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Review

The lateral prefrontal cortex and complex value-based learning and decision making

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A B S T R A C T

Tremendous progress has been made in discerning the neurocognitive basis of value-based decision making and learning. Although the majority of studies to date have employed simple task paradigms, recent work has started to examine more complex aspects of value processing including: the value of engaging rule-based cognitive control; the integration of multiple pieces of information (e.g., reward magnitude and delay) to discern the best course of action; pursuing future rewards; valuation of abstract concepts (e.g., fairness); and comparing the value of executed versus imagined alternative actions. We provide a comprehensive review of functional neuroimaging, electrophysiological, and lesion evidence suggesting that the lateral prefrontal cortex (LPFC) plays a critical role in these complex aspects of value processing. In particular, we focus on the specific information that the LPFC represents, and argue that it includes both cognitive and value-based information. We also discuss how the role of the LPFC is distinct from other value-related regions. Finally, we articulate a framework for understanding the contribution of subregions along the rostro-caudal axis of the LPFC, and thereby bridge the cognitive control and decision making literatures.

Contents

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1. Introduction

In the last decade, there has been an explosion of interest in the neurocognitive basis of value-based learning and decision making. Considerable work has examined the neurocognitive mechanisms underlying the capacity to represent and update the expected value of outcomes predicted by stimuli (Gottfried et al., 2003; O'Doherty et al., 2004; Pessiglione et al., 2006; Plassmann et al., 2010; Rangel et al., 2008), the distinction between habitual (model-free) versus goal-directed (model-based) learning (Balleine and O'Doherty, 2010; Daw et al., 2005; Hampton et al., 2006; McDannald et al., 2012; Rangel et al., 2008), and the extent to which there is convergence in value-based mechanisms across species (Balleine and O'Doherty, 2010; Wallis, 2012). Additionally, this work has identified a core network of regions involved in value-based processes including the ventromedial prefrontal cortex (VMPFC), orbitofrontal cortex (OFC), ventral striatum, insula, amygdala, and several sub-regions of the cingulate cortex (Behrens et al., 2007; Gottfried et al., 2003; Kable and Glimcher, 2007; Knutson and Greer, 2008; O'Doherty et al., 2004; Plassmann et al., 2010; Preuschoff et al., 2008; Rangel et al., 2008; Rushworth et al., 2011).

Increasingly, studies have begun to examine more complex aspects of value-based processes; there is a growing appreciation that in many real world situations, optimal outcomes can only be obtained by instantiating complex cognitive operations. These studies have examined: (1) the reward-value of engaging cognitive control mechanisms (e.g., the use of explicit rules for action); (2) the integration of multiple pieces of information (e.g., reward magnitude and delay) to discern the best course of action; (3) pursuing future rewards instead of immediate gratification; (4) valuation of abstract concepts (e.g., fairness); and (5) comparing the value of executed actions and imagined alternative actions. A consistent finding across these studies is the prominent involvement of the lateral prefrontal cortex (LPFC).

The traditional perspective is that the LPFC is a "cognitive" region that does not directly represent value-based information. Based on this perspective, a reasonable argument for why the LPFC is activated during complex valuation tasks is that it supports the cognitive element of the tasks, and that the core valuation regions noted above represent the specific value-related elements. Indeed, many of these studies suggest that the LPFC supports the cognitive control (or top-down regulation) of processing occurring in other value-related brain regions (e.g., Hare et al., 2009). However, we argue that a strict "cognitive" account cannot fully explain the involvement of the LPFC, especially when considering the LPFC from a representational perspective. Specifically, we propose that the data is most consistent with the idea that the *LPFC represents both cognitive and value-based information*. For example, the LPFC may represent associations between task-rules and predicted motivational outcomes, and thereby provide an overarching context that influences more basic value processing and action selection in other regions. This idea builds upon traditional theories linking the LPFC to cognitive control (Miller and Cohen, 2001), as well as several excellent reviews of electrophysiological work demonstrating that the LPFC represents both cognitive and reward-related information (Seo and Lee, 2008; Watanabe and Sakagami, 2007). Additionally, recent human neuroimaging work is also starting to recognize that the LPFC may directly represent value information (Hutcherson et al., 2012; McClure et al., 2004; Plassmann et al., 2010; Tobler et al., 2009).

