

perch height was recorded for all observed individuals on all 12 islands; in addition, perch height was recorded for marked individuals on four islands (two experimental, two control) in July. Islands were visited multiple times but (with a few exceptions) only once per day. Data were taken for the location at which lizards were first observed; lizards that apparently were disturbed (that is, that appeared to be moving in response to our presence) when first seen were not included.

Also before the introductions, we captured lizards (>33 mm snout-vent length (svl)) on each island ($n = 9-51$, 342 total). Hindlimb span (length from insertion of limb in body wall to tip of claw on the fourth toe) was measured on males. Lizards were individually marked by injecting elastomer tags (Northwest Marine Technologies) subdermally in two limb segments. In November, we exhaustively sampled individuals on each island to recapture marked individuals. We estimated survival proportion as the fraction of originally marked individuals (that is, marked in May) found during the November study period, divided by the marginal recapture rate for the last complete census (see Supplementary Information for details on calculation of this rate); if this estimate was smaller than the final number actually found, we used the latter instead.

To measure the effect of curly-tailed lizards on survival selection, we treated the six-month interval as an episode of selection and calculated standardized selection gradients^{20,21,26} separately for each sex on each island. These coefficients were then used as the data points for subsequent statistical analyses²⁷. We also attempted to calculate selection gradient coefficients using logistic regression²⁶, but the regression analyses failed to converge for analyses on several islands, so that estimates could not be obtained. For females, gradients were calculated only for svl, whereas for males they were calculated (in a multiple regression) for svl and relative hindlimb length (= residual of hindlimb length versus svl using the regression for individuals from all islands (analysis of covariance detects no heterogeneity of slopes among islands in the relationship between hindlimb length and svl)). Individuals not recaptured were considered to have died, with the exception that because of the loss of one of the two marks, the identity of five surviving females could not be established. On the basis of the frequency of mark loss, we estimate that one to two individuals in the study may have lost both marks and thus may have been incorrectly categorized as non-survivors. We measured selection at the intermediate time of six months, when mean survival on the islands averaged 45%, because we expected that this period was long enough for selective differences to become apparent, but not so long that marked cohorts would have mostly or entirely disappeared, thereby vitiating measurement of selection.

To test statistically the effect of *L. carinatus* on *A. sagrei* traits, we analysed selection gradient coefficients and mean perch heights from each island (one value per island) with the null hypothesis that mean values would not differ between experimental and control populations^{28,29}. We first ran analyses of covariance on each dependent variable using island area (log transformed) as a covariate. This covariate was deleted from the model when $P > 0.10$; it was retained only in the model for male relative hindlimb length. Because the variance of an estimated regression coefficient is inversely proportional to sample size, each selection coefficient for a given island was weighted by the number of individuals measured on that island; the weighting method does not change the degrees of freedom in the analysis³⁰ and statistical significance at the 0.05 level is the same in unweighted analyses. All P -values are one-tailed based on a priori hypotheses on the direction of the effect of *L. carinatus* on a given variable.

Received 21 July; accepted 16 September 2004; doi:10.1038/nature03039.

