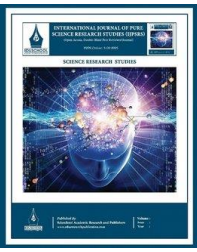
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Magnetoreception and Navigation in Migratory Animals: Mechanisms and Evidence

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Abstract

Animals as different as songbirds, sea turtles, salmon and butterflies reach destinations they have never seen, and part of the information they use comes from the geomagnetic field. This review separates the two capacities involved, a compass that reads direction and a map that estimates position, and examines the evidence for each. Behavioural work in orientation cages established that the avian compass responds to the inclination of field lines rather than to their polarity, that it requires light of short wavelength, and that it is disrupted by weak radio-frequency fields. These properties point to a quantum mechanism in which a light-induced radical pair interconverts between singlet and triplet states at a rate that depends on the orientation of the molecule in the field, and cryptochrome proteins from the retina of a migratory songbird show magnetic sensitivity in vitro. A second mechanism based on biogenic magnetite is supported by conditioning experiments and by trigeminal recordings, though the cells once identified as receptors in the pigeon beak proved to be macrophages. Displacement experiments in reed warblers, sea turtles and salmon indicate a magnetic map based on inclination and declination. No receptor has been confirmed in any species.

Keywords: Magnetoreception, Radical Pair, Cryptochrome, Magnetite, Animal Navigation

1. INTRODUCTION

Long-distance migration presents an orientation problem that improves little with experience for the individuals that most need to solve it. Many songbirds migrate alone and at night on their first journey, without parental guidance, and arrive in a wintering area used by their species. Sea turtles hatch on a beach, spend years at sea, and return to nest within tens of kilometres of their natal site. Solving such problems requires directional information and, for the return leg, some estimate of position.

Animals use several cues in combination, including the position of the sun, the pattern of polarised light at dusk, the rotation of the star field, olfactory gradients and landmarks. The geomagnetic field is distinctive among them because it is available at all times, in all weather, and at any depth or altitude. Its usefulness was established when European robins tested in orientation cages under a controlled artificial field oriented according to that field rather than to any visual cue .[1]

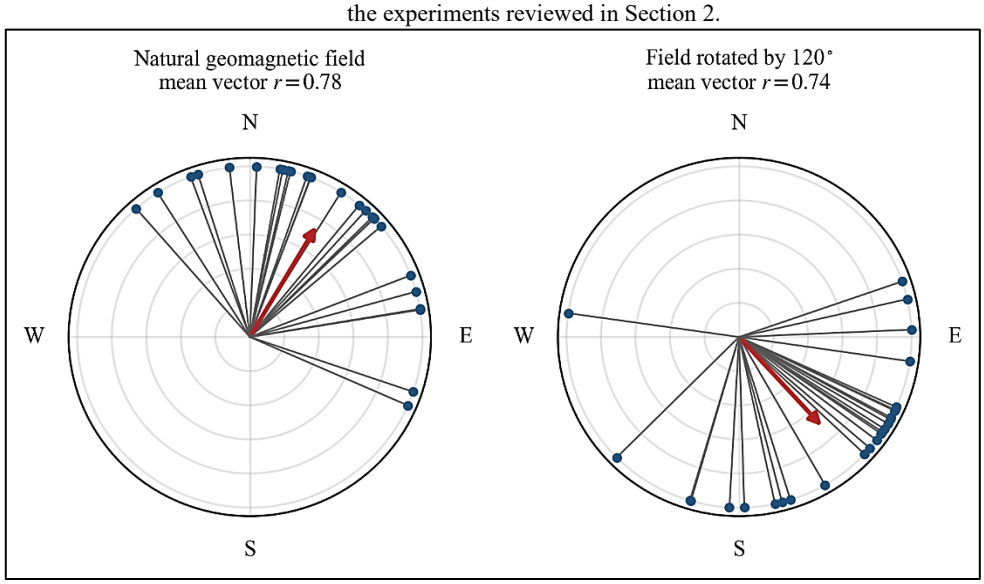
Two capacities must be distinguished. A compass converts a field into a direction. A map converts local field values into an estimate of position relative to a goal, which requires the animal to compare measurements against learned or inherited reference values. The two need not share a receptor, and current evidence suggests they do not. This review examines each in turn, then considers what remains unresolved .[2]

