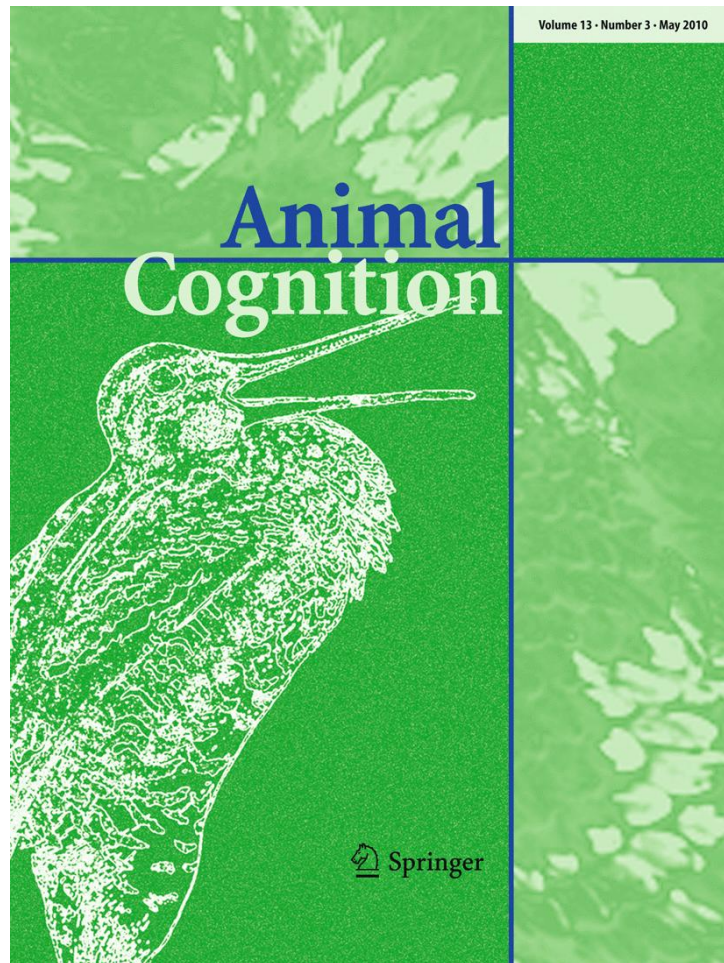


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Learning of magnetic compass directions in pigeons

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Abstract A proof of magnetic compass learning by pigeons under laboratory conditions has been attempted for decades, but all experiments have failed so far. The aim of the present study was to test whether pigeons can learn magnetic compass directions in an operant chamber if magnetic cues are presented as true spatial cues. Experimental sessions were carried out in the local geomagnetic field and in magnetic fields with matched total intensity and inclination, but different directions generated with Helmholtz-coils. Birds demonstrated successful learning with a performance level comparable to that in learning studies with magnetic anomalies. In addition, we compared the data from magnetic learning in the laboratory with performance from homing experiments in the field. The birds that were more successful in the learning experiment had vanishing bearings farther away from the home direction than the group mean at unfamiliar, but not at familiar sites. This might suggest that better learners explore unknown locations in a

different way. Our findings represent the first evidence for operant magnetic compass learning in pigeons and also provide a link between behavioural data from the field and the laboratory.

Keywords Magnetic compass · Pigeon · Operant learning · Homing

Introduction

Magnetic cues are important for orientation in all major groups of vertebrates (Wiltschko and Wiltschko 1995). Especially birds have been studied in great detail. Since the discovery of a magnetic compass in European robins (Wiltschko 1968), a host of studies investigated magnetic orientation during migration and homing. These experiments suggest that birds not only use the magnetic field as a compass cue, but also incorporate magnetic parameters as position cues into their navigational map (Wiltschko and Wiltschko 2007a).

Two separate receptor systems provide birds with magnetic information (see Wiltschko and Wiltschko 2005, 2007a; Mouritsen and Ritz 2005): a radical pair mechanism based on spin-correlated chemical reactions possibly located in the eye (Wiltschko et al. 2002) derives directional information from the magnetic field (Ritz et al. 2000, 2004; Thalau et al. 2005); an iron mineral-based mechanism located in the upper beak detects the intensity of the ambient magnetic field (Fleissner et al. 2003, 2007; Mora et al. 2004; but see Wallraff 2005; Gagliardo et al. 2006).

