

RESEARCH ARTICLE

Magnetic compass orientation in two strictly subterranean rodents: learned or species-specific innate directional preference?

Ludmila Oliveriusová¹, Pavel Němec^{2,*}, Zuzana Králová² and František Sedláček¹

¹Department of Zoology, Faculty of Science, University of South Bohemia, CZ-370 05 Ceske Budejovice, Czech Republic and

²Department of Zoology, Faculty of Science, Charles University in Prague, CZ-128 44 Praha 2, Czech Republic

*Author for correspondence (pgnemoc@natur.cuni.cz)

SUMMARY

Evidence for magnetoreception in mammals remains limited. Magnetic compass orientation or magnetic alignment has been conclusively demonstrated in only a handful of mammalian species. The functional properties and underlying mechanisms have been most thoroughly characterized in Ansell's mole-rat, *Fukomys anselli*, which is the species of choice due to its spontaneous drive to construct nests in the southeastern sector of a circular arena using the magnetic field azimuth as the primary orientation cue. Because of the remarkable consistency between experiments, it is generally believed that this directional preference is innate. To test the hypothesis that spontaneous southeastern directional preference is a shared, ancestral feature of all African mole-rats (Bathyergidae, Rodentia), we employed the same arena assay to study magnetic orientation in two other mole-rat species, the social giant mole-rat, *Fukomys mechowii*, and the solitary silvery mole-rat, *Heliophobius argenteocinereus*. Both species exhibited spontaneous western directional preference and deflected their directional preference according to shifts in the direction of magnetic north, clearly indicating that they were deriving directional information from the magnetic field. Because all of the experiments were performed in total darkness, our results strongly suggest that all African mole-rats use a light-independent magnetic compass for near-space orientation. However, the spontaneous directional preference is not common and may be either innate (but species-specific) or learned. We propose an experiment that should be performed to distinguish between these two alternatives.

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INTRODUCTION

Diverse animals, including birds, mammals, reptiles, amphibians, fish, crustaceans and insects, use the Earth's magnetic field for directional orientation and navigation (Wiltschko and Wiltschko, 1995; Wiltschko and Wiltschko, 2005; Lohmann et al., 2007). Despite the remarkable progress that has been accomplished during the past decade, evidence for magnetoreception in mammals remains fairly limited. Magnetic compass orientation has been convincingly demonstrated in only two species of distantly related subterranean rodents (Burda et al., 1990; Kimchi and Terkel, 2001), two epigeic rodent species (Deutschlander et al., 2003; Muheim et al., 2006) and three bat species (Holland et al., 2006; Holland et al., 2010; Wang et al., 2007). More recently, magnetic alignment has been demonstrated in larger mammals, namely cattle and deer (Begall et al., 2008; Begall et al., 2011; Burda et al., 2009), and in hunting foxes (Červený et al., 2011). Likewise, the mechanisms of magnetoreception in mammals have been less studied than those of other vertebrates (Johnsen and Lohmann, 2005; Mouritsen and Ritz, 2005; Němec et al., 2005). Indeed, except for two recent papers providing evidence for a magnetite-based polarity compass in bats (Wang et al., 2007; Holland et al., 2008), our current knowledge about the underlying mechanisms comes from the study of a single subterranean species – Ansell's mole-rat, *Fukomys anselli*.

Ansell's mole-rat has proved to be an excellent model with which to investigate magnetic orientation because of its robust, spontaneous

drive to construct nests in the southeastern sector of a circular arena using magnetic field azimuth as the primary orientation cue (Burda et al., 1990). In marked contrast to birds (Ritz et al., 2010), its magnetic compass is light independent, polarity based and insensitive to magnetic fields oscillating in the MHz range (Marhold et al., 1997a; Marhold et al., 1997b; Thalau et al., 2006). However, a brief magnetic pulse designed to alter the magnetization of single-domain magnetite can lead to a long-term (≥ 3 months) deflection of mole-rat directional preference (Marhold et al., 1997b). Together, these functional properties strongly suggest that the mole-rat possesses a magnetite-mediated compass. It is also the only mammalian species in which the neural basis of magnetic orientation has been analyzed. It has been shown that magnetic information is integrated with multimodal sensory and motor information into a common spatial representation of allocentric space within the superior colliculus, the head direction system and the entorhinal–hippocampal spatial representation system (Němec et al., 2001; Burger et al., 2010). Although magnetoreceptors remain unknown, recent experiments involving anaesthesia of the eye have suggested the cornea to be a candidate receptor site (Wegner et al., 2006a).

