

PIGEON HOMING: EFFECTS OF MAGNETIC PULSES ON INITIAL ORIENTATION

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ABSTRACT.—After treatment with a 0.5-T magnetic pulse, homing pigeons (*Columbia livia*) showed headings that deviated from the mean direction of untreated controls. These deflections ranged up to 60° and were most pronounced at distances beyond 100 km from the home loft. When birds treated with a pulse south-anterior and birds treated with south-left were released together, they deviated to opposite sides of the untreated controls, indicating that the direction of the pulse determined its specific effects. On the day of treatment, a south-left pulse caused a significantly larger deflection than a south-anterior pulse. The duration of the effects was not entirely clear; the number of releases with significant deflections seemed to decrease as time passed and birds had made additional homing flights. Our findings agree with the hypothesis that magnetite-based receptors provide the pigeons with orientational information. The manifestations of the effect indicate that the magnetic “map” rather than the magnetic compass is involved. Apparently, the pulse specifically alters map information. Received 24 September 1996, accepted 30 January 1997.

AN INCREASING BODY OF EVIDENCE indicates that birds can detect the earth’s magnetic field and extract meaningful directional information from it. Compass orientation based on the magnetic field has been demonstrated in various species of migratory birds and in the nonmigratory homing pigeon (*Columba livia*; see R. Wiltschko and W. Wiltschko 1995). However, directional information is not the only type of information the magnetic field can provide. In the last century, Viguier (1882) proposed that pigeons might use magnetic parameters that have gradients, such as total intensity and inclination, for determining position and deriving their home direction after displacement. This idea led to the model of a navigational “map” for bicoordinate navigation (see Wallraff 1974), with at least one component being magnetic (e.g. Yeagley 1947). Experimental data indeed suggest that magnetic parameters are involved in the pigeon’s map (see R. Wiltschko and W. Wiltschko 1995).

The use of magnetic map factors would require birds to detect minute differences in total intensity and/or inclination. Whether pigeons are able to do this is unclear, because the transducer mechanisms for magnetoreception are not known. Of the potential mechanisms that

have been discussed, the two hypotheses currently receiving the most attention are: (1) magnetoreception via excited-state photopigments (Leask 1977, Schulten 1982), and (2) magnetoreception via ferrimagnetic material such as magnetite (Gould et al. 1978, Kirschvink and Gould 1981). Electrophysiological (Semm and Demaine 1986) and behavioral evidence (W. Wiltschko and R. Wiltschko 1981, 1995; Wiltschko et al. 1993) so far suggest that light-dependent mechanisms provide the directional information. Magnetic material, at least some of it magnetite, has been reported from several species of birds, including pigeons (Walcott et al. 1979, Ueda et al. 1982, Beason and Brennan 1986, Edwards et al. 1992). Hence, a magnetite-based mechanism appears to be a promising candidate for providing birds with magnetic map information. The amount of material that has been found, if it is single-domain magnetite and connected to the nervous system, is sufficient to permit the sensitivity needed for magnetic navigation (Yorke 1979, 1981; Kirschvink and Gould 1981).

Initial attempts to treat pigeons before release with strong magnetic fields in order to affect their navigation has produced mixed results. Kiepenheuer et al. (1986) reported a significant deflection in vanishing bearings and an increase in scatter for pigeons subjected to a 10-T (tesla) magnetic field, compared with con-

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trols. Walcott et al. (1988) subjected pigeons to strong steady or alternating fields, or to a steep magnetic gradient, and found no effects. The latter findings seem to argue against magnetite-based receptors, but the effectiveness of the treatments may have been minimized by the manner in which the magnetic fields were applied. Electromagnets were used, and, as current is supplied, the intensity of the field increased gradually. Single-domain magnetite particles that have been reported in pigeons (Walcott et al. 1979) are of small size and, consequently, have small angular momentum. If such particles were free to move, then they could have aligned themselves with the applied external field so that their magnetic axes remained unaltered; afterwards, they would return to their original orientations so that the applied field would only have temporarily rotated them, not changed their magnetization.

This problem can be overcome by magnetizing the birds with a brief pulse (Kirschvink 1983). In the present study, we used a pulse that was sufficiently strong to alter the magnetization of single-domain magnetite. The pulse had a rise time of nanoseconds so that the viscosity of the cytoplasm should have prevented the particles from rotating fast enough to align themselves before they were remagnetized. Consequently, the magnetization of particles incorporated in magnetoreceptors should have been altered, which, in turn, should have affected the pigeons' detection of any magnetic component in the map. Given these results, differences in map information would be reflected by changes in initial orientation in pigeons that are released away from their loft.

