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REVIEW

The magnetic map sense and its use in fine-tuning the migration programme of birds

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Abstract The Earth's magnetic field is one of several natural cues, which migratory birds can use to derive directional ("compass") information for orientation on their biannual migratory journeys. Moreover, magnetic field effects on prominent aspects of the migratory programme of birds, such as migratory restlessness behaviour, fuel deposition and directional orientation, implicate that geomagnetic information can also be used to derive positional ("map") information. While the magnetic "compass" in migratory birds is likely to be based on radical pair-forming molecules embedded in their visual system, the sensory correlates underlying a magnetic "map" sense currently remain elusive. Behavioural, physiological and neurobiological findings indicate that the sensor is most likely innervated by the ophthalmic branch of the trigeminal nerve and based on magnetic iron particles. Information from this unknown sensor is neither necessary nor sufficient for a functional magnetic compass, but instead could contribute important components of a multifactorial "map" for global positioning. Positional information could allow migratory birds to make vitally important dynamic adaptations of their migratory programme at any relevant point during their journeys.

Keywords Magnetoreception · Navigation · Orientation · Migratory restlessness · Migratory fuelling

Introduction

Migratory birds display remarkable behavioural and physiological changes in their migratory programme to accomodate the challenges they face during their journeys between wintering and breeding grounds. The fact that many first-year migratory birds undertake successful migration alone strongly implies that many of these behavioural and physiological changes are associated with circannual clock-based mechanisms entrained by the ambient photoperiod (Gwinner 1996) and genetic programs (Berthold 1974; Gwinner 1996). This "migratory syndrome" consists of a package of tightly integrated adaptive traits (Piersma et al. 2005) and can be observed even in captivity without access to external cues.

On a bird's migratory journey, positional (or "map") information is of vital importance, e.g. to dynamically adapt behaviour and/or physiology. However, genetic programs and endogenous circannual rhythms alone will be affected by navigational mistakes (e.g. Rabøl 1978) and intrinsic (e.g. fuel load) as well as extrinsic (e.g. wind) factors (Schmaljohann and Naef-Daenzer 2011) and will, therefore, not be accurate enough to provide reliable information on geographical position and thus require the use of fine-tuning mechanisms from external cues. One of these cues, which could theoretically help a bird to determine its geographical position, is the Earth's magnetic field. Indeed, prominent aspects of the birds' migratory programme,

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such as migratory restlessness behaviour, fuel deposition, and/or directional orientation have been shown to be modified by magnetic fields (Perdeck 1958; Mewaldt 1964; Beck and Wiltschko 1988; Wiltschko and Wiltschko 1992; Fransson et al. 2001; Kullberg et al. 2003; Thorup et al. 2007; Boström et al. 2010; Henshaw et al. 2010; Kishkinev et al. 2015; Bulte et al. 2017). Thus, in addition to the well-known magnetic "compass" sense (Wiltschko and Wiltschko 1972; Cochran et al. 2004; Zapka et al. 2009), it is conceivable that birds could use magnetic "map" or "signpost" parameters for global positioning and to adapt their behaviour accordingly.

How does a magnetic map work?

Generating a map based on geomagnetic field parameters is not far-fetched. Apart from naturally occuring magnetic anomalies and irregular daily changes, which will set a lower limit of > 10 km for the accuracy of a magnetic map (Mouritsen 2013, 2015), in many regions on Earth, magnetic parameters (declination, inclination and/or intensity) form a more or less consistent grid of isolines, whose values gradually and predictably change (see e.g. Boström et al. 2012). To use this grid as a basis for a map, birds will have to sample and store magnetic values from various locations on exploratory flights around their home area (Mukhin et al. 2005) and during various stages of their migration. Theoretically, a magnetic map could work in two different ways. Either, a bird would detect the alignments of geomagnetic parameters, and form a mental grid by extrapolating the learned magnetic gradients onto its species-specific migratory range (Phillips 1996). Based on this information, the bird could use locally perceived magnetic parameters to determine its approximate geographical position on its mental magnetic map and derive the required compass direction leading to the desired goal at any timepoint during its migratory journey (Benhamou 2003). Alternatively, a bird could store absolute values of geomagnetic parameters from its goal area. Once being over unknown territory, it would head off in a random direction to measure, how magnetic parameters change, and would choose a particular direction, once the perceived magnetic parameters approach those of the goal ("trial and error" hypothesis; Benhamou 1997). However, displacement experiments showing that birds can correct their orientation when tested inside Emlen funnels (Chernetsov et al. 2008b; Kishkinev et al. 2013, 2015) following a displacement speaks against the "trial and error" hypothesis, since the birds would not be able to move far enough in the funnel to detect any magnetic gradients. None of both hypotheses has been unequivocally shown to explain the mechanisms used by free-flying migratory birds (for review, see Kishkinev 2015).