In spite of behavioural and physiological data indicating that pigeons do use magnetic information (e.g. Walcott and Green 1974; Walcott 1978; Visalberghi and Alleva 1979; Wiltschko et al. 1981), most learning experiments in the

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laboratory were unsuccessful (e.g. Griffin 1982; Carman et al. 1987; Moore et al. 1987; Couvillon et al. 1992). The only positive results involved magnetic intensities and magnetic anomalies (Bookman 1977; Mora et al. 2004; Thalau et al. 2007). Directional training with pigeons has failed so far (e.g. Kreithen and Keeton 1974; Beaugrand 1976; Alsop 1987). A likely reason for this failure is that the cues were not presented as spatial cues in these experiments. Recently, individuals of two other bird species, the domestic chicken (*Gallus gallus*) and the zebra finch (*Taeniopygia guttata*), could be trained to search in specific magnetic directions in square-shaped arenas (Freire et al. 2005, 2008; Voss et al. 2007), although birds learned the correct axis but not the specific goal direction.

The present study addressed three questions. Firstly, a definite proof of operant magnetic compass learning in pigeons was required. Secondly, it was of interest whether pigeons, like chicks and zebrafinches, would show an axial effect in that they preferred the compass direction opposite to the goal direction as much as the goal direction. Thirdly, as the birds were experienced in homing experiments in the field, there was the unique opportunity to compare learning performance in the laboratory with homing performance in the field. Pigeons had to distinguish four feeding locations in a square-shaped operant box, with the position of the accessible feeder indicated by magnetic compass directions only. Thus, the magnetic field was a true spatial cue. Also, consistent with the properties of the natural magnetic field, the experimental magnetic fields were kept constant during sessions (Wiltschko and Wiltschko 2007b).

Materials and methods

Subjects

The subjects were eleven adult homing pigeons (*Columba livia f. domestica*) from the Frankfurt loft. All birds were familiar to regular handling. During their first year of life, all of them had participated in flock training up to 40 km in the cardinal directions. Later on they had taken part in different homing studies, being released singly from various directions and distances. None of the birds had previously been used in learning experiments in the laboratory. The birds used in the present study were housed as a group that also included their breeding partners in a large wooden pen with free entrance to an open air aviary. They were kept at water ad libitum and at least 85% of their free-feeding weight. They were fed with a grain mixture for pigeons during experimental sessions and received supplemental feedings after the experiments. The experimental procedures complied with current German regulations for animal welfare and were carried out in accordance with the

European Communities Council Directive of 24 November 1986 (86/609/EEC).

Apparatus

The training experiments were carried out in a wooden hut outside the zoology building where the local geomagnetic field was undisturbed. The experimental apparatus was a large square-shaped operant chamber (Fig. 1). The 45 × 45-cm aluminium box, 44 cm high, consisted of four identically constructed side walls each provided with a pecking key in the height of the pigeons head and a feeder placed on the ground. All mechanical devices in or close to the operant chamber were operated pneumatically in order to prevent disturbances of the magnetic field. The pecking keys were circular semitransparent plastic discs, 2.5 cm in diameter, which could be illuminated from the back. The operant box was lit by a halogen lamp with a wavelength spectrum close to natural daylight. It passed a diffuser of white plexiglas that was integrated into the lid covering the box. The floor of the apparatus was covered with paper for easy cleaning. Input and output devices in the box were controlled by a remote computer, which also allowed online monitoring by the experimenter.

Magnetic field conditions

We used four magnetic conditions: the local geomagnetic field with magnetic North in the geographic North and three