METHODS

Test birds.—A total of 30 releases was performed in spring and summer from 1989 to 1992, all under sunny skies so that the pigeons could have used their sun compass. The test birds were housed in the loft at the University of Frankfurt (50°40'N, 8°40'E). They were adult pigeons at least one year old and experienced at homing. During their first months of life, they had participated in a standard training program up to 40 km around their loft; additionally, they homed from distances up to 150 km in various directions, with the number of such flights increasing with increasing age.

Treatment with a magnetic impulse.—The magnetic impulse was produced by a solenoid composed of 150 turns of 1.2-mm diameter copper wire wound on

a 10-cm diameter plastic pipe (similar to the design of Kirschvink 1983). A bank of seven electrolytic capacitors (1,100 μ F each) connected in parallel was charged to 300 V, then discharged through the solenoid using a silicon-controlled rectifier. A diode across the solenoid maintained a unidirectional field within the solenoid and prevented the capacitors from reverse-charging. The intensity of the pulse was approximately 0.5 T, its duration about 5 ms.

The effectiveness of the apparatus was tested by magnetizing the frozen head of a Bobolink (*Dolichonyx oryzivorus*) and comparing the resulting isothermal remanent magnetization induced with that produced by subjecting the same frozen head to a 0.7-T magnetic field of a calibrated electromagnet. There was no difference in the amount of remanent magnetization produced by either treatment, indicating that the pulse magnetizer was saturating the material in the heads.

For all experiments, the solenoid was oriented with its main axis east-west and so that the pulse induced a magnetic south pole toward the west end of the solenoid. The birds were placed in from the east. Thus, when their heads were straight, the magnetization was *south-anterior*. In some experiments, the bird's head was turned 90° to the right, resulting in a *south-left* magnetization. All experimental birds were treated only once; completely untreated birds served as controls to evaluate the effect of the treatment.

Release procedure.—The birds were treated in the morning before departure for the first release. Sixteen such tests were performed on the day of treatment. In eight tests, birds that homed from the first release were released again for a second homing flight from another site one or two days later. In six cases, such birds were released a third time from a third site between the fourth and the seventh day after treatment.

The release sites were 40 to 170 km from the home loft in various directions (Fig. 1). The birds were released singly, alternating experimentals and controls, and observed by one or two people using 10 \times 40 binoculars until the birds vanished from sight. Their vanishing bearings were measured with a compass to the nearest 5°, and the vanishing intervals were recorded with a stopwatch. Helpers at the loft recorded the birds upon return.

Data analysis.—For each release and each group of pigeons, a mean vector was calculated by vector addition from the vanishing bearings. This vector was tested with the Rayleigh test for significant directional preference. The vectors of experimentals and controls were tested with the Watson-Williams test for differences in direction, or, if one of the vectors did not reach 0.65, with the Mardia-Watson-Wheeler test for differences in distribution (Batschelet 1981). Vanishing intervals were compared using a Mann-Whitney *U*-test.