2. THE COMPASS AND HOW IT IS MEASURED

Most behavioural evidence comes from orientation cages of the type introduced by Emlen and Emlen, in which a bird in migratory condition hops on an inked or scratch-sensitive surface and leaves a record of its preferred heading .[3] Headings from many individuals are analysed by circular statistics, and the length of the mean vector measures how concentrated they are. Fig. 1 illustrates the logic: when the ambient field is rotated, headings rotate with it, which demonstrates that the birds are reading the field rather than an uncontrolled cue.

The avian compass has three properties that constrain any mechanism proposed for it. First, it responds to the inclination of the field lines relative to gravity and not to their polarity, so it distinguishes poleward from equatorward rather than north from south. Second, it requires light, and it works under short-wavelength illumination but fails under long-wavelength light. Third, it is disrupted by oscillating fields in the megahertz range that are far weaker than the geomagnetic field itself .[4] The last property is the most diagnostic, since a simple magnetic particle would be unaffected by such a weak oscillating field, while a system whose behaviour depends on electron spin would not.

Fig 1: Orientation-cage logic. Each line marks the heading of one individual and the arrow shows the mean vector. When the ambient field is rotated, the distribution rotates with it, as reported in the experiments reviewed in Section 2.



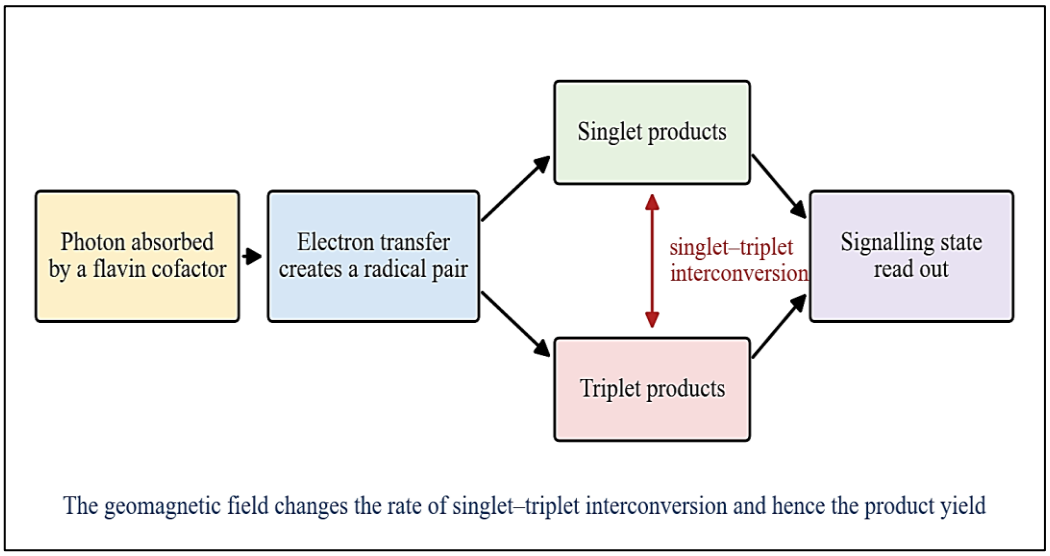
3. THE RADICAL-PAIR MECHANISM

Ritz, Adem and Schulten proposed that the light-dependent compass operates through a photochemical reaction producing a pair of radicals whose unpaired electron spins are initially correlated .[5] The pair interconverts between singlet and triplet configurations, and the rate of interconversion depends on the angle between the molecule and the external field, because hyperfine coupling to nearby nuclei makes the spin dynamics anisotropic. Since the two configurations yield different chemical products, the yield becomes a function of orientation. Fig. 2 shows the scheme. The mechanism explains all three behavioural properties at once: it requires light to create the radical pair, it is insensitive to polarity because the axis and not the direction matters, and it is disrupted by radio-frequency fields tuned near the electron spin transitions .[6]

