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Research Report

Evidence for rostro-caudal functional organization in multiple brain areas related to goal-directed behavior

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ABSTRACT

The functional organization of brain areas supporting goal-directed behavior is debated. Some accounts suggest a rostro-caudal organization, while others suggest a broad recruitment as part of a multiple demand network. We used fMRI and an anatomical region of interest (ROI) approach to test which account better characterizes the organization of key brain areas related to goal-directed behavior: the lateral prefrontal cortex (LPFC), medial prefrontal cortex (MPFC), cingulate cortex, and insula. Subjects performed a cognitive control task with distinct trial events corresponding to rule representation, rule maintenance, action execution, and monitoring progress towards an overarching motivational goal. The use of ROIs allowed us to look for evidence of rostro-caudal gradients during each event separately. Our results provide strong evidence for rostro-caudal gradients in all regions. During the action execution period, activation was robust in caudal ROIs and decreased linearly moving to rostral ROIs in the LPFC, cingulate cortex, and MPFC. Conversely, during the goal monitoring period, activation was weak in caudal ROIs and increased linearly moving to the rostral ROIs in the aforementioned regions. The insula exhibited the reverse pattern. These findings provide evidence for rostro-caudal organization in multiple regions within the same study. More importantly, they demonstrate that rostro-caudal gradients can be observed during individual trial events, ruling out confounding factors such as task difficulty.

1. Introduction

Goal-directed behavior involves the representation of a motivational goal (i.e., a desired outcome), forming rules for guiding actions, physical execution of those actions, and monitoring feedback indicating progress towards the motivational goal. The neural network underlying these processes includes the lateral prefrontal cortex (LPFC), insula, cingulate cortex, and medial prefrontal cortex (MPFC), among other regions (Badre and D'Esposito, 2007; Bunge et al., 2003; Cole and Schneider, 2007; Dixon and Christoff, 2012, 2014; Dosenbach et al., 2006; Duncan, 2010; Koechlin et al., 2003; Kouneiher et al., 2009; Rushworth et al., 2007). A fundamental goal for cognitive neuroscience is understanding the precise functional organization of these

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regions. Two prominent theories have been put forth, providing two contrasting perspectives.

The rostro-caudal organization theory suggests that rostral parts of a given area support different (usually more complex) functions than caudal parts. For example, evidence suggests that the caudal LPFC supports simple concrete rules for action, whereas rostral LPFC supports more abstract rules and goals (Badre, 2008; Badre and D'Esposito, 2007, 2009; Christoff and Gabrieli, 2000; Christoff and Keramatian, 2007; Christoff et al., 2009; Eiselt and Nieder, 2013; Koechlin et al., 2003; Kouneiher et al., 2009; Petrides, 2005; Race et al., 2009). One model of dorsal cingulate/MPFC functional organization (Venkatrama et al., 2009) suggests that caudal areas regulate action execution, whereas rostral areas support high-level decision making and strategic processes (for an alternate model see Kouneiher et al., 2009). Finally, the posterior insula has been implicated in sensory-motor and interoceptive processes (e.g., viscero-somatic sensations related to heartbeat and respiration), whereas the anterior insula may integrate this viscero-somatic information with higher-order cognitive information during goal-directed action (Craig, 2002; Critchley et al., 2004; Dosenbach et al., 2006; Farb et al., 2013; Menon and Uddin, 2010; Singer et al., 2004).

An alternative theory suggests that brain areas related to goal-directed behavior are broadly recruited as part of a 'multiple demand' network to support current task demands (Crittenden and Duncan, 2014 Duncan, 2010; Farooqui et al., 2012). According to this theory, task relevant information is represented by a distributed pattern of activity in each of these brain areas, and does not conform to a rostro-caudal gradient. Evidence for this theory includes the finding that simple task difficulty manipulations can result in widespread increases in multiple demand network activation (Crittenden and Duncan, 2014). Reynolds and colleagues have also provided evidence that the LPFC is not organized along a rostro-caudal axis, but rather, is sensitive to temporal dynamics, exhibiting either transient or sustained activation depending on task demands (Reynolds et al., 2012).

