

1 Transduction of the Geomagnetic Field as Evidenced from 2 Alpha-band Activity in the Human Brain

3 Connie X. Wang¹, Isaac A. Hilburn², Daw-An Wu^{1,3}, Yuki Mizuhara⁴, Christopher P. Cousté²,
4 Jacob N. H. Abrahams², Sam E. Bernstein⁵, Ayumu Matani⁴, Shinsuke Shimojo^{1,3*}, & Joseph L.
5 Kirschvink^{2,6*}

6 ¹Computation & Neural Systems, California Institute of Technology, Pasadena, CA, USA. ²Division of Geological
7 & Planetary Sciences, California Institute of Technology, Pasadena, CA, USA. ³Division of Biology & Biological
8 Engineering, California Institute of Technology, Pasadena, CA, USA. ⁴Graduate School of Information Science and
9 Technology, the University of Tokyo, Bunkyo-ku, Tokyo, Japan. ⁵Department of Computer Science, Princeton
10 University, Princeton NJ, USA. ⁶Earth-Life Science Institute, Tokyo Institute of Technology, Ookayama, Meguro,
11 Tokyo, Japan. * Corresponding Authors: pmag.contact@caltech.edu
12
13
14

15 Abstract

16 Magnetoreception, the perception of the geomagnetic field, is a sensory modality well-
17 established across all major groups of vertebrates and some invertebrates, but its presence in
18 humans has been tested rarely, yielding inconclusive results. We report here a strong, specific
19 human brain response to ecologically-relevant rotations of Earth-strength magnetic fields.
20 Following geomagnetic stimulation, a drop in amplitude of EEG alpha oscillations (8-13 Hz)
21 occurred in a repeatable manner. Termed alpha event-related desynchronization (alpha-ERD),
22 such a response is associated with sensory and cognitive processing of external stimuli.
23 Biophysical tests showed that the neural response was sensitive to the dynamic components and
24 axial alignment of the field but also to the static components and polarity of the field. This
25 pattern of results implicates ferromagnetism as the biophysical basis for the sensory transduction
26 and provides a basis to start the behavioral exploration of human magnetoreception.
27

28 Introduction

29 Magnetoreception is a well-known sensory modality in bacteria (Frankel & Blakemore,
30 1980), protozoans (Bazylinski, Schlezinger, Howes, Frankel, & Epstein, 2000) and a variety of
31 animals (Johnsen & Lohmann, 2008; Walker, Dennis, & Kirschvink, 2002; R. Wiltschko & W.
32 Wiltschko, 1995), but whether humans have this ancient sensory system has never been
33 conclusively established. Behavioral results suggesting that geomagnetic fields influence human
34 orientation during displacement experiments (Baker, 1980, 1982, 1987) were not replicated
35 (Able & Gergits, 1985; Gould & Able, 1981; Westby & Partridge, 1986). Attempts to detect
36 human brain responses using electroencephalography (EEG) were limited by computational

37 methods of the time (Sastre, Graham, Cook, Gerkovich, & Gailey, 2002). Twenty to thirty years
38 after these previous flurries of research, the question of human magnetoreception remains
39 unanswered.

40 In the meantime, there have been major advances in our understanding of animal
41 geomagnetic sensory systems. An ever-expanding list of experiments on magnetically-sensitive
42 organisms has revealed physiologically-relevant stimuli as well as environmental factors that
43 may interfere with magnetosensory processing (Lohmann, Cain, Dodge, & Lohmann, 2001;
44 Walker et al., 2002; R. Wiltschko & W. Wiltschko, 1995). Animal findings provide a potential
45 feature space for exploring human magnetoreception – the physical parameters and coordinate
46 frames to be manipulated in human testing (J. Kirschvink, Padmanabha, Boyce, & Oglesby,
47 1997; W. Wiltschko, 1972). In animals, geomagnetic navigation is thought to involve both a
48 compass and map response (Kramer, 1953). The compass response simply uses the geomagnetic
49 field as an indicator to orient the animal relative to the local magnetic north/south direction
50 (Lohmann et al., 2001; R. Wiltschko & W. Wiltschko, 1995). The magnetic map is a more
51 complex response involving various components of field intensity and direction; direction is
52 further subdivided into inclination (vertical angle from the horizontal plane; the North-seeking
53 vector of the geomagnetic field dips downwards in the Northern Hemisphere) and declination
54 (clockwise angle of the horizontal component from Geographic North, as in a man-made
55 compass). Notably, magnetosensory responses tend to shut down altogether in the presence of
56 anomalies (e.g. sunspot activity or local geomagnetic irregularities) that cause the local magnetic
57 field to deviate significantly from typical ambient values (Martin & Lindauer, 1977; W.
58 Wiltschko, 1972), an adaptation that is thought to guard against navigational errors. These
59 results indicate that geomagnetic cues are subject to complex neural processing, as in most other
60 sensory systems.

61 Physiological studies have flagged the ophthalmic branch of the trigeminal system (and
62 equivalents) in fish (Walker et al., 1997), birds (Beason & Semm, 1996; Elbers, Bulte, Bairlein,
63 Mouritsen, & Heyers, 2017; Mora, Davison, Wild, & Walker, 2004; Semm & Beason, 1990) and
64 rodents (Wegner, Begall, & Burda, 2006) as a conduit of magnetic sensory information to the
65 brain. In humans, the trigeminal system includes many autonomic, visceral and proprioceptive
66 functions that lie outside conscious awareness (Fillmore & Seifert, 2015; Saper, 2002). For

67 example, the ophthalmic branch contains parasympathetic nerve fibers and carries signals of
68 extraocular proprioception, which do not reach conscious awareness (Liu, 2005).

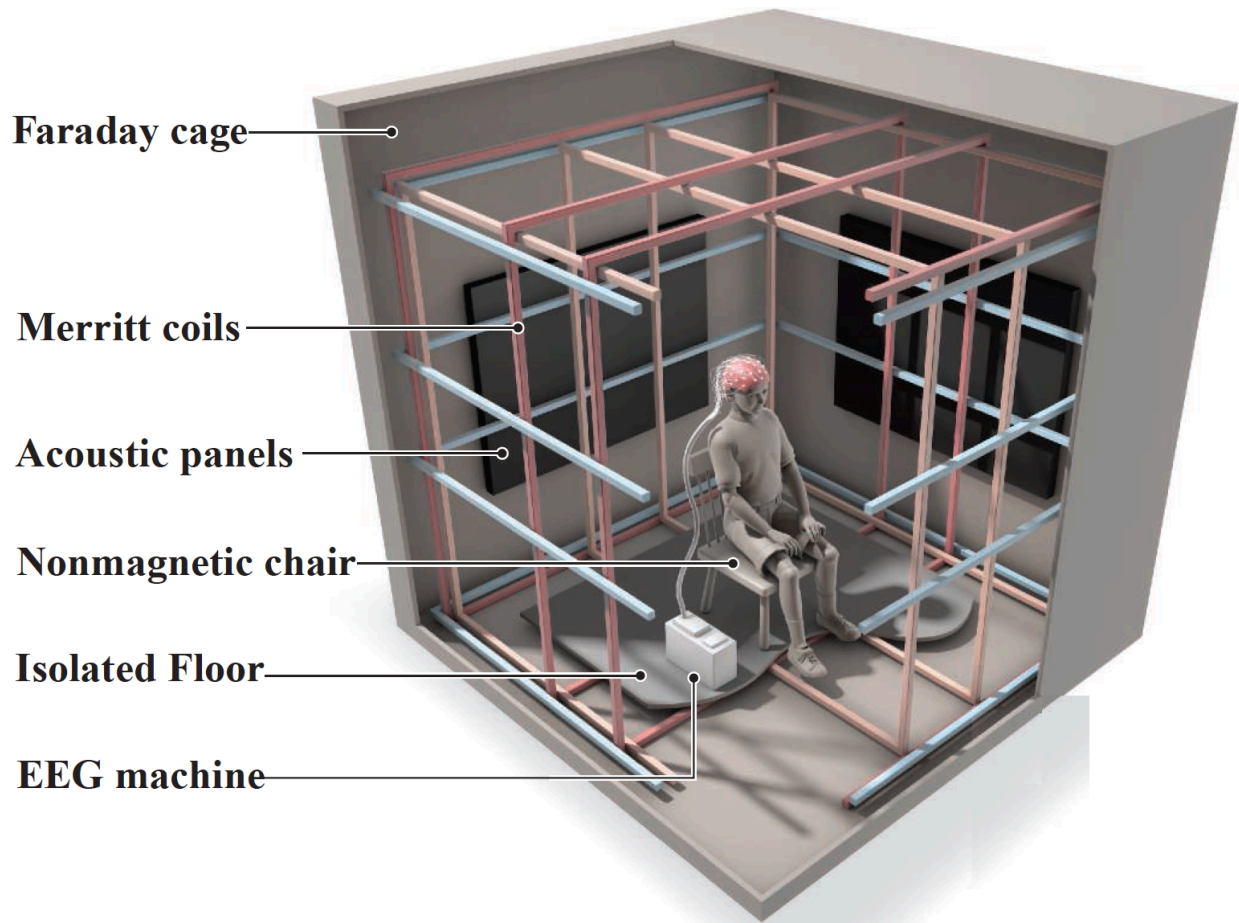
69 If the physiological components of a magnetosensory system have been passed from
70 animals to humans, then their function may be either subconscious or only weakly available to
71 conscious perception. Behavioral experiments could be easily confounded by cognitive factors
72 such as attention, memory and volition, making the results weak or difficult to replicate at the
73 group or individual levels. Since brain activity underlies all behavior, we chose a more direct
74 electrophysiological approach to test for the transduction of geomagnetic fields in humans.

75

76 **Materials and Methods**

77 We constructed an isolated, radiofrequency-shielded chamber wrapped with three nested
78 sets of orthogonal square coils, using the four-coil design of Merritt *et al.* (Merritt, Purcell, &
79 Stroink, 1983) for high central field uniformity (Fig. 1, and in the section on *Extended Materials*
80 *and Methods* below). Each coil contained two matched sets of windings to allow operation in
81 Active or Sham mode. Current ran in series through the two windings to ensure matched
82 amplitudes. In Active mode, currents in paired windings were parallel, leading to summation of
83 generated magnetic fields. In Sham mode, currents ran antiparallel, yielding no measurable
84 external field, but with similar ohmic heating and magnetomechanical effects as in Active mode
85 (J.L Kirschvink, 1992). Active and Sham modes were toggled by manual switches in the distant
86 control room, leaving computer and amplifier settings unchanged. Coils were housed within an
87 acoustically-attenuated, grounded Faraday cage with aluminum panels forming the walls, floor
88 and ceiling. Participants sat upright in a wooden chair on a platform electrically isolated from
89 the coil system with their heads positioned near the center of the uniform field region and their
90 eyes closed in total darkness. (Light levels within the experimental chamber during experimental
91 runs were measured using a Konica-Minolta CS-100A luminance meter, which gave readings of
92 zero, e.g. below $0.01 \pm 2\%$ cd/m².) The magnetic field inside the experimental chamber was
93 monitored by a three-axis Applied Physics SystemsTM 520A fluxgate magnetometer. EEG was
94 continuously recorded from 64 electrodes using a BioSemiTM ActiveTwo system with electrode
95 positions coded in the International 10-20 System (e.g. Fz, CPz, etc.). Inside the cage, the
96 battery-powered digital conversion unit relayed data over a non-conductive, optical fiber cable to

97 a remote control room, ~20 meters away, where all power supplies, computers and monitoring
98 equipment were located.



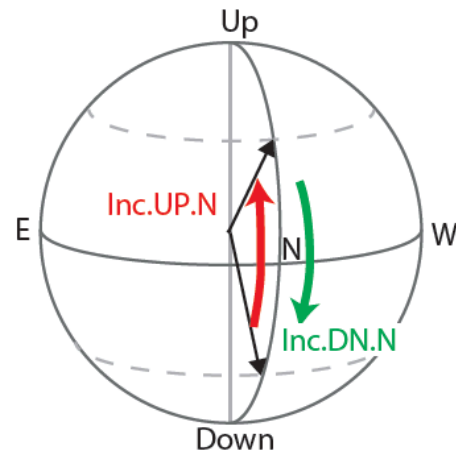
99
100 **Fig. 1.** Schematic illustration of the experimental setup. The ~1 mm thick aluminum panels of
101 the electrically-grounded Faraday shielding provides an electromagnetically “quiet”
102 environment. Three orthogonal sets of square coils ~2 m on edge, following the design of Merritt
103 *et al.* (Merritt *et al.*, 1983), allow the ambient geomagnetic field to be altered around the
104 participant’s head with high spatial uniformity; double-wrapping provides an active-sham for
105 blinding of experimental conditions (J.L Kirschvink, 1992). Acoustic panels on the wall help
106 reduce external noise from the building air ventilation system as well as internal noise due to
107 echoing. A non-magnetic chair is supported on an elevated wooden base isolated from direct
108 contact with the magnetic coils. The battery-powered EEG is located on a stool behind the
109 participant and communicates with the recording computer via an optical fiber cable to a control
110 room ~20 m away. Additional details are available in the *Extended Materials and Methods*
111 section, and Fig. 5 below. This diagram was modified from the figure “Center of attraction”, by
112 C. Bickel (Hand, 2016), with permission.
113
114

115 A ~1 hour EEG session consisted of multiple ~7 minute experimental runs. In each run
116 of 100+ trials, magnetic field direction rotated repeatedly between two preset orientations with
117 field intensity held nearly constant at the ambient lab value (~35 μ T). In SWEEP trials, the
118 magnetic field started in one orientation then rotated smoothly over 100 milliseconds to the other
119 orientation. As a control condition, FIXED trials with no magnetic field rotation were
120 interspersed amongst SWEEP trials according to pseudorandom sequences generated by
121 software. Trials were separated in time by 2-3 seconds. The experimental chamber was dark,
122 quiet and isolated from the control room during runs. Participants were blind to Active vs. Sham
123 mode, trial sequence and trial timing. During sessions, auditory tones signaled the beginning and
124 end of experiment runs, and experimenters only communicated with participants once or twice
125 per session between active runs to update the participant on the number of runs remaining.
126 When time allowed, Sham runs were matched to Active runs using the same software settings.
127 Active and Sham runs were programmatically identical, differing only in the position of
128 hardware switches that directed current to run parallel or antiparallel through paired loops. Sham
129 runs served as an additional control for non-magnetic sensory confounds, such as sub-aural
130 stimuli or mechanical oscillations from the coil system. (Note that experimental variables
131 differing *between* runs are denoted in camel case as in DecDn, DecUp, Active, Sham, etc.,
132 whereas variables that change *within* runs are designated in all capitals like FIXED, SWEEP,
133 CCW, CW, UP, DN, etc.). In Active runs, an electromagnetic induction artifact occurred as a 10-
134 20 microvolt fluctuation in the EEG signal during the 100 ms magnetic field rotation. This
135 induction artifact is similar to that observed in electrophysiological recordings from trout
136 whenever magnetic field direction or intensity was suddenly changed in a square wave pattern
137 (Walker et al., 1997). Strong induced artifacts also occur in EEG recordings during transcranial
138 magnetic stimulation (TMS) (Veniero, Bortoletto, & Miniussi, 2009). In all cases, the artifact
139 can only be induced in the presence of time-varying magnetic fields and disappears once the
140 magnetic field stabilizes ($\partial B/\partial t=0$). In our experiments, EEG data following the 100 ms field
141 rotation interval were not subject to effects from the induction artifact. Furthermore, the
142 induction artifact is phase-locked like an event-related potential and does not appear in analyses
143 of non-phase-locked power, which we used in all subsequent statistical tests. Further discussion
144 of electrical induction is in section 4 of *Extended Materials and Methods*, below.

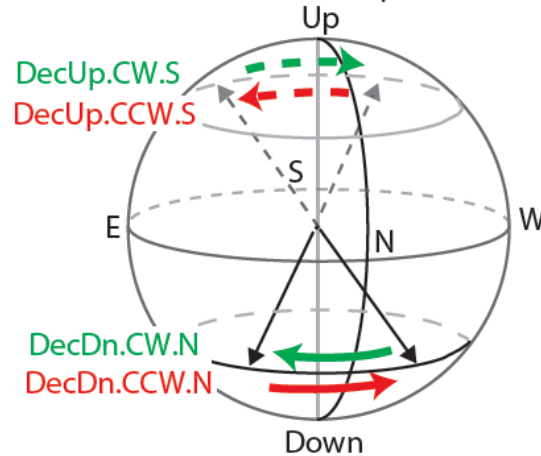
145 Fig. 2 shows the magnetic field rotations used. In inclination (Inc) experiments (Fig.
146 2A), declination direction was fixed to North (0° declination in our coordinate system), and
147 participants sat facing North. Rotation of the field vector from downwards to upwards was
148 designated as an ‘Inc.UP.N’ trial and the return sweep as ‘Inc.DN.N’, with UP/DN indicating the
149 direction of field rotation. In declination (Dec) experiments (Fig 2B, 2C), we held inclination
150 (and hence the vertical component of the field vector) constant, while rotating the horizontal
151 component clockwise or counterclockwise to vary the declination. For trials with downwards
152 inclination (as in the Northern Hemisphere), field rotations swept the horizontal component 90°
153 CW or CCW between Northeast and Northwest, designated as ‘DecDn.CW.N’ or
154 ‘DecDn.CCW.N’, respectively, with ‘.N’ indicating a Northerly direction. To test biophysical
155 hypotheses of magnetoreception as discussed below, we conducted additional declination
156 rotation experiments with static, upwards inclination. As shown in Fig. 2B, rotating an upwards-
157 directed field vector between SE and SW (‘DecUp.CW.S’ and ‘DecUp.CCW.S’) antiparallel to
158 the downwards-directed rotations provides tests of the quantum compass biophysical model,
159 while sweeping an upwards vector between NE and NW (‘DecUp.CW.N’ and ‘DecUp.CCW.N’)
160 provides a general test for electrical induction (Fig. 2C).

