of selective pressure for simplicity and informativeness (*55*–*57*). Studying the evolution of kin classification systems may reveal additional constraints on attested systems; for example, there may be systems that are near-optimal according to our analysis but unattested because they are not the outcomes of plausible evolutionary sequences (*41*).

We have relied here on kinship-specific realizations of the principles of simplicity and informativeness. Appropriate realizations of the same general principles may apply to semantic domains other than kinship, and some evidence suggests that they do. It has been proposed that color naming systems in the world's languages reflect partitions of perceptual color space that are near-optimally informative (*58*), and recent analyses support this view (*6*), including an analysis of lightness terms (*59*) that relies on a variant of the communication game in Fig. 1. A similar analysis of color terms should be possible within our framework, where communication is considered successful to the extent that the color inferred by the hearer is close in perceptual space to that intended by the speaker. The domains of kinship and color are different in fundamental respects: Kin terms describe relations between discrete individuals, whereas color terms pick out regions of a continuous perceptual space. The fact that the same general principles help to explain semantic category systems in such dissimilar domains opens up the possibility of a domain-general foundation for categorization across cultures.

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Supplementary Materials

www.sciencemag.org/cgi/content/full/336/6084/1049/DC1
Materials and Methods
Figs. S1 to S9
Tables S1 to S6
References (*60*–*64*)

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Neural Correlates of a Magnetic Sense

Le-Qing Wu and J. David Dickman*

Many animals rely on Earth's magnetic field for spatial orientation and navigation. However, how the brain receives and interprets magnetic field information is unknown. Support for the existence of magnetic receptors in the vertebrate retina, beak, nose, and inner ear has been proposed, and immediate gene expression markers have identified several brain regions activated by magnetic stimulation, but the central neural mechanisms underlying magnetoreception remain unknown. Here we describe neuronal responses in the pigeon's brainstem that show how single cells encode magnetic field direction, intensity, and polarity; qualities that are necessary to derive an internal model representing directional heading and geosurface location. Our findings demonstrate that there is a neural substrate for a vertebrate magnetic sense.

Behavioral studies have shown that many animals derive geopositional information using cues from Earth's magnetic field (*1*–*5*). Geomagnetic inclination varies from 0° at the magnetic equator to ±90° at the magnetic poles (Fig. 1), and these direction angle variations could be used to derive latitude information (*6*). Geomagnetic intensity also varies uniformly from the equator to the poles (Fig. 1), and local intensity variations exist that seem to be used by some animals for positional determination (*7*). To be functional, a neural system subserving magnetoreception must be sensitive to both of these magnetic field qualities. Although several regions of the central nervous system are activated by magnetic stimulation (*8*–*12*), until now there has been no clear evidence for magnetic sense neural correlates in the vertebrate brain.

A number of studies have suggested that retinal (*13*, *14*), beak (*15*, *16*), and possibly inner ear receptors (*17*, *18*) all transduce magnetic field information in birds. Thus, we recently delivered a rotating magnetic field to alert pigeons and used an early-release gene marker for neural activation

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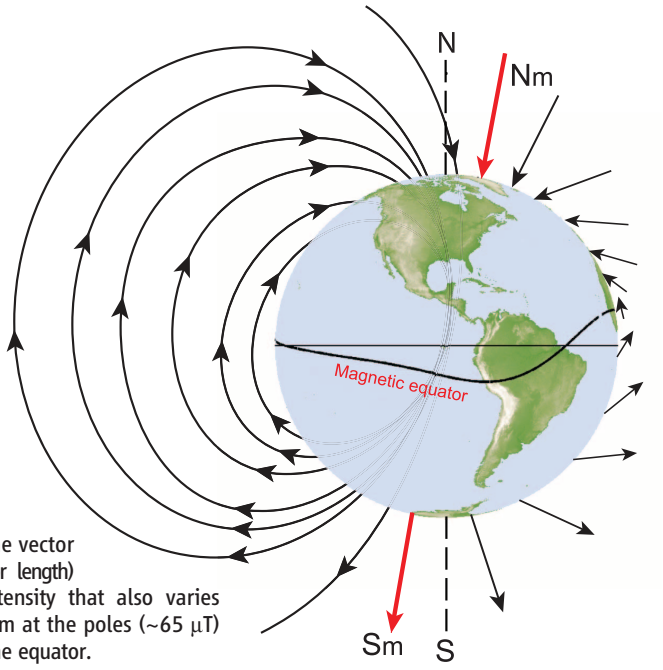


