



Neurobiology of habit formation

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Our knowledge of the brain changes that enable habits to be formed continues to grow rapidly. As a key hub for habits, many studies have focused on neurobiological processes related to habits in the striatum. Attention has been paid to the contributions of the direct and indirect pathways, interneurons, dopaminergic inputs, and potential cortical and amygdala influences. We highlight this research here and conclude with a discussion of several additional topics that are also being addressed to propel our understanding of habits further forward.

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Advances in research on habits are being made in many realms. There is a growing understanding of how habit formation relates to molecular and physiological mechanisms of neuronal plasticity as well as how varieties of neurons and neural pathways contribute to habits [1–4], which we review here. Several major behavioral assays for habits have been in use in order to provide operational measures that distinguish behaviors that are habitual versus those that are purposeful or cognitively driven. One measure for habits is to show that behavior is insensitive to changes in the expected value of the earned outcome. For tasks that involve learning behaviors to achieve rewards, outcome revaluation involves a deflation or inflation of the reward value (e.g. through conditioned taste aversion, satiety, hunger) that occurs outside of the task conditions. The test is whether subjects incorporate that new knowledge about reward value into their learned task behavior routine where the changed reward is the outcome; when behavior immediately adjusts to reflect the new outcome value (e.g. is reduced when the reward has been devalued), it is thought to be goal-directed and rooted in associations that had been learned between the

action and the specific outcome. When behavior remains the same as before, and is insensitive to the new outcome change, it is regarded as habitual and driven by stimulus-response associations. In some cases, habits are also inferred when a learned behavior is insensitive to changes in the received outcome. This occurs, for example, when behavior persists despite the outcome co-occurring with punishment (e.g. a footshock). Similar assays test behavioral flexibility in response to a change in the action-outcome contingency; purposeful behaviors adjust rapidly to reflect new contingencies, while habits do not. On maze tasks, habits are also inferred when navigation is driven by a response rule (e.g. turn right) rather than a place rule (e.g. use environmental cues to signal reward locations). Finally, high performance optimality and vigor can also be a marker of habits. Habitual behavior will exhibit trial-to-trial consistency in rapid and routed responses, accurate responses, and responses that lack vicarious trial-and-error head movements (i.e. deliberations toward choice options before action selection, VTEs).

The basal ganglia

Dorsal striatum

In the brain, ground-zero for habits is the dorsolateral striatum (DLS; primate putamen homologue), a basal ganglia input structure, as it has been implicated in all of the behavioral indices of habits noted above. DLS disruption causes animals to favor the use of spatial cues over response-based rules for navigation, to increase sensitivity to outcome value and action-outcome contingency changes, to reduce responding for an outcome paired with punishment, and to increase variance in action structure [1,2,5–7]. This habit promoting role is specific to the DLS within the larger striatum. In fact, an adjacent area, the dorsomedial striatum (DMS; caudate homologue), instead promotes flexibility and goal-directed behavior. For instance, disruption of DMS activity reduces outcome-sensitivity and space-based navigation, resulting in a reliance on habits instead [2]. It is unlikely that the DMS simply serves to oppose habits as neural recording and imaging studies routinely implicate activity in this brain area as signaling relationships between action choice and outcomes, suggesting an active role in goal-directed behavior [8]. Thus, the general consensus is that parallel and competing circuits exist in the brain for habits and goal-directed actions, the former DLS-related and the latter DMS-related.

A series of recent studies have attempted to uncover how activity in the DLS, and the broader circuits within which it is embedded, represent habit learning. This line of