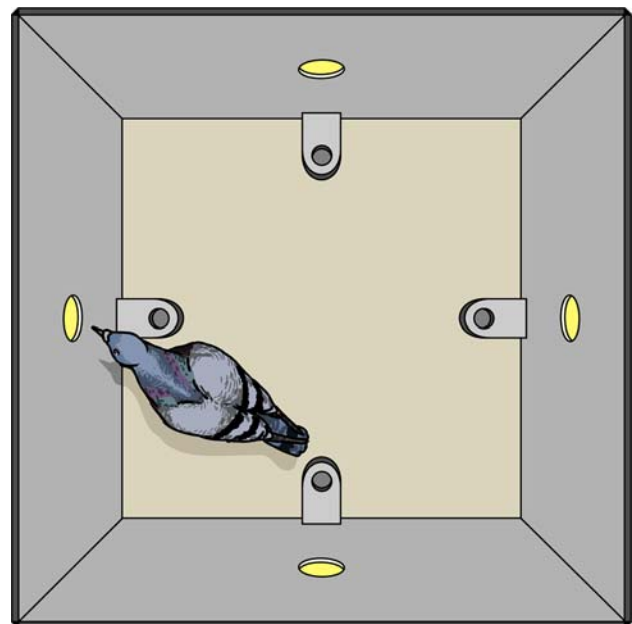


Fig. 1 Operant box for learning magnetic compass directions, seen from above. Each wall was 45 cm long and equipped with a central pecking key and a pneumatically driven feeder. Graph by Robert Nippoldt

experimental fields with magnetic North in the geographic East, South and West, respectively. The apparatus was situated in the centre of two pairs of Helmholtz-coils, 2 m in diameter with 1 m clearance, with the axes aligned horizontally in N–S and E–W, respectively. This allowed a deflection of magnetic North by 90, 180 and 270° without altering the intensity and the inclination of the magnetic field.

The test fields were always established before an individual bird was placed into the box and were held constant within the experimental sessions but changed between sessions in a balanced manner.

Habituation and pre-training

Birds were trained and tested singly. First they were habituated to the experimental situation by placing them repeatedly into the operant box for five minutes. As in later training and testing, birds were caught from their aviary before sessions and placed in wooden containers equipped with water cups where they waited for being set into the box. During habituation to the operant box, a few grains of food were placed near the opening of each of the feeders. As soon as the animals repeatedly consumed the grains within the given time of five minutes, they were judged to be familiarized with the apparatus and pre-training started.

Each pre-training session consisted of 24 trials. At the beginning of a session, the pigeon was placed into the apparatus, and the central light was turned on. After a randomized waiting delay of 10–20 s, one of the pecking keys was illuminated for 5 s. The position of the lit key always corresponded to the pre-assigned magnetic direction. If the animal pecked against the key within this time, the feeder was activated for 3 s. In the first trials, pecking of the key was encouraged by fixing a grain at the pecking key for those individuals that did not peck spontaneously at the lit key. Also, in the first pre-training sessions, additional activations of the feeder were elicited by the experimenter in case the birds acted in the vicinity of the pecking key but did not hit the key (shaping). The criterion for successful pre-training was at least twelve activations of the feeder by the animal within a session. Habituation and pre-training took place in the local geomagnetic field.

Training birds to magnetic directions

Following successful pre-training, each animal was trained to one of the magnetic compass directions, which remained the same over sessions with regard to the magnetic direction but changed between sessions in terms of the geographic direction by experimentally turning of the magnetic field. One bird was trained to go to the magnetic North, another to the magnetic East, etc., and at least one male and

one female were allocated to each of the compass directions. The geographic directions in which the trained magnetic direction was presented changed from session to session in a fully balanced pseudorandom sequence. All geographic directions were used equally often, the same direction was never used more than two times in a row, and the change compared to the preceding session was equally often in a clockwise or counter-clockwise manner.

A session consisted of 12 trials. The number of choices to find the correct magnetic direction was chosen as the primary measure of learning success. This score has the advantage that it integrates all relevant choices within a session into a single value. Furthermore, it turned out to be very stable in pilot experiments. Therefore, it was also used to monitor the birds' progress during training. After successful pre-training, learning sessions started in which all four pecking keys were lit for 5 s. Now the magnetic compass was the only cue indicating the correct direction. If an individual chose a wrong direction, this was regarded as an error leading to a time-out with 5 s of darkness inside the box. After a correct choice, access to the feeder was given for 3 s. As in pre-training, an intertrial interval with a variable duration of 10–20 s was used. The computer recorded a detailed trial-by-trial protocol of all operations, in particular the number of choices made, the position chosen and the exact sequence of choices (Software: Olcus, FBI science).

Each bird ran four sessions per day. Depending on how often the birds were active during experimental sessions, they received a total of 82 ± 9 sessions (median and standard error of the median). For the evaluation of individual performances, we included the last 10 sessions for each magnetic condition. Thus, a total of 40 sessions was used per bird, except for three pigeons that had completed the tests in 23, 16 and 17 sessions. Also, in these birds, the data were balanced across directions.

