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1 **Over 50 years of behavioural evidence on the magnetic sense in animals – What has been** 2 **learnt?**

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7
8 **Abstract** Magnetoreception is a key element in the sensory repertoire of many organisms, and it has
9 been shown to play a role particularly in animal navigation. While the first data to demonstrate a
10 magnetic compass in songbirds through behavioural measures has been presented already decades
11 ago, studies of behaviour are still the main source of information in learning about the magnetic
12 senses. The behavioural evidence is, however, scattered with sometimes contradictory results. Partly,
13 this is a consequence of a wide spectrum of methods used across multiple research groups studying
14 different model organisms. This has limited the ability of researchers to pin down exactly how and
15 why animals use the Earth's magnetic field cues. Here we lay out how a range of methods for testing
16 behaviour spanning from field observations to laboratory manipulations can be used to test for a
17 magnetic sense in animals. To this end, we discuss the principal limitations of behavioural testing in
18 telling us how animals sense the magnetic field, and we argue that behaviour must go hand in hand
19 with other fields to advance our understanding of the magnetic sense.

20 21 **Introduction**

22 More than 50 years ago, the first clear evidence that animals respond to changes in the Earth's
23 magnetic field was provided [1]. Surprisingly, behavioural responses to changes in the magnetic field
24 remain the clearest evidence that animals have a magnetic sense. This behavioural evidence is
25 widespread but is scattered with contradictory results. Partly, this is a consequence of a wide
26 spectrum of methods used across multiple research groups studying different model organisms. This
27 has limited the ability of researchers to pin down exactly how and why animals use the Earth's
28 magnetic field. Here we look at how a range of experimental methods for testing behaviour can be
29 used to test for the magnetic sense in animals and ask if they have provided answers to the follow key
30 questions:

31 **I. Are animals sensitive to magnetic fields?**

32 Is there clear support for the hypothesis that an animal is behaving in response the Earth's magnetic
33 field, or could behaviours that are suggestive of a magnetic sense be due to a side-effect of the testing
34 method itself?

35 **II. Does the behavioural evidence suggest a use for their magnetic sense?**

36 If it is established that an animal is sensitive to magnetic fields, does the behavioural evidence give
37 clear indications about whether an animal is using their sense for a purpose; why they possess this
38 sense? Does the evidence explain how it contributes to their wider ecology, or evolutionary fitness?

39 **III. What is the physiological mechanism that underpins this sense?**

40 There are multiple established theories for the mechanism by which a magnetic sense might work.
41 These are the radical-pair hypothesis [2], [3], the magnetic particle-based magnetoreception
42 hypotheses [4], and electromagnetic induction [5]. Is it possible, using experiments assessing animal
43 behaviour, to determine if an animal possesses one of these sensing mechanisms?

44 **IV. Where is it located?**

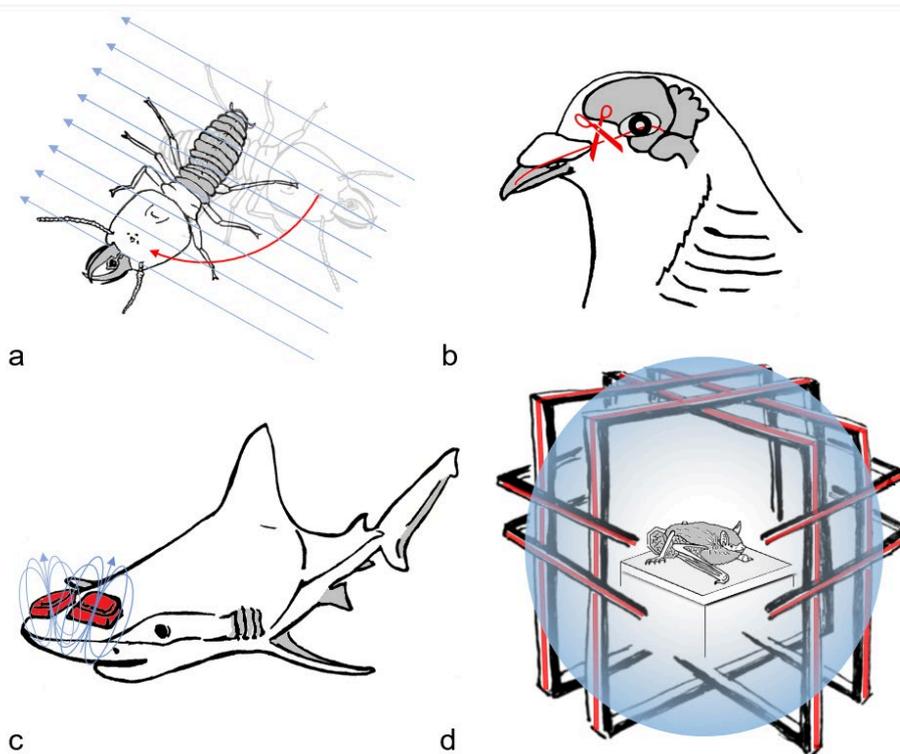
45 There are many possible locations for a magnetoreceptor and these vary across species. To what
46 extent can the behavioural evidence provide answers to the physiological location of an animals'
47 magnetic sense?

