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1 **Animal Navigation: A Noisy Magnetic Sense?**

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Abstract

Diverse organisms use Earth’s magnetic field as a cue in orientation and navigation. Nevertheless, eliciting magnetic orientation responses reliably, either in laboratory or natural settings, is often difficult. Many species appear to preferentially exploit non-magnetic cues if they are available, suggesting that the magnetic sense often serves as a redundant or ‘backup’ source of information. This raises an interesting paradox: Earth’s magnetic field appears to be more pervasive and reliable than almost any other navigational cue. Why then do animals not rely almost exclusively on the geomagnetic field, while ignoring or downplaying other cues? Here we explore a possible explanation: that the magnetic sense of animals is ‘noisy’, in that the magnetic signal is small relative to thermal and receptor noise. Magnetic receptors are thus unable to instantaneously acquire magnetic information that is highly precise or accurate. We speculate that extensive time-averaging and/or other higher-order neural processing of magnetic information is required, rendering the magnetic sense inefficient relative to alternative cues that can be detected faster and with less effort. This interpretation is consistent with experimental results suggesting a long time-course for magnetic compass and map responses in some animals. Despite possible limitations, magnetoreception may be maintained by natural selection because the geomagnetic field is sometimes the only source of directional and/or positional information available.

Keywords: magnetoreception, orientation, migration, signal-to-noise

Summary statement: *Magnetic orientation responses in animals are often weak and difficult to elicit experimentally. A possible explanation is that the magnetic compass is ‘noisy’ and cannot acquire precise magnetic information over short time periods.*

52 *Introduction*

53 Numerous organisms detect Earth’s magnetic field and use it to guide their movements
54 over a wide range of spatial scales (reviewed by Johnsen and Lohmann, 2005; Mouritsen 2013;
55 Nordmann et al., 2017). In many ways, the geomagnetic field appears to be an ideal navigational
56 cue. In contrast to most other sensory cues, it exists everywhere on Earth, is continuously present
57 throughout the day and night, and is largely unaffected by season and weather (though
58 potentially affected by solar storms that wax and wane over an 11-year cycle – e.g. Granger et al.
59 [2020]). Moreover, the magnetic field can potentially provide animals with both directional and
60 positional information (Lohmann et al., 2007). Indeed, humans have used the geomagnetic field
61 as a simple but powerful source of directional information for centuries.

62 The pervasiveness and reliability of Earth’s magnetic field leads to an interesting
63 paradox. Specifically, given that the geomagnetic field is a ubiquitous sensory cue that is
64 potentially available for all animals to exploit in orientation and navigation, why do so few
65 species appear to rely exclusively or even primarily on magnetic cues for guiding their
66 movements? In addition, why is it often difficult to reliably produce magnetic orientation and
67 navigation responses under laboratory conditions?

68 Three examples illustrate the essence of the enigma. The desert ant *Cataglyphis*, a
69 famous insect navigator, begins its adult life with a functional magnetic compass sense that is
70 used as it transitions from underground life to foraging above ground (Fleischmann et al., 2018).
71 Nevertheless, older adult ants undertaking foraging trips orient their movements relative to a
72 celestial compass instead of the geomagnetic field (Wehner et al., 1996). Why do ants switch
73 from using a magnetic compass to using a celestial compass despite the fact that the geomagnetic
74 field is constantly available?

75 Similarly, studies have revealed that several birds, including homing pigeons, appear to
76 use a combination of input from multiple compasses to select a direction instead of relying on the
77 magnetic compass alone (Munro and Wiltschko, 1993; Wiltschko and Wiltschko, 2001). Why is
78 deriving input from multiple compasses in these birds advantageous relative to relying
79 exclusively on the magnetic compass?

80 Finally, loggerhead sea turtles have a well-developed magnetic sense that provides both
81 directional and positional information (Lohmann, 1991; Lohmann and Lohmann, 2012; 2019).
82 Yet hatchling turtles, when leaving the beach and swimming offshore, guide themselves seaward
83 by swimming into ocean waves (Lohmann and Lohmann, 1992), even though the offshore
84 migration could be guided by magnetic cues instead.

85 In this Commentary, we explore the question of why magnetic field information,
86 although potentially available to all animals, often seems to be used either as a ‘backup’ cue or as
87 one of several different sources of information. For simplicity we will focus primarily on the
88 ability of animals to maintain directional headings relative to Earth’s field, or what is often called
89 the ‘magnetic compass sense’, as this represents the simplest use of magnetic information by
90 animals (see Box). We propose a novel hypothesis: that the magnetic compass sense of animals
91 is ‘noisy’, meaning that magnetic receptors are unable to instantaneously acquire magnetic
92 information that is highly precise or accurate because the magnetic signal is small relative to
93 thermal and receptor noise. As a simple analogy, imagine a human-built compass in which the
94 needle does not point unerringly toward the north; instead, the needle points north *on average*,
95 swinging erratically among a variety of directions, so that the reading at any specific instant is
96 unreliable. Such a compass can still be used in orientation, but extracting a useful signal requires
97 some kind of processing -- for example, averaging a series of readings over time -- that might

98 make the magnetic compass harder to use and inefficient relative to alternative cues that can be
99 detected instantly. We argue that a scenario similar to this is consistent with some of the most
100 persistently mysterious aspects of magnetic orientation behavior.