Data analysis

From the session protocols, we derived the following measures:

1. The *number of choices to find the correct direction*. This measure has the advantage of integrating all relevant choices within a session. It is a robust and reliable measure in spatial orientation tests with more than two response alternatives. It has, for example, been used in studies on spatial memory during food-storing (e.g. Clayton 1995). In the present experiment, above random performance on this measure was only possible by using the magnetic cues. In the case with four response options, scores can vary between one and four with a chance level of 2.5. With the conservative assumption that the birds keep perfectly track of their orientation,

the probability for the four different choice patterns is as follows. For a correct choice in the beginning, it is 0.25; for a correct choice on the second try, it is 0.75 (probability of an incorrect choice in the beginning) * 0.33 (probability for a correct choice after a first incorrect choice) = 0.25; and so on.

2. The *directions of first choices of a session*. This measure allowed for assessing as to whether the birds showed a specific preference for the goal direction or an axial effect. In addition, any above chance performance on this measure (axial effect or not) like the first measure indicates magnetic learning. Also on this measure, significant performance can only be achieved by magnetic cue use.

For the comparison with field data, we used all available data from homing flights where the respective birds had been released as members of the control group without any specific treatment. The releases had taken place in the last 3 years before magnetic learning in the laboratory. Release sites were situated in all cardinal compass directions from the home loft at an average distance of 47 km. For a subset of release sites, magnetic anomalies were known. The comparison focused on three parameters:

1. The *deviation from the mean heading of the group with regard to home*, defined as the angular difference between the individual's vanishing bearing and the group mean, with a positive sign indicating that the deviation was to the side opposite of home and a negative sign that it was towards home. These data required that the group showed a significant directional preference by the Rayleigh test (Batschelet 1981) and was only used in these cases. We used these values rather than the deviation from home because at many sites, control pigeons regularly prefer directions that deviate significantly from the true home direction, so-called release site biases (Keeton 1973), with this deviations mostly in the range of 30°, but occasionally up to 60° and more.
2. The *vanishing interval*, i.e. the time between release and the moment the pigeons had moved so far that it vanished from sight for two observers using 10 × 40 binoculars.
3. The *homing speed* in km/h; it was calculated by dividing the recorded homing time by the distance of the release site from the loft.

We calculated parametric correlations between the learning scores given by the mean number of choices until the first correct choice and the three parameters of homing flights. As the angular differences, which represent the appropriate parametric measure of the vanishing bearings (c.f. Batschelet 1981), can vary into the one or other direction, we first

calculated correlations with unsigned angular differences. After having found a significant correlation between the unsigned correlations and magnetic orientation in the laboratory, we tested a directed hypothesis with signed angular differences. These calculations were done for familiar and unfamiliar sites separately. As the overall set of field data that were available contained data from releases within magnetic anomalies where the behaviour is often atypical, we made separate correlations for all releases and for those outside the anomalies. Table 1 shows the number of releases for each bird and the individuals' representative scores for the different parameters and conditions calculated as the median over these releases.

For all statistical tests, a significance level of $\alpha < 0.05$ was selected.

Results

Learning to search in magnetic compass directions

Figure 2a shows the performance level for all birds as the average number of choices to find the correct direction. Unfilled symbols show the performance during initial training (two blocks with 20 trials). At the beginning of training, performance increased slowly. For the first 20 sessions, the group mean was still close to random (2.43 choices to find correct direction; one-sample *t*-test, $t_8 = 0.65$, $P = 0.27$). Further increase was steady in some of the birds and discontinuous in others with phases of better performance and phases with performance back to random. During the test phase (filled circle), which included 40 tests in eight of the birds and 23, 16, and 17 tests in the three other birds, a stable performance level was achieved with no difference between the first and second half of the tests (paired *t*-test, $t_{11} = -1.14$, $P = 0.28$). Comparison with random performance level of 2.5 confirmed significant learning (one-sample *t*-test, $t_{11} = 4.91$, $P < 0.001$). In one bird, performance remained close to random (mean: 2.6). Individual standard errors over the 40 test sessions ranged from 0.15 to 0.18. The number of completed training trials before the test phase was 40.3 sessions on the average.