48 **V. Is there emphatic proof that an animal is *not* magneto-sensitive?**

49 If a behavioural response suggests that an animal is not responding to a magnetic treatment, then
50 how context specific might this be? Could there be other contexts in which it might be expected that
51 a magneto-responsive behaviour is present, and to what degree can it be concluded, on the
52 behavioural evidence produced, that an animal does not possess a magnetic sense?

53

54 **1. Types of behavioural experiments**



55

56 **Fig. 1** Behavioural testing of animal magnetic sensing in the laboratory and the wild. Typically,
57 measures range from **a** observing body alignment in inactive or moving animals, e.g., in termites
58 which occupy resting positions perpendicular to the magnetic field direction [6], to
59 manipulations of the animal or its immediate surroundings. Numbing or removing the
60 (nerve)tissues **b** or organs, or knocking out genes, thought to form the basis of a magnetic
61 sensory system allows the localisation of body parts involved (e.g., [7] or [8]). Direct alteration of
62 the perceivable magnetic field can be achieved by attaching magnets to the body (typically the

63 head **c**, e.g. [9] or [10]) or placing magnets in the near environment (e.g., [11]). Magnets are
64 thought to disrupt magnetoreception, leading to impaired orientation and navigation. In
65 contrast, controlled manipulation of field cues (intensity, inclination and polarity angles) using
66 magnetic coil systems **d** enables experimenters also to predict directions of movement: Inside
67 the altered magnetic field (e.g., [12] or [13]), or even outside of a coil system, if the effect on the
68 biomagnetic sensory system is longer lasting such as after a so-called magnetic pulse (e.g., [14]),
69 or in case a compass system is calibrated for later use (e.g., [14])
70

71 **2.1. Alignment observations**

72 Magnetic alignment is a behavioural observation that animals may align their bodies in some
73 consistent orientation in the Earth's magnetic field (Fig. 1a). This phenomenon tends to occur when
74 animals are at rest, or not exhibiting behaviours that would otherwise mask such an underlying
75 orientation [15]. Magnetic alignment can be tested by direct observation, analysing satellite images,
76 using GPS, or many other tracking methodologies. In the laboratory, it could also be tested using
77 magnetic orientation shifts, e.g. in Helmholtz coils (see section 2.4). Indirectly, the shielding of study
78 animals from the natural magnetic field, e.g. using a Mu-metal chamber, may serve as a test for the
79 abandonment of magnetic alignment behaviour [6], [16]. Magnetic alignment along the North/South
80 axis has been observed in cows when grazing and deer when resting [17], Dogs were reported to show
81 North/South magnetic alignment when defecating [18], and also in preparation for homing [19].
82 Although magnetic alignment appears to play a role in a number of vertebrate species [20]–[23],
83 recent attempts at replication, e.g. on cows [24], [25] and dogs [26], failed to obtain similar results.
84 Careful consideration of the observational circumstances are needed so that environmental factors
85 (e.g., the slope of the terrain or close proximity to powerlines), measurement inaccuracies, animal
86 social behaviour, and unconscious observer bias do not confound the result [26]–[28]. Similarly,
87 pigeons have been found to align along field lines prior to homing [29], and ducks before landing on
88 water [30]. Foxes tend to align their bodies in a North Easterly direction when pouncing on prey, and
89 in the cases when they do this they are more successful in their hunting [31]. Magnetic alignment has
90 been documented in many insect taxa, this includes resting termites [6], mosquitos [32], bees [33] and
91 sandhoppers [34].

