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It's a matter of time: Reframing the development of cognitive control as a modification of the brain's temporal dynamics

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ABSTRACT

Cognitive control is a process that unfolds over time and regulates thought and action in the service of achieving goals and managing unanticipated challenges. Prevailing accounts attribute the protracted development of this mental process to incremental changes in the functional organization of a cognitive control network. Here, we challenge the notion that cognitive control is linked to a topologically static network, and argue that the capacity to manage unanticipated challenges and its development should instead be characterized in terms of inter-regional functional coupling dynamics. Ongoing changes in temporal coupling have long represented a fundamental pillar in both empirical and theoretical-based accounts of brain function, but have been largely ignored by traditional neuroimaging methods that assume a fixed functional architecture. There is, however, a growing recognition of the importance of temporal coupling dynamics for brain function, and this has led to rapid innovations in analytic methods. Results in this new frontier of neuroimaging suggest that time-varying changes in connectivity strength and direction exist at the large scale and further, that network patterns, like cognitive control process themselves, are transient and dynamic.

1. Introduction

Cognitive control – the capacity to consciously adapt thought and action in the face of unanticipated challenge – follows a protracted developmental trajectory (Diamond, 2013). Like many developing intellectual skills, cognitive control is a robust longitudinal predictor of intellectual, social, and health-related outcomes (Moffitt et al., 2011). What makes cognitive control unique among intellectual skills is that it deals with exceptions – computational challenges for which there are no single, ready-made solutions. Almost by definition then, the development of cognitive control must be linked to an emerging ability to flexibly explore alternative configurations of a problem space. A prominent view, built on theoretical and empirical foundations (Johnson, 2001), links the development of cognitive control to age-related changes within a distributed set of linked cortical and subcortical regions collectively referred to as the cognitive control network (CCN) (Cole and Schneider, 2007; Dwyer et al., 2014; Fair et al., 2007). But what is occurring across the CCN to enable cognitive flexibility and what changes in the brain, either functional or structural, are linked to the development of cognitive control?

The present perspective argues that cognitive control should not be reduced to a fixed topology that is incrementally optimized over development. Instead, we suggest that cognitive control can be reframed as an ongoing and dynamic interplay of distributed regions (including those outside the traditional CCN) whose temporal features, ("chronnectome"; Calhoun et al., 2014) are modified as a function of age. We first introduce the CCN and its study in relation to development – empirical investigations dominated by functional magnetic resonance imaging (fMRI) approaches. We argue that although previous studies provide unprecedented insight into developmental changes in brain organization, they do not adequately capture brain activity that unfolds at the shorter timescales in which cognitive control is actually realized. Dynamic approaches that consider time-varying changes in functional connectivity (FC) and initial explorations using this framework are then discussed before outlining questions that deserve continued exploration.

2. The cognitive control network over development

2.1. Cognitive control network defined

The CCN can be defined as a structurally and functionally distinct set of cortical and subcortical brain regions that is linked to

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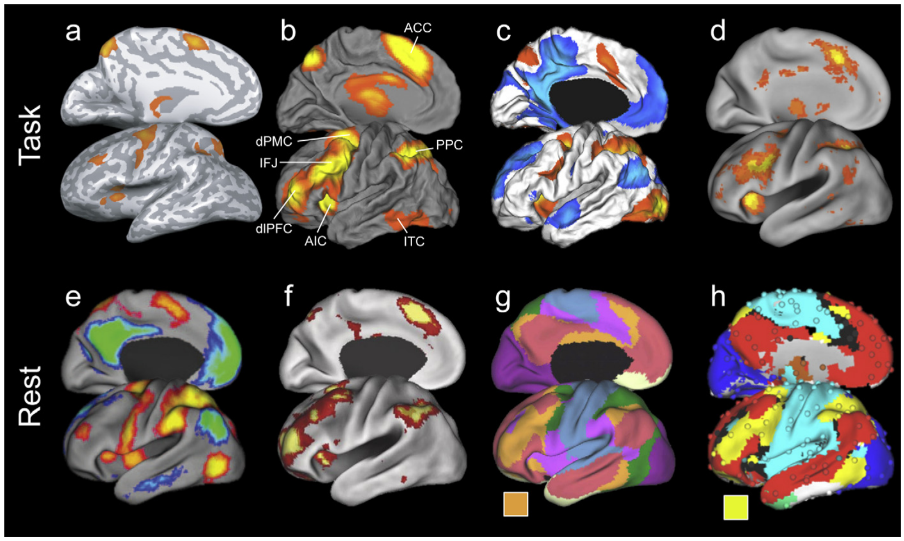

