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Supplemental Information

The Role of the Magnetite-Based Receptors in the Beak in Pigeon Homing

Roswitha Wiltschko, Ingo Schiffner, Patrick Fuhrmann, and Wolfgang Wiltschko

Supplemental Information Part 1: Magnetic Conditions at the Test Sites

The Vogelsberg anomaly originates from repeated ancient lava flow of an extinct volcano. The geomagnetic field in this anomaly is highly irregular, changing from positive to negative intensity values, with very steep local gradients in varying directions. Maximum positive intensity deviations are in the range of up to 850 nT, the negative ones in a range of up to 375 nT, with steep local gradients of up to 3280 nT/km. With the physical properties of the rocks not known, changes in declination and inclination can only be roughly estimated. Declination, the deviation of magnetic north from true north, is probably not measurably affected; the changes of inclination are estimated to be in the range of less than 1°.

From the six release sites within the anomaly used in a previous study [S1], we choose the sites A2, A4, A5 and A6. We also selected four control sites in comparable distances in regions where the geomagnetic field is more or less regular; with control site C identical with the one used before [S1]. Details on the local magnetic situation at these sites are given in Figure 2 in the main text, the respective numerical data are included in Table S1. The magnetic data are based on digital data giving the differences of magnetic intensity from the reference field for 100 x 100 m squares, provided by the Leibniz-Institute for Applied Geophysics, Hannover, Germany. They were obtained by mapping the local intensity from a plane at an altitude of 1000 m above NN, i.e. between about 410 and 815 m above ground at the test sites, and are based on the defined geomagnetic reference field after DGRF (1980.0). At the altitude where the pigeons fly, the differences may be even larger.

Table S1. Test Sites: Position and Local Magnetic Conditions

			Position		Max. positive diff. within 2.5 km		Max. negative diff. within 2.5 km		Conditions within 2.5 km	
Release site		Altitude	α_{home}	dis_{home}	ΔB	Dir.	ΔB	Dir.	ΔB	SD (ΔB)
Anomaly sites										
A2	Ober-Lais	296 m	225°	44.8 km	+150	244°	- 90*	148°	240	48.2
A4	Ulmbach II	420 m	241°	61.1 km	+80*	281°	- 54	334°	134	34.8
A5	Eichelhain	590 m	220°	65.9 km	+155	293°	-170*	183°	325	67.2
A6	Groß-Felda	368 m	212°	68.2 km	+262	206°	- 70*	297°	332	69.7
Control sites										
C	Lich	185 m	192°	40.6 km	+24*	18°	- 22*	53°	46	11.5
C2	Essenheim	249 m	61°	42.2km	+5	138°	- 7	247°	12	4.2
C3	Beselich	230 m	133°	53.3 km	+16	349°	-9*	338°	25	3.5
C4	Bickenbach	419 m	91°	81.5 km	+12	42°	- 11	206°	23	3.0

Altitude of the site is given above NN; α_{home}, dis_{home}, home direction and distance. The column Max. positive diff. within 2.5 km indicates the maximum positive difference in intensity within 2.5 km in nanoteslas, with * indicating that the maximum is closer than 2.5. km; Dir. gives the direction in which the maximum difference is found. The column max. negative diff. within 2.5 km gives the respective data for the maximum negative difference in intensities. In the last columns, ΔB indicates the maximum absolute difference within a 2.5 km radius and SD (ΔB) gives the standard deviation of the intensity values within this radius, both in nanoteslas.

Supplemental Information Part 2: The Nature of the Magnetic ‘Map’ Factors

Magnetic intensity and inclination both show gradients running roughly from the magnetic poles to the magnetic equator; hence they could be used, theoretically at least, as magnetic components in the navigational ‘map’. Magnetic declination also shows spatial variation and could be included in the ‘map’.

Magnetic declination appears to be the least likely candidate for a ‘map’ factor. Being defined in relation to true North, its determination would require that birds are able to determine this reference direction as well as the magnetic direction with sufficient accuracy. Yet birds have no easy means of determining true north. The sun compass can hardly be used, since it is established by learning processes with the magnetic field as reference for recording the sun’s changing position in the course of the day [S2]. The magnetic compass itself may not be accurate enough to record the required small changes in direction, as its accuracy is estimated to be in the range of ± 10° to 15° (see [S3]). Also, in the many parts of the world, changes in declination are extremely small.

