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Report

Magnetoreception in an Avian Brain in Part Mediated by Inner Ear Lagena

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Summary

Many animals use the Earth's geomagnetic field for orientation and navigation, but the neural mechanisms underlying that ability remain enigmatic [1, 2]. Support for at least two avian magnetoreceptors exists, including magnetically activated photochemicals in the retina [3, 4] and ferrimagnetic particles in the beak [5, 6]. The possibility of a third magnetoreceptor in the inner ear lagena organs has been suggested [7]. The brain must process magnetic receptor information to derive constructs representing directional heading and geosurface location. Here, we used the c-Fos transcription factor, a marker for activated neurons [8], to discover where in the brain computations related to a specific set of magnetic field stimulations occur. We found that neural activations in discrete brain loci known to be involved in orientation, spatial memory, and navigation may constitute a major magnetoreception pathway in birds. We also found, through ablation studies, that much of the observed pathway appears to receive magnetic information from the pigeon lagena receptor organs.

Results and Discussion

Birds appear to use magnetic cues to determine heading direction and location [2, 9]. Two avian magnetoreception mechanisms have been proposed: a photoreceptor, where cryptochrome molecules form radical pairs in certain wavelengths of light within a magnetic field [3, 4], and a ferrimagnetic receptor in the beak that is innervated by the trigeminal nerve [5, 6]. In addition, the vestibular lagena of the inner ear contains possible ferrimagnetic compounds that could stimulate directionally selective receptor cells [7]. Indeed, lagena ablation has been shown to disrupt bird's homing ability [10]. Consistent with a role for retinal and beak magnetoreceptors, the visual pallium [11], accessory optic system [12], and trigeminal brainstem complex [13] have all demonstrated magnetosensitivity. Yet, the primary neural pathways for magnetoreception remain largely unknown. Here, we used the c-Fos immediate early gene as a neuroanatomical marker [8] to delineate where in the pigeon brain geomagnetic information is processed. We also tested the hypothesis that lagena receptors function as magnetoreceptors through lesion studies. Experiments were conducted with awake, head-fixed pigeons in total darkness to minimize the response from retinal photopigments and an artificial rotating angle magnetic field was used to maximize responses to field inclination [14] as well as to minimize intensity responses [6]. The rotating magnetic field was delivered along differing elevations for 72 min (Figure 1), then the animals were immediately euthanized and the brain processed for c-Fos-labeled neurons.

Magnetic Activation in the Brain

Serial brain sections of each animal were examined for c-Fos expression. In 10 pigeons either 1.5 (Mag3x; n = 7) or 0.5 (Mag1x, n = 3) Gauss magnetic field stimulation was found to elicit consistent neural activation in only four brain loci; including the posterior vestibular nuclei, dorsal thalamus, hippocampus, and visual hyperpallium (Figure 2A). Because these activated neurons may also have included cells involved in homeostasis, arousal, or other neural tasks, c-Fos expression in control rest birds (n = 5) receiving no artificial magnetic field stimulation was also examined. In rest animals, fewer c-Fos neurons were observed in all brain regions (Figure 2B and Figure S2, available online). To quantify neural activation, we counted c-Fos-labeled cells in three alternate unilateral sections for each brain region (Figure 2E). Left and right side counts were averaged separately and statistical comparisons showed that there were no differences between side counts for any region ($p = 0.91$, analysis of variance [ANOVA]), thus the bilateral measures were pooled. Brainstem magnetic field-activated neurons were primarily located in the posterior medial and descending vestibular nuclei (Figure 2A). Significantly more activated cells in both the Mag3x (171 ± 9, mean ± standard error of the mean [SEM]) and Mag1x (62 ± 12) stimulated birds were observed as compared to the rest condition (14 ± 2) (Mag3x: $F(1,36) = 493$, Mag1x: $F(1,36) = 29.8$, $p < 0.001$; Figure 3A). Further, there were nearly triple the mean number of activated neurons in the Mag3x as compared to the Mag1x pigeons, suggesting a proportional response to field intensity. In the thalamus, activated neurons were clustered in the posterior dorsomedial, dorsointermedial, and dorsolateral thalamic regions (Figure 2A). On average, more thalamic cells were activated in Mag3x (158 ± 8) than in Mag1x (78 ± 6) birds, both being significantly higher as compared to 31 ± 4 cells in rest control birds ($p < 0.001$, ANOVA; Figure 4A). Mag3x and Mag1x-activated hippocampal neurons (Figure 2A) averaged 388 ± 21 and 233 ± 8, respectively, both significantly higher than the 119 ± 10 cells observed in the rest birds ($p < 0.001$, ANOVA; Figure 3A). In the dorsal hyperpallium (Figure 2A), a mean of 477 ± 22 Mag3x and 228 ± 15 Mag1x-activated neurons were observed, as compared to 109 ± 8 for control rest (Figure 2B) birds ($p < 0.001$, ANOVA; Figure 3A). There was a striking absence of cells in the hyperpallium apicale (primary visual Wulst). The mean density of neural activation in the hippocampus (431 ± 13 cells/mm^2) was significantly higher than either the vestibular nuclei (119 ± 3 cells/mm^2), thalamus (76 ± 3 cells/mm^2), or hyperpallial (239 ± 5 cells/mm^2) regions ($p < 0.001$, ANOVA).