101

102

103 *Magnetic orientation responses in the laboratory*

104 Despite the pervasive and reliable nature of the geomagnetic field, behavioral responses
105 of animals in magnetic orientation experiments are typically weak. Informally, the data have a
106 large spread around the mean angle of orientation resulting from different individual animals
107 selecting a wide range of directions. More formally, the confidence interval of the mean angle
108 can be large relative to that seen in studies of orientation to other cues (e.g. Figure 1). This
109 dispersion results in low statistical power when comparing orientation data from different
110 magnetic treatments, which in turn creates several problems for the researcher. For example,
111 unless large numbers of individuals are used, an effect can easily be missed.

112 The relatively weak responses also make it difficult to use magnetic behavior in a single
113 individual as an assay, unlike, for example, vision, where one can illuminate the retina of one
114 individual and get a repeatable response that can then be used to examine the effects of various
115 manipulations (e.g. measurement of a spectral sensitivity curve). Indeed, there is currently no
116 species that has a magnetic response so robust that it can easily be used as a model system to
117 study the underlying physiological, biophysical and genetic basis of the sense. Additionally,
118 there is no species in which magnetoreception is definitively known not to exist, making it
119 difficult to establish negative control species for comparative studies. Again, this contrasts with
120 vision, in which blind species are well known and usually easy to identify. Within a
121 magnetoreceptive species, nulled magnetic fields can of course be used as an experimental

122 control, but we do not currently have the ability to say that magnetoreception has been
123 evolutionarily lost in a given environment, the way we can – for example – say that vision has
124 been lost in certain cave-dwelling species.

125 Another unusual aspect of magnetoreception, found in both behavioral studies and
126 neurobiological assays in certain species, is that the responses to changes in the magnetic field
127 sometimes have a long time-constant (Figure 2). Although species vary significantly in the
128 speed at which they interact with the environment, ranging from darting swifts to lumbering sea
129 slugs, the rate of response within a species tends to be relatively independent of the sensory
130 modality cuing the response (though of course there are exceptions). However, an insect or
131 lobster that may respond within milliseconds to a visual stimulus may take several minutes to
132 respond to an altered magnetic field (Lohmann et al., 1995; Vácha, 2006; Dreyer et al., 2018).
133 Similarly, in the marine mollusc *Tritonia*, one of the few neurobiological model systems for
134 magnetoreception, several identified neurons respond with enhanced electrical activity to
135 changes in Earth-strength magnetic fields, but only after a latency of several minutes (Lohmann
136 et al., 1991; Popescu and Willows, 1999; Wang et al., 2003; 2004). Similarly long latencies
137 from a change in the magnetic field to the onset of an electrophysiological response have been
138 reported in several other animals (e.g. Semm et al., 1980; Semm, 1983; Korall and Martin,
139 1987), although it should be noted that shorter latencies have also been observed (Semm and
140 Beason, 1990; Walker et al., 1997; Wu and Dickman, 2012).

141 Together the weakness and, in some cases, slowness of the magnetic response have
142 contributed to the challenge of determining the sensor involved. Given the lack of an identified
143 magnetoreceptor that can be studied directly, most of the evidence for and against different
144 hypothesized sensor mechanisms has been behavioral. Thus, the fact that the behavioral data are

145 sometimes difficult to interpret has complicated efforts to determine the physiological basis of
146 the magnetic sense.

147

148 *Low signal relative to noise as a potential explanation*

149 Most human experience of magnetic field detection is based on observing the steady
150 needle of a handheld compass, but an interesting possibility is that biological magnetoreceptors
151 do not yield the same consistent and reliable signal. Instead, as mentioned above, the ‘needle’ of
152 the biological compass may move rapidly and seemingly randomly over large angles about the
153 correct direction. In engineering terms, the signal-to-noise ratio (SNR) of the compass may be
154 low. This term is relatively uncommon in much of biology, but is critically important for
155 understanding sensory processes such as vision under low light, a research area for two of the
156 authors. For example, although visual scenes under daylight appear smooth and continuous to the
157 human eye or a camera, those under starlight appear grainy and coarse. This reduction in detail is
158 due to the signal being smaller relative to the noise; the signal decreases because the scene is
159 darker, and the noise – which arises from receptor noise and the random arrival of photons –
160 remains constant. In this situation, one cannot simply increase the brightness of the image to
161 recover the lost detail; doing so only results in a brighter but still coarse image. Instead, visual
162 systems and cameras must sample the scene for a longer period of time, and it is well-known that
163 the temporal resolution (i.e. the ‘speed of the shutter’) of many animal visual systems decreases
164 as the illumination level decreases, meaning that the scene is sampled for longer periods
165 (Warrant 1999).