Fig. 1. Schematic illustration of Earth's geomagnetic field. View of American continents with the north (Nm) and south (Sm) magnetic poles (red vectors), magnetic equator (thick line), Earth spin axis (N-S dashed line), and hemispheric equator (thin line). Magnetic force lines (left field arrows) exit through the Sm pole and enter into the Nm pole. The magnetic field vector (right arrows) direction represents the magnetic inclination angle (relative to gravity) that varies uniformly between ±90° at the poles (Sm and Nm) and 0° at the magnetic equator. The vector magnitude (shown as vector length) represents geomagnetic intensity that also varies uniformly between maximum at the poles (~65 μT) and minimum (~20 μT) at the equator.

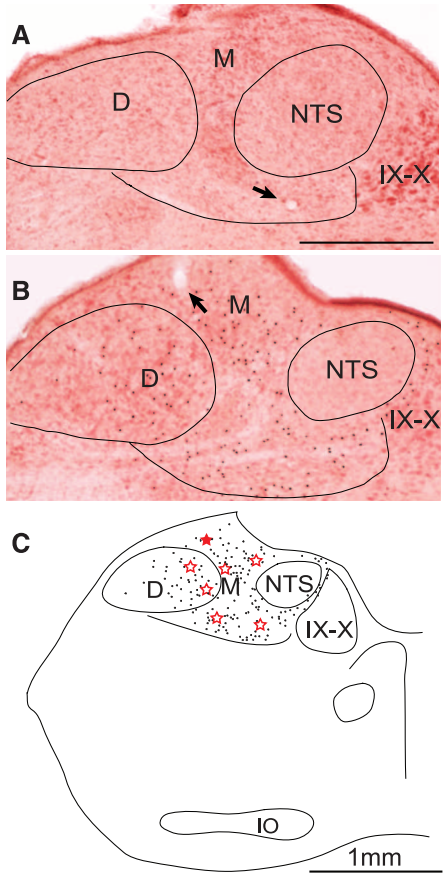
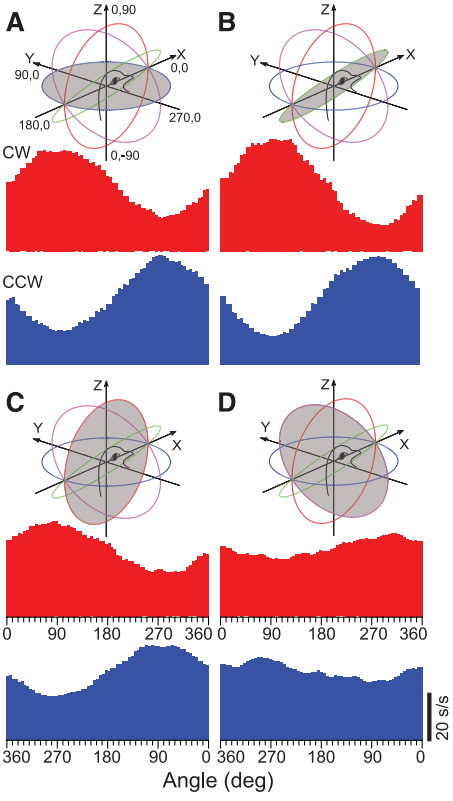


Fig. 2. Recording site verification and c-Fos expression in response to magnetic field stimulation. (**A** and **B**) Vestibular brainstem sections from two pigeons, each with an electrolytic lesion (arrows) made from a recording electrode on the last experimental day. In (B), the brain was processed to show c-Fos transcription factor (black dots), a marker for neural activation, after 72 min of magnetic field stimulation (*18*). (**C**) Anatomical reconstruction of section B, with c-Fos–positive cell locations (black dots) and recording site lesion locations (red stars) for all seven birds (collapsed onto one representative section). D, descending vestibular nucleus; IO, inferior olivary nucleus; M, medial vestibular nucleus; NTS, nucleus of the solitary tract; IX-X, glossopharyngeal-vagal nuclei. Scale bar = 1 mm.



