ACADEMIC PRESS

Available online at www.sciencedirect.com

SCIENCE DIRECT®

Neurobiology of Learning and Memory 79 (2003) 109–117

Neurobiology of Learning and Memory

www.elsevier.com/locate/ynlme

Does the radial arm maze necessarily test spatial memory?

Diane Dubreuil, Céline Tixier, Gérard Dutrieux, and Jean-Marc Edeline*

Laboratoire de Neurobiologie de l'Apprentissage, de la Mémoire et de la Communication, UMR CNRS 8620, Université Paris-Sud, Bât 446, 91405 Orsay cedex, France

Abstract

Since its design 25 years ago (Olton & Samuelson, 1976), the eight-arm radial maze has become very popular and is now widely used to assess spatial memory in rodents. Two versions of the full-baited maze protocol are present in the literature: with or without confinement between the visit of each arm. The confinement was introduced by Olton himself as early as 1977 (Olton, Collison, & Werz, 1977) to eliminate stereotypic behaviors that he had previously observed. It is widely regarded that the confinement prevents rodents from developing these response patterns, and as such it is considered an improved procedure to test spatial memory. Surprisingly, to the best of our knowledge, no study has been especially designed to demonstrate the efficacy of the confinement in blocking the stereotypic behaviors of the animals. The present study compares the strategies of rats trained with or without a confinement procedure. The results show that, after nine days of training, rats submitted to a 5- or a 10-s confinement reach the same level of performance as rats without confinement. The confinement totally prevents stereotypic behaviors like clockwise serial searching strategies which are often observed without confinement. Even a 0-s confinement is sufficient to prevent clockwise strategies, but rats seem to develop other stratagems which do not imply spatial memory. Furthermore, rats previously trained without confinement are unable to perform the task when confinement is introduced on a test day. In contrast, rats previously trained with confinement perform the task correctly when the confinement is no longer present. Thus, without confinement, good levels of performance can be achieved without precise spatial representations.

Keywords: Radial arm maze; Spatial learning; Strategy; Clockwise; Confinement; Delay; Rat

1. Introduction

Spatial representation is one aspect of cognition where the abilities of humans and animals have been extensively compared (Poucet, 1993; Tolman, 1948). For more than two decades, various behavioral tasks have been designed for rodents in order to investigate the brain structures critically involved in spatial representation (for review, see Poucet & Benhamou, 1997). The discovery of 'place cells' in the rat hippocampus (O'Keefe & Dostrovsky, 1971) and the fact that hippocampal lesions can impair spatial learning have initiated large avenues of research looking at the neuronal substrates of spatial representations (Castro, Silbert, McNaughton, & Barnes, 1989; Morris, Hagan, & Rawlins, 1986; Moser, Trommald, & Andersen, 1994). In addition, spatial learning tasks have been used increasingly to investigate the involvement of neurotransmitters in cognitive functions (some examples from the cholinergic system: Ammassari-Teule, Amoroso, Forloni, Rossi-Arnaud, & Consolo, 1993; Page, Everitt, Robbins, Marston, & Wilkinson, 1991; Wellman, Logue, & Sengelaub, 1995; and the noradrenergic system: Belotti & Galey, 1996; Compton, Dietrich, Smith, & Davis, 1995; Przybyslawski, Roullet, & Sara, 1999; Przybyslawski & Sara, 1997; Roberts, Price, & Fibiger, 1976).

Historically, the two behavioral apparatuses used to assess spatial learning in rodents are the Morris water maze (Morris, 1984) and the radial arm maze (Olton & Samuelson, 1976). In the radial arm maze (RAM), memory is usually inferred from the day-to-day improvement in performances in an eight-arm RAM. In the most classic task, described in the pioneering work

* Corresponding author. Fax: +33-1-69-15-77-26.
E-mail address: jean-marc.edeline@ibaic.u-psud.fr (J.-M. Edeline).