Fig. 1. Maps of the cognitive control network derived using rest (top row) and task-based (bottom row) functional imaging approaches. Images are taken from Cole and Schneider (2007) (a), Satterthwaite et al. (2013) (b), Dwyer et al. (2014) (red–yellow, c), a forward inference meta-analysis using the using the Neurosynth platform (www.neurosynth.org) with a search term 'cognitive control' (d), Fox et al. (2005) (red–yellow, e), Vincent et al. (2008) (f), Yeo et al. (2011) (orange, g), Power et al. (2011) (yellow, h). Abbrev.: ACC, anterior cingulate cortex; AIC, anterior insular cortex; dlPFC, dorsal lateral prefrontal cortex; dPMC, dorsal premotor cortex; IFG, inferior frontal junction; ITC, infero-temporal cortex; PPC, posterior parietal cortex.

the capacity for exerting control (for similar definition, see Cole and Schneider, 2007), where the term "network" indicates a collection of items with pairwise temporal relationships (for discussion, see Power et al., 2010). Constituent regions include selected parts of frontal (dorsolateral prefrontal, inferior frontal junction, dorsal premotor), insular (anterior insula), cingulate (anterior cingulate cortex), temporal (infero-temporal cortex), and parietal (posterior parietal cortex) cortex (see Fig. 1), as well as thalamic nuclei and the basal ganglia. While convergent with what Fox et al. refer to as the task-positive network (Fox et al., 2005), this definition is admittedly broad, and encompasses what is likely a family of cognitive control networks. Indeed several whole-brain parcellation schemes subdivide the CCN (Cole and Schneider, 2007) or task-positive network (Fox et al., 2005) into a number of structurally and functionally distinct subnetworks, variously termed: (1) fronto-parietal, dorsal attention, and ventral attention networks (see Yeo et al., 2011; 7-network parcellation); (2) fronto-parietal task control, dorsal attention, and ventral attention networks (see Power et al., 2011; graph-based parcellation); (3) cingulo-opercular task-set maintenance and fronto-parietal moment-to-moment adjustment networks (Dosenbach et al., 2007); (4) executive control and dorsal visual stream components (Beckmann et al., 2005); and (5) salience and executive control networks (Seeley et al., 2007). While acknowledging the importance of subdividing the CCN, points of contrast between static and dynamics approaches to FC that will be made in this discussion remain true whether the CCN is defined broadly or as a family of subnetworks. Therefore, in the interest of economy, we will use the term CCN to refer to this distributed set of regions.

2.2. The CCN and its development

Questions concerning its precise demarcation notwithstanding, there is a general consensus that the CCN is a stable feature of the human connectome, important for cognitive control, and subject to developmental change. These ideas rest largely on three related lines of evidence: (1) task-based fMRI activation studies; (2) resting-state fMRI (rsfMRI) FC studies of intra-network connectivity; and (3) task-based and rsfMRI studies of inter-network connectivity, especially those focused on interactions between the CCN and the default network (DN).

2.2.1. CCN: evidence from task-based activation studies

Task-based fMRI activation studies provide consistent evidence that almost all regions of the CCN are more active when demands on cognitive control are high as compared to when they are low (Fig. 1, top row). How these profiles of activity change with age is less clear (for review, see Crone and Dahl, 2012). Some studies report age-related increases in activity, consistent with the idea that children engage cognitive control processes more robustly as they develop, whereas other studies demonstrate age-related decreases in activation, suggesting, perhaps, that the CCN functions more efficiently over time. Firm conclusions concerning the importance of age must, however, be drawn with caution in light of age-correlated differences in task performance. Indeed, inter-individual variability in task performance controlled for age is a much more robust predictor of CCN activity than age controlled for differences in performance (Satterthwaite et al., 2013). These issues notwithstanding, regions comprising the CCN readily show correlated increases in activity as demands in cognitive control increase.

2.2.2. CCN: evidence from rsfMRI studies of intra-network connectivity

A persuasive source of evidence concerning the existence of the CCN comes rsFC analysis (e.g., Vincent et al., 2008; Yeo et al., 2011; Power et al., 2011; Spreng et al., 2013). The method is based on the finding that regions that co-activate in association with task administration also exhibit correlated intrinsic BOLD activity in the absence of an explicit task (Biswal et al., 1995; for review see Fox and Raichle, 2007). In early work examining the CCN with a rsfMRI approach, Fox et al. (2005) extracted spontaneous BOLD time courses from three regions, the intra-parietal sulcus, the frontal eye fields, and the middle temporal region and correlated these with time courses from every other voxel encompassing the brain (a seed-based approach). The resulting map showed a set of regions whose time courses correlated positively with each of the seed-regions and was highly convergent with maps of the CCN generated using task-based techniques (Fig. 1e). This has since been