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Review

Learning robust cortico-cortical associations with the basal ganglia: An integrative review

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ABSTRACT

This article focuses on the interaction between the basal ganglia (BG) and prefrontal cortex (PFC). The BG are a group of nuclei at the base of the forebrain that are highly connected with cortex. A century of research suggests that the role of the BG is not exclusively motor, and that the BG also play an important role in learning and memory. In this review article, we argue that one important role of the BG is to train connections between posterior cortical areas and frontal cortical regions that are responsible for automatic behavior after extensive training. According to this view, one effect of BG trial-and-error learning is to activate the correct frontal areas shortly after posterior associative cortex activation, thus allowing for Hebbian learning of robust, fast, and efficient cortico-cortical processing. This hypothesized process is general, and the content of the learned associations depends on the specific areas involved (e.g., associations involving premotor areas would be more closely related to behavior than associations involving the PFC). We review experiments aimed at pinpointing the function of the BG and the frontal cortex and show that these results are consistent with the view that the BG is a general purpose trainer for cortico-cortical connections. We conclude with a discussion of some implications of the integrative framework and how this can help better understand the role of the BG in many different tasks.

1. Introduction

The basal ganglia (BG) are a group of nuclei at the base of the forebrain that are highly connected with cortex. Early on, the BG were assigned a role in motor functions, whereas cortex was assigned a more 'cognitive' role (e.g., Vogt, 1911; Wilson, 1912). However, a subsequent century of research suggests that the role of the BG is not exclusively motor, and that the BG also play an important role in learning and memory (Helie, Chakravarthy, & Moustafa, 2013; Packard & Knowlton, 2002). For example, Wise, Murray, and Gerfen (1996) have argued that 'rules' are represented in frontal cortex and that the BG are a context detector that are involved in changing the appropriate rule in cortex as a function of context – e.g., to

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disengage from the current behavior by switching to a new rule. In this review article, we argue that the role of the BG is not restricted to learning contexts using trial-and-error learning, but also to train connections between posterior cortical areas and frontal cortical regions that are responsible for automatic behavior after extensive training (Ashby, Ennis, & Spiering, 2007). According to this view, one effect of BG trial-and-error learning is to activate the correct frontal areas (e.g., rules or responses) shortly after posterior associative cortex activation (e.g., the context or stimulus), thus allowing for Hebbian learning of robust, fast, and efficient cortical–cortical processing. This hypothesized process is general, and the content of the learned associations depends on the specific areas involved (e.g., associations involving premotor areas would be more closely related to behavior than associations involving the prefrontal cortex; PFC).

In this article, we review experiments aimed at pinpointing the function of the BG and the frontal cortex and show that these results are consistent with the view that the BG is a general purpose trainer for cortico-cortical connections. The remainder of this article is organized as follows. First, we review relevant anatomy of the BG and frontal cortex. Next, we detail how the anatomy and connectivity of the BG and frontal cortex supports the learning of cortico-cortical associations. Following this presentation, we review and re-interpret data collected with the goal of elucidating the conditions under which the BG can be used to train cortico-cortical connections. This presentation is followed by possible alternative accounts of the data, including the view that automaticity is characterized by a progressive transfer between anterior and posterior striatum. We conclude with a discussion of the theoretical impact of this integrative role of the BG and frontal cortex and propose future experiments that would provide a direct test of the new integrative framework.

2. Anatomy

2.1. Frontal cortex

2.1.1. PFC

The PFC is a central hub in the brain that is connected to all other cortical areas except for the primary sensory areas and the primary motor area (Miller & Cohen, 2001). While there are many ways to identify the PFC, in this article we define the PFC as the cortical region receiving afferent connections from the medial dorsal nucleus (MDN) of the thalamus (Fuster, 2008). A schematic of the frontal cortex, and its subdivisions, is shown in Fig. 1.

The PFC is typically separated into lateral PFC (Brodmann areas 8, 9, 10, 44, 45, and 46), medial PFC (areas 8m, 9m, 10m, 11m, and 12), and orbitofrontal PFC (areas 10, 11, and 47). The principal neurons in the PFC are pyramidal neurons and stellate neurons. The pyramidal neurons are excitatory (glutamatergic) whereas the stellate cells are inhibitory (GABAergic) interneurons. The pyramidal neurons are connected with other PFC neurons, but also with neurons in other brain regions (e.g., MDN of the thalamus, associative sensory areas). In contrast, the stellate neurons mostly synapse within the PFC. Note that most subdivisions of the PFC are heavily interconnected. Hence, the PFC as a whole can be considered as a single, unified brain area. The separation is mostly functional and based on connectivity with other brain areas (although cytoarchitectonic differences are also present).

2.1.2. Premotor areas (area 6)

The premotor areas (area 6) are caudally adjacent to area 4 (primary motor cortex) and rostrally adjacent to areas 8, 9, and 44 of the PFC. The cytoarchitecture of area 6 allows for the identification of at least three different structures (Barbas & Pandya, 1987). First, area 6 can be divided into a ventral and a dorsal area. The ventral premotor area (PMv) has an emergent layer IV that separates layers III and V, whereas layers III and V merge to form a prominent central band in the dorsal premotor areas. In addition, the pyramidal neurons in the dorsal areas are generally smaller than in the PMv, and the myelin content is less dense. These architectonic features suggest that the dorsal premotor areas are more similar to motor cortex, whereas PMv is more closely related to sensory cortex (Barbas & Pandya, 1987).

The dorsal premotor areas can be further subdivided into a lateral and a medial part. The medial part is called the supplementary motor area (SMA) and contains prominent medium-size pyramidal neurons in layers III and V that are more compact and darkly stained when compared with the lateral part of dorsal premotor area (PMd). In addition, the SMA is often split into a rostral and a caudal region using the vertical commissure anterior (VCA) (Nachev, Kennard, & Husain, 2008). The portion of SMA caudal to the VCA is simply called the SMA and produces movement when a current is

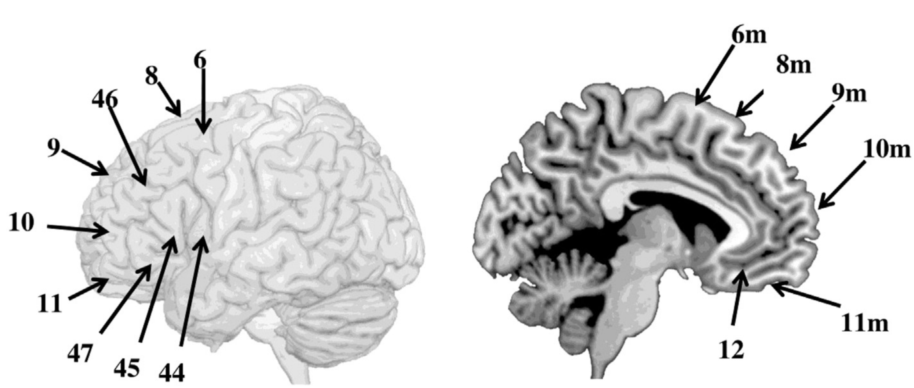

Fig. 1 – Subdivisions of frontal cortex. Numbers refer to Brodmann areas.