The present study used functional magnetic resonance imaging (fMRI) to test which theoretical account better characterizes the functional organization of the LPFC, insula, cingulate cortex, and MPFC. We examined activation patterns during a cognitive control task composed of several distinct trial events relevant to goal-directed behavior: (1) rule representation; (2) rule maintenance; (3) action execution; and (4) monitoring progress towards an overarching motivational goal (earning $60 by the end of the experiment) (see Fig. 1 and Section 4).

Our study expands upon prior work in several important ways. First, prior studies have typically used different task conditions to look for rostro-caudal organization (e.g., low versus high complexity rule demands). However, one limitation of this approach is that the conditions often differ in difficulty, complicating the interpretation of observed differences in activation between rostral and caudal regions. To avoid this problem, we used *a priori* defined regions of interest (ROIs) (see Fig. 2 and Table 1), and compared activation levels in rostral and caudal ROIs during the *identical* trial event (e.g., during action execution). This allows for a straightforward interpretation of results: if rostral and caudal regions have different functions, then they should respond differently to the identical event. Additionally, prior studies have often examined the LPFC as a whole, whereas we partitioned the LPFC into its constituent gyri (inferior, middle, and superior) and examined each as a separate rostro-caudal stream. This may provide more insight into the specific functional organization of the LPFC, which is pertinent given a recent study showing that the ventral and dorsal LPFC exhibit separate (parallel) rostro-caudal patterns of functional connectivity with the cingulate cortex/MPFC (Blumenfeld et al., 2012). Furthermore, the ROI approach allowed us to examine rostro-caudal organization during several distinct trial events in a theoretically agnostic manner, thereby revealing the component of goal-directed behavior to which each brain area is most sensitive.

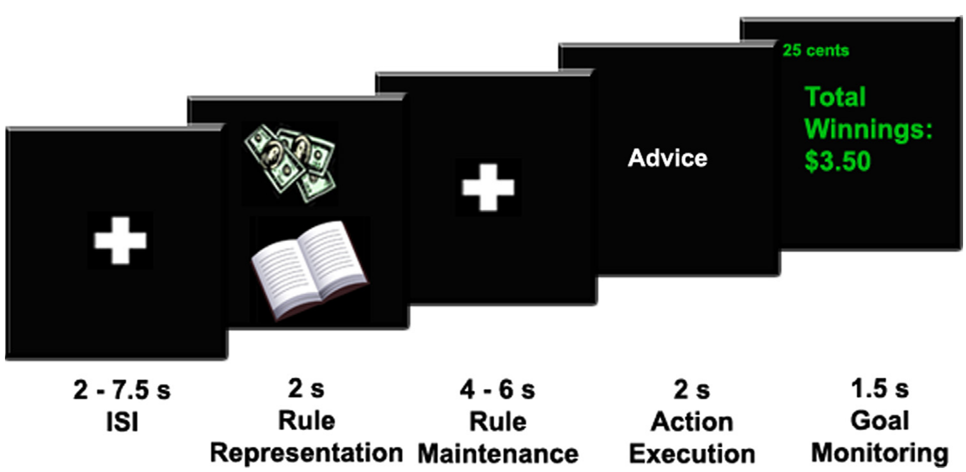

Fig. 1 – Illustration of the trial events. After a variable duration fixation cross, there was a 'rule representation' period during which an instruction cue signaled the currently relevant rules (e.g., book=abstract/concrete rule) and whether or not to expect a monetary reward (e.g., bills=25¢). This was followed by a variable duration delay period ('rule maintenance'). Then a word or face stimulus appeared, and participants made a button response ('action execution'). Finally, a screen revealed whether money had been earned on that trial and cumulative winnings; participants were told to focus on their progress towards the overarching motivational goal of earning the maximum amount of money possible, which was $60 ('goal monitoring').