BRAIN RESEARCH 1621 (2015) 294–308

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Brain Research

Research Report

Telencephalic neurocircuitry and synaptic plasticity in rodent spatial learning and memory

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ARTICLE INFO

Article history:
Accepted 9 January 2015
Available online 22 January 2015

Keywords:
Spatial learning and memory
Synaptic plasticity
Hippocampus
Prefrontal cortex
Striatum
Telencephalic neurocircuitry
Alzheimer's disease
Schizophrenia

ABSTRACT

Spatial learning and memory in rodents represent close equivalents of human episodic declarative memory, which is especially sensitive to cerebral aging, neurodegeneration, and various neuropsychiatric disorders. Many tests and protocols are available for use in laboratory rodents, but Morris water maze and radial-arm maze remain the most widely used as well as the most valid and reliable spatial tests. Telencephalic neurocircuitry that plays functional roles in spatial learning and memory includes hippocampus, dorsal striatum and medial prefrontal cortex. Prefrontal–hippocampal circuitry comprises the major associative system in the rodent brain, and is critical for navigation in physical space, whereas interconnections between prefrontal cortex and dorsal striatum are probably more important for motivational or goal-directed aspects of spatial learning. Two major forms of synaptic plasticity, namely long-term potentiation, a lasting increase in synaptic strength between simultaneously activated neurons, and long-term depression, a decrease in synaptic strength, have been found to occur in hippocampus, dorsal striatum and medial prefrontal cortex. These and other phenomena of synaptic plasticity are probably crucial for the involvement of telencephalic neurocircuitry in spatial learning and memory. They also seem to play a role in the pathophysiology of two brain pathologies with episodic declarative memory impairments as core symptoms, namely Alzheimer's disease and schizophrenia. Further research emphasis on rodent telencephalic neurocircuitry could be relevant to more valid and reliable preclinical research on these most devastating brain disorders.

This article is part of a Special Issue entitled SI: Brain and Memory.

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1. Introduction

Learning is often seen as a process of behavioral change resulting from experience, which includes cognitive as well as motivational aspects. Memory, on the other hand, is the capacity to retain and recall facts, previous experiences, events, impressions, etc. (Markovitsch, 2000). Neuropsychologists classically distinguish between declarative (explicit) and non-declarative (implicit, procedural) memory. Although these terms refer to the ability to speak, both aspects of memory have been identified and modeled in animals as well. Declarative memory comprises semantic and episodic subsystems (Tulving, 1984). The latter refers to the (conscious) recollection of experiences (i.e., what, where and when), and has been found to be especially sensitive to cerebral

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http://dx.doi.org/10.1016/j.brainres.2015.01.015
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List of abbreviations

aCC	anterior cingulate cortex
AD	Alzheimer's disease
AMPA	α-amino-3-hydroxyl-5-methyl-4-isoxazole-propionate
APP/PS1	amyloid precursor protein presenilin 1
CA1/3	area cornu ammonis 1/3
CaMKII	calmodulin-dependent protein kinase II
DG	dentate gyrus
DLS	dorsolateral striatum
DMS	dorsomedial striatum
DSM	diagnostic and statistical manual of mental disorders
EC	entorhinal cortex
GABA	gamma-amino butyric acid
HC	hippocampus
IL	infralimbic cortex
LTP	long-term potentiation
LTD	long-term depression
MK-801	dizocilpine
mPFC	medial prefrontal cortex
MSNs	medium spiny neurons
MWM	Morris water maze
NMDA	*N*-methyl D-aspartate
NVHL	neonatal ventral hippocampus lesion
PD	postnatal day
PFC	prefrontal cortex
PL	prelimbic cortex
RAM	radial arm maze
Zif268	zinc finger transcription factor 268

aging, neurodegeneration, and various neuropsychiatric diseases (Pause et al., 2013).

The identification of complex cognitive abilities in animals that are analogous, homologous or precursory to essentially human functions remains controversial. However, most researchers consider spatial learning and memory in rodents to be at least a close equivalent of human declarative memory abilities (see Morellini, 2013). Spatial memory generally refers to information about the spatial properties of the environment, which is crucial for an animal's ability to navigate in space, and has obvious ecological importance for heavily predated and burrowing murid species.

2. Spatial learning and memory tests in laboratory rodents

Researchers devised hundreds of arenas and protocols to investigate spatial learning and memory in laboratory rodents. However, Morris water maze (MWM) and radial-arm maze (RAM) remain the most widely used. We will briefly review these two tests below, but refer to Hodges (1996) for a thorough comparison between them.

First described by Morris in the early 1980s, MWM consists of a pool filled with opaque water with a submerged escape platform (Morris, 1984; D'Hooge and De Deyn, 2001). In order to locate the hidden platform, rodents need to associate distal environmental cues with its location. During acquisition training in the hidden-platform version of the task (see Fig. 1), most authors have used performance measures such as time required to locate the hidden-platform (i.e., escape latency), path length and velocity. However, rodents have different ways to improve their performance as a result of training, and not all of these actually involve the use of spatial reference memory (Garthe and Kempermann, 2013; Stover et al., 2012). Therefore, some authors implemented more elaborate methods to assess the use of spatial search strategies (Janus, 2004; Brody and Holtzman, 2006; Garthe et al., 2009; Garthe and Kempermann, 2013; Lo et al., 2013, Stover et al., 2012; Van der Jeugd et al., 2013). These can be segregated in spatial strategies, (non-spatial) systematic strategies and repetitive looping. During the course of training, and related to increasing accuracy and directionality, normal rodents will use spatial strategies incrementally, whereas cognitively compromised animals tend to stick to non-spatial strategies (Janus, 2004; Lo et al., 2013; Stover et al., 2012).

Many deviations of the MWM task have been described that assess different aspects of learning and memory. By providing a visible platform the animal learns to swim to a cued goal, an ability that is unrelated to place learning (although mice have been shown to acquire spatial memory during this version of the task as well). Moving the platform to an alternative position (usually the opposite quadrant), the animal has to update its spatial memory during a process called reversal learning. Furthermore, working memory can be assessed using multiple-location place-learning or delayed matching-to-sample procedures, during which the platform is moved to a new location on each training session. A final example of an interesting MWM protocol variant is extinction of spatial preference following platform removal. During such extinction protocols, inhibitory learning suppresses the behaviors that were learned during acquisition (Callaerts-Vegh et al., 2006; Vorhees and Williams, 2006; Morellini, 2013).

Spatial learning and memory can also be reliably assessed in the dry-land RAM (Olton and Samuelson, 1976). A typical RAM device consists of several arms (4–8, or more) symmetrically situated around a central chamber. The commonly used win-shift version of this task requires food-deprived animals to learn to collect rewards from baited arms as efficiently as possible. The most efficient strategy in this version of the task is obviously by visiting each arm only once. The number of revisited arms (errors), and the time required for retrieving the food are measured. Alternatively, when not all arms are baited, animals must learn to avoid entering non-baited arms (Peele and Baron, 1988). Visiting non-baited arms can then be counted as reference memory errors and revisits as working memory errors. Visual or tactile stimuli can be provided to cue animals about visited and unvisited arms (Olaman and McNaughton, 2001; Packard et al., 1989). In the win-stay version of this test, animals need to return to a previously rewarded location (McDonald and White, 1993), instead of avoiding the previously rewarded location as in

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