- Wyles, J. S., Kunkel, J. G. & Wilson, A. C. Birds, behavior, and anatomical evolution. *Proc. Natl Acad. Sci. USA* **80**, 4394-4397 (1983).
- Wcislo, W. T. Behavioral environments and evolutionary change. *Annu. Rev. Ecol. Syst.* **20**, 137-169 (1989).
- West-Eberhard, M. J. Phenotypic plasticity and the origins of diversity. *Annu. Rev. Ecol. Syst.* **20**, 249-278 (1989).
- Wake, D. B., Roth, G. & Wake, M. H. On the problem of stasis in organismal evolution. *J. Theor. Biol.* **101**, 211-224 (1983).
- Brandon, R. in *The Role of Behavior in Evolution* (ed. Plotkin, H. C.) 51-71 (MIT Press, Cambridge, USA, 1988).
- Huey, R. B., Hertz, P. E. & Sinervo, B. Behavioral drive versus behavioral inertia in evolution: A null model approach. *Am. Nat.* **161**, 357-366 (2003).
- Eldredge, N. *Macroevolutionary Dynamics: Species, Niches, & Adaptive Peaks* (McGraw-Hill, New York, 1989).
- Coope, G. R. in *Extinction Rates* (eds Lawton, J. H. & May, R. M.) 55-74 (Oxford Univ. Press, Oxford, 1995).
- Leviton, J. S. *Genetics, Paleontology, and Macroevolution* 2nd edn (Cambridge Univ. Press, Cambridge, UK, 2001).
- Harvey, P. H. & Pagel, M. D. *The Comparative Method in Evolutionary Biology* (Oxford Univ. Press, Oxford, 1991).
- Webb, C. O., Ackerly, D. D., McPeck, M. A. & Donoghue, M. J. Phylogenies and community ecology. *Annu. Rev. Ecol. Syst.* **33**, 475-505 (2003).
- Schoener, T. W. Presence and absence of habitat shift in some widespread lizard species. *Ecol. Monogr.* **45**, 233-258 (1975).
- Pacala, S. W. & Roughgarden, J. Population experiments with the *Anolis* lizards of St. Maarten and St. Eustatius. *Ecology* **66**, 129-141 (1985).
- Losos, J. B. & Spiller, D. Differential colonization success and asymmetrical interactions between two lizard species. *Ecology* **80**, 252-258 (1999).
- Losos, J. B. Integrative approaches to evolutionary ecology: *Anolis* lizards as model systems. *Annu. Rev. Ecol. Syst.* **25**, 467-493 (1994).
- Schoener, T. W., Spiller, D. A. & Losos, J. B. Predators increase the risk of catastrophic extinction of prey populations. *Nature* **412**, 183-186 (2001).
- Schoener, T. W., Spiller, D. A. & Losos, J. B. Predation on a common *Anolis* lizard: Can the food-web effects of a devastating predator be reversed? *Ecol. Monogr.* **72**, 383-408 (2002).

- Schoener, T. W., Slade, J. B. & Stinson, C. H. Diet and sexual dimorphism in the very catholic lizard genus *Leiocephalus* of the Bahamas. *Oecologia* **53**, 160-169 (1982).
- Garland, T. Jr & Losos, J. B. in *Ecological Morphology: Integrative Organismal Biology* (eds Wainwright, P. C. & Reilly, S.) 240-302 (Univ. Chicago Press, Chicago, USA, 1994).
- Lande, R. & Arnold, S. J. The measurement of selection on correlated characters. *Evolution* **37**, 1210-1226 (1983).
- Brodie, E. D. III, Moore, A. J. & Janzen, F. J. Visualizing and quantifying natural selection. *Trends Ecol. Evol.* **10**, 313-318 (1995).
- Schoener, T. W. & Schoener, A. The ecological correlates of survival in some Bahamian *Anolis* lizards. *Oikos* **39**, 1-16 (1982).
- Williams, E. E. in *Lizard Ecology: Studies of a Model Organism* (eds Huey, R. B., Pianka, E. R. & Schoener, T. W.) 326-370 (Harvard Univ. Press, Cambridge, USA, 1983).
- Irschick, D. J. & Losos, J. B. Do lizards avoid habitats in which performance is submaximal?: The relationship between sprinting capabilities and structural habitat use in Caribbean anoles. *Am. Nat.* **154**, 293-305 (1999).
- Hurlbert, S. H. Pseudoreplication and the design of ecological field experiments. *Ecol. Monogr.* **54**, 187-211 (1984).
- Janzen, F. J. & Stern, H. S. Logistic regression for empirical studies of multivariate selection. *Evolution* **52**, 1564-1571 (1998).
- DeWitt, T. J. & Langerhans, R. B. Multiple prey traits, multiple predators: keys to understanding complex community dynamics. *J. Sea Res.* **49**, 143-155 (2003).
- Rundle, H. D., Vamosi, S. M. & Schluter, D. Experimental test of predation's effect on divergent selection during character displacement in sticklebacks. *Proc. Natl Acad. Sci. USA* **100**, 14943-14948 (2003).
- Bolnick, D. I. Can intraspecific competition drive disruptive selection? An experimental test in natural populations of sticklebacks. *Evolution* **58**, 608-618 (2004).
- Littell, R. C., Freund, R. J. & Spector, P. C. *SAS System for Linear Models* 3rd edn (SAS Institute Inc., Cary, North Carolina, 1999).

Supplementary Information accompanies the paper on www.nature.com/nature.

Acknowledgements We thank the National Science Foundation and the National Geographic Society for support, J. Chase, T. Knight and B. Pinder for assistance, R. B. Langerhans for suggesting the approach to study selection and helping in its implementation, D. Bolnick, J. Chase, B. Fitzpatrick, F. Janzen, T. Knight, B. Langerhans, M. Leal, M. Turelli and the Turelli labgroup, for constructive comments on previous drafts, and the Bahamian government for permission to conduct this research.