Inclination, defined as the angular difference between the direction of the magnetic vector and the horizontal, also requires determining magnetic directions against a reference direction. Using the horizon itself appears rather unlikely, since the horizon line is often modified by structures of the terrain. Using the downward direction indicated by gravity seems more likely, because most animals have a sense of gravity. However, the differences in inclination to be detected are extremely small - e.g. in the region of Frankfurt, Germany (50°08'N, 8°40'E), the gradient of inclination is 0.7°/100 km or 0.007°/km. It seems highly unlikely that the combination of determining gravity and magnetic directions can reach the required accuracy in particular in flying animals. At least the birds’ ability to determine directions in the horizontal appears to be far less accurate [S3]. It makes no sense to postulate an extremely accurate mechanism to determine magnetic directions in the vertical, but to assume one by powers of ten less accurate in the horizontal. This speaks against the use of inclination as a navigational factor.

Magnetic intensity is the only factor that does not require a reference. In the Frankfurt region, the intensity gradient of the reference field is about 2.5 nT/km. - Electrophysiological recordings from the ophthalmic nerve, the branch of the *nervus trigeminus* that innervates the receptors in the upper beak, indeed produced answers to changes in magnetic intensity. Significant responses to differences of 200 nT are reported; smaller differences were not tested [S4]. Behavioural data, however, suggest a markedly greater accuracy in detecting intensity changes: when pigeons were released repeatedly from the same site, their vanishing bearings were found to be correlated with temporal fluctuations of the geomagnetic field. These fluctuations were seldom more than 70 nT and commonly less than 40 nT [S5], so that a sensitivity of pigeons in this range is suggested.

In summary, theoretical considerations as well as experimental data point to intensity being the magnetic factor included in the navigational ‘map.’

Supplemental Information Part 3: Data of the Individual Releases

Tables S2 and S3 give the mean vectors, the median vanishing intervals, the median homing speed and the return rate of the individual releases within the magnetic anomaly and outside in magnetically quiet terrain, marking samples that are significantly oriented by the Rayleigh test. Significant differences between experimental birds released with their upper beak anesthetized and untreated control birds are indicated.

Table S2. Data from the Individual Releases within the Magnetic Anomaly

			Vanishing bearings						
Date	Tr.	n (n_b)	α_m	Δh	r_m	Sign. diff.?	Vanishing interval (min:s)	Homing speed (km/h)	Return rate
A2 Ober-Lais, 225°, 44.8 km									
3.5.2007	C (fr)	13 (10)	133°	- 92°	$0.17^{n.s.}$		7:11	46.4	77%
	Xy	13 (10)	216°	- 9°	0.91***	*	3:59 **	48.0	92%
14.8.2007	C fr	12 (10)	57°	- 68°	$0.20^{n.s}$		9:45	35.8	100%
	Xy	11 (10)	229°	+4°	$0.27^{n.s}$		5:43	42.0	91%
8.5.2008	C m	15 (10)	231°	+6°	$0.27^{n.s}$		6:25	47.2	100%
	Xy	15 (10)	246°	+21°	0.82***	*	3:54 *	54.9	100%
A4 Ulmbach, 241°, 61.1 km									
24.5.2007	C uf	10	224°	-17°	0.91***		3:02	14.5	100%
	Xy	12 (10)	205°	- 36°	0.88***		2:06 *	39.0 *	100%
23.4.2008	C fr	10	212°	- 29°	0.73**		4:31	39.8	90%
	Xy	10	185°	- 56°	0.92***	**	3:46	35.6	100%
7.5.2009	C uf	12 (10)	231°	- 10°	$0.45^{n.s.}$		9:14	19.9	92%
	Xy	13 (10)	271°	+30°	0.56 *		6:21	33.9	92%
A5 Eichelhain, 222°, 65.9 km									
30.4.2007	C (fr)	11 (10)	136°	- 86°	$0.26^{n.s.}$		4:34	36.6	100%
	Xy	12 (10)	172°	- 50°	0.81***	**	3:38	52.7 **	100%
19.6.2007	C uf	12 (11)	166°	- 56°	0.91***		6:30	26.2	100%
	Xy	13 (10)	184°	- 38°	0.74**		5:06	26.7	92%
5.5.2008	C uf	13 (10)	110°	- 112°	$0.42^{n.s.}$		9:32	52.7	100%
	Xy	11 (10)	209°	- 13°	0.71 **	*	6:21 *	47.1	100%
A6 Groß-Felda, 212°, 68.2 km									
1.9.2006	C uf	11 (10)	184°	- 28°	$0.48^{n.s.}$		10:24	30.3	100%
	Xy	12 (10)	64°	-148°	$0.09^{n.s.}$		5:12 **	35.9	100%
25.4.2007	C uf	14 (10)	132°	- 80°	0.65 *		9:49	23.5	86%
	Xy	13 (10)	159°	- 53°	0.72**		9:14	16.4	77%
17.6.2009	C fr	10	187°	- 25°	0.79***		10:02	32.5	100%
	Xy	12 (10)	196°	- 16°	0.87***	*	7:04 *	42.2	83%