Figure 2b shows the preferred magnetic directions of the birds. In this comparison, all 10 birds were included whose performance on the number of choices to find the correct direction was higher than the random level. For each individual, choices to each direction were summed over independent sessions from the last block of 40 sessions, and the percentages of choices allocated to the different directions were calculated for each of the birds. Data show a significant preference for the goal direction. Only the goal direction was chosen significantly above chance (one-sample

Table 1 Performance on flights from unfamiliar release sites and their correlation with learning performance as given by the number of choices until the first correct choice, see Fig. 2a

Pigeon	All releases				Releases outside of anomalies			
	<i>N</i>	$\Delta\alpha_m$	Van. int. min:s	Homing speed	<i>N</i>	$\Delta\alpha_m$	Van. int. min:s	Homing speed
A	4 (3)	+2°	4:36	25.4	2 (1)	-21°	4:36	41.5
B	5 (4)	+2°	4:19	48.0	3	+4°	5:17	51.9
C	4 (3)	-16°	3:30	39.8	2 (1)	-16°	3:30	38.9
D	2	+18°	4:18	42.9	-	- (-)	-	-
E	4 (3)	+15°	3:07	51.1	1 (0)	- (-)	-	53.7
F	3 (2)	-12°	4:12	48.3	1	-16°	3:46	55.8
G	5	+7°	5:11	51.4	2	+62°	5:50	14.3
H	4 (3)	-1°	6:33	41.1	3 (2)	-1°	5:30	49.1
I	5 (4)	-13°	5:03	38.3	2 (1)	-11°	4:53	49.0
J	8 (5)	-8°	5:37	19.5	3 (2)	-9°	5:52	10.0
K	6	-5°	4:25	41.5	3	+13°	5:04	25.8
<i>r</i>		-0.593	0.066	-0.150		-0.689	-0.202	0.675
<i>P</i>		0.027*	0.846	0.660		0.020*	0.602	0.032*

Data for the individual pigeons are given as median; *N* number of releases, in parentheses number of data for initial orientation, if different; $\Delta\alpha_m$, deviation from the mean heading of the group, with + indicating that the heading of the pigeons was further from the home direction and—that it was closer to the home direction; van. int., vanishing interval; the homing speed is given in km/h. Statistics: Pearson product moment-correlation, two-tailed ($\Delta\alpha_m$ one-tailed); *r* coefficient of correlation

* $P \leq 0.05$

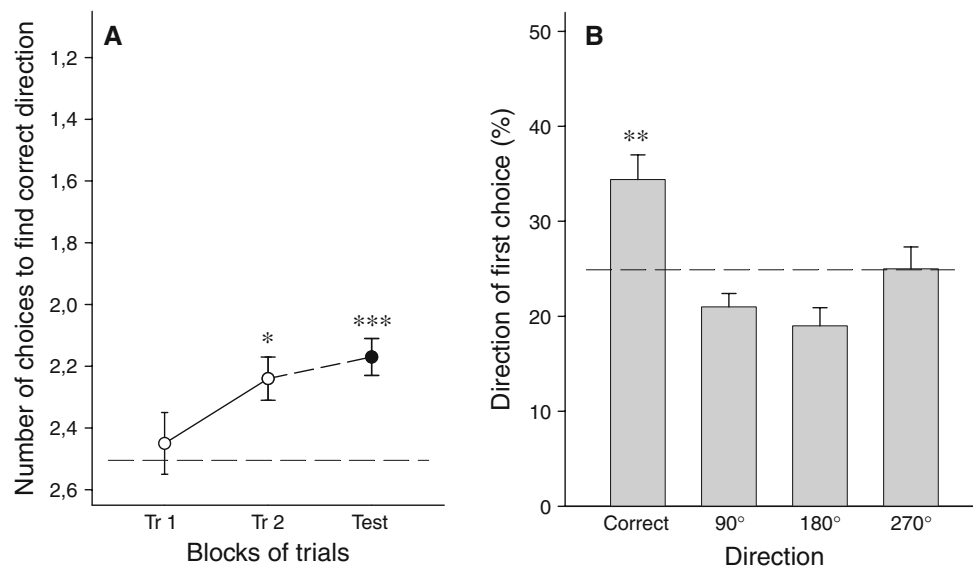


Fig. 2 **a** Number of choices to find the correct direction. Performance increased during training (unfilled circles, mean and SEM) and was significantly above random in the second phase of training and in the test phase (filled circles; mean and SEM). **b** Pigeons preferred the correct direction over the other three directions, and scores on the other

directions were not different from random or from each other. Bars show group mean and SEM. The directions are labelled clockwise with the goal direction at 0°. Dashed lines show random performance level and asterisks indicate significant deviation from chance; * $P < 0.05$, ** $P < 0.01$ and *** $P < 0.001$

t-test, $t_{10} = 3.55$, $P = 0.003$, one-tailed) as well as more often than the other directions. (paired *t*-tests, $t_{10} = 4.11$, $P = 0.002$, $t_{10} = 1.86$, $P = 0.048$, $t_{10} = 4.23$, $P = 0.001$, one-tailed). The other directions did not differ from each other ($t_{10} = 0.67$, $P = 0.52$, $t_{10} = 2.17$, $P = 0.058$, $t_{10} = 1.75$, $P = 0.11$).