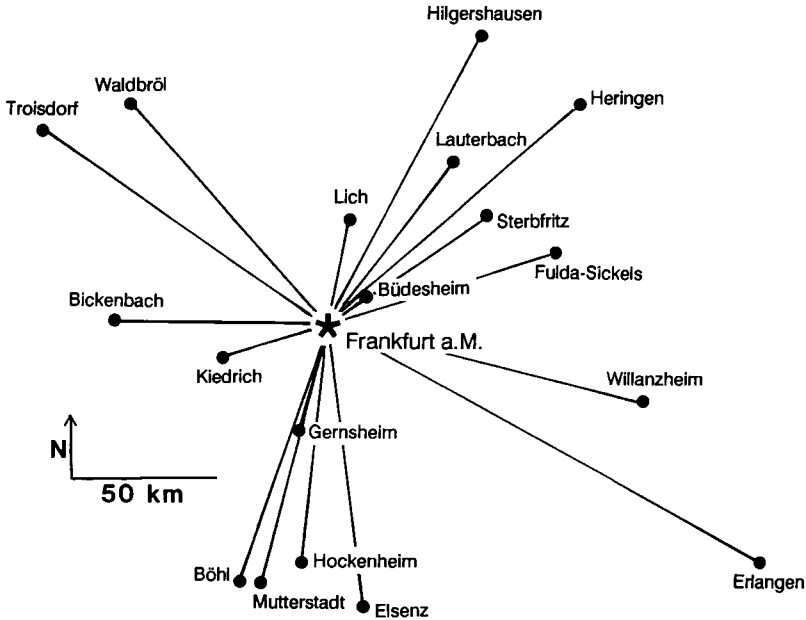


FIG. 1. Locations of pigeon release sites relative to the home loft at Frankfurt, Germany.

Further analysis of the deflections was based on the angular difference between mean directions of the experimentals and controls (δC). Here, we considered only δC s that were based on two vectors that were statistically significant ($P < 0.05$) by the Rayleigh test. The sizes of the deviations produced by the two types of magnetization—south-anterior and south-left—were compared using Mann-Whitney U -tests. Relationships between δC and distance were tested with Spearman rank correlation. Variables such as vector lengths and median vanishing intervals were compared with Wilcoxon tests.

RESULTS

The great variability of the effect was striking; sometimes it was highly significant, and in other cases it was negligible. Considering only cases when vectors for both the controls and the experimentals were significant, differences ranged from 1° to 59° . Some trends were evident, however. First, the effect appeared to manifest itself only at greater distances. Within 100 km of the loft, significant differences between experimental birds and controls were rare, whereas beyond 100 km, most of the releases resulted in significant deflections, at least within the first two days after treatment (Fig. 2). The south-anterior birds released on the day of treatment showed a significant cor-

relation between deflections and distance from the loft ($r_s = 0.748$, $n = 12$, $P < 0.01$), but no such correlation existed in the south-left birds ($r_s = -0.058$, $n = 6$, $P > 0.05$). After the first homing flight, the deflections were not correlated with distance in either group.

Second, the orientation of treatment determined the direction and extent of the responses. When south-anterior and south-left birds were released together, the two groups deviated from the controls to different sides (e.g. Fig. 3). The difference between the two groups was significant in all tests on the day of treatment (Table 1) and in three of four tests performed within the following two days (see Table 2). On the day of treatment, the south-left groups showed significantly greater deflections (median 37°) than did the south-anterior groups (median 12° ; Mann-Whitney test, $P < 0.01$). This also was true when only the releases beyond 50 km were considered. The difference disappeared after one or two days and one homing flight.

There did not seem to be a constant relationship between the direction of treatment and the deflection induced. For example, of the groups treated south-anterior and released beyond 50 km on the day of treatment, four showed a clockwise and five a counterclockwise devia-

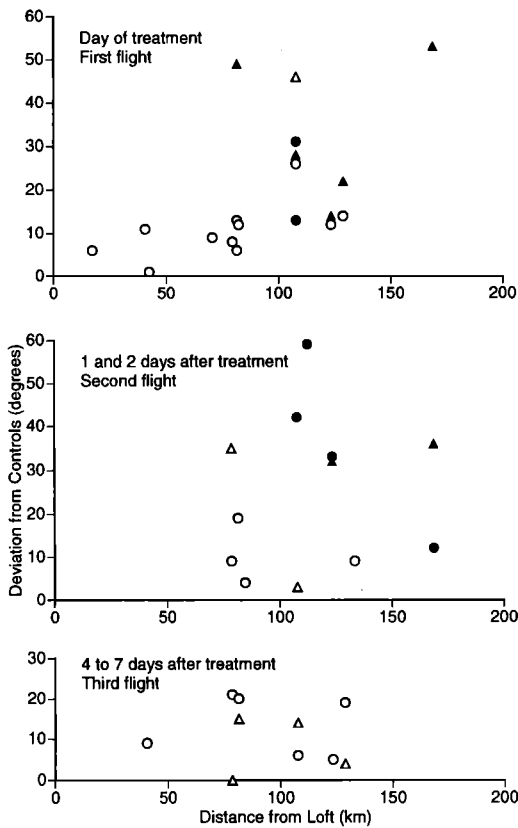


FIG. 2. Deflections from the mean of untreated control pigeons induced by treatment with a magnetic pulse south-anterior (circles) and south-left (triangles) at various distances. Filled symbols indicate significant differences between experimental and control pigeons ($P < 0.05$), and open symbols indicate nonsignificant differences.

tion from the controls. For the birds treated south-left, the corresponding data were four clockwise and two counterclockwise. In addition, no relationship existed between the side of the deflection and the home direction. However, the effect seemed to be release-site specific; i.e. south-anterior groups always deviated counterclockwise at the Elsenz site and clockwise at the Bickenbach site (see Tables 1 and 2).