Competing interests statement The authors declare that they have no competing financial interests.

Correspondence and requests for materials should be addressed to J.B.L. (losos@biology.wustl.edu).

Magnetoreception and its trigeminal mediation in the homing pigeon

Cordula V. Mora^{1*}, Michael Davison², J. Martin Wild³ & Michael M. Walker¹

¹School of Biological Sciences, ²Department of Psychology, ³Anatomy Department, School of Medicine, University of Auckland, Private Bag 92019, Auckland, New Zealand

* Present address: Department of Biology, Coker Hall, CB 3280, University of North Carolina, Chapel Hill, North Carolina 27599-3280, USA

Two conflicting hypotheses compete to explain how a homing pigeon can return to its loft over great distances. One proposes the use of atmospheric odours¹ and the other the Earth's magnetic field²⁻⁴ in the 'map' step of the 'map and compass' hypothesis of pigeon homing⁵. Although magnetic effects on pigeon orientation^{6,7} provide indirect evidence for a magnetic 'map', numerous conditioning experiments⁸ have failed to demonstrate reproducible responses to magnetic fields by pigeons. This has led to suggestions that homing pigeons and other birds have no useful sensitivity to the Earth's magnetic field⁹⁻¹¹. Here we demonstrate that homing pigeons (*Columba livia*) can discriminate between the presence and absence of a magnetic anomaly in a conditioned choice experiment. This discrimination is impaired by attachment of a magnet to the cere, local anaesthesia of the upper beak area, and bilateral section of the ophthalmic branch of

the trigeminal nerve, but not of the olfactory nerve. These results suggest that magnetoreception (probably magnetite-based) occurs in the upper beak area of the pigeon. Traditional methods of rendering pigeons anosmic might therefore cause simultaneous impairment of magnetoreception so that future orientation experiments will require independent evaluation of the pigeon's magnetic and olfactory systems.

We made a series of modifications to an existing operant conditioning procedure¹² to fulfil two conditions that seem to be vital for magnetic discrimination learning in non-avian species^{13–15}. These are that (1) the magnetic stimulus discriminated is a localized, non-uniform magnetic anomaly superimposed on the uniform background field of the Earth, and (2) movement by the experimental subjects is necessary to produce the behavioural response measured in the experiments. Although this combination of experimental parameters mitigates against rapid achievement of powerful discrimination by separating the stimulus, response and reinforcement in both space and time—compared with standard key-pecking experiments—failure to fulfil either or both of the above conditions has characterized all the unsuccessful or irreproducible attempts to condition pigeons and many other species to magnetic fields^{8,12}.

Using a Yes–No signal-detection procedure¹⁶ (see Supplementary Methods), four individually trained pigeons were required to discriminate between the presence and absence of an induced magnetic field anomaly while freely walking in a wooden tunnel (Fig. 1). The intensity profile of the anomaly was 'wave-shaped' and peaked in the centre of the tunnel at 189 micro tesla (μT) (background level of $44 \mu\text{T}$) with an inclination of -80° (background level of -64°). The birds were conditioned to jump onto a platform at one end of the tunnel when the anomaly was present and onto an identical platform at the other end of the tunnel when the anomaly was absent. Choice of the correct platform was rewarded with food whereas incorrect choices were punished with a time penalty.

Over 24 consecutive conditioning sessions, the percentage of correct choices made by the pigeons fell mostly between 55% and 65% (mean of 59.81% with upper and lower 95% confidence limits 58.78% and 60.83%) and occasionally approached 70% (Fig. 2a). Mean discrimination performance was therefore significantly greater than the chance level of 50% ($P < 0.0001$) with the birds

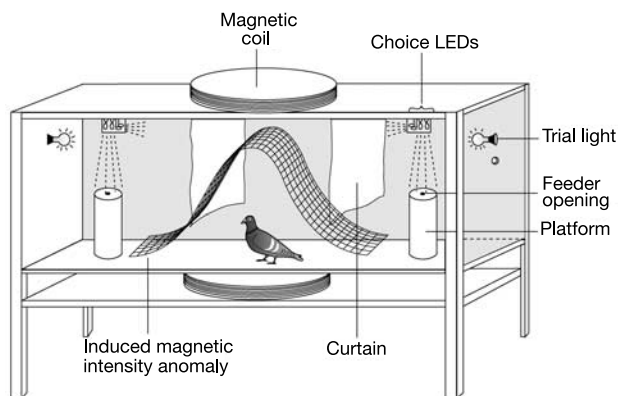


Figure 1 Experimental tunnel used in conditioned choice discrimination of magnetic stimuli. Four individually trained homing pigeons (*C. livia*) discriminated the presence and absence of a magnetic field anomaly, which was wave-shaped in its intensity profile and located centrally in the tunnel (peak intensity and inclination varied from $44 \mu\text{T}$ to $189 \mu\text{T}$ and -64° to -80° respectively). The birds were required to mount one of the two feeder platforms depending on the magnetic field present in the tunnel during a discrete trial. Correct choices were rewarded with food from a feeder opening in the top of the platform whereas incorrect choices resulted in a time penalty.