166 The hypothesis that magnetoreceptors have a low SNR appears plausible for several
167 reasons. First, the geomagnetic field at the earth’s surface is weak, much as light levels are low at

168 night or in the deep sea. More importantly, the interaction of magnetic fields with biological
169 tissue is extraordinarily weak. For example, although magnetic fields can split the energy states
170 of atomic orbitals (known as Zeeman splitting), the energy resulting from this is only one five-
171 millionth that of the thermal noise at human body temperature. In other words, any magnetic
172 compass composed of standard biological molecules would be buffeted about by thermal forces
173 that are many orders of magnitude larger. The only materials that interact strongly with magnetic
174 fields are the elements iron, nickel, cobalt, gadolinium and dysprosium, , and some of their
175 compounds. Ferromagnetic materials, in particular the mineral magnetite (Fe_3O_4), have been
176 proposed as a possible basis of magnetoreception, but an important constraint is that animals do
177 not appear to have the ability to magnetize macroscopic amounts of these materials. Instead, they
178 must use crystals that are either of single-domain size (~50 nm diameter) or smaller, but such
179 small crystals are again vulnerable to the randomizing effects of thermal noise (Kirschvink and
180 Gould, 1981; Kirschvink and Walker, 1985; Yorke, 1985). Magnetotactic bacteria and other
181 single-cell organisms that move along magnetic field lines (Bellini, 1963; Blakemore, 1975)
182 partly overcome this limitation by forming chains of single-domain magnetite crystals, but the
183 general situation in metazoans appears to be one of nano-scale objects being influenced by weak
184 magnetic fields in the presence of relatively large amounts of Brownian motion.

185 Magnetoreception mediated by chemical reactions (known as the ‘radical pair’
186 hypothesis) faces similar or perhaps even larger hurdles because this mechanism does not have
187 the advantage of the unusually large coupling between ferromagnetic minerals and magnetic
188 fields. Nevertheless, analyses suggest that chemical magnetoreception is viable from a
189 theoretical standpoint and that high sensitivity with such a system might be possible (Weaver et
190 al., 2000; Ritz et al., 2000). Of course, receptors in many sensory modalities detect quite small

191 stimuli; for example, photoreceptors respond to individual photons. However, many sensory
192 receptors have focusing/amplifying structures (lenses, outer ears, nostrils) and signal
193 amplification pathways, both of which function to significantly improve signal-to-noise ratio.
194 For the magnetic sense, mechanisms for focusing or amplifying magnetic signals have not been
195 discovered; moreover, they appear unlikely due to the weak interaction between biological tissue
196 and magnetic fields.

197 In sum, an animal magnetic compass (whatever its form) might oscillate significantly and
198 randomly around the correct bearing angle due to the presence of levels of thermal and receptor
199 noise that are high relative to the magnetic signal itself. This in turn might contribute to the large
200 dispersion in directional responses often observed in orientation studies. It might also explain the
201 slow responses to changes in the magnetic field, because the animal may have to integrate the
202 signal over a long time course to increase the reliability of the signal, much as eyes integrate over
203 longer periods under dim light. A reliable compass reading, possibly acquired through
204 integration, is necessary for an efficient path of travel (Figure 3).

205 In the context of this discussion, a distinction should perhaps be drawn among three
206 separate time courses: (1) the time required for the transduction process itself; (2) the time
207 required for the nervous system to integrate and analyze the signal, which depends in part on
208 SNR; and (3) the time needed for a behavioral response, which depends on context, motivation
209 and navigational task. At present, both theoretical and empirical studies suggest that the
210 transduction process itself is likely to require only fractions of a second (e.g. Johnsen and
211 Lohmann, 2008; Slaby et al., 2018). Nevertheless, whether an animal can detect the new
212 direction of the ambient field the instant that it changes, or instead must average signals over
213 time to extract compass information, remains unclear. To our knowledge, no experimental

214 results exist in which a change in the direction of the ambient magnetic field results in a nearly
215 instantaneous change in the heading of an animal. Indeed, experiments with lobsters and moths
216 have revealed a latency of more than a minute between the time that the field direction is
217 changed and the time that the animal changes its direction of travel (Figures 2 and 4).

218 It is also important to note that a magnetoreceptor may not itself be any noisier than
219 receptors for other sensory modalities, inasmuch as thermal and receptor noise are common to all
220 biological receptors. Instead, the central challenge with the magnetic sense might be that the
221 signal is weak, due to the weakness of the geomagnetic field and the limited interaction of
222 biological materials with magnetic fields. Thus, the magnetic sense might be operating under
223 challenging signal-to-noise circumstances, much like the eyes of deep-sea fish or nocturnal
224 moths.

225

226 *Low signal-to-noise and navigational strategies*

227 If receptor and thermal noise in magnetoreception are indeed high relative to the signal
228 then this might influence how the sense is used. Specifically, if the magnetic sense does not
229 provide a continuous and rapid source of information, then it might be easier for animals to use
230 other cues for orientation whenever a choice exists. In this context it is worth noting that
231 pigeons, juvenile sea turtles and young salmon can all maintain headings using both magnetic
232 and celestial compasses, but celestial compasses are often used when both cues are available
233 (Keeton, 1971; Quinn, 1980; Aves and Lohmann, 2003; Mott and Salmon, 2011).

