The Journal of Experimental Biology 215, 2399-2404
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doi:10.1242/jeb.068312

RESEARCH ARTICLE

Conditioned response to a magnetic anomaly in the Pekin duck (*Anas platyrhynchos domestica*) involves the trigeminal nerve

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SUMMARY

There have been recent calls to develop protocols that collect unambiguous measures of behaviour using automatic techniques in conditioning experiments on magnetic orientation. Here, we describe an automated technique for recording the behaviour of Pekin ducks in a conditioning test that allows them to express unrestricted searching behaviour. Pekin ducks were trained to find hidden food in one corner of a square arena below which was placed a magnetic coil that produced a local magnetic anomaly. The trigeminal nerve was anaesthetised by injection of lignocaine hydrochloride 2–3 mm caudal to the medial canthus of each eye, medial to the globe, prior to the presentation of unrewarded tests. Lignocaine-treated ducks showed no initial preference for the magnetic anomaly whereas saline-treated control ducks showed a significant preference at the same age. A second experiment was undertaken in which the trigeminal nerve was surgically severed and 2–3 mm removed, and this surgery abolished the previously observed preference for the corner with the magnetic coil in a small number of ducks. These data show that Pekin ducks are able to detect and use magnetic stimuli to guide unrestricted search behaviour and are consistent with a hypothesis of magnetoreception involving a putative cluster of magnetite in the upper beak.

Key words: behavioural scoring, magnetoreception, trigeminal nerve, birds.

Received 15 November 2011; Accepted 21 March 2012

INTRODUCTION

Conditioning birds to respond to magnetic intensity has only recently been achieved in the laboratory, and usually requires animals to move in response to an experimentally presented magnetic anomaly (Mora et al., 2004) or to move to a location with a different magnetic intensity and inclination in order to obtain a reward (Thalau et al., 2007; Denzau et al., 2011).

Magnetoreception in the above tests is believed to be derived from particles of magnetite, a form of iron oxide that can align to magnetic fields, in the cells of birds (Heyers et al., 2010; Kirschvink et al., 2001). Magnetite has been found in the ethmoid region of the beaks of some 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 (Mora et al., 2004; Semm and Beason, 1990). With respect to their role in natural behaviour, recent evidence suggests that these receptors in the beak mediate magnetic map information such as for guiding homing behaviour in pigeons (Wiltschko et al., 2010).

Conditioning birds to respond to magnetic direction has similarly only recently been achieved by training animals to move in a certain magnetic direction in order to obtain a reward (Freire et al., 2005; Voss et al., 2007; Wilzeck et al., 2010). This response appears to be modulated by chemical reactions that respond to Earth-strength magnetic fields and forms the basis of the avian magnetic compass (Rodgers and Hore, 2009). In the domestic chicken, chemical magnetoreception appears to involve the visual system and is unaffected by anaesthetising the beak region with lignocaine, suggesting a mechanism analogous to that found in passerine migrants (Wiltschko et al., 2007). Recently, the Pekin duck (*Anas platyrhynchos domestica*), derived from the widely dispersed and sometimes migratory mallard duck (*Anas platyrhynchos*) (Bellrose, 1980), was successfully trained to magnetic directions and again these responses were not affected by the application of lignocaine to the beak (Freire and Birch, 2010).

As described above, the free and unrestricted movement of birds appears to be crucial to the success of conditioning tests of both magnetic intensity and direction, and may also more closely emulate the natural behaviour in which magnetic intensity and direction provide information used for orientation. However, the requirement for free and unrestricted movement presents a challenge to researchers as to how to record this behaviour while ensuring objectivity (Marsh and Hanlon, 2007; Sheldrake, 1998). Recently, there have been calls to use automatic techniques in conditioning experiments on magnetic orientation to provide greater consistency of experimental control and data capture (Kirschvink et al., 2010). The adoption of automated and reproducible protocols for measuring responses to magnetic cues is expected to have a significant impact on the field of magnetic orientation in animals.