The duration of the effect and the possible influence of additional homing flights were not entirely clear from the data. Significant differences between groups were found only on the day of treatment and during the next two days, i.e. during the first and second homing flights. When pigeons were released a third time, any differences were no longer significant. How-

ever, although the range appeared to decrease, the median deflection of the south-anterior group remained more or less constant between the first and third homing flights (Table 3).

There was no systematic effect on the other variables such as vanishing intervals and vector lengths (Wilcoxon tests, $P > 0.05$). Apparently, the birds treated with a magnetic pulse vanished just as fast and without hesitation as did the controls, and in general, they agreed just as well among each other, even if some cases appeared to have more scatter than others. The homing performance was not always recorded. However, when it was recorded, a difference between treatment birds and controls was not indicated.

DISCUSSION

Our results, although involving a certain amount of variability, clearly indicate that treatment with a magnetic impulse can affect the initial orientation of pigeons by influencing the direction they select. Thus, the results confirm an earlier report that was based on limited data (Wiltschko and Beason 1991).

Receptors based on magnetite?—The treatment with the short, strong pulse was designed to alter the magnetization of single-domain magnetite and thus influence the configuration of a magnetite-based magnetoreceptor. The response of our pigeons was in agreement with the assumption that such a receptor exists. In an earlier study by Walcott et al. (1988), treatments with a stronger field produced by an electromagnet failed to affect the orientation of pigeons. The difference in results can be accounted for if the magnetic particles were free to rotate to some extent.

From histological studies (e.g. Walcott and Walcott 1982, Beason and Nichols 1984, Beason and Brennan 1986), the magnetite particles in the ethmoid region would seem promising candidates for being part of a magnetite-based receptor. This idea is supported by electrophysiological studies on the Bobolink that recorded responses to changes in magnetic intensity by neurons of the trigeminal ganglion and from the ophthalmic nerve, a branch of the nervus trigeminus that innervates the region where iron-containing material was found (see Beason and Semm 1987, Semm and Beason 1990). A recent study shows that application of a local

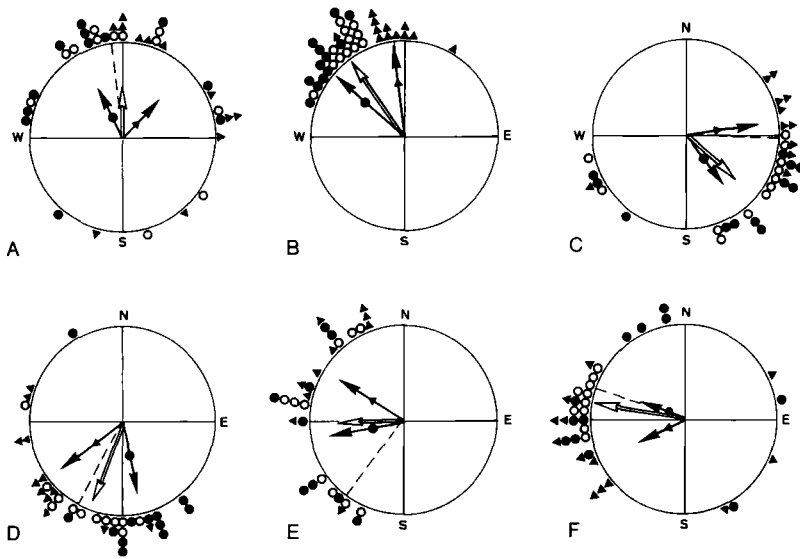


FIG. 3. Pigeons treated with a *south-anterior* pulse (filled circles) and those treated with a *south-left* pulse (filled triangles) released together deviate to different sides of the untreated controls (open symbols). The home direction is indicated by a dashed radius. Symbols at the periphery of the circle indicate vanishing bearings of individual birds, and arrows represent the mean vector proportional to the radius of the circle. Upper diagrams depict birds tested on the day of treatment: (A) Elsenz, 7 August 1990; (B) Elsenz, 29 August 1990; and (C) Bickenbach, 12 September 1990. Lower diagrams depict the same groups of birds tested on their second flight one or two days after treatment: (D) Hilgershausen, 9 August 1990; (E) Lauterbach, 30 August 1990; and (F) Erlangen, 14 September 1990. See Tables 1 and 2 for numerical data.

