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Brain Research Bulletin 65 (2005) 41–58

BRAIN
RESEARCH
BULLETIN

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Egocentric spatial orientation in a water maze by rats subjected to transection of the fimbria-fornix and/or ablation of the prefrontal cortex

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Received 14 September 2003; received in revised form 28 October 2004; accepted 10 November 2004
Available online 16 December 2004

Abstract

The acquisition of a water maze based task requiring egocentric spatial orientation in the absence of distal cues was studied in four groups of rats: animals in which the fimbria-fornix had been transected, rats that received bilateral ablations of the anteromedial prefrontal cortex, animals in which both of these structures had been lesioned, and a sham-operated control group. Isolated lesions of both the anteromedial prefrontal cortex and the hippocampus were associated with a significantly impaired task acquisition. Both of these individually lesioned groups did, however, eventually demonstrate full functional recovery by reaching the task proficiency of the sham-operated control group. In contrast, the group in which both of these structures had been lesioned failed to demonstrate full functional recovery and was severely and long-lastingly impaired when compared to all other groups. Behavioural challenges in the form of a no-platform session and two reversals of platform position demonstrated that while the sham-operated control group and the group subjected to fimbria-fornix transections in isolation utilized rather pure egocentric orientation strategies, the two prefrontally lesioned groups (and especially the combined lesion group) employed a different set of solution strategies which at least partly relied on a "circling" method. Even in the behaviour of the prefrontally lesioned groups, however, indications of a certain level of cognitive representations of the platform positions were seen. It is concluded that both the prefrontal cortex and the hippocampus contribute to the mediation of egocentric spatial orientation. Furthermore, the hippocampus is a significant and potentially irreplaceable part of the neural substrate of functional recovery of the presently studied task after prefrontal lesions—while the prefrontal cortex may play a similar role with respect to hippocampal lesions.

Keywords: Prefrontal cortex; Hippocampus; Fimbria-fornix; Egocentric spatial orientation; Water maze; Behavioural strategies; Functional recovery; Rat

1. Introduction

Most studies addressing the neural substrate of egocentric orientation and egocentrically based problem solving by rats in water mazes (e.g., [2,4,6,29]) have utilized procedures in which the swimming animal is allowed to view the distal cues of the experimental room. The rat is, however, prevented from utilizing such cues for navigational purposes by a procedure in which the platform constantly changes its position relative to the distal cues—while remaining in a fixed position relative to the start position of a given trial. Such a procedure precludes proficient task solution based on allocentric methods of spatial orientation. Consequently, the animal is forced to utilize egocentric orientation in order to solve the task. One should, however (as pointed out elsewhere [23]) be aware that the experimental setup in these studies may invite a competition between the application of allocentric and ego-

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doi:10.1016/j.brainresbull.2004.11.010

centric solution strategies. Therefore, proficient task solution may depend critically on structures involved in the mediation of selection of and shifts between behavioural strategies. Additionally, the activity of structures primarily involved in the mediation of allocentric spatial orientation may influence the quality of task performance negatively. A more "pure" test of egocentric spatial orientation can be obtained in the absence of distal cues—e.g., when access to such cues is eliminated by a curtain spanning the circumference of the maze [23].