The adaptive significance of magnetic orientation in the underground ecotope seems to be obvious (Moritz et al., 2007). In a dark world deprived of most of the sensory cues that are normally available aboveground, the Earth's magnetic field provides the only

reliable and omnipresent source of directional information. Indeed, the strictly subterranean mode of life has resulted in a decreased reliance on vision associated with microphthalmia and a severely reduced visual system that is poorly equipped for visually guided navigation (Němec et al., 2007; Němec et al., 2008). Thus, magnetic cues likely enable subterranean dwellers to orientate when digging long tunnels, to interconnect damaged tunnels, to bypass effectively obstacles, and possibly to find their way back home after rare surface activities (e.g. dispersal, mate-seeking excursions and foraging above ground). The need for efficient orientation underground is further accentuated by a patchy distribution of food resources and high metabolic costs of burrowing (Sedláček, 2007; Zelová et al., 2007; Zelová et al., 2010). Indeed, it has been repeatedly shown that strictly subterranean rodents use magnetic field azimuth as an external directional reference both for orientation in a circular arena or a radial maze (Burda et al., 1990; Marhold et al., 1997a; Marhold et al., 1997b; Marhold et al., 2000; Kimchi and Terkel, 2001) and for the path integration (Kimchi et al., 2004). Not surprisingly, the spontaneous directional preference has been demonstrated in strictly subterranean, congenitally microphthalmic mole-rats (aforementioned citations) but not in more visual subterranean rodents that regularly forage aboveground (Schleich and Antinuchi, 2004). It is generally believed that this directional preference is innate.

In this study, we investigated magnetic compass orientation in two African mole-rats (Bathyergidae, Rodentia), the social giant mole-rat, *Fukomys mechowii*, and the solitary silvery mole-rat, *Heliophobius argenteocinereus*, and thereby tested the hypothesis that spontaneous southeastern directional preference is a shared, ancestral feature of all Afrotropical mole-rats.

MATERIALS AND METHODS

Animals

The silvery mole-rat (*Heliophobius argenteocinereus* Peters 1846) inhabits southern Kenya, Tanzania, Malawi, southeastern Democratic Republic of the Congo, eastern Zambia and northern Mozambique; the giant mole-rat [*Fukomys mechowii* (Peters 1881)] inhabits northern Zambia, southern Democratic Republic of the Congo and Angola (Bennett and Faulkes, 2000). Both model species feature very similar ecologies but differ markedly in their life histories: the silvery mole-rat is solitary, whereas the giant mole-rat is a social cooperative breeder. Their biology has been reviewed recently (Kawalika and Burda, 2007; Šumbera et al., 2007).

A total of 10 silvery mole-rats (five males and five females) and 10 pairs of giant mole-rats were used in this study. The silvery mole-rats were wild caught in Malawi in Mpalanganga estate, Zomba (15°27'S, 35°15'E), Zomba plateau (15°20'S, 35°16'E) and Mulanje–Chipoka (16°02'S, 35°30'E) in 2000 and 2005. The giant mole-rats were born in captivity and originate from a stock captured in Ndola, Zambia. All experimental animals were at least 1 year old.