1074-7427/02/$ - see front matter © 2002 Elsevier Science (USA). All rights reserved.
PII: S1074-7427(02)00023-0

of Olton and Samuelson (1976), the maze is fully baited and the animal has to visit each arm only once within a trial to find the food reward. Several interesting versions of this task have been developed subsequently (Olton & Collison, 1979; Packard & White, 1990), but the RAM is still largely used in a simplified version of the original design (see for example, Ammassari-Teule & Caprioli, 1985; Lavenex & Schenk, 1995). The full-baited version can be used to assess accurate hippocampal lesions (Gisquet-Verrier & Schenk, 1994), to determine the involvement of a particular gene or a particular protein in memory traces (Davis, Rodger, Hicks, Mallet, & Laroche, 1996; Davis et al., 1998; Nogues, Micheau, & Jaffard, 1994), or to test whether the electromagnetic fields emitted by cellular phones produce memory deficits (Dubreuil, Jay, & Edeline, 2002; Lai, Horita, & Guy, 1994; Sienkiewicz, Blackwell, Haylock, Saunders, & Cobb, 2000). Thus, this test has become a standard protocol for assessing memory processing in a variety of research areas.

In the literature, spatial learning in rodents is assessed by two versions of the full-baited RAM task: one version includes a between-choice confinement of a few seconds whereas the other does not (these two versions appear to be chosen arbitrarily). In fact, the confinement procedure was first introduced by Olton and colleagues as early as 1977 in the aim to interrupt rats stereotypic behaviors that they had observed (Olton et al., 1977). From this time, all the studies using confinement procedure implicitly assumed that this confinement is required for testing spatial memory without interference from stereotypic behaviors. Surprisingly, if we except the anecdotal observations by Walker and Olton (1979) and by Bolhuis, Bijlsma, and Ansmink (1986), the efficacy of the confinement procedure to prevent stereotypic behaviors has never been demonstrated. Furthermore, no demonstration has ever been made to confirm that rats trained with and without confinement indeed performed the task with different strategies.

The present study aimed to evaluate the consequences of introducing a between-choice confinement in the full-baited RAM task. We compared, in two experiments, the learning performance and strategies of groups of rats engaged in a spatial learning task with or without a between-choice confinement. By "strategy," we mean the way rats explore the maze and perform the task. The rats with no between-choice confinement were free to visit the maze and to perform the task without any constrains. In contrast, the rats with a between-choice confinement could not explore the maze freely. In a first experiment, the between-choice confinement lasted 10 s. To confirm these first results, a second experiment was carried out with two further between-choice confinement delays: a 0- and a 5-s confinement.

2. Experiment 1

2.1. Methods

2.1.1. Subjects

Twenty-four male Sprague–Dawley rats (Iffa Credo, France), weighing 150 g on arrival to the laboratory, were used as subjects. They were naive at the beginning of the experiment. Daily handling was systematically performed. They were housed in pairs in wire-mesh cages in the laboratory vivarium (12/12 h light/dark cycle, light from 8:00 a.m. to 8:00 p.m.). One week after their arrival, they were progressively food-deprived until they reached 85% of their 'ad libitum' body-weight. Chocolate flavored crisp rice cereal (Chocopops, Kellogg's) was used as the food reinforcement.

2.1.2. Apparatus

The apparatus was a custom-made automated radial arm maze elevated 66 cm above the floor. It consisted of eight identical arms (80×12.5 cm) radiating from a circular platform (30 cm in diameter). The arms and the central platform were made of beige polyprey (stratified wood covered by a 2 mm thick plastic layer). The central platform included a weight detection area (20 cm in diameter) in which four pressure-detectors signaled the presence of the rat in the center of the maze. The pressure detector threshold was set to detect the animal when at least half of its body was on the weight detection area. Doors made of transparent Plexiglas (25 cm high) were located at the entrance of each arm. Each arm was equipped with three infrared diodes located: (i) 15 cm away from the beginning of the arm, (ii) in the middle of the arm, and (iii) 5 cm from the end of the arm. Each diode was placed 2 cm from the floor. Each arm was surrounded by a transparent wall (8 cm high), allowing the animal to see visual cues placed in the room. A small plastic food cup (the same color as the maze floor) was placed at the extremity of each arm; the infrared beam of the third diode was located just above the center of the cup. Another infrared diode was also placed within the food cup to determine whether or not the reward was still present in the food cup after the rat had visited a given arm. Automation of the radial arm maze allowed: (i) the location of the animal to be deduced from the crossing of the infrared beams and visualized on a computer screen, (ii) the doors controlling the entrance of each arm to be operated by a home-made software, and (iii) the presence of a food reward in the food cup to be detected by the software. The TTL pulses generated by the crossing of each infrared beam were sent to the acquisition board (PClab, PCL 720) of a 33 MHz 486 PC computer, which provided an on-line display of the animal's location.

Two halogen lights illuminated the ceiling of the room and were placed to prevent any shadow within the