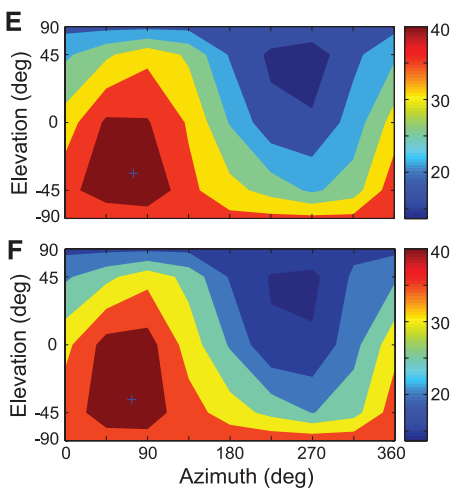


Fig. 3. Stimulus protocol and neural responses to magnetic field stimulation. (**A** to **D**) Schematic illustration of rotating magnetic field vector stimulation for the four great planes tested (top). Azimuth and elevation values [shown in (A)] were referenced to rotations about the positive *x* (0,0), *y* (90,0), and *z* (0,90) axes, corresponding to nasal area, left ear, and vertex, respectively. Zero degrees azimuth and elevation corresponds to a vector directed along the positive *x* axis, whereas an azimuth of 0 and elevation of –90 was a downward- (–*z*) directed stimulus vector. At the base of each panel, response post-stimulus time histograms (mean firing rate as a function of vector orientation) for an example MR neuron to CW (red) and CCW (blue) magnetic vector rotations for each great plane (gray) are shown. (**E** and **F**) Directional tuning contour map (Lambert cylindrical equal-area projection) computed for CW (E) and CCW (F) responses in (A) to (D). Each color contour corresponds to the mean firing rate in spikes per second (s/s) as a function of magnetic field vector elevation and azimuth. The blue cross corresponds to the spatial location of the 3D preferred direction vector.

(the c-Fos transcription factor) to delineate where in the pigeon's brain magnetic field information is processed (*18*). Four main magnetoreception brain regions were identified, including the lateral hyperpallium, hippocampus, dorsal thalamus, and caudal vestibular nuclei, which are all known to be involved in spatial orientation and navigation functions. We also found that lesions of the inner ear lagena receptor (a vestibular otolith organ) eliminated magnetic field activation in several of these regions (*18*), including the vestibular nuclei, where lagena afferents terminate (*19*). We used these findings to hypothesize that this vestibular brainstem region serves as a primary magnetoreception processing center and to begin our search for a neural substrate encoding the avian magnetic sense.

We recorded single-cell extracellular responses from vestibular neurons in seven awake pigeons during magnetic field stimulation. The birds' heads were fixed in place in order to eliminate transient vestibular activation (*20*), and the birds were

placed in total darkness to minimize possible retinal photopigment activation (*13*, *14*). We histologically verified the recording sites (electrolytic lesions) in all seven animals and found them to be located in the caudal descending (D) and medial (M) vestibular nuclei (Fig. 2, A to C). In one pigeon (Fig. 2B), both a marking lesion and c-Fos expression after magnetic field stimulation (*18*) were colocalized, which verified that the recording site was among magnetically activated cells.

To stimulate magnetoreception neurons, a three-dimensional (3D) coil system was used to actively cancel the natural geomagnetic field and then generate an artificial magnetic field, with a vector whose elevation, azimuth, and magnitude could be independently manipulated. The magnetic field vector was stepped in 10° direction-angle increments (100 ms per step) through 360° to complete one revolution (a 3.6-s period) in one of four great circle planes (horizontal, sagittal, and 45° tilts) relative to the center of the bird's head (Fig. 3). For each great circle plane, both clockwise (CW; increasing inclination angle) and counterclockwise (CCW; decreasing inclination angle) magnetic field vector rotations were presented at multiple repetitions. We recorded from 53 vestibular brainstem neurons [magnetic response (MR) cells] that exhibited significant response modulations above the baseline firing rate to magnetic stimulation [analysis of variance (ANOVA), $P < 0.001$]. An additional 276 cells were unresponsive to magnetic stimulation. Figure 3 and fig. S1 show a representative brainstem neuron that responded to the eight CW and CCW magnetic vector rotations (Fig. 3, A to D) by modulating most in one great circle plane (Fig. 3B) and least to an orthogonal plane (Fig. 3D). Further, there was a smooth modulation in firing rate for each stimulus plane, with one magnetic vector direction eliciting the maximal neural response and the opposite direction producing the minimum response (movie S1). To determine whether MR cells respond to the spatial orientation of the magnetic field vector, and not to a higher-order derivative (such as vector velocity), responses to both CW and CCW rotation directions were compared for each stimulus plane. We observed that MR cell responses were proportional to the orientation of the magnetic field vector, regardless of rotation direction (Fig. 3, A to D).