The animals were kept in a breeding room with moderate temperature (25±1°C) under a 12h:12h light:dark regime at the University of South Bohemia. The silvery mole-rats were housed individually in Plexiglas mazes, and the pairs of giant mole-rats were housed in glass terrariums. The mole-rats were fed with carrots, potatoes, lettuce, apples and rodent pellets *ad libitum*, and provided with bedding (horticultural peat) and nest material (filter paper). The giant mole-rats were tested in pairs so as to avoid stress from isolation. All experiments were approved by the Institutional Animal Care and Use Committee of the University of South Bohemia, and the Ministry of Education, Youth and Sports (no. 12923/2007-30).

Behavioural assay

The behavioural test designed to assess magnetic compass orientation in mole-rats has been described in detail previously (Burda et al., 1990). Briefly, individual silvery mole-rats or pairs of the giant mole-rats were released in a circular arena (80 cm diameter and 40 cm high; made of plastic impervious to light) placed in the centre of a pair of Helmholtz coils. The arena was filled with a thin layer of horticultural peat as litter, scattered slips of tissue papers as nest material, and randomly distributed pieces of carrots and potatoes as food. Animals were allowed to explore the novel environment overnight (from 19:00 to 07:00 h). In the giant mole-rat, which exhibits a spontaneous drive to build nests, the nest position was taken as a proxy for assessing spontaneous directional preference. In the silvery mole-rat, which does not build nests under described laboratory conditions, the sleeping position was taken as a proxy for spontaneous directional preference. Video surveillance was used to monitor the nest and sleeping positions. The first 5 min of each experimental hour were automatically recorded by an overhead infrared-sensitive CCD video camera equipped with an infrared diode. The whole experiment was performed in total darkness (in a basement room without windows).

Magnetic conditions

The mole-rats were tested in four different magnetic fields: the natural magnetic field [magnetic north (mN)=0 deg] and three shifted fields with magnetic north at geographic east (mN=90 deg), south (mN=180 deg) or west (mN=270 deg). The three shifted fields were produced by adding a horizontal artificial field aligned 135 deg clockwise (east field), 180 deg (south field) or 135 deg counterclockwise (west field) to the ambient magnetic field; the total intensity (~47 µT) and the inclination (+66 deg) remained unchanged. The artificial fields were generated by a pair of horizontal Helmholtz coils. The coils were powered by a Voltcraft DPS-8003 PFC current-regulated power supply (Conrad Electronic, Hirschau, Germany). The magnetic fields were measured using an Elimag F-1 single axis magnetometer (Elidis, Prague, Czech Republic) after each experiment. Each animal (or pair in the case of the giant mole-rats) was tested only once in each magnetic condition. The sequence of the magnetic fields tested was randomized.

Statistics

Directional responses were analyzed using circular statistics (Batschelet, 1981). The Rayleigh test was used to assess significant deviations from a random distribution of bearings. The Watson–Williams *F*-test was used to compare the mean bearings between tests performed under different magnetic field conditions and between species. These tests were calculated with Oriana 3.0 (Kovach Computing Services, Anglesey, UK). Because the directional preferences of the same animal under different magnetic conditions are not statistically independent, a permutation-type test for uniformity of repeated circular measurements (Follmann and Proschan, 1999) was utilized to analyze the circular distribution of the pooled bearings. To assess significant deviations from a random distribution, the mean vector length of the observed bearings was compared with a null reference distribution of mean vector lengths (supplementary material Fig. S1) obtained by simulation in Python 2.7 (www.python.org/getit/releases/2.7).

RESULTS

The giant mole-rat

These social mole-rats spontaneously gathered the nesting material and built a nest within one to a few hours. In the local geomagnetic