Some migratory birds seem to use magnetic parameters to increase fat deposition prior to geographical obstacles or longer than expected journeys

Fuel deposition plays a vital role during migration. Migratory birds will have to store additional amounts of fat when, e.g. being faced with an ecological barrier, which prevents them finding food. This requires that birds can determine their geographical position prior to the obstacle so that they do not miss their chance to refuel. Fransson et al. (2001) and Kullberg et al. (2003) could show that first-autumn Thrush Nightingales (*Luscinia luscinia*) can use geomagnetic cues to fine-tune their migratory fuel deposition: experimental birds constantly held in the local geomagnetic field of Sweden showed significantly less gain in body mass compared to individuals which were gradually "moved" by mimicking the respective geomagnetic field parameters along their southbound migratory route. Their body masses peaked when being virtually displaced to Northern Egypt, which is an important stopover site just before the crossing of the Sahara desert. These body mass increases largely corroborate observations of increased fuelling rates prior to geographical obstacles in various free-flying bird species (e.g. Bairlein 1991, 2003; Delingat et al. 2006, 2008; Yohannes et al. 2009). Likewise, Northern Wheatears (*Oenanthe oenanthe*) were shown to cope with a longer, albeit "virtual" migratory journey, by increasing their migratory fuel deposits after being magnetically displaced north of their breeding range in southern Sweden during autumn migration (Boström et al. 2010). It should, however, be noted, that such effects may differ between species with different migration and fuelling strategies (Kullberg et al. 2007; Bulte et al. 2017).

Some migratory birds increase their restlessness behaviour in response to an apparent lack of geographical progress

Migratory restlessness is a prominent behavioural aspect of the migratory program and reflects a bird's innate urge to migrate during its migratory cycles (Berthold 1988a; Eikenaar et al. 2014, 2016; Schmaljohann et al. 2015). The amount of migratory restlessness behaviour expressed by captive birds has been shown to correlate with the migratory distance a species or population has to migrate in the wild (Berthold et al. 1972; Berthold 1973, 1974, 1988b; Berthold and Querner 1981; Gwinner 1990; Maggini and Bairlein 2010; Bulte and Bairlein 2013).

An impact of geomagnetic field parameters on the amount of migratory restlessness behaviour was recently suggested to occur in Northern Wheatears: birds from a

Norwegian population held in a magnetic field, which was gradually changed to simulate their natural species-specific migratory route from southern Norway to Mauritania (Bakken et al. 2006), decreased their amount of migratory restlessness, whereas conspecifics constantly kept in the local geomagnetic field of Northern Germany during autumn migration significantly increased their amount of migratory restlessness behaviour with progression of the migratory season (Bulte et al. 2017). These findings were interpreted as the birds' attempt to compensate for the lack of geographical progress during migration.

Experienced migratory birds are capable of correcting for geographical displacements and magnetic information seems to be involved