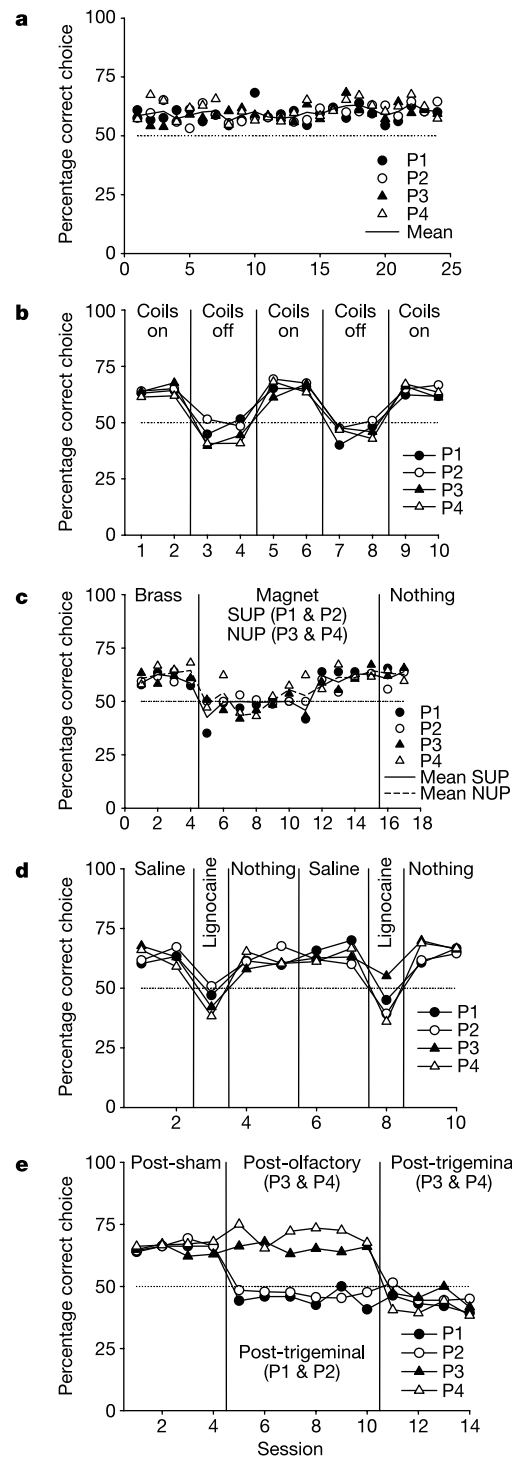


Figure 2 Percentage of correct choices by four individually trained homing pigeons (P1–P4) discriminating the presence and absence of a magnetic field anomaly over consecutive daily sessions. The horizontal line at 50% indicates the level of chance performance. **a**, Baseline magnetic choice discrimination performance. **b**, Coil control sessions with resistors replacing coil load (to test for use of extraneous cues in discrimination). **c**, Magnet impairment sessions in which brass weights (control) or magnets (SUP for P1 and P2, NUP for P3 and P4) have been attached to the top of the cere. **d**, Anaesthetic impairment sessions in which the olfactory mucosa is bathed in a 2% lignocaine hydrochloride solution, physiological saline (control) or nothing. **e**, Nerve sectioning sessions in which sham operations followed by conditioning sessions act as controls for subsequent bilateral sectioning of the olfactory nerve (NI) and the ophthalmic branch (V1) of the trigeminal nerve (NV).

clearly being able to discriminate the presence and absence of the magnetic anomaly in the tunnel. Mean discrimination performance continued to improve ($t_{\text{obs}} = 9.112$, $P < 0.001$) over the control sessions of the subsequent impairment experiments (Fig. 2b–e), reaching 75% after olfactory nerve sectioning (Fig. 2e). This result is close to the 80% value reported as the upper range of discrimination performance seen in pigeons for difficult discrimination tasks with other sensory systems¹⁷. Acquisition of discrimination is not evident in Fig. 2a because the birds had gained extended exposure to the stimuli and their associated reinforcements while the procedure was being developed. As a consequence, their percentage of correct choices abruptly rose above 50% once the final modification to the discrimination procedure was made that revealed discrimination of the stimuli by the birds.