1.1. The prefrontal cortex

The prefrontal cortex of the rat appears to play a significant role in mediation of the acquisition of spatial tasks requiring egocentric orientation in water mazes. This has been demonstrated utilizing both the procedure allowing a free view of distal cues while preventing navigation based on such cues [2,4,6,29] and utilizing a procedure eliminating the availability of distal cues altogether [23]. Additionally, it has been demonstrated that with the latter procedure lesions of the anteromedial prefrontal cortex of the rat also impairs the retention of a preoperatively acquired task requiring egocentric orientation [23]. These results agree well with the model proposed by Poucet [35]—which suggests that the prefrontal cortex is primarily involved in the mediation of egocentric spatial orientation as opposed to more allocentric forms of orientation. Studies addressing allocentric spatial orientation of the mapping type (a type of allocentric place learning occurring when the experimental situation offers an abundance of three-dimensionally arranged distal cues) have generally speaking demonstrated a marginal or absent impairment of task acquisition after prefrontal lesions (e.g., [2–4,6,7,10,14,17,18,21]—see, however, [11–13,37]). Place learning based on allocentric orientation of the "non-mapping" type (a type of allocentric place learning occurring in experimental situations offering only a restricted number of distal cues arranged in a less three-dimensional manner than what is the case in the "standard" water maze setup) is more severely impaired by prefrontal cortical lesions [24]. It might be speculated that instances in which more pronounced impairments of task acquisition have been observed under circumstances where allocentric orientation has been presumed to be of the mapping type may, in reality, be the consequence of experimental setups provoking a task solution by strategies of a "non-mapping" type (see further discussion in [17]).

1.2. Hippocampus

Studies addressing the involvement of the hippocampus in allocentrically based place learning of the mapping type in water mazes (e.g., [1,5,8,21,22,27,28,31,37–41]) have consistently demonstrated lesions of the hippocampus to be associated with major impairments of task acquisition. When, however, allocentrically based place learning is performed under circumstances causing a "non-mapping" strategy to be applied, hippocampally lesioned animals acquire the task as proficiently as sham-operated controls [42]. Rats with lesions of the hippocampus in the form of transection of the fimbria-fornix [2] were rather unimpaired in acquisition of an egocentrically based spatial orientation task in a water maze when offered access to—irrelevant—distal cues. This pattern of results agrees with both the model of Poucet [35] and other demonstrations that hippocampally lesioned or inactivated rats are more impaired in tasks requiring allocentric than egocentric spatial orientation (e.g., [32]). As argued above and elsewhere [23] situations in which the availability of distal cues may invite the application of (irrelevant) allocentrically based solution strategies are not optimal for studies of the neural substrate of egocentric spatial orientation. Consequently, the apparent lack of a hippocampal involvement in the mediation of egocentric spatial orientation in water mazes should be addressed under experimental circumstances preventing the animal from viewing distal cues.

1.3. Posttraumatic functional recovery

The present study addressed aspects of the neural substrate of rats' egocentric navigation in water mazes by studying the acquisition of a task requiring egocentric spatial orientation under circumstances preventing the swimming animals from viewing any distal cues (utilizing a procedure similar to the one of Mogensen et al. [23]). We studied rats with bilateral transections of the fimbria-fornix—thereby examining whether the unimpaired acquisition by such animals of the task of de Bruin et al. [2] might be dependent on the availability of cues in inviting a competing allocentric solution strategy. We also examined two other lesion groups: one subjected to bilateral ablations of the anteromedial prefrontal cortex and one in which bilateral transections of the fimbria-fornix were combined with bilateral ablations of the anteromedial prefrontal cortex. These groups were included for two reasons. Firstly, we wanted to be able to compare directly the task acquisition of hippocampally lesioned animals and animals subjected to prefrontal ablations (a lesion we based on our previous study utilizing the same experimental procedures [23] predicted would cause a major lesion-associated impairment of task acquisition). Secondly, we wanted to address the issue whether the hippocampus contributes to the posttraumatic functional recovery of egocentric spatial orientation seen after ablations of the prefrontal cortex [23]. And, in case an impairment should be seen after hippocampal lesions, whether or not the prefrontal cortex participates in the mediation of a potential functional recovery after such lesions. If either of the single lesion groups would be significantly impaired in the acquisition of this task but would subsequently reveal a complete or partial functional recovery, it would be of interest to see whether the "combined lesion" group would reveal the same level of functional recovery. It would, for instance, be of interest to compare the degree of functional recovery seen in the prefrontal lesion alone group to the potential functional recovery seen in the combined lesion group. A significantly smaller (or even absent) func-