution sufficient for position determination) more difficult, because pigeons would have to extract intensity estimates from a noisier total signal. It is possible that the increases in disoriented flight which occur in response to magnetic perturbations (Keeton *et al.* 1974; Walcott & Green 1974; Walcott 1978; Kiepenheuer 1982; Lednor & Walcott 1983) result from the difficulties pigeons experience as they attempt to assess the intensity field in a more complex magnetic ‘topography’.

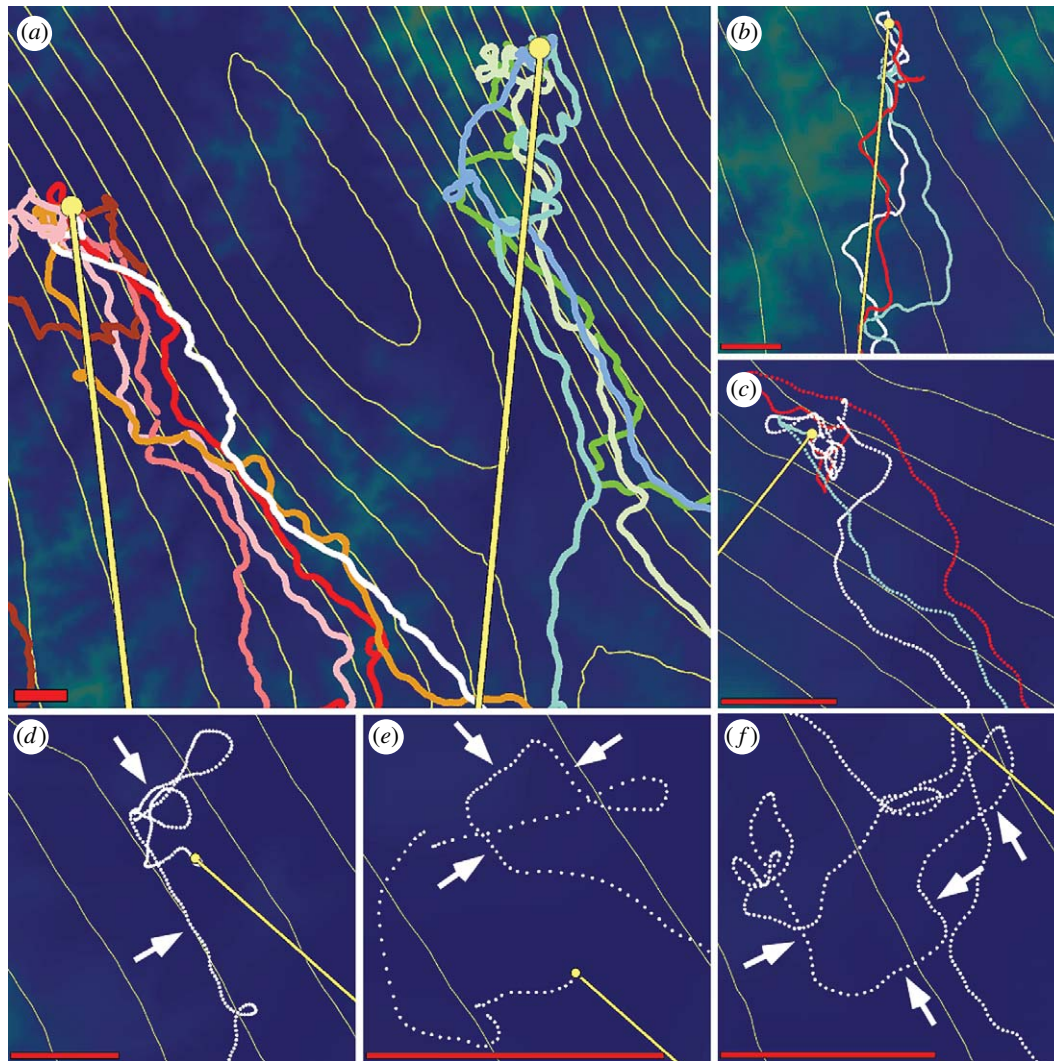


Figure 1. Examples of the orientation of pigeon flight trajectories to isopleths of geomagnetic intensity. Single-colour lines and points signify individual flight trajectories and position fixes, respectively. Yellow circles show the location of release sites whereas yellow lines designate the straight-line direction to the home loft. Pale-green lines depict intensity isopleths at 10 nT intervals. Background colour depicts relative elevation (low-elevation areas are blue and high-elevation areas are red). Red scale bars are 500 m. Arrows indicate locations of alignment of individual birds; (a) Long-distance alignment at a linear 'ridge' of the anomaly (includes incomplete trajectories excluded from analysis); (b, c) Parallel and/or perpendicular alignments from at two other release sites; (d–f). Fine-scale details of L-shaped and box alignments.

Table 1. Results of randomization analyses to determine the significance of alignment of individual trajectories to isodynamics.

distance (km)	alignment parameter (degrees/percent)	no. of significantly aligned birds
4	4.5/5	44
4	9/10	51
4	13.5/15	59
4	18/20	58
2	4.5/5	35
2	9/10	51
2	13.5/15	59
2	18/20	47

When comparing the results of our study with similar work (Wiltschko & Wiltschko 2003) which employed more conventional methods of flight-trajectory description (e.g. vanishing bearings), it is immediately clear that short-lived, spatially complex behaviours such as the alignment behaviour described in this study cannot be characterized

adequately using single, or at best only a very few, observations of relative position. Future research, using very high resolution movement data, into how animals respond to environmental gradients as they are actively homing or migrating should lead to much greater understanding of the cues they use for long-distance navigation.

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