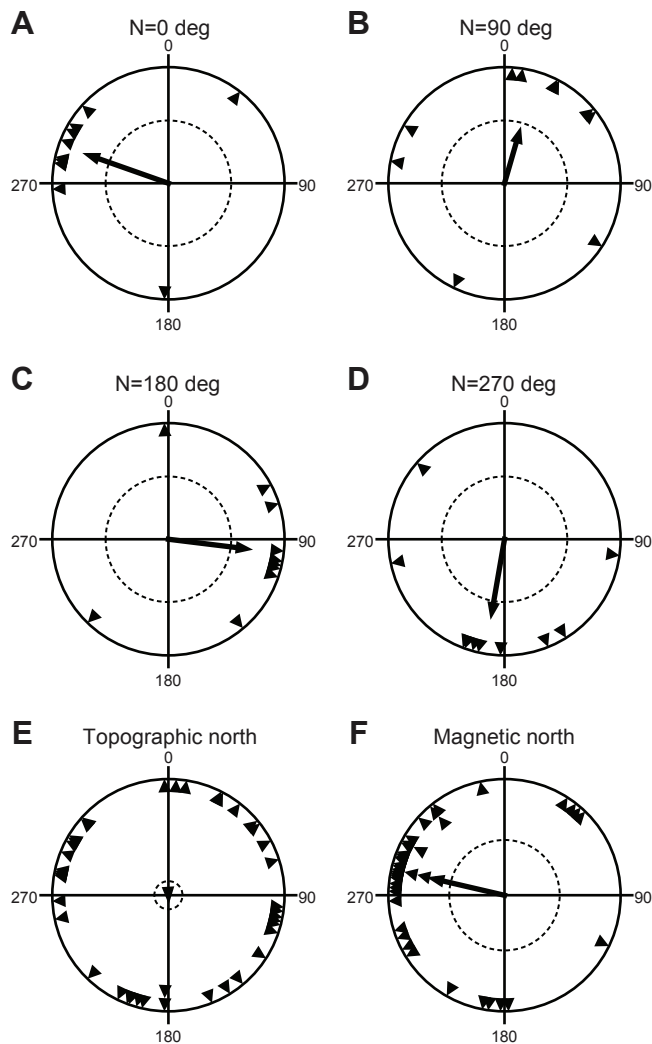


Fig. 1. Magnetic orientation of the giant mole-rat, *Fukomys mechowii*, in a visually symmetrical circular arena. Each triangle represents the position of a nest built by a sibling pair of mole-rats. (A–D) Bearings of 10 mole-rat pairs under different magnetic conditions: the natural magnetic field (A) and three shifted fields with magnetic north at geographic east (B), south (C) or west (D). (E) Topographic distribution of all bearings in the arena plotted irrespective of the experimental magnetic field conditions. (F) All bearings plotted relative to the magnetic north in the arena (standardized to 0 deg). Arrows indicate the mean vector for the distribution of the nests; the length of the mean vector (r) provides a measure of the degree of clustering in the distribution of the nests. The inner dashed circles mark the 5% significance border of the Rayleigh test (note that in A–D it refers to the tabulated critical r values for the given sample size, whereas in E and F it is derived from a simulated null reference distribution of the mean vector lengths for the pooled data; see supplementary material Fig. S1); the arrows exceeding these circles indicate significant directional orientation.

field, they exhibited a clear preference for building their nests in the western sector of the arena (Fig. 1A). When tested in one of three altered magnetic fields created by rotating north 90, 180 or 270 deg, mole-rats changed their directional preferences accordingly (Fig. 1B–C). The mean bearings were significantly different (Watson–Williams F -test, $P < 0.05$; supplementary material Table S1) and differed by approximately 90 deg. The directional preferences were significant in all but one ($mN = 90$ deg) of the fields tested (Rayleigh test, $P < 0.05$; Table 1). When the four data sets were pooled, the topographic distribution of the nests in the arena was

indistinguishable from random (Fig. 1E, Table 1), indicating the absence of non-magnetic orientation cues in the testing arena. By contrast, when the nest bearings were pooled with respect to magnetic north in the arena (standardized to 0 deg), the bearings were strongly westerly oriented (Fig. 1F, Table 1).

