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Species differences in egocentric navigation: The effect of burrowing ecology on a spatial-cognitive trait in mice (In Press, Animal Behaviour May 2017)

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ABSTRACT

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, *M. 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 over-winter survival of young mound-building mice depends. The results of this study highlight the importance of ecological adaptations to the evolution of cognitive traits.

Keywords: Learning, memory, mound-building, *Mus spicilegus*, route-based navigation, spatial ecology

INTRODUCTION

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 non-sessile organisms. To accomplish these non-random movements, animals use allocentric (external) cues, such as the sun, stationary terrestrial objects, or odor 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 et al., 1998, 1996; 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 et al., 1990; migratory behavior, Pravosudov et al., 2006; foraging ecology, Clayton & Krebs, 1994; Pravosudov & Clayton, 2002; environmental complexity, Bruck & Mateo, 2010; du Toit et al., 2012; predation pressure, Brown & Braithwaite, 2005). For example, seed-caching birds learn the locations of hidden seeds with greater precision than non-caching species (Jones et al., 2002), benthic three-spined stickleback learn to locate a hidden reward twice as fast as limnetic ecomorphs that occupy less complex microenvironments (Odling-Smee et al., 2008), and eusocial Damaraland mole-rats, a species with complex burrow architecture, learn a spatial task faster and exhibit higher retention than Cape mole-rats, a solitary species with relatively simple burrows (Costanzo et al., 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; c.f. 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 et al., 2003; Muntyanu, 1990; Poteaux et al., 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 behavior. 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 et al., 2011; Szenczi, Kopcso, Bánszegi, & Altbäcker, 2012). 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 till the following spring (Garza et al., 1997; Muntyanu, 1990; Poteaux et al., 2008). In midwinter, mounds can contain as many 21 mice (Canaday et al., 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 behavioral experiments. To minimize potential litter effects (e.g., Lazic & Essioux 2013), we avoided using same sex litter mates 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 lib* water and chow (Rodent Diet 5001, Harlan Teklad). To enhance motivation for the food reward (see below), seeds that were provided 2-3 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) and maze trials were run during the light phase (between 0900 and 1300). 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

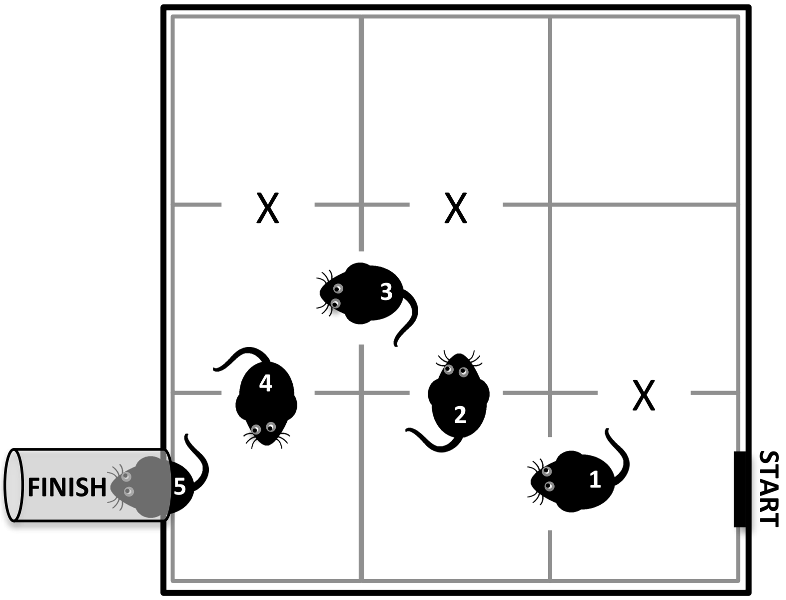

Figure 1. Maze used to test for species differences in spatial learning and memory in *Mus spicilegus* and *M. m. musculus*. Numbers indicate the points at which mice could either take the correct route (indicated by the orientation of the mice) or make one or more errors. An error was scored each time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

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 3x3 grid of nine 13.5x13.5x11 cm boxes with 6.5 cm diameter holes for the animals to move through (Figure 1) and a reward zone (a Habitrail® 5cm 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 the reward tube led us to conclude that a navigation-useful odor gradient was not perceptible by subjects. Furthermore, given the non-direct route of the maze (Figure 1) and its open-air configuration, the use of an odor gradient would not be particularly informative for subjects. Mice were tested in the maze under total darkness (0 lux, dark condition; measured with Pyle Lux Meter PLMT21), or with lights on (150 lux, light condition). No subject was used in both conditions.