We next plotted the locations of all c-Fos-positive cells throughout the brain onto anatomical tracings for each bird, as shown for one representative Mag3x animal in Figure 4. Outside the four brain loci described above, magnetic field-activated neurons were less consistently observed in several additional brain areas (Figure S1). For example, in five out of seven birds, we observed c-Fos-labeled cells in the principal

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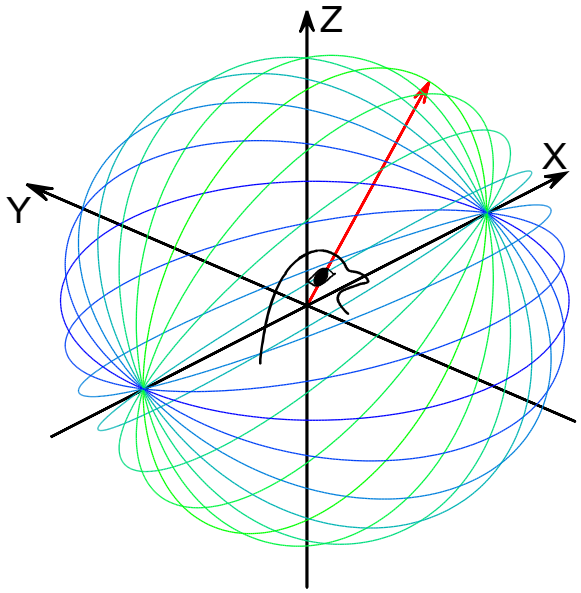

Figure 1. Magnetic Field Stimulation

Schematic illustration of rotating (360° azimuth plane) magnetic field vector (red arrow) for 12 different elevations (blue and green lines). Thirty-six different vector planes were used for each stimulation, 12 directed along each of the x (shown), y, and z axes, referenced to the pigeon's head that was centered in the coil frame.

trigeminal nucleus (PrV), with a mean of 24 ± 2 cells in the Mag3x birds as compared to 3 ± 1 cells in rest birds ($p < 0.001$, ANOVA). These findings are consistent with Heyers et. al. [13] who found a reduction in PrV activation after sectioning the ophthalmic branch of the trigeminal nerve. Avian trigeminal neural responses to magnetic field stimulation have been observed [15] as well as a dependence upon trigeminal nerve function to behaviorally detect local magnetic anomalies [16]. Taken together, these studies all support the existence of beak magnetoreceptors. We also observed magnetic field activation (Figure S1) in the nucleus of the basal optic root (n = 3), optic tectum (n = 3), amygdaloid complex (n = 3), ventral tegmental area (n = 3), lateral anterior thalamic nucleus (n = 3), and superficial parvocellular nucleus (n = 6).