92 Whilst a finding of magnetic alignment does suggest that an animal is in some way sensitive to
93 magnetic fields, the purpose of this behaviour is not always clear. An unconscious ability to rest or
94 move in a particular direction may be an incredibly useful orientational tool. For example, groups of
95 animals could benefit if group members act well-coordinated, i.e. directed, in dangerous situations
96 such as landing manoeuvres [30] or flight from potential predators [35]. However, behavioural
97 evidence of magnetic alignment alone is insufficient to confirm much more than an ability to sense
98 magnetic fields. Furthermore, a lack of behavioural evidence for magnetic alignment in an animal does
99 not mean that they cannot sense magnetic fields as there may be many other contexts in which a
100 behavioural response to magnetic fields would occur.

101 **2.2. Magnets**

102 Attaching a magnet to an animal is perhaps the most basic experimental manipulation to test for a
103 magnetic sense (Fig. 1c). Remarkably, this simple technique has produced conflicting results even
104 within animals of the same species. Experiments on domestic pigeons possibly above all others have

105 created divides within the scientific community regarding their use (or not) of a magnetic sense for
106 navigation [36]–[38]. Testing whether magnetoreception is used for navigation in pigeons is
107 deceptively difficult because in the hierarchy of navigational cues, experiments suggest that the
108 Earth’s magnetic field tends to fall below many others such as visual landmarks, the sun compass, and
109 olfactory cues. It may be that only when alternative cues are unavailable will an animal turn to using
110 magnetoreception. In the case of magnets on a pigeon, experiments have shown that when cloudy,
111 magnets cause disorientation, but not when skies are clear [39]. Attempts to repeat this finding failed
112 to obtain the same results [40]. It was later reported that different placements of magnets on the
113 pigeons’ bodies can alter their disruptive effect [41]. Other experiments using magnets, investigating
114 the degree to which a magnetic sense can alleviate orientation error in clock-shifted pigeons, have
115 also both failed [37] and succeeded [36], [38], [42] in finding an effect. It has been suggested that
116 magnets may not provide sufficient disruption to disable the ability to navigate using a magnetic sense
117 [43], which may explain the disparity in results or indirectly points towards the magnetoreception
118 pathway at play. One attempt of increasing the disruptive effect were “mobile magnets”: magnets in
119 a capsule that change their position on the head of a bird when the bird moves its head. However,
120 when applied to freely flying wandering albatrosses, this refinement did also not interfere with their
121 homing ability [44]. Despite this, in more controlled experiments where a species of songbird did not
122 move freely it was demonstrated that magnets fixed on the bird’s heads have a disruptive effect on
123 their ability to orient [10].

124 There have been many other experimental uses of magnets for the testing of a magnetic sense
125 in animals other than birds. The magnetic object assay investigates the magnetic sense of animals by
126 placing a magnet in their vicinity and looking at how the animal behaves around the magnetic object
127 vs controls. This method has revealed that several rodent species are attracted to the presence of a
128 magnet [11]. Magnets placed in the habitat of nudibranchs alter their movement [45], and
129 magnetotaxis has been observed in *Caenorhabditis elegans* [46]. It is even possible to train dogs to
130 locate magnets [47].