anesthesia to the ophthalmic nerve suppresses the effect of the pulse treatment (Beason and Semm 1996), which indicates that this nerve is indeed involved in mediating the effect of pulse magnetization. However, because specific receptor structures or connections to the nervous system have not been identified, a role of these particles in magnetoreception is still in question.

Although our findings are in accordance with the magnetite hypothesis, they are not proof for the involvement of single-domain magnetite. Other interpretations cannot be completely excluded. The manifestation of the response—mainly deflections rather than disorientation, a clear influence of the pulse direction, and mostly normal vector length indicating normal agreement among birds—argues against nonspecific effects, however. Also, any disturbing effect would be expected to influence an animal's motivation rather than the direction it selects. Interference with nonmagnetite-based receptors is possible, but it is unclear how a pulse would have lasting aftereffects on mechanisms that are not based on permanent

magnetic material. Nonetheless, 3-h exposures to alternating fields of maximum strength below 200,000 nT have been reported to have aftereffects on pigeon orientation for several hours (e.g. Papi et al. 1983, Ioalè and Guidarini 1985, Ioalè and Teyssèdre 1989). The specific cause of these aftereffects is unexplained, but they do not seem to be based on magnetic particles, because the fields were too weak to alter the magnetization of magnetite. Although we cannot exclude other possibilities, our results suggest that a magnetite-based receptor mechanism is by far the most plausible interpretation.

Interference with the navigational "map"?—Our results raise several important questions. Specifically, what type of information would such a magnetite-based receptor convey, and which component of the navigational system is affected? Does the magnetic pulse interfere with the navigational map? Because the pigeons were released under sunny skies and thus would use their preferred sun-compass mechanism (see Schmidt-Koenig et al. 1991), one would not expect a compass effect from magnetic treatment.

TABLE 1. Orientation data for homing pigeons treated with a magnetic impulse the morning before being released away from their home loft.^a

Treatment	n ^b	Mean vector ^c		Deviation ^d			Vanishing interval ^e
		α_m	r_m	Δh	ΔC	ΔSA	
Büdesheim (231°, 17.2 km, 6 September 1992)							
Control	13 (10)	200	0.95***	-31			5:41
South-anterior	10 (10)	206	0.91***	-25	+6		5:52
Lich (192°, 40.6 km, 2 September 1989)							
Control	13 (12)	201	0.64**	+9			4:49
South-anterior	15 (12)	190	0.80***	-2	-11		3:07
Gernsheim (16°, 42.0 km, 9 April 1991)							
Control	12 (12)	59	0.29	(+43)			3:53
South-anterior	15 (12)	317	0.10	(-59)	(-102)		5:38
Kiedrich (76°, 42.4 km, 10 April 1991)							
Control	19 (12)	115	0.93***	+39			4:13
South-anterior	18 (12)	116	0.82***	+40	+1		3:55
Sterbritz (253°, 70.6 km, 18 June 1992)							
Control	13 (9)	267	0.91***	+14			5:40
South-anterior	14 (9)	276	0.54	(+23)	(+9)		6:08
Mutterstadt (15°, 79.5 km, 27 August 1989)							
Control	15 (12)	23	0.92***	+8			3:19
South-anterior	16 (12)	31	0.92***	+16	+8		3:20
Bickenbach (91°, 81.5 km, 12 September 1990)							
Control	14 (12)	130	0.68**	+39			4:02
South-anterior	15 (12)	143	0.67**	+52	+13		4:04
South-left	17 (12)	81	0.80***	-10	-49*	-62**	4:36
Bickenbach (91°, 81.5 km, 26 June 1992)							
Control	16 (12)	84	0.76***	-7			5:22
South-anterior	11 (8)	90	0.92***	-1	+6		5:07
Fulda-Sickels (236°, 82.3 km, 2 July 1992)							
Control	12 (8)	47	0.66*	+171			3:31
South-anterior	11 (11)	35	0.75***	+159	-12		5:00
Hockenheim (7°, 90.0 km, 16 June 1992)							
Control	15 (8)	1	0.26	(-6)			5:04
South-anterior	13 (11)	315	0.62*	-52	(-36)		3:30
Elsenz (353°, 107.8 km, 17 August 1989)							
Control	15 (12)	10	0.86***	+15			4:12
South-anterior	16 (12)	339	0.96***	-14	-31**		4:17
Elsenz (353°, 107.8 km, 7 August 1990)							
Control	15 (12)	359	0.54*	+6			5:41
South-anterior	16 (12)	333	0.59*	-20	-26		6:16
South-left	15 (12)	45	0.59*	+52	+46	+72*	6:22
Elsenz (353°, 107.8 km, 29 August 1990)							
Control	13 (12)	324	0.98***	-29			2:40
South-anterior	12 (12)	311	0.99***	-42	-13*		1:59
South-left	15 (12)	352	0.97***	-1	+28**	+41***	2:15
Hilgershausen (208°, 123.5 km, 30 July 1990)							
Control	17 (12)	210	0.89***	+2			5:11
South-anterior	14 (12)	222	0.62*	+14	+12		5:46
South-left	14 (12)	196	0.94***	-12	-14*	-26**	4:44

