A strong magnetic anomaly affects pigeon navigation

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SUMMARY

Pigeons were released in a strong magnetic anomaly with fast changes in intensity and gradients directions, about 60 km from their loft, and, for comparison, at the border of the anomaly and at a control site. The vanishing bearings were found to be closely related to the home direction, but unrelated to the local gradient directions. The vector lengths and the vanishing intervals, however, were significantly correlated with the maximum difference in intensity within a 2.5 km radius around the release site. This correlation was negative for the vector lengths and positive for the vanishing intervals, indicating that steep local gradients increase scatter between pigeons and delay their departure. These findings suggest that an irregular, fast changing magnetic field as found in the anomaly leads to confusion during the navigational processes. This, in turn, implies that pigeons can sense the respective changes in magnetic intensity. Magnetic cues seem to be included in the normal navigational processes that determine the departure direction.

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INTRODUCTION

Pigeons are well known for their ability to return home from distant, unfamiliar sites. For navigation, they appear to rely on a multitude of cues which they use in an opportunistic way, but the nature of these cues is still the subject of considerable controversy. One of the earliest factors proposed as a component of the avian navigational system was the geomagnetic field (Viguier, 1882), because it appears highly suitable to convey navigational information: both, total intensity and inclination show gradients running roughly north-south in most parts of the world – if birds (and other animals) could detect these magnetic parameters, they would obtain information equivalent to 'magnetic latitude' telling them whether they are north or south of home.

Magnetic navigational factors are of increased interest today in view of the ongoing debate on magnetoreception. Several authors, have described iron-rich structures containing crystals of magnetite in the skin of the upper beak and in the nasal cavity of pigeons and other birds, which have been proposed as putative magnetoreceptors (e.g. Beason and Nichols, 1984; Hanzlik et al., 2000; Williams and Wild, 2001; Fleissner et al., 2003; Fleissner et al., 2007; Stahl et al., 2007; Tian et al., 2007). Their complex structure implies an important biological function, and reading the magnetic field for navigational purposes would be the most plausible one.

Several papers discussing the theoretical considerations of their possible functions have been published in recent years (e.g. Shcherbakov and Winklhofer, 1999; Davila et al., 2003; Fleissner et al., 2007; Solov'yov and Greiner, 2007; Walker, 2008), but practical evidence of the functioning of these iron-rich structures and how they affect behavior is scarce. In electrophysiological studies, Semm and Beason obtained responses from the nerve innervating these structures as a result of changes in magnetic intensity (Semm and Beason, 1990), while a possible involvement in the avian magnetic compass is at variance with behavioral findings (e.g. Beason and Semm, 1996; Munro et al., 1997; R. Wiltschko et al., 2007; R. Wiltschko et al., 2008). This has led to the assumption

that they possibly provide information to be used as a component of the navigational 'map', the mechanisms birds use to determine their position and derive the course to their goal.

Experimental evidence supporting a use of magnetic intensity in avian navigation is rare, however. Manipulations of the magnetic field around the pigeons' head during the homing flight [for summary, see Wallraff (Wallraff, 1983), and treatments with a strong magnetic pulse (Beason et al., 1997) produced only small effects. Positive evidence comes mainly from studies within magnetic anomalies. Several authors (e.g. Wagner, 1976; Frei and Wagner, 1976; Dennis et al., 2007) reported a tendency of pigeons to fly along local magnetic gradients; recently, flight along isolines were also observed (Dennis et al., 2007). Walcott released pigeons in strong anomalies in the New England region of the USA, and reported that the vector lengths calculated from the vanishing bearings were negatively correlated with the steepness of the gradient of total intensity 1 km in the home direction, with very steep gradients leading to disorientation (Walcott, 1978). Kiepenheuer also observed disorientation of pigeons within an anomaly in southern Germany (Kiepenheuer, 1982). These findings suggest an effect of the local magnetic situation on the pigeons' orientation behavior. However, a study comparing the behavior of pigeons from different lofts released at the same site within a magnetic anomaly revealed that not all pigeons respond in the same way; some appear to be unaffected by the anomaly (Walcott, 1986; Walcott, 1992).

A recent study at a magnetic anomaly at Gernsheim, about 40 km south of our loft in Frankfurt, Germany, revealed little effect of the local magnetic conditions (Wiltschko and Wiltschko, 2003). However, this anomaly was very different from the anomalies where Walcott and Kiepenheuer did their studies: these anomalies are stronger and very 'rugged', with frequent changes between positive and negative values and locally very steep gradients. The Gernsheim anomaly, by contrast, is a small positive anomaly with smooth, regular slopes to all sides. Also, it is much closer to the loft and

lies within a very characteristic landscape, which could have promoted the use of other, non-magnetic navigational factors. Hence the study (R. Wiltschko and Wiltschko, 2003) did not provide a definitive answer to the question of the pigeons' use of magnetic parameters.

About 60 km northeast of our Frankfurt loft lies the Vogelsberg anomaly, one of the strongest anomalies in Germany, with a very irregular magnetic field, similar to the anomalies used by Walcott (Walcott, 1978; Walcott, 1992). In view of the possible use of magnetic navigational factors, we began a series of releases at sites within this anomaly and, for comparison, at its edge and at a magnetically undisturbed site. Here we report our first results.

MATERIALS AND METHODS

The releases of pigeons (*Columba livia* f. *domestica* L.) were performed during the summers of 2002 and 2004, from April to September on sunny days with mostly little cloud cover so that the sun compass was available.

Test sites

Vogelsberg is a part of the central German highlands, with a maximum altitude of 770 m above NN. It is a region of about 20 km, with its center at about 60 km northeast of our Frankfurt loft. It is an extinct volcano and because of the ancient lava flows, the magnetic field is highly irregular, changing from positive to negative anomaly values, with very steep local gradients of varying directions. There is, however, no detectable effect on magnetic north. Since we did the study in the traditional way by observing pigeons with

binoculars (see below), we had to use sites that provided good visibility in all directions. We choose six sites within the anomaly, sites A1 to A6, between 40 and 70 km from the loft, two sites at the border of the anomaly, sites B1 and B2, about 40 and 80 km, and the control site C, 40 km north of the loft. Fig. 1 and Table 1 give the exact position of the nine sites.

In our region, the reference field increases with a gradient of $2.5\,nT\,km^{-1}$ towards 15° north-northeast. However, the geomagnetic field itself is never totally regular. For the conditions at our loft in Frankfurt am Main (50°08′N, 8°40′E) see figure 1 in R. Wiltschko and Wiltschko (R. Wiltschko and Wiltschko, 2003). The conditions within the anomaly, characterized by very irregular gradients, and those at the other sites are presented in Fig. 1. Table 1 gives the local magnetic data for the test sites: the largest positive and negative differences in nT within a 1 km and 2.5 km radius around the release point and the directions in which they are found. Within the anomaly, these values are generally considerably higher than at the border or outside. Also, because of the anomaly, the largest increase and decrease in intensity seldom lie in opposite directions. The difference in intensity between the home loft and the release points is also given. Since all test sites lie northeast of the loft, the total intensity is expected to be higher at the test sites, which is the case at all sites except A6, where it is slightly lower (see Table 1). The difference in intensity 1 km in the home direction, the parameter Walcott (Walcott, 1978) found to be correlated with vector lengths, is likewise included.

Table 1 is based on very accurate digital data giving the differences of magnetic intensity from the reference field for 100×100 m squares,
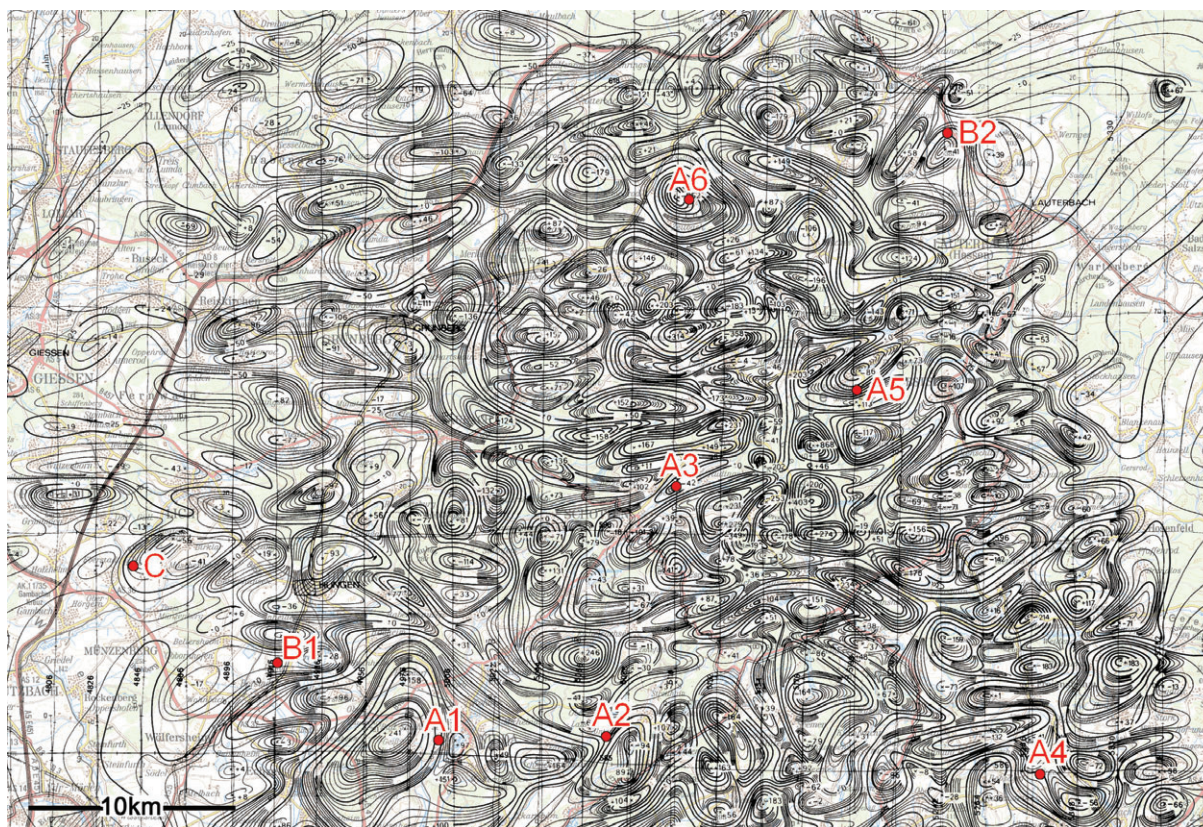
Fig. 1. Map with magnetic isolines superimposed on a topographic map showing the Vogelsberg area and the location of the nine test sites, the control site outside the anomaly, C, the two sites at the border of the anomaly, B1 and B2, and the six sites within the anomaly, A1 to A6. Thin isolines are 5 nT apart, thick isolines are 25 nT apart. For direction and distance to the Frankfurt loft and for details on the magnetic field around the release sites, see Table 1.

