Species differences in egocentric navigation: the effect of burrowing ecology on a spatial cognitive trait in mice

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Efficient navigation is a critical component of fitness for most animals. While most species use a combination of allocentric (external) and egocentric (internal) cues to navigate through their environment, subterranean environments present a unique challenge in that visually mediated allocentric cues are unavailable. The relationship between egocentric spatial cognition and species differences in ecology is surprisingly understudied. We used a maze-learning task to test for differences in egocentric navigation between two closely related species of mice, the eastern house mouse, *Mus musculus musculus*, and the mound-building mouse, *Mus spicilegus*. The two species are sympatric in Eastern Europe and overlap in summer habitat use but differ dramatically in winter space use: whereas house mice occupy anthropogenic structures, mound-building mice survive the winter underground in intricate burrow systems. Given species differences in burrowing ecology, we predicted that *M. spicilegus* would learn the maze significantly faster than *M. m. musculus* when tested in complete darkness, a condition that eliminated allocentric spatial information and served as a proxy for the subterranean environment. We found strong support for this prediction. In contrast, the two species performed equally well when different mice were tested in the same maze with lights on. This context-specific species difference in spatial cognition suggests that enhanced egocentric navigation in *M. spicilegus* is an adaptation to the burrow systems on which the overwinter survival of young mound-building mice depends. The results of this study highlight the importance of ecological adaptations to the evolution of cognitive traits.

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From the long-distance migrations of pelagic seabirds, to a newborn wallaby's journey from mother's birth canal to teat (Croxall, Silk, Phillips, Afanasyev, & Briggs, 2005; Egevang et al., 2010; Schneider, Fletcher, Shaw, & Renfree, 2009; Tyndale-Biscoe & Renfree, 1987), the ability to navigate from one location to another is a critical component of fitness for most nonsessile organisms. To accomplish these nonrandom movements, animals use allocentric (external) cues, such as the sun, stationary terrestrial objects or odour trails, and egocentric (internal) signals from the proprioceptive, vestibular or somatosensory systems (Shettleworth, 2010). Whereas allocentric navigation can incorporate multimodal sensory information from both local and distant cues, egocentric navigation relies on input generated by an organism's own movement. Experimental studies subdivide egocentric navigation into path integration (colloquially, 'dead reckoning') and route-based

navigation. While both rely on the ability to update spatial position based on input from the proprioceptive and/or vestibular systems, path integration is tested by displacing test subjects from a starting point and measuring homing ability, whereas route-based navigation tests subjects' ability to learn and remember a series of turns in a point-to-point system such as a maze (Benhamou, 1997; Shettleworth, 2010).

Few organisms use just one type of cue and most combine allocentric and egocentric information to form a spatial representation, or cognitive map, of their surroundings (Etienne, Maurer, & Seguinot, 1996; Etienne et al., 1998; Shettleworth, 2010). Yet most work on the evolution and mechanistic basis of vertebrate spatial abilities has focused on allocentric cue use. In this context, comparative studies in a wide range of taxa suggest that species, population and sex differences in spatial learning ability, and reliance on different types of external cues for navigation, are shaped by differences in ecology as it relates to space use (e.g. social structure: Gaulin, FitzGerald, & Wartell, 1990; migratory behaviour: Pravosudov, Kitaysky, & Omanska, 2006; foraging ecology: Clayton & Krebs, 1994; Pravosudov & Clayton, 2002; environmental complexity: Bruck & Mateo, 2010; du Toit,

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Bennett, Nickless, & Whiting, 2012; predation pressure: Brown & Braithwaite, 2005). For example, seed-caching birds learn the locations of hidden seeds with greater precision than noncaching species (Jones, Antoniadis, Shettleworth, & Kamil, 2002), benthic three-spined stickleback learn to locate a hidden reward twice as fast as limnetic ecomorphs that occupy less complex microenvironments (Odling-Smee, Boughman, & Braithwaite, 2008), and eusocial Damaraland mole-rats, *Fukomys damarensis*, a species with complex burrow architecture, learn a spatial task faster and exhibit higher retention than Cape mole-rats, *Georychus capensis*, a solitary species with relatively simple burrows (Costanzo, Bennett, & Lutermann, 2009).

Although path integration has been demonstrated in several mammalian orders, including rodents (Alyan, 1996; Bardunias & Jander, 2000; Etienne, Maurer, Saucy, & Teroni, 1986; Kimchi & Terkel, 2004; Mittelstaedt & Mittelstaedt, 1980) and primates (Israël, Grasso, Georges-François, Tsuzuku, & Berthoz, 1997), most work on egocentric navigation has been conducted in invertebrates (e.g. Müller & Wehner, 1988; Wehner & Srinivasan, 1981, 2003; reviewed in ; Srinivasan, 2015; cf. ; Kimchi & Terkel, 2002; Presotto & Izar, 2010). Importantly, ecologically motivated tests for species differences in egocentric spatial ability are surprisingly lacking.

