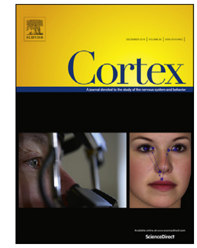
Available online at www.sciencedirect.com

ScienceDirect

Journal homepage: www.elsevier.com/locate/cortex



Research report

A neural mechanism of cognitive control for resolving conflict between abstract task rules

Yi-Shin Sheu [a,*] *and Susan M. Courtney* [a,b,c]

[a] *Department of Psychological & Brain Sciences, Johns Hopkins University, Baltimore, MD, USA*
[b] *F.M. Kirby Research Center for Functional Brain Imaging, The Kennedy Krieger Institute, Baltimore, MD, USA*
[c] *Department of Neuroscience, Johns Hopkins University, Baltimore, MD, USA*

ARTICLE INFO

Article history:
Received 11 December 2015
Reviewed 11 February 2016
Revised 19 April 2016
Accepted 21 September 2016
Action editor Sarah MacPherson
Published online 1 October 2016

Keywords:
Prefrontal cortex
Cognitive control
fMRI
Task rule
Right inferior frontal gyrus

ABSTRACT

Conflict between multiple sensory stimuli or potential motor responses is thought to be resolved via bias signals from prefrontal cortex (PFC). However, population codes in the PFC also represent abstract information, such as task rules. How is conflict between active abstract representations resolved? We used functional neuroimaging to investigate the mechanism responsible for resolving conflict between abstract representations of task rules. Participants performed two different tasks based on a cue. We manipulated the degree of conflict at the task-rule level by training participants to associate the color and shape dimensions of the cue with either the same task rule (congruent cues) or different ones (incongruent cues). Phonological and semantic tasks were used in which performance depended on learned, abstract representations of information, rather than sensory features of the target stimulus or on any habituated stimulus-response associations. In addition, these tasks activate distinct regions that allowed us to measure magnitude of conflict between tasks. We found that incongruent cues were associated with increased activity in several cognitive control areas, including the inferior frontal gyrus, inferior parietal lobule, insula, and subcortical regions. Conflict between abstract representations appears to be resolved by rule-specific activity in the inferior frontal gyrus that is correlated with enhanced activity related to the relevant information. Furthermore, multi-voxel pattern analysis of the activity in the inferior frontal gyrus was shown to carry information about both the currently relevant rule (semantic/phonological) and the currently relevant cue context (color/shape). Similar to models of attentional selection of conflicting sensory or motor representations, the current findings indicate part of the frontal cortex provides a bias signal, representing task rules, that enhances task-relevant information. However, the frontal cortex can also be the target of these bias signals in order to enhance abstract representations that are independent of particular stimuli or motor responses.

* *Corresponding author*. Department of Neurology, Cognitive Neuroscience, Johns Hopkins School of Medicine, 1620 McElderry Street, Reed Hall West, Room 102, Baltimore, MD, 21205, USA.
E-mail addresses: yishin.sheu@gmail.com (Y.-S. Sheu), courtney@jhu.edu (S.M. Courtney).
http://dx.doi.org/10.1016/j.cortex.2016.09.018

1. Introduction

Goal-directed behavior is thought to depend on the ability of the brain to represent and implement the task rules that would produce appropriate behavior for a given situation. Studies have shown that neurons in the prefrontal cortex (PFC) can encode abstract task rules that are not bounded by a specific set of stimuli or overlearned stimulus-response associations. Rather, these rule representations support generalization of task performance to familiar and novel situations alike (Asaad, Rainer, & Miller, 2000; Bunge, Kahn, Wallis, Miller, & Wagner, 2003; Hoshi, Shima, & Tanji, 2000; Wallis, Anderson, & Miller, 2001). It has been proposed that this abstract representation of task rule within the PFC biases processing throughout the rest of the brain by selectively enhancing activity of brain areas that encode the task-relevant information (Miller & Cohen, 2001). This is supported by neuroimaging studies in humans demonstrating rule-dependent interaction between PFC and posterior sensori-motor regions responsible for task execution (e.g., Chiu, Esterman, Han, Rosen, & Yantis, 2011; Egner & Hirsch, 2005; Miller, Vytlacil, Fegen, Pradhan, & D'Esposito, 2011; Nelissen, Stokes, Nobre, & Rushworth, 2013; Sakai & Passingham, 2003, 2006; Stroop, 1935; Waskom, Kumaran, Gordon, Rissman, & Wagner, 2014), and transcranial magnetic stimulation studies in humans showing disruption of PFC causally modulates the neural activity in posterior sensory cortex (Higo, Mars, Boorman, Buch, & Rushworth, 2011; Lee & D'Esposito, 2012; Zanto, Rubens, Thangavel, & Gazzaley, 2011).