234 Another possible way to accommodate a low-SNR magnetic compass is to use it as one cue
235 in a set of multimodal cues. An interesting example consistent with this possibility comes from
236 recent studies with the Bogong moth (*Agrotis infusa*), a nocturnal Australian moth that migrates

237 long distances between summer and winter habitats (Warrant et al., 2016, Dreyer et al., 2018).
238 In initial studies, moths were tested in a flight arena with a largely unobstructed view of the sky;
239 under these conditions, rotating the ambient magnetic field had little or no apparent effect on
240 orientation. By contrast, when a conspicuous visual cue was deliberately placed into the arena as
241 a visual landmark, it emerged that moths changed orientation when the field and landmark were
242 moved together, but became disoriented after 2–3 minutes when either the magnetic field or the
243 visual landmark was shifted alone (Dreyer et al., 2018; Figure 4). These findings suggest that,
244 for Bogong moths, magnetic orientation is one component of a multimodal navigational strategy
245 that also involves visual landmarks. An intriguing possibility is that moths periodically consult
246 their magnetic compasses to ensure that they are moving in the right general direction, but prefer
247 to use visual cues for moment-to-moment maintenance of headings, in much the same way that
248 humans hiking through forests intermittently consult a compass but then, rather than continually
249 peering at the compass as they walk, use visual landmarks to maintain the chosen course.

250 Such a multimodal navigational strategy might actually be the preferred strategy in
251 situations when all available compass cues have low SNR, as might occur in the dimly lit
252 nocturnal habitats of migratory birds or moths or in the murky underwater habitats of sea turtles.
253 In this case, an optimal integration of these low-SNR multimodal cues could be performed to
254 maximize the reliability of the combined information; indeed, by knowing the uncertainty
255 inherent in each compass, such integration can be used to estimate the optimal steering direction
256 (Collett 2012; Ernst and Banks, 2002; Hoinville and Wehner, 2018). Interestingly, homing
257 pigeons have been proposed to simultaneously use a sun compass and magnetic compass under
258 some conditions (Wiltschko and Wiltschko, 2001); indeed, mathematical models have suggested

259 that avian navigation is a complex process that relies on simultaneous use of at least four or five
260 different factors (Schiffner et al., 2011).

261

262 *High-precision magnetic maps?*

263 In addition to having a magnetic compass, some animals also have a ‘magnetic map’, defined
264 as an ability to derive positional information from Earth’s magnetic field (Lohmann et al., 2007).
265 Magnetic maps can be used for a variety of purposes, from changing migratory direction at an
266 appropriate location (Lohmann et al., 2001; 2012; Putman et al., 2014; Naisbett-Jones et al.,
267 2017) to navigating toward a specific home area (Lohmann et al., 2004).

268 The concept of a low-SNR magnetic compass might, at first glance, seem inconsistent
269 with findings suggesting that a few animals can use magnetic information to determine their
270 geographic position when displaced relatively short distances from a home area. For example,
271 lobsters and newts displaced short distances (12 to 45 km) from a home area were able to orient
272 in the homeward direction, apparently by using magnetic cues (Phillips et al., 1995; Fischer et
273 al., 2001; Boles and Lohmann, 2003). If magnetic maps do indeed function over such small
274 distances, then animals presumably can detect the very small differences in the magnetic fields
275 that exist at nearby locations, implying high-precision sensing.

276 An important distinction must be drawn, however, between the precision of a system and
277 the speed with which the precision is achieved. In homing experiments with newts and lobsters,
278 animals remained in the magnetic field of the location to which they had been moved either
279 overnight (lobsters; Boles and Lohmann, 2003) or for several days (newts; Phillips et al., 1995)
280 prior to testing. In principle, this extended duration in the local field might have provided an
281 opportunity for the animals to repeatedly sample the field and, perhaps, average the results. To

282 our knowledge, all demonstrations that animals derive positional or ‘map’ information from
283 Earth’s field (e.g., Lohmann et al., 2001; Putman et al., 2014) have involved experiments in
284 which animals had a period of at least several minutes in which to assess the field. Thus, we
285 caution that an ability to detect magnetic fields with high precision does not, by itself, preclude
286 the possibility that the magnetic sense is noisy; it might mean only that an animal has a
287 mechanism that enables it to extract a high-quality signal through averaging or other means.

288

289 *Implications for the performance of magnetoreception research*

290 If the magnetic compass does indeed have a low SNR, and especially if it is used in
291 combination with other cues, then one practical lesson for experimentalists might be that the
292 standard practice of testing for magnetic orientation in the absence of other sensory cues may not
293 be optimal. As with the Bogong moth, removing ‘competing’ cues may inadvertently create an
294 environment in which animals are less likely, rather than more likely, to express magnetic
295 orientation behavior. Instead, treating the magnetic field as one part of a multi-modal orientation
296 system, and designing experiments that combine magnetic cues with others in a
297 conflict/concordance design, may prove productive.

298 Another suggestion is to undertake experiments with significantly longer time courses,
299 allowing the animal time to assess the field and any changes in it. This may improve the odds of
300 finding a species that has a repeatable response that can be used as an assay to probe the
301 underlying mechanisms.

302 An additional issue is that the SNR of the magnetoreceptor is likely to be under natural
303 selection. Diurnal, terrestrial species that always (or usually) have access to multiple directional
304 cues (e.g. birds) may be under less selective pressure to have a reliable magnetic compass than

305 those that have access to fewer navigational cues, such as nocturnal species or those that inhabit
306 subsurface ocean habitats (e.g. sea turtles, lobsters). Therefore, it would be interesting to study
307 whether the confidence intervals in aquatic and nocturnal species (for example) are smaller than
308 those in terrestrial and diurnal species, although differences in experimental protocols may make
309 such a comparison difficult.

