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Intramaze cue utilization in the water maze: Effects of sex and estrous cycle in rats

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Abstract

Rats can use a wide spectrum of intra- and extramaze information while navigating through the environment. The current study examined the relative contribution of an intramaze cue with regard to its proximity to the goal. Three experiments were conducted and the impact of intramaze cue removal or rotation on water maze search was examined. In males, the effect of the intramaze cue declined monotonically in relation to the proximity of the cue to the goal. A more complex relationship between cue location and utilization was found in estrous and proestrus females. Estrous females showed a strong effect of the cue only when it was near the goal, ignoring it when it was situated further away. Conversely proestrus females were affected by the cue under all conditions. It is concluded that previous reports of behavioral differences may stem from the fact that proestrus females are affected by and attend to a wider range of stimuli, while estrous females are more affected by salient stimuli.

Keywords: Estrogen; Landmark; Learning; Navigation; Spatial; Hippocampus

Introduction

When searching for food or finding their way back home, animals can use a wide spectrum of strategies that allow them to successfully navigate through their environment. For example, food storing birds use visual landmarks and the sun compass (Sherry and Duff, 1996), bats use echolocation (Gallistel, 1990), honeybees use visual landmarks and path integration (Collett and Collett, 2002). Even when one limits the task to spatial navigation, and the species to rats, there are a multitude of cues the animal can attend to. Some studies show that rats ignore landmark information and preferentially encode the geometric layout of the environment defined by large areas (e.g., walls) and corners (Cheng, 1986; Gallistel, 1990; Margules and Gallistel, 1988). Other studies show that landmarks are important for navigation (Greene and Cook, 1997) and that rats are able to encode the spatial information derived from the geometric relations among landmarks (Benhamou and Poucet, 1998; Greene and Cook, 1997). One possible reason for the differences in these studies is that the landmarks differed in their salience, location to the horizon, and proximity to the goal, all of which could affect how much the rats will rely on these stimuli.

In the above studies, the subjects were male rats. When females were tested on these types of tasks, a picture of sexually dimorphic spatial navigation emerges. Using a plus maze, Tropp and Markus (2001) found that during early exposure to an environment, female rats attend to many different types of cues and with additional training they rely more on distal visual information, while male rats predominantly used the distal visual information at all times. Williams et al. (1990) used a 12-arm radial maze with only 8 arms reinforced and showed that male rats selectively attend to the geometry of the room and ignore the distal landmarks, while females attend to both room geometry and distal landmarks. Kanit et al. (1998) showed that female rats relied more on a local visual cue than males

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in a water maze task. These findings indicate sex differences in navigation.

It has been known for some time that the hippocampus is an important structure for spatial navigation (O'Keefe and Nadel, 1978; Sutherland and Rudy, 1989). More recently, it has been shown that in female rats there are periodical morphological changes that are concomitant with the hormonal changes across the estrous cycle (Gould et al., 1990; Woolley and McEwen, 1992). Specifically, the estradiol level peak during the proestrus stage is accompanied by an approximate 30% increase in synaptic density on the apical dendrites of the pyramidal cells in the CA1 region of the hippocampus (Woolley and McEwen, 1992). During estrus, both estradiol levels and spine density return to basal levels. Electrophysiological changes are also observed in hippocampus. During proestrus, there is an increase in hippocampal plasticity and long-term potentiation (Cordoba Montoya and Carrer, 1997; Good et al., 1999; Warren et al., 1995), and a decrease of the seizure threshold (Terasawa and Timiras, 1968).

Consequently, rather than simply look for sex differences in navigation, it is important to consider the female rats' stage of the estrous cycle. Previous studies (Frye, 1995; Markus and Zecevic, 1997; Warren and Juraska, 1997) showed that female rats performed better on spatial tasks during low estrogen phases of the estrous cycle than during proestrus phase, when levels of estrogen are high. Other studies failed to find a difference in performance across estrous cycle (Berry et al., 1997; Schwegler et al., 1993; Stackman et al., 1997). There are also studies that show that proestrus animals are better at spatial tasks (Frick and Berger-Sweeney, 2001; Korol and Kolo, 2002). One possible source of the discrepancies may be related to the type of task used (Desmond and Levy, 1997; Dohanich, 2002). Generally, studies using stressful/aversive tasks (i.e., water maze, fear conditioning) show a detrimental effect of ovarian hormones on performance (Chesler and Juraska, 2000; Frye, 1995; Markus and Zecevic, 1997; Warren and Juraska, 1997). Conversely, studies using appetitive motivation report enhanced performance associated with high levels of ovarian hormones (Daniel and Dohanich, 2001; Daniel et al., 1997). Another possible factor is the type of memory task used. Estrogen has been shown to improve performance on working memory in the radial arm maze (Dohanich, 2002; Fader et al., 1999; Luine et al., 1998), T-maze (Fader et al., 1998), and water maze (Sandstrom and Williams, 2001), while having no effect on reference memory (Dohanich, 2002; Fader et al., 1999; Luine et al., 1998), or having a detrimental effect on reference memory in the water maze (Daniel et al., 1999; Frye, 1995; Warren and Juraska, 1997). However, neither the type of reinforcement nor the type of memory tested can account for all the data. The present study examines whether the source of these discrepancies is differences in the degree to which different landmarks are attended to.

The current experiments compare how male and female rats use landmark information when navigating through an environment. Three experiments were conducted, employing a water maze task and manipulating the spatial location of a salient intramaze landmark in relation to the goal. The manner in which the location of the landmark, sex, and the hormonal stage affected cue use was examined.

Methods

Subjects

Fifty-seven female and twenty male 344 Fischer rats (Harlan Sprague–Dawley, IN) were included in the study. All rats were 5 months old at the beginning of the study. They were single-housed in clear Plexiglas cages and the colony was maintained on a 12-h light/dark cycle (lights on at 06:30). Water and food were available ad libitum. The behavioral testing was performed between 14:00 and 18:30. Because of the constraints imposed on the available testing time by the estrous cycle, Experiment 1 was run in 3 batches and Experiment 2 was run in 2 batches. All procedures performed in this study were approved by the University of Connecticut Institutional Animal Care and Use Committee.

Apparatus

The water maze was a round blue polyethylene tank, 77.5 cm height, 122 cm diameter at the water level. The tank was filled to a depth of 48 cm with water (19–21°C). In Experiment 1, a white circular platform (15 cm diameter) with an attached perpendicular white rectangle (14 × 5 cm) was placed in the tank, 0.5 cm above the water level, in the center of one of the four quadrants. In Experiments 2 and 3, a transparent circular platform (15 cm diameter) was placed in the center of an adjacent quadrant in the tank, 1.5 cm below the water level.

All experiments were run in the same large room (size 4.5 × 5 m), with many extramaze cues available (door, cabinets, computer, lamp, posters on the walls). For Experiments 2 and 3, the pool was moved to a different corner of the room and the room was made to look different by adding a large white partition (174 × 170 cm) and changing the pattern and source of lighting. The new location of the platform was shifted from its previous location in relation to the real world, as well as in relation to major cues in the room. A camera (Panasonic) was placed above the center of the pool at each location and sent images to a SMART (Panlab, Spain) tracking system for behavioral analysis.

Procedure

Before behavioral testing, females were lavaged daily for at least 2 complete cycles. During the experiment, females