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Material-specific interference control is dissociable and lateralized in human prefrontal cortex



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ABSTRACT

The prefrontal cortex (PFC) plays a key role in the ability to pursue a particular goal in the face of competing alternatives, an ability that is fundamental to higher-order human behavior. Whether this region contributes to cognitive control through material-general mechanisms, or through hemispheric specialization of component abilities, remains unclear. Here we show that left or right ventrolateral PFC damage in humans leads to doubly dissociable deficits in two classic tests of interference control. Patients with damage centered on left ventrolateral prefrontal cortex had exaggerated interference effects in the color-word Stroop, but not the Eriksen flanker task, whereas patients with damage affecting right ventrolateral prefrontal cortex showed the opposite pattern. Thus, effective interference resolution requires either right or left lateral PFC, depending on the nature of the task. This finding supports a lateralized, material-specific account of cognitive control in humans.

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1. Introduction

1.1. Theoretical underpinnings and clinical relevance of interference control

Resistance to interference, defined as “the ability to ignore or inhibit irrelevant information while executing a plan”, is essential for successful human behavior (Dempster and Corkill, 1999, p. 397). Research on interference control spans over a hundred years and permeates the field of psychology: changes in susceptibility to interference have been used to explain development of cognitive abilities, age-related cognitive decline and psychiatric disorders including attention-deficit/hyperactivity disorder, obsessive-compulsive disorder, autism, and schizophrenia (Barkley, 1997; Ciesielski and Harris, 1997; Darowski et al., 2008; Dempster, 1995; Enright and Beech, 1993; Nestor and O'Donnell, 1998; Ridderinkhof et al., 1997). A central question in the study of interference control and, more generally, executive function remains: is resistance to interference a unitary, domain-general function or is it instead supported by dissociable, material-specific processes? This fundamental question has important

implications for the way we conceptualize, diagnose, assess, and treat disorders of cognitive control.

1.2. Support for interference control as a domain-general process

Behavioral studies in healthy subjects suggest a close relationship between different forms of resistance to interference. A classic paper by Friedman and Miyake (2004) sought to address the unity and diversity among tasks of interference control, including two of the most commonly used tests in clinical psychology and cognitive neuroscience, the Stroop (Stroop, 1935) and Eriksen flanker tasks (Eriksen and Eriksen, 1974). Using latent variable analysis of individual differences, they showed a tight relationship between tasks requiring suppression of prepotent verbal responses, whether triggered by verbal (Stroop interference) or spatial (flanker interference) distractors. This raises the possibility of a common neural mechanism for these two forms of interference control. Functional imaging and single-unit studies argue that a suite of frontal and parietal brain regions alternatively termed multiple-demand (Duncan, 2001), task-positive (Fox et al., 2005), or the cognitive control network (Cole et al., 2013; Cole and Schneider, 2007) is broadly engaged across a range of tasks that require cognitive flexibility. This frontoparietal network includes ventrolateral prefrontal cortex (VLPFC) and is engaged by tasks requiring interference control, including Stroop (Duncan, 2010;

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Fedorenko et al., 2013). A different line of inquiry also supports the functional generality of prefrontal cortex (PFC); single-unit recordings in primate VLPFC show that these neurons can flexibly code task-relevant information (Asaad et al., 2000; Cromer et al., 2010; Freedman et al., 2001; Fuster et al., 2000). In sum, this work argues that interference control is domain-general, with VLPFC part of a network that is engaged to implement control across diverse tasks.

1.3. Evidence for multiple-process and material-specific accounts of interference control

Others have argued that interference control involves multiple processes, relying on distinct PFC regions (Petrides, 2005; Stuss et al., 1995). This is supported by human functional imaging and lesion studies that show dissociable PFC contributions to interference control. Work by Kok (1999) points to multiple cortical and subcortical systems that interact over different time-scales from the processing of early sensory information to response-selection. Lesion studies also support the existence of dissociable component processes in interference control: damage to the right frontal operculum results in dissociable deficits in attentional capture and stimulus–response conflict (Michael et al., 2014). This finding shows the independence of sensory and motor processing stages in interference control. Congruent with this hypothesis, a quantitative meta-analysis of 47 fMRI studies of tasks requiring interference resolution, including Stroop and flanker tasks, showed low correlation of brain activation across tasks (Nee et al., 2007) suggesting that different forms of interference control depend on different PFC sub-regions. The authors also found hemispheric differences across tasks, with right and left lateralized foci in flanker and Stroop meta-analyses respectively; they concluded that differential patterns of activation in dorsolateral PFC (DLPFC), VLPFC, and anterior cingulate cortex (ACC) across tasks might reflect distinct cognitive processes. Taken together these findings argue against a unified network for cognitive control and instead support the existence of multiple component processes underlying resistance to interference.