Cryptochromes are the candidate molecules. They are flavoproteins present in the retina, and light absorption by the flavin cofactor produces a radical pair through a chain of electron transfers along conserved tryptophan residues. Purified cryptochrome 4 from the European robin responds to applied magnetic fields in vitro, and the response is weaker in the corresponding proteins from non-migratory chicken and pigeon, which is the closest link so far between the molecule and the behaviour .[7] The magnetic effects observed in isolated protein are nevertheless produced by fields stronger than the geomagnetic one, and how the sensitivity is amplified in the intact retina is unknown.

Neuroanatomy supports a visual pathway. Lesion experiments in European robins showed that birds without a functioning trigeminal nerve still orient by the magnetic compass, while lesions to a forebrain region called cluster N, which receives input from the eyes and is active during night-time orientation, abolish the ability .[8] Tracing studies confirm that this region is connected to the retina through the thalamofugal pathway .[9] The compass therefore appears to be a visual function in birds, a conclusion consistent with reports that low-frequency electromagnetic noise in urban environments disrupts orientation and that shielded huts restore it .[10]

Fig 2: The radical-pair scheme proposed for the light-dependent compass .[5,6] Product yields depend on the orientation of the molecule relative to the field.



4. MAGNETITE-BASED RECEPTION

A second mechanism uses crystals of biogenic magnetite, which experience a torque in an external field that could be transduced by mechanoreceptors .[11] Unlike the radical-pair system this mechanism is sensitive to polarity and does not require light, so it is the natural candidate for a map sense that must measure field intensity.

The evidence is mixed. Conditioning experiments show that pigeons can be trained to discriminate magnetic anomalies, and that this ability depends on the trigeminal nerve and on an intact upper beak .[12] Recordings from the pigeon brainstem identified neurons whose firing encoded field direction and intensity .[13] Against this, the iron-rich cells in the upper beak that were widely reported as candidate receptors were shown by systematic histology to be macrophages rather than neurons, a result that removed the main anatomical support for the model .[14]

The current position is that behavioural and electrophysiological evidence for a magnetite-based sense is reasonably strong while the cellular identification is absent. The receptor may be rare, small and distributed, which would explain the difficulty. As one review put the matter, this is a sense without a known receptor .[15]

5. EVIDENCE FOR A MAGNETIC MAP

Position sensing requires at least two independent field parameters that vary in different directions. Inclination and total intensity vary mainly with latitude, while declination, the angle between magnetic and geographic north, varies with longitude in many regions. Displacement experiments provide the key evidence. Eurasian reed warblers displaced eastwards by more than a thousand kilometres corrected their heading appropriately, and birds held in a field where only declination was altered behaved as if displaced along the longitude that the altered declination implied.[16] A later study showed that the same species extrapolates beyond the range of values it has experienced, which implies a gradient map rather than a memorised set of local values .[17]

Marine examples are equally instructive. Hatchling loggerhead turtles placed in fields replicating locations around their oceanic migration route swam in directions appropriate to each location, indicating inherited responses to regional field values .[18] Analysis of nesting records showed that turtles return to beaches whose field signature matches that of their natal site, and that gradual drift of the geomagnetic field is accompanied by corresponding shifts in nesting distributions, which supports imprinting on a magnetic signature .[19] In Pacific salmon, juveniles with no prior ocean experience oriented according to fields representing the northern and southern edges of their range, again indicating an inherited map .[20] Monarch butterflies possess a light-dependent inclination compass, demonstrating that the mechanism is not confined to vertebrates .[21] Table 1 summarises the evidence by mechanism.

Magnetic information is never used alone. Birds recalibrate their magnetic compass against the pattern of polarised light near sunset, and the direction of that calibration differs between species and seasons. Olfactory cues contribute to homing in pigeons and to navigation in seabirds, and experienced individuals rely more on learned landmarks than first-year migrants can. The hierarchy among cues shifts with conditions, which is one reason that removing a single cue in an experiment often produces a smaller effect than the importance of that cue would suggest .[2] Interpreting negative results in this field therefore requires care, since redundancy between systems can mask the loss of any one of them.

