Journal of Theoretical Biology 399 (2016) 141–147

Contents lists available at ScienceDirect

Journal of Theoretical Biology

journal homepage: www.elsevier.com/locate/yjtbi

Shifted magnetic alignment in vertebrates: Evidence for neural lateralization?

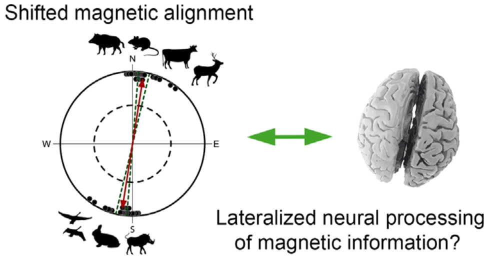
E. Pascal Malkemper [a,b], Michael S. Painter [c], Lukas Landler [c,d,*]

[a] Department of General Zoology, Faculty of Biology, University of Duisburg-Essen, Universitätsstrasse. 2, 45117 Essen, Germany
[b] Department of Game Management and Wildlife Biology, Faculty of Forestry and Wood Sciences, Czech University of Life Sciences Prague, Kamýcká 129, 165 21 Prague 6, Czech Republic
[c] Department of Biological Sciences, Virginia Tech, Blacksburg, Virginia, United States of America
[d] Research Institute of Molecular Pathology (IMP), Vienna Biocenter (VBC), 1030 Vienna, Austria

HIGHLIGHTS

- Many vertebrate taxa consistently align along the magnetic north-south axis.
- Meta-analysis shows a consistent mean clockwise rotation from magnetic north-south.
- Consistent shift may be due to lateralized magnetic processing in the nervous system.

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:
Received 5 January 2016
Received in revised form 13 March 2016
Accepted 28 March 2016
Available online 6 April 2016

Keywords:
Magnetoreception
Magnetic alignment
Lateralization
Geomagnetic field
Cortical hemispheres
Spatial orientation
Central sensory processing

ABSTRACT

A wealth of evidence provides support for magnetic alignment (MA) behavior in a variety of disparate species within the animal kingdom, in which an animal, or a group of animals, show a tendency to align the body axis in a consistent orientation relative to the geomagnetic field lines. Interestingly, among vertebrates, MA typically coincides with the north–south magnetic axis, however, the mean directional preferences of an individual or group of organisms is often rotated clockwise from the north–south axis. We hypothesize that this shift is not a coincidence, and future studies of this subtle, yet consistent phenomenon may help to reveal some properties of the underlying sensory or processing mechanisms, that, to date, are not well understood. Furthermore, characterizing the fine structure exhibited in MA behaviors may provide key insights to the biophysical substrates mediating magnetoreception in vertebrates. Therefore, in order to determine if a consistent shift is exhibited in taxonomically diverse vertebrates, we performed a meta-analysis on published MA datasets from 23 vertebrate species that exhibited an axial north–south preference. This analysis revealed a significant clockwise shift from the north–south magnetic axis. We summarize and discuss possible competing hypotheses regarding the proximate mechanisms underlying the clockwise shifted MA and conclude that the most likely cause of such a shift would be a lateralization in central processing of magnetic information.

1. Background

Many animals use the Earth's magnetic field to orient in their environment (Wiltschko and Wiltschko, 2012). For instance, migrating birds use a magnetic compass during seasonal migrations

* Corresponding author.
E-mail address: lukas.landler@imp.ac.at (L. Landler).

http://dx.doi.org/10.1016/j.jtbi.2016.03.040

(Wiltschko and Wiltschko, 1972), hatchling sea turtles use navigational markers provided by components of the Earth's magnetic field to guide innate migration along the Atlantic gyre (Lohmann et al., 2012), and newts possess a magnetic compass and a magnetic map which is used during navigation (Phillips et al., 2002a). In addition to the so-called 'goal oriented' magnetic behaviors, many animals show spontaneous magnetic responses (Begall et al., 2013), often referred to as 'magnetic alignment' (MA). As used in this article, MA describes a spontaneous, non-goal directed magnetic response, such as the tendency of animals to spontaneously align their body axis relative to the Earth's magnetic field. Magnetic alignment was first described over 50 years ago in insects (i.e. in European cockchafer, *Melolontha melolontha*, (Schneider, 1963)), and today evidence suggests that this behavior is commonplace among animals across diverse taxa (Begall et al., 2013). However, although widespread within the animal kingdom, little is known about the sensory mechanisms and the functional significance of MA behaviors. Insects often exhibit quadrimodal spontaneous orientation, aligning along cardinal or anticardinal magnetic axes, (Becker et al., 1996, 1964; Becker and Speck, 1964; Painter et al., 2013; Vácha et al., 2010), whereas vertebrates show preferences to align their body along the north–south magnetic axis (Begall et al., 2008, 2011; Burda et al., 2009; Hart et al., 2012, 2013a, 2013b; Slaby et al., 2013). The same directional tendencies have been shown in spontaneous directional nest construction of some mammals when tested in visually symmetric circular arenas (Malkemper et al., 2015; Oliveriusová et al., 2014). Even though it is controversial whether nest-building preferences represent a form of magnetic alignment equivalent to the alignment behaviors discussed above [see (Begall et al., 2013)], in the current discussion they are considered spontaneous directional responses to the geomagnetic field, and therefore are included in our definition and analysis.

