

Conditioning to magnetic direction in the Pekin duck (*Anas platyrhynchos domestica*)

Rafael Freire* and Tessa E. Birch

School of Animal and Veterinary Sciences, Charles Sturt University, Wagga Wagga, New South Wales 2678, Australia

*Author for correspondence (rfreire@csu.edu.au)

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SUMMARY

The ability of ducks to derive magnetic direction information was tested in a conditioned procedure and the functional properties of the mechanism of magnetoreception investigated using common manipulations. Twelve ducks were trained to find a hidden imprinting stimulus behind one of three screens in a round arena. Once a criterion was reached, the directional choices of ducks were recorded in four treatments presented in a random order, separated with rewarded training trials to avoid extinction. In tests in the geomagnetic field, ducks preferred the screen in the training direction ($P=0.005$). In the crucial tests of magnetic orientation with the magnetic field experimentally shifted by 120 deg, ducks showed a significant difference in the choice for the correct magnetic direction between treatments ($P=0.002$). More specifically, they chose the correct magnetic direction more often than expected by chance ($P=0.03$), indicating that they were deriving directional information from the magnetic field. Ducks also chose the correct magnetic direction more often than expected by chance in tests with the shifted field after the upper bill was anaesthetised with lignocaine ($P=0.05$) or when the right eye was covered ($P=0.005$), indicating that these manipulations did not impair the ability to choose the correct magnetic direction. Thus, Pekin ducks can be conditioned to magnetic directions, and the results are consistent with the hypothesis that magnetic orientation is based on a chemical magnetoreception mechanism that is not restricted to the right eye.

Key words: magnetoreception, ducks, orientation behavior.

INTRODUCTION

The Earth works as a giant magnet with magnetic field lines that originate and end near the rotational poles, providing directional information that many animals can use for orientation (Wiltschko and Wiltschko, 1995). Although birds have been shown respond to magnetic direction, the mechanisms by which they do so have only recently started to be understood. The magnetite-based mechanism assumes that magnetoreception is derived from particles of magnetite, a form of iron oxide that can align to magnetic fields, present in the cells of animals (Kirschvink et al., 2001). Magnetite has been found in the ethmoid region of the beaks of many birds (Falkenberg et al., 2010), and anaesthetising this region with lignocaine or severing of the trigeminal nerve to the beak has been found to abolish some magnetoreception responses (Beason et al., 1995; Mora et al., 2004). The chemical magnetoreception mechanism assumes that magnetoreception is derived from chemical reactions that are modulated by Earth-strength magnetic fields (for a review, see Rodgers and Hore, 2009). Chemical magnetoreception appears to involve the visual system (Wiltschko et al., 2005; Zapka et al., 2009; Heyers et al., 2007) and possible only the left eye in some birds (Wiltschko et al., 2002; Mouritsen et al., 2004; Rogers et al., 2008).

Response to magnetic direction has been demonstrated in more than 20 species of birds (for a review, see Wiltschko and Wiltschko, 1995), with most of these being passerine migrants. The preference for migrating species of birds as a research model is that orientation in the migratory direction is a reliable behaviour that provides a means for analysing the underlying magnetic orientation mechanism. By contrast, conditioning birds to magnetic directions using magnetic stimuli was initially largely unsuccessful (Wiltschko

and Wiltschko, 1996). More recently, however, conditioning to a magnetic direction was first demonstrated in the domestic chicken, *Gallus gallus*, by training chicks to locate an imprinting stimulus hidden behind one of four screens in a square arena (Freire et al., 2005). In crucial unrewarded tests with the magnetic field experimentally shifted by 90 deg to the east, chicks shifted their search accordingly, indicating that they were deriving directional information from the magnetic field. Further research with the chicken showed that orientation is disrupted by covering of the left eye but is not disrupted by anaesthetising the beak with lignocaine, suggesting that chickens possess a chemical magnetoreception mechanism similar to that used by passerine migrants (Wiltschko et al., 2007a). In the current study, we investigated magnetoreception in another precocial bird, the Pekin duck (*Anas platyrhynchos domestica*), derived from the widely dispersed mallard ducks (*Anas platyrhynchos*), which show migratory behavior, such as from North America to Mexico for the winter (Drilling et al., 2002).

The ability of ducks to learn to use magnetic direction information was tested in a conditioned procedure based on that used by Wiltschko and colleagues (Wiltschko et al., 2007a), only with three, rather than four, screens. This improvement was introduced to remove the difficulty that birds appear to have in differentiating between the two screens on the same magnetic axis. Common techniques that disrupt the putative chemical magnetoreception mechanism, the covering of the right eye (Wiltschko et al., 2002; Rogers et al., 2008), and that disrupt the putative magnetite-based mechanism, the application of lignocaine to the upper beak (Beason et al., 1995; Mora et al., 2004), were also used to investigate the mechanism used by the ducks.