Lagena Lesions

In five birds, the lagena organs were extirpated bilaterally and a 3 day survival period provided to allow lesion activation to subside [17]. Then, a Mag3x stimulation was applied. Figures 2D and 3A show that lagena ablation significantly reduced the number of activated neurons in the vestibular nuclei, dorsal thalamus, and hippocampus, as compared to both the Mag3x and Mag1x birds ($p < 0.001$, ANOVA). In the hyperpallium, lagena lesion reduced the number of activated neurons significantly for the Mag3x birds ($p < 0.001$, ANOVA), but was equivalent to that observed for the Mag1x condition. Next, we subtracted the rest condition means from the Mag3x means (propagation error formula) to obtain cell count estimates due to magnetic field stimulation only (Figure 3B). Similar mean subtractions for lagena lesion values from Mag3x values provided an estimate of activated neurons due to lagena-only stimulation. We found that Mag3x and lagena-responsive mean activations were similar for the vestibular nuclei, thalamus, and hippocampus regions ($p > 0.94$, standard equivalency test [SET], Figure 3B). Only the hyperpallium was significantly higher ($p < 0.01$, SET). This suggests that the magnetic field activation we observed in the vestibular nuclei, thalamus, and hippocampus was primarily due to lagena receptors, given the current test conditions, whereas the additional activated neurons in the hyperpallium probably arose from retina and/or beak magnetoreceptors (Figure S3).

As a control, sham lesion surgeries in which the lagena organs were not extracted, were performed in three birds, and the birds were then exposed to the Mag3x stimulation following 3 days of recovery. No significant differences in the number of activated neurons in any the four major brain regions were observed between Mag3x and sham operated birds ($p > 0.05$, ANOVA; Figures 2C and 3A).

Neural Pathway for Magnetoreception

Here, we describe a magnetoreception neural pathway in homing pigeons that includes loci known to be involved with orientation, spatial memory, and navigation functions. In the brainstem, vestibular nuclei neurons receive lagena afferent terminations [18], project to the avian dorsal thalamus [19], and have been reported to respond to both motion and magnetic field stimulation [20]. Thalamic regions receiving vestibular afferents in turn, project to the hippocampus [21] and to the lateral hyperpallium [22]. The dorsal lateral thalamus also receives projections from visual motion cells in the nucleus of the basal optic root [23] and optic tectum [24]. Tectal neurons respond to light-dependent magnetic field stimulation [12]. The hippocampus is involved in spatial navigation [25] that appears to depend upon functional vestibular input [26]. Hippocampal neurons also respond to magnetic field stimulation [27] and receive indirect projections from the vestibular nuclei through the thalamus [24]. Lastly, we observed magnetic field-activated neurons in the hyperpallium, including Cluster N, a region that is involved in light-dependent magnetoreception [11, 28]. Lesions of cluster N have been shown to disrupt compass orientation in birds, whereas disruption of the ophthalmic branch of the trigeminal nerve did not [29]. Here, our data support findings in the garden warbler [13], suggesting that retina-mediated magnetoreception projects through the thalamofugal visual pathway because we observed magnetic field-activated neurons in the nBOR, lateral dorsal thalamus, and dorsal hyperpallium [30]. Interestingly, in pigeons, neither hippocampal nor hyperpallium apicale (visual Wulst) lesions affected stored navigational map information, as initial homeward orientation from distant release sites was not significantly challenged [31]. However, hippocampal loss does affect landmark navigation, homing performance, and formation of new navigational maps [32, 33].

Lagena Function as a Magnetoreceptor

Geomagnetic field lines systematically vary in both intensity and direction depending upon Earth surface location [34]. An inclination compass measures the angle (elevation) of the geomagnetic field that varies between 0° at the equator and ± 90° (opposite polarity) at the north and south magnetic poles. The lagena is the third otolith organ found in fish, amphibians, reptiles, birds, and monotremes, but is not present in other mammals. In pigeons, the lagena lies at the base of the basilar papilla with receptor cells oriented in a parasagital plane [7, 35]. Lagena receptors are directionally tuned to changes in head tilt relative to gravity and translational motion [36]. We propose that lagena ferrimagnetic particles (not found in utricle or saccule) [7] stimulate lagena receptors whose