Animals were brought from the colony room to the adjacent testing room in their home cages immediately before each trial and were placed in the apparatus by an experimenter who then left the room. For the dark condition, we used small strips of glow in the dark tape on the outside of the apparatus to mark where the animals needed to be placed to start the maze. A second experimenter timed and scored each trial from a different room using a remote live video feed (Panasonic HC-W850 with night vision capability to a 32 inch Phillips 720p HDTV model 32PF9631D or Samsung UN22F5000 LEDTV). Both experimenters were blind to sex and species identity, although species differences in size were evident to experienced observers.

Mice were given a maximum of 10 minutes to complete the maze, defined as head inside the reward tube. To minimize uneven experience with the maze and reduce handling stress, animals were returned to their home cages in the reward tube within approximately one minute of completion. To successfully run the maze, a mouse must have completed the task in 30 s or less with one or fewer errors. An error was defined as backtracking through the maze or entering a dead end box (Figure 1). Entering a box was defined as the animal placing its head through the hole between the sections. Each animal was run once daily until it either completed the task successfully on two consecutive days, or until 21 days had elapsed. For mice that met our criteria for successful maze completion, the number of days until the first completion was taken as a dependent measurement (see Bruck & Mateo, 2010, for analogous test criterion). Mice that did not meet our criterion received a nominal score of 21. Mazes were washed with warm soapy water between each individual trial and maze orientation was rotated

180° daily to prevent the animals from using magnetic sensory input to navigate (e.g., Kimchi et al. 2004; Muheim, Edgar, Sloan, & Phillips, 2006).

Analysis

The effects of species and sex on the number of trials required to successfully complete the maze (trials to criterion) under each condition (dark or light) were explored with mixed models in which litter ID was included as a random effect. Survival models were used for final analyses because this approach accounts for incomplete or right-censored data; in the case of this study, mice that did not meet criterion before the end of the three-week period. We fit a parametric survival model with a Fréchet (inverse Weibull) distribution and tested for effects of species, sex, and their interaction on trials to criterion under each condition. The same model was used to test for an effect of condition within species. Mice that did not meet criterion by 21 days were coded as censored. Significance was evaluated with likelihood ratio tests (LRT). Analysis of variance (ANOVA) was used for *post hoc* tests for sex differences within species. $P \leq 0.05$ was considered significant. All analyses were carried out in JMP 12 (SAS Institute Inc.).

Ethical Note

Animal care and experimental procedures were approved by the Oklahoma State University Institutional Animal Care and Use Committee under protocol numbers AS1310 and AS141. Mice were tested in the maze daily for a maximum of 22 days. During this time they were housed singly. After serving in the experiment, mice were returned to the main colony and used as breeders.

RESULTS

Of the 56 mice that started the maze trials, five were disqualified due to incorrect maze set up. Final sample sizes for the dark condition were 16 *M. spicilegus* (8/sex) from 10 litters and 15 *M. m. musculus* (8 males, 7 females) from five litters. Final sample sizes for the light condition were 11 *M. spicilegus* (5 males, 6 females) from seven litters and nine *M. m. musculus* (4 males, 5 females) from six litters. In the dark trials, 75% (12/16) of *M. spicilegus* reached criterion (maze completion in ≤ 30 s with ≤ 1 error on two consecutive days) before the end of the trial period whereas only 53.3% (8/15) of *M. m. musculus* reached criterion. In the light trials, 90.9% (10/11) of *M. spicilegus* and 77.7% (7/9) of *M. m. musculus* reached criterion (see supplemental materials for error and latency summaries).

The cumulative proportions of *M. spicilegus* and *M. m. musculus* that reached criterion under each condition are shown in Figure 2. Summary statistics and sample sizes for each species split