Here, we propose an automated technique for recording the location of Pekin ducks in a conditioning test that allows them free and unrestricted movement. The technique is based on automatic image recognition and data entry. We trained ducks to associate the presence of a localised experimental magnetic anomaly with hidden food, and in unrewarded tests compared the duck's preference for this magnetic anomaly with their preference for a control coil that does not generate a magnetic field. In Experiment 1, trained ducks were tested once a day for 10 consecutive days following injection of either lignocaine or saline (control treatment) to an area beside the trigeminal nerve. In Experiment 2, the findings of Experiment 1 were further explored by surgical severing of the trigeminal nerve.

MATERIALS AND METHODS

Experiment 1: anaesthesia of the nerve

Study animals and maintenance

Eighteen Pekin ducks (*Anas platyrhynchos domestica*) of unknown sex obtained from Nulkaba hatchery as 1 day old ducklings (Cessnock, NSW, Australia) were randomly assigned to three groups of six ducks and placed in 70×150×60 cm pens lined with wood shavings. Temperature was maintained at 25–30°C and lighting on a 16 h light:8 h dark cycle. Water was available *ad libitum* from a poultry drinker.

Training phase

The arena for training and testing was made of 20 mm white laminated chipboard and had a square bottom with sides of 80 cm, and was 75 cm high. The walls of the arena were lined with black paper up to a height of 25 cm above the floor, with the remainder of the walls being white. A dark grey substrate consisting of a mixture of peat and wood dust covered the floor. An overhead camera was placed above the centre of the arena and was used to record the duck's behaviour on a laptop computer.

A black plastic feeding dish (15 cm diameter) was placed at each of the four corners of the arena. Underneath two of these dishes at opposite corners (and under the floor of the arena) was fixed a magnetic coil or a control coil. The magnetic coil comprised copper wire wound around a wooden wheel to create a 15 cm wide coil with 60 revolutions of wire. A DC current of 1 A was run through the coils to produce a magnetic anomaly. A fluxgate magnetometer (MAG-01H, Bartington Instruments, Witney, UK) was used to measure the strength of the anomaly 100 mm above the coil at approximately the height of the duck's head. The anomaly was measured at the local maximum (north orientation, 65 deg inclination) vertical and horizontal (north direction) positions (Fig. 1A). The control coil was made with identical copper wire wound 30 times in one direction and 30 times in the opposite direction. Double wrapping in this way cancels out the magnetic field generated by the current, and controls for possible effects such as warmth, hum or vibration.

The training procedure involved placing each duck in the centre of the arena in a clear plastic start cage measuring 15×15 cm for 20 s before it was released. Poultry starter crumbs had previously been placed in the dish located above the magnetic coil. The remaining dishes contained the dark grey substrate covering the floor. For day 1 (the day of arrival from the hatchery) and day 2, the food was uncovered and ducks were in pairs and allowed to remain in the arena until they had finished eating (usually 10–15 min). From days 3 to 5, each duck was trained individually two times a day and had access to starter crumbs out of the dish located above the magnetic coil until the duck had finished eating (usually 3–6 min). On each subsequent day, additional dark grey substrate was placed over the food to encourage searching for the food. The amount of time taken to find the food was recorded and the duck was removed after it had finished eating, and returned to its home pen. The location of the magnetic coil was changed every day according to a random sequence.