MATERIALS AND METHODS

Subjects and imprinting procedure

Twelve Pekin ducks of unknown sex obtained from Nulkaba hatchery (Cessnock, NSW, Australia) were reared in isolation from about 20 h after hatching in pens (40×60×40 cm) with wood-shavings on the floor and opaque walls. A red table tennis ball, 4 cm in diameter, was suspended by nylon string 10 cm above the floor in the centre of the pen to provide the imprinting stimulus. Temperature was maintained at 25–30°C and lighting was on a 16 h:8 h light:dark cycle. The ducks were fed chick starter crumbs on a round (15 cm diameter) dish, and water was available *ad libitum* from an externally mounted drinker.

Apparatus

The ducks were trained to locate the imprinting stimulus (red ball) behind one of three screens in a round testing arena in the local geomagnetic field of Wagga Wagga, NSW, Australia (58000 nT, –66 deg inclination). The testing arena was a white round pen with a diameter of 80 cm and height of 40 cm. Wood shavings were used to cover the floor. Three white screens (15 cm wide, 25 cm high) were positioned perpendicular to the centre and 15 cm from the side walls of the arena. One screen was positioned at the magnetic north, and the other two screens were 120 deg and 240 deg from this screen. The upper 35 cm of the arena comprised four walls that could be opened to introduce and remove the ducks. Lighting in the arena was provided by four incandescent lamps (40 W) above a light diffuser. Care was taken to make the arena as uniform as possible so as to reduce the effect of spatial cues and an overhead camera (Kobi DSP) was placed above the centre of the arena, with the lens positioned through a hole of diameter 5 cm in the light diffuser and was used to observe the behavior of the ducks on a monitor.

Training phase

Training and testing were undertaken when ducks were 5–20 days of age. Training involved placing a duck in the centre of the arena in a clear plastic start cage (20×20×25 cm) for 20 s next to the red ball. The ball was then slowly moved behind one screen and the duck released and allowed to search for the ball (this was termed a ‘visual displacement trial’). One minute after approaching to within 5 cm of the ball, or after 3 min, the duck was picked up and returned to the home pen.

After completion of three visual displacement trials, the duck was placed in the start cage with the ball already behind a screen. After 20 s, the duck was released and allowed to search for the ball (this was termed a ‘relocation trial’). One minute after the duck had approached to within 5 cm of the ball, it was returned to its home pen. If a duck failed to approach the ball within 3 min of release, it was shown the location of the ball before being put back in its home pen.

Each duck continued to receive relocation trials until it approached to within 5 cm of a ball in less than 20 s of release on three consecutive relocation trials (‘criterion’). Trials in which a duck moved behind other screens not concealing a ball before locating the ball were scored as incorrect and not used to determine whether criterion was reached. In order to minimize the impact of other cues within the arena, the arena was rotated by 120 deg or 240 deg between trials according to a pseudorandom sequence. Additionally, the side of the arena from which the duck was handled was also determined by a pseudorandom sequence.

Testing phase

The testing phase consisted of unrewarded (no ball) tests interspersed by relocation trials (in order to prevent extinction of the conditioned

response). Four ducks were trained to locate the ball behind each of the three screens. Tests were identical to relocation trials except that there was no imprinting stimulus behind a screen. After a test, the duck was returned to the home pen with the ball for a few minutes before being placed in the start cage again and presented with a relocation trial, as described above – that is, in the local geomagnetic field with a ball placed behind the correct screen. After this, it was returned to its home pen for a few minutes and then presented with another test. This continued every day until a full complement of 20 tests was obtained for each duck, which took 2–4 days.

Each duck received five tests of each of four treatments presented in a random sequence: (1) in the natural geomagnetic field (geomagnetic tests), (2) in an experimental magnetic field with magnetic north rotated by 120 deg clockwise (shifted-north tests), (3) in an experimental field [as in (2)] with the right eye covered with a cone-shaped piece of masking tape (left-eye tests) and (4) in an experimental field [as in (2)] with 2% lignocaine hydrochloride solution (lignocaine tests; Illium Lignocaine, Troy Laboratories PTY Limited, Smithfield NSW, Australia).