161 **Fig. 2.** Magnetic field rotations used in these
 162 experiments. In the first ~100 ms of each
 163 experimental trial, the magnetic field vector
 164 was either: 1) rotated from the first preset
 165 orientation to the second (SWEEP), 2) rotated
 166 from the second preset orientation to the first
 167 (also SWEEP), or 3) left unchanged
 168 (FIXED). In all experimental trials, the field
 169 intensity was held constant at the ambient lab
 170 value (~35 uT). For declination rotations, the
 171 horizontal rotation angle was +90 degrees or -
 172 90 degrees. For inclination rotations, the
 173 vertical rotation angle was either +120
 174 degrees / -120 degrees, or +150 degrees / -150
 175 degrees, depending on the particular
 176 inclination rotation experiment. (A)
 177 Inclination rotations between $\pm 60^\circ$ or $\pm 75^\circ$.
 178 The magnetic field vector rotates from
 179 downwards to upwards (Inc.UP.N, red) and
 180 vice versa (Inc.DN.N, green), with declination
 181 steady at North (0°). (B) Declination
 182 rotations used in main assay (solid arrows)
 183 and vector opposite rotations used to test the
 184 quantum compass hypothesis (dashed
 185 arrows). In the main assay, the magnetic field
 186 rotated between NE (45°) and NW (315°) with
 187 inclination held downwards ($+60^\circ$ or $+75^\circ$) as
 188 in the Northern Hemisphere (DecDn.CW.N
 189 and DecDn.CCW.N); vector opposites with
 190 upwards inclination (-60° or -75°) and
 191 declination rotations between SE (135°) and
 192 SW (225°) are shown with dashed arrows
 193 (DecUp.CW.S and DecUp.CCW.S). (C)
 194 Identical declination rotations, with static but
 195 opposite vertical components, used to test the
 196 electrical induction hypothesis. The magnetic
 197 field was shifted in the Northerly direction
 198 between NE (45°) and NW (315°) with
 199 inclination held downwards ($+75^\circ$,
 200 DecDn.CW.N and DecDn.CCW.N) or
 201 upwards (-75° , DecUp.CW.S and
 202 DecUp.CCW.S). The two dotted vertical
 203 lines indicate that the rotations started at the
 204 same declination values. In both (B) and (C),
 205 counterclockwise rotations (viewed from
 206 above) are shown in red, clockwise in green.

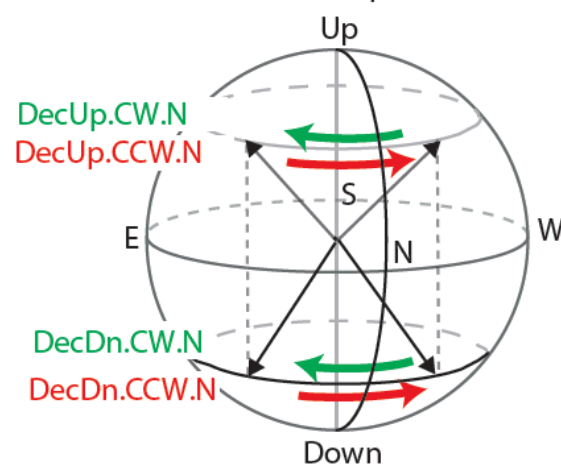
A. Inclination rotations with fixed declination



B. Antipodal Declination Rotations
(A test of the 'Quantum Compass')



C. Identical Declination Rotations
(A test of an Induction Compass)



207 During magnetic field rotations, EEG was recorded from participants in the eyes-closed
208 resting state. Auditory cues marked the beginning and end of each ~7 minute run, but
209 participants were not informed of run mode, trial sequence or stimulus timing. EEG was
210 sampled at 512 Hz from 64 electrodes arrayed in the standard International 10-20 positions using
211 a Biosemi™ ActiveTwo system. The experimental protocol was approved by the Caltech
212 Institutional Review Board (IRB), and all participants gave written informed consent.

213 We used conventional methods of time/frequency decomposition (Morlet wavelet
214 convolution) to compute post-stimulus power changes relative to a pre-stimulus baseline interval
215 (–500 to –250 ms) over a 1-100 Hz frequency range. We focused on non-phase-locked power by
216 subtracting the event-related potential in each condition from each trial of that condition prior to
217 time/frequency decomposition. This is a well-known procedure for isolating non-phase-locked
218 power and is useful for excluding the artifact from subsequent analyses (Cohen, 2014).
219 Following the identification of alpha band activity as a point of interest (detailed in Results), the
220 following procedure was adopted to isolate alpha activity in individuals. To compensate for
221 known individual differences in peak resting alpha frequency (8 to 12 Hz in our participant pool)
222 and in the timing of alpha wave responses following sensory stimulation, we identified
223 individualized power change profiles using an automated search over an extended alpha band of
224 6-14 Hz, 0-2 s post-stimulus. For each participant, power changes at electrode Fz were averaged
225 over all trials, regardless of condition, to produce a single time/frequency map. In this cross-
226 conditional average, the most negative time-frequency point was set as the location of the
227 participant’s characteristic alpha-ERD. A window of 250 ms and 5 Hz bandwidth was
228 automatically centered as nearly as possible on that point within the constraints of the overall
229 search range. These time/frequency parameters were chosen based on typical alpha-ERD
230 durations and bandwidths. Alpha power activity in each individualized window was used to test
231 for significant differences between conditions. For each condition, power changes were
232 averaged separately within the window, with trials subsampled and bootstrapped to equalize trial
233 numbers across conditions. Outlier trials with extreme values of alpha power (typically caused
234 by movement artifacts or brief bursts of alpha activity in an otherwise low-amplitude signal) in
235 either the pre- or post-stimulus intervals were removed by an automated algorithm prior to
236 averaging, according to a threshold of 1.5X the interquartile range of log alpha power across all
237 trials. Further details are provided in sections 1-5 of *Extended Materials and Methods*, below.

238 **Results**

239 In initial observations, several participants (residing in the Northern Hemisphere)
240 displayed striking patterns of neural activity following magnetic stimulation, with strong
241 decreases in EEG alpha power in response to two particular field rotations: (1) Inclination
242 SWEEP trials (Inc.UP.N and Inc.DN.N), in which the magnetic vector rotated either down or up
243 (e.g. rotating a downwards pointed field vector up to an upwards pointed vector, or vice versa;
244 Fig. 2A red and green arrows), and (2) DecDn.CCW.N trials, in which magnetic field declination
245 rotated counterclockwise while inclination was held downwards (as in the Northern Hemisphere;
246 Fig 2B, solid red arrow). Alpha power began to drop from pre-stimulus baseline levels as early
247 as ~100 ms after magnetic stimulation, decreasing by as much as ~50% over several hundred
248 milliseconds, then recovering to baseline by ~1 s post-stimulus; this is visualized by the deep
249 blue color on the time-frequency power maps (Fig. 3). Scalp topography was bilateral and
250 widespread, centered over frontal/central electrodes, including midline frontal electrode Fz when
251 referenced to CPz. Fig. 3A shows the whole-brain response pattern to inclination sweeps and
252 control trials (Inc.SWEEP.N and Inc.FIXED.N) of one of the responsive participants, with the
253 alpha-ERD exhibited in the SWEEP but not FIXED trials. Similarly, Fig. 3B and 3C show the
254 declination responses of a different participant on two separate runs (labeled Runs #1 and #2) six
255 months apart. Response timing, bandwidth and topography of the alpha-ERD in the CCW
256 sweeps, with negative FIXED controls, were replicated across runs, indicating a repeatable
257 signature of magnetosensory processing in humans. After experimental sessions, participants
258 reported that they could not discern when or if any magnetic field changes had occurred.

259

260

261

262

263

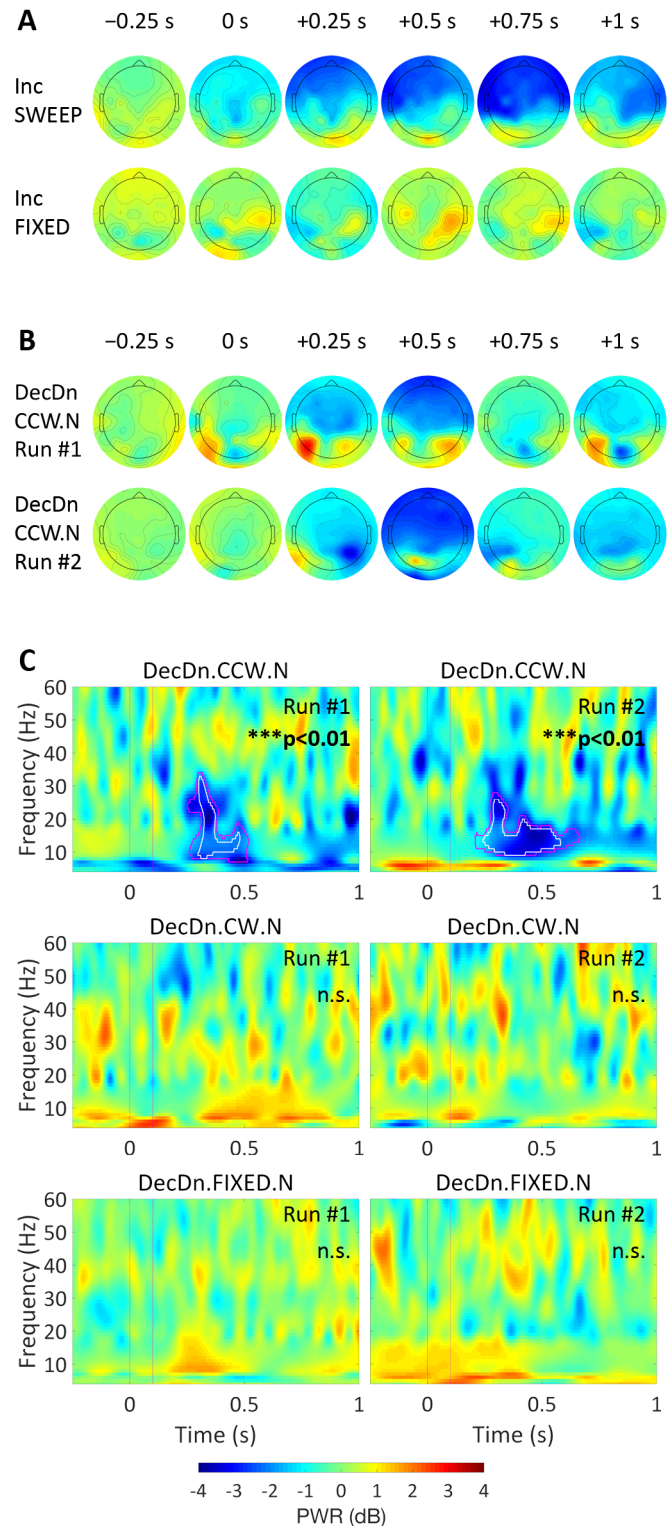
264

265

266

267

268 **Fig. 3.** Alpha-ERD as a neural response to
269 magnetic field rotation. Post-stimulus power
270 changes (dB) from a pre-stimulus baseline (-500
271 to -250 ms) plotted according to the ± 4 dB color
272 bar at bottom. **(A)** Scalp topography of the
273 alpha-ERD response in an inclination
274 experiment, showing alpha power at select time
275 points before and after field rotation at 0 s.
276 Alpha-ERD (deep blue) was observed in
277 SWEEP (top row), but not FIXED (bottom row),
278 trials. **(B)** Scalp topography of the alpha-ERD
279 response for two runs of the declination
280 experiment, tested 6 months apart in a different
281 strongly-responding participant. DecDn.CCW.N
282 condition is shown. In both runs, the response
283 peaked around +500 ms post-stimulus and was
284 widespread over frontal/central electrodes,
285 demonstrating a stable and reproducible
286 response pattern. **(C)** Time-frequency maps at
287 electrode Fz for the same runs shown in (B).
288 Pink vertical lines indicate the 0-100 ms field
289 rotation interval. Pink/white outlines indicate
290 significant alpha-ERD at the $p < 0.05$ and $p < 0.01$
291 statistical thresholds, respectively. Separate runs
292 shown side by side. Significant alpha-ERD was
293 observed following downwards-directed
294 counterclockwise rotations (outlines in top row),
295 with no other power changes reaching
296 significance. Significant power changes appear
297 with similar timing and bandwidth, while
298 activity outside the alpha-ERD response, and
299 activity in other conditions is inconsistent across
300 runs.



301
302
303
304
305
306

307 The alpha rhythm is the dominant human brain oscillation in the resting state when a
308 person is not processing any specific stimulus or performing any specific task (Klimesch, 1999).
309 Neurons engaged in this internal rhythm produce 8-13 Hz alpha waves that are measurable by
310 EEG. Individuals vary widely in the amplitude of the resting alpha rhythm. When an external
311 stimulus is suddenly introduced and processed by the brain, the alpha rhythm generally decreases
312 in amplitude compared with a pre-stimulus baseline. (Hartmann, Schlee, & Weisz, 2012;
313 Klimesch, 1999; Pfurtscheller, Neuper, & Mohl, 1994). This EEG phenomenon, termed alpha
314 event-related desynchronization (alpha-ERD), has been widely observed during perceptual and
315 cognitive processing across visual, auditory and somatosensory modalities (Peng, Hu, Zhang, &
316 Hu, 2012). Alpha-ERD may reflect the recruitment of neurons for processing incoming sensory
317 information and is thus a generalized signature for a shift of neuronal activity from the internal
318 resting rhythm to external engagement with sensory or task-related processing (Pfurtscheller &
319 Lopes da Silva, 1999). Individuals also vary in the strength of alpha-ERD; those with high
320 resting-state or pre-stimulus alpha power tend to show strong alpha-ERDs following sensory
321 stimulation, while those with low alpha power have little or no response in the alpha band
322 (Klimesch, 1999).

323 Based on early observations, we formed the hypothesis that sensory transduction of
324 geomagnetic stimuli could be detectable as alpha-ERD in response to field rotations – e.g. the
325 magnetic field rotation would be the external stimulus, and the alpha-ERD would be the
326 signature of the brain beginning to process sensory data from this stimulus. This hypothesis was
327 tested at the group level in data collected from 29 participants in the inclination rotation
328 conditions (Fig 2A) and 26 participants in the declination rotation conditions (Fig. 2B, solid
329 arrows).

330 For inclination experiments, we collected data from matched Active and Sham runs
331 (N=29 of 34; 5 participants were excluded due to time limits that prevented the collection of
332 sham data). We tested for the effects of inclination rotation (SWEEP vs. FIXED) and magnetic
333 stimulation (Active vs. Sham) using a two-way repeated-measures ANOVA. We found a
334 significant interaction of inclination rotation and magnetic stimulation ($p<0.05$). Post-hoc
335 comparison of the four experimental conditions (Active-SWEEP, Active-FIXED, Sham-SWEEP,
336 Sham-FIXED) revealed significant differences between Active-SWEEP and all other conditions
337 ($p<0.05$). Downwards/upwards rotations of magnetic field inclination produced an alpha-ERD

338 ~2X greater than background fluctuations in the FIXED control condition and all the Sham
339 conditions. Results are summarized in Table 1 and Fig. 4A.

340 In declination experiments (Fig. 4B), we observed a strikingly asymmetric response to
341 the clockwise (DecDn.CW.N) and counterclockwise (DecDn.CCW.N) rotations of a downwards-
342 directed field sweeping between Northeast and Northwest. Alpha-ERD was ~3X greater after
343 counterclockwise than after clockwise rotations, the latter producing alpha power changes
344 indistinguishable from background fluctuations in the FIXED control condition. Over the
345 participant pool (N=26 of 26 who were run in this experiment), we ran a one-way repeated-
346 measures ANOVA with three conditions (DecDn.CCW.N, DecDn.CW.N, and DecDn.FIXED.N)
347 to find a highly significant effect of declination rotation ($p < 0.001$) (Table 1). As indicated in
348 Fig. 4B, the counterclockwise rotation elicited a significantly different response from both the
349 clockwise rotation ($p < 0.001$) and FIXED control ($p < 0.001$). Fig. 4D shows the stimulus-locked
350 grand average across all participants for each condition; an alpha-ERD is observed only for
351 counterclockwise rotations of a downwards-directed field (left panel). Sham data were available
352 for 18 of 26 participants in the declination experiments; no major changes in post-stimulus power
353 were observed in any of the sham conditions (Fig. 4E).

354

355

356

357

358

359

360

361

362

363

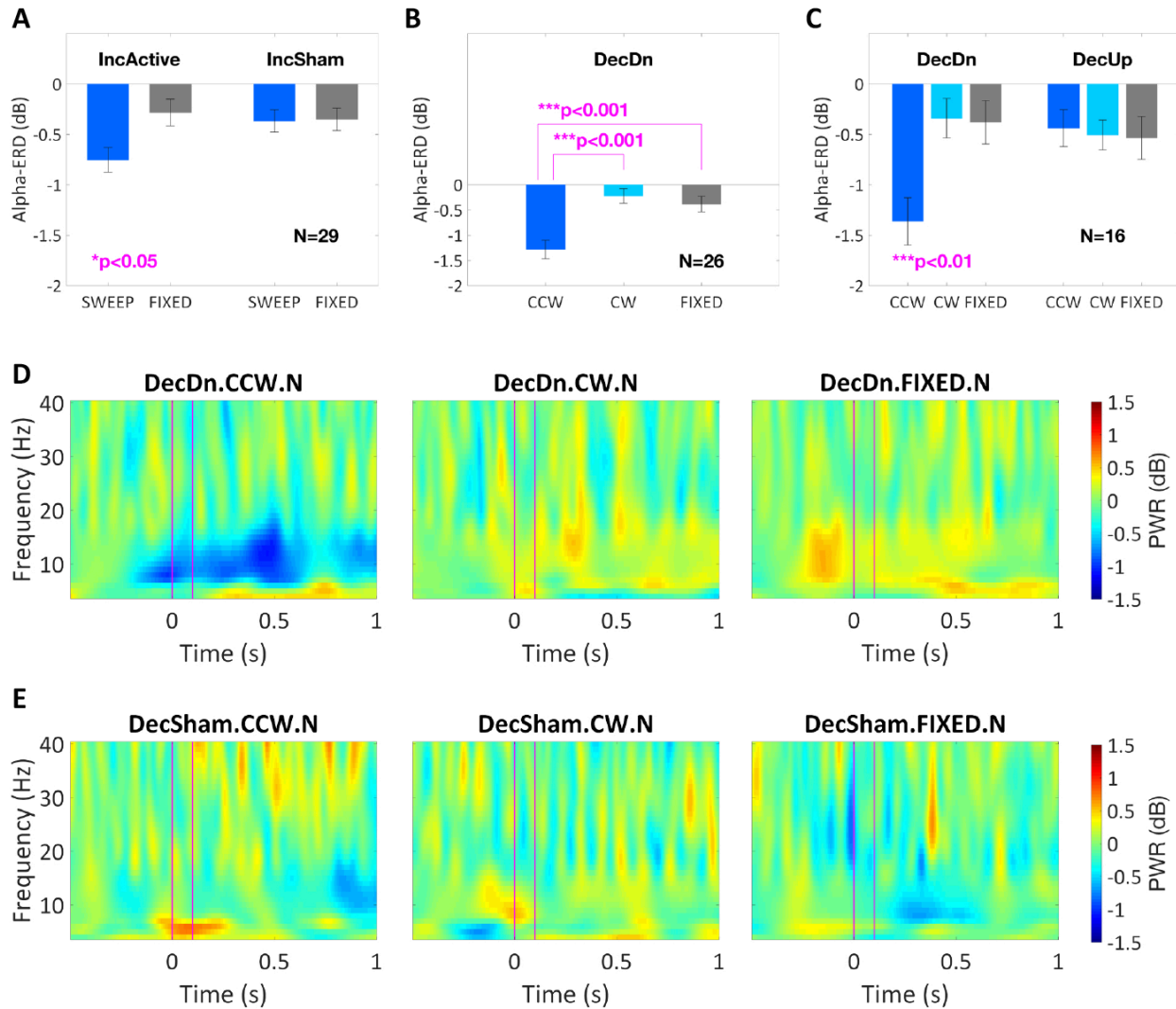
364

365

366

367

368



369

370 **Fig. 4.** Group results from repeated-measures ANOVA for the effects of geomagnetic
 371 stimulation on post-stimulus alpha power. (A) Average alpha-ERD (dB) at electrode Fz in the
 372 SWEEP and FIXED conditions of inclination experiments run in Active or Sham mode. Two-
 373 way ANOVA showed an interaction ($p < 0.05$, $N = 29$) of inclination rotation (SWEEP vs. FIXED)
 374 and magnetic stimulation (Active vs. Sham). According to post-hoc testing, only inclination
 375 sweeps in Active mode produced alpha-ERD above background fluctuations in FIXED trials
 376 ($p < 0.01$) or Sham mode ($p < 0.05$). (B) Average alpha-ERD (dB) at electrode Fz in the
 377 declination experiment with inclination held downwards (DecDn). One-way ANOVA showed a
 378 significant main effect of declination rotation ($p < 0.001$, $N = 26$). The downwards-directed
 379 counterclockwise rotation (DecDn.CCW.N) produced significantly different effects from both
 380 the corresponding clockwise rotation (DecDn.CW.N, $p < 0.001$) and the FIXED control condition
 381 (DecDn.FIXED.N, $p < 0.001$). (C) Comparison of the declination rotations with inclination held
 382 downwards (DecDn) or upwards (DecUp) in a subset ($N = 16$ of 26) of participants run in both
 383 experiments. Two-way ANOVA showed a significant interaction ($p < 0.01$) of declination
 384 rotation (CCW vs. CW vs. FIXED) and inclination direction (Dn vs. Up). Post-hoc testing
 385 showed significant differences ($p < 0.01$) between the DecDn.CCW.N condition and every other
 386 condition, none of which were distinct from any other. This is a direct test and rejection of the