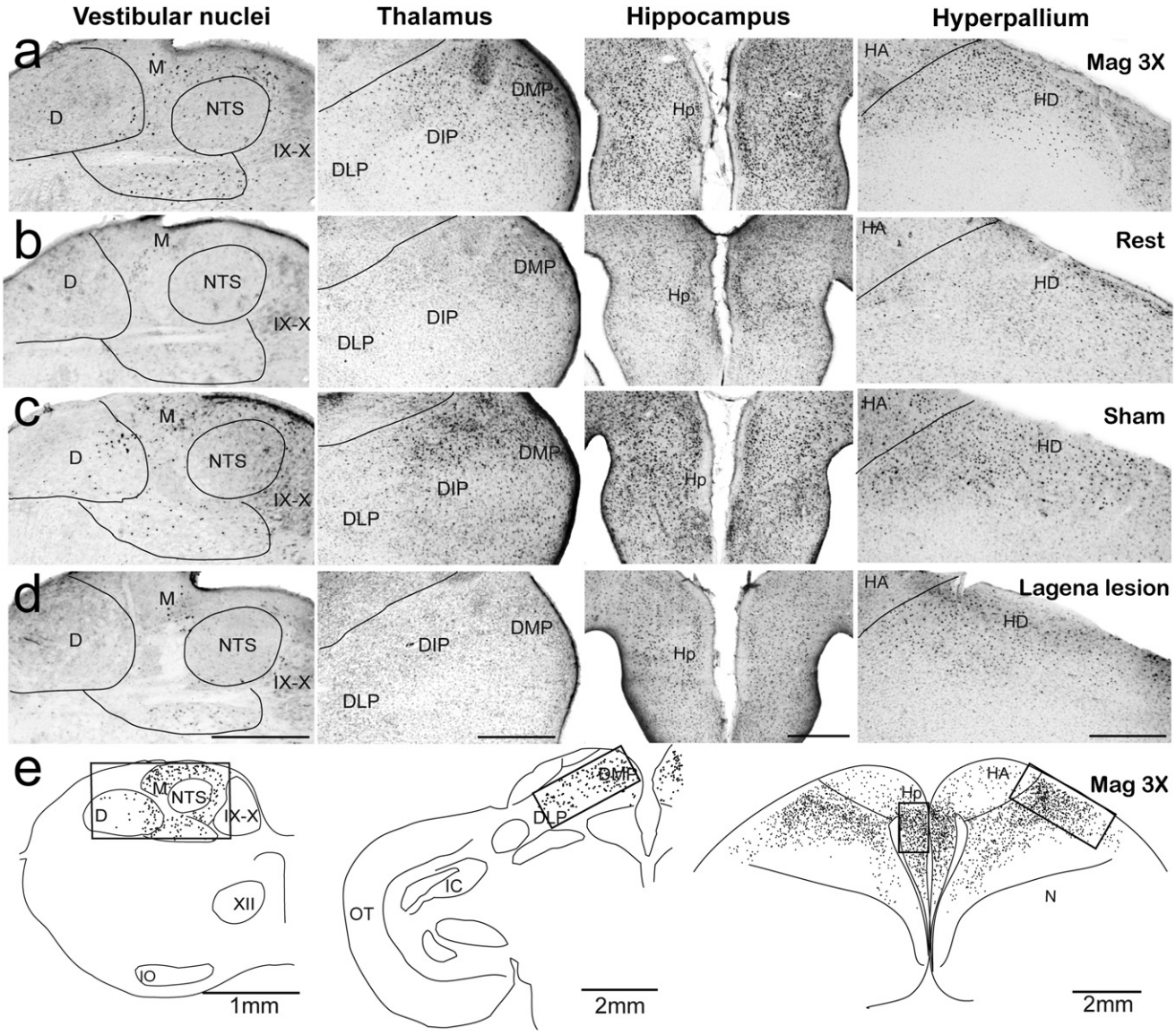

Figure 2. Photomicrographs and Anatomical Tracings for c-Fos-Positive Neurons

(A–D) Images arranged in columns for the vestibular nuclei, dorsal thalamus, hippocampus, and hyperpallium (left–right), for four stimulus conditions including Mag3x (A), rest (B), sham surgery (C), and lagena lesion (D). c-Fos-positive neurons identified by dark-stained nuclei (immunolabel bound to the expressed c-Fos protein) are clearly visible with the highest activation patterns exhibited in the Mag3x and sham condition birds. Reconstructions of transverse sections with activated neurons (black dots) in the posterior vestibular nuclei (far left), dorsal thalamus (center left), hippocampus (center right), and dorsal hyperpallium (far right). Counting frames (boxes) used for quantification of activated cell counts are indicated. The following abbreviations are used: D, descending vestibular nucleus; DLP, dorsolateral posterior thalamic nucleus; DIP, dorsointermediate posterior thalamic nucleus; DMP, dorsomedial posterior thalamic nucleus; HA, hyperpallium apicale; HD, hyperpallium densocellulare; Hp, hippocampus; IO, inferior olivary nucleus; M, medial vestibular nucleus; N, nidopallium; NTS, nucleus tractus solitarius; OT, optic tectum; XII, hypoglossal nucleus; IX-X, glossopharyngeal and vagal motor nuclei. The scale bar represents 500 μm for (A–D). The scale bars in (E) are as indicated.