To quantify the differences in CW/CCW responses, we computed directional tuning curves separately for rotation direction. The mean firing rates for both CW and CCW responses were then plotted as a function of magnetic field vector azimuth and elevation in color contour maps (Fig. 3, E and F; Lambert equal-area projections). Separate 3D cosine functions were fit to the CW and CCW responses to calculate the mean maximum sensitivity (S_{max}) and preferred direction values. A significant linear regression [Pearson correlation coefficient (R) = 0.996, $P < 0.001$] relating the maximum sensitivity values for CW and CCW vector rotations for all 53 MR cells was observed, with a slope that was not statistically distinguishable from unity [slope = 0.98, coefficient of determination (R^2) = 0.99, 95% confidence interval (CI) = (0.97, 1.01); Fig. 4A]. Because CW and CCW responses were equivalent, a single cosine function was fit to the averaged CW and CCW responses to calculate the total S_{max} and preferred direction measures for each MR cell ($R^2 > 0.82$ for 93% of the cells and $R^2 > 0.62$ for the remaining cells). For the example cell of Fig. 3, a peak modulation of 17.6 spikes/s above and below the baseline occurred when the magnetic field stimulus vector was directed out (azimuth of 74.2°) and below (–33.7° elevation) the left ear. For all MR cells, the maximal sensitivities to magnetic stimulation ranged between ±1.3 and ±22.1 spikes/s, with a mean of ±13.2 spikes/s (SD ± 4.8). The absolute 3D angular difference in preferred tuning directions (excitatory peak) between CW and CCW neural responses was compared, and 89% (47 out of 53) of MR cells had identical preferred directions, with 4% more being within one 10° angle step (Fig. 4B).

The strength of the preferred direction tuning for each MR cell was quantified with a direction discrimination index (DDI). The DDI ranges from 0 to 1, where larger DDI values indicate a neuron's stronger selectivity for magnetic field vector orientation. MR cells exhibited strongly tuned DDIs that were equivalent (pairwise sign test, $P = 0.83$) for both CW and CCW vector rotation directions (regression slope 1.05, $R^2 = 0.89$), whereas cells that exhibited no response to magnetic stimulation did not (Fig. 4C). For the population of MR cells, CW and CCW values were averaged to calculate a mean DDI of 0.82 ± 0.12 (SD, n =