Tr., treatment: C, control pigeons without treatment, Xy pigeons with the upper beak anesthetized with Xylocain; fr, familiar with the region: birds that had homed from another site within the anomaly before; uf, unfamiliar with the region: birds homing from within the anomaly for the first time (parentheses indicate that this applies to all but one birds of the sample); m, a mixture of familiar and unfamiliar birds. n (n_b). number of pigeons released and, in parentheses, number of vanishing bearings, if not identical; α_m, mean bearing; Δh, mean bearing with respect to the home direction, with + indicating a clockwise and – a counter-clockwise deviation, r_m , mean vector length, with asterisks indicating significance by the Rayleigh test [S6]; asterisks in the column 'Sign. diff.?' indicate significant differences in vanishing bearings, and asterisks at vanishing intervals and homing speed indicate significant differences in these two parameters between experimentals and controls by the Mann Whitney U-test. Significance level: *, $p < 0.05$; **, $p < 0.01$, ***, $p < 0.001$; n.s., not significant.

Table S3. Data from the Individual Releases in Magnetically Quiet Terrain outside the Anomaly

			Vanishing bearings			Sign. diff.?	Vanishing interval (min:s)	Homing speed (km/h)	Return rate
Date	Tr.	n (n_b)	α_m	Δh	r_m				
C Lich, 192°, 40.2 km									
27.8.2007	C	10	236°	+44°	0.98***		2:33	31.7	100%
	Xy	11 (10)	225°	+33°	0.93***		3:53 **	38.3	100%
30.7.2007	C	10	223°	+31°	0.73**		7:02	43.1	100%
	Xy	10	234°	+42°	0.68**		5:50	20.8 *	100%
30.4.2008	C	15 (10)	191°	-1°	0.67**		6:23	33.4	100%
	Xy	14 (10)	213°	+31°	0.49 $^{\text{n.s.}}$		6:50	39.9	93%
C2 Essenheim, 61°, 42.2 km									
24.8.2007	C	12 (10)	63°	+2°	0.85***		4:04	18.1	100%
	Xy	11 (10)	72°	+11°	0.90***		4:25	44.4	100%
6.4.2008	C	11 (10)	68°	+7°	0.88***		4:04	26.1	100%
	Xy	10	97°	+36°	0.76**	*	3:26	27.2	100%
24.4.2009	C	11 (10)	93°	+32°	0.93***		6:02	32.5	100%
	Xy	11 (10)	93°	+32°	0.80***		4:22	42.9 *	100%
C3 Beselich, 135°, 51.9 km									
13.9.2007	C	12 (10)	191°	+56°	0.31 $^{\text{n.s.}}$		7:38	14.0	75%
	Xy	12 (10)	170°	+35°	0.79***		10.45	13.1	83%
7.5.2008	C	14 (10)	171°	+36°	0.76**		6:23	34.2	93%
	Xy	12 (10)	217°	+82°	0.71**		4:13	24.0	83%
20.5.2009	C	11 (10)	197°	+62°	0.94***		3:37	12.5	55%
	Xy	10	179°	+44°	0.70**	**	4:59 *	16.7	90%
C4 Bickenbach, 91°, 81.5 km									
14.9.2007	C	11 (10)	121°	+30°	0.84***		7:51	34.0	92%
	Xy	10	146°	+55°	0.36 $^{\text{n.s.}}$	**	10:13	7.0	80%
3.5.2008	C	12 (10)	109°	+18°	0.88***		4:49	27.3	75%
	Xy	10	155°	+64°	0.55 *	*	7:03 *	32.2	100%
14.4.2009	C	12 (10)	176°	+85°	0.89***		4:52	28.8	92%
	Xy	11 (10)	192°	+101°	0.81***		6:09 *	13.8	82%

Symbols and abbreviations as in Table S2.