research has begun to suggest that the DLS signals several different aspects of habits in different ways, highlighting what we have described as a multi-component structure of habitual behavior [4]. Two major distinctions include signaling related to the DLS role in performance optimization and the role in producing behavior that is insensitive to changes in outcome value or action-outcome contingency. For example, activity in DLS medium spiny neurons (MSNs), the GABAergic projection neurons of the striatum, can signal specific movements from specific body parts, likely as a consequence of major inputs arriving from the sensorimotor cortex [9]. However, as those movements are put to use in learning a task for reward, the neurons cease responding to each movement occurrence [9]. This change in neuronal signaling occurs as the movements become consistent and repetitive, suggesting a role in representing performance optimization. Yet these changes do not appear to be related to the degree of outcome-insensitivity of the behaviors. For example, the change occurs in head-related activity during a head-movement task for reward, in which head movements become outcome-insensitive, but also occurs in lick-related neurons during a licking task for reward in which licking remains outcome-sensitive [10,11]. A similar conclusion has been reached through analysis of another type of activity change in the DLS, one consistently linked with the optimality and vigor of behavior across several animal species: the emergence of a ‘chunking’ pattern of spiking that emphasizes the boundaries of a learned action sequence [12]. This pattern has been shown to relate closely to the vigor of a given action routine as it occurs, increasing in strength in close correspondence with an increasing fluidity and consistency of behavior as it is repeated [13,14*,15,16]. Even at the single trial level, the strength of DLS chunking activity, particularly the activity at the initiation of behavior, correlates with faster performance and, notably, an absence of VTEs that indicate purposefulness in behavior. Such findings support the notion that the chunking patterns represent the linking together of an action chain into a single habitual unit [12]. Curiously, though, the chunking pattern is not related to how sensitive the behavior is to outcome value at the trial level, but its emergence does coincide across days with the development of outcome-insensitivity that can serve to define a habit [14*]. Consistent with this, measurements of the overall magnitude of activity in the DLS during task behavior, in both human imaging and rodent neuronal recording studies, shows a positive relationship with the development of the outcome sensitivity measure of habit [17,18]. These collective findings raise the question of how to integrate signals in the DLS that represent movement vigor with the outcome-insensitivity of habits, which we touch on below.

Direct-pathway and indirect-pathway striatal neurons

Additional work has begun to dissect the habit-related contributions of different types of MSNs within the

striatum. Two main MSN populations of interest include those of the basal ganglia direct pathway (striatonigral MSNs) and those of the indirect pathway (striatopallidal MSNs) [19]. Classically, the direct-pathway MSNs are thought to promote the performance of chosen movements while the indirect-pathway MSNs inhibit movement or promote alternate movement options [19]. New methodologies have paved a way for monitoring and manipulating these MSNs by capitalizing on their distinct molecular profiles. For example, direct-pathway MSNs contain the excitatory G-protein-coupled dopamine D1 receptor, while indirect pathway MSNs instead contain the inhibitory G-protein-coupled D2 receptor (as well as the adenosine A2A receptor) [20]. Traditionally, the view is that movements are facilitated by dopamine influx that increases activity in the direct-pathway (via D1 receptors) and decreases activity in the indirect pathway (via D2 receptors). Yet, for habits, the story is more nuanced.

In one study on striatum-wide signaling, reduced outcome-sensitivity that occurs after dopamine stimulation (i.e. habit enhancement, see also below) was found to be related to activity in both MSN populations. Habit enhancement was blocked by antagonism of D1 receptors, which would inhibit direct-pathway MSNs. In contrast, outcome insensitivity was augmented by antagonism of D2 receptors, which would increase activity in indirect-pathway MSNs [21]. Several additional studies report a necessary role for the indirect pathway in habit expression based on measures of both insensitivity to outcome value and action-outcome contingencies [22,23]. One recent example highlighting a potentially nuanced role for both MSN populations is an experiment that focused specifically on the DLS. Stimulation of direct-pathway MSNs increased task acquisition rate and biased behavior toward an action paired with optogenetic stimulation (i.e. enhanced performance optimality), while stimulation of indirect-pathway MSNs decreased task acquisition rate and increased non-rewarded actions [24]. Moreover, relative to one another, animals with indirect-pathway stimulation were less sensitive to action-outcome contingency degradation compared to animals with direct-pathway stimulation. These results suggest an action optimization role for direct pathway activity, and a distinct role for indirect pathway activity in diluting the representation of action-outcome contingencies. As both behavioral optimization and action-outcome insensitivity can be important features of an overall habit, these findings point toward the direct-pathway and indirect-pathway MSNs as potentially contributing distinct but complementary functions for habit formation. Indeed, there is evidence that both MSN populations can be engaged in tandem during optimized behaviors, particularly at the point of action initiation [25,26], further suggesting that both populations contribute meaningfully to habits. Intriguingly, there may be a

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