We performed additional tests in order to control for the possibility that any hidden cues inside or outside the operant box might have contributed to the birds performance. Firstly, we checked as to whether certain geographic directions might overall have been chosen more often than

expected by chance. Choices were distributed evenly across the four directions ($\chi^2 = 2.70$, $df = 3$, $P = 0.44$). Secondly, we tested as to whether the correct first choices were distributed evenly across geographic directions. Also in this case, there was no significant difference between directions neither for the overall distribution ($\chi^2 = 1.58$, $df = 3$, $P = 0.66$, pooled data) nor for individual birds (all non-significant).

In summary, these data from operant learning show significant magnetic learning on a moderate performance level and unequivocal evidence that magnetic compass learning in pigeons leads to specific learning of the unimodal goal direction.

Comparison with field data

Table 1 compares the performance in the field at unfamiliar sites and learning scores in the current experiment. For a comparison with the laboratory data, only homing measures were of interest that show some consistent trend over repeated releases, and thus reflect individual differences in the ability or proneness to use certain cues and strategies. Therefore, the median performance over all releases available for a bird was used. Considering all releases, vanishing intervals and homing speed did not correlate with learning performance. There was, however, a relation between spatial operant learning and the vanishing bearings. We first looked at the correlation between learning scores and the general deviation of vanishing bearings from the home direction, regardless of the direction of the deviation. The higher the performance was in the spatial operant task the greater was the deviation of the vanishing bearings from the home direction ($N = 11$, $r = -0.723$, $P = 0.012$). This suggested the presence of a directed biasing factor, which was more effective in better magnetic learners than in poorer magnetic learners. Therefore, we then tested the specific hypothesis whether better magnetic learners showed a greater than average deviation into the direction of the group's release site bias. In order to test for such directed effect, we calculated the deviation from the mean heading of the group for each individual and each single release. Deviations from home greater than the group mean received a positive sign and smaller deviations a negative sign. There was a significant correlation with magnetic operant learning score ($N = 11$, $r = -0.593$, $P = 0.027$, one-tailed; Fig. 3). As in the learning scores lower values mean better learning, this correlation expresses that the better a pigeon had learnt the task, the farther its bearings deviated from the mean of the group away from the home direction into the direction of the group's deviation. Table 1 also gives the data of the releases outside magnetic anomalies separately. Again, there was no correlation with the vanishing intervals ($N = 9$, $r = -0.202$, $P = 0.602$) and a significant

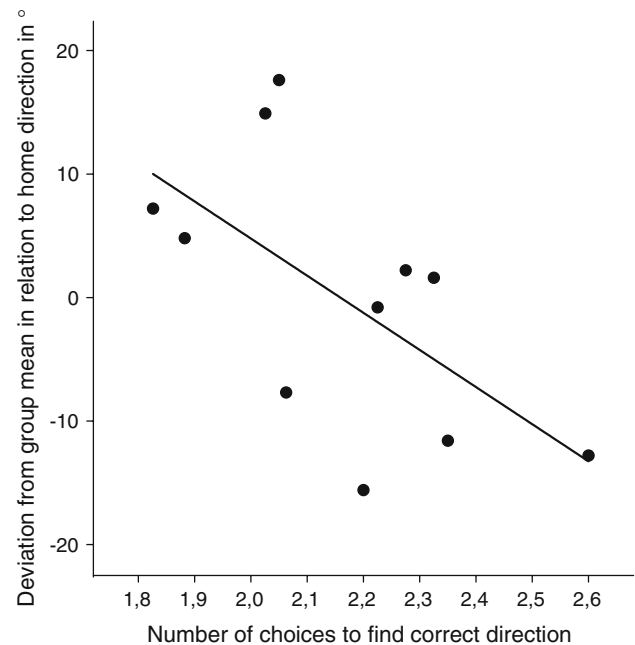


Fig. 3 Median angular difference of the individual pigeon's heading from the mean heading of the group at unfamiliar release sites, with a *positive sign* indicating a deviation from the home direction that was larger than that of the group mean and a *negative sign* indicating a deviation that was smaller. The median angular difference was significantly correlated with the performance of learning magnetic directions in the laboratory

