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Network mechanisms of intentional learning

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ABSTRACT

The ability to learn new tasks rapidly is a prominent characteristic of human behaviour. This ability relies on flexible cognitive systems that adapt in order to encode temporary programs for processing non-automated tasks. Previous functional imaging studies have revealed distinct roles for the lateral frontal cortices (LFCs) and the ventral striatum in intentional learning processes. However, the human LFCs are complex; they house multiple distinct sub-regions, each of which co-activates with a different functional network. It remains unclear how these LFC networks differ in their functions and how they coordinate with each other, and the ventral striatum, to support intentional learning. Here, we apply a suite of fMRI connectivity methods to determine how LFC networks activate and interact at different stages of two novel tasks, in which arbitrary stimulus-response rules are learnt either from explicit instruction or by trial-and-error. We report that the networks activate *en masse* and in synchrony when novel rules are being learnt from instruction. However, these networks are not homogeneous in their functions; instead, the directed connectivities between them vary asymmetrically across the learning timecourse and they disengage from the task sequentially along a rostro-caudal axis. Furthermore, when negative feedback indicates the need to switch to alternative stimulus–response rules, there is additional input to the LFC networks from the ventral striatum. These results support the hypotheses that LFC networks interact as a hierarchical system during intentional learning and that signals from the ventral striatum have a driving influence on this system when the internal program for processing the task is updated.

Introduction

Humans have a remarkable ability to learn new tasks rapidly. We often perform them near flawlessly based on instruction, observation, mental simulation, or the outcomes of individual attempts. These intentional forms of learning involve flexible cognitive systems, which rapidly adapt to encode temporary programs for processing non-automated tasks in a controlled manner.

There is a wealth of evidence for the role of the lateral frontal cortex (LFC) in coding for these temporary programs (Duncan, 2001). For example, at the resolution of multi-unit electrophysiology, populations of neurons within the primate LFCs represent task-relevant information, including the stimuli, responses, and rules that constitute the task (Freedman et al., 2001; Miller and Cohen, 2001). They can adapt rapidly, switching from representing one aspect of a task to another in a fraction of a second (Stokes et al., 2013). At the regional-anatomical scale, neuropsychological research has shown that frontal lobe damage leads to cognitive inflexibility; that is, the inability to learn new behaviours or to override those that are habitual (Gaffan and Harrison, 1988; Halsband and Freund, 1990; Halsband and Passingham, 1982; Petrides, 1985, 1990, 1997). Furthermore, functional magnetic resonance imaging (fMRI) has demonstrated that the human LFCs are strongly activated during a variety of tasks that require the intentional control of thoughts and actions (Duncan and Owen, 2000; Fedorenko et al., 2013) including when tasks are being performed based on instructed rules (Rowe et al., 2007; Zhang et al., 2013). Most relevantly, when simple cognitive tasks are being performed in the scanner, the LFCs respond more at the beginning of the experiment, when stimulus–response rules are novel (Fig. 1), with little or no response towards the end, when they are routine (Boettiger and D'Esposito, 2005; Erika-Florence et al., 2014; Toni and Passingham, 1999; Toni et al., 2001).

Although it is well established that the LFCs are involved in intentional learning, the mechanisms by which they interact and adapt are not yet fully understood. This is in part because the functional organisation of the human LFCs is often conceptually simplified to enable

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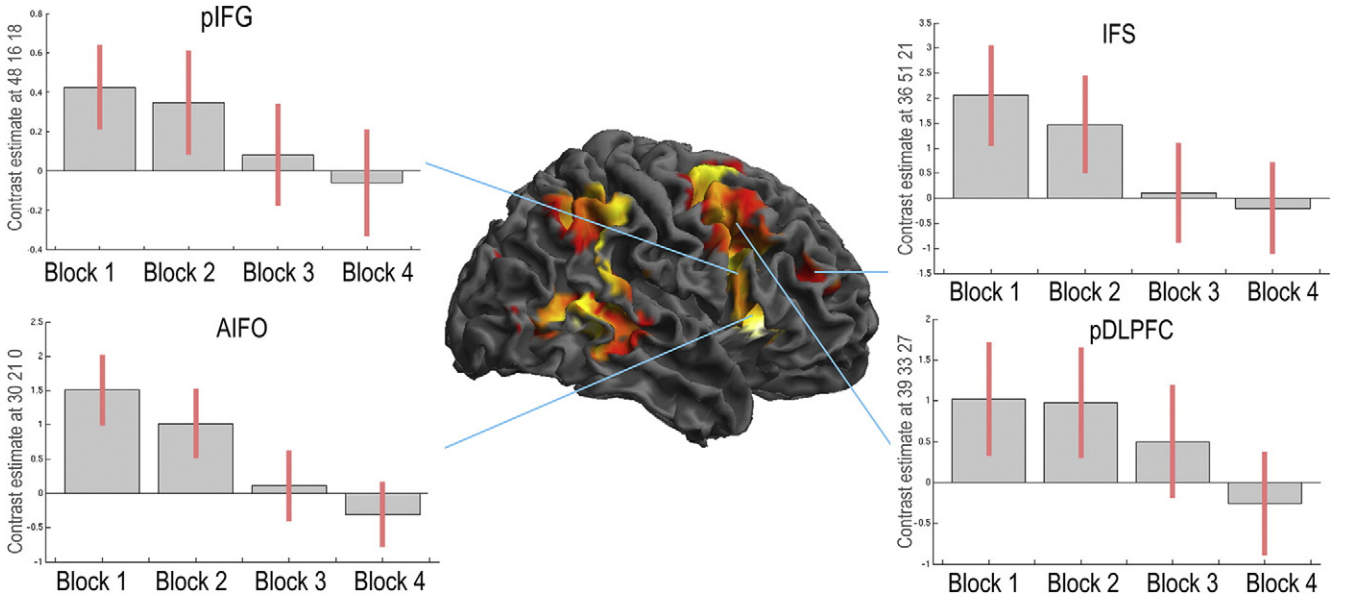