We used a spatial learning task to test for differences in egocentric navigation between two closely related, but ecologically distinct, species of Old World mice: the eastern house mouse, *Mus musculus musculus*, and the mound-building mouse, *Mus spicilegus*. The two species are sympatric throughout the range of *M. spicilegus* (Eastern Europe, from Hungary to the Ukraine) and locally syntopic in crop fields during the spring and summer (Gouat, Katona, & Poteaux, 2003; Muntyanu, 1990; Poteaux, Busquet, Gouat, Katona, & Baudoin, 2008) but exhibit major differences in burrowing ecology. While house mice will dig and construct burrows under experimental conditions (Bouchard & Lynch, 1989; Schmid-Holmes, Drickamer, Robinson, & Gillie, 2001), their commensal relationship with humans typically precludes this behaviour. In sympatry with *M. spicilegus*, *M. m. musculus* overwinters in haystacks, farm buildings and other anthropogenic structures (Muntyanu, 1990). In contrast, *M. spicilegus* survives the winter in complex burrow systems topped by mounds of soil and vegetation that serve a thermoregulatory function (Szenczi, Kopcso, Bánszegi, & Altbäcker, 2012; Szenczi et al., 2011). The burrow systems typically reach a depth of 1–2 m with exit holes up to 1.5 m away from the central mound (Muntyanu, 1990; Szenczi et al., 2011). Construction takes several days to weeks and involves multiple related individuals, primarily young of the year that delay reproduction until the following spring (Garza et al., 1997; Muntyanu, 1990; Poteaux et al., 2008). In midwinter, mounds can contain as many 21 mice (Canaday, Mosansky, & Stamlo, 2009). Mounds and burrows are constructed during the autumn (September – November) and are occupied until spring (March – April; Muntyanu, 1990; Szenczi et al., 2011). Thus, mound-building mice spend at least half of the year living underground in a spatially complex and completely dark environment in which allocentric cues are largely unavailable.

We tested for species differences in a maze-learning task performed in complete darkness without access to allocentric cues. Given the specialized burrowing ecology of *M. spicilegus,* we predicted that this species would learn the task faster than *M. m. musculus.* To control for more general species differences in spatial ability, we repeated the experiment using different individuals with lights on (i.e. with access to allocentric cues both inside and external to the maze). Given that both species forage above ground and occupy the same habitat for part of the year, we did not expect to find species differences in maze learning with allocentric cues available.

METHODS

Animals

A total of 27 *M. m. musculus* from 10 litters and 29 *M. spicilegus* from 16 litters were used in this study. Both species were represented by wild-derived inbred strains, obtained from Jackson Laboratory (*M. m. musculus*: PWK/PhJ) and the Montpellier Wild Mice Genetic Repository (*M. spicilegus*: ZRU), and maintained at Oklahoma State University since 2013. Subjects were sexually naïve young adults (*M. m. musculus*, 55–166 days; *M. spicilegus* 57–167 days) that had not been used in prior behavioural experiments. To minimize potential litter effects (e.g. Lazic & Essioux, 2013), we avoided using same-sex littermates in the same light condition whenever possible.

Mice were housed in polycarbonate cages bedded with Sani-chips® (Harlan Teklad, Madison, WI, U.S.A.) and were provided with nesting material (cotton nestlets and alfalfa hay) and ad libitum water and chow (Rodent Diet 5001, Harlan Teklad). To enhance motivation for the food reward (see below), seeds that were provided two to three times/week as enrichment to other mice in the colony were not given to test subjects; animals were not otherwise food restricted. The colony was maintained on a 12:12 h light:dark cycle (lights on at 0900 hours) and maze trials were run during the light phase (between 0900 and 1300 hours). This schedule was chosen because *Mus* species spend most daylight hours inside a nest or burrow, the environment we were attempting to approximate with the maze.

Apparatus and Procedure

To test the subjects' egocentric navigation abilities we used performance learning on a two-dimensional maze task. The maze (Ware Manufacturing, www.waremfginc.com) consisted of a 3 × 3 grid of nine 13.5 × 13.5 × 11 cm boxes with 6.5 cm diameter holes for the animals to move through (Fig. 1) and a reward zone (a Habitrail® 5 cm diameter plastic tube and endcap) with wild bird seeds and bedding from each subject's home cage (see Mateo, 2008, for comparable methodology). During pilot testing, the large number of errors that occurred with animals in the last box before
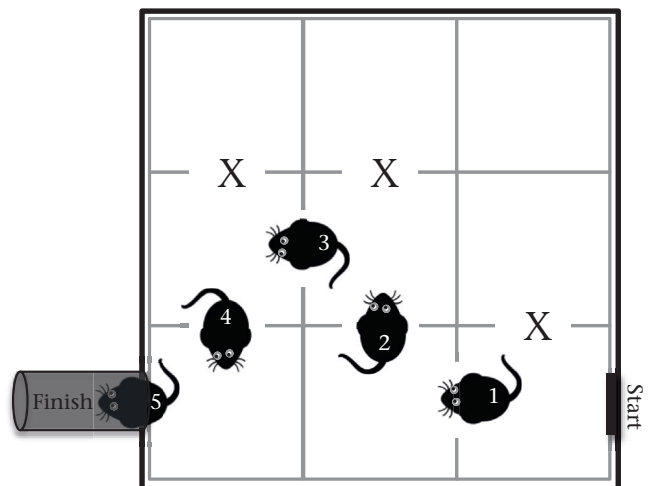

Figure 1. Maze used to test for species differences in spatial learning and memory in *Mus spicilegus* and *M. m. musculus*. Numbers indicate the points at which mice could either take the correct route (indicated by the orientation of the mice) or make one or more errors. An error was scored each time a mouse backtracked in the maze or entered a dead end box (indicated with Xs).