131 Unusual or disrupted behaviour in the presence of a magnet is certainly suggestive of a
132 sensitivity to magnetic fields. It is difficult, however, to ascertain whether or not behavioural changes
133 to magnets are a conscious response with an adaptive purpose, or a discomfort, disorientation, or
134 interest-in the presence of unusual stimuli. Furthermore, it is also difficult to draw any conclusions
135 about the sensing mechanism by which the magnetic sense is based using magnets. It is theorised that
136 magnets may not fully disrupt the ability of a radical pair mechanism to be used as a navigational cue,
137 but because some disruption is still possible, the possibility of a radical pair mechanism cannot be
138 eliminated [43]. The same is true for the theory of a magnetic induction mechanism, which was once
139 thought to be unaffected by magnets, but this has been called into question [48]. The location of
140 magnets can also have an effect on behavioural response especially if attached to larger animals [41],
141 but it may be difficult to achieve the precision necessary to use magnets to pin down the location of
142 a magneto-receptor. Considering that both positive and negative results have been obtained in the
143 same animal species for the effect of magnets, it might be unwise to rule out a magnetic sense in an
144 animal that has not had a behavioural response to the presence of a magnet [44].

145 **2.3. Sensory ablation**

146 Theories on the bodily location of a magnetoreceptor have inspired scientists to try to disable the
147 behavioural response to magnetic fields by removing or numbing the respective physiological organ.

148 It has been proposed that a magnetite-based receptor may be located in the cornea of some magneto-
149 sensitive animals [49]. Anesthetising the eyes of mole-rats has been shown to cause magnetically
150 responsive behaviour to cease, while other behaviours remained stable [50]. The same result in mole-
151 rats has also been obtained by surgically removing their eyes [51]. The navigational ability of migrating
152 bats, thought to be in-part aided by a magnetic sense, based on data from non-migratory species [14],
153 is also affected by the numbing of the cornea [52]. In pigeons, anaesthesia to the upper beak and
154 surgery to the trigeminal nerve was reported to disable their ability to detect magnetic fields in a
155 discrimination experiment (Fig. 1b), suggesting that a sensor based on magnetite was located in their
156 upper beak [53]. However, other researchers found that surgically disabling the trigeminal nerve did
157 not impact upon navigation performance in pigeons [54]. It was later discovered that the architecture
158 hypothesised for magnetosensitivity in birds at the time was not present in the upper beak of pigeons
159 [55], calling into question the results of previous behavioural experiments, and opening the door to
160 other possible sources of the magnetic sense in birds. Other than surgical ablation, in invertebrates,
161 genetic manipulations to silence the *Cry* gene have also been used to disable magnetosensitive
162 behaviour [56]–[58]

163 Whilst there are clear ethical questions regarding surgery as a method for removing the
164 presumed organ involved in magnetic sensing, it is preferred by some to anesthetising because of the
165 short-lasting and possible non-specific effect of drugs [51], [59]. Clearly, however, non-specific
166 behavioural effects are also likely to be present in the case of surgical removal of organs, especially
167 the eyes. Sensory ablation can allow researchers to narrow down the location of an animal's magnetic
168 sense, but it may be difficult to be sure that only the magnetic sense has been removed, and therefore
169 that behavioural changes are not caused by other sensory or structural damage.

170 **2.4. Magnetic coil systems**

171 Controlling and re-creating a magnetic field is a powerful tool for the behavioural testing of a magnetic
172 sense (Fig. 1d). Helmholtz or Merritt coils, for example, allow the Earth's magnetic field to be altered
173 [60]. Researchers may change the orientation of the field, create a new magnetic field that resembles
174 one elsewhere on Earth, or create unusual field conditions. The main limitation of this technique is
175 that the magnetic field is altered within a limited space between the coils. This space can be large
176 enough for arena experiments on small animals, like insects, but for larger animals this can limit the
177 scope for possible behaviours that can be tested and observed. Birds can be tested for the presence
178 of a magnetic sense inside a magnetic coil using an Emlen funnel. Within this inverted cone, a bird
179 who is motivated to fly will make marks or scratches on the side of the funnel which can then be
180 assessed in order to determine the orientation of their preferred movement direction [61]. Using this
181 technique, many species of birds have been shown to use the Earth's magnetic field as a navigational
182 cue [12], [13], [62], particularly also in combination with sensory ablation [63], [64]; see section 2.3.
183 Usage of environmental magnetic fields can be both as a compass, and a map. A magnetic compass is
184 investigated by changing the orientation of the magnetic field or cancelling out its horizontal
185 component [65]. A magnetic map can be examined by performing a virtual displacement, whereby the
186 parameters of the magnetic field are shifted to resemble those that exist elsewhere. This technique
187 has shown that different values of magnetic intensity and inclination can cause the orientation of
188 many animals to shift in relation to the physical location on Earth that matches the new magnetic
189 parameters. Because it is possible to change the magnetic inclination and intensity within a magnetic
190 coil system independently, researchers can examine whether a magnetic sense is responsive to