To control for the possibility that the birds might use cues from the apparatus that were unrelated to the magnetic field anomaly, the birds were tested after substitution of equivalent resistors for the magnetic coils in the electrical circuit (Fig. 2b). Over ten sessions, the birds readily discriminated the presence and absence of the anomaly when the coils were carrying current from the power supply (sessions 1, 2, 5, 6, 9, 10). In contrast, they failed to make correct responses more than 50% of the time when the resistors were present (sessions 3, 4, 7, 8; $F_{\text{obs}} = 266.21$, $P < 0.0001$). Successful impairment of the pigeons' magnetic discrimination performance (see below) also argues against the use of extraneous cues associated with the experimental apparatus.

Successful discrimination of the anomaly by the birds permitted a series of impairment experiments to investigate the probable location and mechanism of the pigeons' magnetic sense. First, small but strong rare-earth magnets (NdFeB cylinders of 3-mm diameter and 2-mm length with a field strength of 2,500 μT at 1-cm distance) were attached to the cere for the duration of each of eleven conditioning sessions (sessions 5–15; Fig. 2c). The orientation of the magnet was south-up (SUP) for two pigeons and north-up (NUP) for the other two birds. With this magnet attached to the cere, the pigeons' discrimination performance immediately dropped to chance level ($P = 0.1103$), indicating that the magnet impaired the ability of the pigeons to discriminate magnetic fields. Control sessions where the birds carried brass weights of equivalent size (sessions 1–4; Fig. 2c) or, following magnetic impairment, nothing at all (sessions 16–17; Fig. 2c) showed an average discrimination performance significantly greater than chance (both $P < 0.0001$) and indistinguishable from baseline performance (Fig. 2a). Mean performance during the brass weight sessions was significantly better than that with attached magnets ($F_{\text{obs}} = 8.00$, $P = 0.0048$). Magnetic impairment was temporary, however, as performance gradually recovered over several sessions (sessions 9–11; Fig. 2c) to the level achieved previously. This change in behaviour over time was confirmed by a large, statistically reliable covariance (36.94, $Z_{\text{obs}} = 1.88$, $P = 0.0297$) for the mean performance over the magnet sessions, whereas the covariances over the brass weight and untreated sessions were effectively zero. No effect of the orientation of the magnet (NUP or SUP) was detected ($F_{\text{obs}} = 0.70$, $P = 0.4071$).

Second, to assess whether observed effects of the magnet were on hypothesized magnetoreceptors located either in the eye¹⁸ or in the upper beak area^{19,20}, we locally anaesthetized the olfactory cavity using a 2% lignocaine hydrochloride solution. The birds performed normally after bathing the olfactory cavity in physiological saline (sessions 1, 2, 6, 7; Fig. 2d) and during untreated control sessions (sessions 4, 5, 9, 10; Fig. 2d), but performed poorly after local anaesthesia of the olfactory cavity (sessions 3, 8, $F_{\text{obs}} = 28.93$, $P < 0.0001$; Fig. 2d). Discrimination was thus reversibly abolished by anaesthesia of the olfactory cavity.

The final experiment aimed to identify the afferent nerve that carries magnetic field information to the brain by separately sectioning the trigeminal and olfactory nerves before they become

closely associated in the upper beak area (Fig. 3). Sham operations followed by four conditioning sessions (sessions 1–4; Fig. 2e) in which the birds continued to discriminate the magnetic field anomaly after recovery (both groups $P < 0.0001$) provided a control for the effects of surgery on discrimination. Bilateral sectioning of the ophthalmic branch (V1) of the trigeminal nerve (NV) in two pigeons was followed by discrimination performance slightly below chance level (sessions 5–14, $P = 0.0034$; Fig. 2e), whereas bilateral sectioning of the olfactory nerve (NI) in the other two birds had no such effect (sessions 5–10, $P < 0.0001$; Fig. 2e). Discrimination subsequently failed in the olfactory nerve-sectioned birds after bilateral section of the ophthalmic branch of the trigeminal nerve (sessions 11–14, $P = 0.0029$; Fig. 2e). The differences in discrimination performance between these three treatment stages, as designated by the vertical lines in Fig. 2e, were significant ($F_{\text{obs}} = 222.32$, $P < 0.0001$).

