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Over 50 years of behavioural evidence on the magnetic sense in animals: what has been learnt?

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

1 Introduction

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

1.1 Are animals sensitive to magnetic fields?

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

1.2 Does the behavioural evidence suggest a use for their magnetic sense?

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

1.3 What is the physiological mechanism that underpins this sense?

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

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1.4 Where is it located?

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

1.5 Is there emphatic proof that an animal is not magneto-sensitive?

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

2 Types of behavioural experiments

2.1 Alignment observations

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

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

2.2 Magnets

Attaching a magnet to an animal is perhaps the most basic experimental manipulation to test for a magnetic sense (Fig. 1c). Remarkably, this simple technique has produced conflicting results even within animals of the same species. Experiments on domestic pigeons possibly above all others have created divides within the scientific community regarding their use (or not) of a magnetic sense for navigation [36–38]. Testing whether magnetoreception is used for navigation in pigeons is deceptively difficult because in the hierarchy of navigational cues, experiments suggest that the Earth's magnetic field tends to fall below many others such as visual landmarks, the sun compass, and olfactory cues. It may be that only when alternative cues are unavailable will an animal turn to using magnetoreception. In the case of magnets on a pigeon, experiments have shown that when cloudy, magnets cause disorientation, but not when skies are clear [39]. Attempts to repeat this finding failed to obtain the same results [40]. It was later reported that different placements of magnets on the pigeons' bodies can alter their disruptive effect [41]. Other experiments using magnets, investigating the degree to which a magnetic sense can alleviate orientation error in clock-shifted pigeons, have also both failed [37] and succeeded [36, 38, 42] in finding an effect. It has been suggested that magnets may not provide sufficient disruption to disable the ability to navigate using a magnetic sense [43], which may explain the disparity in results or indirectly points towards the magnetoreception pathway at play. One attempt of increasing the disruptive effect was "mobile magnets": magnets in a capsule that change their position on the head of a bird when the bird moves its head. However, when applied to freely flying wandering albatrosses, this refinement did also not interfere with their homing ability [44]. Despite this, in more controlled experiments where a species of songbird did not move freely, it was demonstrated that magnets fixed on the bird's heads have a disruptive effect on their ability to orient [10].

There have been many other experimental uses of magnets for the testing of a magnetic sense in animals

