



Sex differences on the competitive place task in the water maze: The influence of peripheral pool time on spatial navigation performance in rats



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ABSTRACT

This study investigated sex differences on the competitive place version of the Morris water maze task to determine whether potential strategy differences would emerge during any phase of the study but in particular on the competitive place phase. Previous findings indicate that this version of the task is highly sensitive to measures that disrupt NMDA-dependent synaptic plasticity within the hippocampus during memory consolidation (McDonald et al., 2005). The present findings revealed significant sex differences during all phases of the study, including Phase I with standard place training to locate a hidden platform/goal, Phase II mass training to a new place with the platform/goal relocated to the diagonally opposite quadrant and Phase III, competitive place probe test with the platform removed to measure spatial behaviour directed at either location. The findings showed no sex difference in escape latency and other standard performance measures during the first two phases, initial place acquisition and mass training to a new location. A very subtle male advantage in visiting both Old and New place locations during the third phase place competition test was observed, however, in the time spent swimming in the periphery of the pool, the pool wall (Zone C – outer third radial distance) was increased for females during all phases of the study, suggesting a general effect may have influenced place location search behaviour of the females. Increased peripheral pool time may represent a female preference for approaching the wall, a local cue. Alternatively, the possibility that increased peripheral swimming/thigmotaxis may represent hormonal influences interacting with strategic preferences were discussed, though no definitive conclusions about sex differences in cognitive-spatial performance or memory consolidation were inferred from the present findings. The findings suggest that mixed results reported in the literature by others may be due in part to an interaction with a persistent peripheral pool swimming response demonstrated in female rats.

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1. Introduction

Sex differences in spatial performance have long been associated with brain structure and function (Kimura, 1992). Recent findings in rats (Keeley et al., 2015a) and humans (Driscoll et al., 2005) support this view and point to further interactions with the organizational and activational effects of hormones, stress, age, strategy preferences, environmental enrichment, spatial/landmark/geometric cues and various neurotransmitter, drug and brain plasticity processes (e.g., Rahman and Koerting, 2008; Wang et al., 2016; Chamizo et al., 2016, 2014; Sneider et al., 2015,

2011; Keeley et al., 2015a, 2013; Mannix et al., 2014; Macuchova et al., 2014; Nowak et al., 2014; Warner et al., 2013; Burke et al., 2013; Grissom et al., 2013; Chow et al., 2013; Hawley et al., 2012; Rodriguez et al., 2013, 2010).

The interaction of sex/gender differences with other factors likely contributes to the mixed results reported in the literature. A meta-analysis of the behavioural and biological data on sex differences claimed to reveal a robust male advantage on spatial tasks such as the water maze and radial maze (Jonasson, 2005). However, this assertion has been questioned based on the literature cited (Blokland et al., 2006), with more variable findings reported. For example, approximately half the studies cited in part of the Jonasson (2005) review actually reported no difference between male and female rats, as noted by Blokland et al. (2006). These latter authors tested Wistar rats on cued, egocentric and place versions of the water maze and found no sex difference on the former

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two tasks in their first experiment nor in the acquisition phase of cue and place tasks in their second experiment. Despite the lack of effect, male rats spent more time near the previous platform position than the female rats during a place task probe trial. Based on these findings, the authors concluded that male Wistar rats were better at using a place-based strategy than females.

Several studies using the water maze have concluded that strategy use interacts with other factors in determining sex/gender differences (e.g., Grissom et al., 2013; Hawley et al., 2012; Kanit et al., 2005; Keeley et al., 2013). Although the water maze is considered to be a “cognitive mapping” task by some, there is significant variation in the processes that contribute to spatial learning and cognition (Mackintosh, 2002). Further, there is now overwhelming evidence of a nexus between genes, development and the environment, a GDE tripartite model (McDonald et al., 2004) in the expression of sex differences across studies, contributing to the mixed and misunderstood research findings. Despite the complexity of interactions, compelling evidence indicates that hormones may interact with environmental stress (Beiko et al., 2004; Burke et al., 2013; Cimadevilla et al., 1999; Wang et al., 2016; Snihur et al., 2008), with genetic strain and brain morphology also contributing to the differences observed, further influencing anxiety and the responses to pharmacological manipulations (Keeley et al., 2015a,b,c; Keeley and McDonald, 2015; Wartman et al., 2012). Although there is little doubt that these biological interactions with the environment contribute to sex differences, the present study focused on the potential strategies that may differ between the sexes/gender as an extension of individual differences in the types of cues utilized during different phases of training, retraining and competition testing in learning multiple place representations.