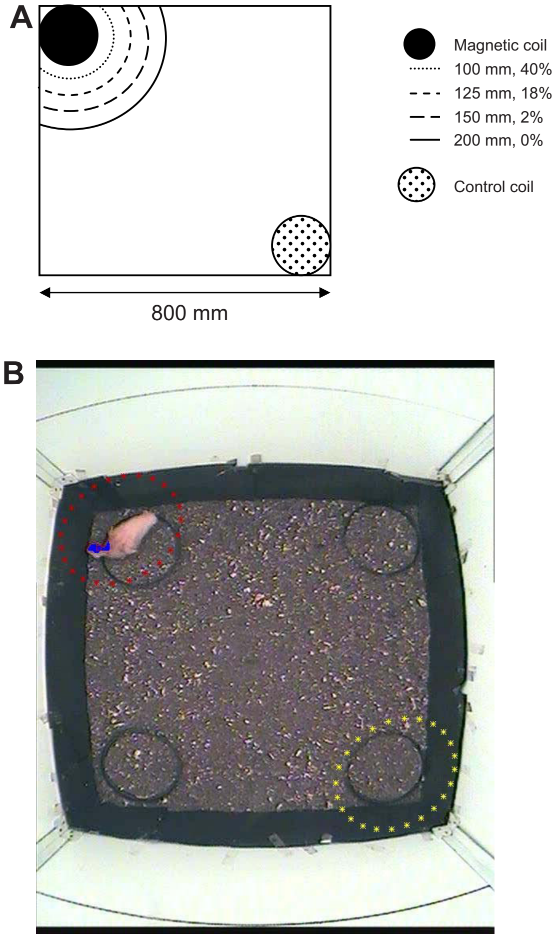

Fig. 1. (A) Intensity of the magnetic anomaly generated by the magnetic coil. The anomaly was measured at the local maximum (north orientation, 65 deg inclination), vertical and horizontal (north direction) positions. These three measurements were summed and compared with identical measurements with the centre of the coil at 100, 125, 150 and 200 mm from the probe. The percentage increase in the strength of the magnetic anomaly relative to the local field is presented. (B) Image of the contours of the duck's head identified by the sampling program (blue) and approximate extent of the magnetic anomaly (red dotted circle) and its equivalent around the control coil (yellow dotted circle).

Testing phase

Testing was unrewarded (no food) with all four dishes filled with dark grey substrate. Ducks were placed in the arena for 2 min each day for 10 days (6–15 days of age). Each of the 18 ducks received one of two treatments on each day of testing. Each duck received each treatment for 5 days (i.e. five lignocaine and five saline observations from each duck), according to a pseudo-random sequence, and on each day the position of the magnetic coil was changed according to a random sequence. Lignocaine treatment involved injection of 0.2 ml of 20 mg ml^{-1} lignocaine hydrochloride (Ilium Lignocaine 20, Troy Laboratories, Smithfield, NSW, Australia) 2–3 mm caudal to the medial canthus of each eye, medial to the globe. Saline treatment involved the injection of 0.2 ml sterile saline solution to the same area. Ducks were marked with red hairspray to the top of the head, in area of approximately 10×20 mm. An observer recorded the number of bouts of head scanning in the 2 min tests in real time. A bout of head scanning was defined as a number of side-to-side turns of the bird's head at an angle more than 60 deg to the left or right, followed by the subsequent return of the head to the normal position. Head scanning is a rapid movement and it is difficult to count individual turns of the head in real time. Instead, we counted bouts of these behaviours separated by a period in which the head was in the normal straight position for more than 3 s at the end of the bout. Each bout usually comprised 3–4 side-to-side movements. Two hours after the completion of the tests, individual ducks were returned to the arena, with food above the magnetic coil in order to receive a training trial as described above.

Statistical analysis

Automatic image recognition was used to detect the centroid of the red area on the duck's head every 5th frame (i.e. 0.2 s) to give 600 locations for each 2 min test. The centroid locations were transformed to actual distances from the centre of the magnetic coil, following correction for the geometric distortion introduced by the lens. The number of times that the centroid of the red mark of each duck was within 150 mm of the centre of the magnetic coil, as depicted in Fig. 1B, and control coils was automatically recorded and tabulated. The location data were in the form of the number of times that the duck was recorded above the magnetic coil and control coil, with a maximum of 600 per 2 min test. These 'counts' data have a binomial distribution with the total counts being the sum of the number of counts above the magnetic coil and the number of counts above the control coil. It should be noted that the proportion of counts above the magnetic coil ranges from 0 to 1 with 0.5 representing a random distribution. A generalised linear mixed model (GLMM; Genstat 13, VSN International, www.vsni.co.uk) was used to analyse these counts with treatment and days as fixed effects and duck as a random factor. A *post hoc* binomial test on the number of ducks that spent more time above the magnetic coil than above the control coil (i.e. the proportion of counts above the magnetic coil that were >0.5) was used as a conservative method to identify significant preferences for the magnetic coil. Head-scanning bouts met assumptions for parametric analysis and were analysed in a generalised linear model (GLM) with treatment and age as fixed effects factors and duck as a random factor.