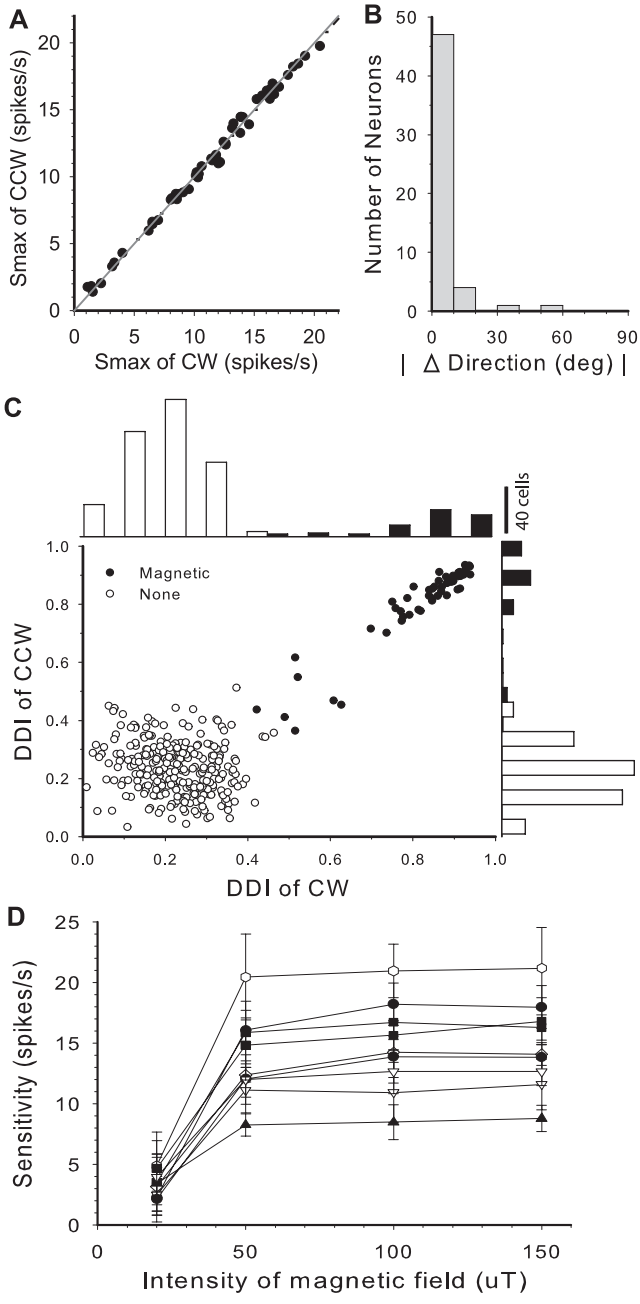


Fig. 4. Sensitivity, preferred direction, tuning strength, and intensity functions for MR cells. (**A**) Maximum sensitivity for MR cells (n = 53) to CW and CCW magnetic field rotation directions. No significant difference between slopes [r^2 = 0.99, 95% CI = (0.97, 1.01)] for ideal unity ratio (black line) and regression (dashed gray line) indicates equivalent cell response for both directions. (**B**) Difference in maximum sensitivity preferred directions for CW and CCW magnetic vector rotations. (**C**) DDI values (peak sensitivity) for nonmagnetic (open circles) and MR cells (solid circles) to CW and CCW magnetic field vector rotation. DDI values range from zero (no significant directional tuning) to 1 (highly tuned). Top and side histograms show marginal distributions. Scale bar = 40 cells. (**D**) MR cell (n = 9) intensity functions for peak sensitivity (CW and CCW combined).

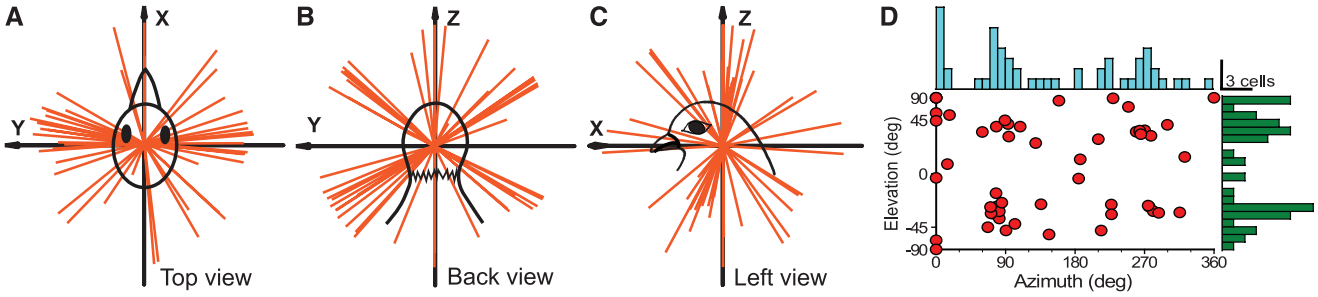


Fig. 5. Spatial orientation of 3D preferred direction vectors and distributions. (**A** to **C**) 3D preferred direction unit vectors plotted in Cartesian coordinate projections onto the *x-y* (top), *y-z* (back), and *x-z* (left) cardinal head planes. (**D**) Distribution of MR cell preferred directions in spherical coordinates plotted as a function of azimuth and elevation (Lambert cylindrical equal-area projection). Histograms on top and right sides show the marginal distributions. Scale bar = 3 cells.

53 cells). Distributions show that 87% of the MR neurons had DDI values above 0.7, indicating highly tuned selectivity. In contrast, none of the nonresponsive cells were selective, with significantly lower DDI values (mean = 0.22, SD ± 0.05, $F_{(1,327)} = 1695$, $P < 0.001$) that were independent of magnetic vector rotation ($R^2 = 0.02$). Taken together, these findings indicate that MR cells respond to magnetic vector direction by encoding the elevation (inclination angle), the azimuth, and the polarity (cosine tuning) of the applied magnetic field.

