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Comparison of direction and distance estimation across spatial tasks: Absence of sexually dimorphic self-movement cues processing

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ABSTRACT

Animals use many sources of information to maintain spatial orientation, including cues from the environment and cues generated by self-movement. In general, sexual dimorphisms have been observed in humans and rodents in tasks that afford access to environmental and self-movement cues. As of yet, no studies have directly compared sex differences in a task that restricts access to self-movement cues. The current study used motion capture software to characterize sex differences in a food-hoarding task under complete dark conditions, which require the use of self-movement cues. A similar analysis was applied to behavior observed in a place learning version of the water maze. Several sex differences in general aspects of performance were observed on both spatial tasks; however, there was no evidence of sex differences in measures of direction and distance estimation on either task. These results are discussed in light of several factors that may mediate sexual dimorphic performance in spatial tasks.

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Sexually dimorphic performance in rodents has been observed across multiple spatial learning tasks (for reviews see Andreano & Cahill, 2009; Jonasson, 2005; Voyer, Voyer, & Bryden, 1995; Williams & Meck, 1991). In place learning tasks, such as the water maze and the radial arm maze, male rats tend to show better performance than females (Beiko, Lander, Hampson, Boon, & Cain, 2004; Bimonte, Hyde, Hoplight, & Denenberg, 2000; Cimadevilla et al., 1999; Frye, 1995; McFadden et al., 2011; Perrot-Sinal, Kostenuik, Ossenkopp, & Kavaliers, 1996; Roof, 1993; Roof & Havens, 1992; Saucier, Shultz, Keller, Cook, & Binsted, 2008; however, see Faraji, Metz, & Sutherland, 2010). Multiple sources of information can be used to maintain spatial orientation on these spatial tasks and this helps improve performance (Gallistel, 1990). Environmental cues (e.g., visual, olfactory, auditory) and their relationships provide sources of information. Movement of the animal through the environment generates self-movement cues (e.g., vestibular, sensory flow, and proprioception) and provides another source of information to guide behavior. Interestingly, previous work has demonstrated that the accuracy of self-movement cue processing influences learning the relationships between environmental cues. Specifically, procedures that disrupt vestibular system function have been shown to disrupt encoding an array of landmarks (Biegler & Morris, 1996; Semenov & Bures, 1989) and attenuate environmental tuning of place cells and head direction cells (Stackman, Clark, & Taube, 2002). The







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availability of both sources of information in the water maze and radial arm maze makes it difficult to infer the mechanism that mediates sexually dimorphic performance.

Several behavioral mechanisms have been advanced to explain the differences in performance on spatial tasks observed between females and males. Previous work has suggested that male and female rodents engage in sex-specific organization of movement (Field, Whishaw, & Pellis, 1996; Field, Whishaw, Forgie & Pellis, 2004; Wallace, Köppen, Jones, Winter, & Wagner, 2010). Food protection behavior has previously been used to evaluate this hypothesis. Work has shown that male and female rats pivot differently in their attempts to avoid the loss of a food item to a conspecific (Field et al., 1996). Although body size has been speculated as contributing to movement differences, other work has provided evidence suggesting that sex differences in size may not account for sex-specific organization of movement. Specifically, pregnant females (approximately of the same size as a male) were observed to pivot similarly to a normal female, rather than a male (Field et al., 2004). Thus, the body size of male and female rats is unlikely the mechanism that mediates the sex differences in movement patterns. Instead, these results suggest a sex-specific organization of movement that may reflect a dimorphic manner in the way that females and males move through their environment.

Further analysis of performance parameters in the water maze task provides additional support for sex differences in movement organization. For example, male rats locate the hidden platform significantly faster, swim shorter distances to find the platform, and have lower heading errors relative to female rats (Köppen, Winter, Loda, et al., 2013; Köppen, Winter, Stuebing, Cheatwood, & Wallace, 2013). Interestingly, both male and female rats exhibited a similar response bias when the pool is shifted within the room. These results suggest that aspects of movement organization, rather than memory, vary between male and female rats. Therefore differences in spatial organization may be due to variability in processing self-movement cues. As of yet, no studies have selectively evaluated sex differences in self-movement cue processing.

Previous work has used the spontaneous food hoarding behavior of rats to dissociate the use of environmental and self-movement cue processing (Köppen, Winter, Loda, et al., 2013; Köppen, Winter, Stuebing, et al., 2013; Maaswinkel & Whishaw, 1999; Maaswinkel, Jarrard, & Whishaw, 1999; Wallace, Hines, Pellis, & Whishaw, 2002). Under dark conditions, rats use self-movement cues generated while searching for a food item to estimate direction and distance to return to the refuge (Barlow, 1964; Gallistel, 1990; Potegal, 1982; Shettleworth, 1998). The homeward segment reflects how accurately self-movement cues were processed while the rat searched for the food pellet. Thus the food hoarding task under dark conditions provides a novel approach to evaluate whether differences in self-movement cue processing is a factor that may contribute to sexually dimorphic performance observed in spatial tasks.

Therefore, the current study used kinematic analysis to characterize female and male rat performance in two spatial tasks, the food-hoarding task under dark conditions, which assessed online self-movement cue processing, and the water maze task, which assessed place learning and has been shown previously to detect sexually dimorphic performance (Beiko et al., 2004; Cimadevilla et al., 1999; Frye, 1995; McFadden et al., 2011; Saucier et al., 2008, however see Faraji et al., 2010). Further, although females and males were tested on both spatial tasks, testing order was counterbalanced to evaluate the effects of prior experience on performance. Finally, the estrous cycle was monitored throughout the food hoarding task to evaluate whether specific phases of the cycle were associated with changes in food hoarding accuracy.

Materials and methods

Subjects

Twenty-four Long–Evans rats (12 female and 12 male), obtained from the Northern Illinois University vivarium at 90 days of age, were used in the current study. Rats were pair-housed in Plexiglas cages in a room maintained on a 12-h light/dark cycle. Food and water were provided ad libitum unless otherwise noted. The NIU Institutional Animal Care and Use Committee acting, in accordance with the National Institutes of Health's Guide for the Care and Use of Laboratory Animals, approved all of the experimental procedures described in the following section.

Food hoarding table

The food hoarding apparatus was a large circular table (200 cm in diameter), positioned 75 cm above the floor. The table was located in a lightproof room with multiple visual cues: posters on the walls, wooden door, chair, and experimenter. A night vision camera was attached to the ceiling and provided a video feed to a DVD recorder located in an adjacent room. Night-vision goggles were used to handle and observe each rat's behavior under dark testing conditions. A small opaque box ($20 \text{ cm} \times 29 \text{ cm} \times 22 \text{ cm}$) located at the periphery of the table provided refuge for the rat to establish a home base. The box was positioned below the surface of the table, with an open top and a short ramp that could be climbed to gain access to the surface of the table.

Water maze

The water maze apparatus was a large circular pool (1.73 m diameter \times 0.60 m height) filled with water (19 °C) made opaque by the addition of white non-toxic paint. The hidden escape platform (15 cm diameter and 28 cm in height) was submerged 2 cm below the surface of the water. The water maze was located in a rectangular room (2.77 m \times 4.42 m) with

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