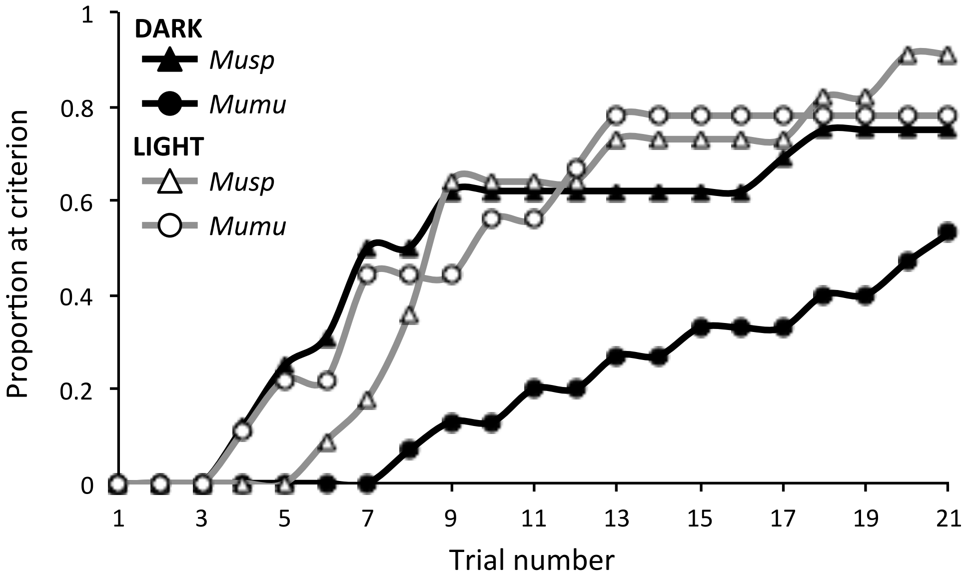

Figure 2. The cumulative proportions of *Mus spicilegus* (triangles, *Musp*) and *M. m. musculus* (circles, *Mumu*) that met criterion for successful maze completion under dark (black lines, filled shapes) or light (grey lines, open shapes) conditions.

by sex and condition are in Table 1. Analysis with mixed models found a significant effect of species in the dark condition ($F_{1,31} = 5.71$, $P = 0.037$): *M. spicilegus* learned the maze faster than *M. m. musculus*. Neither sex nor the interaction between species and sex were significant in the dark (sex, $F = 0.30$, $P = 0.59$; species*sex, $F = 2.42$, $P = 0.13$), and none of these terms were significant in the light condition (species, $F_{1,20} = 0.002$, $P = 0.95$; sex, $F = 0.33$, $P = 0.58$; species*sex, $F = 0.21$, $P = 0.65$).

Table 1. Mean (SD) number of trials to reach criterion for *M. spicilegus (Musp)* and *M. m. musculus (Mumu)* males (M) and females (F) that successfully completed the maze task under dark or light conditions.

	Dark				Light			
	Musp F	*Musp* M	*Mumu* F	*Mumu* M	*Musp* F	*Musp* M	*Mumu* F	*Mumu* M
Trials to criterion	6.6 (4.54)	8.0 (5.24)	16.0 (3.61)	12.0 (5.7)	9.5 (5.24)	10.0 (4.69)	8.3 (3.86)	6.0 (3.0)
$n_{\text{criterion}}^{*}$	7	5	3	5	6	4	4	3
n_{total}	8	8	7	8	6	5	5	4
$n_{litters}$	7	8	4	4	3	5	4	4

[*] Number that reached criterion

Using survival analysis to account for mice that failed to reach criterion by the end of the trial increased the effect of species on trials to criterion in the dark (LRT: $X^2_{(1,\, n = 31)} = 11.48$, $P = 0.0007$). The effect of sex remained non-significant ($X^2 = 0.03$, $P = 0.9$) but the interaction between species and sex was marginally significant ($X^2 = 3.99$, $P = 0.046$). This interaction was explained by a tendency for *M. m. musculus* males that met criterion to do so earlier than females, whereas this pattern was reversed in *M. spicilegus* (Table 1). However, there was no significant difference between the sexes in either species (ANOVA: *M. m. musculus,* $F_{(1,8)} = 1.15$, $P = 0.3$; *M. spicilegus,* $F_{(1,12)} = 0.26$, $P = 0.6$). In the light condition there was no effect of species, sex, or their interaction (species, $X^2_{(1,\, n = 20)} = 1.79$, $P = 0.2$; sex, $X^2 = 0.004$, $P = 0.95$; species*sex, $X^2 = 1.34$, $P = 0.3$). Within species, there was no effect of condition on trials to criterion for *M.*

spicilegus ($X^2_{(1,\ n\ =\ 27)}$ = 1.72, *P* = 0.2), whereas *M. m. musculus* performed significantly better in the light ($X^2_{(1,\ n\ =\ 24)}$ = 7.62, *P* = 0.006).