negative correlation with the vanishing bearings (deviation from home: $N = 9$, $r = -0.784$, $P = 0.602$; deviation from the mean heading of the group: $N = 9$, $r = -0.689$, $P = 0.020$, one-tailed). But here we additionally found a significant correlation with homing speed: better laboratory learners took more time to return ($N = 10$, $r = 0.675$, $P = 0.032$, see Table 1).

Regarding releases from familiar sites, we focused on the releases from sites outside anomalies as there were only few data from sites with anomalies. There was no correlation between learning performance in the laboratory and vanishing interval ($N = 10$ animals; $r = 0.400$, $P = 0.252$) or homing speed ($N = 11$; $r = 0.020$, $P = 0.953$). The deviation from the group mean with regard to home also was not significant ($N = 10$; $r = 0.535$, $P = 0.055$, one-tailed).

Discussion

Our findings show that pigeons can learn magnetic compass directions in an operant task. Furthermore, findings show that during magnetic learning pigeons acquire a specific preference for the goal direction. And finally, there seems to be a relationship between magnetic compass learning in the laboratory and homing performance in the field.

Why was it successful this time?

There have been earlier attempts to train pigeons to magnetic directions (e.g. Kreithen and Keeton 1974; Beaugrand 1976; Alsop 1987; see Wiltschko and Wiltschko 1995, Chap 8, 1996; for a review); our study is the first successful one. This raises the question about the reasons for the lack of success of earlier studies. Inevitably, the spatial scale in laboratory studies of magnetic orientation is much smaller than in the natural situation for which orientation behaviour has evolved. The more important is that laboratory experiments attempt to match other relevant factors of the natural situation. Regarding this, experiments on magnetic compass orientation should (1) require the birds to turn into a certain direction that is related to the orientation of the magnetic field and (2) avoid unnatural magnetic conditions. None of the earlier laboratory experiments (Kreithen and Keeton 1974; Beaugrand 1976; Alsop 1987) with pigeons met these criteria.

Test design involving a spatial task

Compared to earlier studies, our test design was more naturalistic in that it included components of a spatial task, requiring magnetic compass use in a context where it is naturally used. The birds had to move to a goal in a certain direction based on their perception of magnetic compass, a design that had also worked with chickens and zebra finches (Freire et al. 2005; Voss et al. 2007). In one of the few earlier studies that used *operant* discrimination of magnetic directions, Alsop (1987) had pigeons respond to the left or the right key at the same wall of a Skinner box-like operant chamber. Thus, there was no meaningful relationship between the magnetic directions and the directions the birds had to turn to. One aspect that might generally impede conditioning to magnetic directions is that the magnetic compass is a component of the navigational system that is usually employed in orientation over extended distances. As magnetic cues might not typically be used by pigeons during search for food on a small spatial scale, the likelihood to build a link between the magnetic compass direction and the feeding sites may not be high. For another compass system, the sun compass, such a link could be shown in several species including homing pigeons. In octagonal outdoor aviaries, the birds relied on the directional information to find a food goal (Bingman and Jones 1994; Chappell and Guilford 1995). Here, in larger environments, the tasks were essentially a spatial task of locating a specific site, and it seems likely that the compass direction was not associated with the food itself, but with the site where food was to be found. Corvids caching food spontaneously rely on the sun compass to remember their caches, indicating that compass orientation is a component

of spatial memory (Wiltschko et al. 1999). This may have facilitated successful learning in the larger aviaries. In the commonly used smaller operant chambers, however, establishing a link between directions indicated by the sun compass and a food reward has always been problematic and often failed (see e.g. Rawson 1954; Kramer 1957; Schmidt-Koenig 1958). Despite these limitations, the present findings clearly show that pigeons can be trained to prefer magnetic directions also in a small spatial environment if a test design with characteristics of a spatial task is used.

