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Research report

Dorsolateral striatum and dorsal hippocampus: A serial contribution to acquisition of cue-reward associations in rats

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HIGHLIGHTS

- Rats with dorsolateral striatum lesions were impaired in procedural and declarative-like memories.
- Rats with dorsal hippocampal lesions were impaired in declarative-like memory.
- Rats with dorsal hippocampal lesions were not impaired procedural memory.
- Establishment of a procedural may be a prerequisite for a declarative-like memory.

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ABSTRACT

In laboratory rodents, procedural and declarative-like memory processes are often considered operating in dual, sometimes even competing with each other. There is evidence that the initial approach of a repetitive task first engages a hippocampus-dependent declarative-like memory system acquiring knowledge. Over repetition, there is a gradual shift towards a striatum-dependent response memory system. In the current experiment, Long-Evans male rats with bilateral, fiber-sparing ibotenic acid-induced lesions of the dorsolateral striatum or the dorsal hippocampus were trained in an olfactory associative task requiring the acquisition of both a procedural and a declarative-like memory. Rats with dorsolateral striatum lesions, and thus an intact hippocampus, were impaired on both sub-categories of memory performance. Rats with dorsal hippocampal lesions exhibited a substantial deficit in learning the declarative-like cue-reward associations, while the acquisition of the procedural memory component of the task was not affected. These data suggest that the dorsolateral striatum is required to acquire the task rule while the dorsal hippocampus is required to acquire the association between a given stimulus and its associated outcome. The finding is that the dorsolateral striatum and the dorsal hippocampus most probably contribute to successful learning of cue-reward associations in a sequential (from procedural to declarative-like memory) order using this olfactory associative learning task.

1. Introduction

Damage to hippocampal and retrohippocampal structures in rodents causes selective impairments in a variety of spatial and non spatial declarative-like learning tasks [1–4]. Such damage, however, was also shown to have little or no effects on other types of learning [5,6], including olfactory associative learning [7–10]. An example is provided by the effects of such lesions in the successive go/no go olfactory discrimination task [11]. In this task, animals are successively presented with individual odor stimuli, which are paired (i.e., indicative of go trials) or not (i.e., indicative of no go trials) with reinforcement. The prerequisite for successful learning of go/no go tasks after hippocampal damage is that the cues are presented with a short inter-trial interval. Indeed, when rats with hippocampal damage have to manage the successive odor presentations with long inter-trial intervals (>15 s), the odor-reward association is not acquired [9,10]. These observations confirmed earlier findings in both rats and monkeys subjected to fornix or hippocampal lesions [12]. Surprisingly, there are only a few studies which aimed at identifying the brain regions involved in this type of hippocampus-independent learning [13].

One candidate structure is the striatum, the rodent equivalent of the caudate–putamen in primates. In rats, lesions of the striatum,

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Table 1
Coordinates and injection volumes for ibotenate lesions of the dorsolateral striatum or the dorsal hippocampus. Coordinates are given in mm anterior and lateral to Bregma (Paxinos and Watson, 1998) and from the skull surface in depth.

Structure	Anteriority	Laterality	Depth	Volume (μL)
Dorsolateral striatum	+0.5	±3.9	−5.2	0.4
	+1.2	±3.6	−5.2	0.4
Dorsal hippocampus	−2.6	±1.0	−3.8	0.06
	−3.1	±3.0	−2.8	0.06
	−3.0	±1.4	−3.2; −2.4	0.06 each
	−3.8	±3.7	−2.8	0.06
	−3.8	±2.6	−3.0; −2.5	0.06 each
	−4.1	±4.0	−3.2	0.08
	−4.1	±2.5	−2.5	0.08

and more specifically of its dorsal regions, impair the acquisition or/and retrieval of several operant tasks that are not or only poorly affected by hippocampal lesions [2]. These include tasks based on avoidance responses [14–19], brightness discrimination [20], processing of visual cues in the Morris water maze [21,22], and visual/olfactory conditioning of emotional responses [23].

Our associative olfactory task [9] enables separate assessment of performance linked to procedural or declarative-like memory contributions. Using this task, a first experiment assessed performance after fiber-sparing lesions of the dorsolateral striatum. Given the outcome of this experiment (i.e., the impairment of procedural learning prevented acquisition of the hippocampus-dependent declarative-like component of the task), we performed a complementary experiment in which the effects of dorsal hippocampus lesions were assessed according to exactly the same protocol. Following hippocampal lesions, we expected normal procedural learning but no acquisition of the hippocampus-dependent, declarative-like component of the task. Our results suggest a serial implication of the striatum and the hippocampus in cue-reward associations learning.