387 quantum compass hypothesis. (D) Grand average of time-frequency power changes across the
388 26 participants in the DecDn experiment from (B). Pink vertical lines indicate the 0-100 ms field
389 rotation interval. A post-stimulus drop in alpha power was observed only following the
390 downwards-directed counterclockwise rotation (left panel). Wider spread of desynchronization
391 reflects inter-individual variation. Convolution involved in time/frequency analyses causes the
392 early responses of a few participants to appear spread into the pre-stimulus interval. (E) Grand
393 average of time-frequency power changes across the 18 participants with sham data in the
394 declination experiments; no significant power changes were observed.

395
396
397
398
399
400
401
402
403
404
405
406
407
408
409
410
411
412
413
414
415
416
417
418
419
420
421
422
423
424
425
426
427
428
429
430
431
432

Group Results for Effects of Magnetic Field Rotation on Post-Stimulus Alpha Power			
ANOVA #1: Inclination Rotation x Magnetic Stimulation (N=29)			
Two-Way Repeated Measures ANOVA	F	p	η_p^2
Main Effect of Inclination Rotation (SWEEP vs. FIXED)	3.26	0.08	0.19
Main Effect of Magnetic Stimulation (Active vs. Sham)	2.47	0.13	0.09
Inclination Rotation x Magnetic Stimulation (Interaction)	5.67	0.02*	0.17
ANOVA #2: Declination Rotation (N=26)			
One-Way Repeated Measures ANOVA	F	p	η_p^2
Main Effect of Declination Rotation (CCW vs. CW vs. FIXED)	13.09	0.00003***	0.34
ANOVA #3: Declination Rotation x Inclination Direction (N=16)			
Two-Way Repeated Measures ANOVA	F	p	η_p^2
Main Effect of Declination Rotation (CCW vs. CW vs. FIXED)	3.77	0.03*	0.24
Main Effect of Inclination Direction (Dn vs. Up)	0.89	0.36	0.06
Declination Rotation x Inclination Direction (Interaction)	6.49	0.004***	0.30

433
434 **Table 1. Group results from repeated-measures ANOVA for the effects of magnetic field**
435 **rotation on post-stimulus alpha power.** ANOVA #1 shows a significant interaction of
436 inclination rotation (SWEEP vs. FIXED) and magnetic stimulation (Active vs. Sham) in the
437 inclination experiments. Based on post-hoc testing, alpha-ERD was significantly greater in
438 SWEEP trials in Active mode, compared with all other conditions ($p < 0.05$). ANOVA #2 shows a
439 significant main effect of declination rotation when inclination is static and downwards as in the
440 Northern Hemisphere. Alpha-ERD was significantly greater following counterclockwise
441 rotations ($p < 0.001$). ANOVA #3 shows a significant interaction of declination rotation and
442 inclination direction in declination experiments designed to test the “Quantum Compass”

443 mechanism of magnetoreception. A significant alpha-ERD difference ($p < 0.01$) between
444 counterclockwise down (DecDn.CCW.N) and counterclockwise up (DecUp.CCW.S) argues
445 against this hypothesis in humans.

446
447

448 The asymmetric declination response provided a starting point for evaluating potential
449 mechanisms of magnetosensory transduction, particularly the quantum compass hypothesis,
450 which has received much attention in recent years (Hore & Mouritsen, 2016; Ritz, Adem, &
451 Schulten, 2000). Because the quantum compass cannot distinguish polarity, we conducted
452 additional declination rotation experiments in which the fields were axially identical to those in
453 the preceding DecDn experiments, except with reversed polarity (Fig. 2B; reversed polarity
454 rotations shown as dashed arrows). In the additional DecUp conditions, Magnetic North pointed
455 to Geographic South and up rather than Geographic North and down, and the upwards-directed
456 field rotated clockwise (DecUp.CW.S) or counterclockwise (DecUp.CCW.S) between SE and
457 SW. In later testing, we ran 16 participants in both the DecDn and DecUp experiments to
458 determine the effects of declination rotation and inclination direction in a two-way repeated
459 measures ANOVA with six conditions (DecDn.CCW.N, DecDn.CW.N, DecDn.FIXED.N,
460 DecUp.CCW.S, DecUp.CW.S, and DecUp.FIXED.S). A significant interaction of declination
461 rotation and inclination direction ($p < 0.01$) was found (Fig. 4C and Table 1). DecDn.CCW.N
462 was significantly different from all other conditions ($p < 0.01$), none of which differed from any
463 other. Thus, counterclockwise rotations of a downwards-directed field were processed
464 differently in the human brain from the same rotations of a field of opposite polarity. These
465 results contradict the quantum compass hypothesis, as explained below in Biophysical
466 Mechanisms.

467 From previous EEG studies of alpha oscillations in human cognition, the strength of
468 alpha-ERD is known to vary substantially across individuals (Klimesch, 1999; Klimesch,
469 Doppelmayr, Russegger, Pachinger, & Schwaiger, 1998; Pfurtscheller et al., 1994). In
470 agreement with this, we observed a wide range of alpha-ERD responses in our participants as
471 well. Some participants showed large drops in alpha power up to ~60% from pre-stimulus
472 baseline, while others were unresponsive with little change in post-stimulus power at any
473 frequency. Histograms of these responses are provided in Fig. 6-8 of *Extended Materials and*
474 *Methods* below.

475 To confirm that the variability across the dataset was due to characteristic differences
476 between individuals rather than general variability in the measurement or the phenomenon, we
477 retested the strongly-responding participants to see if their responses were stable across sessions.
478 Using permutation testing with false discovery rate (FDR) correction at the $p < 0.05$ and $p < 0.01$
479 statistical thresholds, we identified participants who exhibited alpha-ERD that reached
480 significance at the individual level and tested them ($N=4$) again weeks or months later. An
481 example of separate runs on the same participant is shown in Figs. 3B and 3C, and further data
482 series are shown in the Fig 9 of *Extended Materials and Methods*. Each participant replicated
483 their results with similar response tuning, timing and topography, providing greater confidence
484 that the observed effect was specific for the magnetic stimulus in the brain of that individual.
485 While the functional significance of these inter-individual differences is unclear, the
486 identification of strongly responding individuals gives us the opportunity to conduct more
487 focused tests directed at deriving the biophysical characteristics of the transduction mechanism.

488

489 **Biophysical Mechanisms**

490 Three major biophysical transduction hypotheses have been considered extensively for
491 magnetoreception in animals: (1) various forms of electrical induction (Kalmijn, 1981;
492 Rosenblum, Jungerman, & Longfellow, 1985; Yeagley, 1947), (2) a chemical/quantum compass
493 involving hyperfine interactions with a photoactive pigment (Schulten, 1982) like cryptochrome
494 (Hore & Mouritsen, 2016; Ritz et al., 2000), and (3) specialized organelles based on biologically-
495 precipitated magnetite similar to those in magnetotactic microorganisms (J.L. Kirschvink &
496 Gould, 1981). We designed the declination experiments described above to test these
497 hypotheses.

498 *Electrical Induction.* According to the Maxwell-Faraday law ($\nabla \times \mathbf{E} = -\partial\mathbf{B}/\partial t$), electrical
499 induction depends only on the component of the magnetic field that is changing with time
500 ($\partial\mathbf{B}/\partial t$). In our declination experiments, this corresponds to the horizontal component that is
501 being rotated. The vertical component is held constant and therefore does not contribute to
502 electrical induction. Thus, we compared brain responses to two matched conditions, where the
503 declination rotations were identical, but the static vertical components were opposite (Fig 2C). A
504 transduction mechanism based in electrical induction would respond identically to these two
505 conditions. Video 1 shows the alpha-ERD magnetosensory response of one strongly-responding

506 individual to these two stimulus types. In the top row, the static component was pointing
507 upwards, and in the bottom row, the static field was pointing downwards. In the DecDn.CCW.N
508 condition (lower left panel), the alpha-ERD (deep blue patch) starts in the right parietal region
509 almost immediately after magnetic stimulation and spreads over the scalp to most recording sites.
510 This large, prolonged and significant bilateral desynchronization ($p < 0.01$ at Fz) occurs only in
511 this condition with only shorter, weaker and more localized background fluctuations in the other
512 conditions (n.s. at Fz). No alpha-ERD was observed following any upwards-directed field
513 rotation (DecUp.CCW.N and DecUp.CW.N, top left and middle panels), in contrast to the strong
514 response in the DecDn.CCW.N condition. Looking across all of our data, none of our
515 experiments (on participants from the Northern Hemisphere) produced alpha-ERD responses to
516 rotations with a static vertical-upwards magnetic field (found naturally in the Southern
517 Hemisphere).

518 These tests indicate that electrical induction mechanisms cannot account for the neural
519 response. This analysis also rules out an electrical artifact of induced current loops from the
520 scalp electrodes, as any current induced in the loops would also be identical across the matched
521 runs. Our results are also consistent with many previous biophysical analyses, which argue that
522 electrical induction would be a poor transduction mechanism for terrestrial animals, as the
523 induced fields are too low to work reliably without large, specialized anatomical structures that
524 would have been identified long ago (Rosenblum et al., 1985; Yeagley, 1947). Other potential
525 confounding artifacts are discussed in sections 6 and 7 of the *Extended Materials and Methods*,
526 below.

527 *Quantum Compass.* From basic physical principles, a transduction mechanism based on
528 quantum effects can be sensitive to the axis of the geomagnetic field but not the polarity (Ritz et
529 al., 2000; Schulten, 1982). In the most popular version of this theory, a photosensitive molecule
530 like cryptochrome absorbs a blue photon, producing a pair of free radicals that can transition
531 between a singlet and triplet state, with the transition frequency depending on the local magnetic
532 field. The axis of the magnetic field – but not the polarity – could then be monitored by
533 differential reaction rates from the singlet vs. triplet products. This polarity insensitivity, shared
534 by all quantum-based magnetotransduction theories, is inconsistent with the group level test of
535 the quantum compass presented above. The data (Table 1 and Figure 4C, dark blue bars) showed
536 clearly distinct responses depending on polarity. We additionally verified this pattern of results

537 at the individual level. Video 2 shows the alpha-ERD magnetosensory response in another
538 strongly-responding individual. Only the DecDn.CCW.N rotation (lower left panel) yields a
539 significant alpha-ERD ($p < 0.01$ at Fz). Lack of a significant response in the axially identical
540 DecUp.CCW.S condition indicates that the human magnetosensory response is sensitive to
541 polarity. This means that a quantum compass-based mechanism cannot account for the alpha-
542 ERD response we observe in humans.

543

544 **Response Selectivity**

545 The selectivity of brain responses for specific magnetic field directions and rotations may
546 be explained by tuning of neural activity to ecologically relevant values. Such tuning is well
547 known in marine turtles in the central Atlantic Ocean, where small increases in the local
548 geomagnetic inclination or intensity (that indicate the animals are drifting too far North and are
549 approaching the Gulf Stream currents) trigger abrupt shifts in swimming direction, thereby
550 preventing them from being washed away from their home in the Sargasso Sea (Light, Salmon,
551 & Lohmann, 1993; Lohmann et al., 2001; Lohmann & Lohmann, 1996). Some migratory birds
552 are also known to stop responding to the magnetic direction if the ambient field intensity is
553 shifted more than $\sim 25\%$ away from local ambient values (W. Wiltschko, 1972), which would
554 stop them from using this compass over geomagnetic anomalies. From our human experiments
555 to date, we suspect that alpha-ERD occurs in our participants mainly in response to geomagnetic
556 fields that reflect something close to "normal" in the Northern Hemisphere where the North-
557 seeking field vector tilts downwards. This would explain why field rotations with a static
558 upwards component produced little response in Northern Hemisphere participants. Conducting
559 similar experiments on participants born and raised in other geographic regions (such as in the
560 Southern Hemisphere or on the Geomagnetic Equator) could test this hypothesis.

561 Another question vis-à-vis response selectivity is why downwards-directed CCW
562 (DecDn.CCW.N), but not CW (DecDn.CW.N), rotations elicited alpha-ERD. The bias could
563 arise either at the receptor level or at higher processing levels. The structure and function of the
564 magnetoreceptor cells are unknown, but biological structures exhibit chirality (right- or left-
565 handedness) at many spatial scales – from individual amino acids to folded protein assemblies to
566 multicellular structures. If such mirror asymmetries exist in the macromolecular complex
567 interfacing with magnetite, they could favor the transduction of one stimulus over its opposite.

568 Alternatively, higher-level cognitive processes could tune the neural response towards
569 counterclockwise rotations without any bias at the receptor level. As of this writing, we cannot
570 rule out the possibility that some fraction of humans may have a CW response under this or other
571 experimental paradigms, just as some humans are left- instead of right-handed. We also cannot
572 rule out the existence of a separate neural response to CW rotations that is not reflected in the
573 alpha-ERD signature that we assay here.

574 The functional significance of the divergent responses to CW and CCW is also unclear. It
575 may simply arise as a byproduct during the evolution and development of other mirror
576 asymmetries (such as north-up vs. north-down), which serve a clearer functional, ecologically
577 relevant purpose with a lower biological cost. It may also be that the alpha-ERD response
578 reflects non-directional information, such as a warning of geomagnetic anomalies, which can
579 expose a navigating animal to sudden shifts of the magnetic field comparable to those used in our
580 experiments. For example, volcanic or igneous terranes are prone to remagnetization by
581 lightning strikes, which produce magnetic fields powerful enough to leave local, 1-10 m scale
582 remnant (permanent) magnetizations strong enough to warp the otherwise uniform local
583 geomagnetic field. A large-scale example is the Vredefort Dome area in South Africa
584 (Carporzen, Weiss, Gilder, Pommier, & Hart, 2012) where lightning remagnetization has been
585 studied extensively. Such anomalies are common in areas with volcanic or igneous basement
586 rock and can be located by simply wandering around with a hand compass held level at waist
587 height and observing abnormal swings of the compass needle from magnetic north. An animal
588 moving through isolated features of this sort would experience paired shifts; the magnetic field
589 direction and intensity would change as the anomaly is entered and then return to normal upon
590 exiting. If the magnetosensory system evolved in the brain as a warning signal against using the
591 magnetic field for long-range navigation while passing through local field anomalies, sensitivity
592 to only one directional excursion is needed. Future experiments could test this speculation by
593 sweeping field intensity through values matching those of lightning-strike and other anomalies to
594 check for asymmetric patterns of alpha desynchronization.

595 A further question is whether the response asymmetry occurs only in passive experiments
596 when participants experience magnetic stimulation without making use of the information or also
597 in active experiments with a behavioral task, such as judging the direction or rotation of the
598 magnetic field. Behavioral tasks with EEG recording could be used to explore the

599 magnetosensory system in more detail and may uncover the unknown function of the observed
600 response and its asymmetry.

601

602 **General Discussion**

603 As noted above, many past attempts have been made to test for the presence of human
604 magnetoreception using *behavioral* assays, but the results were inconclusive. To avoid the
605 cognitive and behavioral artifacts inherent in testing weak or subliminal sensory responses, we
606 decided to use EEG techniques to see directly whether or not the human brain has passive
607 responses to magnetic field changes. Our results indicate that human brains are indeed collecting
608 and selectively processing directional input from magnetic field receptors. These give rise to a
609 brain response that is selective for field direction and rotation with a pattern of neural activity
610 that is measurable at the group level and repeatable in strongly-responding individuals. Such
611 neural activity is a necessary prerequisite for any subsequent behavioral expression of
612 magnetoreception, but such magnetically-triggered neural activity does not demand that the
613 magnetic sense be expressed behaviorally or enter an individual's conscious awareness.