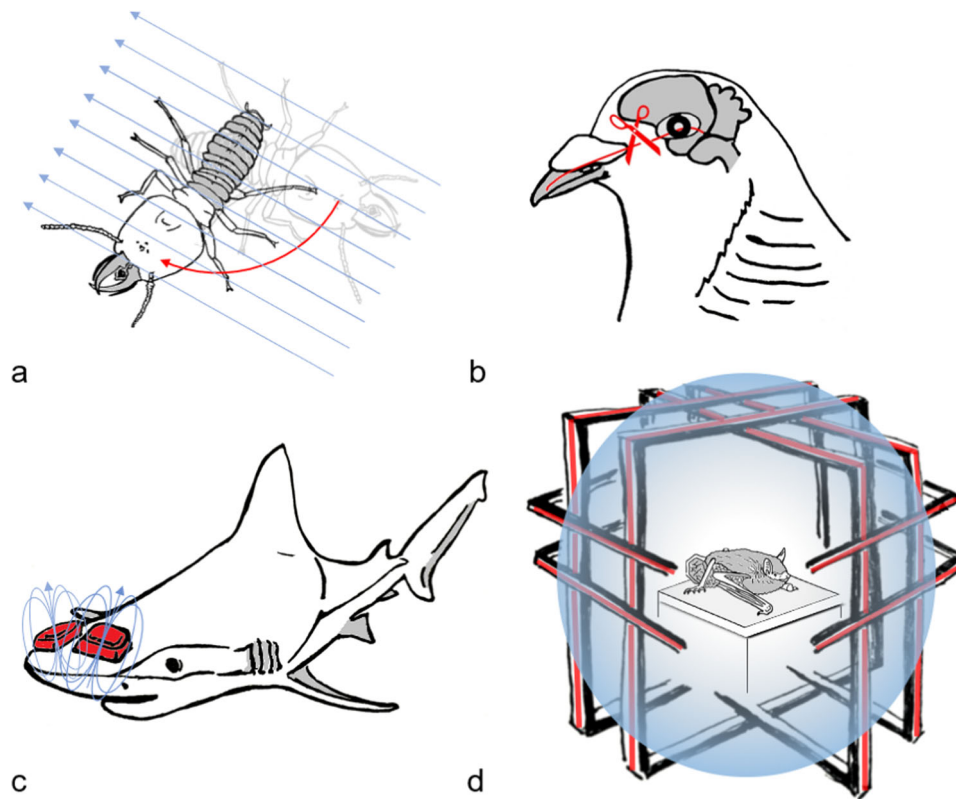


Fig. 1 Behavioural testing of animal magnetic sensing in the laboratory and the wild. Typically, measures range from **a** observing body alignment in inactive or moving animals, e.g. in termites which occupy resting positions perpendicular to the magnetic field direction [6], to manipulations of the animal or its immediate surroundings. Numbing or removing the (nerve)tissues **b** or organs, or knocking out genes, thought to form the basis of a magnetic sensory system allows the localisation of body parts involved (e.g. [7] or [8]). Direct alteration of the perceivable magnetic field can be achieved by attaching magnets to the body (typically the head **c**, e.g. [9] or [10]) or placing magnets in the near environment (e.g. [11]). Magnets are thought to disrupt magnetoreception, leading to impaired orientation and navigation. In contrast, controlled manipulation of field cues (intensity, inclination and polarity angles) using magnetic coil systems **d** enables experimenters to predict directions of movement inside the altered magnetic field (e.g. [12] or [13]), or even outside of a coil system if the effect on the biomagnetic sensory system is longer lasting such as after a so-called magnetic pulse (e.g. [14]), or in the case of a compass system which is calibrated for later use (e.g. [14])

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

Unusual or disrupted behaviour in the presence of a magnet is certainly suggestive of a sensitivity to magnetic fields. It is difficult, however, to ascertain whether or not behavioural changes to magnets are a conscious response with an adaptive purpose, or a discomfort, disorientation, or interest-in the presence of unusual stimuli. Furthermore, it is also difficult to draw any conclusions about the sensing mechanism by which the magnetic sense is based using magnets. It is theorised that magnets may not fully disrupt the ability of a radical

pair mechanism to be used as a navigational cue, but because some disruption is still possible, the possibility of a radical pair mechanism cannot be eliminated [43]. The same is true for the theory of a magnetic induction mechanism, which was once thought to be unaffected by magnets, but this has been called into question [48]. The location of magnets can also have an effect on behavioural response especially if attached to larger animals [41], but it may be difficult to achieve the precision necessary to use magnets to pin down the location of a magneto-receptor. Considering that both positive and negative results have been obtained in the same animal species for the effect of magnets, it might be unwise to rule out a magnetic sense in an animal that has not had a behavioural response to the presence of a magnet [44].

2.3 Sensory ablation

Theories on the bodily location of a magneto-receptor have inspired scientists to try to disable the behavioural response to magnetic fields by removing or numbing the respective physiological organ. It has been proposed that a magnetite-based receptor may be located in the cornea of some magneto-sensitive animals [49]. Anaesthetising the eyes of mole-rats has been shown to cause magnetically responsive behaviour to cease, while other behaviours remained stable [50]. The same result in mole-rats has also been obtained by surgically removing their eyes [51]. The navigational ability of migrating bats, thought to be in-part aided by a magnetic sense, based on data from non-migratory species [14], is also affected by the numbing of the cornea [52]. In pigeons, anaesthesia to the upper beak and surgery to the trigeminal nerve was reported to disable their ability to detect magnetic fields in a discrimination experiment (Fig. 1b), suggesting that a sensor based on magnetite was located in their upper beak [53]. However, other researchers found that surgically disabling the trigeminal nerve did not impact upon navigation performance in pigeons [7]. It was later discovered that the architecture hypothesised for magnetosensitivity in birds at the time was not present in the upper beak of pigeons [54], calling into question the results of previous behavioural experiments, and opening the door to other possible sources of the magnetic sense in birds. Other than surgical ablation, in invertebrates, genetic manipulations to silence the *Cry* gene have also been used to disable magneto-sensitive behaviour [55–57].

