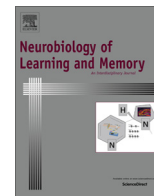




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Review

Habit learning and memory in mammals: Behavioral and neural characteristics



Antonella Gasbarri ^{a,b,*}, Assunta Pompili ^{a,b}, Mark G. Packard ^c, Carlos Tomaz ^{d,e}

^a Department of Applied Clinical and Biotechnological Sciences, University of L'Aquila, Italy

^b European Center for Brain Research, Santa Lucia Foundation IRCCS, 00143 Rome, Italy

^c Department of Psychology, Texas A&M University, College Station, TX 77843, USA

^d Laboratory of Neurosciences and Behavior, Institute of Biology, University of Brasília, Brasília, DF, Brazil

^e Brazilian Institute of Neuropsychology and Cognitive Sciences (IBNeuro), Brasília, DF, Brazil

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ABSTRACT

Goal-directed behavior and habit learning represent two forms of instrumental learning; whereas the former is rapidly acquired and regulated by its outcome, the latter is reflexive, elicited by antecedent stimuli rather than their consequences. Habit learning can be generally defined as the acquisition of associations between stimuli and responses. Habits are acquired via experience-dependent plasticity, occurring repeatedly over the course of days or years and becoming remarkably fixed. The distinction between habit learning, as a product of a procedural learning brain system, and a declarative learning system for encoding facts and episodes is based on the hypothesis that memory is composed of multiple systems that have distinct neuroanatomy and operating principles. Here we review recent research analyzing the main behavioral and neural characteristics of habit learning. In particular, we focus on the distinction between goal-directed and habitual behavior, and describe the brain areas and neurotransmitters systems involved in habit learning. The emotional modulation of habit learning in rodents and primates is reviewed, and the implications of habit learning in psychopathology are briefly described.

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1. Introduction

Habit learning can be broadly defined as the acquisition of associations between stimuli and responses (Hull, 1943). It represents in part one of the two systems of instrumental conditioning, one of which is considered to involve a goal-directed system that acquires associations between responses and the incentive value of outcomes, and a second habit system that acquires S–R associations (Adams & Dickinson, 1981). Habit formation refers to the incremental strengthening of a stimulus–response (S–R) bond, according to the reinforcement contingencies operating in a given learning situation.

Habits typically involve acquisition of sequential, repetitive, and motor behaviors elicited by external or internal triggers that, once released, can go to completion without constant conscious oversight (Graybiel, 2008). The characteristics of habits include that they occur repeatedly over the course of days or years,

becoming remarkably fixed. Moreover, fully acquired habits are performed almost automatically, virtually non-consciously, allowing attention to be focused elsewhere. Thus, habits help to free up the cognitive loads during the expression of routine procedures and allow organisms to focus on novel situations and tasks. They tend to involve an ordered, structured action sequence that is prone to being elicited by a particular stimulus. Habits may also potentially include expressions of routine “thoughts” as well as motor expressions of routine behaviors (Graybiel, 2008).

The classic distinction between habit learning, as a product of a procedural learning brain system, and a declarative memory brain system for encoding facts and episodes is based on the hypothesis that memory is not a unitary faculty of the brain, but it is composed of multiple systems that have distinct neuroanatomy and psychological operating principles (for reviews see Gasbarri & Tomaz, 2012; Packard & Knowlton, 2002; Squire, 2009; White & McDonald, 2002). Declarative memory supports the learning of relationships among items and events, whereas habit memory is typically acquired gradually over many trials through the establishment of S–R associations that may develop outside of awareness, and are rigidly organized. In the case of non-declarative memory, experience modifies behavior without requiring any

* Corresponding author at: Department of Applied Clinical and Biotechnological Sciences, University of L'Aquila, via Vetoio, Coppito, 67100 L'Aquila, Italy. Fax: +39 0862 433433.

E-mail address: antonella.gasbarri@cc.univaq.it (A. Gasbarri).

conscious memory content or even the experience that memory is being used. Non-declarative memory is expressed through performance, while declarative memory is expressed through recollection, as a way of modeling the external world. The different memory systems support behavior operating in parallel (Squire, 2009; White & McDonald, 2002). Scientists in different fields have been attracted to the study of habits due both to their crucial role in behavior and the dichotomy between the conscious, voluntary control over behavior, considered the essence of higher-order deliberative behavioral control, and lower-order behavioral control that is hardly available to consciousness. Importantly, repetitive behaviors can also appear as cardinal symptoms in a broad range of neurological and neuropsychiatric illness.

2. Instrumental learning: from goal-directed action to habitual behavior

The automaticity of behavior, after repetitive practice, is considered a consequence of the gradual shift from goal-directed to habitual control of action (Adams & Dickinson, 1981; Balleine & Dickinson, 1998a). It is very well known that in everyday life frequently repeated behaviors are characterized by a relative resistance to change, which may be due to the fact that, with extended practice, behaviors become more automatic, shifting from explicit to implicit control. This so-called proceduralization of behavior is considered an indicator of successful learning (Anderson, 1987), since it sets cognitive resources free for other tasks, even though there is a decrease of flexibility and cognitive control, which can reduce the speed in the reaction to modifications in the environment.