The results from these impairment experiments are consistent with the detection of magnetic fields using magnetite located in the front of the head^{19–21} and electrophysiological experiments that have demonstrated responses to magnetic field stimuli in V1 of the bobolink²². They are not consistent, however, with the use of light-mediated magnetoreception for magnetic discrimination. We therefore suggest that magnetoreception in pigeons, and possibly in birds in general, is at least in part dependent on magnetite located in the upper beak area with the ophthalmic branch of the trigeminal nerve carrying magnetic field information to the brain. The magnetic sense of pigeons thus shares a similar location (the nasal region) and afferent nerve (the trigeminal) with at least the teleost fishes^{15,23}. Field experiments^{8,24} and a theoretical model²⁵ suggest that this magnetite-based system could form the basis for a magnetic 'map' in homing pigeons. Now that the pigeon's magnetic sense can finally be studied in the laboratory in the same way as other sensory modalities, the sensitivity of homing pigeons to magnetic fields can be analysed in psychophysical studies and compared with theoretical requirements for use in a 'map'. The transduction mechanism of the pigeon's magnetic

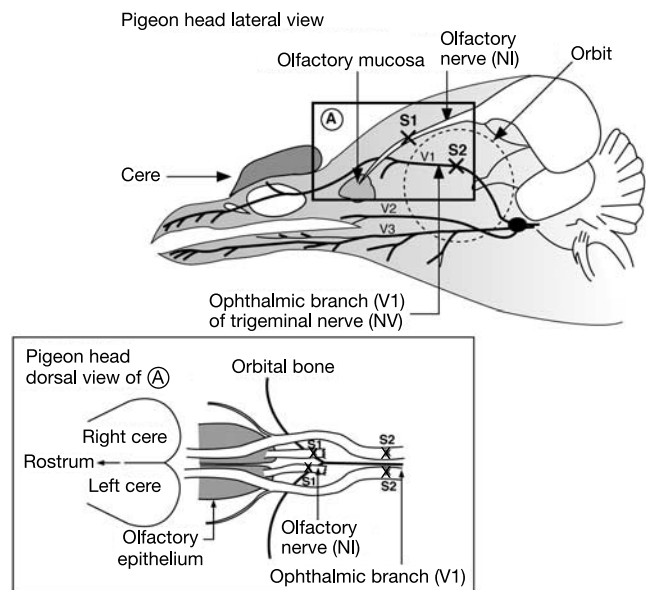


Figure 3 Lateral and dorsal (insert) views of the anatomical relationship between the ophthalmic branch (V1) of the trigeminal nerve (NV), the olfactory nerve (NI) and the olfactory mucosa in the head region of the homing pigeon (*C. livia*). Crosses S1 and S2 indicate the points of bilateral nerve sectioning for the olfactory and ophthalmic nerves, respectively.

compass remains to be determined, and we note that a separate, light-mediated pathway has been suggested from work with migratory birds^{8,18}.

Our results also suggest that interpretation of previous magnetic and olfactory impairment experiments in homing pigeons and possibly other species, such as sea turtles²⁶, albatrosses²⁷ and petrels^{28,29} requires caution. There is a possibility that attached magnets, even when applied close enough to the magnetoreceptor to elicit an effect on orientation behaviour, will produce only temporary or incomplete impairment of the magnetic sense. Moreover, as first suggested by ref. 30, induction of anosmia by local anaesthesia, application of zinc sulphate to the olfactory mucosa, or olfactory nerve sectioning at the base of the beak, might simultaneously impair the magnetic sense because the olfactory and trigeminal structures are in close proximity in the nasal cavity (Fig. 3). If magnetite is present in the olfactory mucosa of the pigeon, as it is in rainbow trout^{15,23}, or if the magnetoreceptors are found in nearby regions¹⁹, any of the above treatments or even mechanical plugging of the nostrils may potentially directly affect the operation of the magnetoreceptors themselves. To overcome the above difficulties in interpreting magnetic and olfactory impairment experiments and resolve the debate over use of magnetic and olfactory stimuli in homing pigeons, independent sectioning or blocking of the olfactory nerve and the ophthalmic branch of the trigeminal nerve will be required. We suggest that our work provides the basis for detailed studies of both the operation and use of the magnetic sense in homing pigeons and possibly migratory bird species. □

Methods

Experimental birds

Two female and two male experienced racing pigeons, aged 3–7 yr, were given water *ad libitum* while their food intake was restricted to maintain each animal at 85% ± 15 g of its free-feeding body weight.