Whilst there are clear ethical questions regarding surgery as a method for removing the presumed organ involved in magnetic sensing, it is preferred by some to anaesthetising because of the short-lasting and possible non-specific effect of drugs [51, 58]. Clearly, however, non-specific behavioural effects are also likely to be present in the case of surgical removal of organs, especially the eyes. Sensory ablation can allow researchers to narrow down the location of an animal's magnetic sense, but it may be difficult to be sure that only the magnetic sense has been removed, and therefore that behavioural changes are not caused by other sensory or structural damage.

2.4 Magnetic coil systems

Controlling and re-creating a magnetic field is a powerful tool for the behavioural testing of a magnetic sense (Fig. 1d). Helmholtz or Merritt coils, for example, allow the Earth's magnetic field to be altered [59]. Researchers may change the orientation of the field, create a new magnetic field that resembles one elsewhere on Earth, or create unusual field conditions. The main limitation of this technique is that the magnetic field is altered within a limited space between the coils. This space can be large enough for arena experiments on small animals, like insects, but for larger animals this can limit the scope for possible behaviours that can be

tested and observed. Birds can be tested for the presence of a magnetic sense inside a magnetic coil using an Emlen funnel. Within this inverted cone, a bird who is motivated to fly will make marks or scratches on the side of the funnel which can then be assessed in order to determine the orientation of their preferred movement direction [60]. Using this technique, many species of birds have been shown to use the Earth's magnetic field as a navigational cue [12, 13, 61], particularly also in combination with sensory ablation [8, 62]; see Sect. 2.3. Usage of environmental magnetic fields for navigation can be both as a compass, and a map. A magnetic compass is investigated by changing the orientation of the magnetic field or cancelling out its horizontal component [63]. A magnetic map can be examined by performing a virtual displacement, whereby the parameters of the magnetic field are shifted to resemble those that exist elsewhere. This technique has shown that different values of magnetic intensity and inclination can cause the orientation of many animals to shift in relation to the physical location on Earth that matches the new magnetic parameters. Because it is possible to change the magnetic inclination and intensity within a magnetic coil system independently, researchers can examine whether a magnetic sense is responsive to inclination [56] and/or intensity [64]. When celestial cues are present, then an animal's sensitivity to magnetic declination can also be tested with manipulation of the field orientation or celestial cue location. If used as part of a navigational map, declination can significantly improve its usefulness for precise localisation. This is because inclination and intensity have strikingly similar gradients of change in many areas across the Earth's surface, and so used alone, they may not translate to precise locations [65]. Helmholtz coils have been used to show that Eurasian reed warblers can be sensitive to changes in magnetic declination [13]. Arena experiments with smaller animals, or simplified coils, can be used to train animals to learn to use the orientation of the magnetic field within the arena as a navigational cue [66]. Experiments are also possible that allow a virtual gradient of a magnetic field within a coil by tracking the location of the animal inside the coil and modifying the parameters of the magnetic field accordingly [67].

Whilst magnetic coil systems have the potential to reveal many aspects of an animal's magnetic sense, they are not without limitations. Sudden changes of magnetic fields are known to initiate stress responses, among many other physiological and behavioural reactions [68–71] that may influence orientation response and, therefore, confound results [72]. Even in humans, it has been shown that unusual changes in the magnetic field, such as those that occur to people within the International Space Station, have a psychophysiological impact [73]. Furthermore, it has been shown that in physical displacement experiments, diurnal animals that have been kept in the dark, and therefore potentially stressed and/or unable to update their magnetic map enroute, have unusual orientations compared to those with access to daylight [74]. It is therefore important to highlight that a sudden change in the magnetic

field, as is standard practice for virtual displacement experiments, is an unnatural event that has the potential to cause unwanted physiological and behavioural side effects. It is also important to note that a magnetic coil is not sufficient to determine whether or not an animal has a magnetic sense. There are many contexts that are extremely difficult to model inside a coil setup, such as unrestricted flight or behaviour of large animals, that may be necessary in order for a magnetic sense to reveal itself.