The silvery mole-rat

The results were generally congruent with those described above for the giant mole-rats, although the scatter in the distribution of bearings was greater in the silvery mole-rats (Fig. 2, Table 1). It is unclear whether the greater scatter reflects species-specific differences or the mere fact that sleeping position provides a less reliable measure of directional preference. Individual directional decisions may also be less precise and consistent than those resulting from interactions between two siblings in the giant mole-rat. The silvery mole-rats slept preferentially in the western sector of the arena in the local geomagnetic field and they significantly changed the preferred sleeping positions as predicted in the shifted magnetic fields (Fig. 2A–D). The directional preferences were significant in the geomagnetic field and in the field shifted by 180 deg, and borderline significant in the field shifted by 270 deg (Table 1). Pooled data were random with respect to topographic north, but significantly westerly oriented with respect to magnetic north (Fig. 2E, F, Table 1).

Interspecific comparison

When tested under the same magnetic conditions, both species tended to prefer the same direction. Indeed, the 95% confidence intervals largely overlapped and the mean bearings were not significantly different (Watson–Williams F -test, $P > 0.05$; supplementary material Table S1).

DISCUSSION

The arena assays performed in this study show that two bathyergid species, *F. mechowii* and *H. argenteocinereus*, use a light-independent magnetic compass for near-space orientation. Both species exhibited spontaneous western directional preference and, importantly, deflected their directional preference according to shifts in the direction of magnetic north, clearly indicating that they were deriving directional information from the magnetic field. Because all the experiments were performed in total darkness, the functional properties of their magnetic compass appear the same as those of other strictly subterranean mole-rats (Marhold et al., 1997a; Kimchi and Terkel, 2001). Interestingly, the preferred direction of both studied species differed from the southeastern preference of the Ansell's mole-rat (Burda et al., 1990; Marhold et al., 1997a; Marhold et al., 1997b; Thalau et al., 2006). This finding indicates that the directional preference is not a common, ancestral feature of Afrotropical mole-rats and raises the question as to whether it is innate or learned.

Two magnetic compass mechanisms in mammals?

Among subterranean mammals, magnetic compass orientation has been hitherto demonstrated in three species of African mole-rats (Burda et al., 1990) (present study) and in the Eurasian blind mole rat, *Spalax ehrenbergi* (Kimchi and Terkel, 2001). All of these species are strictly subterranean, i.e. inhabiting self-constructed burrow systems isolated from the aboveground environment by mounds of soil, and the animals feed almost exclusively on underground storage organs of plants (Nevo, 1999; Bennett and Faulkes, 2000). Because mole-rats are rarely exposed to light, it is not surprising that their magnetic compass orientation is light

Table 1. Orientation of the African mole-rats in different magnetic field conditions

Test conditions	<i>Fukomys mechowii</i>				<i>Heliophobius argenteocinereus</i>			
	μ (deg)	r	P	N	μ (deg)	r	P	N
Magnetic north=0 deg	289	0.717	0.003	10	272	0.685	0.006	10
Magnetic north=90 deg	16	0.445	0.139	10	7	0.467	0.112	10
Magnetic north=180 deg	97	0.666	0.008	10	138	0.598	0.024	10
Magnetic north=270 deg	190	0.637	0.013	10	196	0.526	0.059	10
Topographic bearings*	177	0.011	0.979	40	219	0.15	0.405	40
Magnetic bearings*	283	0.614	0.004	40	288	0.54	1.3×10^{-4}	40

μ , mean orientation; r, mean vector length; P, probability of the Rayleigh test; N, number of animals/animal pairs tested.

*Note that the pooled data were analyzed using a uniformity test for repeated circular measurements (see Materials and methods for details).

independent. However, whether this property implicating a magnetite-mediated transduction mechanism can be generalized to other mammals remains unclear. As noted above, a light-independent, magnetite-based compass has also been reported in microphthalmic echolocating bats (Wang et al., 2007; Holland et

al., 2008). By contrast, recent evidence suggests that the magnetic compass of epigeic rodents such as the Siberian hamster, *Phodopus sungorus*, and C57BL/6J mice has more in common with birds than with mole rats; most notably it seems to be disrupted by low-level fields oscillating in the MHz range (Phillips et al., 2010) (J. B. Phillips, unpublished). These findings point to an intriguing possibility that two fundamentally different mechanisms, namely a light-independent, magnetite-based mechanism (for reviews, see Kirschvink et al., 2001; Winklhofer and Kirschvink, 2010) and a light-induced, photoreceptor-based mechanism (Ritz et al., 2000), underlie magnetic compass orientation in rodents.