191 inclination [57] and/or intensity [66]. When celestial cues are present, then an animal's sensitivity to
192 magnetic declination can also be tested with manipulation of the field orientation or celestial cue
193 location. If used as part of a navigational map, declination can significantly improve its usefulness for
194 precise localisation. This is because inclination and intensity have strikingly similar gradients of change
195 in many areas across the Earth's surface, and so used alone, they may not translate to precise
196 locations [67]. Helmholtz coils have been used to show that Eurasian reed warblers can be sensitive
197 to changes in magnetic declination [13]. Arena experiments with smaller animals, or simplified coils,
198 can be used to train animals to learn to use the orientation of the magnetic field within the arena as
199 a navigational cue [68]. Experiments are also possible that allow a virtual gradient of a magnetic field
200 within a coil by tracking the location of the animal inside the coil and modifying the parameters of the
201 magnetic field accordingly [69].

202 Whilst magnetic coil systems have the potential to reveal many aspects of an animal's
203 magnetic sense, they are not without limitations. Sudden changes of magnetic fields are known to
204 initiate stress responses, among many other physiological and behavioural reactions [70]–[73] that
205 may influence orientation response and therefore confound results [74]. Even in humans, it has been
206 shown that unusual changes in the magnetic field, such as those that occur to people within the
207 International Space Station, have a psychophysiological impact [75]. Furthermore, it has been shown
208 that in physical displacement experiments, diurnal animals that have been kept in the dark, and
209 therefore potentially stressed and/or unable to update their magnetic map enroute, have unusual
210 orientations compared to those with access to daylight [76]. It is therefore important to highlight that
211 a sudden change in the magnetic field, as is standard practice for virtual displacement experiments, is
212 an unnatural event that has the potential to cause unwanted physiological and behavioural side
213 effects. It is also important to note that a magnetic coil is not sufficient to determine whether or not
214 an animal has a magnetic sense. There are many contexts that are extremely difficult to model inside
215 a coil setup, such as unrestricted flight or behaviour of large animals, that may be necessary in order
216 for a magnetic sense to reveal itself.

217 **2.5. Magnetic interference – pulsing and RF fields**

218 If an animal possesses a magnetite-based receptor, then it is thought that their ability to sense
219 magnetic fields will be disrupted by a magnetic pulse designed to temporarily re-polarise a magnet,
220 whilst a radical pair type receptor would be unaffected [77]. Some researchers have also suggested
221 that a magnetic pulse can disrupt an animal's ability to use a magnetic map, but not a magnetic
222 compass [78]. In contrast, a radical pair mechanism is understood to be disrupted by weak radio-
223 frequency (RF) fields [3], but no disruption should be caused to an animal with a magnetite-based
224 receptor. Assessment of behavioural responses to applications of magnetic pulses and RF fields has
225 therefore become a popular technique for investigating the source and use of a magnetic sense. This
226 may become less informative, however, when considering that some animals may possess both a
227 magnetite and radical pair mechanism [79]. Bird navigation, for example, is disrupted both by RF fields
228 [80], [81] and magnetic pulsing [77], [82], [83]. In addition, the presence of many negative results
229 where bird behaviour has not been altered by magnetic interference further confounds any attempts
230 to make taxon-wide conclusions [84]–[86]. In animals possessing both receptor types, it may be that
231 one is preferred or used in different contexts or roles, such as either a map or compass ability.
232 Evidence that pulses affect adult but not juvenile migrating birds is one such context [83], [87].
233 However, this may be another oversimplification, as despite arguments to the contrary [78], both

234 magnetite and radical pair receptors have the potential to attain both map and compass information
235 [2], [88]. Therefore, without extremely careful and well controlled experimental design, it may be
236 challenging to gain great insights from behavioural experiments using magnetic interference, and
237 again, any behavioural responses to magnetic interference should be interpreted in light of the many
238 psychophysiological effects that can result from magnetic field exposure [89]–[91].