2.5 Magnetic interference: pulsing and RF fields

If an animal possesses a magnetite-based receptor, then it is thought that their ability to sense magnetic fields will be disrupted by a magnetic pulse designed to temporarily re-polarise a magnet, whilst a radical pair type receptor would be unaffected [75]. Some researchers have also suggested that a magnetic pulse can disrupt an animal's ability to use a magnetic map, but not a magnetic compass [76]. In contrast, a radical pair mechanism is understood to be disrupted by weak radio-frequency (RF) fields [3], but no disruption should be caused to an animal with a magnetite-based receptor. Assessment of behavioural responses to applications of magnetic pulses and RF fields has, therefore, become a popular technique for investigating the source and use of a magnetic sense. This may become less informative, however, when considering that some animals may possess both a magnetite and radical pair mechanism [77]. Bird navigation, for example, is disrupted both by RF fields [78, 79] and magnetic pulsing [75, 80, 81]. In addition, the presence of many negative results where bird behaviour has not been altered by magnetic interference further confounds any attempts to make taxon-wide conclusions [82–84]. In animals possessing both receptor types, it may be that one is preferred or used in different contexts or roles, such as either a map or compass ability. Evidence that pulses affect adult but not juvenile migrating birds is one such context [81, 85]. However, this may be another oversimplification, as despite arguments to the contrary [76], both magnetite and radical pair receptors have the potential to attain both map and compass information [2, 86]. Therefore, without extremely careful and well-controlled experimental design, it may be challenging to gain great insights from behavioural experiments using magnetic interference, and again, any behavioural responses to magnetic interference should be interpreted in light of the many psychophysiological effects that can result from magnetic field exposure [87–89].

2.6 Light exposure

The radical pair mechanism is reliant upon certain wavelengths of light in order to function correctly as a magnetic sense [2, 90]. Controlling the light which reaches an animal is used as a possible test of whether or not they possess a radical pair-based magnetic sense. Light has been shown to control the magnetic sense in

many animals [91], which has been recently reported even for humans [92]. The effect of light is not a binary switch; however, it is possible that magnetically responsive behaviours can continue for as long as 24 h since light was present [93, 94].

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

2.7 Observation: other

Other behavioural evidence to support a magnetic sense can be found in correlations between animal movement trends and changes in the Earth's magnetic field over time [95]. The locations of ringed birds over the last century have shown that birds use inclination as a ‘stop sign’ to inform when to end their migration [96, 97]. A species of whale was reported to become stranded more frequently on days when strong solar storms alter the Earth's magnetic field [98], and pigeon homing performance is also reduced during solar storms [99]. This method seems unlikely to be able to make strong inferences about the nature of the magnetic sense, however suffering the same limitations as the other techniques.

3 Summary

There is certainly a vast collection of behavioural evidence to show that many animals are sensitive to magnetic fields. The magnetic sense appears to have a wide variety of uses, from navigation [100], to a role in helping to catch prey [31]. This array of ecological uses for a magnetic sense can conversely make it difficult to detect, even though it may be more likely that an animal has a magnetic sense than not. Behaviours associated with magnetic cues can prioritise other environmental cues, and may be revealed only when an animal has nothing else to rely on. This makes designing behavioural experiments that are both realistic (not so unnatural that an animal is deterred from reacting to a treatment), and successful (enough environmental stimuli is controlled so that an animal will respond to magnetic cues) a challenging task. Furthermore, the context in which an animal may respond to magnetic fields may be elusive and hard to predict. There are also a variety of psychophysiological effects of magnetic fields that may lead to both false positives and negatives in behavioural experiments. As model organisms for the study of magnetoreception become established, with predictable and easily repeatable behavioural responses, then a combination

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

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