310

311 *Conclusions*

312 From uncertain beginnings, the study of magnetoreception has developed into a vibrant
313 field with the potential to unearth a sensor with a completely novel design. Despite advances,
314 however, progress has been hindered by the complexities and inconsistencies of the behavioral
315 data. We suggest that this complexity may not be a failing of the research, but might instead
316 reflect the natural behavioral output of a sensory system with an unusually low level of signal
317 relative to receptor and thermal noise.

318 Because magnetoreceptors have not yet been identified with certainty in any animal, it is
319 not yet possible to test this hypothesis directly using cellular recording techniques. However, it
320 may be possible to test the hypothesis indirectly using behavioral assays similar to those that
321 have been used to measure temporal resolution in vision. For example, certain three-color light
322 emitting diodes consist of both a red and green light emitting circuit, wired in opposite polarity,
323 such that DC current in one direction creates red light, DC current in the opposite direction
324 creates green light. Thus, a 60 Hz AC current creates an amber mixture because the alternating
325 flashing of the red and green circuits is above the temporal resolution of the human eye. One can
326 then use these LEDs run at different AC frequencies in a forced choice conditioning trial to

327 assess temporal resolution behaviorally. An analog experiment using alternating magnetic fields
328 may be possible, and is currently under development by the authors.

329 The concept of a low SNR magnetic compass represents a possible unifying explanation
330 for a variety of peculiarities in magnetoreception research, including consistently weak magnetic
331 orientation behavior, long time courses for behavioral responses and the finding that few if any
332 animals rely solely on magnetic orientation when alternative cues are present. Considering this
333 possibility may provide new insights into the conditions under which animals use their magnetic
334 sense and the ways in which magnetoreception can most effectively be studied.

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BOX: A Quick Guide to Magnetoreception

Earth’s magnetic field provides two types of information that can be exploited by animals in orientation and navigation. Animals that use the geomagnetic field as a source of *directional* information, for example to maintain headings to the north or south, are said to have a ‘magnetic compass’. By contrast, animals that derive *positional* information from Earth’s magnetic field are said to have a ‘magnetic map’ (Lohmann et al., 2007). Magnetic maps can be used by animals to change direction at appropriate locations along migratory routes (e.g., Lohmann et al., 2001; 2012; Putman et al., 2014) or to navigate to specific locations (e.g., Lohmann et al., 2004; Kishkinev et al., 2015).

Despite abundant behavioral evidence that animals sense magnetic fields, little is known about how they do so. More than one mechanism may exist, perhaps even in the same animal (Lohmann et al., 2010). Most research has focused on three possibilities.

Electromagnetic Induction: When an electrically conductive object such as a fish moves through Earth’s magnetic field, negatively and positively charged particles migrate to opposite sides of the object, resulting in a constant voltage determined by speed and direction relative to the magnetic field. This might provide the basis for a magnetic sense in elasmobranch fish (e.g., sharks), which have highly sensitive electroreceptors (Kalmijn 1974; 1984; Johnsen and Lohmann, 2008). Electromagnetic induction might also underlie magnetoreception in birds, with the crucial detection process occurring in the fluid-filled inner ear (Nimpf et al., 2019).

373 **Magnetite:** The magnetite hypothesis proposes that particles of magnetite (Fe_3O_4) underlie
374 magnetoreception. Single-domain magnetite crystals act as tiny magnets that twist into
375 alignment with the Earth's magnetic field if allowed to rotate freely. In principle, such crystals
376 might transduce magnetic information to the nervous system by exerting torque or pressure on
377 secondary receptors (such as stretch receptors, hair cells, or mechanoreceptors) or by opening ion
378 channels directly if, for example, cytoskeletal filaments connect the crystals to the channels (e.g.,
379 Kirschvink et al. 2001; Johnsen and Lohmann 2005; Walker 2008).

380

381 **Chemical Magnetoreception:** Another hypothesis is that magnetoreception involves unusual
382 chemical reactions that are influenced by Earth's magnetic field. Because the proposed reactions
383 involve pairs of free radicals as short-lived intermediates, this idea is sometimes referred to as
384 the radical pairs hypothesis. Details are complex and have been described elsewhere (e.g., Ritz et
385 al., 2010; Hore and Mouritsen, 2016). Many of the best-known radical-pair reactions begin with
386 electron transfers that are induced by the absorption of light; thus, chemical magnetoreceptors
387 might also be photoreceptors and magnetoreception might be tied to the visual system.
388 Photoreceptive proteins known as cryptochromes have been proposed as a possible
389 magnetoreceptive substrate (Ritz et al., 2000).