Experiment 2: nerve section

Five pekin ducks, different from those used in Experiment 1, were reared in groups of 2–3 in 70×150×60 cm pens lined with wood shavings. Maintenance and training to find food were in the testing arena from days 1 to 5, as in Experiment 1. The ducks were then tested on day 6, again following the same procedure as in Experiment 1, and their location recorded automatically. The number of head scans was also recorded. The ducks continued to receive training trials as in Experiment 1 until day 11. On day 11, the trigeminal nerves were sectioned as described below. Ducks were returned to their home pens on day 12 to recover. On days 13–15, they received a testing trial in the morning, and a training trial 2 h later, following the procedure in Experiment 1.

Surgery

All surgical procedures were approved by the Charles Sturt University Animal Care and Ethics Committee. Anaesthesia was induced by inhalation of isoflurane (Baxter Australia, Toongabbie, NSW, Australia) in oxygen administered *via* a mask made from a latex sheet stretched over a small feline anaesthetic mask and split to admit the bird's beak and nares. Once a sufficient plane of anaesthesia had been achieved, the duckling was placed on a heating pad at 42°C and an assistant held the mask and head to allow the procedure to be performed.

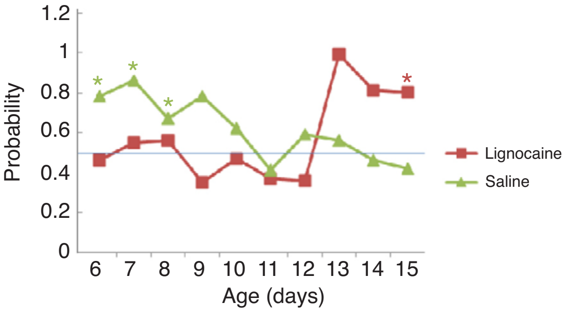

Fig. 2. Back-transformed means of probabilities for observations in which the centroid of the mark on the duck's head was within 150 mm of the magnetic coil following treatment with lignocaine or saline (means from GLMM, see Materials and methods). The probability of 0.5 (i.e. no preference) is marked with a blue line. *Post hoc* binomial test comparisons in which probability was significantly greater than 0.5 are marked with an asterisk ($P<0.05$).

The surgical procedure was performed using an operating microscope. An incision was made through the skin from 3–4 mm rostral to, and level with, the medial canthus of the eye to 3–4 mm caudal and just dorsal to the upper eyelid along the line of the orbit. The subcutaneous tissues were gently dissected with Potts scissors to reveal the dorsal rim of the orbit. The dissection was continued into the orbit, medial to the conjunctival sac whilst gentle caudal and lateral retraction was applied to the globe to allow adequate visualisation. The trigeminal nerve was identified coursing rostrally from the middle of the orbit, behind the globe, toward an area just ventral to the medial canthus. Using Potts scissors the nerve was transected and a 2–3 mm section removed, taking care not to sever a small artery associated with the nerve. If the artery was accidentally transected, gentle pressure was applied for 2–3 min to control bleeding. At the conclusion of the procedure, 0.1 ml of bupivacaine (Pfizer Australia, West Ryde, NSW, Australia) was instilled into the area and the skin closed with 4/0 monofilament glyconate (Monosyn, B. Braun Australia, Bella Vista, NSW, Australia) in a cruciate pattern. The duck was then turned over and the opposite trigeminal nerve sectioned in the same way. At the conclusion of the procedure the bird was given 2–3 ml of Hartmann's solution (Baxter Australia) by injection, subcutaneously on the lateral side of the body under each wing. Once the bird was conscious, a single dose of meloxicam (Metacam, Boehringer Ingelheim, North Ryde, NSW, Australia) was given by subcutaneous injection at a dose of 0.1 mg kg^{-1}.

