



## Evidence for plasticity in magnetic nest-building orientation in laboratory mice

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Previous studies have shown that mammals exhibit two distinct forms of magnetic behaviour: spontaneous magnetic alignment and learned magnetic compass orientation. However, it remains to be determined whether the type of magnetic response is species specific (i.e. species exhibit either learned magnetic compass responses or spontaneous magnetic orientation). Alternatively, learned and spontaneous magnetic orientation may be context dependent and expressed in the same species under different conditions, e.g. motivational, physiological and/or environmental. Using C57BL/6J laboratory mice, we provide evidence for multiple spatial responses to magnetic cues in the same species. In a series of three similar nest-building experiments in which mice were trained to construct nests in one of four magnetic directions, mice either positioned nests along a fixed northeast–southwest magnetic axis (Series 1), independent of the trained direction, and similar to spontaneous magnetic alignment responses in other vertebrates, or exhibited learned magnetic compass orientation in the direction away from (Series 2) or towards (Series 3) the sheltered end of the magnetic axis they had been exposed to during the training period. Importantly, the responses elicited in each series paralleled changes in the experimental protocols and may help to explain the variation in magnetic behaviours. Furthermore, the plasticity in the magnetic orientation exhibited by laboratory mice suggests that magnetic cues play important role in the spatial ecology of epigeal rodents. Characterizing the factors that elicit these responses will shed light on the adaptive significance of spontaneous magnetic alignment, a widespread but poorly understood spatial behaviour. In addition, future studies with similar nest-building assays will likely play a role in helping to determine whether magnetic compass orientation and spontaneous magnetic alignment are mediated by the same underlying mechanisms of magnetoreception.

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Use of magnetic cues for spatial orientation has been demonstrated in multiple classes of vertebrates, as well as in a variety of invertebrates (for review see [Wiltschko & Wiltschko, 2005](#)). In mammals, two types of magnetic responses have been reported: spontaneous magnetic alignment and goal-directed magnetic compass orientation. Until recently, most of the evidence for magnetosensitivity in mammals has come from spontaneous (i.e. nonlearned, non-goal-oriented) magnetic nest-building responses

of subterranean mole-rats (genus *Fukomys*). Mole-rats have been shown to position nests inside circular arenas in a fixed direction relative to the magnetic field, typically southeast ([Burda, Marhold, Westenberger, Wiltschko, & Wiltschko, 1990](#); [Marhold, Wiltschko, & Burda, 1997](#); [Thalau, Ritz, Burda, Wegner, & Wiltschko, 2006](#); but see [Oliveriusová, Němec, Králová, & Sedláček, 2012](#)). However, evidence collected over the past decade indicates that spontaneous magnetic alignment is widespread in epigeal mammals (i.e. mammals active at or above the soil surface). For example, a spontaneous preference for nest construction along the ~north–south magnetic axis has been demonstrated in wood mice, *Apodemus sylvaticus*, and bank voles, *Clethrionomys glareolus*, in both ambient and experimentally rotated magnetic fields ([Malkemper](#)

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et al., 2015; Oliveriusová, Němec, Pavelková, & Sedláček, 2014). In addition to laboratory assays, a wealth of field studies have reported spontaneous body alignment along the ~north–south axis in a variety of free-roaming mammals, although direct evidence for the involvement of magnetic cues underlying these responses is lacking (Begall, Červený, Neef, Vojtěch, & Burda, 2008; Begall, Malkemper, Červený, Němec, & Burda, 2013; Červený, Begall, Koubek, Nováková, & Burda, 2011; Červený et al., 2017; Obleser et al., 2016). Indirect evidence, however, comes from disruption of ~north–south alignment of cattle and deer in proximity to high-voltage power lines that disturb the local magnetic field and from alignment data collected from northern latitudes (where there is considerable variation in magnetic declination), revealing that magnetic north is a better predictor of north–south alignment than geographical north (Begall et al., 2008; Burda, Begall, Červený, Neef, & Němec, 2009). Taken together, the laboratory and field studies suggest that magnetic cues play an important role in mammalian spontaneous alignment. And while the functional significance of this seemingly widespread behaviour is not understood, a variety of hypotheses have been proposed (Begall et al., 2013; Červený et al., 2011; Hart et al., 2013; Malkemper, Painter, & Landler, 2016; Painter, Dommer, Altizer, Muheim, & Phillips, 2013; Phillips, Muheim, & Jorge, 2010).

In addition to spontaneous magnetic orientation, evidence for learned magnetic compass responses has come from studies of the C57BL/6J strain of laboratory mice. In nest-building and modified 'plus' Morris water maze assays, mice readily learned the magnetic compass direction of a shelter or submerged platform, respectively (Muheim, Edgar, Sloan, & Phillips, 2006; Phillips et al., 2013). What remains to be determined, however, is whether the forms of magnetic responses expressed in mammals are species specific (i.e. whether a species exhibits either learned magnetic compass responses or spontaneous magnetic orientation). Or alternatively, whether learned magnetic compass orientation and spontaneous magnetic alignment can be expressed under different contexts by the same species, as appears to be the case in amphibians and birds (Phillips, Borland, Freake, Brassart, & Kirschvink, 2002; Wiltschko, Thorsten, Stapput, Thalau, & Wiltschko, 2005).