The masking tape cone was attached to the feathers around the eye approximately 5 min before the test and did not press on the eye. Most ducks initially attempted to remove the cone, but, after about 5 min, such activities were not observed and the ducks showed normal behavior in the home pens. Immediately after each monocular test, the eye patch was removed with care. Lignocaine was applied to the underside of the upper bill with a cotton bud 10 min before the test, and the ducks did not show any adverse effect to this procedure. Lignocaine has been used for analgesia in various bird species and is considered to have a relatively short (i.e. less than 30 min) effect when applied topically, and there was a delay of at least 2 h after a lignocaine test before presentation of another test.

The experimental magnetic field was generated by sets of Helmholtz coils with a diameter of 2 m and a clearance of 1 m. The coils were positioned around the arena, with their axis horizontally oriented towards 150 deg so that magnetic north could be shifted by 120 deg clockwise, with minimal changes to inclination and intensity.

Statistical analysis

For each duck and each test, the treatment (geomagnetic, shifted-north, left-eye and lignocaine), order (1–20) and response were recorded. The response was the direction of the screen that the duck first walked behind (i.e. direction chosen) and was the training direction (TD), the correct magnetically shifted direction (i.e. 120 deg shifted clockwise from the training direction, ‘SD’, shifted direction) or the screen in the other direction (‘OD’). Analysis was required to test for differences between treatments, so treatment was included in models as a fixed effect. To account for possible variation between ducks (in training ability), duck was included in models as a random effect (as in repeated measures analysis, for example). The number of times the TD or SD was chosen in a given number of tests has a binomial distribution (i.e. x number of times chosen out of y number of tests). Therefore, the number of tests in which TD was chosen was analysed using Binomial Generalised Linear Mixed Models (GLMMs), and the same analysis then performed for the number of times that SD was chosen. Further analysis to determine whether choices differed from random was undertaken using the estimates of the logit of the proportion of choices of TD and SD for each treatment. These were compared with the logit of ‘1/3’ (i.e. random) by using established normal theory for the distribution of parameter estimates [Z tests, where Z is the standard (0,1) distribution]. The duration taken to make a choice was log transformed to meet modelling assumptions and analysed in a linear

mixed model with ‘treatment’ as a fixed effect and ‘duck’ as a random effect.

RESULTS

In visual displacement tests, ducks readily called and searched for the imprinting stimulus, indicating that the imprinting procedure had been effective. Ducks also learnt to search readily for the imprinting stimulus in relocation trials, reaching criterion of three consecutive successes in 3–16 trials (mean 8.5±1.3). Ducks were reasonably accurate at finding the ball in relocation trials between the tests, requiring on average 1.5±0.06 trials before being presented with another test. Ducks were also motivated to move behind a screen in tests, although they took significantly longer to make a choice in left-eye tests (back-transformed predicted mean 9.4 s, GLMM: $F_{3,224}=14.3$, $P<0.001$) than in geomagnetic tests (3.2 s), lignocaine (3.7 s) or shifted-north tests (3.3 s).

Table 1 shows the directional choices of ducks in the four treatments – for one duck (number 2) only four lignocaine tests were completed owing to experimenter error. The crucial test of magnetic orientation – the ability to chose the shifted direction (SD) in shifted-north tests – revealed a significant difference between the four treatments (GLMM: $F_{3,224}=5.03$, $P=0.002$, Fig. 1). Further analysis shows that ducks chose the SD screen significantly more often than expected by chance in shifted-north tests ($Z=2.2$, $P=0.03$) but chose the SD screen significantly less often than expected by chance in tests in the geomagnetic field ($Z=-2.33$, $P=0.02$). Interestingly, ducks also chose the SD screen significantly more often than expected by chance in lignocaine ($Z=2.8$, $P=0.005$) and left-eye ($Z=1.96$, $P=0.05$) tests.

Ducks chose the screen in the training direction (TD) more often than expected by chance in the tests in the geomagnetic field ($Z=2.8$, $P=0.005$), indicating the effectiveness of the conditioning procedure. Not surprisingly, because, as described above, ducks preferred the SD in the three treatments with the experimental magnetic field, ducks did not choose the training direction a significantly different number of times from chance level in lignocaine ($Z=0.88$, $P=0.38$), left-eye ($Z=1.57$, $P=0.12$) or shifted-north tests ($Z=-0.27$, $P=0.79$). The number of choices of the TD screen did not differ significantly between the four conditions (GLMM: $F_{3,224}=1.7$, $P=0.17$).

