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Discussion forum

Parts to principles: Anatomical origins of prefrontal organization

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1. Introduction

In "The Organisation of the Mind," Shallice and Cooper (2011; henceforth S&C) identify "isolable cognitive subsystems" of higher-level cognition that are definable computationally, dissociable neuroanatomically, and functionally important for domains as diverse as semantic and episodic memory, working memory maintenance and manipulation, reasoning and planning, and supervisory processes and consciousness. Hence, the book provides an integrative view of the neurocognitive underpinnings of higher-level cognition, as gleaned from the cognitive neuroscience approach.

The isolable subsystems in PFC identified by S&C undoubtedly reflect differences in its intrinsic and extrinsic cortico-cortical connectivity (e.g., Yeterian et al., 2012). However, as discussed below, the focal loops that interlink PFC with striatum (e.g., Middleton and Strick, 2002) are central to PFC function. Thus, the anatomical organization of these loops is also a key determinant of the functional organization of PFC subsystems.

2. Policy abstraction and dorsal PFC

As reviewed by S&C, abundant neuroimaging and neuropsychological data indicate that increasingly rostral subregions of the dorsal PFC are recruited when task demands become more abstract (e.g., Koechlin et al., 2003; Badre and D'Esposito, 2007; S&C p. 350–360). Although controversy surrounds the precise definition of abstraction (S&C, p. 358), one framework for understanding these effects invokes the concept of policy abstraction (Badre et al., 2010; Badre and Frank, 2012; Frank and Badre, 2012).

By this view, rostral areas of dorsal PFC represent abstract state-to-action mappings – i.e., policies – specifying optimal *collections* of actions given a state or context (e.g., on Monday morning [state], make coffee [action]; Fig. 1A). Caudal areas of dorsal PFC represent concrete state-to-action mappings selecting specific actions (e.g., when using the French press, grind coffee beans coarsely). This hierarchical decomposition of large state-to-action mapping problems improves learning (fewer actions/action classes are considered in solving subproblems) and generalization (subproblem solutions can be reused independently) (Botvinick, 2008).

Policy abstraction may emerge from dynamics in a series of nested, topographically-organized frontostriatal loops. Such loops are a hypothesized mechanism for selective updating of working memory: the basal ganglia "gate" task-relevant information into PFC-based working memory and keep irrelevant information out (e.g., O'Reilly and Frank, 2006). Thus, for a concrete policy where color but not shape of a stimulus determines the correct keypress, this loop would gate color (but not shape) information into working memory to select a response. Nesting these loops can allow for abstract policy: information maintained in rostral PFC can influence gating in more caudal frontostriatal loops (e.g., when shape, as maintained in rostral PFC, determines whether color or orientation is gated into the more caudal response-selection loop). Thus, the observed rostrocaudal gradient in PFC could be an emergent property of nested frontostriatal loops.

Indeed, simulations of these frontostriatal loops predict behavioral and neuroimaging results from hierarchical tasks (Badre and Frank, 2012), and hierarchical nesting in these loops accelerates learning (Frank and Badre, 2012). Moreover, high-definition diffusion spectrum tractography has provided initial evidence for this nested anatomical pattern in

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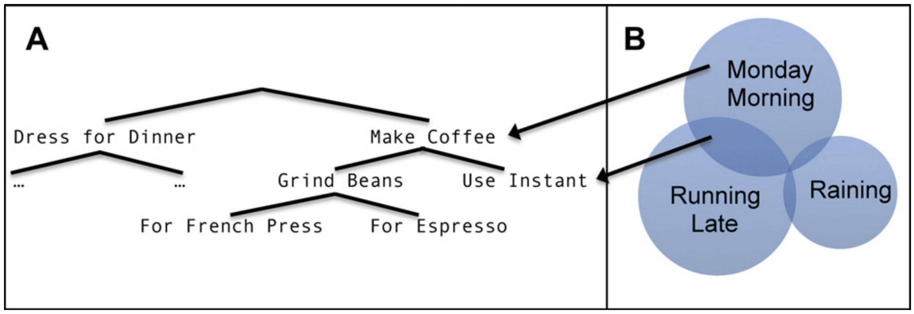

Fig. 1 – The coffee-making example of policy abstraction (A) and its interaction with state abstraction (B).

frontostriatal connectivity (Verstynen et al., 2012). Thus, the isolable nature of dorsal PFC subsystems may emerge from their hierarchical interactions with highly-topographic striatal circuits (Middleton and Strick, 2002).

But what about the ventrolateral prefrontal cortex, where rostrocaudal gradients are less commonly observed (e.g., S&C, p. 358)?

3. State abstraction and ventral PFC

In contrast to the highly-topographic striatal pathway innervated by dorsal PFC (involving the internal globus pallidus; GPi), the pathway innervated by ventral PFC (involving the substantia nigra reticulata; SNr; Kitano et al., 1998; Middleton and Strick, 2002) is far less topographic. These two pathways may also differ functionally, with the GPi-mediated pathway being more central to action-side processing, and the SNr pathway more involved in sensory-side processing (e.g., SNr's unique projections to inferotemporal cortex and sensory hallucinations arising from SNr lesions; Middleton and Strick, 2000). This implies that a more integrative and sensory-related ventral subsystem operates alongside a more segmented, hierarchical, and action-related dorsal subsystem.

Why might the brain complement a rostrocaudally-segmented policy abstraction hierarchy in dorsal PFC with a more integrative ventral system? Learning is enhanced not only by nesting actions into more abstract action classes (i.e., through policy abstraction), but also by collapsing across irrelevant distinctions in contextual state, so that only relevant features of the state are considered. For example, instant coffee may be preferable when running late; this feature of the state (i.e., timeliness) should be preferentially selected among less-relevant contextual features (e.g., the weather; Fig. 1B) in setting the appropriate task. Similarly, many categorization problems involve learning about classes of inputs that can be similarly acted upon. Such "state abstraction" also requires the highly integrative monitoring of context and transitions, so that non-identical contexts can be treated equivalently only as long as that is itself contextually appropriate (Botvinick, 2008; Gureckis and Love, 2010).

A ventral PFC subsystem for state abstraction seems consistent with much neuropsychological data (e.g., the mnemonic selection functions ascribed to this region [S&C, p. 375–8], as well as the ventral PFC foci of the state-related "monitoring" and "task-setting" functions [S&C, p. 367–8]). Neuroimaging offers additional support: activity in ventral PFC does not differentiate irrelevant distinctions between stimuli of the same abstract class, unlike dorsal PFC (Hon et al., 2012). Multivariate patterns in ventral PFC are so abstract as to be highly similar across fully distinct actions (e.g., response commission and response inhibition; Chatham et al., 2012) as though this area is tasked with identifying, selecting, or monitoring states themselves, largely independent of their precise mappings to action.

4. Conclusions

PFC subsystems may reflect in part their dissociable patterns of frontostriatal connectivity. Dorsal PFC participates in a set of GPi-mediated corticostriatal loops that preserve rostrocaudal topography and give rise to policy abstraction, operating alongside a more integrative SNr-mediated ventrofronto-striatal circuit for state abstraction. This framework provides a computationally-, neuropsychologically-, and neuroanatomically-grounded basis for identifying isolable subsystems in higher-level cognition.

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