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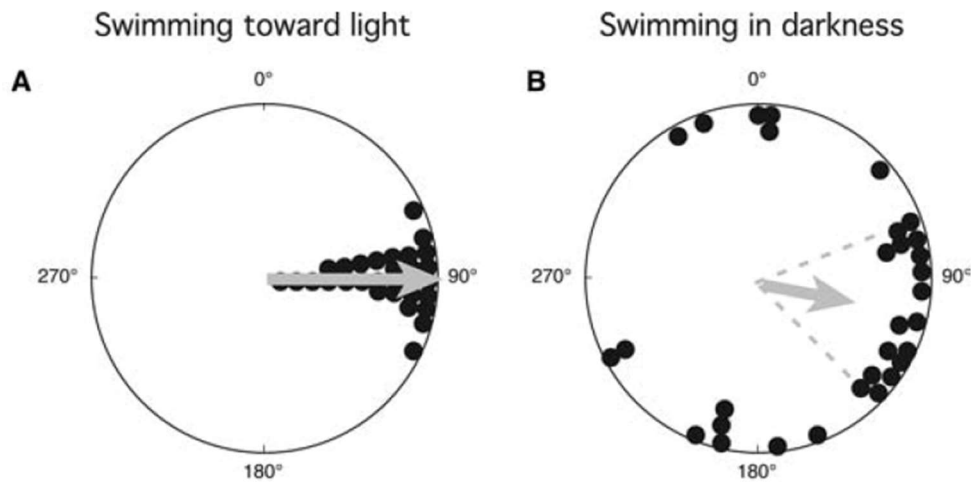
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579 **Figure 1: Orientation of hatchling loggerhead sea turtles (*Caretta caretta*) under conditions**

580 **in which turtles rely on different sensory cues to orient eastward.** In both cases, turtles were

581 placed into cloth harnesses and tethered to an electronic tracking device in a circular water-filled

582 arena. (A) Orientation of turtles when dim illumination (a white LED) was present in the east.

583 Under these conditions, turtles are known to use visual cues to swim toward the light; if the

584 ambient magnetic field is reversed while the light is present, turtles do not change direction

585 (KJL, unpublished data), implying either that they do not use their magnetic compass in this

586 situation or, if they do, that visual cues take precedence. (B) Orientation of the same turtles

587 subsequently tested in complete darkness. Turtles tested under these conditions, after exposure

588 to light in the east, are known to orient eastward using Earth's magnetic field (Lohmann, 1991;

589 Light et al., 1993; Lohmann and Lohmann, 1994), but the dispersion of the turtles increases

590 strikingly when they are forced to rely on their magnetic compasses. Data are from Irwin and

591 Lohmann (2005). The comparison between sensory cues is not perfect, inasmuch as it is

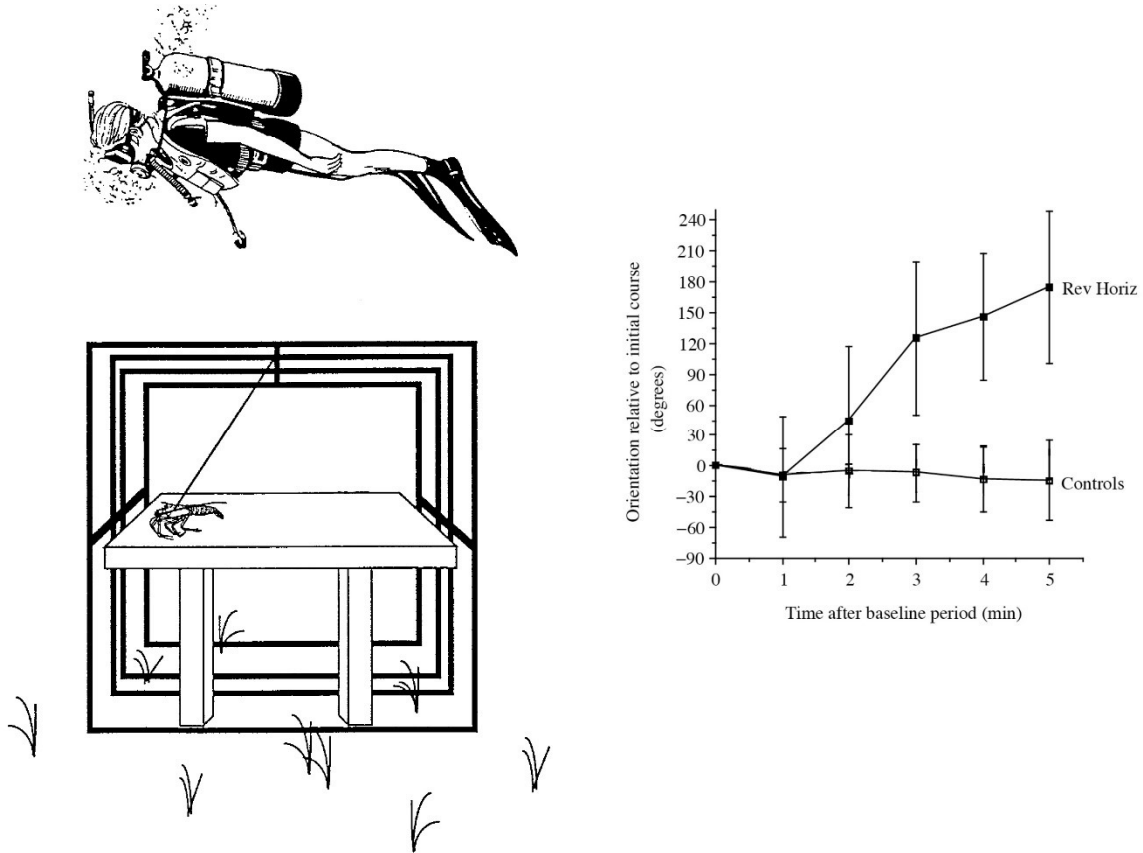
592 conceivable that turtles are differentially motivated (for unknown reasons) to swim east under

593 the two conditions, or that having access to magnetic cues and light cues together yields stronger

594 orientation than magnetic cues alone (even though reversing the magnetic field when the light is

595 present has no effect). These caveats aside, similar comparisons suggest that sea turtles are often
596 more strongly oriented while using visual cues to crawl across the beach (Lucas et al., 1992) or
597 while using wave cues to orient offshore (Lohmann et al., 1990; Lohmann and Lohmann, 1992)
598 than they are while using magnetic compass orientation.