Table 1. The local geomagnetic field at the nine sites

Position	Release site	α_{home}	d_{home} (km)	ΔB to home (nT)	Max. positive difference (nT)				Max. negative difference (nT)				Max difference (nT) within a radius of		Difference in 1 km in home direction
					1 km		2.5 km		1 km		2.5 km				
					ΔB	Dir.	ΔB	Dir.	ΔB	Dir.	ΔB	Dir.	1 km	2.5 km	
C	Lich-Eberstadt	192°	40.6		+22	307°	+23	21°	−16*	58°	−22*	54°	38	45	+8
B1	Hungen-Utphe	204°	38.4	+104	+31	163°	+98	127°	−3	79°	−14*	79°	34	112	+18
B2	Lauterbach	219°	78.7	+192	+23	287°	+51*	247°	−45	191°	−49*	16°	68	100	−27*
A1	Nidda	217°	39.1	+245	+79	287°	+109*	288°	−37*	117°	−73	99°	116	182	+22*
A2	Ober Lais	225°	44.8	+133	+72	233°	+150	244°	−71	107°	−90*	148°	143	240	+68
A3	Schottenring	219°	56.2	+131	+120	127°	+281	132°	−17*	360°	−17*	58°	137	291	+63
A4	Ulmbach II	241°	61.1	+122	+17	209°	+79*	284°	−23	119°	−54	334°	40	133	+15
A5	L.-Eichelhain	222°	65.9	+216	+64*	202°	+155	293°	−130	354°	−169*	180°	194	324	+62*
A6	Groß-Felda	212°	68.2	−5	+90	29°	+262	206°	−70*	297°	−70*	291°	160	378	−76

C, control site outside of the anomaly; B, site at the border of the anomaly; A, site within the anomaly. α_{home}, d_{home}, direction and distance to the loft, respectively. ΔB to home, difference in magnetic intensity to the home site; ΔB, the maximum difference in intensity in nT within 1 and 2.5 km, with * indicating that the maximum difference is closer than 1 or 2.5 km, respectively; Dir., the direction in which the maximum difference is found. Max. differences within 1 and 2.5 km, the maximum difference of intensities within a radius of 1 and 2.5 km around the release point, respectively; the last 2 columns indicate the differences in home direction.

provided by the Leibniz-Institute for Applied Geophysics, Hannover, Germany. These data were obtained by mapping the local intensity from a plane at an altitude of 1000 m above NN, which means between about 850 and 400 m above ground at the test sites (see altitude data included in Table 2) and are based on the defined geomagnetic reference field of the epoch 1980.0 (DGRF 1980.0). The map in Fig. 1 illustrates the deviations from this reference field, i.e. from the values expected if the magnetic field were completely regular. The deviations from the reference field will be even greater at 30–40 m above ground, the normal flying altitude of pigeons.

Test birds and release procedure

The test birds were adult pigeons in their second year of life and older. During their first year of life, they had participated in a standard training program up to 40 km in the cardinal compass directions; additionally they had completed several training flights each spring. The vast majority had also homed singly a varying number of times from various directions and distances in previous experiments, the number of these flights increasing with increasing age. For the present study, we distinguish between birds familiar to the release site (fs) that had been released at the respective release site once before, and birds unfamiliar to the site (ufs).

Three sites within the anomaly, site A1, A2 and A4, the two sites at the border and the control site had already been used before this study began. The respective data of adult pigeons are included in Fig. 2 in the result section (supplementary material Table S1). Our analysis, however, is based only on the data from the present study for the homogeneity of samples, as pigeons from the same groups with similar pre-experience were released at all nine sites. The number of releases per site varied because we performed more releases at the three new sites within the anomaly.

The release procedure was the traditional one: the pigeons were transported to the release site in a VW van and released singly. They were watched by two observers using 10×40 binoculars (Zeiss Dyalit) until they vanished from sight, which was usually about 2.5 km from the release point. Their bearings after 1 min and their vanishing bearings were recorded with the help of a compass to the nearest 5°, and the vanishing intervals were recorded with a stop watch. We continued to release pigeons until we had obtained 10 evaluable bearings per release. An observer at the loft recorded the return of the birds.

Data analysis and statistics

From the 10 vanishing bearings and the bearings after 1 min, we calculated mean vectors of the respective release, which were tested for directional preference by the Rayleigh test (Batschelet, 1981). From the 10 vanishing intervals and the homing speeds, medians are given because these data are not normally distributed.

To compare the behavior at the nine sites, we determined the following data for each site: (1) the center of distribution of the mean vectors of the vanishing bearings; (2) the second order mean vector based on the mean bearings at vanishing; (3) the median of the mean vector lengths at vanishing; (4) the median of the median vanishing intervals; (5) the median homing speed and return rate.

In a second order analysis, the centers of distribution of vanishing bearings were tested for significant agreement using the Hotelling test for bivariate samples; they were compared using the Mardia test for bivariate samples (Batschelet, 1981). The second order mean vectors at each site were set in relation to the home directions and to the directions of the increasing and decreasing magnetic gradient at the respective sites. This was done by testing the angular differences to home and to the gradient directions at 2.5 km from the release site with the Rayleigh test (Batschelet, 1981), with significance indicating a relationship.

The bearings 1 min after release were analyzed in the same way as the vanishing bearings and correlated with the greatest differences in intensity at 1 km because a pigeons can only fly about 1 km within 1 min.

The data on vector lengths at vanishing as well as the vanishing intervals were correlated with the local magnetic data given in Table 1 using the non-parametric Spearman rank correlation.

RESULTS

The data of all releases of the present study are listed in Table 2 (for the data of the previous releases at the test sites, see supplementary material Table S1). Table 3 shows the center of distribution of the mean vectors of the releases at each site, together with the medians of vector lengths, the median of the median vanishing intervals as well as the medians of return rate and homing speed.

Data obtained at the nine sites

The mean vectors at vanishing are given in Fig. 2, together with the direction of the highest increase and decrease of intensity at 2.5 km

