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Rapid learning and flexible memory in "habit" tasks in rats trained with brain stimulation reward

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Abstract

Two groups of rats, one rewarded with sweetened food and the other rewarded with medial forebrain bundle (MFB) stimulation, were trained to home in on and dig for a buried object coated with a target odor. After each group had 15 training trials, MFB rats searched with greater accuracy and speed than food-rewarded rats. MFB rats were subsequently tested (1) after 6 weeks with no additional practice; (2) with food or non-food distractor odors, and (3) with major spatial alterations to the search environment, and in all cases searched with the same high accuracy, short search time, and low level of distractibility as in baseline. These results suggest that the high motivation provided by MFB reward engenders rapidly formed, long-lasting, and surprisingly flexibly deployable "habit" memories.

Keywords: Medial forebrain bundle; Memory; Habit; Motivation; Reinforcement; Olfaction; Rats

1. Introduction

Over the last several decades, the results of many studies have supported an anatomical and functional dissociation between "declarative," hippocampally dependent memory, and "procedural," or "habit," basal ganglia-dependent learning [1–4], in rats as well as primates [1,3,5,6]. These two forms of learning and memory were thought to differ psychologically in several fundamental respects: Declarative memories were conscious, relational, generalizable to novel contexts, and capable of being learned in a single trial (or "episode"; hence its alternative name "episodic memory"), whereas habit acquisition and execution were thought to be subconscious, specific to the training environment, and learned slowly over the course of many (e.g. 100 or more) training trials [4]. Habit tasks, also called "stimulus–response" tasks [3], are defined as tasks in which subjects are trained to execute a specific motor action (e.g. a turn) whenever they perceive a reward-associated sensory cue (e.g. a lit arm of a radial maze), with the context-appropriate performance of the motor act bringing the reward [4].

Recent mechanistic findings from studies testing the role of particular basal ganglia cellular classes and synapses in procedural learning appear to substantiate the view that habit learning would be "inflexible"–specific to the sensory environment and other task contingencies used in training–as well as "compulsive"–repetitively executed with little consideration given to trial-specific information during the decision-making process–particularly when the reinforcer used in the behavioral task was medial forebrain bundle (MFB) stimulation or addictive drugs. For example, several studies have suggested that the large quantity of dopamine released into the nucleus accumbens shell and core during

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MFB stimulation as opposed to during the experience of natural rewards such as food would make the learned habit both more rigidly executed and compulsive in response to the sensory stimuli present during training [7,8], much as learned sensory cues exert powerful control over behavior with drugs of abuse [9]. Another set of findings supporting the rigidity of procedural learning is that cholinergic, tonically active interneurons in the striatum play a crucial role in linking highly specific sensory cues to sensing the reward delivered after a correct motor response [10,11]. Indeed, both brain stimulation reward and narcotic reinforcers are considered to be "habit-forming" and much more powerfully addicting when administered as rewards in operant tasks as opposed to passive paradigms [8,12].

Earlier studies indicated that if a task was a well-defined habit task, the hippocampus could be ablated with no perceptible loss in performance, and vice versa [e.g. Refs. 2,13]. These studies were initially interpreted to mean that hippocampally dependent processes played no role in normal (basal ganglia-dependent) habit learning and execution. However, recent evidence has revealed that hippocampal encoding of multiple task parameters occurs even when the animals' task is designed to be strictly a habit task [4]. For instance, some evidence indicates that hippocampally dependent declarative memories are formed even when the context they encode cannot be used to solve the task. An example of "context" would be a configuration of prominent visual cues in stable locations in the training room. Theoretically, it was expected that if a rat learned a habit task in which it had to turn into a radial-maze arm that was lit (the S+), and the lit arm varied randomly from trial to trial, the location of distal spatial cues would be irrelevant to performance of the task. However, McDonald et al. have found evidence to the contrary [4]. They showed that if the distal cues change their position across testing trials, proactive interference was created in which the rat confused prior trials with the current trial. Thus, this experimental manipulation exposed the possibility that the hippocampus was encoding this set of distal cues despite their lack of utility in the habit task. Confirming this hypothesis, the authors found that when the hippocampus was subsequently lesioned, the proactive interference across trials vanished.

Some evidence suggests that in tasks with stronger motivation, multiple types of learning might take place and be deployed together to result in a higher rate of obtaining the reward. For example, in Olds and Milner's classic 1954 study [14] demonstrating the power of MFB conditioning over bar-pressing in rats, many animals learned the task in 1–2 trials, suggesting that hippocampal, episodic memory may have aided in the acquisition of a traditional habit (bar-pressing) task. Furthermore, a recent study by Talwar et al. [15] demonstrated that MFB-seeking behavior can be surprisingly flexible despite the habit nature of the task the rats were taught. In this study, rats were trained to move forward and turn left or right in response to electrical stimulation of their left or right somatosensory cortices for MFB stimulation reward. Although the directional locomotor behavior was trained in a two-dimensional figure-eight maze, rats rapidly generalized this behavior to any tested ground plane, e.g. when released into environments such as grassy fields, sands, and the open laboratory. Moreover, they generalized their learning to three-dimensional as well as two-dimensional contexts, e.g., climbing up ladders and trees and jumping off ledges, when an MFB pulse train indicated moving "forward."

In the current experiment, we addressed the nature of MFB-rewarded versus food-rewarded learning in habit task-digging in woodchips at the location of a buried, specific conditioned odor for either sweetened cereal or brain stimulation reward. We then probed the MFB rats under multiple conditions that required cognitive flexibility beyond that thought to be possible for pure habit learning. Our findings suggest that MFB rats make use of multiple memory systems in learning and performing this habit task in order to maximize the amount of reward.

2. Materials and methods

2.1. Animal treatments

Nine female Long–Evans rats (starting weight 280–300 g), 5 experimental animals and 4 controls, were used. Under isoflurane anesthesia, experimental animals (henceforth, "MFB rats") received bilateral electrode implants in their medial forebrain bundles (MFBs, stereotaxic coordinates 3.8 mm posterior to bregma, 1.6 mm lateral to the midline, and 8.2 mm deep) and ventral tegmental areas (VTAs, coordinates 5.2 mm posterior, 0.9 mm lateral, and 8.2 mm deep). Each brain structure on each side received a single Teflon-coated, stainless steel microwire (100 μm in diameter) as part an electrode array custom-fabricated in our laboratory. A week after experimental animals underwent surgery, both food-rewarded and MFB animals were food-deprived to 90% of free-feeding body weight and were maintained at that body weight throughout the duration of the experiment. During the course of probe condition testing, one of the MFB rats died, leaving four experimental animals for the remainder of the study. All procedures were conducted in accordance with the NIH Guide for the Care and Use of Laboratory Animals and the experimental protocol approved by the Institutional Animal Care and Use Committee at SUNY Health Science Center.

2.2. Brain stimulation technique

Remote stimulation was delivered to implanted rats via a two-component stimulation system. The system consisted of a transmitter connected to a laptop PC through its serial port, and an integrated receiver-microprocessor backpack