614 The fact that alpha-ERD is elicited in a specific and sharply delineated pattern allows us
615 to make inferences regarding the biophysical mechanisms of signal transduction. Notably, the
616 alpha-ERD response differentiated clearly between sets of stimuli differing only by their static or
617 polar components. Electrical induction, electrical artifacts and quantum compass mechanisms
618 are totally insensitive to these components and cannot account for the selectivity of brain
619 responses. Indeed, while birds have evolved a method of navigation that would allow them to
620 navigate by combining a non-polar magnetic sense with gravity, that strategy would not be able
621 to distinguish our test stimuli (see section 8 of the *Extended Materials and Methods*). In
622 contrast, ferromagnetic mechanisms can be highly sensitive to both static and polar field
623 components, and could distinguish our test stimuli with differing responses. Finally, magnetite-
624 based mechanisms for navigation have been characterized in animals through neurophysiological
625 (Walker et al., 1997), histological (Diebel, Proksch, Green, Neilson, & Walker, 2000) and pulse-
626 remagnetization studies (Beason, Wiltschko, & Wiltschko, 1997; Ernst & Lohmann, 2016; R. A.
627 Holland, 2010; R.A. Holland & Helm, 2013; R. A. Holland, Kirschvink, Doak, & Wikelski,
628 2008; Irwin & Lohmann, 2005; J.L. Kirschvink & Kobayashi-Kirschvink, 1991; Munro, Munro,
629 Phillips, Wiltschko, & Wiltschko, 1997; Munro, Munro, Phillips, & Wiltschko, 1997; W.

630 Wiltschko, Ford, Munro, Winklhofer, & Wiltschko, 2007; W. Wiltschko, Munro, Beason, Ford,
631 & Wiltschko, 1994; W. Wiltschko, Munro, Ford, & Wiltschko, 1998, 2009; W. Wiltschko,
632 Munro, Wiltschko, & Kirschvink, 2002; W. Wiltschko & R. Wiltschko, 1995), and biogenic
633 magnetite has been found in human tissues (Dunn et al., 1995; Gilder et al., 2018; J. L.
634 Kirschvink, Kobayashi-Kirschvink, & Woodford, 1992; Kobayashi & Kirschvink, 1995; Maher
635 et al., 2016; Schultheiss-Grassi, Wessiken, & Dobson, 1999).

636 These data argue strongly for the presence of geomagnetic transduction in humans,
637 similar to those in numerous migratory and homing animals. Single-domain ferromagnetic
638 particles such as magnetite are directly responsive to both time-varying and static magnetic fields
639 and are sensitive to field polarity. At the cellular level, the magnetomechanical interaction
640 between ferromagnetic particles and the geomagnetic field is well above thermal noise (J.L.
641 Kirschvink & Gould, 1981; J. L. Kirschvink, Winklhofer, & Walker, 2010), stronger by several
642 orders of magnitude in some cases (Eder et al., 2012). In many animals, magnetite-based
643 transduction mechanisms have been found and shown to be necessary for navigational behaviors,
644 through neurophysiological and histological studies (Diebel et al., 2000; Walker et al., 1997). A
645 natural extension of this study would be to apply the pulse-remagnetization methods used in
646 animals to directly test for a ferromagnetic transduction element in humans. In these
647 experiments, a brief magnetic pulse causes the magnetic polarity of the single-domain magnetite
648 crystals to flip. Following this treatment, the physiological and behavioral responses to the
649 geomagnetic field are expected to switch polarity. These experiments could provide
650 measurements of the microscopic coercivity of the magnetite crystals involved and hence make
651 predictions about the physical size and shape of the crystals involved (Diaz Ricci & Kirschvink,
652 1992 203), and perhaps their physiological location.

653 Previous attempts to detect human magnetoreception may have been confounded by a
654 number of factors. Response specificity and neural tuning to the local environment (Block,
655 1992) make it likely that tests using stimuli outside the environmental range would likely fail,
656 and past computational methods were not as good at isolating the neural activity studied here
657 (Boorman et al., 1999; Sastre et al., 2002), further discussed in section 9 of the *Extended*
658 *Materials and Methods*, below. Other experiments were conducted in unshielded conditions and
659 may have been subject to radio-frequency noise which has been shown to shut down

660 magnetoreceptivity in birds and other animals (Engels et al., 2014; Landler, Painter, Youmans,
661 Hopkins, & Phillips, 2015; Tomanova & Vacha, 2016; R. Wiltschko et al., 2015).

662 At this point, our observed reduction in alpha-band power is a clear neural signature for
663 cortical processing of the geomagnetic stimulus, but its functional significance is unknown. In
664 form, the activity is an alpha-ERD response resembling those found in other EEG investigations
665 of sensory and cognitive processing. However, the alpha-ERD responses found in literature take
666 on a range of different spatiotemporal forms and are associated with a variety of functions. It is
667 likely that the alpha-ERD seen here reflects the sudden recruitment of neural processing
668 resources, as this is a finding common across studies. But more research will be needed to see if
669 and how it relates more specifically to previously studied processes such as memory access or
670 recruitment of attentional resources.

671 Further, alpha-ERD probably represents only the most obvious signature of neural
672 processing arising from geomagnetic input. A host of upstream and downstream processes need
673 to be investigated to reveal the network of responses and the information they encode.
674 Responses independent from the alpha-ERD signature will likely emerge, and those might show
675 different selectivity patterns and reflect stimulus features not revealed in this study. Does human
676 magnetoreceptive processing reflect a full representation of navigational space? Does it contain
677 certain warning signals regarding magnetic abnormalities? Or have some aspects degenerated
678 from the ancestral system? For now, alpha-ERD remains a blank signature for a wider,
679 unexplored range of magnetoreceptive processing.

680 Future experiments should examine how magnetoreceptive processing interacts with
681 other sensory modalities in order to determine field orientation. Our experimental results suggest
682 the combination of a magnetic and a positional cue (e.g. reacting differently to North-up and
683 North-down fields). However, we cannot tell if this positional cue uses a reference frame set by
684 gravity sensation or is aligned with respect to the human body. In birds, orientation behavior
685 reflects a magnetic inclination compass that identifies the steepest angle of magnetic field dip
686 with respect to gravity (R. Wiltschko & W. Wiltschko, 1995; W. Wiltschko, 1972), and this
687 compass can operate at dips as shallow as 5° from horizontal (Schwarze et al., 2016). Because
688 magnetism and gravity are distinct, non-interacting forces of nature, the observed behavior must
689 arise from processing of neural information from separate sensory systems (J. L. Kirschvink et
690 al., 2010). Evolution has driven many of the known sensory systems down to their physical

691 detection limits with astounding specificity (Block, 1992). Gravitational information is known to
692 arise in the utricle and saccule of the vertebrate vestibular system due to the motions of dense
693 biominerals activating hair cells (Lopez & Blanke, 2011), and a magnetite-based
694 magnetosensory organ has been localized at the cellular level in fish (Diebel et al., 2000; Eder et
695 al., 2012; Walker et al., 1997). The neural processing of magnetic with gravitational sensory
696 cues could perhaps be addressed by modifying the test chamber to allow the participant to rest in
697 different orientations with respect to gravity or by running the experiment in the zero-gravity
698 environment of the international space station.

699 In the participant pool, we found several highly responsive individuals whose alpha-ERD
700 proved to be stable across time: 4 participants responded strongly at the $p < 0.01$ level in repeated
701 testing over weeks or months. Repeatability in individual participants suggests that the alpha-
702 ERD did not arise due to chance fluctuations in a single run, but instead reflects a consistent
703 individual characteristic, measurable across multiple runs. A wider survey of individuals could
704 reveal genetic/developmental or other systematic differences underlying these individual
705 differences.

706 The range of individual responses may be partially attributed to variation in basic alpha-
707 ERD mechanisms, rather than to underlying magnetoreceptive processing. However, some
708 participants with high resting alpha power showed very little alpha-ERD to the magnetic field
709 rotations, suggesting that the extent of magnetoreceptive processing itself varies across
710 individuals. If so, distinct human populations may be good targets for future investigation. For
711 example, studies of comparative linguistics have identified a surprising number of human
712 languages that rely on a cardinal system of environmental reference cues (e.g. North, South,
713 East, West) and lack egocentric terms like front, back, left, and right (Haviland, 1998; Levinson,
714 2003; Meakins, 2011; Meakins & Algy, 2016; Meakins, Jones, & Algy, 2016). Native speakers
715 of such languages would (e.g.) refer to a nearby tree as being to their North rather than being in
716 front of them; they would refer to their own body parts in the same way. Individuals who have
717 been raised from an early age within a linguistic, social and spatial framework using cardinal
718 reference cues might have made associative links with geomagnetic sensory cues to aid in daily
719 life; indeed, linguists have suggested a human magnetic compass might be involved (Levinson,
720 2003). It would be interesting to test such individuals using our newly-developed methods to see
721 if such geomagnetic cues might already be within their conscious awareness, aiding their use of

722 the cardinal reference system. In turn, such experiments might guide the development of training
723 procedures to enhance geomagnetic sensitivity in individuals raised in other language and
724 cultural groups, advancing more rapidly studies on the nature of a human magnetic sense.

725 In the 198 years since Danish physicist Hans Christian Ørsted discovered
726 electromagnetism (March 1820), human technology has made ever-increasing use of it. Most
727 humans no longer need to rely on an internal navigational sense for survival. To the extent that
728 we employ a sense of absolute heading in our daily lives, external cues such as landmarks and
729 street grids can provide guidance. Even if an individual possesses an implicit magnetoreceptive
730 response, it is likely to be confounded by disuse and interference from our modern environment.
731 A particularly pointed example is the use of strong permanent magnets in both consumer and
732 aviation headsets, most of which produce static fields through the head several times stronger
733 than the ambient geomagnetic field. If there is a functional significance to the magnetoreceptive
734 response, it would have the most influence in situations where other cues are impoverished, such
735 as marine and aerial navigation, where spatial disorientation is a surprisingly persistent event
736 (Poisson & Miller, 2014). The current alpha-ERD evidence provides a starting point to explore
737 functional aspects of magnetoreception, by employing various behavioral tasks in variety of
738 sensory settings.

739

740 **Conclusion**

741

742 We conclude that at least some modern humans transduce changes in Earth-strength
743 magnetic fields into an active neural response. Given the known presence of highly-evolved
744 geomagnetic navigation systems in species across the animal kingdom, it is perhaps not
745 surprising that we might retain at least some functioning neural components, especially given the
746 nomadic hunter/gatherer lifestyle of our not-too-distant ancestors. The full extent of this
747 inheritance remains to be discovered.

748

749

750

751

752

753 **Extended Materials and Methods.**

754 Detailed additional instructions concerning the custom-built equipment and instrumentation are
755 provided below. All experiments were performed in accordance with relevant guidelines and
756 regulations following NIH protocols for human experimentation, as reviewed and approved
757 periodically by the Caltech Administrative Committee for the Protection of Human Subjects
758 (Caltech IRB, protocols 13-0420, 17-0706, and 17-0734). All methods were carried out in
759 accordance with relevant guidelines and regulations. Informed consent using forms approved by
760 the Institutional Review Board was obtained from all subjects. No subjects under the age of 18
761 were used in these experiments.

762

763 **1. Magnetic Exposure Facility.** We constructed a six-sided Faraday cage shown in Figs. 1 and
764 5 out of aluminum, chosen because of: (1) its high electrical conductivity, (2) low cost and (3)
765 lack of ferromagnetism. The basic structure of the cage is a rectangular 2.44 m x 2.44 m x 2.03
766 m frame made of aluminum rods, 1.3 cm by 1.3 cm square in cross-section, shown in Fig. 5A.
767 Each of the cage surfaces (walls, floor and ceiling) have four rods (two vertical and two
768 horizontal) bounding the perimeter of each sheet. On the cage walls three vertical rods are
769 spaced equally along the inside back of each surface, and on the floor and ceiling three
770 horizontal rods are similarly spaced, forming an inwards-facing support frame. This frame
771 provides a conductive chassis on which overlapping, 1 mm thick aluminum sheets (2.44 m long
772 and 0.91 m wide) were attached using self-threading aluminum screws at ~0.60 m intervals with
773 large overlaps between each sheet. In addition, we sealed the seams between separate aluminum
774 panels with conductive aluminum tape. The access door for the cage is a sheet of aluminum that
775 is fastened with a 2.4 m long aluminum hinge on the East-facing wall such that it can swing
776 away from the cage and provide an entrance/exit. Aluminum wool has been affixed around the
777 perimeter of this entrance flap to provide a conductive seal when the flap is lowered (e.g. the
778 cage is closed). Ventilation is provided via a ~3 m long, 15 cm diameter flexible aluminum tube
779 (Fig. 5E) that enters an upper corner of the room and is connected to a variable-speed ceiling-
780 mounted fan set for a comfortable but quiet level of airflow. The end of the tube in contact with
781 the Faraday cage is packed loosely with aluminum wool that allows air to pass and provides
782 electrical screening. LED light strips (Fig. 5H) provide illumination for entrance and exit. These
783 lights are powered by a contained lithium ion battery housed in an aluminum container attached

784 at the top end of the Faraday cage, adjacent to the entrance of the ventilation air duct (seen as the
785 red battery in Fig. 5E).

786 In all experiment sessions, power to the lights was switched off. A small USB-powered
787 infrared camera and microphone assembly (Fig. 5G) mounted just inside the cage on the North
788 wall allows audiovisual monitoring of participants inside the room. Instructions to the
789 participants are given from a pair of speakers mounted outside the Faraday cage (Fig. 5F),
790 controlled remotely by experimenters and electrically shorted by a computer-controlled TTL
791 relay when not in use. Acoustic foam panels are attached to the vertical walls to dampen echoes
792 within the chamber as well as to reduce the amplitude of external sound entering the chamber.
793 To complete the Faraday shielding, we grounded the cage permanently at one corner with a 2.6
794 mm diameter (10 AWG) copper wire connected to the copper plumbing in the sub-basement of
795 the building. RMS noise measurements from the cage interior using a Schwarzbeck Mess™
796 Elektronik FMZB 1513 B-component active loop Rf antenna, a RIGOL™ DSA815/E-TG
797 spectrum analyzer, and a Tektronix™ RSA503A signal analyzer indicated residual noise
798 interference below 0.01 nT, in the frequency range from 9 kHz to 10 MHz.

799 Electrical cables entering the Faraday cage pass through a side gap in the aluminum
800 ventilation duct and then through the aluminum wool. Rf interference is blocked further on all
801 electrical cables entering the room using pairs of clip-on ferrite chokes (Fair-Rite™ material #75,
802 composed of MnZn ferrite, designed for low-frequency EMI suppression, referred from here-on
803 as ferrite chokes) and configured where possible using the paired, multiple-loop “pretty-good
804 choke” configuration described by Counselman (Counselman, 2013) (Fig. 5I). Inside the
805 shielded space are located a three-axis set of square coils approximately 2 m on edge following
806 the Merritt *et al.* four-coil design (Merritt et al., 1983) (using the 59/25/25/59 coil winding ratio)
807 that provides remarkably good spatial uniformity in the applied magnetic field (12 coils total,
808 four each in the North/South, East/West, and Up/Down orientations as seen in Fig. 5A). The
809 coils are double-wrapped inside grounded aluminum U-channels following a design protocol that
810 allows for full active-field and sham exposures (J.L Kirschvink, 1992); they were constructed by
811 Magnetic Measurements, Ltd., of Lancashire, U.K. (<http://www.magnetic-measurements.com>).
812 This double-wrapped design gives a total coil winding count of 118/50/50/118 for all three-axes
813 coil sets.

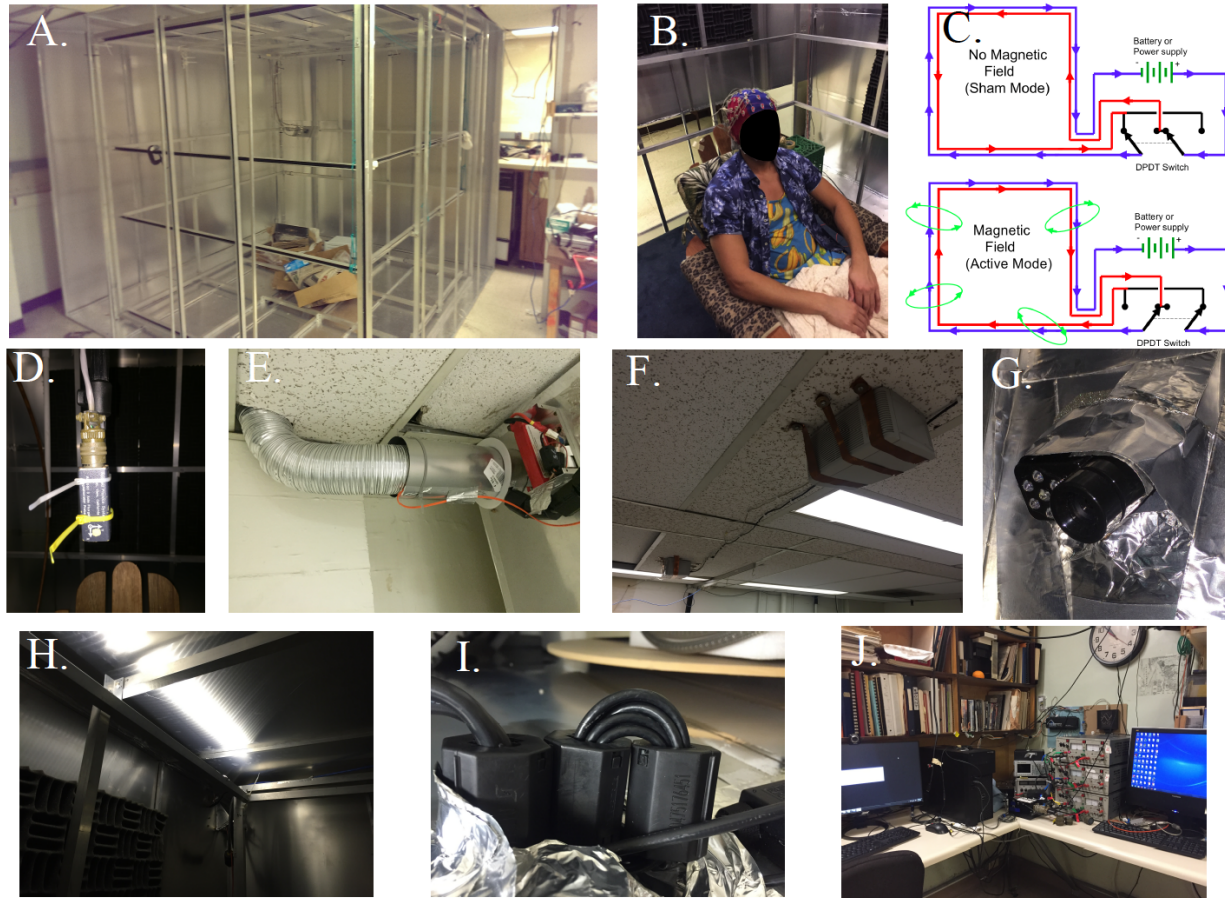
814 To provide a working floor isolated from direct contact with the coils, we suspended a
815 layer of ~2 cm thick plywood sheets on a grid work of ~ 10 x 10 cm thick wooden beams that
816 rested on the basal aluminum plate of the Faraday shield that are held together with brass screws.
817 We covered this with a layer of polyester carpeting on top of which we placed a wooden
818 platform chair for the participants (Fig. 5B). Non-magnetic bolts and screws were used to fasten
819 the chair together, and a padded foam cushion was added for comfort. The chair is situated such
820 that the head and upper torso of most participants fit well within the ~1 m³ volume of highly
821 uniform magnetic fields produced by the coil system (J.L Kirschvink, 1992) while keeping the
822 participants a comfortable distance away from direct contact with the Merritt coils.