Finally, ducks significantly avoided the other direction (OD) in shifted-north tests ($Z=2.06$, $P=0.04$), left-eye tests ($Z=3.48$, $P=0.0001$) and lignocaine tests ($Z=2.97$, $P=0.003$) but did not choose the OD a significantly different number of times from random in geomagnetic tests ($Z=0.59$, $P=0.55$, Fig. 1).

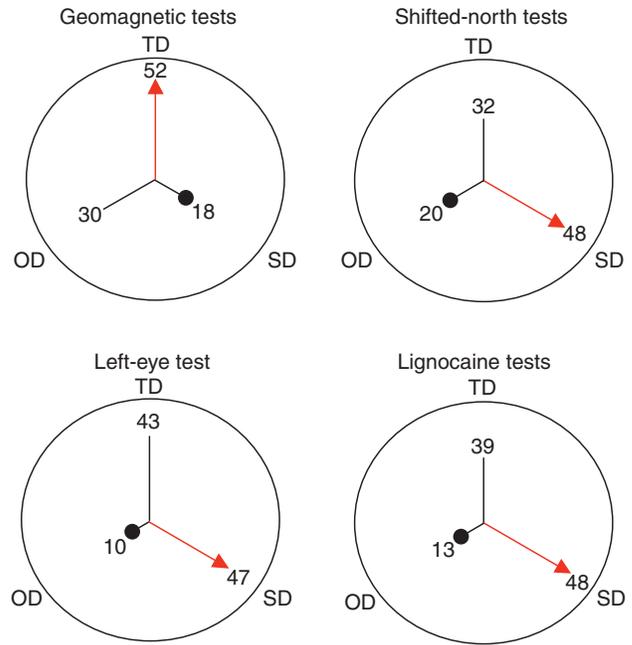


Fig. 1. The back-transformed mean of the number of choices for each screen in the magnetic direction test presented as a percentage. Choices for the screen in the training direction (TD), shifted direction 120 deg from the training direction (SD) or the screen in the other direction (OD) for each of the four treatments (geomagnetic field, shifted-north, lignocaine and left-eye tests) are shown. Red lines and arrows indicate samples with a significant preference for a particular direction, black lines and rounded endings indicate significantly fewer choices than expected by chance. Black lines with a straight ending indicate choices that do not differ from chance level.

DISCUSSION

In summary, ducks chose the screen in the training direction in tests in the local geomagnetic field and, crucially, when the magnetic field was shifted by 120 deg, chose the screen in the correct magnetic direction, indicating that they were deriving directional information from the magnetic field. Ducks also chose the screen in the correct magnetic direction significantly more than expected by chance in tests in which the upper bill was anaesthetised with lignocaine or in tests in which the right eye was covered, indicating that these manipulations did not impair the ability to derive directional information from the magnetic field.

Table 1. Directional choices of the individual ducks (#N) trained to each of the three training directions (TD)

| #N | TD | Geomagnetic tests | | | | | | Lignocaine tests | | | | | | Left-eye tests | | | | | | Shifted-north tests | | | | | |
|----|----|-------------------|---|---|---|---|---|------------------|---|---|---|---|---|----------------|---|---|---|---|---|---------------------|---|--|--|--|--|
| 1 | E | E | E | n | E | n | e | e | n | W | e | W | n | e | W | e | n | W | W | W | e | | | | |
| 2 | E | n | E | E | E | n | e | e | n | W | e | W | e | e | W | W | n | n | e | W | W | | | | |
| 3 | E | E | E | E | n | E | W | W | e | W | e | e | W | W | e | n | e | e | e | n | e | | | | |
| 4 | E | E | E | w | E | E | n | W | e | e | W | e | W | W | e | n | n | e | W | W | e | | | | |
| 5 | N | e | w | e | w | w | E | n | n | E | E | E | n | E | n | E | E | E | E | E | E | | | | |
| 6 | N | w | e | N | N | N | E | E | n | n | E | n | E | E | n | E | n | E | E | E | E | | | | |
| 7 | N | N | N | N | e | e | E | n | E | E | E | n | E | n | n | E | n | E | E | E | n | | | | |
| 8 | N | N | e | N | N | w | E | E | n | n | n | E | n | E | n | E | n | E | n | E | n | | | | |
| 9 | W | n | e | e | n | e | N | N | e | N | N | w | w | w | w | e | e | N | e | N | N | | | | |
| 10 | W | W | W | e | e | e | e | w | w | e | w | w | w | N | e | w | N | N | e | e | w | | | | |
| 11 | W | W | W | W | e | n | w | N | N | w | w | N | N | N | N | e | w | e | N | N | N | | | | |
| 12 | W | e | n | W | W | W | N | N | e | e | N | w | w | N | N | N | e | e | w | w | N | | | | |

Choices are shown for the four treatments. Choices of the correct magnetic direction are indicated by uppercase letters and incorrect ones by lower-case letters. The order of presentation of the treatments was randomised, but the order is not shown in this table.