TABLE 1. Continued.

Treatment	n ^b	Mean vector ^c		Deviation ^d			Vanishing interval ^e
		α_m	r_m	Δh	ΔC	ΔSA	
Heringen (229°, 128.9 km, 27 July 1990)							
Control	14 (12)	270	0.96***	+41			3:11
South-anterior	16 (12)	256	0.92***	+27	-14		3:55
South-left	15 (12)	292	0.97***	+63	+22**	+36***	3:26
Erlangen (289°, 168.7 km, 31 August 1989)							
Control	14 (12)	276	0.88***	-13			3:38
South-anterior	14 (12)	149	0.21	(-140)	(-127)*		3:42
South-left	17 (12)	329	0.62**	+40	+53*	(180)*	3:59

*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

^a Boldface headings denote release site (direction and distance to home loft, date of release).

^b Number of pigeons released (number of bearings evaluated).

^c α_m = direction (°) of mean vector; r_m = length of mean vector. Asterisks denote significance by the Rayleigh test.

^d Δh = deviation (°) from home direction; ΔC = deviation (°) from mean of controls; ΔSA = deviation (°) from mean of birds treated with south-anterior pulse. Differences not based on two significant mean vectors are in parentheses; asterisks denote significance by the Watson-Williams test or the Mardia-Watson-Wheeler test (see Methods).

^e Median vanishing time (minutes:seconds).

Furthermore, the variability in the effect and the observation that greater effects occur at longer distances from home also argue against an influence on the magnetic compass, because the compass is used in a similar way at all distances, and the compass effect should be more uniform. Thus, from the circumstances of the releases and the nature of the effect, it appears that the map rather than the compass is affected, which agrees with the hypothesis that magnetic factors are part of a bird's navigational map (R. Wiltschko and W. Wiltschko 1995). Interestingly, magnetization with different orientations produced deflections to different sides. Apparently, the treatment did not deprive the pigeons of magnetic information altogether. Instead, the responses suggest that each experimental group interpreted the magnetic map information differently.

An effect on magnetic components of the navigational map also would explain the great variability we observed. The map system includes a variety of factors that appear to be used in a flexible way, with different rankings and combinations at various sites (see Wiltschko and Wiltschko 1994). Thus, the effect of altering one factor would depend on the other factors used at a given site. In view of this, the variable effect we observed is precisely what one might expect if one factor in a multifactorial system is disturbed. Variability and site-specificity are typical for effects associated with the navigational map, and they are not restricted to magnetic factors. For example,

Wiltschko et al. (1987) reported that anosmia affected the behavior of Frankfurt pigeons only at specific sites in a particular region, and Schöps and Wiltschko (1994) observed that partly depriving pigeons of infrasound affected their orientation differently in various regions around the loft. The deflections we observed were of a similar size to those usually associated with magnetic map factors, namely those observed after treatments interfering with natural magnetic information under sun, such as releasing birds with magnets or small, battery-operated coils (e.g. Walcott 1977, Visalberghi and Alleva 1979).