Fig. 1. Paradigms that are used to probe LFC function often treat learning effects as nuisance variables. This can lead to overly static interpretations of LFC function. For example, one prominent hypothesis states that a sub-region of the right inferior frontal gyrus (pIFG) is involved in the effortful cancellation of dominant motor responses. The Stop Signal Task is designed to probe motor inhibition processes and shows significant activation within this region. However, the pIFG is most active when the task is initially being learnt. Other LFC sub-regions, including the anterior insula inferior frontal operculum (AIFO), inferior frontal sulcus (IFS) and posterior dorsolateral prefrontal cortex (pDLPFC), show similar learning effects. Behavioural performance measures correlate with changes in functional connectivity between these LFC sub-regions. These results (Erika-Florence et al., 2014) indicate that distributed LFC networks work in a coordinated manner to support novel tasks. As a task becomes automated, the involvement of these networks diminishes.

experimental tractability (Passingham and Wise, 2012). For example, classic studies focused on mapping functional dissociations across large-scale dorsal-ventral and anterior–posterior axes within the LFCs. However, data-driven analyses have shown that the LFCs are more complex than this (Hampshire and Sharp, 2015); they contain multiple, functionally distinct sub-regions, which each co-activate with a different large-scale connectivity network (Beckmann and Smith, 2004; Dosenbach et al., 2006, 2008; Erika-Florence et al., 2014; Hampshire et al., 2012b; Laird et al., 2011; Smith et al., 2009). Three of these LFC networks (Fig. 2) include brain regions that are known to play particularly flexible roles in cognition (Duncan, 2001; Duncan and Owen, 2000; Fedorenko et al., 2013) and that are implicated in learning (Toni and Passingham, 1999; Toni et al., 2001). One network includes the anterior insular/inferior frontal operculum, the anterior cingulate cortex and the temporal-parietal junction bilaterally (AIFO network). Another includes the inferior frontal sulcus, the inferior parietal cortex and the ventral caudate bilaterally (IFS network). The third includes the lateral frontopolar cortex, the posterior dorsolateral prefrontal cortex and the superior parietal cortex bilaterally (LFPC network). It remains unclear how these networks differ in their functions and how they coordinate with each other to support controlled modes of behaviour such as intentional learning.

The ventral striatum has also been implicated in the learning of novel tasks and is richly connected to several LFC regions. However, it also reliably dissociates from the LFCs under some cognitive conditions (Hampshire et al., 2012a). For example, it has been reported that parameters from computational simulations of model-based and model-free reinforcement learning predict regional brain activations within the LFCs and the ventral striatum respectively (Glascher et al., 2010). More broadly, the ventral striatum has been implicated in the processing of task feedback, particularly reward prediction errors (O'Doherty et al., 2003; Schonberg et al., 2007; Seymour et al., 2004). Based on this, it has been proposed that the LFCs and the ventral striatum carry distinct learning signals (Glascher et al., 2010). However, less is known about how the LFCs and ventral striatum interact when these learning signals must be integrated: for example, when feedback signals the requirement to modify the temporary internal program for performing the task.

Here, we address these questions by applying a combination of fMRI analysis methods to examine LFC network activity and connectivity across consecutive stages of two stimulus–response learning tasks. First, we use a combination of precisely controlled contrasts and analyses of global network synchrony to test the hypothesis that LFC networks are more active and functionally interconnected during the simplest form of intentional learning, in which stimulus–response rules are applied based on explicit instruction at the start of each learning block with no reinforcement from feedback. Then, we use focused regions of interest (ROI) and psychophysiological interaction (PPI) analyses to test the hypothesis that striatocortical connections are engaged when the stimulus–response rules are being established based on feedback (O'Doherty et al., 2003; Schonberg et al., 2007; Seymour et al., 2004). Finally, we apply dynamic causal modelling (DCM) with Bayesian model selection to test whether LFC sub-regions interact in a hierarchical manner during learning from instruction and to examine how negative feedback impacts on striatocortical interactions during learning by trial and error.

Materials and methods

Participants

17 healthy participants (7 female and 10 male) aged 19–27 years completed Study 1 and 14 participants (5 female and 9 male) aged 20–35 years completed Study 2. All participants were right handed English speakers with normal or corrected to normal eyesight. Volunteers were excluded if they had a history of neurological or psychiatric illness, were taking psychoactive medications or did not meet MRI safety criteria. The local research ethics board approved this study. Participants gave informed consent prior to entering the fMRI scanner.

Task designs

In Study 1 (Fig. 3a), participants were presented with a simple discrimination rule for 4 s (e.g. yellow shapes = left button response and orange shapes = right button response) followed by a sequence of coloured shapes. There were 4 compound stimuli per rule, constructed from 2 exemplars per dimension. There was no feedback post response. Stimuli were presented in randomised order at a rate of 1 per 1.7 s with