Table 2. Data of the releases

Site	Date	Fam?	N (N_b)	α	Δh	r	Van. int.	Home	Speed
C, Lich-Eberstadt	29.7.2002	ufs	12 (10)	233°	+41°**	0.79**	3:09	92%	47.8
192°, 40.6 km	9.8.2002	ufs	10	239°	+47°**	0.96***	3:16	100%	40.6
185 m	20.8.2002	fs	10	225°	+33°*	0.84***	3:26	100%	53.0
	30.6.2004	ufs	11 (10)	216°	+24°*	0.90***	3:10	100%	54.8
B1, Hungen-Utphe	18.4.2002	ufs	11 (10)	(249°)	(+44°)	0.29ⁿ·ˢ·	3:18	100%	16.2
204°, 38.4 km	22.4.2002	ufs	11 (10)	208°	+4°	0.86***	4:35	100%	52.4
150 m	14.6.2002	ufs	11 (10)	199°	−5°	0.95***	4:10	100%	56.2
	23.8.2002	fs	12 (10)	207°	+3°	0.97***	3:10	100%	60.6
	25.6.2004	ufs	16 (10)	189°	(−15°)	0.82***	6:21	100%	31.6
	7.7.2004	ufs	11 (10)	205°	+1°	0.98***	4:11	100%	52.4
B2, Lauterbach-R.	25.4.2002	ufs	10	209°	−10°	0.89***	4:07	100%	23.0
219°, 78.7 km	21.5.2002	ufs	12 (10)	193°	−26°**	0.96***	3:26	100%	47.8
380 m	29.7.2002	fs	13 (10)	206°	−13°	0.93***	2:53	100%	53.6
	2.9.2004	ufs	13 (10)	216°	−3°	0.94***	3:19	100%	51.9
A1, Nidda	22.4.2002	ufs	11 (10)	191°	−26°*	0.94***	5:30	100%	35.0
217°, 39.1 km	13.+15.5.	ufs	19 (10)	(223°)	(+6°)	0.42ⁿ·ˢ·	8:11	100%	36.1
177 m	14.8.2002	ufs	10	214°	−3°	0.83***	8.02	100%	34.5
	20.8.2002	fs	10	236°	+19°*	0.96***	6:37	100%	45.1
	30.6.2004	ufs	14 (10)	(204°)	(−13°)	0.43ⁿ·ˢ·	10:09	100%	39.1
	7.7.2004	ufs	17 (10)	212°	−5°	0.91***	5:23	100%	51.0
A2, Ober Lais	22.4.2002	ufs	11 (10)	163°	−62°**	0.69**	6:40	100%	28.0
225°, 44.8 km	9.5.2002	ufs	11 (10)	(138°)	(−88°)	0.15ⁿ·ˢ·	4:32	100%	34.9
296 m	14.8.2002	ufs	12 (10)	(244°)	(+19°)	0.45ⁿ·ˢ·	6:11	100%	48.9
	23.8.2002	fs	10	242°	+17°*	0.95***	4:32	100%	42.0
	2.9.2004	ufs	15 (10)	(273°)	(+48°)	0.42ⁿ·ˢ·	6:31	100%	50.7
A3, Schottenring	18.4.2002	ufs	10	214°	−5°	0.59*	5:43	100%	36.8
219°, 56.5 km	9.5.2002	ufs	11 (10)	218°	−1°	0.74**	5:29	82%	36.8
434 m	26.6.2002	ufs	10	189°	−30°	0.75**	5:00	100%	52.5
	9.7.2002	ufs	12 (10)	216°	−3°	0.84***	4:31	100%	47.7
	3.9.2002	fs	13 (10)	218°	−1°	0.99***	6:19	100%	56.6
	14.6.2004	ufs	12 (10)	217°	−2°	0.83***	3:28	100%	48.4
	5.7.2004	ufs	10	217°	−2°	0.98***	6:52	100%	28.7
	22.8.2004	ufs	10	215°	−4°	0.88***	2:49	90%	44.6
	17.9.2004	ufs	12 (10)	214°	−5°	0.74**	3:18	100%	44.6
A4, Ulmbach II	8.5.2002	ufs	12 (10)	(273°)	(+32°)	0.15ⁿ·ˢ·	3:10	100%	19.6
241°, 61.1 km	16.5.2002	ufs	13 (10)	165°	−76°***	0.71**	4:52	100%	45.3
420 m	15.8.2002	ufs	11 (10)	222°	−19°	0.59*	6:52	91%	46.4
	13.9.2002	fs	12 (10)	276°	+35°***	0.94***	3:50	100%	69.7
	28.7.2004	ufs	12 (10)	187°	−54°***	0.98***	3:45	100%	57.3
A5, L.-Eichelhain	18.4.2002	ufs	12 (10)	(180°)	(− 42°)	0.26ⁿ·ˢ·	4:44	75%	32.4
222°, 65.9 km	8.5.2002	ufs	11 (10)	(117°)	(−105°)	0.24ⁿ·ˢ·	3:47	82%	54.9
590 m	30.5.2002	ufs	11 (10)	200°	−22°	0.62*	6:06	91%	38.4
	26.6.2002	ufs	13 (10)	157°	−65°***	0.76**	5:40	100%	47.6
	29.7.2002	fs	11 (10)	173°	−49°*	0.68**	5:23	100%	48.2
	14.6.2002	ufs	10	(184°)	(−38°)	0.42ⁿ·ˢ·	3:30	100%	48.2
	28.6.2004	ufs	10	(179°)	(−43°)	0.3ⁿ·ˢ·	5:32	100%	43.9
	22.7.2004	ufs	10	(162°)	(−60°)	0.51ⁿ·ˢ·	5:34	90%	39.5
	9.9.2004	ufs	12 (10)	(96°)	(−126°)	0.17ⁿ·ˢ·	3:50	100%	54.2
A6, Groß Felda	25.4.2002	ufs	11 (10)	203°	−9°	0.66**	5:34	100%	37.2
212°, 68.2 km	21.5.2002	ufs	14 (10)	190°	−22°	0.55*	7:55	93%	52.5
368 m	30.5.2002	ufs	12 (10)	214°	+2°	0.75**	6:17	100%	49.9
	9.7.2002	ufs	10	222°	+10°	0.80**	8:52	100%	46.0
	30.8.2002	fs	12 (10)	218°	+6°	0.98***	5:20	100%	51.2
	14.6.2004	ufs	14 (10)	190°	−22°	0.80***	5:59	100%	39.7
	28.6.2004	ufs	15 (10)	187°	−25°*	0.92***	11:28	100%	37.2
	22.7.2004	ufs	11 (10)	185°	−27°*	0.86***	5:26	100%	36.5
	9.9.2004	ufs	13 (10)	223°	+11°	0.94***	8:08	100%	46.5

First column: positions of the release sites with respect to the anomaly: C, control site outside anomaly; B, sites at the border of the anomaly; A, sites within the anomaly; names of the release sites, home direction and distance to home, altitude above NN. Fam?, the familiarity of the birds with the site: ufs, unfamiliar with the site; fs, familiar with the site. N (N_b), number of pigeons released and, in parentheses, number of evaluable bearings; α, mean vanishing bearing; Δh, their difference to the home direction, with + indicating a difference to the right and − a difference to the left and non-significant mean bearings given in parentheses; r, length of mean vector, with asterisks indicating significance by the Rayleigh test (Batschelet, 1981). Van. int., median vanishing interval in minutes:seconds; Home, percentage of pigeons that returned; Speed, median homing speed in $km\,h^{-1}$. Significance levels: *$P<0.05$; **$P<0.01$; ***$P<0.001$; n.s. not significant.
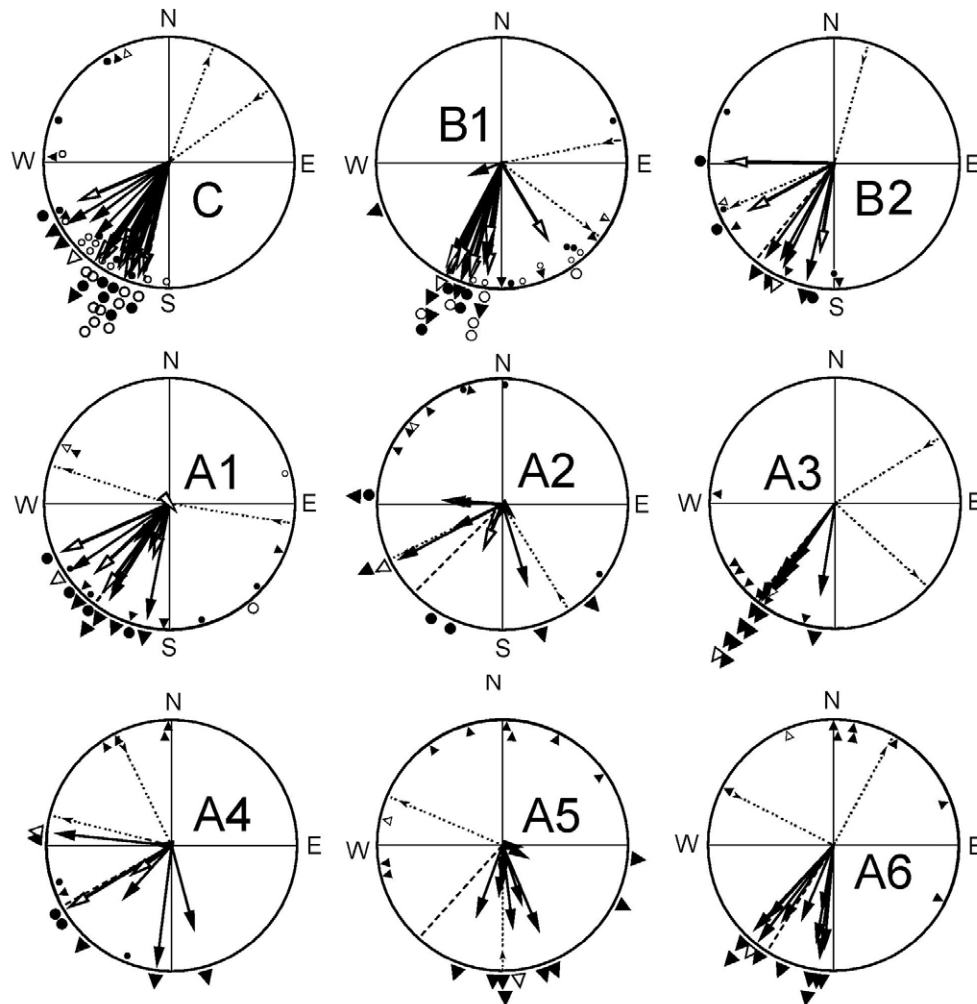
Fig. 2. Mean vectors of the releases performed at the nine sites; the releases of the present study are represented by arrows with a solid heads, their mean directions are indicated by triangles; those performed prior to this study are represented by arrows with open heads and their mean directions are indicated by round symbols. Open symbols, pigeons familiar with the site; solid symbols, birds unfamiliar with the site. The home direction is indicated by a dashed radius, the gradient directions at 2.5 km are indicated by dotted radii with arrowheads, the arrowhead pointing outward indicating the direction of the maximum of increasing intensity at 2.5 km, those pointing inward the respective direction of decreasing intensity.

from the release point. The vectors of the vanishing bearings at the control site and at the border of the anomaly are mostly long and lie fairly close together, indicating good agreement between the pigeons within each sample. The same is largely true for the sites A1, A3 and A6 within the anomaly, whereas the vectors at the other sites are mostly shorter. At the sites A2 and A5, the majority of the samples were not statistically significant ($P>0.05$, Rayleigh test; see Table 2), indicating no pronounced directional preference. In the second order analysis, the center of the vectors at vanishing at the sites A2 and A4 were not significantly different from random by the Hotelling test (see Table 3), indicating large variance in behavior.