Experimental apparatus

Daily conditioning sessions were conducted in a wooden tunnel¹² (3.30 m length × 1.06 m width × 0.96 m height) (Fig. 1) with two identical platforms (48 cm high) located at opposite ends. Each platform was fitted with microswitches to detect the weight of a pigeon, and a rotating feeder disc controlling access to the food reservoir through a feeder opening. Two transparent curtains suspended from the ceiling of the tunnel forced the pigeons to walk, not fly, between the platforms. Trial lights at either end of the tunnel signalled the stimulus-sampling period, while four white light-emitting diodes (LEDs) directly over each platform signalled both the availability of the platforms for the choice response and whether or not the correct response had been made. Insulation of the coils and location of electronic equipment in a separate room minimized the possibility that the birds could detect any thermal or auditory cues.

Discriminative stimuli

The magnetic field intensity anomaly was produced by two identical single-wrapped (100 turns of 0.05-mm copper wire) circular coils of 1.11-m diameter, located just above and below the centre of the tunnel (Fig. 1). With the coils wired in parallel and a constant, direct current of 3.0 A passing through them, the fields projected into the central region of the tunnel by the two coils summed to produce a distinctive magnetic field anomaly in which both intensity and inclination changed markedly from background values of 44 μT and -64° to 189 μT and -80°, respectively. During the control experiment, five 6.8 Ω resistors were wired in parallel to match the effect of the coils' load (1.5 A at a resistance of 1.36 Ω per coil) on the power source.

Nerve sectioning

Under general anaesthesia, the paired olfactory nerves (NI) were approached via a midline burr hole made in the rostral skull. The thin, bony canals housing the nerves were opened and a 2-mm section of each nerve was removed (Fig. 3). The ophthalmic branch (V1) of the trigeminal nerve (NV) behind the left eye was approached after an incision through the upper eyelid and orbital fascia and gentle depression of the globe. A 3-mm piece of nerve was removed (Fig. 3). V1 running behind the right eye was sectioned via the left orbit after removal of a small part of the interorbital bone. V1-sectioning did not impair the ability of the birds to mount the feeder platform or to consume the food reward. Sham operations involved the same procedures, except that the nerves were not cut. All birds were given 60 h to recover from sham surgery and nerve sectioning before conditioned choice testing.

Statistical analysis

A linear mixed model was fitted to each normally distributed data set using the Statistical

Analysis System (SAS). The model permitted us to test first for differences between the mean percentage of correct choices made by the birds and the 50% correct choice expected from chance performance. We could then examine the data for the occurrence of learning, detected as changes in behaviour over time, and estimate and accommodate any autocorrelation between sessions.

Further data analysis and computer simulations (not shown) were conducted to determine the cause of the slightly below-chance performance in the coils-off sessions in the control experiment, the magnetic and anaesthesia impairment sessions and the sessions after V1 sectioning. These revealed that this below-chance performance resulted from the interaction between the birds switching to a pattern of frequent alternation between platforms independent of stimulus presentation during impairment sessions, and slight, unexpected non-randomness in the balanced quasi-random order of stimulus presentation used in this study.

Received 4 May; accepted 4 October 2004; doi:10.1038/nature03077.