823 We suspended the three-axis probe of a fluxgate magnetometer (Applied Physics
824 Systems™ model 520A) on a non-magnetic, carbon-fiber, telescoping camera rod suspended
825 from the ceiling of the Faraday cage (Fig. 5D). This was lowered into the center of the coil
826 system for initial calibration of field settings prior to experiments and then raised to the edge of
827 the uniform field region to provide continuous recording of the magnetic field during
828 experiments. Power cables for the coils and a data cable for the fluxgate sensor pass out of the
829 Faraday cage through the ventilation shaft, through a series of large Rf chokes (Counselman,
830 2013), a ceiling utility chase in the adjacent hallway, along the wall of the control room, and
831 finally down to the control hardware. The control hardware and computer are located ~20 m
832 away from the Faraday cage through two heavy wooden doors and across a hallway that serve as
833 effective sound dampeners such that participants are unable to directly hear the experimenters or
834 control equipment and the experimenters are unable to directly hear the participant.

835 In the remote-control room, three bipolar power amplifiers (Kepco™ model BOP-100-
836 1MD) control the electric power to the coil systems (Fig. 5J) and operate in a mode where the
837 output current is regulated proportional to the control voltage, thereby avoiding a drop in current
838 (and magnetic field) should the coil resistance increase due to heating. Voltage levels for these
839 are generated using a 10k samples per channel per second, 16-bit resolution, USB-controlled,
840 analog output DAQ device (Measurement Computing™ Model USB-3101FS), controlled by the
841 desktop PC. This same PC controls the DC power supply output levels, monitors and records the
842 Cartesian orthogonal components from the fluxgate magnetometer, displays video of the
843 participant (recordings of which are not preserved per IRB requirements), and is activated or
844 shorted, via TTL lines, to the microphone/speaker communication system from the control room

845 to the experimental chamber. As the experimenters cannot directly hear the participant and the
846 participant cannot directly hear the experimenters, the microphone and speaker system are
847 required (as per Caltech Institute Review Board guidelines) to ensure the safety and comfort of
848 the participant as well as to pass instructions to the participant and answer participants' questions
849 before the start of a block of experiments. The three-axis magnet coil system can produce a
850 magnetic vector of up to 100 μ T intensity (roughly 2-3X the background strength in the lab) in
851 any desired direction with a characteristic RL relaxation constant of 79-84 ms (inductance and
852 resistance of the four coils in each axis vary slightly depending on the different coil-diameters
853 for each of the three nested, double-wrapped coil-set axes). Active/Sham mode was selected
854 prior to each run via a set of double-pole-double-throw (DPDT) switches located near the DC
855 power supplies. These DPDT switches are configured to swap the current direction flowing in
856 one strand of the bifilar wire with respect to the other strand in each of the coil sets (J.L
857 Kirschvink, 1992) (Fig. 5C). Fluxgate magnetometer analog voltage levels were digitized and
858 streamed to file via either a Measurement Computing™ USB 1608GX 8-channel (differential
859 mode) analog input DAQ device, or a Measurement Computing™ USB 1616HS-2 multifunction
860 A/D, D/A, DIO DAQ device connected to the controller desktop PC. Fluxgate analog voltage
861 signal levels were sampled at 1024 or 512 Hz. Although the experimenter monitors the
862 audio/video webcam stream of the participants continuously, as per Caltech IRB safety
863 requirements, while they are in the shielded room the control software disconnects the external
864 speakers (in the room that houses the experimental Faraday cage and coils) and shorts them to
865 electrical ground during all runs to prevent extraneous auditory cues from reaching the
866 participants. Light levels within the experimental chamber during experimental runs were
867 measured using a Konica-Minolta CS-100A luminance meter, which gave readings of zero
868 (below $0.01 \pm 2\%$ cd/m^2).

869
870
871
872
873
874
875



876

877 **Fig. 5. Additional images of critical aspects of the human magnetic exposure facility at**
878 **Caltech.** A. Partially complete assembly of the Faraday cage (summer of 2014) showing the
879 nested set of orthogonal, Merritt square four-coils (Merritt et al., 1983) with all but two
880 aluminum walls of the Faraday cage complete. B. Image of a participant in the facility seated in
881 a comfortable, non-magnetic wooden chair and wearing the 64-lead BioSim™ EEG head cap.
882 The EEG sensor leads are carefully braided together to minimize electrical artifacts. The chair is
883 on a raised wooden platform that is isolated mechanically from the magnet coils and covered
884 with a layer of synthetic carpeting; the height is such that the participant's head is in the central
885 area of highest magnetic field uniformity. C. Schematic of the double-wrapped control circuits
886 that allow active-sham experiments (J.L Kirschvink, 1992). In each axis of the coils, the four
887 square frames are wrapped in series with two discrete strands of insulated copper magnet wire
888 and with the number of turns and coil spacing chosen to produce a high-volume, uniform applied
889 magnetic field (Merritt et al., 1983). Reversing the current flow in one of the wire strands
890 via a double-pole-double-throw (DPDT) switch results in cancellation of the external field with
891 virtually all other parameters being the same. This scheme is implemented on all three
892 independently controlled coil axes (Up/Down, East/West and North/South). D. Fluxgate
893 magnetometer (Applied Physics Systems 520A) three-axis magnetic field sensor attached to a
894 collapsing carbon-fiber camera stand mount. At the start of each session the fluxgate is lowered
895 to the center of the chamber for an initial current / control calibration of the ambient geomagnetic
896 field. It is then raised to a position about 30 cm above the participant's head during the

897 following experimental trials, and the three-axis magnetic field readings are recorded
898 continuously in the same fashion as the EEG voltage signals. E. Air duct. A 15 cm diameter
899 aluminum air duct ~2 meters long connects a variable-speed (100 W) electric fan to the upper SE
900 corner of the experimental chamber; this is also the conduit used for the major electrical cables
901 (power for the magnetic coils, sensor leads for the fluxgate, etc.). F. & G. An intercom / video
902 monitoring system was devised by mounting a computer-controlled loudspeaker (F) outside the
903 Faraday shield on the ceiling North of the chamber coupled with (G) a USB-linked IR video
904 camera / microphone system mounted just inside the shield. Note the conductive aluminum tape
905 shielding around the camera to reduce Rf interference. During all experimental trials a small
906 DPDT relay located in the control room disconnects the speaker from computer and directly
907 shorts the speaker connections. A second microphone in the control room can be switched on to
908 communicate with the participant in the experimental chamber, as needed. An experimenter
909 monitors the audio and video of participants at all times, as per Caltech IRB safety requirements.
910 H. LED lights, 12 VDC array, arranged to illuminate from the top surface of the magnetic coils
911 near the ceiling of the chamber. These are powered by rechargeable 11.1 V lithium battery packs
912 (visible in E) and controlled by an external switch. I. Ferrite chokes. Whenever possible, these
913 are mounted in a multiple-turn figure-eight fashion (Counselman, 2013) on all conductive wires
914 and cables entering the shielded area and supplemented with grounded aluminum wool when
915 needed. J. Image of the remote control area including (from left to right): the PC for controlling
916 the coils, the DPDT switches for changing between active and sham modes, the fluxgate control
917 unit, the three power amplifiers that control the current in the remote coil room, and the separate
918 PC that records the EEG data. Participants seated in the experimental chamber do not report
919 being able to hear sounds from the control room and *vice versa*.

920

921

922

923

924

925

926

927

928

929

930

931

932

933

934

935

936 **2. Participants.** Participants were 34 adult volunteers (24 male, 12 female) recruited from the
937 Caltech population. This participant pool included persons of European, Asian, African and
938 Native American descent. Ages ranged from 18 to 68 years. Each participant gave written
939 informed consent of study procedures approved by the Caltech Institutional Review Board
940 (Protocols 13-0420, 17-0706, and 17-0734).

941
942 **3. Experimental Protocol.** In the experiment, participants sat upright in the chair with their
943 eyes closed and faced North (defined as 0° declination in our magnetic field coordinate reference
944 frame). The experimental chamber was dark, quiet and isolated from the control room during
945 runs. Each run was ~ 7 minutes long with up to eight runs in a ~ 1 hour session. The magnetic
946 field was rotated over 100 milliseconds every 2-3 seconds, with constant 2 or 3 s inter-trial
947 intervals in early experiments and pseudo-randomly varying 2-3 s intervals in later experiments.
948 Participants were blind to Active vs. Sham mode, trial sequence and trial timing. During
949 sessions, auditory tones signaled the beginning and end of experiments and experimenters only
950 communicated with participants once or twice per session to update the number of runs
951 remaining. When time allowed, Sham runs were matched to Active runs using the same
952 software settings. Sham runs are identical to Active runs but are executed with the current
953 direction switches set to anti-parallel. This resulted in no observable magnetic field changes
954 throughout the duration of a Sham run with the local, uniform, static field produced by the
955 double-wrapped coil system in cancellation mode (J.L Kirschvink, 1992).

956 Two types of trial sequences were used: (1) a 127-trial Gold Sequence with 63 FIXED
957 trials and 64 SWEEP trials evenly split between two rotations (32 each), and (2) various 150-trial
958 pseudorandom sequences with 50 trials of each rotation interspersed with 50 FIXED trials to
959 balance the number of trials in each of three conditions. All magnetic field parameters were held
960 constant during FIXED trials, while magnetic field *intensity* was held constant during inclination
961 or declination rotations. In inclination experiments (Fig. 2A of the main text), the vertical
962 component of the magnetic field was rotated upwards and downwards between $\pm 55^\circ$, $\pm 60^\circ$, or
963 $\pm 75^\circ$ (Inc.UP and Inc.DN, respectively); data collected from runs with each of these inclination
964 values were collapsed into a single set representative of inclination rotations between steep
965 angles. In each case, the horizontal component was steady at 0° declination (North; Inc.UP.N
966 and Inc.DN.N). Two types of declination experiments were conducted, designed to test the

967 quantum compass and electrical induction hypotheses. As the quantum compass can only
968 determine the axis of the field and not polarity, we compared a pair of declination experiments in
969 which the rotating vectors were swept down to the North (DecDn.N) and up to the South
970 (DecUp.S), providing two symmetrical antiparallel data sets (Fig. 2B of the main text). In the
971 DecDn.N experiments, the vertical component was held constant and downwards at $+60^\circ$ or
972 $+75^\circ$, while the horizontal component was rotated between NE (45°) and NW (315°), along a
973 Northerly arc (DecDn.CW.N and DecDn.CCW.N). In DecUp.S experiments, the vertical
974 component was held upwards at -60° or -75° , while the horizontal component was rotated
975 between SW (225°) and SE (135°) along a Southerly arc (DecUp.CW.S and DecUp.CCW.S).
976 Again, runs with differing inclination values were grouped together as datasets with steep
977 downwards or steep upwards inclination. To test the induction hypothesis, we paired the
978 DecDn.N sweeps with a similar set, DecUp.N, as shown on Fig. 2C. These two conditions only
979 differ in the direction of the vertical field component; rotations were between NE and NW in
980 both experiments (DecDn.CW.N, DecDn.CCW.N, DecUp.CW.N and DecUp.CCW.N). Hence,
981 any significant difference in the magnetosensory response eliminates induction as a mechanism.
982

983 **4. EEG Recording.** EEG was recorded using a BioSemi™ ActiveTwo system with 64
984 electrodes following the International 10-20 System (Nuwer et al., 1998). Signals were sampled
985 at 512 Hz with respect to CMS/DRL reference at low impedance <1 ohm and bandpass-filtered
986 from 0.16-100 Hz. To reduce electrical artifacts induced by the time-varying magnetic field,
987 EEG cables were bundled and twisted 5 times before plugging into a battery-powered BioSemi™
988 analog/digital conversion box. Digitized signals were transmitted over a 30 m, non-conductive,
989 optical fiber cable to a BioSemi™ USB2 box located in the control room ~ 20 m away where a
990 desktop PC (separate from the experiment control system) acquired continuous EEG data using
991 commercial ActiView™ software. EEG triggers signaling the onset of magnetic stimulation
992 were inserted by the experiment control system by connecting a voltage timing signal (0 to 5 V)
993 from its USB-3101FS analog output DAQ device. The timing signal was sent both to the
994 Measurement Computing USB-1608GX (or USB-1616HS-2) analog input DAQ device, used to
995 sample the magnetic field on the experiment control PC and a spare DIO voltage input channel
996 on the EEG system's USB2 DAQ input box, which synchronized the EEG data from the optical
997 cable with the triggers cued by the controlling desktop PC. This provided: (1) a precise

998 timestamp in continuous EEG whenever electric currents were altered (or in the case of FIXED
999 trials, when the electric currents could have been altered to sweep the magnetic field direction,
1000 but were instead held constant) in the experimental chamber, and (2) a precise correlation (± 2
1001 ms, precision determined by the 512 samples per second digital input rate of the BioSemiTM
1002 USB2 box) between fluxgate and EEG data.

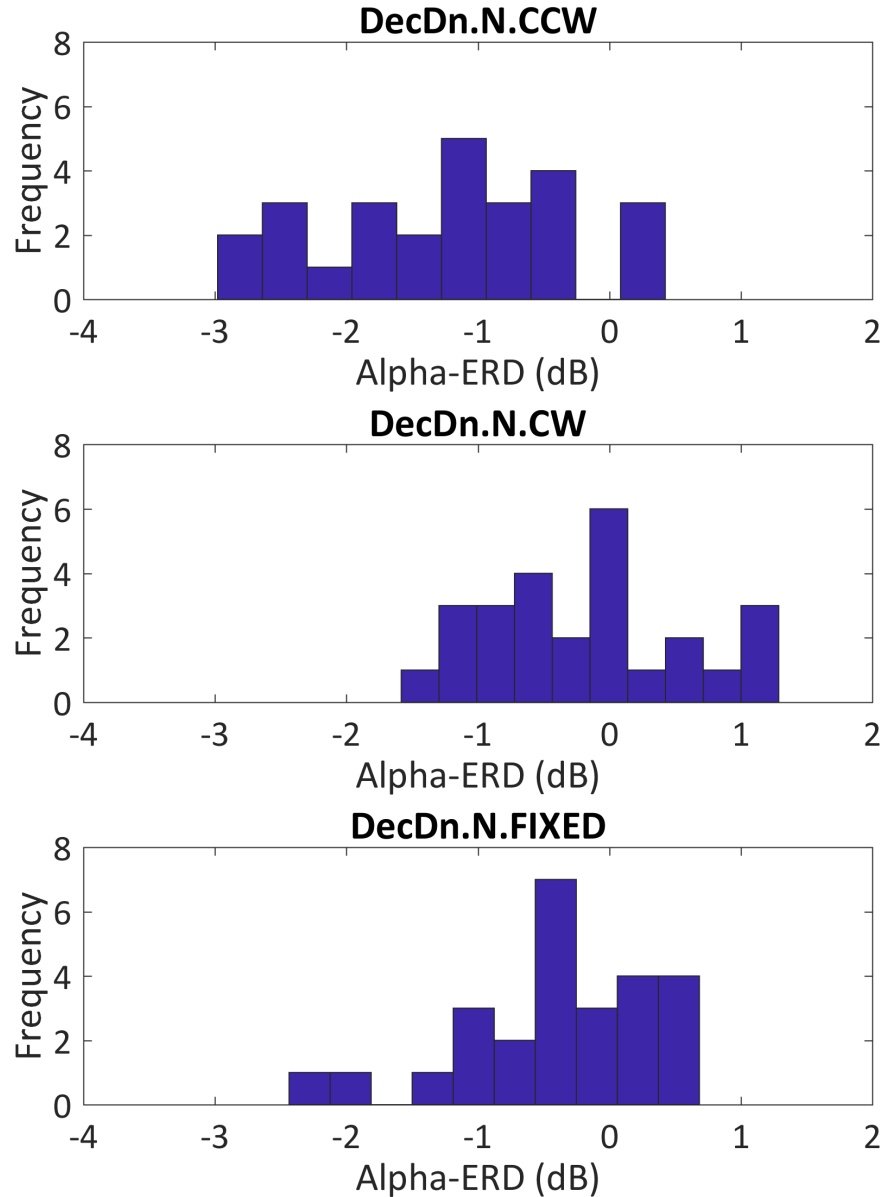
1003
1004 **5. EEG Analysis.** Raw EEG data were extracted using EEGLABTM toolbox for MATLABTM
1005 and analyzed using custom MATLABTM scripts. Trials were defined as 2- or 3-s epochs from
1006 -0.75 s pre-stimulus to $+1.25$ or $+2.25$ s post-stimulus, with a baseline interval from -0.5 s to
1007 -0.25 s pre-stimulus. Time/frequency decomposition was performed for each trial using Fast
1008 Fourier Transform (MATLABTM function *fft*) and Morlet wavelet convolution on 100 linearly-
1009 spaced frequencies between 1 and 100 Hz. Average power in an extended alpha band of 6-14 Hz
1010 was computed for the pre-stimulus and post-stimulus intervals of all trials, and a threshold of
1011 1.5X the interquartile range was applied to identify trials with extreme values of log alpha
1012 power. These trials were excluded from further analysis but retained in the data. After
1013 automated trial rejection, event-related potentials (ERPs) were computed for each condition and
1014 then subtracted from each trial of that condition to reduce the electrical induction artifact that
1015 appeared only during the 100 ms magnetic stimulation interval. This is an established procedure
1016 to remove phase-locked components such as sensory-evoked potentials from an EEG signal for
1017 subsequent analysis of non-phase-locked, time/frequency power representations. Non-phase-
1018 locked power was computed at midline frontal electrode Fz for each trial and then averaged and
1019 baseline-normalized for each condition to generate a time/frequency map from -0.25 s pre-
1020 stimulus to $+1$ s or $+2$ s post-stimulus and 1-100 Hz. To provide an estimate of overall alpha
1021 power for each participant, power spectral density was computed using Welch's method
1022 (MATLABTM function *pwelch*) at 0.5 Hz frequency resolution (Welch, 1967).