The vanishing intervals at the sites within the anomaly are usually longer than at the sites at the border or outside, and the median homing speed is slightly higher, but these differences are not significant because of the large scatter between releases. The return rate remains largely unaffected (see Table 3).

Analysis of directional behavior with respect to the magnetic conditions

Fig. 3 gives the second order mean vectors based on the mean bearings at vanishing for each site in relation to the home direction and the direction of the highest increase and the highest decrease of magnetic intensity at 2.5 km plotted upward. The nine second order mean directions add up to a long, significant vector when set in relation to the home direction, but they do not form significant vectors in relation to the gradient directions 2.5 km from the release point. The same is true when only the vectors from the six sites within the anomaly are considered (Table 4). This indicates that there is no constant relationship between the birds' bearings at vanishing and the direction of the local gradients – apparently, the flight directions are not influenced by the local magnetic situation, whereas they show a close relationship to the home direction.

For the data recorded 1 min after release, see supplementary material Tables S2–S4 and Fig. S1.

Correlations of vector lengths and vanishing intervals with the local magnetic conditions

We also correlated the median vector lengths at vanishing and the vanishing intervals with the magnetic data listed in Table 1; the coefficients of correlation are given in Table 5. None of the parameters is correlated with the difference in magnetic intensity between release point and home loft. With the local differences in

Table 3. Center of vectors and medians of the data recorded at the nine sites

Release site		Position		N	Center of vectors at vanishing			Med. r	Vanish. interval	Homing	
		α_{home}	d_{home}		αh	a	Sign.			Rate	Speed
C	Lich-Eberstadt	192°	40.6	4	+37°	0.86	**	0.87	3:12	100%	50.4
B1	Hungen-Utphe	204°	38.4	6	0°	0.79	**	0.91	4:11	100%	52.4
B2	Lauterbach	219°	78.7	4	−13°	0.92	***	0.94	3:23	100%	49.9
A1	Nidda	217°	39.1	6	−4°	0.72	**	0.87	7:20	100%	37.6
A2	Ober Lais	225°	44.8	5	−1°	0.39	n.s.	0.45	6:11	100%	42.0
A3	Schottenring	219°	56.5	9	−5°	0.81	***	0.83	5:00	100%	44.6
A4	Ulmbach II	241°	61.1	5	−26°	0.49	n.s.	0.71	3:50	100%	46.4
A5	L.-Eichelhain	222°	65.9	9	−53°	0.40	**	0.42	5:23	91%	47.6
A6	Groß-Felda	212°	68.2	9	−8°	0.78	***	0.80	6:17	100%	46.5

Release sites: C, control site outside the anomaly; B, site at the border of the anomaly; A, site within the anomaly; Position: α_{home}, d_{home}, direction and distance (in km) to home; N, number of samples; αh, a, centers of vectors: direction with respect to home (+, clockwise and −, counterclockwise deviation from the home directions) and distance from center. Sign., significant agreement between samples (Hotelling test for bivariate samples) (Batschelet, 1981); Med. r, median vector lengths; Vanish. interval, median vanishing interval (in minutes:seconds); Homing: Rate, median return rate; Speed, median homing speed in km h⁻¹. Significance levels: *$P<0.05$; **$P<0.01$; ***$P<0.001$; n.s., not significant.

intensity, however, we found several significant correlations, the most frequently observed ones being those with the maximum difference in intensity within the 1 and 2.5 km radius around the release site (see Table 5). These correlations are negative for the vector length at vanishing in pigeons unfamiliar with the respective sites, but not in those that had homed from the sites before. The vectors 1 min after release do not show this correlation (see supplementary material Table S5). The vanishing intervals, however, are positively correlated with the maximum difference in intensity within a 1 and a 2.5 km radius, a correlation found in unfamiliar and familiar birds alike. A significant correlation with the steepness of the gradient 1 km in the home direction is only found once; it seems to be an exception (see Table 5).

Significant correlations with other magnetic differences listed in Table 1 usually occur together with significant correlations of maximum difference in intensity within a 1 or 2.5 km radius; their coefficients of correlation are mostly smaller than the ones with the maximum difference. Since the other differences in intensity are included in maximum difference, they seem to reflect the correlations existing between those variables and the maximum difference.

In summary, whereas the directions the pigeons fly seem largely unaffected by the local magnetic conditions, the vector length at

vanishing, reflecting the agreement among pigeons, and the vanishing intervals, reflecting the time taken to leave the release sites, proved significantly correlated with maximum difference in intensity.

DISCUSSION
Our data show that the irregular magnetic field in a strong magnetic anomaly indeed affects the homing process of pigeons. This effect seems to involve the navigational 'map' rather than the compass, since both avian compass mechanisms were available: the differences in intensity are small enough to still fall within the functional window of the magnetic compass found in European robins and domestic chickens (see W. Wiltschko 1978; W. Wiltschko et al., 2007), and the sun was visible during all releases.

Initial orientation in relation to the local gradients
As in our study at the Gernsheim anomaly (R. Wiltschko and Wiltschko, 2003), we did not find a directional relationship between the pigeons' bearings and the local gradients. Wagner (Wagner, 1976) and Frei and Wagner (Frei and Wagner, 1976), released pigeons in weak magnetic anomalies in Switzerland, and reported that their birds roughly followed the gradients in the direction that would decrease the differences to the home value. For the present study, this would mean that we should have expected the pigeons
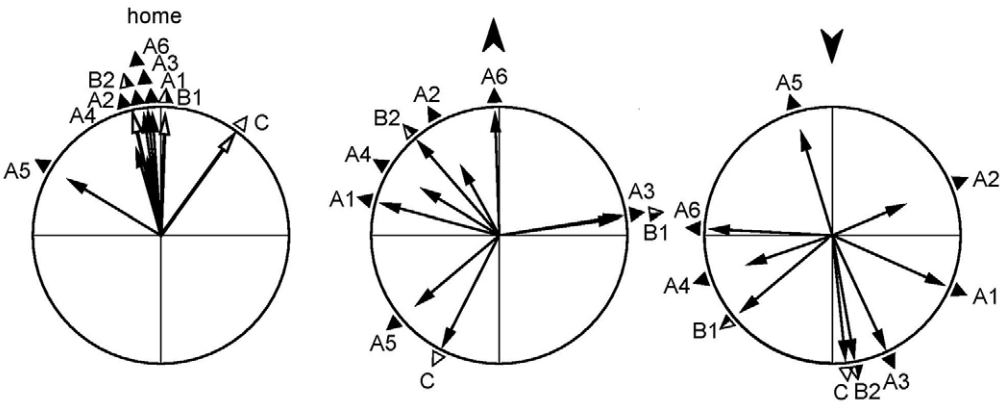

Fig. 3. Second order mean vectors based on the mean bearings of the releases performed at the nine sites with respect to the home direction, the direction of the increasing and of the decreasing intensity gradient, plotted upward. The second order mean vectors are represented by arrows, their mean directions are marked by triangles at the periphery of the circle: open triangles, control site; half-open triangles, sites at the border of the anomaly; solid triangles, sites within the anomaly.

Table 4. Grand mean vectors with respect to home and the gradient directions

Vector	All sites			Anomaly sites only		
With respect to	N	α_N	r_N	N	α_N	r_N
Home	9	+8°	0.92***	6	−10°	0.97***
Increasing gradient	9	−46°	0.35[n.s.]	6	−43°	0.50[n.s.]
Decreasing gradient	9	−171°	0.32[n.s]	6	+64°	0.09[n.s.]