Statistical analysis

Duck number 1, 3 and 4 failed to move within 150 mm of either coil on days 6, 15 and 14, respectively, thereby scoring no observations. As ducks need to be active and move to the corners in order to detect the magnetic anomaly, these ducks would not have been exposed to the magnetic information necessary to make a choice. These three records were therefore treated as missing values. The number of observations (counts) above the magnetic coil was again analysed in a GLMM. In the interests of reducing the number of ducks undergoing surgical procedures, we did not conduct a sham-surgery treatment. Instead, we used the number of observations above the control coil for each duck as a control for comparison. Therefore, the type of coil (magnetic or control) and day were fixed effects in the model, with duck as a random factor.

RESULTS

Experiment 1

Ducks were active during training and fed upon the food, suggesting that they were motivated to find food. Despite making the food searching more difficult on subsequent days by covering the food with substrate, ducks learnt the task quickly. Ducks took 60±21, 26±13 and 9±3 s to start eating on days 3, 4 and 5, respectively.

In tests, a significant treatment–day interaction on the number of counts above the magnetic anomaly was found (GLMM, $F_{9,130}$=2.4, P=0.017). There were no significant main effects of day (GLMM, $F_{9,135}$=1.5, P=0.17) or treatment (GLMM, $F_{1,136}$=0.8, P=0.39) on the number of counts above the magnetic anomaly. *Post hoc* binomial tests on the preference for the magnetic coil over the control coil indicated that ducks treated with saline preferred the magnetic coil in their earlier tests, but that this preference disappeared in later tests (Fig. 2). In contrast, ducks treated with lignocaine showed no preference for the magnetic coil in earlier tests, but showed a preference for this coil in the last test (Fig. 2).

A significant treatment–day interaction was found for the number of head-scanning bouts (GLM, $F_{9,136}$=3.6, P<0.001). There was also a main effect of day on head-scanning behaviour (GLM, $F_{9,132}$=4.1, P<0.001) but not of treatment (GLM, $F_{1,132}$=3.7, P=0.056). The significant interaction suggests that lignocaine-treated ducks showed more head-scanning behaviour on days 6 and 7 than saline-treated ducks, though there also appeared to be considerable between-day variation (Fig. 3).

Experiment 2

On day 6, ducks spent significantly more time above the magnetic coil than above the control coil (GLMM, $F_{1,19}$=19.4, P<0.001; Fig. 4), supporting the results of Experiment 1. After surgery, however, there was no significant difference in the time spent above the magnetic coil compared with time spent above the control coil (GLMM, $F_{1,22}$=0.06, P=0.82; Fig. 4). There was large variation between ducks on days 13–15 as shown in Table 1. There was also no effect of day (GLMM, $F_{1,22}$=0.0, P=1) or day–treatment interaction (GLMM, $F_{1,22}$=2.1, P=0.16) on the amount of time spent above the magnetic coil after surgery. Predicted means for the number of head scans were 5.0 for day 6, 4.6 for day 13, 12.4 for day 14 and 9.0 for day 15 (GLM, $F_{3,12}$=3.3, P=0.059) and were in the range observed in Experiment 1.

DISCUSSION

In summary, for the first 3 days of testing in Experiment 1, ducks treated with saline spent significantly more time above the magnetic coil that had previously indicated the presence of hidden food than above the control coil. In contrast, ducks injected with lignocaine near the trigeminal nerve showed no preference for this magnetic coil compared with the control coil during this time. Lignocaine-treated ducks performed more head-scanning behaviour than saline-treated ducks in these first 2 days, possibly indicating that they were trying to detect the magnetic anomaly. The conditioned response in saline-treated ducks showed a classical extinction curve, with preference becoming extinguished with time. Curiously, lignocaine-treated ducks showed a significant preference for the magnetic coil in the last day of testing, suggesting that they may have been able to detect the magnetic coil at 13–15 days of age. In Experiment 2, we tested ducks at this age following surgical severing of the trigeminal nerve, to test the possible involvement of the trigeminal nerve at this age. Severing the trigeminal nerve did indeed abolish the previously significant preference for the magnetic anomaly. These findings provide objective evidence that a magnetic anomaly can guide unrestricted movement in the duck and that this response requires a functioning and intact trigeminal nerve.