1023 From individual datasets, we extracted post-stimulus alpha power to test for statistically
1024 significant differences amongst conditions at the group level. Because alpha oscillations vary
1025 substantially across individuals in amplitude, frequency and stimulus-induced changes, an
1026 invariant time/frequency window would not capture stimulus-induced power changes in many
1027 participants. In our dataset, individual alpha oscillations ranged in frequency (8 to 12 Hz peak
1028 frequency), and individual alpha-ERD responses started around $+0.25$ to $+0.75$ s post-stimulus.

1029 Thus, we quantified post-stimulus alpha power within an automatically-adjusted time/frequency
1030 window for each dataset. First, non-phase-locked alpha power between 6-14 Hz was averaged
1031 over all trials regardless of condition. Then, the most negative time/frequency point was
1032 automatically selected from the post-stimulus interval between 0 s and +1 or +2 s in this cross-
1033 conditional average. The selected point represented the maximum alpha-ERD in the average over
1034 all trials with no bias for any condition. A time/frequency window of 0.25 s and 5 Hz was
1035 centered (as nearly as possible given the limits of the search range) over this point to define an
1036 individualized timing and frequency of alpha-ERD for each dataset. Within the window, non-
1037 phase-locked alpha power was averaged across trials and baseline-normalized for each condition,
1038 generating a value of alpha-ERD for each condition to be compared in statistical testing.

1039 In early experiments, trial sequences were balanced with nearly equal numbers of FIXED
1040 (63) and SWEEP (64) trials, with an equal number of trials for each rotation (e.g. 32 Inc.DN and
1041 32 Inc.UP trials). Later, trial sequences were designed to balance the number of FIXED trials
1042 with the number of trials of each rotation (e.g. 50 DecDn.FIXED, 50 DecDn.CCW, and 50
1043 DecDn.CW trials). Alpha-ERD was computed over similar numbers of trials for each condition.
1044 For example, when comparing alpha-ERD in the FIXED vs. CCW vs. CW conditions of a
1045 declination experiment with 63 FIXED (32 CCW and 32 CW trials) 100 samplings of 32 trials
1046 were drawn from the pool of FIXED trials, alpha-ERD was averaged over the subset of trials in
1047 each sampling, and the average over all samplings was taken as the alpha-ERD of the FIXED
1048 condition. When comparing FIXED vs. SWEEP conditions of an inclination experiment with 50
1049 FIXED, 50 DN, and 50 UP trials, 200 samplings of 25 trials were drawn from each of the DN
1050 and UP conditions and the average alpha-ERD over all samplings taken as the alpha-ERD of the
1051 SWEEP condition. Using this method, differences in experimental design were reduced,
1052 allowing statistical comparison of similar numbers of trials in each condition. The alpha-ERD
1053 values for each participant in each condition are shown as histograms for the DecDn (Fig. 6),
1054 DecUp (Fig. 7), and Sham declination (Fig. 8) experiments. These values were used in statistical
1055 testing at the group level.

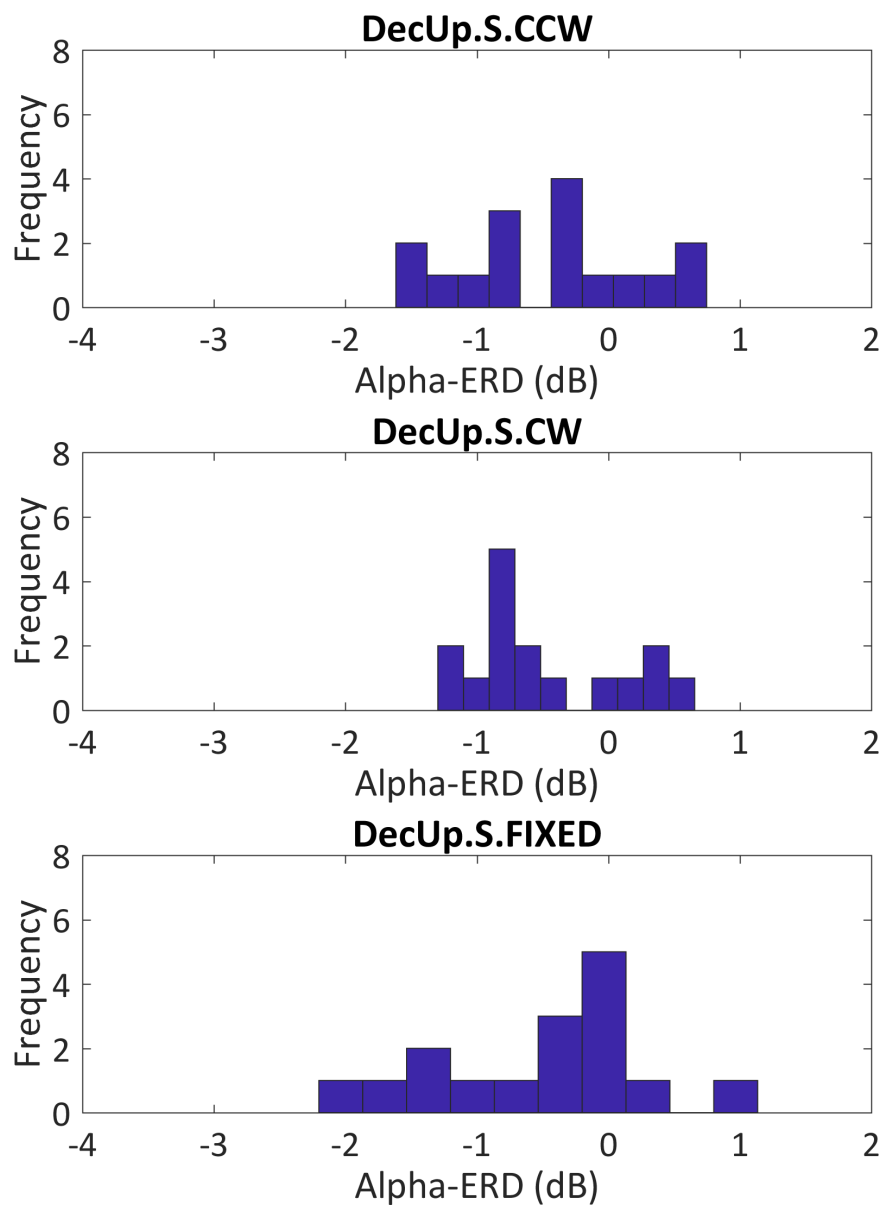
1056
1057
1058
1059



1060

1061 **Fig. 6.** Histogram of alpha-ERD responses over all participants (N=26) in the DecDn
1062 experiment. The panels show the histogram of individual responses for each condition.
1063 Frequency is given in number of participants. Because we looked for a drop in alpha power
1064 following magnetic stimulation, the histograms are shifted towards negative values in all
1065 conditions. The CCW condition shows the most negative average in a continuous distribution of
1066 participant responses, with the most participants having a >2 dB response.
1067

1068



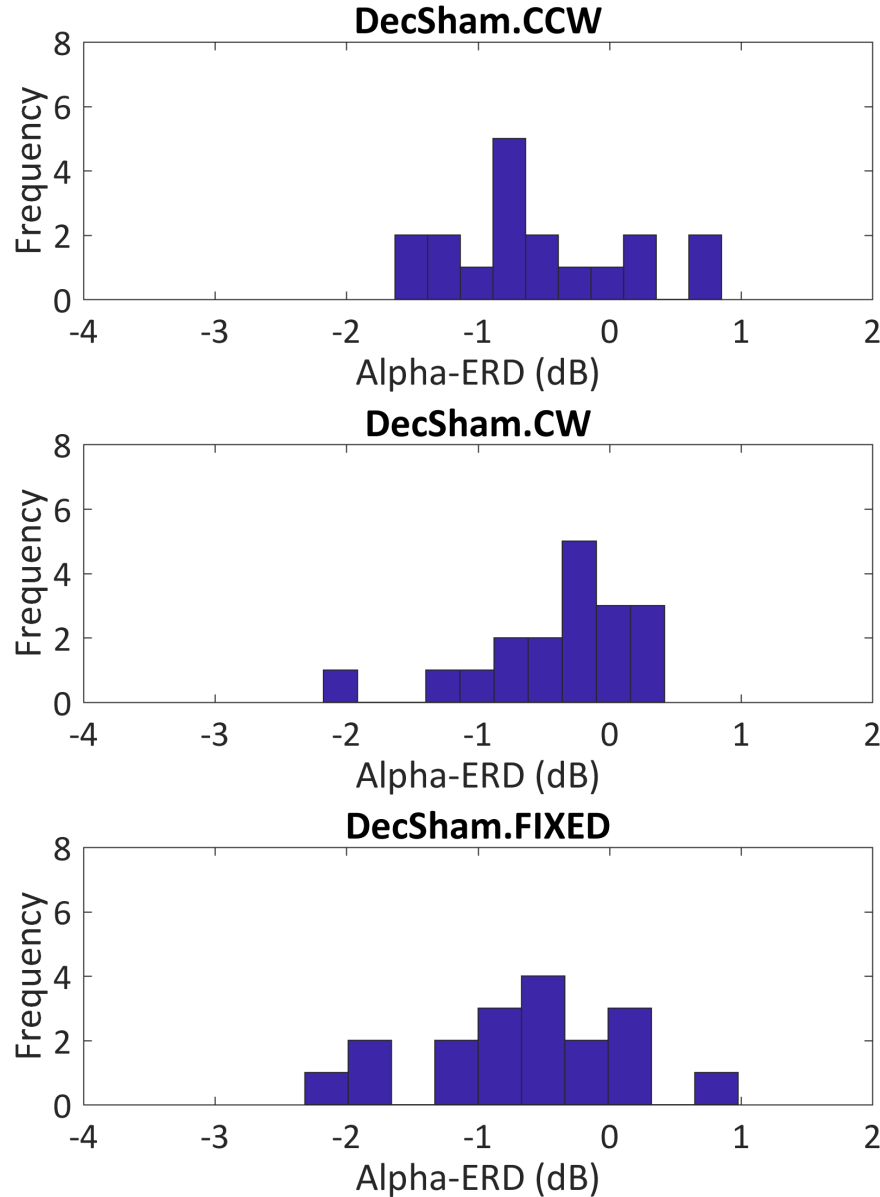
1069

1070 **Fig. 7.** Histogram of alpha-ERD responses over all participants (N=16) in the DecUp
1071 experiment. The panels show the histogram of individual responses for each condition. No
1072 significant magnetosensory response was observed in any condition, and no clear difference is
1073 apparent between the three distributions.

1074

1075

1076



1077

1078 **Fig. 8.** Histogram of alpha-ERD responses over all participants (N=18) in the Sham Declination
1079 experiment. The panels show the histogram of individual responses for each condition. No
1080 significant magnetosensory response was observed in any condition, and no clear difference is
1081 apparent between the three distributions.

1082

1083

1084 Three statistical tests were performed using average alpha-ERD: (1) Inc ANOVA
1085 (N=29), (2) DecDn ANOVA (N=26), (3) DecDn/DecUp ANOVA (N=16). For the inclination
1086 experiment, data were collected in Active and Sham modes for 29 of 34 participants. Due to
1087 time limitations within EEG sessions, sham data could not be collected for every participant, so
1088 those participants without inclination sham data were excluded. A two-way repeated-measures
1089 ANOVA tested for the effects of inclination rotation (SWEEP vs. FIXED) and magnetic
1090 stimulation (Active vs. Sham) on alpha-ERD. Post-hoc testing using the Tukey-Kramer method
1091 compared four conditions (Active-SWEEP, Active-FIXED, Sham-SWEEP and Sham-FIXED)
1092 for significant differences (Tukey, 1949).

1093 For the DecDn experiment, data were collected from 26 participants in Active mode. A
1094 one-way repeated-measures ANOVA tested for the effect of declination rotation (DecDn.CCW
1095 vs. DecDn.CW vs. DecDn.FIXED) with post-hoc testing to compare these three conditions. For
1096 a subset of participants (N=16 of 26), data was collected from both DecDn and DecUp
1097 experiments. The DecUp experiments were introduced in a later group to evaluate the quantum
1098 compass mechanism of magnetosensory transduction, as well as in a strongly-responding
1099 individual to test the less probable induction hypothesis, as shown in Video 1. For tests of the
1100 quantum compass hypothesis, we used the DecDn/DecUp dataset. A two-way repeated-measures
1101 ANOVA tested for the effects of declination rotation (DecDn.CCW.N vs. DecDn.CW.N vs.
1102 DecUp.CCW.S vs. DecUp.CW.S vs. DecDn.FIXED.N vs. DecUp.FIXED.S) and inclination
1103 direction (Inc.DN.N vs Inc.UP.S) on alpha-ERD; data from another strongly-responding
1104 individual is shown in Video 2. Post-hoc testing compared six conditions (DecDn.CCW.N,
1105 DecDn.CW.N, DecDn.FIXED.N, DecUp.CCW.S, DecUp.CW.S and DecUp.FIXED.S).

1106 Within each group, certain participants responded strongly with large alpha-ERD while
1107 others lacked any response to the same rotations. To establish whether a response was consistent
1108 and repeatable, we tested individual datasets for significant post-stimulus power changes in
1109 time/frequency maps between 0 to +2 or +3 s post-stimulus and 1-100 Hz. For each dataset,
1110 1000 permutations of condition labels over trials created a null distribution of post-stimulus
1111 power changes at each time/frequency point. The original time/frequency maps were compared
1112 with the null distributions to compute a p-value at each point. False discovery rate correction for
1113 multiple comparisons was applied to highlight significant post-stimulus power changes at the
1114 $p < 0.05$ and $p < 0.01$ statistical thresholds (Benjamini & Hochberg, 1995). Fig. 9 shows repeated

1115 runs (Run #1 and Run #2) of two different participants (A and B) in the DecDn experiment. The
1116 outlined clusters indicate significant power changes following magnetic field rotation. In each
1117 case, the significant clusters are similar in timing and bandwidth across runs up to six months
1118 apart.

1119

1120

1121

1122

1123

1124

1125

1126

1127

1128

1129

1130

1131

1132

1133

1134

1135

1136

1137

1138

1139

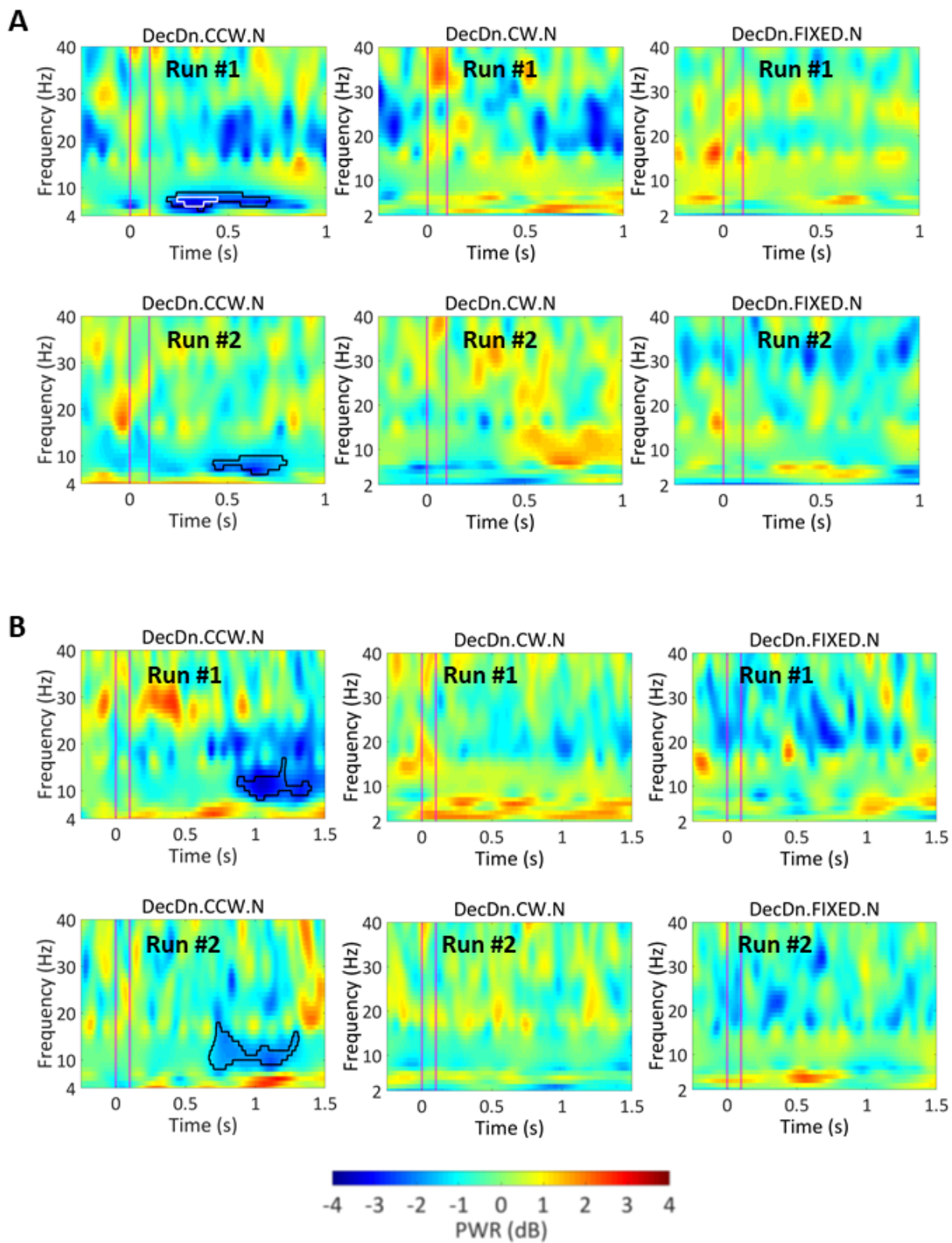
1140

1141

1142

1143

1144



1146 **Fig. 9.** Repeated results from two strongly-responding participants. In both (A) and (B),
1147 participants were tested weeks or months apart under the same conditions (Run #1 and Run #2).
1148 Time/frequency maps show similar timing and bandwidth of significant alpha power changes
1149 (blue clusters in outlines) after counterclockwise rotation, while activity outside the alpha-ERD
1150 response, and activity in other conditions is inconsistent across runs. Black/white outlines
1151 indicate significance at the $p < 0.05$ and $p < 0.01$ thresholds. The participant in (A) had an alpha
1152 peak frequency at < 9 Hz and a lower-frequency alpha-ERD response. The participant in (B) had
1153 an alpha peak frequency > 11 Hz and a higher-frequency alpha-ERD response. Minor power
1154 fluctuations in the other conditions or in different frequency bands were not repeated across runs,
1155 indicating that only the alpha-ERD was a repeatable signature of magnetosensory processing.