Migratory birds can perform true navigation, i.e. they are able to determine the correct heading which leads them to their target destinations even from unfamilar locations (Berthold 1991; Mouritsen and Mouritsen 2000; Mouritsen 2003; Holland 2014). This ability requires, besides a "compass" (to set the migratory direction towards the goal), a "map", which tells the bird its approximate position relative to the goal (Berthold 1991; Mouritsen and Mouritsen 2000; Mouritsen 2003; Holland 2014). The strongest evidence for true navigation abilities have been obtained from geographic displacements when migratory birds were translocated away from their species-specific migratory routes. Experienced free-flying European Starlings (*Sturnus vulgaris*; Perdeck 1958), Golden-crowned Sparrows (*Zonotrichia atricapilla;* Mewaldt 1964), White-crowned Sparrows (*Zonotrichia leucophrys nuttalli*; Mewaldt 1964; Thorup et al. 2007) and Eurasian Reed Warblers (*Acrocephalus scirpaceus*; Chernetsov et al. 2008b; Kishkinev et al. 2013) were shown to correct for large geographical displacements. Furthermore, Pied Flycatchers (*Fidecula hypoleuca*) have been reported to shift their orientation (initiate a "Zugknick") when geomagnetic parameters were used to simulate their natural migration route at about the appropriate time (Beck and Wiltschko 1988, but see; Chernetsov et al. 2008a). Likewise, Garden Warblers (*Sylvia borin*) seemed to reverse their migratory direction when being exposed to a horizontal magnetic field, which simulated an equator crossing (Wiltschko and Wiltschko 1992; but see; Schwarze et al. 2016). Lesser Whitethroats (*Sylvia curruca*) magnetically displaced south of their breeding area showed a seasonally appropriate northward orientation (Henshaw et al. 2010), and Eurasian Reed Warblers (*Acrocephalus scirpaceus*) corrected for a 1000-km virtual eastward magnetic displacement in spring (Kishkinev et al. 2015). Thus, in various components of their migratory program, birds apparently seemed to have used local magnetic field parameters as a "map" sense to estimate their approximate geographical position, and/or as a "signpost" to trigger adaptive changes in their behaviour and/or physiology.

Two magnetic senses for two different tasks

By which mechanism do migratory birds obtain positional information from the Earth's magnetic field? A string of studies with Eurasian Reed Warblers (*Acrocephalus scirpaceus*) recently provided direct indications of putative neuronal correlates underlying a magnetic "map" sense in migratory birds. First, Chernetsov et al. (2008b) could show that Eurasian Reed Warblers were able to compensate for a 1000-km eastward displacement by switching their northeasterly migratory direction in Rybachy on the Baltic coast to Northwest when tested near Moscow. Further studies suggested that an innate clock-based "jetlag" mechanism was not sufficient to explain the compensatory behaviour observed after the physical displacement (Kishkinev et al. 2010), but that geomagnetic information only is sufficient to induce a reorientation response (Kishkinev et al. 2015). Furthermore, Eurasian Reed Warblers with surgically ablated ophthalmic branches of the trigeminal nerves (V1) failed to compensate for a physical geographical displacement. Instead they headed towards the same migratory northeasterly direction as before the displacement (Kishkinev et al. 2013).

Studies using a strong, directed, magnetic pulse thought to remagnetise putative iron-based magnetoreceptors have reported deflected orientation responses (Beason and Semm 1996; Munro et al. 1997; Wiltschko et al. 2009; Holland 2010). In a more detailed study, Holland and Helm (2013) reported that experienced migratory songbirds, which have already acquired a navigational map (Perdeck 1958; Mouritsen 2003; Holland 2014), reacted with a directed, but deflected orientation response (Beason and Semm 1996; Munro et al. 1997; Wiltschko et al. 2009; Holland 2010), whereas juvenile migratory songbirds, which had not yet established a map (Perdeck 1958; Mouritsen 1998, 2003; Mouritsen and Mouritsen 2000; Holland 2014) were unaffected by the pulse treatments (Holland and Helm 2013). To sum up, a growing body of evidence supports the existence of a magnetic "map" sense based on magnetic iron particles associated with the trigeminal system (for reviews, see Wiltschko and Wiltschko 2013; Mouritsen 2015; Mouritsen et al. 2016; Hore and Mouritsen 2016).

This trigeminal-based magnetic sense was long proposed to be based on iron-containing receptors (e.g. Walcott et al. 1979; Kirschvink and Gould 1981). Putative candidate structures were described at six specific spots with strictly bilateral symmetry along the lateral edges of the upper beak of various bird species, which is innervated by V1 (Fleissner et al. 2003, 2007; Falkenberg et al. 2010). Although these structures later turned out to almost certainly be macrophages rather than magnetosensors (Treiber et al. 2012, 2013; Mouritsen 2012), the existence of a magnetic sensor associated with V1 is still supported by behavioural and neurobiological evidence. For instance, in a conditioned-choice paradigm, pigeons were trained to distinguish between the presence/absence of a strong magnetic anomaly. The pigeons could do so, but when V1 was cut bilaterally, the correct choice rate decreased to chance level (Mora et al. 2004).