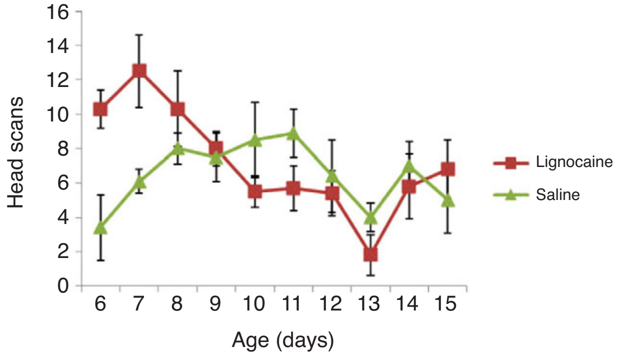

Fig. 3. Mean number of head scans (±s.e.m.) in tests following treatment with lignocaine or saline solution (Experiment 1).

The magnetic coil generated a magnetic field that extended about 15–20 cm away from the centre of the coil and was characterised by changes in magnetic intensity and inclination. Ducks would have needed to move within this distance of the coil in training trials before detecting the stimulus and obtaining the reward, so that conditioning would occur through instrumental learning. The finding that the time taken from the introduction into the arena to commencing feeding decreased with subsequent training trials supports the occurrence of instrumental learning. The required response in tests, unrestricted movement and searching behaviour, is difficult to measure objectively using conventional observer records as described in the Introduction. It is perhaps not surprising that conditioning to magnetic stimuli has been most successful with birds that generally walk more than passerine migrants as for practical reasons there are limitations on the size of experimental apparatuses and the generation of experimental magnetic fields.

The conditioning methods in the study by Mora and colleagues (Mora et al., 2004) and this study yielded similar correct responses or preferences of about 70%. Instrumental (operant) learning protocols where the reward follows the response allow for fast training with little experimenter influence as the response is virtually always paired with the reward. Tests in our protocol were unrewarded to eliminate the possibility of ducks using olfactory or

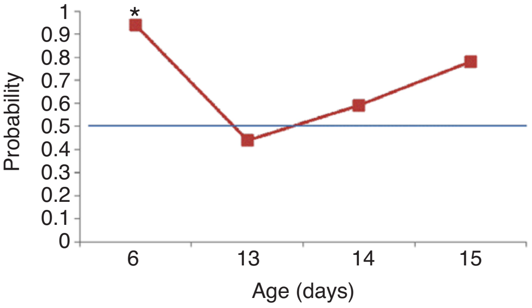

Fig. 4. Back-transformed means of probabilities for observations in which the centroid of the mark on the duck's head was within 150 mm of the magnetic coil before surgery (day 6) and in the 3 days after surgery (days 13–15). It should be noted that only the days on which testing was undertaken are shown on the *x*-axis. The probability of 0.5 (i.e. no preference) is marked with a blue line. Probability significantly greater than 0.5 is marked with an asterisk (P<0.05).

Table 1. Number of counts above the magnetic and the control coil for each duck in Experiment 2

Duck	Age (day)	Magnetic coil	Control coil	% Magnetic coil
2	6	12	0	100
3	6	9	0	100
4	6	76	17	81.7
5	6	176	0	100
1	13	0	33	0
2	13	83	0	100
3	13	22	322	6.4
4	13	155	58	72.8
5	13	69	0	100
1	14	0	25	0
2	14	64	0	100
3	14	13	7	65
5	14	0	25	0
1	15	24	0	100
2	15	0	51	0
4	15	101	0	100
5	15	66	0	100

Day 6 was before treatment, and days 13–15 were after severing of the trigeminal nerve.