α, mean vanishing bearing; r, length of mean vector; asterisks at r_N indicate significance by the Rayleigh test. Significance levels: ***, $P<0.001$; n.s., not significant.

to follows the decreasing gradients at all sites except at site A6. This is obviously not the case; instead the vanishing bearings are closely related to the home direction

At this point, it is worth considering what following magnetic gradients as a navigational strategy would mean. If the navigation task is to reach home in a fast and efficient way, following the local intensity gradient that decrease the difference to the home values makes little sense, especially from a site within a magnetic anomaly. Such a strategy would be helpful only if the magnetic field were completely regular, which is practically nowhere the case. Even smooth, gradual irregularities would lead to detours. If pigeons looking for decreasing gradients entered a magnetic low by chance, they would be 'trapped', as the magnetic factors could not lead them out.

Another problem concerns the ability to detect the directions of the gradients. It is easily conceivable that pigeons record the scalar value of magnetic field intensity at a site, but the directions in which this intensity increases and decreases cannot immediately know – gradients cannot be sensed over a distance. Detecting gradient directions would require extensive flying around in order to scan the local field, compare the recorded values and so determine how intensity changes in the different directions. The distance pigeons would have to fly depends on their still unknown ability to detect minute differences in intensity – the greater their sensitivity, the shorter the distances they have to cover until the difference exceeds the threshold of detection. Hence, even from the theoretical point of view, following magnetic gradients is not to be expected, and it was not found, either in the present study or in the study in the Gernsheim anomaly with its regular magnetic slopes (Wiltschko and Wiltschko, 2003).

A similar problem occurs with the model proposed by Walker, in which the direction of the steepest slope in intensity is assumed to represent one of the crucial coordinates to be compared with the direction of the slope at home (Walker, 1998). Aside from the fact that this model would not work in a highly irregular magnetic field as the Vogelsberg anomaly, the question arises of how pigeons would determine the direction of the steepest slope with sufficient accuracy without scanning a larger part of the area. Dennis and colleagues tracked pigeons with GPS-based flight recorders and reported that they often flew parallel or perpendicular to the local isolines of intensity (Dennis et al., 2007). The tracks occasionally showed loops or what was described as 'box-like' structures, but whether these patterns can be interpreted as scanning is unclear. In the examples given, they only encompass areas with a diameter of little more than 500 m; it would require a remarkable sensitivity to detect differences in intensity over these distances.

Correlation of behavioral parameters with the steepness of magnetic gradients

The indications for an effect of the local magnetic conditions on the pigeons' navigation emerges from the correlation of the vector lengths at vanishing and the vanishing intervals with the maximum difference in magnetic intensity within a 1 and 2.5 km radius around the release site. Similar to Walcott (Walcott, 1978), we find a negative correlation between the vector lengths of birds unfamiliar with the release sites and the range of magnetic intensity: the larger the maximum difference in intensity, i.e. the steeper the local gradients, the shorter the vectors at vanishing. Yet, even if vector lengths decrease, our birds are not generally disoriented within the anomaly. A possible reason is that the anomaly at Iron Mine where Walcott observed disorientation was even stronger (Walcott, 1978; Walcott, 1992). Also, better non-magnetic navigational factors might have been available. Another difference from Walcott (Walcott, 1978) is that our best correlations are not with the difference in magnetic intensity 1 km in the home direction, but with the maximum changes around the release site. The vanishing intervals, a variable Walcott did not study, are also correlated with the range of intensity, and this correlation is positive: the steeper the gradients, the longer are the vanishing intervals, irrespective of the pigeons' previous experience.

Long vanishing intervals mean extensive flying around at the release site and a relatively late decision to leave. Released within the anomaly, the pigeons seem to have problems interpreting the local magnetic conditions: encountering marked changes in intensity resulting from the steep gradients with changing directions obviously delay the birds' decision to depart, rendering the choice of the departure direction more difficult. This implies that pigeons are not only able to detect the local magnetic intensity and its changes, but that they routinely record it and normally include this information in their navigational processes. For example, if they compare the local intensity with the one remembered from their home loft, as predicted by the concept of the gradient map (see Wallraff, 1974), then recording rapidly changing values of intensity while flying around at the release site will be rather confusing. We can only speculate on their response – they may search around more

Table 5. Coefficients of the Spearman rank correlation for vector lengths and vanishing intervals ($N=9$)

Variable	Data set	Difference between home and release site	Range within 1 km radius	Range within 2.5 km radius	1 km in home direction
Vector lengths at Vanishing:	All releases	−0.087	**−0.688***	**−0.679***	−0.454
	birds unfamiliar with the site	−0.233	**−0.667***	**−0.717***	**−0.633***
	birds familiar with the site	−0.300	+0.033	+0.383	+0.100
Vanishing intervals:	all releases	+0.317	**+0.667***	**+0.767***	+0.350
	birds unfamiliar with the site	+0.367	**+0.633***	**+0.717***	+0.483
	birds familiar with the site	+0.383	**+0.633***	**+0.717***	+0.500

Significant coefficients of correlation are given in bold, with asterisks indicating *$P<0.05$.

intensively to check the local situation. This is supported by the significant changes in orientation between 1 min after release and vanishing observed at four at the sites within the anomaly (see supplementary material Table S3).

When the pigeons finally leave and vanish from sight approximately 2.5 km from the release point, they are mostly oriented roughly in the home direction. Yet within the anomaly, this orientation can hardly be attributed to magnetic factors – these are too irregular and ambiguous to provide meaningful information. We must assume that the birds rely on other, non-magnetic factors or fall back on reversing the direction of the outward journey (see Wiltschko and Wiltschko, 1982). This would mean that they finally recognized the local magnetic field as unreliable and no longer include it in their navigational process. Possibly, the more confused they are, the longer they search around, and the later they reach the decision to turn to other cues. Yet a later decision might move the point of decision (see Schiffner and Wiltschko, 2009) farther from the release point and thus lead to less agreement among the birds, resulting in shorter vectors at vanishing, as are observed in the present study.

Altogether, the effect of the magnetic anomaly – longer vanishing intervals and shorter vectors at vanishing – is reflected in the flying behavior at the release site rather than in the vanishing bearings. Pigeons rely on a multitude of cues for navigation, and in a multiple cue system it is very hard to isolate the effect of one type of cue from that of the others. Within the anomaly, the birds could reach meaningful decisions about their departure directions only once they ignored the magnetic cues. Under these conditions, an effect of the local magnetic conditions on the circumstances until such a decision is reached is to be expected, whereas the later directional choices would depend on other factors.

### A possible role of the receptors in the upper beak?

Our data indicate that magnetic factors are normally involved in the pigeons' navigation process. This is in agreement with the role of the magnetite-based receptors suggested by behavioral experiments with migratory birds and domestic chicken (W. Wiltschko et al., 1994; Beason et al., 1995; Beason and Semm, 1996; Munro et al., 1997; R. Wiltschko et al., 2007; W. Wiltschko et al., 2007; W. Wiltschko et al., 2009): they seem to provide information on magnetic intensity as a component of the navigational 'map' rather than magnetic compass information. Our present findings, supporting a role of magnetic intensity in avian navigation, provide a chance to obtain more direct evidence for the biological function of these receptors.

REFERENCES

Batschelet, E. (1981). *Circular Statistics in Biology*. London: Academic Press.

Beason, R. C. and Nichols, J. E. (1984). Magnetic orientation and magnetically sensitive material in a transequatorial migratory bird. *Nature* **309**, 151-153.

Beason, R. C. and Semm, P. (1996). Does the avian ophthalmic nerve carry magnetic navigational information? *J. Exp. Biol.* **199**, 1241-1244.

Beason, R. C., Dussourd, N. and Deutschlander, M. (1995). Behavioural evidence for the use of magnetic material in magnetoreception by a migratory bird. *J. Exp. Biol.* **198**, 141-146.

Beason, R. C., Wiltschko, R. and Wiltschko, W. (1997). Pigeon homing: effects of magnetic pulse on initial orientation. *Auk* **114**, 405-415.

Davila, A. F., Fleissner, G., Winklhofer, M. and Petersen, N. (2003). A new model for a magnetoreceptor in homing pigeons based on interacting clusters of superparamagnetic magnetite. *Phys. Chem. Earth* **28**, 647-652.

Dennis, T. E., Rayer, M. J. and Walker, M. M. (2007). Evidence that pigeons orient to geomagnetic intensity during homing. *Proc. Biol. Sci.* **274**, 1153-1158.

Fleissner, G., Holtkamp-Rötzler, E., Hanzlik, M., Winklhofer, M., Fleissner, G., Petersen, N. and Wiltschko, W. (2003). Ultrastructural analysis of a putative magnetoreceptor in the beak of homing pigeons. *J. Comp. Neurol.* **458**, 350-360.

Fleissner, G., Stahl, B., Thalau, P., Falkenberg, G. and Fleissner, G. (2007). A novel concept of Fe-mineral-based magnetoreception: histological and physicochemical data from the upper beak in homing pigeons. *Naturwissenschaften* **94**, 631-642.

Frei, U. and Wagner, G. (1976). Die Anfangsorientierung von Brieftauben im erdmagnetisch gestörten Gebiet des Monat Jorat. *Rev. Suisse Zool.* **83**, 891-897.

Hanzlik, M., Heunemann, C., Holzkamp-Rötzler, E., Winklhofer, M., Petersen, N. and Fleissner, G. (2000). Superparamagnetic magnetite in the upper beak tissue of homing pigeons. *BioMetals* **13**, 325-331.