Theoretical and empirical evidence from terrestrial vertebrates points to the involvement of two magnetoreception mechanisms relying on different biophysical processes: a magnetite-based mechanism (MBM) and a radical pair-based mechanism (RPM). An MBM is thought to function by means of a single domain or chains of superparamagnetic crystals of magnetite coupled to the cell membrane. The torque exerted on the magnetite crystals by the magnetic field is thought to provide the mechanical linkage responsible for opening or closing membrane channels (Kirschvink, Walker, & Diebel, 2001; Winklhofer & Kirschvink, 2010). Properties consistent with an MBM are found in the magnetic responses of subterranean mole-rats that are (1) independent of light, (2) sensitive to the polarity of the magnetic field, (3) unaffected by exposure to low-level (~85 nT) radiofrequency fields and (4) altered by high-intensity magnetic pulses in the tesla range (Kimchi & Terkel, 2001; Marhold, Burda, Kreilos, & Wiltschko, 1997; Marhold, Wiltschko et al., 1997; Thalau et al., 2006).

In contrast, an RPM involves a photo-induced biochemical reaction, forming radical-pair intermediates sensitive to the alignment of the magnetic field axis and can be affected by low-level radiofrequency (RF) fields (Ritz, Adem, & Schulten, 2000; Schulten, Swenberg, & Weller, 1978; Solov'yov, Thorsten, Schulten, & Hore, 2014). Spontaneous magnetic nest-building behaviour in wood mice has been shown to be sensitive to RF fields in the low-MHz range (Malkemper et al., 2015), and learned magnetic compass orientation by laboratory mice can only be obtained reliably when ambient RF field noise is lowered to less than 1 nT by

electromagnetically shielding the training and testing environments (Muheim et al., 2006; Phillips et al., 2013). Findings from wood mice and laboratory mice are both consistent with a magnetoreception pathway mediated by an RPM (Maeda et al., 2008; Ritz et al., 2000, 2009; Ritz, Thalau, Phillips, Wiltschko, & Wiltschko, 2004; Solov'yov et al., 2014; Thalau, Ritz, Stapput, Wiltschko, & Wiltschko, 2005; Wiltschko et al., 2014). However, this is in contrast to behavioural evidence from amphibians and birds in which learned magnetic compass orientation and spontaneous magnetic alignment appear to be mediated by separate biophysical mechanisms (RPM and MBM; respectively, Phillips et al., 2002; Wiltschko et al., 2005). Therefore, what remains to be determined is whether different forms of magnetic behaviour in mammals can be exhibited in the same species (i.e. spontaneous alignment and learned compass orientation are expressed in the same mammalian species) and, if so, whether the responses are mediated by a common or separate sensory mechanism.

In the present study, we show that both learned magnetic compass orientation and spontaneous magnetic alignment can be expressed in the same strain of laboratory mice. These findings show that the use of magnetic cues in mammals is more flexible than previously realized, providing further indication that magnetic information may play an important role in rodent, and more generally, mammalian spatial behaviour. Development of an assay in which it is possible to elicit both spontaneous and learned magnetic responses will help to further characterize the biophysical mechanism(s) underlying these distinct magnetic responses in an epigeic rodent, which, to date, remains an open question. Furthermore, determining the factors (e.g. environmental, physiological) that cause mice to exhibit spontaneous magnetic orientation will help to shed light on the adaptive significance of this widespread, yet poorly understood, magnetic behaviour.

## METHODS

### *Ethical Note*

All Methods were approved by the Virginia Tech Institute of Animal Care and Use Committee (Research Protocol No. 15-025).

### *General Methods*

#### *Training*

Male C57BL/6J inbred mice were used in this study and reared in a laboratory colony from stock obtained from the Jackson Laboratory (Bar Harbor, ME, U.S.A.). Therefore, all mice were derived from a common genetic background and possessed nearly identical genotypes. Pups were weaned at a mean of 23 days after birth and raised in same-sex sibling groups until transported to the Behavioral Testing Facility (Blacksburg, VA, U.S.A.) where mice were trained and tested. All mice were between 65 and 90 days of age when tested (mean  $\pm$  SD = 74.6  $\pm$  4.7 days) and were returned to the original colony after each experiment. Mice were trained inside the same building at the Behavioral Testing Facility, however, in the initial experiments (Series 1), training was carried out in an outer ('control') room, whereas mice tested in following experiments (Series 2 and 3) were trained inside an 'inner' room that was buffered from ambient noise and vibrations produced by equipment located in the control room. Testing was carried out in a separate building located at the Behavioral Testing Facility (see below). Male mice were trained for a minimum of 4 days and a maximum of 10 days in translucent polycarbonate cages lined with wood shavings as substrate. Food pellets and water were provided ad libitum. Training cages were placed on one of four sets of partially enclosed nonmagnetic wooden shelves aligned in four

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