Within the anomaly, the control birds are significantly oriented in 5 of the 12 releases, while the experimentals with their beak anesthetized show oriented behaviour in 10 of the 12 releases. At the magnetically quiet control sites, the vast majority of samples was significantly oriented: 11 of the 12 control samples and 10 of the 12 experimental ones.

The differences between experimentals and controls reveal an interesting pattern: within the anomaly (Table S2), in all cases where there is a significant difference in vanishing bearings, the birds with the beak anesthetized have the longer vector indicating better orientation. Also, in all cases with a significant difference in vanishing interval, these birds take less time to vanish from sight. The shorter vectors and the longer vanishing intervals of the untreated controls seem to reflect the confusing effect of the anomalous magnetic situation.

Outside the anomaly, the trend is reversed (see Table S3): in all cases with a significant difference in vanishing bearings and vanishing intervals, the control birds have significantly longer vectors and vanish significantly faster.

Vanishing bearings and vectors of the three releases at the eight sites are given in Figure S1.

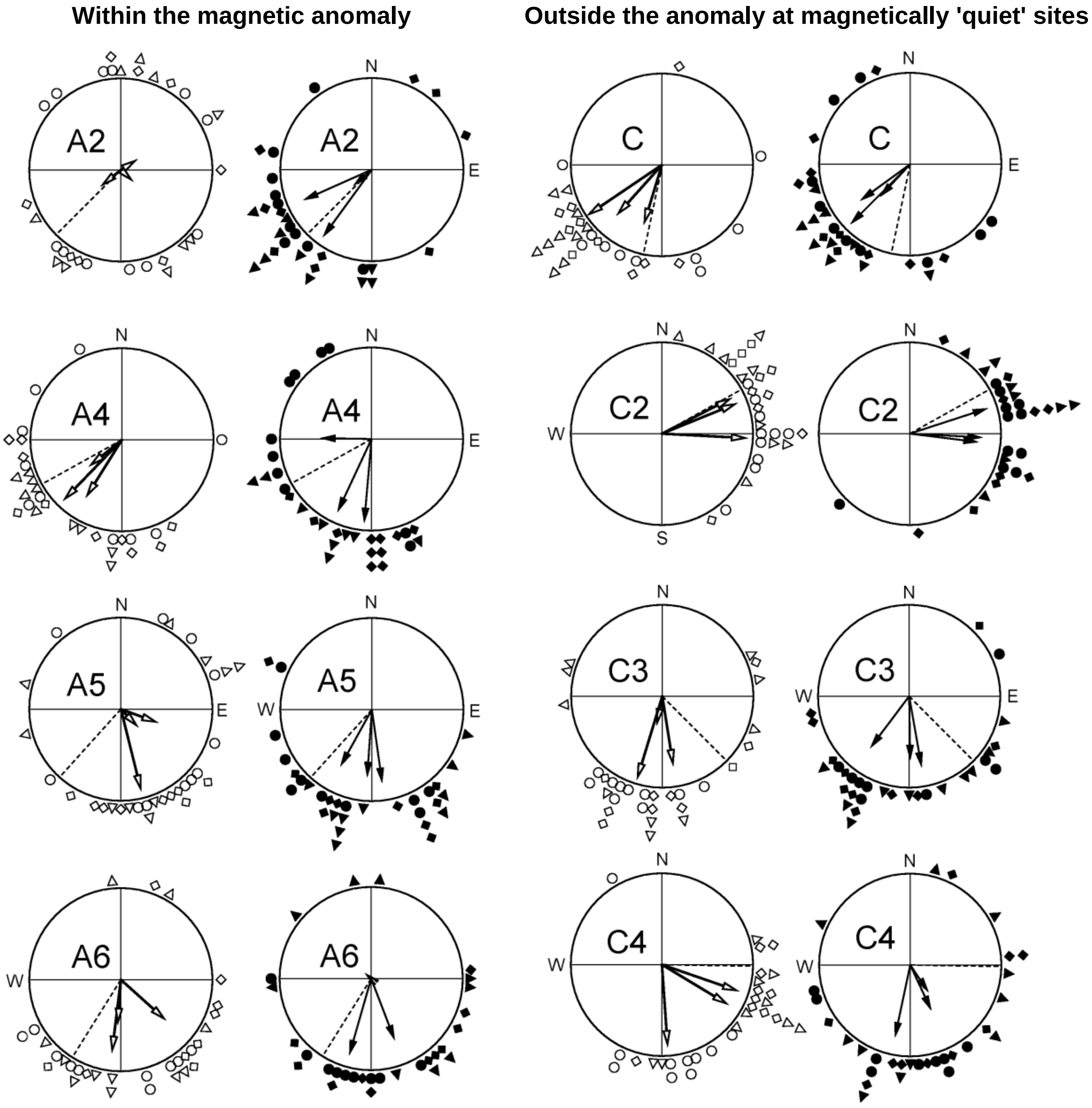

Figure S1. Initial Orientation within and outside the Anomaly
The home direction is given by a dashed radius. The vanishing bearings of the three releases at each of the eight sites are marked in different symbols; the arrows represent the respective mean vectors. Open symbols: untreated control pigeons; solid symbols: experimental pigeons with their upper beak locally anesthetized.

Supplemental Information Part 4: Effect of Familiarity with Other Sites in the Same Anomaly

Lednor and Walcott, who studied the effect of strong magnetic anomalies in America, reported that their pigeons were disoriented when they were released in an anomaly for the first time; if they had homed from another site within the same anomaly, however, they departed significantly oriented [S7]. Kiepenheuer also observed that pigeons released a second time in the Kaiserstuhl anomaly in southern Germany were homeward oriented [S8].

Because of a limited number of test birds, we had to release some pigeons in the anomaly more than once, in our previous [S1] as well as in the present study. In the previous study, we had found that experience at other sites within the anomaly did not affect the behaviour of our pigeons, whereas on a second flight from the same site, the observed correlations of vector lengths and vanishing intervals with the local magnetic conditions disappeared. In the present study, six releases within the anomaly involved pigeons released in the anomaly for the first time and five involved pigeons that had been released within the anomaly before; the respective releases are marked in Table S2. Table S4 compares the median of the various variables of the two groups with the Mann-Whitney U-test.

