Available online at www.sciencedirect.com

ScienceDirect

Current Opinion in Behavioral Sciences

Corticostriatal foundations of habits

Carol A Seger[1,2,3]

Much of our daily behavior is based on habit. This article reviews recent advances in understanding the corticostriatal system's role in habit learning and representation. New methods have led to a better understanding of how striatal circuitry (particularly the direct and indirect basal ganglia pathways) underlies habit learning. Research has established the critical role of perceptual processing in habit learning and has raised the intriguing possibility that some attentional mechanisms are habitual. Habit learning is only one of several mechanisms for acquiring appropriate behaviors; we can now better characterize when habit learning will predominate, and how habit and other learning mechanisms interact.

Addresses
[1] School of Psychology, South China Normal University, Zhongshan Avenue West 55, Tianhe District, Guangzhou, Guangdong Province 510631, China
[2] Department of Psychology, Colorado State University, Fort Collins, CO 80523, USA
[3] Program in Molecular, Cellular, and Integrative Neurosciences, Colorado State University, Fort Collins, CO 80523, USA

Corresponding author: Seger, Carol A. (seger@colostate.edu)

Current Opinion in Behavioral Sciences 2018, **20**:153–160

This review comes from a themed issue on **Habits and skills**

Edited by **Barbara Knowlton** and **Jörn Diedrichsen**

https://doi.org/10.1016/j.cobeha.2018.01.006

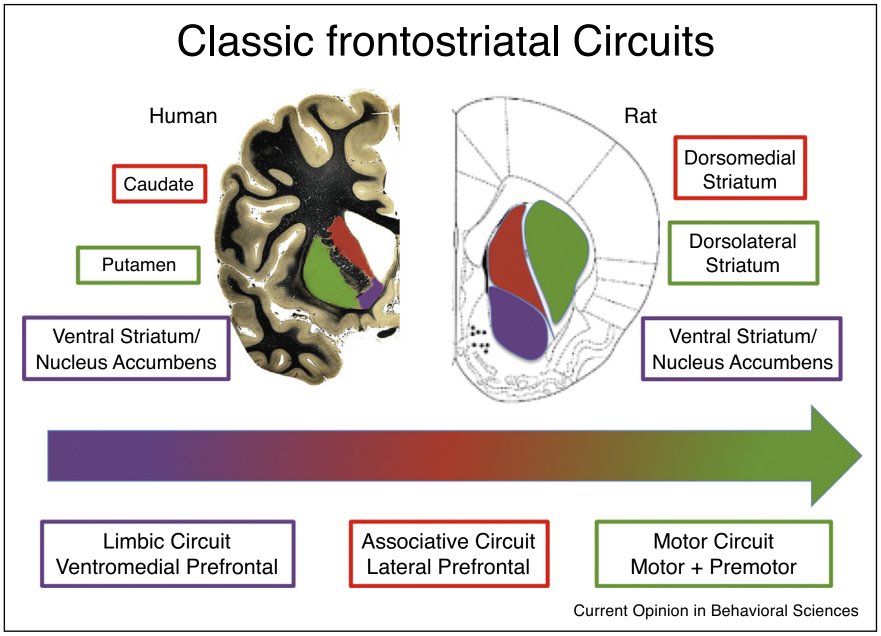
This is an exciting time for neuroscientists studying habit learning. Methodological advances now allow us to delve into the corticostriatal systems underlying habits with unprecedented specificity [4]. This review focuses on habit learning as a function of corticostriatal systems connecting the basal ganglia with cerebral cortex, and especially on recent research from 2015 to mid-2017. It discusses advances made in answering three fundamental questions: How are habit representations acquired in and executed via corticostriatal circuitry? Is perceptual processing integral to corticostriatal mechanisms underlying habits, and is there such a thing as attentional habit learning? And finally, how do the neural systems underlying habit learning interact with other learning and memory systems, in particular those underlying goal-directed behaviors?