That the pulse caused more pronounced deflections beyond 100 km suggests that the importance of magnetic map factors is greater with increasing distances from home. This agrees with the assumption that gradients such as magnetic intensity or inclination can only be used when the difference to the home value exceeds a certain threshold. Phillips (1996) predicted that a large-scale map (i.e. a map that functions at distances of ≥ 100 km from home) derived from the geomagnetic field is unlikely to be useful at distances less than 50 to 75 km of the bird's goal. At shorter distances, the geomagnetic field would not provide reliable map information because local magnetic gradients (5 to 10 km) can vary in ways that are inconsistent with the field gradient on a larger (i.e. regional) scale. Only when a bird is displaced more than 50 to 75 km away from home is it likely to encounter values of total intensity that

TABLE 2. Orientation data for homing pigeons treated with a magnetic impulse the one to seven days before being released away from their home loft.^a

Treatment	n ^b	Mean vector ^c		Deviation ^d			Vanishing interval ^e
		α_m	r_m	Δh	ΔC	ΔSA	
Pigeons that had homed <i>once</i> from another site after treatment with a pulse							
Lauterbach (218°, 78.6 km, 30 August 1990, 1 day)							
Control	12 (10)	268	0.70**	+50			3:36
South-anterior	10 (9)	259	0.80**	+41	-9		3:35
South-left	15 (10)	303	0.81***	+85	+35	+46*	2:55
Bickenbach (91°, 81.5 km, 12 April 1991, 2 days)							
Control	19 (12)	110	0.72***	+19			3:34
South-anterior	16 (12)	129	0.52*	+38	+19		3:46
Böhl (19°, 84.6 km, 12 April 1991, 2 days)							
Control	20 (12)	11	0.57*	-8			3:52
South-anterior	16 (12)	7	0.90***	-12	-4		3:59
Elsenz (353°, 107.8 km, 1 August 1990, 2 days)							
Control	14 (12)	333	0.92***	-20			3:20
South-anterior	14 (12)	291	0.70**	-62	-42*		2:18
South-left	12	336	0.90***	-17	+3	+45*	4:04
Waldbröl (138°, 112.6 km, 19 August 1989, 2 days)							
Control	13 (12)	142	0.74***	+4			4:39
South-anterior	16 (12)	201	0.78***	+63	+59***		4:08
Hilgershausen (208°, 123.5 km, 9 August 1990, 2 days)							
Control	12	201	0.89***	-7			4:54
South-anterior	16 (12)	168	0.79***	-40	-33*		4:02
South-left	13 (12)	233	0.83***	+25	+32*	+65***	2:50
Troisdorf (124°, 133.5 km, 27 August 1989, 2 days)							
Control	14 (12)	105	0.88***	-19			4:04
South-anterior	16 (12)	114	0.77***	-10	+9		4:46
Erlangen (289°, 168.7 km, 14 September 1990, 2 days)							
Control	14 (10)	280	0.98***	-9			2:47
South-anterior	14 (12)	292	0.52*	+3	+12*		2:47
South-left	13	244	0.57*	-45	-36*	-48	2:15
Pigeons that homed <i>twice</i> from another site after treatment with a pulse							
Lich (192°, 40.6 km, 21 August 1989, 4 days)							
Control	15	214	0.96***	+22			2:00
South-anterior	18 (15)	205	0.87***	+13	-9		2:12
Willanzheim (294°, 123.5 km, 15 April 1991, 5 days)							
Control	17 (12)	69	0.66**	+135			3:37
South-anterior	14 (10)	74	0.68**	+140	+5		2:56
Elsenz (353°, 107.8 km, 18 September 1990, 6 days)							
Control	15 (10)	336	0.91***	-17			3:09
South-anterior	9 (8)	342	0.86**	-11	+6		3:53
South-left	13 (10)	350	0.83**	-3	+14	+8	4:31
Lauterbach (218°, 78.6 km, 3 August 1990, 7 days)							
Control	13 (12)	271	0.86***	+53			4:04
South-anterior	14 (12)	250	0.74***	+32	-21		3:12
South-left	14 (11)	271	0.85***	+53	±0	+21	4:32
Bickenbach (91°, 81.5 km, 5 September 1990, 7 days)							
Control	12	94	0.87***	+3			3:26
South-anterior	12 (11)	74	0.97***	-17	-20		4:03
South-left	14 (12)	79	0.94***	-12	-15	+5	3:50

TABLE 2. Continued.