Converging evidence demonstrates that flanker and Stroop tasks, despite sharing a requirement for interference control, rely on at least partly distinct, and potentially lateralized, material-specific neural substrates. Behavioral evidence shows low within subject correlation of interference control across Stroop and flanker tasks, and no interaction between these two forms of interference in a combined Stroop and flanker paradigm (Fan et al., 2003). fMRI studies show that right VLPFC (RVLPFC) activation is associated with resolution of flanker interference (Bunge et al., 2002; Hazeltine et al., 2003; Hazeltine et al., 2000; Ullsperger and von Cramon, 2001) whereas left VLPFC (LVLPFC) activation is associated with Stroop interference (Brass and von Cramon, 2004; Derrfuss et al., 2005; Leung et al., 2000; Roberts and Hall, 2008; Zysset et al., 2001). An fMRI study by Morimoto et al. (2008) observed hemispheric specialization in VLPFC for flanker interference using color words or color patches as stimuli: the color word flanker produced left VLPFC activation and the non-verbal color patch flanker activated right VLPFC (Morimoto et al., 2008). Taken together, this work fails to support the strongest forms of unitary models of interference control, instead arguing for a more functionally specific view of at least the VLPFC contribution. In contrast to fMRI work, human lesion studies can test whether a region of interest is necessary for a particular function, and so can provide stronger evidence for dissociability claims. One prior case report showed a single dissociation with interference control disrupted in a verbal, but not nonverbal task after left VLPFC damage, arguing that resistance to interference is not a common, general process engaged across tasks (Hamilton and Martin, 2005).

1.4. Aims of the present study

Here we sought evidence to disentangle competing hypotheses concerning the structure–function relationship of VLPFC and interference control. We tested whether right or left VLPFC is differentially required for the performance of two classic tests of interference control (color-word Stroop and Eriksen flanker) in patients with focal damage to these regions. If left and right VLPFC play a domain-general role in cognitive control, we would expect that damage to either region would produce either increased interference effects regardless of the task, or no effect if the intact hemisphere can fully compensate for damage in the other. On the other hand, if lateralized prefrontal regions make unique contributions to cognitive control depending on the nature of the material being processed, then the lesion–deficit relationship should be dissociable across tasks.

2. Materials and methods

2.1. Participants in Experiment 1

Eight right-handed patients with damage centered on the left ($N=3$) or right ($N=5$) VLPFC and 21 right-handed healthy controls were recruited from the McGill Cognitive Neuroscience Research Registry for the main experiment. The Edinburgh Handedness Inventory (Oldfield, 1971) was available for a subset of the total sample ($N=17$); the mean laterality inventory was 93.4 (range 80–100). The control sample included 6 men and 15 women, the LVLPFC group comprised 1 man and 2 women, and the RVLPFC sample included 1 man and 4 women. Patients were included if they had focal brain lesions affecting right or left VLPFC, as determined by structural CT and/or MRI scans. Subjects were tested at least 1 year (mean 3.3 years, range 1.2–6.3 years) after brain injury. The mean lesion volume did not differ significantly between groups (RVLPFC=67 cc, range 27–113 vs. LVLPFC 40 cc, range 13–75, $U=4.0$, $P=0.30$). Larger lesion volume did not predict greater Stroop or flanker interference effects. Individual patient lesion characteristics are described in Table 1 and Fig. 1 (A and B). One RVLPFC participant had been on a low dose of a selective serotonin reuptake inhibitor for 17 years and was euthymic. Exclusion of this subject did not alter the statistical significance of our main findings. All other patients did not take psychoactive medication and were free from psychiatric or other neurologic illness.

A summary of patient demographic information and performance on a neuropsychological battery screening for aphasia, inattention and neglect is provided in Table 2. These variables were compared across all three groups (LVLPFC, RVLPFC, Controls) using nonparametric Kruskal–Wallis H tests. Mann–Whitney U tests were applied for pairwise comparisons between patient groups. There were no significant differences between patient groups and controls with respect to age ($P=0.79$) or years of education ($P=0.96$). There were also no significant differences in forward digit span, BDI, letter cancellation tasks, sentence comprehension, or naming performance between LVLPFC and RVLPFC groups (all $P>0.10$). The LVLPFC group showed a trend towards reduced phonological fluency (FAS: $U=2.0$; $P=0.099$), semantic fluency (animals: $U=2.0$; $P=0.099$), and significantly lower backwards digit span ($U=1.0$; $P=0.046$) compared to RVLPFC. Controls scored above 25/30 on the Montreal Cognitive Assessment (Nasreddine, et al., 2005), did not take psychoactive medication and had no history of neurological or psychiatric illness. All

Table 1
Lesion characteristics of patients in the main experiment.

Subject	Etiology	Years since injury	Lesion volume (cc)	Brodmann's areas
RVLPFC 1	Stroke	1.4	47.1	45, 44, 47, 38
RVLPFC 2	Low-grade glioma	1.3	113.1	11, 47, 20, 38, 21
RVLPFC 3	Stroke	4.4	27.2	47, 45, 46
RVLPFC 4	Stroke	4.0	78.6	45, 46, 44, 6, 9
RVLPFC 5	Meningioma resection	6.4	59.5	47, 45, 11, 46
LVLPFC 1	Stroke	3.0	30.5	44, 45, 47, 6
LVLPFC 2	Stroke	4.4	75.2	45, 47, 38, 46, 21
LVLPFC 3	Stroke	1.2	13.1	47, 45

Brodmann's areas are ordered from largest to smallest affected regions. The reported Brodmann's areas represent over 80% of the cortical lesion volume in each subject. Lesion volume was not significantly different between right and left VLPFC ($P=0.3$). RVLPFC=right ventrolateral prefrontal cortex; LVLPFC=left ventrolateral prefrontal cortex.

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