1156
1157 **Video 1.** Test of the electrical induction mechanism of magnetoreception using data from a
1158 participant with a strong, repeatable alpha-ERD magnetosensory response. Bottom row shows
1159 the DecDn.CCW.N, DecDn.CW.N and DecDn.FIXED.N conditions (64 trials per condition) of
1160 the DecDn.N experiment; top row shows the corresponding conditions for the DecUp.N
1161 experiment. Scalp topography changes from -0.25 s pre-stimulus to $+1$ s post-stimulus. The
1162 CCW rotation of a downwards-directed field (DecDn.CCW.N) caused a strong, repeatable alpha-
1163 ERD (lower left panel, $p < 0.01$ at Fz); weak alpha power fluctuations observed in other
1164 conditions (DecDn.CW.N, DecDn.FIXED.N, DecUp.CW.N, DecUp.CCW.N and
1165 DecUp.FIXED.N) were not consistent across multiple runs of the same experiment. If the
1166 magnetoreception mechanism is based on electrical induction, the same response should occur in
1167 conditions with identical $\partial \mathbf{B} / \partial t$ (DecDn.CCW.N and DecUp.CCW.N), but the response was
1168 observed only in one of these conditions: a result that contradicts the predictions of the electrical
1169 induction hypothesis.

1170
1171 **Video 2.** Test of the quantum compass mechanism of magnetoreception using data from
1172 another strongly-responding participant. Bottom vs. top rows compare the DecDn.N and
1173 DecUp.S experiments in the CCW, CW and FIXED conditions (DecDn.CCW.N, DecDn.CW.N,
1174 DecDn.FIXED.N, DecUp.CW.S, DecUp.CCW.S and DecUp.FIXED.S with 100 trials per
1175 condition). The quantum compass is not sensitive to magnetic field polarity, so magnetosensory
1176 responses should be identical for the DecDn.CCW.N and DecUp.CCW.S rotations sharing the
1177 same axis. Our results contradict this prediction. A significant, repeatable alpha-ERD is only
1178 observed in the DecDn.CCW.N condition (lower left panel, $p < 0.01$ at Fz), with no strong,
1179 consistent effects in the DecUp.CCW.S condition (top left panel) or any other condition.

1180

1181

1182

1183

1184 **Extended Discussion**

1185

1186 **6. Controlling for Magnetomechanical Artifacts.** A question that arises in all studies of
1187 human perception is whether confounding artifacts in the experimental system produced the
1188 observed effects. The Sham experiments using double-wrapped, bonded coil systems controlled
1189 by remote computers and power supplies indicate that obvious artifacts such as resistive
1190 warming of the wires or magnetomechanical vibrations between adjacent wires are not
1191 responsible. In Active mode, however, magnetic fields produced by the coils interact with each
1192 other with maximum torques occurring when the moment \mathbf{u} of one coil set is orthogonal to the
1193 field \mathbf{B} of another (torque = $\mathbf{u} \times \mathbf{B}$). Hence, small torques on the coils might produce transient,
1194 sub-aural motion cues. Participants might detect these cues subconsciously even though the coils
1195 are anchored to the Faraday cage at many points; the chair and floor assemblies are mechanically
1196 isolated from the coils; the experiments are run in total darkness, and the effective frequencies of
1197 change are all below 5 Hz and acting for only 0.1 second. No experimenters or participants ever
1198 claimed to perceive field rotations consciously even when the cage was illuminated and efforts
1199 were made to consciously detect the field rotations. Furthermore, the symmetry of the field
1200 rotations and the asymmetric nature of the results both argue strongly against this type of artifact.
1201 During the declination experiments, for example, the vertical component of the magnetic field is
1202 held constant while a constant-magnitude horizontal component is rotated 90° via the N/S and
1203 E/W coil axes. Hence, the torque pattern produced by DecDn.CCW.N rotations should be
1204 identical to that of the DecUp.CW.S rotations, yet these conditions yielded dramatically different
1205 results. We conclude that magnetomechanical artifacts are not responsible for the observed
1206 responses.

1207

1208 **7. Testing for Artifacts or Perception from Electrical Induction.** Another source of artifacts
1209 might be electrical eddy currents induced during field sweeps that might stimulate subsequent
1210 EEG brain activity in the head or perhaps in the skin or scalp adjacent to EEG sensors. Such
1211 artifacts would be hard to distinguish from a magnetoreceptive structure based on electrical
1212 induction. For example, the alpha-ERD effects might arise via some form of voltage-sensitive
1213 receptor in the scalp subconsciously activating sensory neurons and transmitting information to
1214 the brain for further processing. However, for any such electrical induction mechanism the

1215 Maxwell-Faraday law holds that the induced electric field \mathbf{E} is related to the magnetic field
1216 vector, $\mathbf{B}(t)$, by:

1217

$$1218 \quad \nabla \times \mathbf{E} = -\partial\mathbf{B}(t)/\partial t \quad (1).$$

1219

1220 During a declination rotation, the field vector $\mathbf{B}(t)$ is given by: $\mathbf{B}(t) = \mathbf{B}_V + \mathbf{B}_H(t)$, where \mathbf{B}_V is
1221 the constant vertical field component, t is time, $\mathbf{B}_H(t)$ is the rotating horizontal component, and
1222 the quantities in **bold** are vectors. Because the derivative of a constant is zero, the static vertical
1223 vector \mathbf{B}_V has no effect, and the induced electrical effect depends only on the horizontally-
1224 rotating vector, $\mathbf{B}_H(t)$:

1225

$$1226 \quad \nabla \times \mathbf{E} = -\partial\mathbf{B}_V/\partial t - \partial\mathbf{B}_H(t)/\partial t = -\partial\mathbf{B}_H(t)/\partial t \quad (2).$$

1227

1228 As noted in the main text, Video 1 shows results for the induction test shown in Fig. 2C
1229 for which the sweeps of the horizontal component are identical, going along a 90° arc between
1230 NE and NW (DecDn.CCW.N and DecUp.CCW.N). The two trials differ only by the direction of
1231 the static vertical vector, \mathbf{B}_V , which is held in the downwards orientation for the bottom row of
1232 Video 1 and upwards in the top row. As only the DecDn.CCW.N sweep elicits alpha-ERD, and
1233 the DecUp.CCW.N sweep does not elicit alpha-ERD, electrical induction cannot be the
1234 mechanism for this effect either via some artifact of the EEG electrodes or an intrinsic
1235 anatomical structure.

1236 We also ran additional control experiments on “EEG phantoms,” which allow us to
1237 isolate the contribution of environmental noise and equipment artifacts. Typical setups range
1238 from simple resistor circuits to fresh human cadavers. We performed measurements on two
1239 commonly-used EEG phantoms: a bucket of saline, and a cantaloupe. From these controls, we
1240 isolated the electrical effects induced by magnetic field rotations. The induced effects were
1241 similar to the artifact observed in human participants during the 100 ms magnetic stimulation
1242 interval. In cantaloupe and in the water-bucket controls, no alpha-ERD responses were observed
1243 in Active or Sham modes suggesting that a brain is required to produce a magnetosensory
1244 response downstream of any induction artifacts in the EEG signal.

1245

1246 **8. Non-polar magnetoreceptivity (attributed to birds) cannot explain the present data.**

1247 Birds and some other animals display a magnetic inclination compass that identifies the
1248 steepest angle of magnetic field dip with respect to gravity (R. Wiltschko & W. Wiltschko, 1995;
1249 W. Wiltschko, 1972), and as noted earlier this compass can operate at dips as shallow as 5° from
1250 horizontal (Schwarze et al., 2016). This allows a bird to identify the direction of the closest pole
1251 (North or South) without knowing the polarity of the magnetic field. If a bird knows it is in the
1252 (e.g.) Northern Hemisphere, it can use this maximum dip to identify the direction of geographic
1253 North. However, this mechanism could not distinguish between the antipodal (vector opposite)
1254 fields used in our biophysical test of polarity sensitivity. If we create a field with magnetic north
1255 down and to the front, the bird would correctly identify North as forward. However, if we point
1256 magnetic north up and to the back, the bird would still identify North as forward because that is
1257 the direction of maximum dip.

1258 Because magnetism and gravity are distinct, non-interacting forces of nature, the
1259 observed behavior must arise from neural processing of sensory information from separate
1260 transduction mechanisms (J. L. Kirschvink et al., 2010). If polarity information is not present
1261 initially from a magnetic transducer or lost in subsequent neural processing, it cannot be
1262 recovered by adding information from other sensory modalities. As an illustration, if we gave
1263 our participants a compass with a needle that did not have its North tip marked, they could not
1264 distinguish the polarity of an applied magnetic field even if we gave them a gravity pendulum or
1265 any other non-magnetic sensor.

1266 At present our experimental results in humans suggest the combination of a magnetic and
1267 a positional cue. However, we cannot tell if this positional cue is a reference frame using gravity
1268 or one aligned with respect to the human body. This could perhaps be addressed by modifying
1269 the test chamber to allow the participant to rest in different orientations with respect to gravity.

1270
1271 **9. Sastre *et al.* EEG Study.** Our results perhaps shed light on a previous study attempting to
1272 detect the presence of a low-frequency magnetic stimulus on human brainwaves, which found no
1273 significant effects. As part of a major initiative to investigate possible electromagnetic effects on
1274 cancer by the US National Institute of Health and the Department of Energy during the 1990's,
1275 Sastre *et al.* (Sastre et al., 2002) analyzed EEG signals for power changes in several frequency
1276 bands averaged over 4 s intervals before and after changes in the background magnetic field.

1277 However, they did not do the time/frequency analysis that we report here nor averaging of
1278 repeated rotations over many trials; wavelet methods were not used as frequently at that time.
1279 To test the impact of these differences in data analysis algorithms, we analyzed our data using
1280 the techniques in Sastre *et al.* These analyses did not reveal any significant differences in total or
1281 band-specific power between any conditions. Thus, our results are consistent with previous
1282 findings.

1283 Other differences between our studies lie in the stimulation parameters. In four of seven
1284 conditions from Sastre *et al.* (A, B, C and D), the field intensities used (90 μ T) were twice as
1285 strong as the ambient magnetic field in Kansas City (45 μ T) and were well above intensity
1286 alterations known to cause birds to ignore geomagnetic cues (W. Wiltschko, 1972).
1287 Additionally, Sastre *et al.* chose to use clockwise but not counterclockwise rotations (conditions
1288 B and C). In our study, rotating the declination clockwise did not yield statistically significant
1289 effects although the reasons are not yet understood (Table 1).

1290
1291

1292 **Acknowledgements.** This work was supported directly by Human Frontiers Science Program
1293 grant HFSP-RGP0054/2014 to S.S., J.L.K. and A.M., and more recent analysis of data was
1294 supported by DARPA RadioBio Program grant (D17AC00019) to JLK and SS, and Japan
1295 Society for the Promotion of Science (JSPS) KAKENHI grant 18H03500 to AM. Previous
1296 support to J.L.K. from the Fetzer institute allowed construction of an earlier version of the 2 m
1297 Merritt coil system. C.X.W. and S.S. have been partly supported by JST.CREST. We thank
1298 Dragos Harabor, James Martin, Kristján Jónsson, Mara Green and Sarah Crucilla for work on
1299 earlier versions of this project and other members of the Kirschvink, Shimojo, and Matani labs
1300 for discussions and suggestions. We also thank James Randi, co-founder of the Committee for
1301 the Scientific Investigation of Claims of the Paranormal (CSICOP), for advice on minimizing
1302 potential artifacts in the experimental design. Dr. Heinrich Mouritsen of the University of
1303 Oldenberg gave valuable advice for construction of the Faraday cage and input on an earlier draft
1304 of the manuscript.

1305

1306 **Author Contributions.** J.L.K. initiated, and with S.S. and A.M., planned and directed the
1307 research. C.X.W., D.A.W. and I.A.H. largely designed the stimulation protocols and conducted

1308 the experiments and data analysis. C.P.C., J.N.H.A., S.E.B. and Y.M. designed and built the
1309 Faraday cage and implemented the magnetic stimulation protocols. All authors contributed to
1310 writing and editing the manuscript.

1311
1312 **Online Content:** All digital data are available at <https://data.caltech.edu/records/930> and
1313 <https://data.caltech.edu/records/931> , including MatLab™ scripts used for the automatic data
1314 analysis.

1315
1316 **References**

- 1317
1318 Able, K. P., & Gergits, W. F. (1985). Human Navigation: Attempts to Replicate Baker's
1319 Displacement Experiment. In J. L. Kirschvink, D. S. Jones, & B. J. MacFadden (Eds.),
1320 *Magnetite Biomineralization and Magnetoreception in Organisms: A New*
1321 *Biomagnetism* (pp. 569-572). New York: Plenum Press.
1322 Baker, R. R. (1980). Goal orientation by blindfolded humans after long-distance
1323 displacement: possible involvement of a magnetic sense. *Science*, *210*(4469), 555-
1324 557.
1325 Baker, R. R. (1982). *Human navigation and the 6th sense*: Simon and Schuster.
1326 Baker, R. R. (1987). Human Navigation and Magnetoreception - the Manchester
1327 Experiments Do Replicate. *Animal Behaviour*, *35*, 691-704. doi:Doi 10.1016/S0003-
1328 3472(87)80105-7
1329 Bazylinski, D. A., Schlezinger, D. R., Howes, B. H., Frankel, R. B., & Epstein, S. S. (2000).
1330 Occurrence and distribution of diverse populations of magnetic protists in a
1331 chemically stratified coastal salt pond. *Chemical Geology*, *169*(3-4), 319-328. doi:Doi
1332 10.1016/S0009-2541(00)00211-4
1333 Beason, R. C., & Semm, P. (1996). Does the avian ophthalmic nerve carry magnetic
1334 navigational information? *Journal of Experimental Biology*, *199*(5), 1241-1244.
1335 Beason, R. C., Wiltschko, R., & Wiltschko, W. (1997). Pigeon homing: Effects of magnetic
1336 pulses on initial orientation. *Auk*, *114*(3), 405-415. doi:Doi 10.2307/4089242
1337 Benjamini, Y., & Hochberg, Y. (1995). Controlling the False Discovery Rate - a Practical and
1338 Powerful Approach to Multiple Testing. *Journal of the Royal Statistical Society Series*
1339 *B-Methodological*, *57*(1), 289-300.
1340 Block, S. M. (1992). Biophysical Aspects of Sensory Transduction. In D. P. Corey & S. D.
1341 Roper (Eds.), *Sensory Transduction* (Vol. 45, pp. 424). Marine Biological Laboratory,
1342 Woods Hole, Massachusetts: Rockfeller University Press.
1343 Boorman, G. A., Bernheim, N. J., Galvin, M. J., Newton, S. A., Parham, F. M., Portier, C. J., &
1344 Wolfe, M. S. (1999). *NIEHS Report on Health Effects from Exposure to Power-Line*
1345 *Frequency Electric and Magnetic Fields* (NIEHS Ed. Vol. 99-4493). Research Triangle
1346 Park, NC 27709: Department of Health & Humn Services, US Government.
1347 Carporzen, L., Weiss, B. P., Gilder, S. A., Pommier, A., & Hart, R. J. (2012). Lightning
1348 remagnetization of the Vredefort impact crater: No evidence for impact-generated

- 1349 magnetic fields. *Journal of Geophysical Research-Planets*, 117. doi:Artn E01007
1350 10.1029/2011je003919
- 1351 Cohen, M. X. (2014). *Analyzing Neural Time Series Data Theory and Practice Preface*.
1352 Cambridge, Massachusetts: MIT Press.
- 1353 Counselman, C. (2013). Excellent, Easy, Cheap Common-Mode Chokes. *National Contest*
1354 *Journal of the American Radio Relay League*, 41(1), 3-5.
- 1355 Diaz Ricci, J. C., & Kirschvink, J. L. (1992). Magnetic domain state and coercivity predictions
1356 for biogenic greigite (Fe₃S₄): A comparison of theory with magnetosome
1357 observations. *J. Geophys. Res.*, 97, 17309-17315.
- 1358 Diebel, C. E., Proksch, R., Green, C. R., Neilson, P., & Walker, M. M. (2000). Magnetite defines
1359 a vertebrate magnetoreceptor. *Nature*, 406(6793), 299-302. doi:10.1038/35018561
- 1360 Dunn, J. R., Fuller, M., Zoeger, J., Dobson, J., Heller, F., Hammann, J., . . . Moskowitz, B. M.
1361 (1995). Magnetic material in the human hippocampus. *Brain Res Bull*, 36(2), 149-
1362 153.
- 1363 Eder, S. H., Cadiou, H., Muhamad, A., McNaughton, P. A., Kirschvink, J. L., & Winklhofer, M.
1364 (2012). Magnetic characterization of isolated candidate vertebrate magnetoreceptor
1365 cells. *Proc Natl Acad Sci U S A*, 109(30), 12022-12027.
1366 doi:10.1073/pnas.1205653109
- 1367 Elbers, D., Bulte, M., Bairlein, F., Mouritsen, H., & Heyers, D. (2017). Magnetic activation in
1368 the brain of the migratory northern wheatear (*Oenanthe oenanthe*). *J Comp Physiol*
1369 *A Neuroethol Sens Neural Behav Physiol*, 203(8), 591-600. doi:10.1007/s00359-017-
1370 1167-7
- 1371 Engels, S., Schneider, N. L., Lefeldt, N., Hein, C. M., Zapka, M., Michalik, A., . . . Mouritsen, H.
1372 (2014). Anthropogenic electromagnetic noise disrupts magnetic compass
1373 orientation in a migratory bird. *Nature*, 509(7500), 353-356.
1374 doi:10.1038/nature13290
- 1375 Ernst, D. A., & Lohmann, K. J. (2016). Effect of magnetic pulses on Caribbean spiny lobsters:
1376 implications for magnetoreception. *J Exp Biol*, 219(Pt 12), 1827-1832.
1377 doi:10.1242/jeb.136036
- 1378 Fillmore, E. P., & Seifert, M. F. (2015). Anatomy of the Trigeminal Nerve. In R. S. Tubbs, E.
1379 Rizk, M. Shoja, M. Loukas, N. Barbaro, & R. Spinner (Eds.), *Nerves and Nerve Injuries*
1380 (Vol. 1, pp. 319-350): Academic Press.
- 1381 Frankel, R. B., & Blakemore, R. P. (1980). Navigational Compass in Magnetic Bacteria.
1382 *Journal of Magnetism and Magnetic Materials*, 15-8(Jan-), 1562-1564. doi:Doi
1383 10.1016/0304-8853(80)90409-6
- 1384 Gilder, S. A., Wack, M., Kaub, L., Roud, S. C., Petersen, N., Heinsen, H., . . . Schmitz, C. (2018).
1385 Distribution of magnetic remanence carriers in the human brain. *Scientific Reports*,
1386 8(11363). doi:DOI:10.1038/s41598-018-29766-z 1
- 1387 Gould, J. S., & Able, K. P. (1981). Human homing: an elusive phenomenon. *Science*,
1388 212(4498), 1061-1063.
- 1389 Hand, E. (2016). Polar explorer. *Science*, 352(6293), 1508-1510, 1512-1503.
1390 doi:10.1126/science.352.6293.1508
- 1391 Hartmann, T., Schlee, W., & Weisz, N. (2012). It's only in your head: expectancy of aversive
1392 auditory stimulation modulates stimulus-induced auditory cortical alpha
1393 desynchronization. *Neuroimage*, 60(1), 170-178.
1394 doi:10.1016/j.neuroimage.2011.12.034