The duck proved to be an excellent model species for conditioning to the magnetic direction – they readily sought the imprinting stimulus in the training trials, and all ducks continued to be strongly motivated to search for the imprinting stimulus throughout the tests. The new test used in this study had three screens in a round arena, as opposed to four screens in a square arena, as previously used with chickens (Freire et al., 2005; Wiltschko et al., 2007a). In the latter test, chickens showed axial responses, that is they were unable to differentiate between the correct magnetic direction and the opposite direction (i.e. the screen at 180 deg), which is difficult to interpret from a biological perspective as choosing the correct magnetic axis also corresponds to sometimes going in the wrong (i.e. 180 deg to the correct) direction. This axial response also complicates the training trials as two imprinting stimuli are required, one behind the correct screen and one behind the screen opposite it, to prevent the conditioned response becoming extinguished. The new methodology, and the use of ducks that are derived from a migratory species, we hope will offer a new research model for the investigation of magnetic compass orientation in birds that is not restricted to the migratory seasons. Additionally, the use of a commercially available species represents some benefits in terms of the ethics of animal research in that these birds were (1) domestically hatched and reared and (2) showed little fear of human handlers owing to their domestication.

We unexpectedly found that ducks showed magnetic compass orientation even with the right eye covered, even though magnetic compass orientation is disrupted by covering the right eye in European robins [*Erithacus rubecula* (Wiltschko et al., 2002)], silvereyes [*Zosterops lateralis* (Wiltschko et al., 2003)] and chickens [*Gallus gallus* (Rogers et al., 2008)]. The slightly longer time taken by ducks to choose a screen in the left-eye tests compared with the other treatments probably indicates the difficulty in walking with one eye covered, rather than an effect on magnetic orientation. These findings indicate that use of the right eye is not crucial for compass orientation in the duck. Recently, night-migrating garden warblers (Hein et al., 2009) and pigeons (Wilzeck et al., 2010) have also shown magnetic orientation using the left eye only, suggesting that the lateralization of magnetic compass orientation might be limited to some bird species. An alternative explanation, that magnetic compass orientation in the duck involves a magnetite-based mechanism would not seem plausible either as anaesthetising the bill with lignocaine did not disrupt magnetoreception, yet this procedure disrupts some magnetoreception responses in homing pigeons [*Columba livia* (Mora et al., 2004)].

An alternative explanation, albeit rather speculative, is that ducks are able to derive magnetic direction information from both the chemical and magnetite-based mechanisms, and were thus able to alternate use of the mechanism that was not disabled in the monocular and lignocaine treatments. If the magnetite-based mechanism is an evolutionary ancient mechanism of magnetic compass orientation (Wiltschko et al., 2007b), it might well be expected to have retained its receptor properties and perhaps guide behavior when the chemical mechanism is not functioning. One such situation in the natural context would be during navigation under low light, such as dusk or night migrations, when there might not be sufficient light for the chemical magnetoreception mechanism to operate. Even if the magnetite-based mechanism does not provide magnetic compass orientation on its own, animals might also be able to use the ‘fixed direction’ information it seems to provide (Wiltschko et al., 2007b) and combine it with other spatial cues to give meaningful orientations. In the wild, it would seem an oversimplification to assume that orientation is based solely on one source of information, and orientation based on a combination of magnetic information and other spatial cues would seem more reliable for orientation (e.g. Biro et al., 2007). In tests with the shifted-

field, ducks showed a significant avoidance of the ‘other direction’ but not the training direction, raising the possibility that they might have also associated some unknown extra-apparatus spatial cue with the training direction. Our tests in the shifted magnetic field would therefore have placed ducks in a conflict situation – extra apparatus cues might have guided the ducks towards the training direction, whereas magnetic cues guided the duck 120 deg from this. One possibility is that the ducks might have been using extra-apparatus cues such as the sound of ducks in the neighbouring room, although the way in which magnetic and other directional information is used for orientation is an area of research needing further examination.

In conclusion, Pekin ducks derived from the migratory Mallard duck showed magnetic compass orientation in a simple conditioning paradigm. Magnetic orientation was observed even after anaesthetising of the bill or covering of the right eye, and these results are consistent with the hypothesis that magnetic orientation is based on a chemical magnetoreception mechanism that is not restricted to the right eye in this species.

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