afferents encode a "geomagnetic vector" in which direction and magnitude are referenced to gravity. The vector direction would encode the difference angle between the geomagnetic field inclination and gravity; independent of head orientation. Vector magnitude would encode field intensity and could aid in location determination due to specific local variations in geomagnetic intensities [2, 34]. Through convergence of multisensory cues, the brain could use lagena information to help determine heading direction and location relative to a geomagnetic map, as needed for accurate navigation [9, 26, 37, 38]. Because many vertebrate species possess lagenas, understanding their role in magnetoreception may be key to learning how these animals know where they are and where they are headed.

Experimental Procedures

Subjects and Stimulation

Twenty-three homing pigeons (*Columba livia*) were used in accordance with the National Institutes of Health Guidelines and the Animal Care and Use Committee at Washington University. In order to eliminate vestibular responses to head motion [39, 40] and to reduce potential contributions from retinal and beak magnetoreceptors [3, 4, 41], each bird was awake

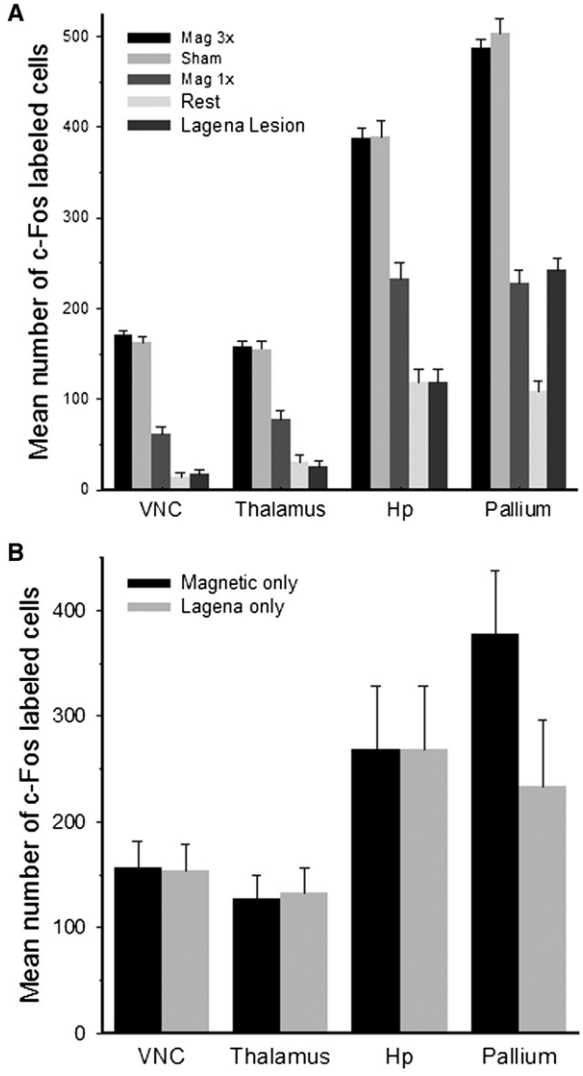

Figure 3. Number of Activated Cells for Different Brain Regions and Stimulus Conditions

(A) Mean number of activated neurons for all birds in the vestibular nuclei, dorsal thalamus, hippocampus, and hyperpallium for Mag3x (black), sham (gray), Mag1x (dark gray), rest (light gray), and lagena lesion (light black) conditions. (B) Mean values (propagation error formula) for magnetic field-only (Mag3x–rest) and lagena-only (Mag3x–lagena lesion) mean number of cells. The error bars represent ±SEM (A) and propogation error (B).

