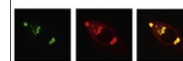


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Research Report

Enhanced adolescent learning and hippocampal axonal projections following preadolescent spatial exposure to a water or dry maze

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ABSTRACT

The present work sought to determine whether preadolescent exposure to a different task in the same spatial environment would lead to enhancement of water-maze performance and changes in hippocampal connectivity. Separate groups of preadolescent (p16–p26) Long Evans rats (LER) were exposed to the same room and arena using either a water-maze (WM) or a dry-maze (DM), while a third group received no exposure to the spatial cues (NT) but were handled. Three weeks later, rats were tested on the WM or DM task in the same room where preadolescent exposure took place. This set up conditions where the DM/WM and WM/DM groups were exposed to the same spatial cues during the preadolescent and adolescent (p40–p44) phases but performed different tests allowing for the dissociation of spatial cue exposure and task familiarity on adolescent performance. When animals experienced similar preadolescent and adolescent conditions (WM/WM or DM/DM), there was improved performance over animals with no preadolescent spatial exposure (NT/WM or NT/DM). In group DM/WM, there was enhanced adolescent performance compared to group NT/WM. In contrast, group WM/DM did not show enhanced adolescent performance. Compared to groups with no preadolescent spatial exposure, groups with both preadolescent and adolescent spatial exposure showed elevated synaptophysin staining in the hippocampal CA3 region indicating an expanded axonal projection in this region. These data suggest the possibility that exposure to spatial cues during the preadolescent period, independent from task-specific requirements, contributes to enhanced adolescent spatial performance on the WM. This appears to be linked with the reorganization of axonal inputs to the CA3 region.

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1. Introduction

Lesions or temporary inactivation of the dorsal hippocampus reliably disrupt performance on spatial tasks (Morris et al., 1982; Sutherland et al., 1982, 1983; McDonald and White, 1994; Moser et al., 1995; Duva et al., 1997; Cassel et al., 1998; Galani et al., 1998; Oswald et al., 2003; Gaskin et al., 2011) suggesting a hippocampal contribution to spatial memory function. Additional evidence that the hippocampus contributes to spatial information processing comes from the study of place cells (Derdikman and Moser, 2010; Rolls, 2010; Burgess and O'Keefe, 2011; Vann and Albasser, 2011) whereby networks within in the hippocampus are activated in response to familiar environments (see also Ramirez-Amaya et al., 2005; Vazdarjanova et al., 2006; Albasser et al., 2010). There is increasing evidence that the axonal input to the dorsal CA3 hippocampus (i.e., the mossy fibers) may regulate spatial learning and memory by remodeling its synaptic connections. Work has shown that training on the spatial version of the water-maze (WM) task is associated with a larger axonal, mossy fiber projection to the dorsal hippocampal CA3 *stratum oriens* (SO) of adult rats (Ramirez-Amaya et al., 1999, 2001; Holahan et al., 2006; Rekart et al., 2007a, 2007b).

In Long Evans rats (LER), prior to any spatial WM training, the mossy fiber terminal field can be observed in the *stratum oriens* (SO), corresponding to the basal dendrites of the CA3 pyramidal cells (Holahan et al., 2006). In an examination of the development of CA3 hippocampal mossy fiber (MF) distribution in LER (Holahan et al., 2007), MF innervation of the *stratum lucidum* (SL) was widespread by postnatal day 12 (p12). Beginning on p15, MF staining was evident in the *stratum pyramidale* (SP) and by p18 and p21, widespread MF staining was observed in the SO. By p24, the SO projection in LER was complete and remained stable into adulthood (Holahan et al., 2006).

The MF development described above has been correlated with the emergence of memory function (Keeley et al., 2010). Using LER, spatial memory function was assessed in a WM task from p16 to p26. From p16 to p19, stable WM performance was observed with moderate improvements in performance. From p18 to p21, there was a dramatic improvement in WM performance to levels seen in adult LER (Holahan et al., 2006; Keeley et al., 2010). The combination of the neuroanatomical and behavioral studies leads to the hypothesis that this developmental time period (p16–p21; preadolescence) represents a sensitive period for hippocampal development and modification. Support for this idea comes from several lines of evidence: (1) maternal separation from p2 to p14 results in a significant reduction in MF connectivity and impairs spatial learning (Huot et al., 2002; McNamara et al., 2002), (2) daily administration of an NMDA-receptor antagonist from p17 to p20 in LER reduces the widespread MF connectivity pattern as observed in controls (Holahan et al., 2007), (3) lateral fluid percussion at p19 results in water maze acquisition and retention impairments 1 month after injury (Giza et al., 2005; see also Cernak et al., 2010), (4) training on the spatial version of the WM task from p16 to p20 results in improved spatial performance when compared to age-matched controls without the early WM

task exposure (Carman and Mactutus, 2001; Keeley et al., 2010). Taken together, these findings suggest that input-dependent processes during a sensitive period between p16 and p20 might enhance hippocampal development and subsequent spatial information processing.

In the Keeley et al. (2010) study, it was not clear whether the improved WM performance in LER as a result of preadolescent exposure was due to task familiarity, spatial familiarity, or both. The improvement may have been due to task-familiarity aspects (e.g., the animal learned how to swim, habituated to the water, the presence of a hidden escape platform) or spatial memory function (e.g., the animal retained a spatial map of the cues around the pool and the location of escape platform). In the present experiment, we sought to determine whether the beneficial effects of preadolescent exposure would be seen when the preadolescent and adolescent task demands differed. To this end, preadolescent animals were exposed to the spatial cues on either a dry maze (DM) or water maze (WM) and the opposite or same task demands were used during the adolescent phase. Because both conditions took place in the same room, this would allow for the dissociation of task familiarity from acquisition of a spatial representation. The distribution of MF was also examined in the adolescent rats to determine if synaptic malleability would take place in association with preadolescent and adolescent spatial exposure on the DM or WM.

2. Results

2.1. Preadolescent DM

No learning-related data were collected during the preadolescent DM condition, as the environment was stable across the 11 sessions and time on the DM was fixed based on the yoking procedure.

2.2. Preadolescent WM

Fig. 3 shows mean escape latencies of the rats that received preadolescent exposure to the WM (Groups WM/WM and WM/DM). Both groups displayed a significant decrease in latency to reach the platform across the 11 WM days. There were no significant differences between the latencies of the WM/WM group and the WM/DM group at any point during the preadolescent phase. Latency data were analyzed using a 2-way mixed analysis of variance (ANOVA) using day as the repeated factor. This revealed a main effect of day ($F(10,10)=9.63$, $p<0.001$) but not group ($F(1,14)=0.19$, $p=0.67$). Notably, there was relatively little change in performance in either group across the first 4 days of WM exposure, followed by a rapid improvement from p19 to p22; similar to previous work (Keeley et al., 2010).

2.3. Adolescent DM

For Days 2–5 of the adolescent DM condition, one object was moved to a new location before each session. This allowed an estimation of a rat's ability to remember the spatial configuration of the objects 24 h earlier, by calculating investigation

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