In this paper, we provide a comprehensive review of electrophysiological, functional magnetic resonance imaging (fMRI), and lesion studies demonstrating that the LPFC plays a fundamental role in complex value-based learning and decision making. We first review the anatomical connections of the LPFC to provide context for understanding its role in valuation. We then review evidence suggesting that the LPFC represents specific reward and punishment outcomes, even during simple tasks with minimal cognitive demands. We then review the role of the LPFC and the information it represents in more complex valuation tasks. Furthermore, we describe how the role of the LPFC differs from other value-related brain regions. Finally, we articulate a preliminary framework for understanding the distinct contribution of subregions situated along the rostro-caudal axis of the LPFC to value-based learning and decision making, and thereby attempt to bridge findings from the decision making and cognitive control literatures.

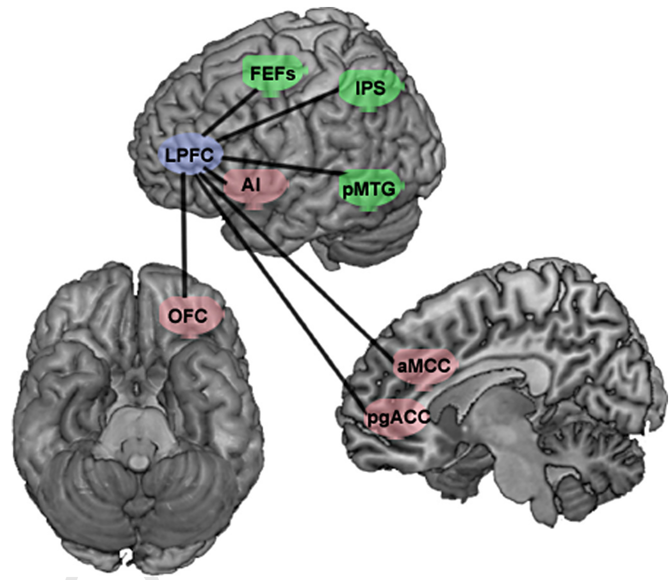

Fig. 1. Schematic Illustration of the anatomical connections of the LPFC. Connections with "cognitive" regions highlighted in green include the frontal eye fields (FEFs), intraparietal sulcus (IPS), and posterior middle temporal gyrus (pMTG). Connections with "motivation" regions highlighted in red include the pregenual anterior cingulate cortex (pgACC), anterior insula (AI), orbitofrontal cortex (OFC) and anterior mid-cingulate cortex (aMCC).

2. Anatomical context for understanding the LPFC in value processing

Fig. 1 provides a schematic illustration of key anatomical connections of the LPFC. The LPFC's anatomical connections with other "cognitive" regions (e.g., lateral temporal, parietal, and premotor cortices) are often emphasized. However, the LPFC also has robust reciprocal connections with key motivation-related regions of the brain. We provide a general overview of these connections based on monkey tracing studies, acknowledging that connections differ to some extent for the ventral and dorsal LPFC, and for the architectonic subdivisions within each of these areas. The LPFC receives strong input from the OFC, especially rostral area 11 (Petrides and Pandya, 1999, 2002, 2007). This pathway may supply the LPFC with information about object-outcome associations (Gottfried et al., 2003; Wallis and Miller, 2003; Walton et al., 2010). The LPFC (especially the mid-dorsolateral prefrontal cortex; mid-DLPFC) is robustly interconnected with area 32 of the pregenual anterior cingulate cortex (Pandya et al., 1981; Petrides and Pandya, 1999, 2002, 2007), a region that plays a role in subjective emotional feeling states including happiness and embarrassment (Amemori and Graybiel, 2012; Damasio et al., 2000; Lane et al., 1997; Sturm et al., 2012). The LPFC is also well connected with the anterior mid-cingulate cortex (aMCC; often referred to as the dorsal ACC) (Pandya et al., 1981; Petrides and Pandya, 1999, 2002), a region that represents the value of actions based on the amount of required effort

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