Kiepenheuer, J. (1982). The effect of magnetic anomalies on the homing behavior of pigeons. In *Avian navigation* (ed. F. Papi and H. G. Wallraff.), pp. 120-128. Berlin: Springer-Verlag.

Munro, U., Munro, J. A., Phillips, J. B., Wiltschko, R. and Wiltschko, W. (1997). Evidence for a magnetite-based navigational 'map' in birds. *Naturwissenschaften* **84**, 26-28.

Schiffner, I. and Wiltschko, R. (2009). Point of decision: when do pigeons decide to head home? *Naturwissenschaften* **96**, 251-258.

Semm, P. and Beason, R. C. (1990). Responses to small magnetic variation by the trigeminal system of the Bobolink. *Brain Res. Bull.* **25**, 735-740.

Shcherbakov, V. P. and Winklhofer, M. (1999). The osmotic magnetometer: a new model for magnetite-based magnetorecptors in animals. *Eur. Biophys. J.* **28**, 380-392.

Solov'yov, I. A. and Greiner, W. (2007). Theoretical analysis of an iron mineral-based magnetoreceptor model in birds. *Biophys J.* **93**, 1493-1509.

Stahl, B., Fleissner, G., Fleissner, G. and Falkenbegr, G. (2007). Cross-species unveiling a putative avian magnetoreceptor. *HASYLAB Annual Report* **2006**, 1269-1270. Hamburg: DESY.

Tian, L., Xiao, B., Lin, W., Zhang, S., Zhu, R. and Pan, Y. (2007). Testing for the presence of magnetite in the upper-beak skin of homing pigeons. *BioMetals* **20**, 197-203.

Viguier, C. (1882). Le sens de l'orientation et ses organes chez les animaux et chez l'homme. *Rev. Philos. France Etranger* **14**, 1-36.

Wagner, G. (1976). Das Orientierungsverhalten von Brieftauben im erdmagnetisch gestörten Gebiete des Chasseral. *Rev. Suisse Zool.* **83**, 883-890.

Walcott, C. (1978). Anomalies in the earth's magnetic field increase the scatter of pigeon's vanishing bearings. In *Animal Migration, Navigation and Homing* (ed. K. Schmidt-Koenig and W. T. Keeton), pp. 143-151. Heidelberg: Springer-Verlag.

Walcott, C. (1986). A review of magnetic effects on homing pigeon orientation. *In Biophysical Effects of Steady Magnetic Fields* (ed. G. Maret, N. Boccara and J. Kiepenheuer), pp. 146-147, Heidelberg: Springer-Verlag.

Walcott, C. (1992). Pigeons at magnetic anomalies: the effects of loft location. *J. Exp. Biol.* **170**, 127-141.

Walker, M. M. (1998). On and a wing and a vector: a model for magnetic navigation by homing pigeons. *J. Theor. Biol.* **192**, 342-349.

Walker, M. M. (2008). A model for encoding magnetic field intensity by magnetite-based magnetoreceptor cells. *J. Theor. Biol.* **250**, 85-91.

Wallraff, H. G. (1974). *Das Navigationssystem der Vögel*. München: Oldenbourg Verlag.

Wallraff, H. G. (1983). Relevance of atmospheric odours and geomagnetic field to pigeon navigation: what is the 'map' basis? *Comp. Biochem. Physiol.* **76A**, 643-663.

Williams, M. N. and Wild, J. M. (2001). Trigeminally innervated iron-containing structures in the beak of homing pigeons and other birds. *Brain Res.* **889**, 243-246.

Wiltschko, R. and Wiltschko, W. (2003). Orientation behavior of homing pigeons at the Gernsheim anomaly. *Behav. Ecol. Sociobiol.* **54**, 562-572.

Wiltschko, R., Stapput, K., Ritz, T., Thalau, P. and Wiltschko, W. (2007). Magnetoreception in birds: different physical processes for different types of directional responses. *HFSP J.* **1**, 41-48.

Wiltschko, R., Munro, U., Ford, H., Stapput, K. and Wiltschko, W. (2008). Light-dependent magnetoreception: orientation behaviour of migratory birds under dim red light. *J. Exp. Biol.* **211**, 3344-3350.

Wiltschko, W. (1978). Further analysis of the magnetic compass of migratory birds. In *Animal Migration, Navigation and Homing* (ed. K. Schmidt-Koenig and W. T. Keeton), pp. 302-310. Heidelberg: Springer-Verlag.

Wiltschko, W. and Wiltschko, R. (1982). The role of outward journey information in the orientation of homing pigeons. In *Avian Navigation* (ed. F. Papi and H. G. Wallraff), pp. 239-252. Heidelberg: Springer-Verlag.

Wiltschko, W., Munro, U., Beason, R. C., Ford, H. and Wiltschko, R. (1994). A magnetic pulse leads to a temporary deflection in the orientation of migratory birds. *Experientia* **50**, 697-700.

Wiltschko, W., Freire, R., Munro, U., Ritz, T., Rogers, L., Thalau, P. and Wiltschko, W. (2007). The magnetic compass of domestic chickens, *Gallus gallus. J. Exp. Biol.* **210**, 2300-2310.

Wiltschko, W., Munro, U., Ford, H. and Wiltschko, R. (2009). Avian orientation: the pulse-effect is mediated by the magnetic-receptors in the upper beak. *Proc. Biol. Sci.* **276**, 2227-2232.
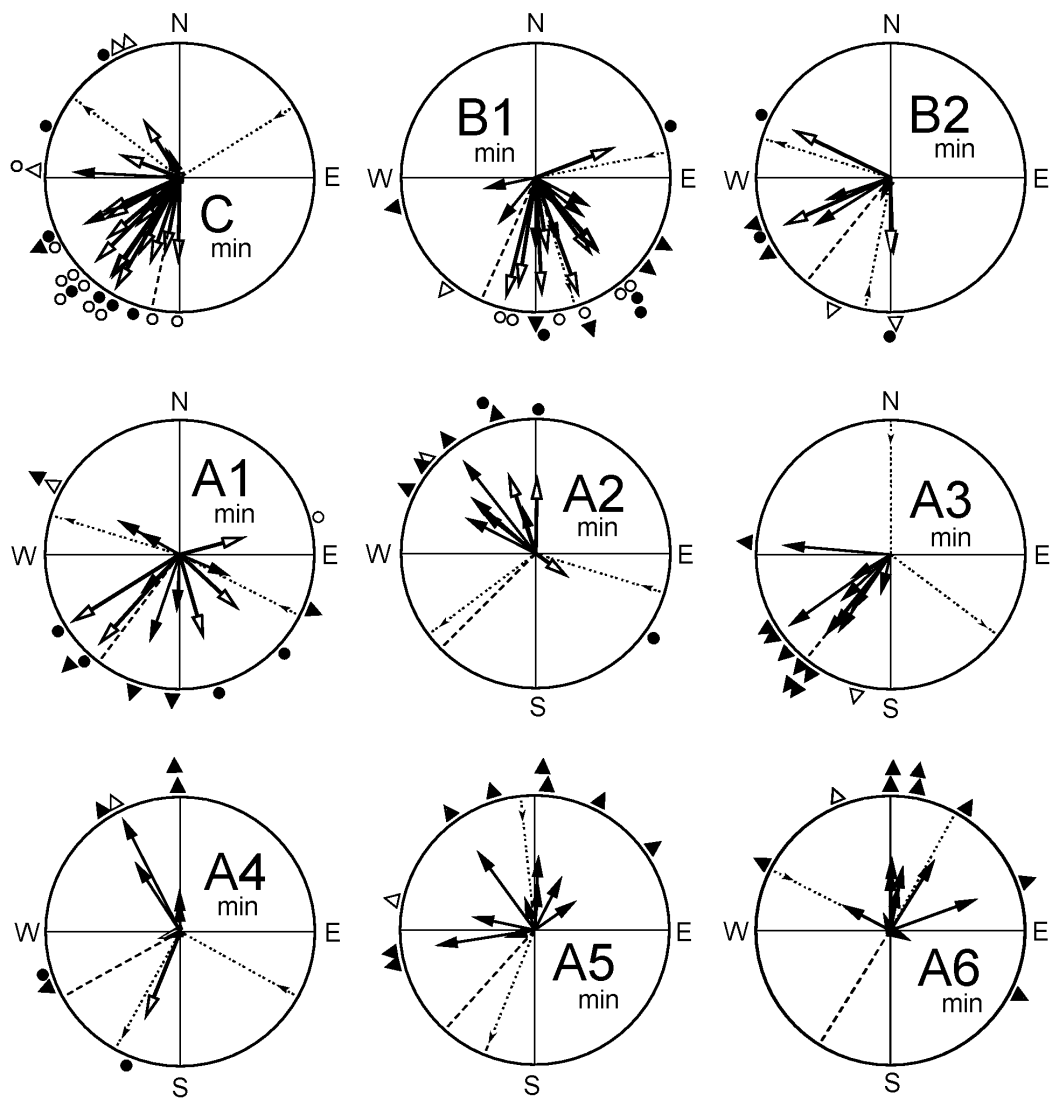
Fig. S1 Mean vectors 1 min after release at the nine site. The releases of the present study are given by arrows with a solid arrowheads, their mean directions are indicated by triangles; those performed prior to this study are given as arrows with open arrow heads and their mean directions are indicated by round symbols. Open symbols, pigeons familiar with the site; solid symbols, birds unfamiliar with the site. The home direction is indicated by a dashed *radius*, the gradient directions at 1 km are given by dotted *radii* with arrowheads, the arrowhead pointing outward indicating the direction of the maximum of increasing intensity at 1 km, those pointing inward the respective direction of decreasing intensity.