Table S4. Effect of Previous Experience within the Anomaly

	Controls				Experimentals			
Variable	first time	repeated	U	p	first time	repeated	U	p
Deviat. home	42°	68°	11	0.268	37°	16°	10	0.214
Vector length	0.57	0.26	8	0.123	0.71	0.87	7	0.089
Vanish. interval	9:23	7:11	13	0.396	5:46	3:59	11	0.268
Homing speed	25.1	36.6	5	0.041 *	35.2	42.2	5	0.041 *

Deviat. home, deviation from the home direction; Vanish. interval, vanishing interval in min:s; Homing speed is given in km/h. U, test statistic of the Mann Whitney U-test; p, probability of error.

Again, we find no significant effect of familiarity with the anomaly on the variables of initial orientation. Only homing speed was significantly increased when the birds had homed from other sites in the anomaly before, which is not surprising, since familiarity with the region is known to usually increase homing speed [S9].

An improved orientation on a second flight as described by our colleagues [S3, S4] was thus not observed. Lednor and Walcott report this phenomenon from two sites without documenting the local magnetic situation; possibly, the magnetic conditions at the two sites were more similar than those at our test sites, where they are very different indeed (see Figure 2 in the main text). Also, it cannot be excluded that the American pigeons have recognized being in the same anomaly and simply flew the net direction that had eventually led them home on their last flight from there [S3]. The same may be true for the pigeons in the Kaiserstuhl anomaly; possibly, these birds were released a second time at the same sites [S4]. Indeed, American pigeons were disoriented in the anomaly when they had homed before from other anomalies with different home directions [S3].

Furthermore, in contrast to the American pigeons and those released at Kaiserstuhl, our birds were not always disoriented when released in anomaly for the first time (see [S1] and Table S2), relying on nonmagnetic cues. Lednor and Walcott [S3] also discussed the use of nonmagnetic cues for their pigeons. The observation that our pigeons could use such cues already when released for the first time is in agreement with the assumption that suitable nonmagnetic cues are easier available in the Vogelsberg anomaly than in the other anomalies.

Supplemental References

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