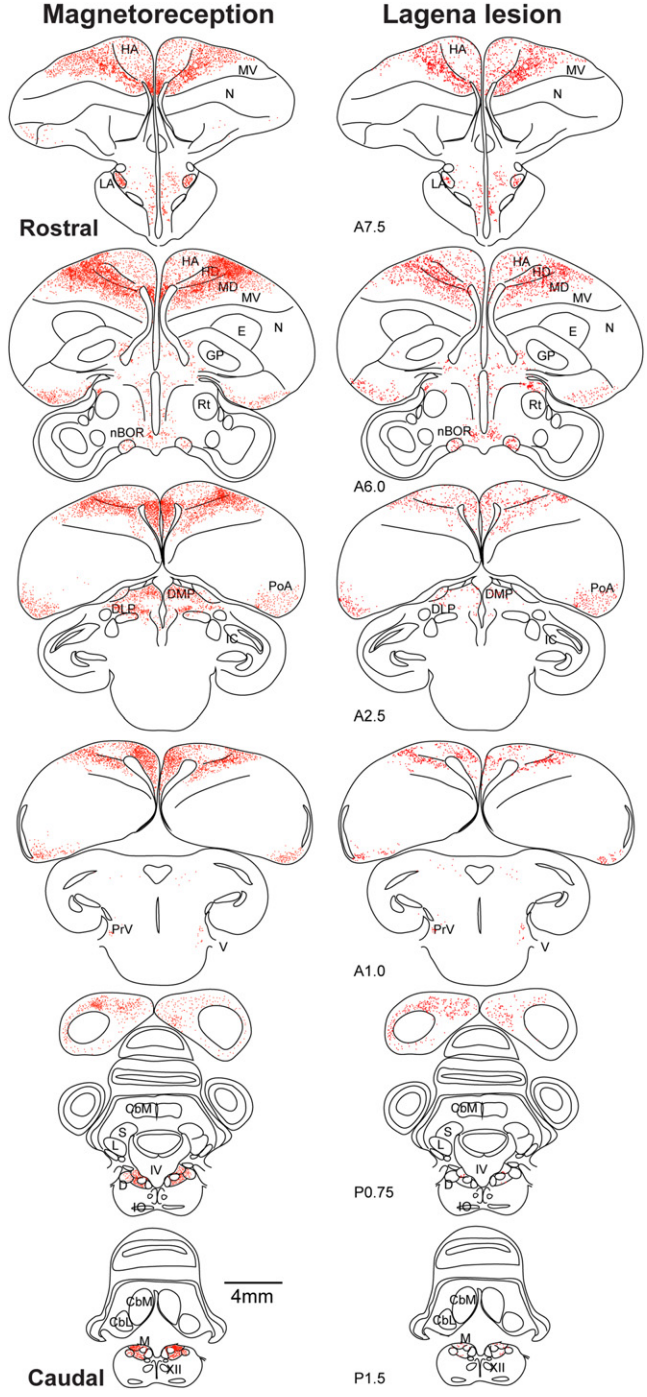

Figure 4. Mag3x and Lagena Lesion Anatomical Tracings

Transverse sections with all activated cells plotted (red dots) by location to yield the neural distributions in representative birds for Mag3x (left) and lagena lesion (right) conditions. Sections are arranged in rostral-to-caudal order, distances relative to AP0 (interaural axis). The following abbreviations are used: CbL, lateral cerebellar n ucleus; CbM, medial cerebellar nucleus; GP, globus pallidus; IC, inferior colliculus; L, lateral vestibular nucleus; LA, lateral anterior thalamic nucleus; nBOR, nucleus of the basal optic root; PoA, amygdaloid complex; PrV, principal trigeminal nucleus; IV, forth ventricle; S, superior vestibular nucleus Other abbreviations as in Figure 2.

and placed head-fixed (implanted head-stud) [39] in the dark in the center of a 3D magnetic coil frame (Figure 1A). The ambient geomagnetic field was measured at the bird's head with a three-axis magnetometer (HMC2003, Honeywell), then was actively canceled. An artificial magnetic field was generated through three pairs of Helmholtz coils (61 cm cube) with a direct current source and consisted of either a 1.5 Gauss (150,000 nT; ~3× intensity of home laboratory) or 0.5 Gauss (50,000 nT) vector that rotated through the 360° azimuth along each of 36 different elevation angles (12 each for x, y, and z axes; 15° increments; Figure 1A). Each magnetic field vector rotation required 2 min duration, for a total stimulation period of 72 (2 × 36) minutes. No confounding radio frequency, acoustic noise, or temperature changes were observed during the magnetic field stimulation.