Table S1. Data from releases at the test sites prior to the present study

Site	Date	Fam?	N (N_b)	α	Δh	r	Van. int.	Return	Speed
C, Lich	26.04.1977	ufs	23 (20)	204°	+12°	0.88***	4:45	96%	22.7
192°, 40.6 km	26.03.1981	ufs	16 (15)	209°	+17°	0.79***	7:40	100%	29.7
	04.07.1981	fs	12 (10)	217°	+25°	0.97***	6:35	100%	34.3
	19.08.1984	fs	20 (10)	193°	+1°	0.91***	6:01	100%	29.7
	22.08.1984	fs	11 (8)	205°	+13°	0.93***	3:30	100%	38.6
	13.05.1986	ufs	23 (17)	195°	+3°	0.94***	3:04	96%	39.9
	25.07.1988	ufs	16 (12)	201°	+9°	0.88***	4:10	100%	29.7
	18.08.1988	ufs	17 (9)	(206°)	+14°	0.48$^{n.s.}$	3:56	100%	Not rec.
	21.08.1989	fs	15	214°	+22°	0.96***	2:00	100%	49.7
	02.09.1989	fs	13 (12)	201°	+9°	0.64 **	4:49	100%	Not rec.
	13.03.1990	fs	16 (13)	205°	+13°	0.81***	3:29	100%	21.5
	31.03.1990	fs	19 (11)	207°	+15°	0.84***	4:40	100%	Not rec.
	01.04.1990	fs	11	200°	+8°	0.80***	2:21	100%	Not rec.
	17.04.1990	fs	16 (11)	199°	+7°	0.92***	4:00	100%	Not rec.
	03.08.1991	ufs	8	247°	+55°	0.78***	2:26	100%	20.5
	08.05.1994	ufs	14 (11)	215°	+22°	0.88***	2:26	93%	42.3
	21.07.2000	fs	10	206°	+14°	0.92***	5:56	100%	65.2
B1, Hungen-Utphe	10.10.1982	ufs	15 (10)	203°	−1°	0.91***	7:50	93%	Not rec.
204°, 38.4 km	11.06.1985	fs	14 (12)	187°	−17°*	0.89***	3:14	93%	42.7
	21.08.1985	ufs	13 (10)	196°	−8°	0.93***	4:52	100%	38.3
	03.07.1986	ufs	17(12)	195°	−9°**	0.97***	3:18	100%	39.1
	10.09.1987	fs	21 (12)	190°	−14°	0.68**	3:54	95%	14.9
	23.09.1987	fs	13 (11)	208°	+4°	0.93***	4:07	100%	28.8
	23.06.1988	fs	12	190°	−14°	0.81***	4:43	100%	47.0
	18.05.1989	fs	10	199°	−5°*	0.99***	2:36	100%	Not rec.
	27.10.1991	fs	11	146°	−58°***	0.72**	3:30	100%	Not rec.
	10.05.1993	ufs	11	206°	+2°	0.99***	3:20	100%	56.2
B2, Lauterbach.	31.07.1990	ufs	18 (12)	241°	+22°	0.78***	3:01	100%	23.9
219°, 78.7 km	03.08.1990	ufs	13 (12)	271°	+52°***	0.86***	4:04	100%	34.4
	12.05.1998	ufs	11 (10)	189°	−30°	0.71**	4:06	73%	44.9
A1, Nidda	26.08.1983	ufs	10	246°	+29°*	0.94***	3:20	100%	31.7
217°, 39.1 km	04.07.1985	ufs	15 (12)	227°	+10°	0.81***	2:34	100%	65.2
	06.05.1986	ufs	11 (10)	(197°)	−20°	0.45$^{n.s.}$	4:39	100%	35.0
	24.09.1987	fs	14 (8)	(141°)	−76°	0.0 8$^{n.s.}$	6:17	100%	17.6
	18.05.1998	ufs	10	217	0°	0.88***	4:45	100%	58.7
A2, Ober Lais	27.05.1977	ufs	21 (10)	226°	+1°	0.61*	4:58	100%	Not rec.
225°, 44.8 km	02.06.1981	ufs	15 (10)	(203°)	−22°	0.39$^{n.s.}$	5:53	100%	28.9
	20.06.1988	ufs	17 (12)	(212°)	−13°	0.21$^{n.s.}$	8:49	100%	38.4
	15.06.1997	ufs	19 (17)	274°	+49°	0.47*	4:45	95%	Not rec.
A4, Ulmbach II	11.06.1987	ufs	17 (12)	239°	−4°	0.40$^{n.s.}$	5:34	100%	27.6
241°, 61.1 km	14.10.1999	ufs	10	234°	−7°	0.96***	4:15	100%	31.1

First column: positions of the release sites with respect to the anomaly: C, control site outside, B, sites at the border of the anomaly, A, sites within the anomaly; names of the release sites, home direction and distance to home. Fam?, the familiarity of the birds with the site: ufs, unfamiliar with the site; fs, familiar with the site. $N(N_b)$, number of pigeons release and, in parentheses, number of evaluable bearings; α, mean vanishing bearing; Δh, their difference to the home direction, with +indicating a difference to the right and − a difference to the left; r, length of mean vector, with asterisks indicating significance by the Rayleigh test (Batschelet, 1981). van. int., median vanishing interval in minutes:seconds; home, percentage of pigeons that returned; speed, median homing speed in km h^{-1}; not rec., indicates that the homing speed was not recorded. Significance levels: *$P<0.05$; **$P<0.01$; ***$P<0.001$; n.s., not significant.

Table S2. Bearings 1 min after release from the present study

Site	Date	Fam?	N_{min}	α_{min}	Δh_{min}	r_{min}	Δ 1 min-v.
C, Lich	29.7.2002	ufs	11	(334°)	(+142°)	$0.25^{n.s.}$	$-101°^{**s}$
192°, 40.6 km	9.8.2002	ufs	10	273°	$+81°^{**}$	0.80^{***}	$-34°^{**}$
	20.8.2002	fs	10	(339°)	(+147°)	$0.22^{n.s.}$	$-114°^{**s}$
	30.6.2004	ufs	10	244°	$+52°^{**}$	0.80^{***}	$-28°^{*}$
B1, Hungen-Utphe	18.4.2002	ufs	11	(258°)	(+54°)	$0.40^{n.s.}$	$-9°^{n.s.}$
204°, 38.4 km	22.4.2002	ufs	10	(129°)	(−75°)	$0.47^{n.s.}$	$+79°^{*}$
	14.6.2002	ufs	10	(118°)	(−86°)	$0.46^{n.s.}$	$+81°^{*s}$
	23.8.2002	fs	12	(219°)	(+15°)	$0.45^{n.s.}$	$-12°^{**s}$
	25.6.2004	ufs	13	160°	−44°	0.53^{*}	$+29°^{*s}$
	7.7.2004	ufs	11	180°	−24°	0.54^{*}	$+25°^{*s}$
B2, Lauterbach-R.	25.4.2002	ufs	10	(204°)	(−15°)	$0.19^{n.s.}$	$+5°^{*}$
219°, 78.7 km	21.5.2002	ufs	12	178°	−41°	0.58^{*}	$+15°^{**s}$
	29.7.2002	fs	12	251°	+32°	0.52^{*}	$-45°^{*s}$
	2.9.2004	ufs	13	238°	+19°	0.68^{**}	$-22°^{n.s.}$
A1, Nidda	22.4.2002	ufs	11	(225°)	(+8°)	$0.41^{n.s.}$	$-34°^{*}$
217°, 39.1 km	13.+15.5.	ufs	16	(113)	(−104°)	$0.36^{n.s.}$	$+110°^{n.s.}$
	14.8.2002	ufs	10	(299°)	(+82°)	$0.35^{n.s.}$	$-85°^{*}$
	20.8.2002	fs	10	(299°)	(+82°)	$0.53^{n.s.}$	$-63°^{*}$
	30.6.2004	ufs	14	(183°)	(−34°)	$0.43^{n.s.}$	$+21°^{n.s.}$
	7.7.2004	ufs	16	199°	−18°	0.69^{***}	$+13°^{n.s.}$
A2, Ober Lais	22.4.2002	ufs	10	(344°)	(+119°)	$0.37^{n.s.}$	$+179°^{**}$
225°, 44.8 km	9.5.2002	ufs	10	297°	$+72°^{*}$	0.59^{*}	$-159°^{*s}$
	14.8.2002	ufs	10	308°	$+83°^{*}$	0.52^{*}	$-64°^{n.s.}$
	23.8.2002	fs	9	311°	$+86°^{**}$	0.64^{*}	$-69°^{**}$
	2.9.2004	ufs	14	322°	+97°	0.88^{***}	$-49°^{**s}$
A3, Schottenring	18.4.2002	ufs	9	275°	$+56°^{**}$	0.81^{***}	$-61°^{n.s.}$
219°, 56.5 km	9.5.2002	ufs	9	(239°)	(+20°)	$0.35^{n.s.}$	$-21°^{*s}$
	26.6.2002	ufs	9	218°	−1°	0.71^{**}	$-29°^{n.s.}$
	9.7.2002	ufs	11	214°	−5°	0.70^{**}	$+2°^{n.s.}$
	3.9.2002	fs	13	(194°)	(−25°)	$0.31^{n.s.}$	$+24°^{**s}$
	14.6.2004	ufs	12	215°	−4°	0.51^{*}	$-2°^{n.s.}$
	5.7.2004	ufs	8	235°	+16°	0.93^{***}	$-18°^{n.s.}$
	22.8.2004	ufs	9	219°	0	0.78^{**}	$-4°^{n.s.}$
	17.9.2004	ufs	12	227	+8°	0.52^{*}	$-13°^{*s}$
A4, Ulmbach II	8.5.2002	ufs	10	327°	$+86°^{**}$	0.62^{*}	$-54°^{**}$
241°, 61.1 km	16.5.2002	ufs	12	(359°)	(+118°)	$0.32^{n.s.}$	$+166°^{**}$
	15.8.2002	ufs	11	(358°)	(+117°)	$0.24^{n.s.}$	$+136°^{n.s.}$