A true compass or magnetic alignment?

It has been repeatedly suggested that magnetic orientation in mole-rats investigated in a circular arena and/or a radial maze may constitute a fixed alignment response rather than true compass (i.e. goal directed) orientation (Deutschlander et al., 2003; Muheim et al., 2006; Phillips et al., 2010). However, unlike typical alignment responses, the orientation of mole-rats is unimodal and does not coincide with the magnetic cardinal directions. Indeed, most experiments have demonstrated a southeastern directional preference (Burda et al., 1990; Marhold et al., 1997a; Marhold et al., 1997b; Kimchi and Terkel, 2001). More importantly, labyrinth experiments and homing tests in a radial maze performed by Kimchi and colleagues (Kimchi and Terkel, 2001; Kimchi et al., 2004) have shown that blind mole rats use the Earth's magnetic field not only as an external directional reference for the path integration but also for navigation towards a nearby goal. Although such evidence is not currently available for African mole-rats, it has been suggested that they use magnetic compass to find their way back home after mate-seeking excursions (Moritz et al., 2007).

Does regression of the visual system impair the light-dependent compass mechanism?

The light-induced radical pair mechanism appears to be intimately coupled with photoreception (Ritz et al., 2000; Rodgers and Hore, 2009) but not necessarily with image-forming vision. Indeed, behavioural evidence strongly suggests that photoreceptors of the pineal organ, which lack image-forming capacity, are implicated in mediating light-dependent magnetic compass responses in amphibians (Deutschlander et al., 1999). Nevertheless, a recent behavioural study demonstrated that avian magnetoreception requires non-degraded image formation/object vision (Stapput et al., 2010).

Strictly subterranean rodents share many convergent sensory adaptations, among which reduced eyes and visual systems are the most conspicuous (for a review, see Nėmec et al., 2007). The blind mole rat *S. ehrenbergi* has subcutaneous eye with a degenerated optical apparatus that has lost the ability of image formation