- Papi, F., Fiore, L., Fiaschi, V. & Benvenuti, S. Olfaction and homing in pigeons. *Monit. Zool. Ital. (N.S.)* **6**, 85–95 (1972).
- Gould, J. L. The case for magnetic sensitivity in birds and bees (such as it is). *Am. Sci.* **68**, 256–267 (1980).
- Moore, B. R. Is the homing pigeon's map geomagnetic? *Nature* **285**, 69–70 (1980).
- Walcott, C. Magnetic orientation in homing pigeons. *IEEE Trans. Magnet.* **16**, 1008–1013 (1980).
- Kramer, G. Wird die Sonnenhöhe bei der Heimfindeorientierung verwertet? *J. Ornithol.* **94**, 201–219 (1953).
- Walcott, C. in *Animal Migration, Navigation, and Homing* (eds Schmidt-Koenig, K. & Keeton, W. T.) 143–153 (Springer, Heidelberg, 1978).
- Keeton, W. T., Larkin, T. S. & Windsor, D. M. Normal fluctuations in the earth's magnetic field influence pigeon orientation. *J. Comp. Physiol.* **95**, 95–103 (1974).
- Wiltschko, R. & Wiltschko, W. *Magnetic Orientation in Animals* (Springer, Heidelberg, 1995).
- Griffin, D. R. Ecology of migration: is magnetic orientation a reality? *Q. Rev. Biol.* **57**, 293–295 (1982).
- Wallraff, H. G. Simulated navigation based on assumed gradients of atmospheric trace gases (Models on pigeon homing Part 2). *J. Theor. Biol.* **138**, 511–528 (1989).
- Papi, F. *Animal Homing* (Chapman and Hall, London, 1992).
- Carman, G. J., Walker, M. M. & Lee, A. K. Attempts to demonstrate magnetic discrimination by homing pigeons in flight. *Anim. Learn. Behav.* **15**, 124–129 (1987).
- Walker, M. M. & Bitterman, M. E. Conditioned responding to magnetic fields by honeybees. *J. Comp. Physiol. A* **157**, 67–71 (1985).
- Walker, M. M. Learned magnetic field discrimination in yellow-fin tuna, *Thunnus albacares*. *J. Comp. Physiol. A* **155**, 673–679 (1984).
- Walker, M. M. *et al.* Structure and function of the vertebrate magnetic sense. *Nature* **390**, 371–376 (1997).
- Davison, M. C. & Tustin, R. D. The relation between the generalized matching law and signal-detection theory. *J. Exp. Anal. Behav.* **29**, 331–336 (1978).
- Delius, J. D. in *Physiology and Behaviour of the Pigeon* (ed. Abs, M.) 327–355 (Academic, London, 1983).
- Ritz, T., Dommer, D. H. & Phillips, J. B. Shedding light on vertebrate magnetoreception. *Neuron* **34**, 503–506 (2002).
- Williams, M. N. & Wild, J. M. Trigeminal innervated iron-containing structures in the beak of homing pigeons, and other birds. *Brain Res.* **899**, 243–246 (2001).
- Fleissner, G. *et al.* Ultrastructural analysis of a putative magnetoreceptor in the beak of homing pigeons. *J. Comp. Neurol.* **458**, 350–360 (2003).
- Walcott, C., Gould, J. L. & Kirschvink, J. L. Pigeons have magnets. *Science* **205**, 1027–1029 (1979).
- Beason, R. C. & Semm, P. Does the avian ophthalmic nerve carry magnetic navigational information? *J. Exp. Biol.* **199**, 1241–1244 (1996).
- Diebel, C. E., Proksch, R., Green, C. R., Neilson, P. & Walker, M. M. Magnetite defines a vertebrate magnetoreceptor. *Nature* **406**, 299–302 (2000).
- Beason, B. C., Wiltschko, R. & Wiltschko, W. Pigeon homing: effects of magnetic pulses on initial orientation. *Auk* **114**, 405–415 (1997).
- Walker, M. M. On a wing and a vector: a model for magnetic navigation by homing pigeons. *J. Theor. Biol.* **192**, 341–349 (1998).
- Papi, F., Luschi, P., Akesson, S., Capogrossi, S. & Hays, G. C. Open-sea migration of magnetically disturbed sea turtles. *J. Exp. Biol.* **203**, 3435–3443 (2000).
- Mouritsen, H., Huyvaert, K. P., Frost, B. J. & Anderson, D. J. Waved albatrosses can navigate with strong magnets attached to their head. *J. Exp. Biol.* **206**, 4155–4166 (2003).
- Benhamou, S., Bonadonna, F. & Jouventin, P. Successful homing of magnet-carrying white-chinned petrels released in the open sea. *Anim. Behav.* **65**, 729–734 (2003).
- Bonadonna, F. & Bretagnolle, V. Smelling home: a good solution for burrow-finding in nocturnal petrels? *J. Exp. Biol.* **205**, 2519–2523 (2002).
- Schmidt-Koenig, K. in *Physiology and Behaviour of the Pigeon* (ed. Abs, M.) 267–283 (Academic, London, 1983).

Supplementary Information accompanies the paper on www.nature.com/nature.

Acknowledgements C.V.M. was formerly Cordula V. Haugh. This work was supported by grants from the Auckland University Research Committee. We thank J. Longville for supplying the pigeons, M. Williams for advice on the use of anaesthetics, B. McArdle for help with statistical analysis, V. Ward for graphical support and R. Mora for technical support.

Competing interests statement The authors declare that they have no competing financial interests.

Correspondence and requests for materials should be addressed to C.V.M. (cvmora@email.unc.edu).