Hence, the purpose of the present study was to test rats on a competitive place variation of the Morris water maze (Morris, 1981) reported by McDonald et al. (2005). These authors used a three phase experiment in which rats received standard place training in Phase I, followed by mass training to locate a new place location in the diagonally opposite quadrant in Phase II, and then tested rats on a competitive place probe test in Phase III to assess the relative spatial bias for visiting the Old versus the New platform locations. This version of the water maze task was highly sensitive to NMDA-mediated synaptic plasticity in the hippocampus, as demonstrated by lesion and intra-hippocampal drug infusions of the NMDA receptor antagonist CCP. Based in part on the findings reported by Blokland et al. (2006) and others showing that male rats may show a stronger spatial bias on probe tests to the original place location, as well as other findings showing that males are persistent in searching at the original location with standard place training (Devan and McDonald, 2001) even when moved to a new room/pool following latent learning (Devan et al., 2002), we hypothesized a male advantage may be based on the original place location, whereas females may show a preference for using more recent spatial working memory (Healy et al., 1999) to search at the new location in a competitive place situation. In addition to escape latency and other standard measures of performance, we also included measures of peripheral pool time to determine if general effects may influence the observation of sex/gender differences in the water maze.

2. Method

2.1. Subjects

Twenty-four Long-Evans hooded rats (Harlan Sprague-Dawley Inc.) weighing 300–350 g were used as subjects. This sample consisted of 12 females and 12 males. All animals were singly housed in Plexiglas cages with access to food (Lab Diet 5001 Rodent Diet)

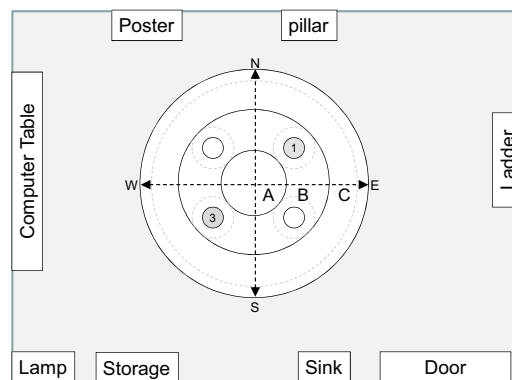


Fig. 1. Diagram of the water maze and room setup. The pool was divided into four quadrants, with the boundaries with the pool wall labelled N, E, S and W (not true compass coordinates), which served as the start positions. The platform was initially positioned at Location 1, grey circle in the NE quadrant, for the first phase of the experiment then moved to the diagonally opposite quadrant at Location 3. The pool was further divided into Zones A, B and C, defined as the inner third, middle third and outer third of the pool diameter, respectively. The room contained several distal cues labelled in the figure that were visible from within the pool, as well as others not shown (e.g., the camera, features of the drop ceiling and the monitors on the computer table and equipment in the storage area).

and tap water ad libitum. The holding cages were located in an environmentally controlled colony room which included a 12:12 h. light-dark cycle (room temperature $\approx 23^\circ\text{C}$). All behavioural training and testing occurred during the light cycle.

2.2. Apparatus

The Morris water maze was a galvanized steel tank, 152 cm in diameter with a wall height of 45 cm. The tank was painted white and filled with water made opaque by the addition of non-toxic white Crayola tempera paint ($\approx 100\text{ mL}$). The tank was positioned on cinder blocks, raising it above the floor to drain and more easily place animals in the pool. The water filled the tank to an approximate depth of 26 cm, making it cover the platform by 1.5 cm. Water temperature was $\approx 23.5 \pm 1.5^\circ\text{C}$. The escape platform was constructed of PVC pipe 12.4 cm in diameter and 25 cm in height.

The experimental room measured $5.08 \times 4.47\text{ m}$ and contained several cues that were visible from within the pool and during transport of subjects to the start positions (Fig. 1). The pool was positioned in the approximate center of the room and the distal environment included both standard room features such as the door, sink and a structural pillar on the North wall and several added cues including a poster, ladder, floor lamp, storage area with equipment and cleaning utilities, and a large stainless steel table with the computer tracking system, including three monitors of different size and a DVD/VHS recorder. Towels were stored on the lower tier of the table. All nonstructural features of the room were considered distal cues that remained at stable locations for the duration of the experiment.

A camera was positioned above the tank and was connected to the DVD/VHS recorder as well as the computer tracking system by HVS Image (VP118, Edinburg, UK, <http://www.hvsimage.com/>) with trial analysis conducted with the HVS 20/20 program. The floor of the room was a continuous sealed surface approved for animal testing and contained a floor drain near the water maze in which pool water was drained on a daily basis. The drop ceiling of the room contained overhead fluorescent lights and metal guides forming square grids in which standard ceiling panels were placed. The overhead camera was mounted just below a ventilation unit directly above the water maze. The camera was contained within a metal housing unit that included three small 30 W spot lights with

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