Conditioning to a constant cue

The natural magnetic field is a factor that remains fairly stable on the time-scale relevant in the experimental sessions. Rapid changes in magnetic stimuli during a session, as in earlier studies, may fail to elicit a proper response because they are in conflict with the birds' normal experience. Because the natural magnetic field is fairly constant in the short-term, it is conceivable that animals consult their magnetic compass only when entering a new environment and, having quickly formed a directionally oriented representation of the lay of the land, further on ignore the magnetic field and its directions (see Wiltschko and Wiltschko 2007b). Similar to the likewise successful studies of Freire et al. (2005) and Voss et al. (2007), we therefore kept the magnetic field constant during testing. The experimental magnetic field was always established before the bird was placed into the apparatus and never changed during the session. This matches the constancy of the natural geomagnetic field and probably proved crucial for successful conditioning to magnetic directions: when a pigeon is reintroduced in the apparatus, the test chamber represents a 'new' environment that requires reorientation and with it, magnetic compass use.

Is the performance level typical for magnetic learning?

Compared to discrimination studies with other sensory modalities, e.g. colour discrimination, the performance in magnetic compass learning is only moderate. For example, even in a dual-task where pigeons discriminated colours in parallel to a spatial working memory task, performance on the colour discrimination was at nearly 90% with 50% random probability (Prior and Güntürkün 2001). However, magnetic compass learning performance seems to be at a similar level as performance during learning of magnetic intensities and magnetic anomalies. Although comparison with other studies involving magnetic conditioning requires some caution as other stimuli, test designs, and rewarding strategies were used the success rates in the studies of Bookman (1977) and Mora et al. (2004) of 67 and 60% with a random probability of 50% are comparable to our

findings on compass learning with success rates of about 35% against a random level of 25%. The only other studies involving learning of magnetic directions with domestic chickens and zebra finches (Freire et al. 2005; Wiltschko et al. 2007; Rogers et al. 2008; Voss et al. 2007) are only superficially similar. In both cases, the birds could choose between four directions like ours, but only a first choice was allowed. In contrast to our pigeons, the behaviour of these birds was axial, and they were rewarded in the correct direction and the opposite one. With a chance level of 50%, the chicks preferred the correct spatial axis in 76% and the zebra finches in 82% of the cases, which appears to be in a similar order of magnitude as the 36% first choices in the correct direction we observed with a chance level of 25%. In general, however, the success rates of conditioning studies with magnetic stimuli appear to be lower than those involving other cues.

Comparison with field data

Those birds that performed better in the magnetic conditioning experiment deviated farther from the home direction than the mean of the group, and, from unfamiliar sites outside magnetic anomalies, returned slower. At first glance, this finding is surprising because one might intuitively assume that good magnetic learners should show smaller deviations. However, homing requires the integration of many different cues and probably a combination of strategies. Although experienced pigeons can determine their home direction by local 'map' factors alone (see Wiltschko and Wiltschko 1985), it is unclear to what extent they might use route-based information when available (see Wiltschko and Wiltschko 2000). At sites where local 'map' factors indicate a direction that deviates from the true home direction (Keeton 1973) route-based information, namely the direction of displacement, can be recorded with the magnetic compass and may help to avoid large deviations.

In particular, the deviations from the group mean away from the home direction might reflect exploratory behaviour, as it was observed at unfamiliar, but not at familiar sites. The role of exploratory behaviour in homing is still only partially understood, but it seems likely that collecting information about local cues is a main aspect. Using a modelling approach, Vergassola et al. (2007) have suggested that in addition to following gradients, animals may use 'infotaxis' as a means of updating their information about cues that undergo local change. During infotaxis, animals move in a way that maximizes information gain on cues with variable distribution and visit patches in the local environment that are not on the beeline course to the goal but provide valuable additional information on relevant orientation cues. Assuming that our pigeons had used an infotaxis strategy, this would mean that good magnetic learners

were more prone to update their information on the local factors that had caused the whole group to deviate from the direct homeward path. Regarding the correlation with magnetic learning in the laboratory, it seems plausible that the cues being updated during the pigeons' infotaxis were of magnetic nature. This remains speculative for the moment but allows for specific tests in follow-up studies.

Overall, our study opens several new perspectives for the study of spatial orientation in birds. The evidence for the learning of magnetic compass directions under laboratory conditions in a species that is well studied for homing in the field brings new momentum into the detailed analysis of the mechanisms of avian spatial orientation, the more as our findings for the first time indicate a link between individual learning in the laboratory and performance in the field.

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