Earth's geomagnetic field systematically varies between approximately 20 microteslas (μT) at the magnetic equator to more than 60 μT at the magnetic poles (International Geomagnetic Reference Field 11 Model, data year 2010). To determine whether magnetic-responsive neurons were sensitive in that range, we derived intensity functions using four different amplitudes (20 to 150 μT) of the rotating magnetic field vector presented to nine MR neurons in each great circle plane for both CW and CCW rotation directions (Fig. 4D). All neurons had low sensitivity to the 20-μT stimuli (mean ± SD, values for three trials), with significantly increased responses to the 50-μT level (repeated measures ANOVA, $F_{(1,8)} = 475.5$, $P < 0.0001$) and further increases for the 100-μT level ($F_{(1,8)} = 13.3$, $P < 0.006$). Exponential curve fits to each cell indicated that many MR neurons reach response saturation between 70 and 120 μT, and there were no significant differences between neural responses at the 100- and 150-μT levels ($P = 0.335$). These intensity functions show that MR cells have a sensitivity bandwidth that spans the current range of Earth's geomagnetic field.

Because we found that MR cells are selectively tuned to magnetic field vector direction, we examined the population spatial distribution by plotting each cell's preferred direction as a unit vector in spherical Cartesian coordinates (three cardinal head planes; Fig. 5, A to C). Although the preferred directions were widely distributed, they were not uniform. For example, many MR cells' preferred vectors were directed at 45° increments above or below the interaural axis (Fig. 5, B and C). Others had preferred directions aligned with either the naso-occipital (Fig. 5, A and C), or dorsal-ventral (Fig. 5, B and C) axes. When viewed in magnetic stimulus space as a function of azimuth and elevation (Fig. 5D), the preferred direction elevations were significantly bimodal, with peaks at 35° and –30° (Silverman's multimodality test, $P < 0.05$). In contrast, the azimuth data were unimodal ($P = 0.284$).

We have shown that single vestibular brainstem neurons encode the direction, intensity, and polarity of an applied magnetic field, which is consistent with a ferrimagnetic particle receptor (*21*), as opposed to a radial-pair cryptochrome mechanism (*14*). Our findings demonstrate that MR neurons are most sensitive within an intensity range that is naturally produced by Earth's magnetic field, a necessary condition for a magnetoreception system to be useful in the derivation of geopositional information. However, Earth's magnetic field varies over time (for instance, there has been a 35% decrease in its strength over the past 2000 years), so it would seem likely that magnetoreception systems adapt to the slowly changing fields through evolution and/or developmental plasticity in order to maximize magnetic sense perception. It is likely that MR neurons receive magnetic information from the inner ear lagena (*18*, *19*); however, signals from the beak and/or retina are also possible (*13*–*16*). Because MR neurons are located in the vestibular nuclei, multimodal integration of magnetic and linear acceleration cues could provide geomagnetic information relative to the fixed constant of gravity (*18*, *22*, *23*). If so, magnetoreception neural constructs would remain stable in a space-fixed reference frame, regardless of head position. We suggest that MR cells encode a geomagnetic vector that could be used by the neural population to computationally derive the bird's position and directional heading. The geomagnetic vector elevation component could provide the bird's latitude (Fig. 1), the vector azimuth component could be used as a magnetic compass to provide heading direction, and the vector magnitude could provide spatial position cues through local variations in intensity (Fig. 1) relative to a learned internal model of geomagnetic space (*4*, *7*, *24*). How MR cell information is used for orientation and navigation remains to be discovered, but our findings demonstrate that there is a direct neural substrate underlying a magnetic sense in the avian brain.

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Supplementary Materials

www.sciencemag.org/cgi/content/full/science.1216567/DC1
Materials and Methods
Fig. S1
References (*25*–*30*)
Movie S1

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Neural Correlates of a Magnetic Sense
Le-Qing Wu and J. David Dickman (April 26, 2012)
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Editor's Summary

Magnetic Sense

Many species orient and navigate using aspects of Earth's magnetic field. Magnetic receptors have been found in the eyes, ears, and bills of birds, but there has been no clear evidence of the neural mechanism by which magnetic signals are translated into direction. Recording from the brainstem within conscious pigeons, **Wu and Dickman** (p. 1054, published online 26 April; see the Perspective by **Winklhofer**) reveal the presence of neurons in the pigeon's brain that encode the inclination angle and intensity of the geomagnetic field. Thus, pigeons––and perhaps other species––can develop an internal model of geopositional latitude to facilitate spatial orientation and navigation based on magnetoreception.