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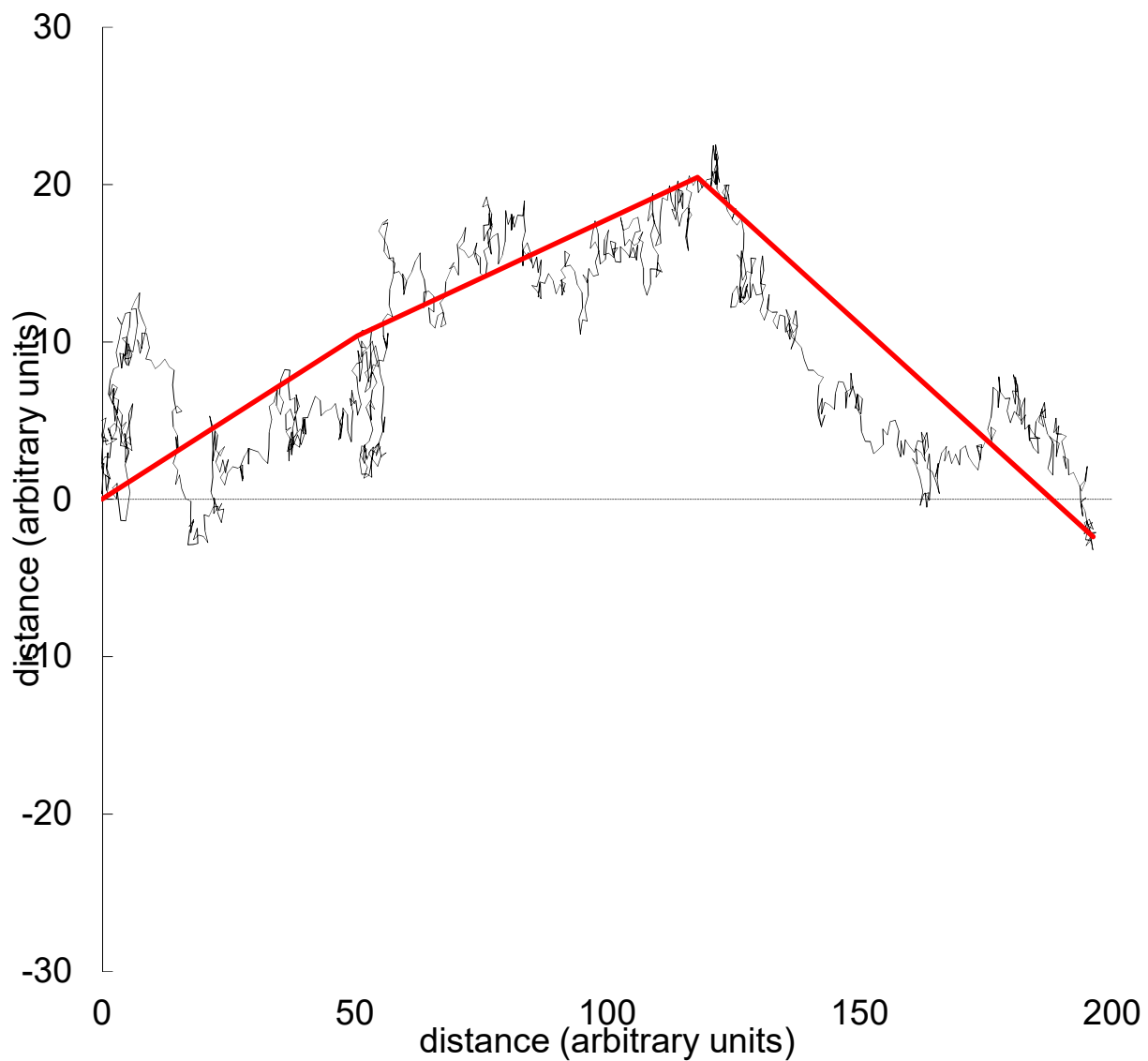


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601 **Figure 2: Orientation of Caribbean spiny lobsters (*Panulirus argus*).** Diagram on the left
 602 shows a lobster walking in place while tethered on a table surrounded by an underwater magnetic
 603 coil system (boxlike structure), with a diver monitoring its orientation behavior. After lobsters
 604 established consistent headings, the coil was used to reverse the direction of the field in some of
 605 the trials; in others, lobsters continued walking in the unaltered local field. In the diagram on the
 606 right, time zero on the x-axis is the time at which the field was reversed for half of the lobsters
 607 (there was no reversal for the controls). The vertical axis indicates the mean angle of all lobsters
 608 in the two groups, with an orientation bearing of zero degrees indicating the previous orientation
 609 of the lobsters. Lobsters that were not exposed to a field reversal (n = 14) continued on similar
 610 headings with little deviation from their initial courses. By contrast, lobsters exposed to the field
 611 reversals (n = 9) began to deviate from their initial headings approximately 1–2 min after the

612 field reversal and, by 5 min after, were walking in directions approximately opposite to their
613 initial direction. Interestingly, the change in direction did not occur immediately after the field
614 was shifted. Data are from Lohmann et al., 1995.