While observing the dark trials we noticed that house mice seemed more hesitant than mound-building mice in moving through the maze when placed in it for the first time. To separate any species differences in initial response to a novel environment from differences in ability to negotiate a dark environment, we tested for an effect of species on the times it took for mice to leave the start box, and to complete the maze, on their first trial. The species did not differ in the amount of time to leave the start box under either condition (ANOVA: dark, $F_{(1,35)}$ = 1.04, *P* = 0.3; light, $F_{(1,21)}$ = 0.03, *P* = 0.9). However, *M. spicilegus* completed the maze significantly faster than *M. m. musculus* on the first day they encountered it under dark conditions, but not under light conditions (ANOVA, dark: $F_{(1,35)}$ = 16.36, *P* = 0.0003; light: $F_{(1,21)}$ = 2.25, *P* = 0.2).

DISCUSSION

We used a maze-learning task to test for differences in spatial ability between a pair of sympatric but ecologically distinct species of mice, the eastern house mouse, *Mus musculus musculus*, and the mound-building mouse, *M. spicilegus*. Given the specialized burrowing ecology of *M. spicilegus* we predicted that this species would perform significantly better than the commensal house mouse when tested in complete darkness without access to allocentric cues. We found strong support for this prediction: in the dark condition, mound-building mice moved through the maze faster when they first encountered it and learned the correct route faster than did house mice. Moreover, there was no species difference when naïve individuals were tested in the same maze with access to visual cues. Together, these results suggest that enhanced ability to navigate using egocentric cues only is an adaptation to life in the burrow systems that mound-building mice construct and occupy for up to half of the year in nature. We discuss these findings in light of the evolutionary ecology and mechanistic basis of egocentric navigation, and the opportunity for future studies of the genetic basis and neural architecture of egocentric navigation and burrow construction in *M. spicilegus*.

Ecological correlates of species differences in egocentric navigation

There is robust evidence that cognitive ability, like any other complex trait, can evolve in response to selection pressures in different environments or social contexts (reviewed in Cauchoix & Chaine, 2016; Morand-Ferron et al., 2016). Species, population, and sex differences in spatial learning and memory abilities have been particularly well studied in this ecological framework (e.g., Bruck & Mateo, 2010; Gaulin et al., 1990; Kimchi & Terkel, 2004; Pravosudov and Clayton, 2002). Yet few studies have asked whether differences in spatial cognition are context- or task-specific (reviewed in Gibson & Kamil, 2009), and the relationship between ecology and egocentric navigation ability has received little attention.

Mound and burrow construction in *M. spicilegus* is presumed to be an adaptation to harsh seasonal environments: soil temperatures under mounds are elevated and stable relative to the surrounding environment, and larger mounds have a higher proportion of mice that survive the winter (Szenczi et al., 2011). Construction and occupation of mound/burrow systems also shape life history and social structure in *M. spicilegus*. Most construction is carried out by young of the year – animals that delay reproduction till they emerge from the mounds the following spring – and there is evidence for individual task-specialization in the process of mound construction (Serra et al., 2012; Hurtado et al., 2013). The results of this study add enhanced egocentric navigation to the suite of behavioral traits that promote overwinter survival in young mound-building mice.

We also found that species differences in spatial learning and memory depend on the types of cues that are available. While house mice performed significantly better with access to allocentric information, mound-building mice performed equally well with or without allocentric cues. To the extent that the maze task approximated spatial problems that each species encounters in nature, these results are consistent with the fact that the two species overlap in aboveground space use where allocentric cues are available, whereas construction and occupation of complex burrows is unique to *M. spicilegus*.

While sex differences in spatial ability are widely reported in lab mice and rats, which sex performs better varies with task, genotype, and age (Ennaceur et al., 2008; reviewed in Jonasson, 2005). Considering that male and female *M. spicilegus* overwinter in the same burrow systems, do not differ in behaviors associated with mound construction (Hurtado et al. 2013), and mate after dispersal from mounds, we did not expect the sexes to differ in egocentric navigation ability. Although we did not detect sex differences in either species under either condition, there was a marginally significant interaction between sex and species in the dark condition: female *M. spicilegus* tended to perform better than male *M. spicilegus*, whereas the opposite was true for *M. m. musculus* females and males. Sex specific sample sizes in this study were small; it is possible that increased sampling might reveal species-specific effects of sex on egocentric navigation. Future studies should explore the intriguing possibility of opposite patterns of sexual dimorphism in egocentric navigation ability in these closely related species.