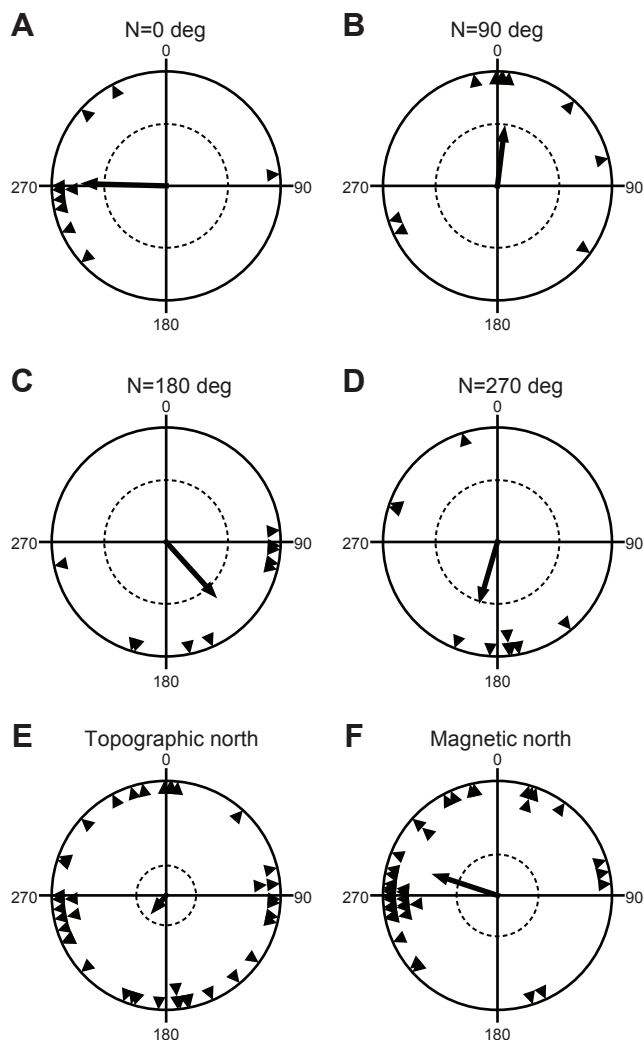


Fig. 2. Magnetic orientation of the silvery mole-rat, *Heliophobius argenteocinereus*, in a visually symmetrical circular arena. Each triangle represents a sleeping position of an individual mole-rat. See Fig. 1 legend for explanation. The inner dashed circles mark the 5% significance border of the Rayleigh test; the arrows exceeding these circles indicate significant directional orientation.

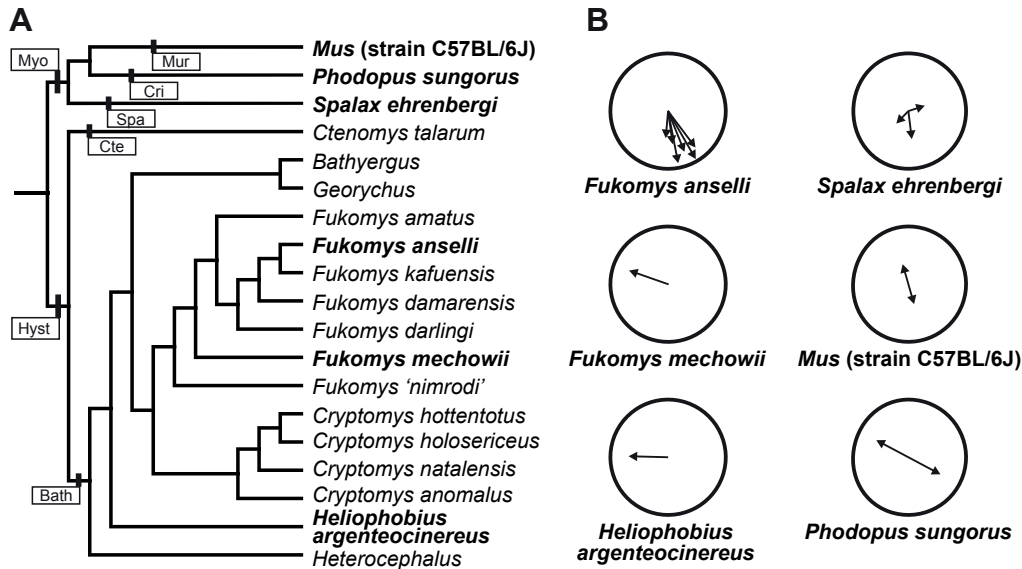


Fig. 3. (A) Taxonomic distribution of rodent species, in which the spontaneous directional preference has been demonstrated (shown in bold). Bath, Bathyergidae; Cri, Cricetidae; Cte, Ctenomyidae; Hyst, Hystricomorpha; Mur, Muridae; Myo, Myomorpha; Spa, Spalacidae. (B) Spontaneous directional choices reported in six rodent species. Arrows indicate the grand mean vectors reported in different experiments; the longer the grand mean vector, the more consistent the orientation choices between family groups (*Fukomys ansellii* and *F. mechowii*) or individuals (the other four species). Double-headed arrows indicate bimodal distribution of choices. Note the remarkably stable directional preference in the Ansell's mole-rat, *F. ansellii*. Data sources vary by species: [*F. ansellii* (Burda et al., 1990; Marhold et al., 1997a; Marhold et al., 1997b; Thalau et al., 2006; Wegner et al., 2006a); *F. mechowii* and *H. argenteocinereus* (present study); *S. ehrenbergi* (Kimchi and Terkel, 2001; Marhold et al., 2000); *Mus* C57BL/6J (Muheim et al., 2006); *P. sungorus* (Deutschlander et al., 2003)].