In the first magnetic stimulation group (Mag3x, n = 7) the 1.5 Gauss intensity field was delivered. In a second group (rest, n = 5), animals were placed head-fixed in the coil frame in the dark, but no artificial magnetic field was applied and the ambient geomagnetic field (inclination 67.193°, mean intensity: 0.5314 G) was not canceled. In a third group (lesion, n = 5), the vestibular lagena receptors were bilaterally removed. A 3 day recovery period followed to allow decline of lesion-induced c-Fos expression [17], then the birds were exposed to Mag3x stimulation. In a fourth group (sham, n = 3), identical surgical lesion procedures were performed except

that the lagenas were not removed; then after 3 days recovery birds were exposed to the Mag3x stimulation. In a fifth group (Mag1x, n = 3), a rotating magnetic field vector of 0.5 Gauss intensity was delivered.

Immunohistochemistry

Each pigeon was immediately perfused following stimulation (4% paraformaldehyde). The brain was blocked 3 mm anterior to the interaural axis (AP0), removed, then postfixed for 12 hr. Serial brain sections (50 μm) were cut, incubated with 0.5% H_2O_2 in 90% methanol [18], followed by 0.5% $NaBH_4$, and permeabilized in 0.05% Tween-20. Sections were then treated in 5% normal goat serum (Vector Laboratories), rinsed, and incubated in anti-c-Fos primary (1:2000, rabbit c-Fos Ab = K-25, sc-253, Santa Cruz, 48 hr). The secondary antibody (Biotin-SP-AffiniPure Goat Anti-Rabbit IgG, Jackson ImmunoResearch Laboratories, 1:400) was applied for 90 min, followed by AB solution (Vector ABC kit, Vector Laboratories) diluted 1:280, then incubated in 0.5 mg/ml diaminobenzidene peroxidase solution to visualize the c-Fos-antibody complexes. Sections were mounted onto slides and counterstained. For nine of the birds, three brain sets (one magnetic field, one lagena lesion, and one sham bird) were processed simultaneously with the same chemistry. Cell counts from these animals were no different from those of similar group conditions processed individually or in pairs, as determined from the 95% confidence intervals.

Analyses

All c-Fos-positive cells in the brain were plotted relative to AP0 in alternate traced sections (60–65/bird) for each animal with video microscopy and an anatomical reconstruction program [18]. For quantification, c-Fos-positive cells were counted in box frames in the vestibular nuclei (1.6 × 0.9 mm), dorsal thalamus (2.3 × 0.9 mm), medial hippocampus (0.9 × 1.0mm), dorsal hyperpallium (2.3 × 0.9 mm), and trigeminal nucleus (1.5 × 0.8 mm). Photomicrographs at equal light intensity for all sections (4×) were converted to gray scale and cropped to the counting frame size for each region. The number of c-Fos-positive cells was quantified, with an automated analysis program written for the Python environment (v2.7.1), by an experimenter blind to stimulation condition. The program compared adjacent pixel contrast within a specified marker size (<5 μm) with a filter threshold (set at 0.3, range from 0 [pure black] to 1.0 [pure white]) and with markers placed on nuclei that passed criterion threshold. For each counting frame, the measurements were repeated and identical values were obtained each time, thus validating the quantification procedure.

Statistical comparisons were made with a multifactor repeated-measures analysis of variance, with planned follow-up comparisons (ANOVA, Statistica). Factors included stimulus condition and left and right sides, whereas brain region was treated as a repeated measure (four levels). Comparisons for the subtraction distribution means were performed with the propagation error formula ($A-B = \sqrt{((SD_A)^2 + (SD_B)^2)}$) and significance was determined with the SET ($|A-B| \leq 2\sqrt{((SD_A)^2 + (SD_B)^2)}$).

Supplemental Information

Supplemental Information includes Supplemental Experimental Procedures and three figures and can be found with this article online at doi:10.1016/j.cub.2011.01.058.

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