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618 **Figure 3: The effects of averaging a noisy signal on the path of an orienting animal.** The
 619 black line shows the simulated 1200-step path of an animal that is attempting to move directly to
 620 the right using a compass whose measurements of a constant field have a normal distribution
 621 with a standard deviation of 120 degrees. The red line shows the path of the animal using the
 622 same underlying measurements, but averaging the field measurements over 400 steps and then
 623 making one large 400-step move. The ratio of the length of the red path to the black path is

624 approximately 5:1. The ratios for magnetic sensors with standard deviations of 10, 30, 60, 120,
625 and 180 degrees are 1.02 ± 0.01 , 1.14 ± 0.02 , 1.7 ± 0.04 , 4.7 ± 0.26 , and 9.6 ± 1.4 respectively (N = 10
626 simulations for each).

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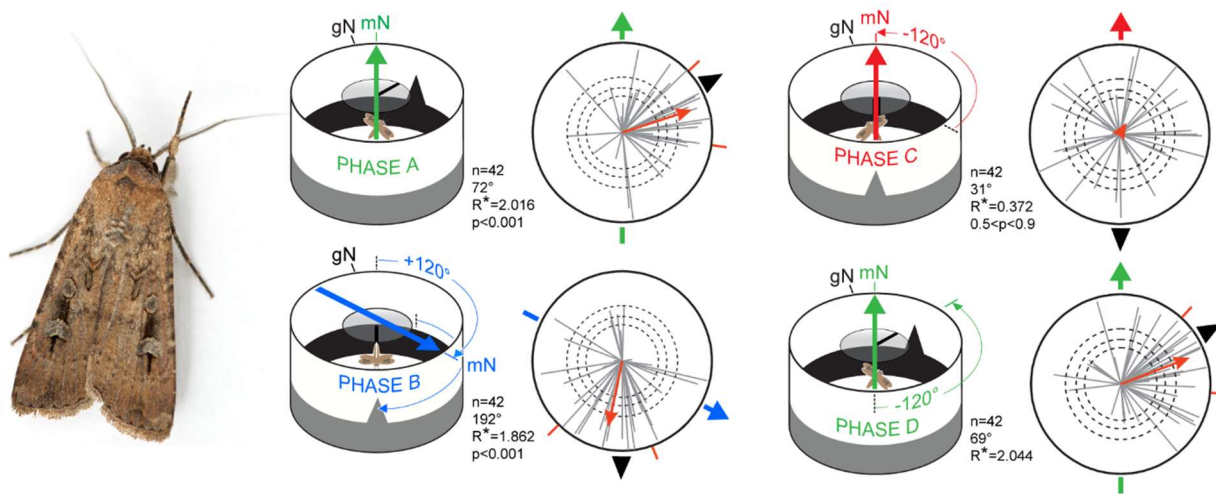
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643 **Figure 4. Migratory orientation in Bogong moths is multimodal.** Individual moths were
 644 tethered at the centre of a cylindrical Perspex flight arena placed vertically on a table outdoors.
 645 Moths were then attached to the end of a vertical shaft connected to an encoder that continuously
 646 measured the instantaneous orientations of steadily flying moths that were free to turn in any
 647 azimuthal direction. Each moth was then subjected to magnetic and visual cues during four 5-
 648 minute phases (A to D) and their directions and directedness (orientation and length,
 649 respectively, of grey vectors in circular plots) measured. When the positions of the magnetic
 650 field (heavy coloured arrows) and visual landmarks (black triangular ‘mountain’ and dorsal
 651 stripe) are correlated and turned together (Phases A, B and D), moths (n=42, grey vectors), the
 652 moth population (grey vectors) remains significantly oriented near the landmarks (as indicated
 653 by the long (highly directed) red population mean vectors; $p < 0.001$). When the two cues are set
 654 in conflict (Phase C), moths become disoriented (as indicated by the short (undirected) red
 655 population mean vector; $0.5 < p < 0.9$). The directedness (length) of the population mean vector is
 656 given by its R^* value: the greater the R^* value, the more directed the population of moths it

657 represents. The R^* value also reveals the likelihood that the mean flight direction of a population
658 of moths – where each moth has its own direction and directedness (direction and length of grey
659 vectors) – differs significantly from a random, undirected population (according to the Moore’s
660 modified Rayleigh test: Moore, 1980). Dashed circles: required R^* value for statistical
661 significance (i.e. the R^* value required to reliably distinguish the directedness of the population
662 from a random, undirected population): $p < 0.05$, $p < 0.01$ and $p < 0.001$, respectively for increasing
663 radius. Outer radius of plots: $R^* = 2.5$. Red radial dashes: 95% confidence interval. gN,
664 geographic North. mN, magnetic North. Data are from Dreyer et al., 2018.
665