What is habit learning? History and current conceptualizations

The term 'habit learning' has its origin in research conducted in the 1960s, meant to encompass forms of learning that were preserved in humans and nonhuman animals with hippocampal lesions and associated impairment in declarative memory function [5,6]. Habits were conceptualized as form of procedural memory and, along with skills, were linked via lesion studies to the basal ganglia [7,8], and later specifically to the sensorimotor basal ganglia circuit through the posterior putamen. In parallel, the concept of habit learning was being developed in instrumental learning theory [9], in which habit is defined as behavior based on stimulus-response associations independent of reward or outcome, in contrast with goal directed behavior based on associations between actions and outcomes. In this theory, the key difference between goal directed and habitual behavior is outcome sensitivity, and habits can be identified by testing if behavior is insensitive to reinforcers. For example, if maze running reinforced with chocolate becomes habitual a rat will continue to run the maze even if it is satiated on chocolate and the reinforcer is no longer of value. Both goal directed and habit learning have been shown to involve portions of the basal ganglia: the anterior caudate and posterior putamen, respectively [10–12], as summarized in Figure 1. The definitions of habit learning as a form of nondeclarative memory and as a form of instrumental learning are largely compatible,[4] and as noted above, both converge on the same corticostriatal system: the motor circuit connecting putamen with premotor and sensorimotor cortices. This review will focus on this motor corticostriatal system and how it supports habit learning, with habits defined in the tradition of instrumental learning, as independent of goal-directed functions that are outcome sensitive.

[4] Although habit learning conceptualized as nondeclarative memory and habit learning conceptualized as non-goal-directed instrumental learning are largely compatible, the reader should not assume this means that declarative memory and goal-directed learning rely on the same neural system. Neurally, declarative memory is associated with medial temporal systems, whereas goal-directed learning is associated with frontoparietal working memory and caudate (dorsomedial) striatal systems. Declarative memory and goal-directed learning can occur independently, for example, short term goal directed learning is preserved in amnesic patients with declarative memory impairment due to hippocampal damage [1]. However, both systems often are required for extended goal directed learning that is dissociable from habit learning [2,3].

Figure 1



Classic three-circuit characterization of frontostriatal loops. Top left: Primary divisions of the human striatum. Top right: Primary divisions of the rodent striatum. Habits recruit the posterior putamen (dorsolateral striatum) and the motor corticostriatal circuit connecting this region with premotor and sensorimotor cortex [70–72]. The anterior caudate (dorsomedial striatum) is associated with executive function broadly, and goal-directed learning in particular, consistent with its connections with the prefrontal cortex in the associative corticostriatal circuit [15]. Finally, the ventral striatum (also known as the nucleus accumbens) underlies reward processing and participates in the limbic circuit with ventromedial prefrontal regions. Bottom: Arrow indicates typical patterns of anatomical interaction between the primary loops, progressing from limbic to associative to motor. Note that this frontal lobe centric view does not include corticostriatal projections from other cortical regions, in particular perceptual regions; see section on 'Perceptual and attentional aspects of habits.'

Because habit learning is defined in contrast with goal-directed learning and declarative memory, and multiple forms of learning can and often do take place simultaneously, in order to study habit learning in the laboratory it is necessary to use tasks in which non-habitual influences on behavior are minimized or in which the habit learning contribution can be estimated separately. Several commonly used habit learning tasks are illustrated in Figure 2. Typically, habit learning is fostered when the material to be learned is not well suited to hypothesis testing or strategic thought due to complexity, reinforcement contingencies are used that are known to preferentially support habit learning (such as interval reinforcement schedules [10]), or additional manipulations are implemented that can interfere with the limited capacity executive functions that goal directed learning relies on (dual task, distraction, stress, time pressure; see [13] for review). Recent computational work has adapted algorithms from reinforcement learning to formally estimate goal directed (or 'model based') and habitual (or 'model free') behavior [14,15]. Behavior is operationally defined as habitual if it can be predicted by the model free algorithm that is solely a function of past reinforcement and an individual's learning rate. Although all these measures do largely measure habit and reduce or minimize goal directed contributions, none is process pure and it is unclear whether they are equivalent [16].

Corticostriatal representations of habits

Recent research has increased our knowledge of how habits are acquired and represented in the corticostriatal system, including within the pathways through the basal ganglia, the striatum, and cerebral cortex.

Roles of the direct and indirect pathways

In the now-classic dual pathway model of the corticostriatal system [17,18] there are two functionally independent parallel pathways between striatum and thalamus: the 'direct' pathway passing from striatum directly to the globus pallidus internal segment (GPi), and the 'indirect' pathway passing through the globus pallidus external segment (GPe) between striatum and GPi. The GPi sends inhibitory projections to the thalamus that modulate cortical activity. Activity in the direct (or 'go') pathway ultimately facilitates cortical excitation and elicits movement, whereas activity in the indirect (or 'no-go') pathway ultimately increases inhibition of cortex and suppresses movement. In the classic view, habits were thought to rely solely on direct pathway activity eliciting the habitual action representation in motor cortex. The