Space use and burrowing behavior during the reproductive season are not well characterized in natural populations of *M. spicilegus*. However, there is no evidence for continued use of winter burrow systems; indeed, one study found a negative association between the presence of mounds and capture rate for adult females (Gouat et al., 2003). Thus, the proposed selective advantage of enhanced egocentric navigation as applied to learning a fixed route may be specific to the life stage bounded by initial dispersal from the nest and first reproduction. Given that parturition and lactation can enhance spatial cognition in female rodents (e.g., Kinsley et al., 1999) it would be of particular interest to test for effects of motherhood on performance of different types of spatial tasks. For example, path integration – the ability to update spatial position relative to a starting point – relies on the same movement-generated input and neural substrates (see below) as the route-based task used here, but also requires flexibility in the formation of a cognitive map. Since updating her location relative to the location of her nest is exactly what a foraging female must accomplish, we might expect this aspect of egocentric navigation to be specifically enhanced in lactating mound-building mice relative to pre-reproductive conspecifics of both sexes.

Mechanisms of species differences in egocentric navigation

M. spicilegus is slightly smaller than *M. m. musculus* and differs in tail length and several cranial characters but does not exhibit any of the external phenotypes associated with sensory adaptations to dark environments (e.g., specialized external pinnae, elaboration of vibrissae or nasal soft tissue, modified foot pads or guard hairs) (Sokolov et al., 1998). Thus, species differences in navigational ability in complete darkness are not readily explained by enhanced auditory or tactile sensitivity in *M. spicilegus*. Indeed, maze dimensions were considerably larger than the body width of the animals, such that extensive somatosensory stimuli were not available as mice moved through the maze (e.g., Kimchi & Terkel, 2004). Likewise, by thoroughly cleaning mazes after each trial and rotating maze position across days, we eliminated cues that could provide allocentric information in the dark condition (e.g., odor trails, extra-maze auditory cues, natural or artificial magnetic fields). These observations suggest that enhanced egocentric navigation in *M. spicilegus* reflects more precise processing, and consolidation into memory, of movement-generated input at the level of the central nervous system.

While the capacity to generate and retain an internal representation of external spatial relations is traditionally attributed to the hippocampus, work in lab mice and rats demonstrates that interactions between the hippocampus and another forebrain region – the striatum – are of particular importance to egocentric navigation (Mizumori et al., 2009; Chersi & Burgess, 2015). The dorsal and ventral regions of the striatum are critical to planned motor output and reward-based learning, respectively. It has been suggested that these two striatal functions are integrated in response learning, the association of body turns with reward (Chersi & Burgess, 2015). Within this circuitry, striatal dopamine is critical to egocentric, but not to allocentric, navigation (Braun et al., 2015). In our study, mice learned to follow a route defined by a series of points at which decisions involving body turns were required. The two species performed equally well when allocentric visual cues were available, but *M. spicilegus* out-performed *M. m.*

musculus when these cues were eliminated and mice were forced to navigate using egocentric input exclusively.

Given the close evolutionary relationship between house mice and mound-building mice, and the fact that *M. spicilegus* is not a subterranean specialist, we would not expect to find species differences in the size or structure of brain regions implicated in egocentric navigation. Instead, the results of this study hint at greater hippocampal-striatal connectivity or sensitivity in *M. spicilegus*, potentially mediated by dopaminergic activity. Co-localization of immediate early gene and dopamine receptor activation by an egocentric navigation task would provide a preliminary test of this hypothesis.

Finally, because the strains of mice used here to represent each species have been maintained in the lab for many generations and individuals used in the experiment were reared under identical standard conditions, our results indicate that species differences in spatial cognition have a genetic basis. While *M. spicilegus* and *M. m. musculus* do not hybridize in nature, crosses are still possible in the lab (Zechner et al., 1996). Therefore, traits unique to *M. spicilegus* are amenable to genetic mapping. Work on the genetics of burrowing behavior in *Peromyscus* mice (Dawson et al., 1988; Weber et al., 2013), nest construction in house mice (Sauce et al., 2012), spatial navigation in rats (Herrera et al., 2013), and olfactory learning and memory in *Nasonia* wasps (Hoedjes et al., 2014) and *Drosophila* (Nepoux et al., 2015), demonstrates the feasibility of this approach for ecologically relevant cognitive traits.

Conclusions

Despite the extensive literature on spatial learning and memory in laboratory rodents, and on patterns of space use in natural populations of many species, few studies have asked whether there is a match between species-specific spatial ecology and species differences in egocentric navigation ability. Here, we show that differences in spatial ability between sympatric mouse species are exclusive to egocentric cue use, and that the direction of this difference is consistent with species differences in burrowing ecology. These results highlight the role of ecological selection in the evolution of cognitive traits, and pave the way for future work on the genetic and neural substrates of behaviors that differ between mound-building mice and their commensal relatives (Tong and Hoekstra, 2012).

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