This mechanism in which feedback from the PFC exerts influence over posterior regions to bias competition in favor of task-relevant sensory and motor representations is well established (for reviews, see Miller, 2000; Ridderinkhof, van den Wildenberg, Segalowitz, & Carter, 2004). It is not clear, however, whether the same mechanism can be applied to situations in which the competition is among abstract representations of task rules. When multiple task rules are simultaneously activated, analogous to when multiple sensory stimulus or motor response representations are activated, how is this competition resolved? Can the type of interaction that occurs between PFC and posterior regions also occur among different regions within the PFC itself, by biasing neural processing towards prefrontal neurons coding the relevant abstract information? It is an important issue because the mechanism responsible for resolving conflicts between abstract representations of non-sensory information might be different from those resolving conflicts between sensory representations of stimuli (for a review, see Kastner & Ungerleider, 2000) or between potential actions (for a review, see Cisek & Kalaska, 2010).

In the current study, we used functional magnetic resonance imaging (fMRI) to investigate the mechanism by which we can select relevant over irrelevant task rules. If the mechanism were similar to the mechanism that is thought to govern selection of sensory and motor representations (Desimone, 1998; Miller & Cohen, 2001), then we would expect to find two specific results. First, conflict between abstract rules would be expected to result in behavioral impairment and be accompanied by increased activity in a cognitive control network that helps to overcome the behavioral impairment. Second, conflict between abstract representations of task rules would be expected to be resolved by PFC interacting with brain regions processing the abstract information needed for the task, which is neither sensory nor motor related. We expected that this process would be achieved by enhancement of relevant abstract information, and perhaps secondarily by inhibition of irrelevant abstract information.

Participants were extensively trained so that strong associations were formed between different cue dimensions and one of two abstract task rules. Conflict was manipulated by having different cue dimensions (color and shape) associated either with the same task rule (congruent) or different ones (incongruent). For the incongruent cues, one cue dimension is mapped onto one task rule and the other cue dimension is mapped onto the other task rule through extensive training. The appearance of an incongruent cue, therefore, can cause automatic activation of both task rule representations. These task rules defined what type of abstract information had to be retrieved for a target word, rather than specifying particular manual response mappings or sensory features, so the conflict occurred at the abstract task-rule level. Participants switched between two tasks according to the rule given by the currently relevant cue dimension (color or shape), which was instructed at the beginning of each block and alternated across blocks. Phonological and semantic tasks were used, as they were previously shown to preferentially activate distinct brain areas (Lau & Passingham, 2007; Sakai & Passingham, 2006), allowing us to measure the degree of conflict between relevant and irrelevant task rules, and the interactions among PFC regions that may enable conflict resolution. By using these abstract rules combined with trial-unique words to which the rules were applied, participants could not learn a specific stimulus-response association, but rather needed to resolve the conflict at a more abstract level of representation.

2. Material and methods

2.1. Participants

Sixteen (12 females, 4 males) right-handed, healthy young adults between 18 and 35 (mean age 20 ± 2.5 years) participated the study. All participants were native English speakers with normal or corrected-to-normal vision, no history of head injury, substance abuse, neurological or psychiatric disorders, and were not taking any medications at the time of the study. The protocol was approved by the Institutional Review Boards of the Johns Hopkins University and the Johns Hopkins Medical Institutions. All participants provided written informed consent.

2.2. Experimental procedure

Participants were asked to make either a phonological or a semantic judgment for a visually presented word, as quickly as possible, while maintaining accuracy. We chose these semantic and phonological tasks because previous studies have shown that they preferentially activate distinctive regions within the frontal cortex (McDermott, Petersen, Watson, &