First column: positions of the release sites with respect to the anomaly: C, control site outside, B, sites at the border of the anomaly, A, sites within the anomaly; names of the release sites, home direction and distance to home. Fam?, the familiarity of the birds with the site: ufs, unfamiliar with the site; fs, familiar with the site. N_{min}, number of bearings 1 min after release; α_{min}, mean vanishing bearings 1 min after release; Δh_{min}, their difference to the home direction, with + indicating a difference to the right and − a difference to the left, and non-significant data given in parentheses; r_{min}, length of mean vector, with asterisks indicating significance by the Rayleigh test (Batschelet, 1981) Δ 1 min-v., change from 1 min after release to vanishing, with asterisks indicating a significant difference by the Watson Williams test if $r > 0.65$, otherwise by the Mardia Watson Wheeler test (Batschelet, 1981).

Table S3. Center of vectors and medians of the vector lengths 1 min after release

Release site		Position			Center of vectors after 1 min				Difference	
		α_{home}	d_{home} (km)	N	αh_{min}	a_{min}	Sign.	Med r_{min}	$\Delta 1$ min-v.	Sign.
C	Lich-Eberstadt	192°	40.6	4	+82°	0.43	n.s.	0.53	−45°	n.s.
B1	Hungen-Utphe	204°	38.4	6	−32°	0.33	*	0.46	+32°	n.s.
B2	Lauterbach	219°	78.7	4	+2°	0.43	n.s.	0.56	−15°	n.s.
A1	Nidda	217°	39.1	6	+5°	0.24	n.s.	0.42	−9°	n.s.
A2	Ober Lais	225°	44.8	5	+90°	0.58	*	0.59	−91°	*
A3	Schottenring	219°	56.5	9	+10°	0.58	***	0.70	−15°	*
A4	Ulmbach II	241°	61.1	5	+93°	0.42	n.s.	0.32	−119°	n.s.
A5	L.-Eichelhain	222°	65.9	9	+107°	0.30	*	0.45	−160°	***
A6	Groß-Felda	212°	68.2	9	+165°	0.33	*	0.46	−173°	***

Release sites: C, control site outside the anomaly; B, site at the border of the anomaly; A, site within the anomaly; Position: α_{home}, d_{home}, direction and distance to home; N, number of samples; αh_{min}, a_{min}, centers of vectors: direction with respect to home (+, clockwise and − counterclockwise deviation from the home directions) and distance from center: Sign., significant agreement between samples (Hotelling test for bivariate samples, Batschelet 1981); med. r_{min}, median vector lengths. Difference $\Delta 1$ min-v., angular difference between vectors 1 min after release and at vanishing with + indicating a clockwise and − a counterclockwise shift between 1 min and vanishing; Sign., significance of this difference [Mardia test for bivariate samples (Batschelet, 1981)]. Significance levels: *$P<0.05$; **$P<0.01$; ***$P<0.001$; n.s., not significant.

Table S4. Bearings 1 min after releases at the test sites prior to the present study

Site	date	Fam?	N_{min}	α_{min}	Δh_{min}	r_{min}	$\Delta 1$ min-van.
C, Lich	26.04.1977	ufs	22	199°	+7°	0.67***	+5°
192°, 40.6 km	26.03.1981	ufs	16	328°	+136°	0.50*	−119°
	04.07.1981	fs	10	(274°)	+82°	0.14$^{n.s.}$	−57°
	19.08.1984	fs	16	181°	−11°	0.63**	+12°
	22.08.1984	fs	10	191°	−1°	0.58*	+14°
	13.05.1986	ufs	21	208°	+16°	0.64***	−13°
	25.07.1988	ufs	14	(224°)	+32°	0.25$^{n.s.}$	−23°
	18.08.1988	ufs	13	(291°)	+99°	0.47$^{n.s.}$	−85°
	21.08.1989	fs	14	210°	+18°	0.95***	+4°
	02.09.1989	fs	12	222°	+30°	0.48$^{n.s.}$	−21°
	13.03.1990	fs	14	225°	+33°	0.88***	−20°
	31.03.1990	fs	18	241°	+49°	0.63***	−34°
	01.04.1990	fs	11	215°	+23°	0.89***	−15°
	17.04.1990	fs	16	230°	+38°	0.70***	−31°
	03.08.1991	ufs	8	246°	+54°	0.62*	+1°
	08.05.1994	ufs	12	214°	+22°	0.89***	+1°
	21.07.2000	fs	10	228°	+30°	0.38$^{n.s.}$	−22°
B1, Hungen-Utphe	10.10.1982	ufs	15	(142°)	(−62°)	0.29	+61°
204°, 38.4 km	11.06.1985	fs	11	139°	−65°**	0.70***	+48°
	21.08.1985	ufs	13	140°	−64°**	0.72***	+56°
	03.07.1986	ufs	13	69°	−135°**	0.62**	+126°
	10.09.1987	fs	12	144°	−60°**	0.70***	+46°
	23.09.1987	fs	13	171°	−33°	0.56*	+37°
	23.06.1988	fs	12	160°	−44°**	0.93***	+30°
	18.05.1989	fs	9	194°	−10°	0.92***	+5°
	27.10.1991	fs	11	189°	−15°	0.82***	−43°
	10.05.1993	ufs	11	177°	−27°*	0.87***	+29°
B2, Lauterbach.	31.07.1990	ufs	18	249°	+30°**	0.86***	−8°
219°, 78.7 km	03.08.1990	ufs	12	296°	+77°**	0.80***	−25°
	12.05.1998	ufs	11	180°	−39°	0.56*	+9°
A1, Nidda	26.08.1983	ufs	8	164°	−53°*	0.64*	+82°
217°, 39.1 km	04.07.1985	ufs	14	222°	+5°	0.89***	+5°
	06.05.1986	ufs	10	133°	−84°**	0.59*	+64°
	24.09.1987	fs	12	75°	−142°	0.50*	+66°
	18.05.1998	ufs	9	238°	+21°*	0.94***	−21°
A2, Ober Lais	27.05.1977	ufs	20	244°	+19°	0.72***	−18°
225°, 44.8 km	02.06.1981	ufs	12	(126°)	(−99°)	0.29$^{n.s.}$	+77°
	20.06.1988	ufs	16	341°	+116°**	0.62**	−129°
	15.06.1997	ufs	17	1°	+136**	0.57**	−87°
A4, Ulmbach II	11.06.1987	ufs	14	252°	−11°	0.16$^{n.s.}$	−13°
241°, 61.1 km	14.10.1999	ufs	9	202°	−39°	0.69**	+32°

First column: positions of the release sites with respect to the anomaly: C, control site outside, B, sites at the border of the anomaly, A, sites within the anomaly; names of the release sites, home direction and distance to home. Fam?, indicates the familiarity of the birds with the site: ufs, unfamiliar with the site and the anomaly; ufs, unfamiliar with the site, but familiar with other sites within the anomaly; fs, familiar with the site. N_{min}, number of bearings 1 min after release; α_{min}, mean vanishing bearings 1 min after release; Δh_{min}, their difference to the home direction, with + indicating a difference to the right and − a difference to the left, and non-significant data given in parentheses; r_{min}, length of mean vector, with asterisks indicating significance by the Rayleigh test (Batschelet, 1981); $\Delta 1$ min-v., change from 1 min after release to vanishing.

Table S5. Coefficients of the Spearman rank correlation for vector lengths 1 min after release (N=9)

Variable	Data set	Difference between home and release site	Range within 1 km radius	Range within 2.5 km radius	1 km in home direction
Vector lengths 1 min after release:	All releases	−0.113	+0.096	−0.029	+0.254
	Birds unfamiliar with the site	−0.321	−0.054	−0.213	−0.004
	Birds familiar with the site	+0.600*	−0.067	−0.167	+0.383

*P=0.05.