2. Material and methods

2.1. Animals

Fifty two young adult Long-Evans rats (R. Janvier, France) weighing 250–275 g at the time of surgery were used. They were individually housed and kept on a 24 h light–dark cycle (lights on at 7:00 am and off at 7:00 pm) in a room held at a constant temperature (22°). After surgery and before testing, each animal was first handled (10 min) daily for three consecutive days. Then it was deprived of water 48 h before the beginning of training. During training of the following days, the rats were given water ad libitum for 30 min per day at 6:30 pm. European guidelines on procedures for animal experimentation were followed, and all efforts were made to minimize the animals' suffering and to reduce the number of animals used while complying with statistical constraints.

2.2. Lesion surgeries

All rats were anaesthetized with an intraperitoneal (ip) administration of pentobarbital (60 mg/kg, i.p.). Once anaesthetized, they were given an intramuscular injection of an antibiotic (Extencilline; 0.3 mL/kg) and were subsequently placed on a stereotaxic apparatus. Their scalp was opened longitudinally with a scalpel and little holes were drilled in the skull at locations where a needle had to be introduced into the brain to perform the ibotenate infusions. The ibotenate solution (5 μg/μL) was infused at the coordinates indicated in Table 1 at a speed of 0.25 μL/min. After each infusion, the needle was left in place for 4 min before being slowly retracted. In the sham-operated rats, the needle was descended into the brain at each of the coordinates used for the lesion, but no infusion was performed. After surgery, the scalp was sutured and all rats were placed in a heated cage until complete recovery from anesthesia. Behavioral training was started 4 weeks after surgery.

2.3. Apparatus and training procedure

The olfactory training apparatus was a rectangular box made of wire mesh (30 cm × 30 cm × 50 cm). A conical odor port (1.5 cm in diameter, 0.5 cm above the floor) was drilled horizontally through a triangular wedge of Plexiglas, mounted in one corner of the cage. A circular (1 cm diameter) water port in the shape of a well was placed directly above the odor port. Responses to the odor presentation

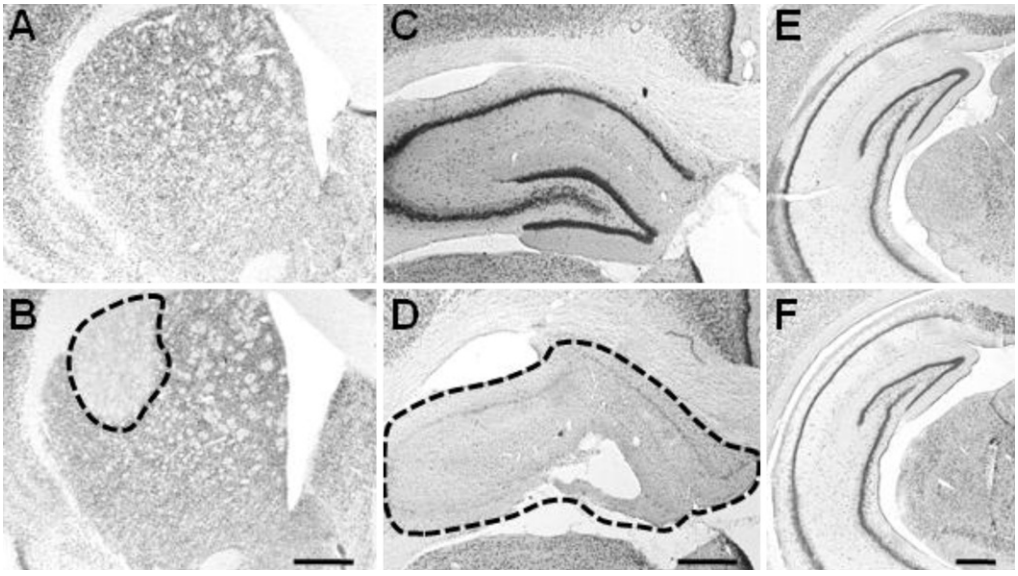

Fig. 1. Representative photographs illustrating lesions following NeuN staining in the groups of SHAM (A, C, E) and lesioned (B, D, F) rats. B and D show typical examples of lesions in the dorsolateral striatum and in the dorsal hippocampus, respectively. Dashed lines indicate the limits of the damaged area. E and F indicate that rostral regions of the hippocampus were not damaged after lesions of the dorsal hippocampus (F) as compared to a sham-operated rat (E). Scale bars at the bottom right of photos B, D and F correspond to 1 μM.