239 **2.6. Light exposure**

240 The radical pair mechanism is reliant upon certain wavelengths of light in order to function correctly
241 as a magnetic sense [2], [92]. Controlling the light which reaches an animal is used as a possible test
242 of whether or not they possess a radical-pair based magnetic sense. Light has been shown to control
243 the magnetic sense in many animals [93], which has been recently reported even for humans [94].
244 The effect of light is not a binary switch however, it is possible that magnetically responsive behaviours
245 can continue for as long as 24 hours since light was present [95], [96].

246 A clear drawback of removing light is that it may be a prerequisite for behaviours that are magnetically
247 responsive, such as navigation, to require light in order for them to be performed in the first place
248 even in nocturnal animals that live just under very “dim” light conditions. Therefore, this method may
249 not be appropriate for some behavioural tests or specific animals. At least, removal of light – also
250 called “total darkness experiments” – require extremely well controlled testing conditions that can be
251 a challenge to create.

252 **2.7. Observation – other**

253 Other behavioural evidence to support a magnetic sense can be found in correlations between animal
254 movement trends and changes in the Earth’s magnetic field over time [97]. The locations of ringed
255 birds over the last century have shown that birds use inclination as a ‘stop sign’ to inform when to end
256 their migration [98], [99]. A species of whale was reported to become stranded more frequently on
257 days when strong solar storms alter the Earth’s magnetic field [100], and pigeon homing performance
258 is also reduced during solar storms [101]. This method seems unlikely to be able to make strong
259 inferences about the nature of the magnetic sense however, suffering the same limitations as the
260 other techniques.

261 **3. Summary**

262 There is certainly a vast collection of behavioural evidence to show that many animals are sensitive to
263 magnetic fields. The magnetic sense appears to have a wide variety of uses, from navigation [102], to
264 a role in helping to catch prey [31]. This array of ecological uses for a magnetic sense can conversely
265 make it difficult to detect, even though it may be more likely that an animal has a magnetic sense than
266 not. Behaviours associated with magnetic cues can prioritise other environmental cues, and may be
267 revealed only when an animal has nothing else to rely on. This makes designing behavioural
268 experiments that are both realistic (not so unnatural that an animal is deterred from reacting to a
269 treatment), and successful (enough environmental stimuli is controlled so that an animal will respond
270 to magnetic cues) a challenging task. Furthermore, the context in which an animal may respond to
271 magnetic fields may be elusive and hard to predict. There are also a variety of psychophysiological
272 effects of magnetic fields that may lead to both false positives and negatives in behavioural
273 experiments. As model organisms for the study of magnetoreception become established, who have
274 predictable and easily repeatable behavioural responses, then a combination of behavioural

275 experiments can allow the underlying physiological mechanisms underpinning magnetic sensing to be
276 revealed, though crossover between mechanisms and differences between species may be limiting.
277 Behavioural evidence for a magnetic sense over the last 50 years is still largely restricted to data
278 supporting the hypothesis that many animals can sense magnetic fields and the way that they can use
279 it. While behaviour has been used to attempt to infer the nature of the magnetic sensing mechanism,
280 this has resulted in equivocal results, and so at this point, it may be concluded that behaviour alone
281 cannot tell us how animals sense the magnetic field. This may change once a clear mechanism or
282 mechanisms for sensing the magnetic field have been revealed however, and so behaviour must go
283 hand in hand with other fields to understand the nature of the magnetic sense.

284

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288

289 Data Availability Statement

290 No Data associated in the manuscript.

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