Few studies have attempted to investigate the magnetoreception mechanism underlying MA. While subterranean rodents (mole-rats) seem to use a magnetite-based mechanism (MBM) (Marhold et al., 1997; Thalau et al., 2006), evidence from other vertebrates, including epigeic mammals, points towards the involvement of a radical pair mechanism (RPM) (Landler et al., 2015; Malkemper et al., 2015). The RPM has also been implicated in the magnetic compass response of migratory birds and amphibians (Phillips et al., 2010b; Ritz, 2011). However, strong support for a magnetite-based mechanism mediating spontaneous nest building responses comes from mole-rats, the best studied group of mammals for magnetoreception to date. It is, however, unclear whether this represents the general mechanism underlying all vertebrate magnetoreception, or rather, if mole-rats represent the exception to the rule given their unique subterranean lifestyle. Birds and newts seem to possess both types of receptors used for different tasks (Phillips, 1986; Wiltschko et al., 2007).

While the underlying mechanisms of MA are poorly understood, even less evidence exists concerning its possible function and biological significance (Begall et al., 2013). The only study linking MA behavior to a biological fitness advantage showed that red foxes were approximately 60 – 70% more successful at catching hidden prey when mousing jumps were directed towards north-east or south-west, compared to mousing attempts in other magnetic directions (Červený et al., 2011). This observation fits quite well with the idea that animals use a visual pattern that receives input from the geomagnetic field to encode their environment (Phillips et al., 2010a). A biophysical mechanism that creates such a visual pattern has been suggested to underlie magnetic compass responses in a variety of vertebrates (Cintolesi et al., 2003; Ritz et al., 2000), and has been proposed to be generated through a radical pair mechanism (RPM) occurring in specialized photoreceptors of the retina or pineal organ (Hart et al., 2013a, 2013b; Nießner et al., 2011; Phillips et al., 2010a, 2001). Behavioral evidence from turtles suggests that the same RPM pattern might be involved in encoding novel environments, where an association is formed between novel places and a particular 'visual' pattern (Landler et al., 2015). In the case of mousing red foxes, the visual pattern generated from an RPM might act as a range finder helping to estimate prey distances and/or guide the trajectory of the jump (Červený et al., 2011) in a similar way as the patterns has been proposed to facilitate the tendency of waterfowl landing along the north–south magnetic axis (Hart et al., 2013a, 2013b).

Interestingly, in cases where animals align axially along the north–south axis, as is the case in most vertebrates, but also reported in some invertebrates (Sandoval et al., 2012), there tends to be a conspicuous shift of the mean alignment clockwise from the magnetic north–south axis. A consistent shift across multiple species during various behaviors (e.g. grazing, sleeping, landing, hunting, nest building) would not be predicted from the hypotheses for the biological function or the underlying receptor mechanism of MA that have been proposed to date. However, such a phenomenon in spatial behaviors might indicate a functional lateralization of the underlying magnetic sensory pathway in vertebrates, as has been suggested in different species of migratory birds but remains a highly debated topic in magnetoreception. While research in different bird species provided evidence for a lateralized magnetic compass located in the right eye (Wiltschko et al., 2002), later evidence challenged these results, possibly suggesting a more complex story involving developmental effects on the underlying sensory mechanism (Gehring et al., 2012; Hein et al., 2011). It is further likely, that there exists a functional lateralization rather than an absolutely lateralized receptor distribution with regard to the magnetic sense, as was deduced from experiments with birds showing ocular dominance, predominantly using one eye over the other depending on the type of magnetic tasks (Wilzeck et al., 2010). Such a functional lateralization might be related to the widespread lateralized central processing of information in vertebrate brains (Halpern et al., 2005; Walker, 1980). Current knowledge about central processing of magnetic information in the brain of vertebrates is limited and mostly based on studies of immediate early gene expression induced by magnetic stimulation (see discussion for details). Based on the findings in birds, two pathways processing magnetic information have been suggested, one for each receptor type (MBM and RPM) (Mouritsen et al., 2015). The pathway for magnetic compass information (mediated by RPM) in the bird brain connects the primary receptors that are believed to reside in the retina via the dorsal lateral geniculate nucleus of the thalamus to the forebrain Cluster N and adjacent hyperpallial areas (Mouritsen et al., 2015). Magnetic map information (mediated by MBM) on the other hand is suggested to be routed via trigeminal brainstem nuclei to the forebrain nucleus basalis and trigeminal parts of the nidopallium (Mouritsen et al., 2015). If these two pathways mediating magnetic information were anatomically and/or functionally lateralized, it would be conceivable that the lateralization results in shifted MA behavior, which could in turn shed light on the enigmatic biological function of vertebrate MA. Here, we performed a meta-analysis of published data after a systematic literature search on vertebrate axial MA responses addressing two main questions: (1) Do mean responses from vertebrate species show a consistent and significant clockwise shift, deviating from the magnetic north–south axis, and (2) what are possible explanations for such a shift in light of evidence on the underlying mechanism and possible adaptive functions?