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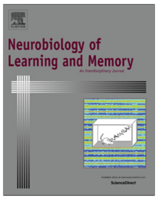

Review

Frontostriatal development and probabilistic reinforcement learning during adolescence

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ABSTRACT

Adolescence has traditionally been viewed as a period of vulnerability to increased risk-taking and adverse outcomes, which have been linked to neurobiological maturation of the frontostriatal reward system. However, growing research on the role of developmental changes in the adolescent frontostriatal system in facilitating learning will provide a more nuanced view of adolescence. In this review, we discuss the implications of existing research on this topic for learning during adolescence, and suggest that the very neural changes that render adolescents vulnerable to social pressure and risky decision making may also stand to play a role in scaffolding the ability to learn from rewards and from performance-related feedback.

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1. Introduction: Adolescence as a time for new learning

Adolescence is the transition from child-like dependence to independence– a period that begins with the onset of puberty and continues into the mid-20s. During childhood, parents provide offspring with basic needs such as food and shelter and help regulate their behavior. During adolescence, there is a developmental shift, whereby teens begin looking to the broader world and society to learn to make their own decisions and increasingly regulate their own behavior. Thus, exploration of new decision spaces becomes essential. It is imperative that adolescents are able to learn efficiently from their new experiences. In this review, our

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goal is to synthesize current literature on the neural correlates of learning during this crucial developmental window. We begin with a brief overview of learning circuitry in adults, followed by changes in this circuitry during adolescence, and finally, a review of the few neuroimaging studies that have made significant inroads in understanding adolescent learning mechanisms.

2. Adult learning

The majority of research on the neural correlates of learning has been conducted in adults. For brevity, we focus on probabilistic learning to draw parallels to the adolescent literature, most of which has focused on this type of learning.

2.1. Probabilistic learning

When navigating the environment, some cues or actions may be more beneficial than others. When a particular stimulus is associated with a desired outcome 100% of the time, a single instance may be all that is required for learning to take place, and all subsequent interactions serve to confirm that initial learning. However, the environment is not always so predictable, or deterministic. When foraging for food in the wild, for instance, an object that is associated with reward on one occasion may not be 100% reliably predictive of that same outcome. Still, that object will be associated with positive outcomes some of the time, and for that reason some objects will be worth repeatedly seeking out. Some facets of academic learning – category learning, skill learning, and statistical learning – often rely in part on accumulated experience with probabilistic contingencies. Learning about such probabilistic outcomes requires accumulated evidence, and such learning is known to depend upon motivational/reward circuitry in the brain.

2.2. Structure and function of component regions of the reinforcement learning network

In adults, a comprehensive body of research has identified the circuits underlying learning from the outcomes of choices (Fig. 1). During learning, stimuli in the environment become associated with rewarding outcomes, which are known to engage a network involving both cortical and subcortical structures (O'Doherty, 2016). These structures play distinct but intertwined roles in the affective and cognitive processing involved in learning from reinforcement. Haber and Behrens (2014) comprehensively reviewed connections among key cortical and subcortical components of the motivational/reward system. These include projections to the ventral striatum (VS) from the orbitofrontal cortex (OFC), ventromedial prefrontal cortex (vmPFC), and anterior cingulate cortex (ACC) - key regions for motivational control and adaptive behavior, which converge with additional inputs from amygdala, hippocampus, and midbrain. The OFC is important for the elicitation of experienced outcome values by stimuli in the environment, whereas the vmPFC plays a role in valuation of and choice between stimuli based on internal states, actively updating values in light of the motivational status of the organism. Activation in vmPFC reflects the "on-line" value system that is used to guide choice. Both the OFC and the vmPFC project to the dorsal ACC (dACC), which contributes to the selection of competing actions.

The VS receives converging projections from OFC, vmPFC, and dACC, allowing for the integration of multiple value signals (Haber & Behrens, 2014). These reward signals from VS feed broadly into the dopaminergic midbrain, which in turn modulates activity of the dorsal striatum, overall cortical functioning, amygdala, and hippocampus. Thus, dopaminergic activity that is guided by ventral striatal signaling stands to affect not just the selection of motor and cognitive actions, but also memory formation.

2.3. Rewards and feedback both engage striatum

Converging evidence from behavioral and cognitive neuroscience has revealed the striatum to be a critical component of the reinforcement learning system, which controls the selection of advantageous responses by updating associations between choices and their outcomes (e.g., O'Doherty, 2004). Adults exhibit increased activation in the striatum during anticipation and receipt of rewards and decreased activation following punishments (e.g., Delgado, Nystrom, Fissell, Noll, & Fiez, 2000). In adults, feedback about performance accuracy engages the striatum in an analogous manner to rewards and punishments, with positive feedback resulting in increased activation relative to negative feedback (e.g., Daniel & Pollmann, 2010; Satterthwaite et al., 2012; Tricomi, Delgado, McCandliss, McClelland, & Fiez, 2006).

2.4. Striatal functioning during learning

Prediction error refers to the discrepancy between an expected reward and actual outcome. Knowledge of these discrepancies is needed to learn about the probability that a particular cue or

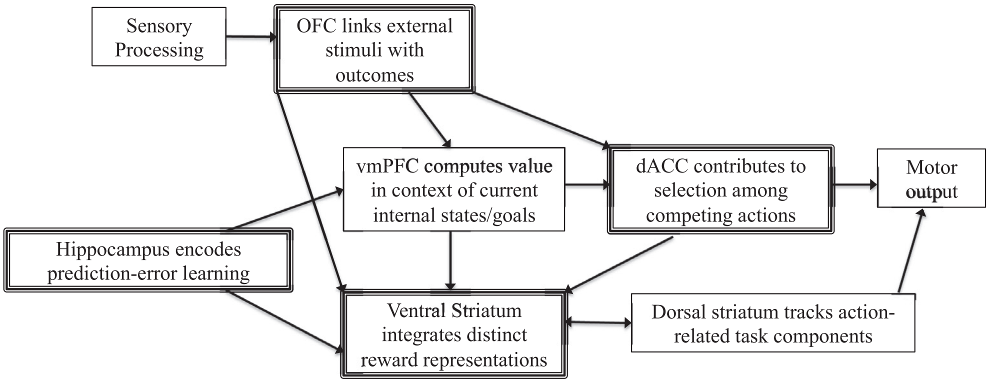

Fig. 1. Simplified overview of frontostriatal connections underlying reward-based learning. OFC receives input from sensory processing to form associations between stimuli and likely outcomes. vmPFC computes value in the context of the current state with input from OFC and projections to VS and dACC. Hippocampus encodes prediction-error learning and sends input to vmPFC and VS. Dorsal striatum tracks action-related task components and has reciprocal connections with VS. Dorsal ACC contributes to the selection of competing actions, with inputs that convey external incentive values (computed by OFC) and their relation to internal states and goals (vmPFC). VS receives input from all these regions, allowing it to integrate multiple types of value representations. Thicker boxes indicate regions that receive dense projections from midbrain dopamine structures. Based on review by Haber and Behrens (2014). For simplicity, not all projections and reciprocal connections are noted.