The last column shows the percentage of counts that were above the magnetic coil out of all the counts obtained for that test day. On three occasions, ducks were not recorded on either coil, and these data are not included in the table (duck 1 on day 6, duck 3 on day 15 and duck 4 on day 14).

visual cues to guide search behaviour in tests, and tests needed to be followed by rewarded training trials to avoid extinction of the response. It has been known for some time that a previously conditioned response can be erased if the response ceases to be associated with the reward (Mackintosh, 1974), and providing training trials between unrewarded tests has been found to offer some protection from extinction learning in pigeons (Rescorla, 2002) and chickens (Freire et al., 2005). However, the fall in preference for the magnetic anomaly following saline treatment on subsequent days suggests that extinction of the conditioned response may have occurred in this study. Future tests should consider alterations to the protocol in order to reduce the chances of the conditioned response becoming extinguished.

In our experiment, injection of lignocaine into an area near the trigeminal nerve abolished the duck's initial ability to detect the magnetic coil. This would suggest that ducks were using the magnetite receptors in the upper beak to detect the magnetic anomaly (Beason et al., 1995; Falkenberg et al., 2010; Mora et al., 2004). Pekin ducks were recently also shown to be able to derive magnetic direction from the magnetic field, and this response was not disrupted by the application of lignocaine to the upper beak (Freire and Birch, 2010). This magnetic response may indicate that ducks are also able to detect magnetic compass directions by a chemical process. Our magnetic anomaly would also have produced local changes to magnetic direction and inclination, so it is feasible that ducks could associate changes detected by this chemical process to locate the food. It is unclear why ducks do not use a chemical process for this task, though the magnetic anomaly may produce a magnetic field that is too strong to be detected by a chemical process as it is considered to have a narrow functional window (Wiltschko et al., 2006).

The reason ducks do not appear to use the chemical process may also be because the response of the beak receptors providing a salient cue and through blocking other less-salient cues is ignored. If so, it is interesting to note that towards the end of testing, lignocaine-treated ducks were able to detect the magnetic anomaly. This raises the intriguing possibility that if magnetic detection provided by the upper beak is blocked with lignocaine, birds can adapt and use a second chemical process to provide an orientation cue. Although plausible, we initially aimed to discount the possibility that the ability of lignocaine-treated ducks to detect the anomaly was simply related to their age. In Experiment 2, we surgically severed the trigeminal nerve and this abolished a preference for the anomaly at 13–15 days of age in a small number of ducks. The ability to detect the magnetic anomaly at 13–15 days of age by lignocaine-treated ducks in Experiment 1 therefore did not appear to be related to changes in age. In the interests of reducing the number of animals undergoing surgery only five ducks were tested in Experiment 2, and further tests perhaps with non-surgical procedures would be beneficial to confirm this effect. Another possible explanation for the above findings is that as the ducks grew, the injections were not deep enough and deposited the lignocaine too far from the nerve to perform its function.

Head scanning in garden warblers is characterised by rapid side-to-side movements of the head (Mouritsen et al., 2004) and a similar head-scanning movement occurs in ducks. Although we expected to see more head scanning in lignocaine-treated ducks, this was only observed in the first 2 days. Confusingly, saline-treated ducks performed little head-scanning behaviour in the first 3 days, when we expected them to conduct more as they were not finding food. Head-scanning behaviour suggests that ducks were seeking relative measures of magnetic intensity or direction, with which to generate a response (Mouritsen and Ritz, 2005). Although head scanning appears to be important in detecting migratory direction in garden warblers (Mouritsen et al., 2004), it is unclear from our findings whether this behaviour assists ducks in detecting the magnetic anomaly.

In conclusion, a protocol based on automatic recording of location as influenced by a magnetic anomaly provides objective evidence that Pekin ducks are able detect and use magnetic information to guide unrestricted search behaviour. This response was modulated by the trigeminal nerve and is consistent with a hypothesis of magnetoreception involving a putative cluster of magnetite in the upper beak.

ACKNOWLEDGEMENTS

We thank the Spatial Data Analysis Network (Charles Sturt University, Wagga Wagga, NSW, Australia) for assistance with the spatial analysis and Ann Cowling for statistical advice.

FUNDING

This research received no specific grant from any funding agency in the public, commercial, or not-for-profit sectors.

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