Studies on instrumental conditioning in rats reported that actions that are instrumental in obtaining access to rewards, such as lever pressing for food, can be controlled by two processes: a goal-directed system, and a habit behavior supported primarily by the orbitofrontal cortex and dorsomedial striatum (DMS), and dorsolateral striatum (DLS), respectively (Balleine & O'Doherty, 2010; Yin & Knowlton, 2006). The main difference between them is that the goal-directed system, which characterizes the initial acquisition, encodes the relationship between an action and the motivational value of the outcome, while the habit behavior implies the association between stimulus and response, without any correlation with the outcome prompted by the response (Balleine & Dickinson, 1998a; Balleine & Dickinson, 1998b; Schwabe & Wolf, 2013). Therefore, instrumental learning has been found to be sensitive both to non-contingent reward delivery and to post-training changes of outcome value (Adams & Dickinson, 1981; Balleine, 2001; Colwill & Rescorla, 1986; Dickinson & Balleine, 1994, 2002). However, after extensive training, control over performance shifts to a stimulus–response mechanism and, as a consequence, actions become habitual and no longer sensitive to changes in either the instrumental contingency or reward value (Balleine & Dickinson, 1998a; Dickinson & Balleine, 1993, 1995; Dickinson, Balleine, Watt, Gonzalez, & Boakes; 1995). Even though goal directed actions, which are supported primarily by the orbitofrontal cortex and dorsomedial striatum (DMS), and habit behavior, that is based mainly on dorsolateral striatum (DLS), are considered antagonistic they may at times compete and at others cooperate in the selection and subsequent evaluation of actions required for normal choice performance (Balleine & O'Doherty, 2010).

In order to distinguish goal-directed and habitual actions, two experimental behavioral paradigms—outcome devaluation and contingency degradation—were developed on the basis of the hypothesis that goal-directed, but not habitual behavior, is responsive to modifications in the motivational value of the outcome and the

action–outcome contingency (for review see Schwabe & Wolf, 2011). The outcome devaluation experiment consists of three phases: (1) training of the subjects in two instrumental actions producing two food outcomes, (2) devaluation of one of the two food outcomes, (3) extinction test, where a reduced frequency of the now devalued action suggest that learning is goal-directed, while the absence of this behavioral sensitivity may indicate habit learning (Schwabe & Wolf, 2013).

In contingency degradation tests, free rewards independent of any action are presented (Balleine, Killcross, & Dickinson, 2003; Yin, Ostlund, Knowlton, & Balleine, 2005). After training in two instrumental actions causing two different outcomes, in the test session one of the outcomes is presented non-contiguously making its probability similar if the previously required action is shown or not. Taking into account that goal-directed, but not habitual behaviors are believed to be sensitive to the contingency action–outcome, a decrease in the response to the action, linked to the non-contiguously presented reward, suggests a goal-directed action, while its absence is indicative of habit behavior.

The entity of training determines the process that controls behavior. In fact, while initial behavior is mostly goal-directed, extensive training decreases the sensitivity to changes in goal value and action–outcome contingency and automatic habit behavior becomes predominant (Adams, 1982; Dickinson, Balleine, Watt, Gonzalez, & Boakes, 1995; Dickinson, Squire, Varga, & Smith, 1998).

The contribution of goal-directed and habitual processes to instrumental action is influenced also by the reinforcement schedule utilized during training (Dickinson, 1985; Yin & Knowlton, 2006). Considering that, in this kind of schedule, the experienced correlation between action and outcome is high, if a response is followed with a certain probability by a reward, goal-directed action is induced. However, due to the fact that in these experimental paradigms the experienced instrumental contingency is generally low, interval schedules where a response is followed by a reward only after a certain time interval facilitate habitual behavior. The evidence that even a modest training on an interval schedule may cause the shift to habitual behavior suggests that habit formation is not necessarily a consequence of practice *per se* (Dickinson, Nicholas, & Adams, 1983). Extensive training may decrease the modification in behavior and then the experienced correlation between action and its outcome. It is not surprising that, if the action–outcome knowledge is absent or decreased, behavior is no longer affected by variations in the value of the outcome or the instrumental contingency (Dickinson, 1985).

3. Neural substrates of habit learning

Neurobiological studies have clearly established that the mammalian brain does not contain a single memory center or brain structure that mediates the acquisition, consolidation, and retrieval of all types of learned information. Rather, extensive evidence suggests that memory is organized in multiple brain systems (for reviews see Packard & Knowlton, 2002; Squire, 2009; White & McDonald, 2002; White, Packard, & McDonald, 2013). Numerous studies have implicated the hippocampal–temporal lobe system in declarative memory and the striatum and connected basal ganglia in procedural learning and habit formation (McDonald & White, 1993; Packard, Hirsh, & White, 1989; Packard & McGaugh, 1992; Yin & Knowlton, 2006). Even though the precise functions of the hippocampal formation (HF) are not completely clear, the weight of evidence favors a role in episodic memory, storing information concerning individually experienced events, set in a specific spatiotemporal context (Eichenbaum, Yonelinas, & Ranganath, 2007; Squire & Wixted, 2011; Tulving & Markowitsch, 1998; Wang & Morris, 2010). By contrast, procedural memories are

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