Treatment	n ^b	Mean vector ^c		Deviation ^d			Vanishing interval ^e
		α _m	r _m	Δh	ΔC	ΔSA	
Heringen (229°, 128.9 km, 6 August 1990, 7 days)							
Control	14 (12)	245	0.81***	+16			3:36
South-anterior	13 (10)	226	0.79***	-3	-19		4:58
South-left	16 (12)	249	0.82***	+20	+4	+23	5:22

*, P < 0.05; **, P < 0.01; ***, P < 0.001.

^a Boldface headings denote release site (direction and distance to home loft, date of release, number of days between treatment with pulse and release).

^b Number of pigeons released (number of bearings evaluated).

^c α_m = direction (°) of mean vector; r_m = length of mean vector. Asterisks denote significance by the Rayleigh test.

^d Δh = deviation (°) from home direction; ΔC = deviation (°) from mean of controls; ΔSA = deviation (°) from mean of birds treated with south-anterior pulse. Asterisks denote significance by the Watson-Williams test or the Mardia-Watson-Wheeler test (see Methods).

^e Median vanishing time (minutes:seconds).

are consistently higher or lower than the home value and that can reliably be used to determine its geographic position relative to home. Moreover, this type of large-scale map would only enable the bird to locate the general vicinity of its home. Some other source of map information and/or an alternative homing mechanism (e.g. searching for familiar landmarks) would have to be used to determine the precise location of home. Also, other cues might have minimized any magnetic effect in the immediate home region. All of the pigeons were thoroughly familiar with the area within 40 to 50 km of their home loft through training early in their life, and the region not far beyond may still have been somewhat familiar from other homing flights. So, even if pigeons normally use magnetic cues in the vicinity of their loft, other cues may have outweighed the manipulated magnetic map information.

Parallel findings in migratory birds.—Our experiments differ from previous studies on the effect of pulse magnetization in that they involve: (1) free-flying birds versus captives tested in cages, and (2) homing over moderate dis-

tances versus migratory orientation. However, there is no *a priori* reason to suppose that different mechanisms would be used for homing versus migration, so long as experienced migrants return to a familiar home area (Perdeck 1958).

By indicating an effect of the treatment on the directions selected, our results are in accordance with those of previous experiments with migratory birds; i.e. treatment with an identical pulse caused considerable deflections in direction, and different orientations of the pulse caused deflections to opposite sides (Wiltschko et al. 1994, Beason et al. 1995, W. Wiltschko and R. Wiltschko 1995). The size of the deflection seemed to be somewhat larger in migrants, because the birds deviated from their normal migratory course up to about 90°. This might be attributed to the fact that the migrants, unlike our pigeons, were tested in closed rooms where other cues that might have dampened the effect outside were not available.

The effect observed in migratory birds also has been interpreted as an interference with the navigational map rather than with the magnet-

TABLE 3. Median angular difference (range in parentheses) between treatment and control homing pigeons released away from their home loft.

Treatment	1st homing flight ^a		2nd homing flight ^b		3rd homing flight ^c	
	n ^d	ΔC ^e	n	ΔC	n	ΔC
South-anterior	12	12° (1 to 31°)	8	16° (4 to 59°)	6	15° (5 to 21°)
South-left	6	37° (14 to 53°)	4	34° (3 to 36°)	4	9° (0 to 15°)

^a Day of treatment.

^b 1 or 2 days after treatment.

^c 4 to 7 days after treatment.

^d Number of pigeons released.

^e Angular difference relative to control sample.

ic compass. Migrants tested in the above-mentioned studies had been caught in the wild, and none was tested during its first migration. This means that they had established a map, were familiar with their goal area, and thus could navigate towards it (Perdeck 1958). Consequently, the observed deflections may be attributed to an interference with the map. When the effect of the pulse was suppressed by anesthetizing the ophthalmic nerve, the birds oriented in their original migratory direction with the magnetic field as the only available cue, which clearly indicated that the magnetic compass was unimpaired by the pulse (Beason and Semm 1996). A recent study with young birds on their first migration also supports this view. The birds had been caught soon after hatching and before they could develop a navigation map by experience (see Wiltschko and Wiltschko 1987). When tested in the absence of cues other than the magnetic field, they continued in their normal migratory direction after the pulse treatment (Munro et al. 1997). This finding, too, strongly suggests that the pulse leaves the magnetic compass intact and interferes only with the map.

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