- 1395 Haviland, J. B. (1998). Guugu Yimithir cardinal directions. *Ethos*, 26(1), 25-47. doi:DOI
1396 10.1525/eth.1998.26.1.25
- 1397 Holland, R. A. (2010). Differential effects of magnetic pulses on the orientation of naturally
1398 migrating birds. *J R Soc Interface*, 7(52), 1617-1625. doi:10.1098/rsif.2010.0159
- 1399 Holland, R. A., & Helm, B. (2013). A strong magnetic pulse affects the precision of departure
1400 direction of naturally migrating adult but not juvenile birds. *Journal of the Royal*
1401 *Society Interface*, 10, 20121047.
- 1402 Holland, R. A., Kirschvink, J. L., Doak, T. G., & Wikelski, M. (2008). Bats use magnetite to
1403 detect the earth's magnetic field. *Plos One*, 3(2), e1676.
1404 doi:10.1371/journal.pone.0001676
- 1405 Hore, P. J., & Mouritsen, H. (2016). The Radical-Pair Mechanism of Magnetoreception. In K.
1406 A. Dill (Ed.), *Annual Review of Biophysics, Vol 45* (Vol. 45, pp. 299-344).
- 1407 Irwin, W. P., & Lohmann, K. J. (2005). Disruption of magnetic orientation in hatchling
1408 loggerhead sea turtles by pulsed magnetic fields. *J Comp Physiol A Neuroethol Sens*
1409 *Neural Behav Physiol*, 191(5), 475-480. doi:10.1007/s00359-005-0609-9
- 1410 Johnsen, S., & Lohmann, K. J. (2008). Magnetoreception in animals. *Physics Today*, 61(3), 29-
1411 35. doi:Doi 10.1063/1.2897947
- 1412 Kalmijn, A. J. (1981). Biophysics of Geomagnetic-Field Detection. *IEEE Transactions on*
1413 *Magnetics*, 17(1), 1113-1124. doi:Doi 10.1109/Tmag.1981.1061156
- 1414 Kirschvink, J., Padmanabha, S., Boyce, C., & Oglesby, J. (1997). Measurement of the
1415 threshold sensitivity of honeybees to weak, extremely low-frequency magnetic
1416 fields. *J Exp Biol*, 200(Pt 9), 1363-1368.
- 1417 Kirschvink, J. L. (1992). Uniform magnetic fields and Double-wrapped coil systems:
1418 Improved techniques for the design of biomagnetic experiments.
1419 *Bioelectromagnetics*, 13, 401-411.
- 1420 Kirschvink, J. L., & Gould, J. L. (1981). Biogenic magnetite as a basis for magnetic field
1421 sensitivity in animals. *Bio Systems*, 13, 181-201.
- 1422 Kirschvink, J. L., & Kobayashi-Kirschvink, A. (1991). Is geomagnetic sensitivity real?
1423 Replication of the Walker-Bitterman conditioning experiment in honey bees.
1424 *American Zoologist*, 31, 169-185.
- 1425 Kirschvink, J. L., Kobayashi-Kirschvink, A., & Woodford, B. J. (1992). Magnetite
1426 biomineralization in the human brain. *Proc Natl Acad Sci U S A*, 89(16), 7683-7687.
- 1427 Kirschvink, J. L., Winklhofer, M., & Walker, M. M. (2010). Biophysics of magnetic
1428 orientation: strengthening the interface between theory and experimental design. *J*
1429 *R Soc Interface*, 7 Suppl 2, S179-191. doi:10.1098/rsif.2009.0491.focus
- 1430 Klimesch, W. (1999). EEG alpha and theta oscillations reflect cognitive and memory
1431 performance: a review and analysis. *Brain Res Brain Res Rev*, 29(2-3), 169-195.
- 1432 Klimesch, W., Doppelmayr, M., Russegger, H., Pachinger, T., & Schwaiger, J. (1998). Induced
1433 alpha band power changes in the human EEG and attention. *Neurosci Lett*, 244(2),
1434 73-76. doi:10.1016/s0304-3940(98)00122-0
- 1435 Kobayashi, A., & Kirschvink, J. L. (1995). Magnetoreception and EMF Effects: Sensory
1436 Perception of the geomagnetic field in Animals & Humans. In M. Blank (Ed.),
1437 *Electromagnetic Fields: Biological Interactions and Mechanisms* (pp. 367-394).
1438 Washington, DC.: American Chemical Society Books.
- 1439 Kramer, G. (1953). Wird die Sonnenhöhe bei der Heimfindeorientierung verwertet? *Journal*
1440 *of Ornithology*, 94, 201-219.

- 1441 Landler, L., Painter, M. S., Youmans, P. W., Hopkins, W. A., & Phillips, J. B. (2015).
1442 Spontaneous magnetic alignment by yearling snapping turtles: rapid association of
1443 radio frequency dependent pattern of magnetic input with novel surroundings. *Plos*
1444 *One*, *10*(5), e0124728. doi:10.1371/journal.pone.0124728
- 1445 Levinson, S. C. (2003). *Space in Language and Cognition*. Cambridge: Cambridge University
1446 Press.
- 1447 Light, P., Salmon, M., & Lohmann, K. J. (1993). Geomagnetic Orientation of Loggerhead Sea-
1448 Turtles - Evidence for an Inclination Compass. *Journal of Experimental Biology*, *182*,
1449 1-9.
- 1450 Liu, G. T. (2005). The trigeminal nerve and its central connections. In N. R. Miller , N. J.
1451 Newman , V. Biousse, & K. J. B. (Eds.), *Walsh & Hoyt's Clinical Neuro-Ophthalmology*,
1452 *6th edition* (6th ed., Vol. 1, pp. 1233-1268). Philadelphia: Lippencott Williams &
1453 Wilkins.
- 1454 Lohmann, K. J., Cain, S. D., Dodge, S. A., & Lohmann, C. M. (2001). Regional magnetic fields as
1455 navigational markers for sea turtles. *Science*, *294*(5541), 364-366.
1456 doi:10.1126/science.1064557
- 1457 Lohmann, K. J., & Lohmann, C. M. F. (1996). Detection of magnetic field intensity by sea
1458 turtles. *Nature*, *380*(6569), 59-61. doi:DOI 10.1038/380059a0
- 1459 Lopez, C., & Blanke, O. (2011). The thalamocortical vestibular system in animals and
1460 humans. *Brain Res Rev*, *67*(1-2), 119-146. doi:10.1016/j.brainresrev.2010.12.002
- 1461 Maher, B. A., Ahmed, I. A., Karloukovski, V., MacLaren, D. A., Foulds, P. G., Allsop, D., . . .
1462 Calderon-Garciduenas, L. (2016). Magnetite pollution nanoparticles in the human
1463 brain. *Proc Natl Acad Sci U S A*, *113*(39), 10797-10801.
1464 doi:10.1073/pnas.1605941113
- 1465 Martin, H., & Lindauer, M. (1977). Der Einfluss der Erdmagnetfelds und die
1466 Schwerorientierung der Honigbiene. *J. Comp. Physiol.*, *122*, , 145-187.
- 1467 Meakins, F. (2011). Spaced Out: Intergenerational Changes in the Expression of Spatial
1468 Relations by Gurindji People. *Australian Journal of Linguistics*, *31*(1), 43-77. doi:Pii
1469 932432693 10.1080/07268602.2011.532857
- 1470 Meakins, F., & Algy, C. (2016). Deadly Reckoning: Changes in Gurindji Children's Knowledge
1471 of Cardinals. *Australian Journal of Linguistics*, *36*(4), 479-501.
1472 doi:10.1080/07268602.2016.1169973
- 1473 Meakins, F., Jones, C., & Algy, C. (2016). Bilingualism, language shift and the corresponding
1474 expansion of spatial cognitive systems. *Language Sciences*, *54*, 1-13.
1475 doi:10.1016/j.langsci.2015.06.002
- 1476 Merritt, R., Purcell, C., & Stroink, G. (1983). Uniform Magnetic-Field Produced by 3-Square,
1477 4-Square, and 5-Square Coils. *Review of Scientific Instruments*, *54*(7), 879-882.
1478 doi:Doi 10.1063/1.1137480
- 1479 Mora, C. V., Davison, M., Wild, J. M., & Walker, M. M. (2004). Magnetoreception and its
1480 trigeminal mediation in the homing pigeon. *Nature*, *432*(7016), 508-511.
1481 doi:10.1038/nature03077
- 1482 Munro, U., Munro, J. A., Phillips, J. B., Wiltschko, R., & Wiltschko, W. (1997). Evidence for a
1483 magnetite-based navigational "map" in birds. *Naturwissenschaften*, *84*(1), 26-28.
1484 doi:DOI 10.1007/s001140050343

- 1485 Munro, U., Munro, J. A., Phillips, J. B., & Wiltschko, W. (1997). Effect of wavelength of light
1486 and pulse magnetisation on different magnetoreception systems in a migratory bird.
1487 *Australian Journal of Zoology*, 45(2), 189-198. doi:Doi 10.1071/Zo96066
- 1488 Nuwer, M. R., Comi, G., Emerson, R., Fuglsang-Frederiksen, A., Guerit, J. M., Hinrichs, H., . . .
1489 Rappelsburger, P. (1998). IFCN standards for digital recording of clinical EEG.
1490 International Federation of Clinical Neurophysiology. *Electroencephalogr Clin*
1491 *Neurophysiol*, 106(3), 259-261. doi:10.1016/s0013-4694(97)00106-5
- 1492 Peng, W., Hu, L., Zhang, Z., & Hu, Y. (2012). Causality in the association between P300 and
1493 alpha event-related desynchronization. *Plos One*, 7(4), e34163.
1494 doi:10.1371/journal.pone.0034163
- 1495 Pfurtscheller, G., & Lopes da Silva, F. H. (1999). Event-related EEG/MEG synchronization
1496 and desynchronization: basic principles. *Clin Neurophysiol*, 110(11), 1842-1857.
1497 doi:10.1016/s1388-2457(99)00141-8
- 1498 Pfurtscheller, G., Neuper, C., & Mohl, W. (1994). Event-related desynchronization (ERD)
1499 during visual processing. *Int J Psychophysiol*, 16(2-3), 147-153. doi:10.1016/0167-
1500 8760(89)90041-x
- 1501 Poisson, R. J., & Miller, M. E. (2014). Spatial disorientation mishap trends in the U.S. Air
1502 force 1993-2013. *Aviat Space Environ Med*, 85(9), 919-924.
1503 doi:10.3357/ASEM.3971.2014
- 1504 Ritz, T., Adem, S., & Schulten, K. (2000). A model for photoreceptor-based
1505 magnetoreception in birds. *Biophys J*, 78(2), 707-718. doi:10.1016/S0006-
1506 3495(00)76629-X
- 1507 Rosenblum, B., Jungerman, R. L., & Longfellow, L. (1985). Limits to induction-based
1508 magnetoreception. In J. L. Kirschvink, D. S. Jones, & B. J. MacFadden (Eds.), *Magnetite*
1509 *Biom mineralization and Magnetoreception in Organisms: A New Biomagnetism* (pp.
1510 223-232). New York: Plenum Press.
- 1511 Saper, C. B. (2002). The central autonomic nervous system: conscious visceral perception
1512 and autonomic pattern generation. *Annu Rev Neurosci*, 25, 433-469.
1513 doi:10.1146/annurev.neuro.25.032502.111311
- 1514 Sastre, A., Graham, C., Cook, M. R., Gerkovich, M. M., & Gailey, P. (2002). Human EEG
1515 responses to controlled alterations of the Earth's magnetic field. *Clin Neurophysiol*,
1516 113(9), 1382-1390. doi:10.1016/s1388-2457(02)00186-4
- 1517 Schulten, K. (1982). Magnetic-Field Effects in Chemistry and Biology. *Festkorperprobleme-*
1518 *Advances in Solid State Physics*, 22, 61-83. doi:DOI 10.1007/BFb0107935
- 1519 Schultheiss-Grassi, P. P., Wessiken, R., & Dobson, J. (1999). TEM investigations of biogenic
1520 magnetite extracted from the human hippocampus. *Biochim Biophys Acta*, 1426(1),
1521 212-216. doi:10.1016/s0304-4165(98)00160-3
- 1522 Schwarze, S., Steenken, F., Thiele, N., Kobylkov, D., Lefeldt, N., Dreyer, D., . . . Mouritsen, H.
1523 (2016). Migratory blackcaps can use their magnetic compass at 5 degrees
1524 inclination, but are completely random at 0 degrees inclination. *Sci Rep*, 6, 33805.
1525 doi:10.1038/srep33805
- 1526 Semm, P., & Beason, R. C. (1990). Responses to small magnetic variations by the trigeminal
1527 system of the bobolink. *Brain Res Bull*, 25(5), 735-740. doi:10.1016/0361-
1528 9230(90)90051-z

- 1529 Tomanova, K., & Vacha, M. (2016). The magnetic orientation of the Antarctic amphipod
1530 *Gondogeneia antarctica* is cancelled by very weak radiofrequency fields. *J Exp Biol*,
1531 219(Pt 11), 1717-1724. doi:10.1242/jeb.132878
- 1532 Tukey, J. W. (1949). Comparing individual means in the analysis of variance. *Biometrics*,
1533 5(2), 99-114. doi:10.2307/3001913
- 1534 Veniero, D., Bortoletto, M., & Miniussi, C. (2009). TMS-EEG co-registration: On TMS-induced
1535 artifact. *Clinical Neurophysiology*, 120(7), 1392-1399.
1536 doi:10.1016/j.clinph.2009.04.023
- 1537 Walker, M. M., Dennis, T. E., & Kirschvink, J. L. (2002). The magnetic sense and its use in
1538 long-distance navigation by animals. *Current Opinion in Neurobiology*, 12(6), 735-
1539 744. doi:10.1016/S0959-4388(02)00389-6
- 1540 Walker, M. M., Diebel, C. E., Haugh, C. V., Pankhurst, P. M., Montgomery, J. C., & Green, C. R.
1541 (1997). Structure and function of the vertebrate magnetic sense. *Nature*, 390(6658),
1542 371-376.
- 1543 Wegner, R. E., Begall, S., & Burda, H. (2006). Magnetic compass in the cornea: local
1544 anaesthesia impairs orientation in a mammal. *J Exp Biol*, 209(Pt 23), 4747-4750.
1545 doi:10.1242/jeb.02573
- 1546 Welch, P. D. (1967). Use of Fast Fourier Transform for Estimation of Power Spectra - a
1547 Method Based on Time Averaging over Short Modified Periodograms. *Ieee*
1548 *Transactions on Audio and Electroacoustics*, Au15(2), 70-+. doi:10.1109/Tau.1967.1161901
- 1550 Westby, G. W. M., & Partridge, K. J. (1986). Human Homing - Still No Evidence Despite
1551 Geomagnetic Controls. *Journal of Experimental Biology*, 120, 325-331.
- 1552 Wiltschko, R., Thalau, P., Gehring, D., Niessner, C., Ritz, T., & Wiltschko, W. (2015).
1553 Magnetoreception in birds: the effect of radio-frequency fields. *J R Soc Interface*,
1554 12(103). doi:10.1098/rsif.2014.1103
- 1555 Wiltschko, R., & Wiltschko, W. (1995). *Magnetic orientation in animals* (Vol. 33). Berlin:
1556 Springer.
- 1557 Wiltschko, W. (1972). The influence of magnetic total intensity and inclination on
1558 directions preferred by migrating European robins (*Erithacus rubecula*). In S. R.
1559 Galler, K. Schmidt-Koenig, G. J. Jacobs, & R. E. Belleville (Eds.), *Animal Orientation*
1560 *and Navigation* (Vol. NASA SP-262, pp. 569-578). Washington, D.C., USA: U.S.
1561 Government Printing Office.
- 1562 Wiltschko, W., Ford, H., Munro, U., Winklhofer, M., & Wiltschko, R. (2007). Magnetite-based
1563 magnetoreception: the effect of repeated pulsing on the orientation of migratory
1564 birds. *J Comp Physiol A Neuroethol Sens Neural Behav Physiol*, 193(5), 515-522.
1565 doi:10.1007/s00359-006-0207-5
- 1566 Wiltschko, W., Munro, U., Beason, R. C., Ford, H., & Wiltschko, R. (1994). A Magnetic Pulse
1567 Leads to a Temporary Deflection in the Orientation of Migratory Birds. *Experientia*,
1568 50(7), 697-700. doi:10.1007/Bf01952877
- 1569 Wiltschko, W., Munro, U., Ford, H., & Wiltschko, R. (1998). Effect of a magnetic pulse on the
1570 orientation of silvereyes, *zosterops l. lateralis*, during spring migration. *J Exp Biol*,
1571 201 (Pt 23)(23), 3257-3261.
- 1572 Wiltschko, W., Munro, U., Ford, H., & Wiltschko, R. (2009). Avian orientation: the pulse
1573 effect is mediated by the magnetite receptors in the upper beak. *Proc Biol Sci*,
1574 276(1665), 2227-2232. doi:10.1098/rspb.2009.0050

- 1575 Wiltschko, W., Munro, U., Wiltschko, R., & Kirschvink, J. L. (2002). Magnetite-based
1576 magnetoreception in birds: the effect of a biasing field and a pulse on migratory
1577 behavior. *J Exp Biol*, 205(Pt 19), 3031-3037.
- 1578 Wiltschko, W., & Wiltschko, R. (1995). Migratory Orientation of European Robins Is
1579 Affected by the Wavelength of Light as Well as by a Magnetic Pulse. *Journal of*
1580 *Comparative Physiology a-Sensory Neural and Behavioral Physiology*, 177(3), 363-
1581 369.
- 1582 Yeagley, H. L. (1947). A Preliminary Study of a Physical Basis of Bird Navigation. *Journal of*
1583 *Applied Physics*, 18(12), 1035-1063. doi:Doi 10.1063/1.1697587
- 1584