Table 1. Evidence for the two proposed magnetoreception mechanisms

Property	Radical pair	Magnetite
Requires light	Yes	No
Sensitive to polarity	No, reads inclination	Yes
Disrupted by radio-frequency fields	Yes [4,6]	Not expected
Candidate molecule identified	Cryptochrome 4 [7]	Biogenic magnetite [11]
Neural pathway	Visual, via cluster N [8,9]	Trigeminal [12,13]
Receptor cell confirmed	No	No, earlier claim withdrawn [14]
Proposed role	Compass	Map and intensity detection

6. MAGNETIC RESPONSES BEYOND BIRDS

Attention to birds reflects the convenience of the orientation cage rather than any restriction of the sense. Comparable evidence exists across vertebrates and in several invertebrate groups.

Bats calibrate their homing direction against the magnetic field. Big brown bats displaced from their roost and exposed to a rotated field at sunset departed in directions rotated accordingly, which indicates that the field is used together with a cue available at dusk.[22] Subterranean mole rats, which live in complete darkness and cannot use celestial cues at all, build nests in a preferred magnetic direction and reverse that preference when the field is reversed; their compass responds to polarity rather than inclination and does not require light, so it is unlikely to share a mechanism with the avian system.[23]

Spontaneous alignment provides a different class of evidence. Analysis of satellite images and field observations found that cattle and deer at rest tend to align along the magnetic north to south axis, an effect that weakened near power lines where the field is distorted.[24] Alignment of this kind carries no obvious navigational function and is best treated as an indication that the field is perceived rather than as evidence of a compass in use.

Among invertebrates the monarch butterfly has a light-dependent inclination compass with the same spectral dependence as the avian system, and social insects, spiny lobsters and several molluscs respond to field manipulation.[21] The distribution of the trait across such distant lineages suggests either an ancient origin or repeated independent evolution, and the mechanistic differences between the avian and the mole rat compasses favour the second interpretation.

7. UNRESOLVED PROBLEMS

Three difficulties stand out. The first is the sensitivity gap. Magnetic effects on isolated cryptochrome require fields well above geomagnetic strength, and the behavioural sensitivity of birds implies that the biological system detects changes of a few percent in a field of about fifty microtesla. Proposed solutions involve ordered arrays of receptor molecules and long-lived spin coherence, but neither has been demonstrated in a retina.

The second is replication. Several influential results in this field have proved difficult to reproduce across laboratories, and the effects are small relative to individual variation in orientation behaviour. Sample sizes in cage experiments are often modest, and the analysis depends on circular statistics whose assumptions are not always checked. Reports of disruption by anthropogenic electromagnetic noise are important for this reason as well as for their conservation implications, since they suggest that ambient conditions in the laboratory may themselves influence outcomes .[10]

The third is the receptor. No cell has been identified in any species that responds to magnetic stimuli and projects to the brain, in contrast with every other sensory modality. The nearest approach came from rainbow trout, where cells containing magnetite were located in the olfactory lamellae and units in the associated branch of the trigeminal nerve responded to changes in field intensity ; the identification has proved difficult to extend to other species, and isolating candidate cells from surrounding tissue remains the main technical obstacle.[25] Until such a cell is described completely, mechanistic accounts remain inferences from behaviour and biochemistry rather than descriptions of a sensory system.

8. CONCLUSION

Magnetic orientation is established beyond reasonable doubt in birds, turtles, salmon and several insects, and the properties of the avian compass constrain its mechanism tightly enough to make the radical-pair proposal the leading explanation. Magnetite-based detection remains the more plausible basis for measuring intensity and hence for the map sense, despite the loss of its principal anatomical evidence. Displacement experiments show that the map uses at least two field parameters and that animals extrapolate from them rather than matching

remembered values. The outstanding requirement is cellular: identification of a receptor and of its afferent pathway would convert a well-supported inference into a described sense, and would also clarify how far anthropogenic fields interfere with migration.

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