On the level of the central nervous system, significantly increased expression levels of immediate early genes reflecting neuronal activation after magnetic stimulation were observed in the principle (PrV) and spinal trigeminal (SpV) sensory brain nuclei of European Robins (*Erithacus rubecula*; Heyers et al. 2010), homing pigeons (*Columba livia*; Lefeldt et al. 2014) and Northern Wheatears (*Oenanthe oenanthe*; Elbers et al. 2017). This magnetic field-triggered activation significantly dropped when either the magnetic field was compensated or when V1 was cut (Heyers et al. 2010; Lefeldt et al. 2014). V1 carries purely sensory information and is the only non-olfactory nerve whose distal endings innervate the upper beak, parts of the facial skin and the nasal cavity. Neuronal connectivity studies across various bird species prove that PrV and SpV represent the primary brain targets of V1 terminals (e.g. Dubbeldam et al. 1976, 1979; Dubbeldam 1980; Wild 1981, 1990; Bottjer and Arnold 1982; Bout and Dubbeldam 1985; Wild and Zeigler 1996; Wild et al. 2001; Heyers et al. 2010; Lefeldt et al. 2014).

In addition to the abovementioned magnetic “map” sense used to assess a bird’s approximate geographical position, birds are also able to derive directional information from the Earth’s magnetic field for maintaining a consistent heading (Wiltschko and Wiltschko 1972; Cochran et al. 2004). This “compass” sense is almost certainly embedded in their visual system (for review, see Hore and Mouritsen 2016; Mouritsen et al. 2016). The primary sensors are located in both eyes (Hein et al. 2010, 2011; Engels et al. 2012) and most likely belong to the flavoprotein group of cryptochrome proteins, which are expressed in subpopulations of specific retinal neurons, and which have been shown to absorb blue light and to form radical pairs upon photoexitation (Mouritsen et al. 2004; Liedvogel et al. 2007b; Niessner et al. 2011, 2016; Maeda et al. 2012; Bolte et al. 2016; Kattnig et al. 2016, for review, see, e.g. Hore and Mouritsen 2016). Retinally perceived magnetic information is transmitted to the brain via the thalamofugal visual pathway (Heyers et al. 2007) to a forebrain area called “Cluster N” (Mouritsen et al. 2005). Cluster N is located in the anterior visual wulst and was shown to exhibit strong neuronal activation in various migratory bird species during magnetic compass orientation (Mouritsen et al. 2005; Heyers et al. 2007; Liedvogel et al. 2007a; Hein et al. 2010; Zapka et al. 2010). Lesioning of Cluster N (Zapka et al. 2009) but not sectioning of V1 (Beason and Semm 1996; Zapka et al. 2009) led to a dysfunctional magnetic compass, which strongly indicates a direct involvement of Cluster N but not the trigeminal system in processing of magnetic compass information (Zapka et al. 2009).

Conclusion

Various migratory bird species display magnetic field-dependent changes in prominent aspects of their migratory programme. Depending on the respective species-specific migratory behaviour, ecology and migration strategy, these can include migratory fuel gain, the amount of migratory restlessness behaviour and/or the directionality of migration. In all cases, the birds apparently seemed to have used local magnetic field parameters as a “map” sense to estimate their approximate geographical position, and/or as a “signpost” to trigger adaptive changes in their behaviour and/or physiology. Among the currently discussed hypotheses on how birds could sense magnetic fields, a currently unknown, probably iron particle-based sensor innervated by the trigeminal nerve is the most likely candidate structure to sense magnetic “map” information. In contrast, the magnetic compass sense is almost certainly embedded in the birds’ visual system. We would like to finish with a cautionary note: in view of the obvious evolutionary advantage of integrating information from all potentially relevant cues which could help the bird navigate successfully, it would be naïve to believe that magnetic cues only are the only map (and compass) cues used for navigation on a bird’s migratory journey. Thus, the birds’ map sense and general navigational skills almost certainly are multifactorial (Mouritsen et al. 2016; Chernetsov 2017).

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