(Sanyal et al., 1990; Cernuda-Cernuda et al., 2002). African mole-rat eyes feature normal properties, indicating the capability of image-forming vision (Cernuda-Cernuda et al., 2003; Peichl et al., 2004). However, their object vision is constrained by extremely low visual acuity (Němec et al., 2008) and severe regression of the visual domains involved in the coordination of the visuomotor reflexes important for the stabilization of the image on the retina (Němec et al., 2004). Therefore, the microphthalmia and regressed visual system may hypothetically impair the light-dependent magnetic compass in these strictly subterranean rodents and possibly other microphthalmic mammals such as echolocating bats, provided that it prevents the perception of contours.

Learned or species-specific innate directional preference?

Southeastern or southern directional preference has been repeatedly reported in Ansell's mole-rat (Burda et al., 1990; Marhold et al., 1997a; Marhold et al., 1997b; Thalau et al., 2006; Wegner et al., 2006a) as well as in the phylogenetically distant blind mole rat *S. ehrenbergi* (Kimchi and Terkel, 2001). These findings suggest that this preference is innate and common to all strictly subterranean rodents. The latter assumption has been disproved by the present study: both the social giant mole-rat, which is closely related to Ansell's mole-rat, and the solitary silvery mole-rat, which represents a basal bathyergid lineage, preferred a westerly direction. The arena assays performed here thus imply that spontaneous directional preference is either species-specific or learned. So far, no studies have been conducted to distinguish between these two alternatives. The strongest, albeit circumstantial, support for a hard-wired, innate preference constitutes the fact that spontaneous directional choice in Ansell's mole-rat is highly consistent between experiments conducted in two laboratories over a period of two decades (Fig. 3). However, results reported in the blind mole rat are less consistent (Kimchi and Terkel, 2001; Marhold et al., 2000). Animals tested

in Tel-Aviv (chromosomal species $2N=58$), Haifa ($2N=60$) and Frankfurt am Main ($2N=60$) preferred southeastern, east-northeastern and southwestern directions, respectively (Fig. 3). Moreover, the directional preference for nest placement is learned in the Siberian hamster and the C57BL/6J mouse (Deutschlander et al., 2003; Muheim et al., 2006). These epigeic rodents exhibit only weak spontaneous preference, but reveal robust magnetic compass orientation once magnetic cues are associated with a light gradient in training cages prior to testing in a circular, visually symmetrical arena. It remains unclear whether, and if so to what degree, holding conditions affect directional preference in subterranean, congenitally microphthalmic mole-rats. Nevertheless, observations that the bathyergid mole-rats tend to be best oriented in the natural magnetic field and exhibit a much higher scatter of bearings in at least some experimental fields [e.g. the east field (present study) and the south field (Burda et al., 1990)] are in line with the notion that the rotated magnetic field may cause a conflict between the magnetic field and some non-magnetic cue the animals have access to, provided that in the north testing field the relative alignment of the magnetic and non-magnetic cues would be the same as it was in the animals' holding cages.

We suggest that the critical test to distinguish these two possibilities should follow the assay introduced in the laboratory mouse (Muheim et al., 2006). Because all four species reported to use a magnetic compass for near-space orientation also exhibit light-avoidance behaviour (Rado et al., 1992; Wegner et al., 2006b; Kott et al., 2010), they should readily associate the magnetic direction with the dark end of a training cage. If spontaneous directional preference is innate, there should be no effect of the holding conditions. If it is learned, animals should orient in the magnetic direction coinciding with the dark end of the training cage, i.e. animals held prior to testing in the holding cages oriented differently relative to the magnetic field should prefer different directions in a

visually symmetrical arena. Such an outcome would also constitute conclusive evidence that the mole-rat magnetic compass orientation is goal-directed. This experimental paradigm thus harbours potential for the better understanding of the nature of magnetic compass orientation in subterranean mammals.

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