



Original Articles

Individual differences in the Simon effect are underpinned by differences in the competitive dynamics in the basal ganglia: An experimental verification and a computational model



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ABSTRACT

Cognitive control is thought to be made possible by the activity of the prefrontal cortex, which selectively uses task-specific representations to bias the selection of task-appropriate responses over more automated, but inappropriate, ones. Recent models have suggested, however, that prefrontal representations are in turn controlled by the basal ganglia. In particular, neurophysiological considerations suggest that the basal ganglia's indirect pathway plays a pivotal role in preventing irrelevant information from being incorporated into a task, thus reducing response interference due to the processing of inappropriate stimuli dimensions. Here, we test this hypothesis by showing that individual differences in a non-verbal cognitive control task (the Simon task) are correlated with performance on a decision-making task (the Probabilistic Stimulus Selection task) that tracks the contribution of the indirect pathway. Specifically, the higher the effect of the indirect pathway, the smaller was the behavioral costs associated with suppressing interference in incongruent trials. Additionally, it was found that this correlation was driven by individual differences in incongruent trials only (with little effect on congruent ones) and specific to the indirect pathway (with almost no correlation with the effect of the direct pathways). Finally, it is shown that this pattern of results is precisely what is predicted when competitive dynamics of the basal ganglia are added to the selective attention component of a simple model of the Simon task, thus showing that our experimental results can be fully explained by our initial hypothesis.

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1. Introduction

Cognitive control depends on the capacity to overcome prepotent behavioral responses that interfere with those required by internal goals. In many cases, the successful resolution of this interference depends on *selective attention*, that is, the capacity to ignore certain features of a stimulus and instead focus on other characteristics, selected on the basis of internal task goals. However, the exact nature of the neural mechanism for resolving interference is still debated. In fact, multiple mechanisms might be recruited for cognitive control, depending on the nature and

demands of the task at hand. In this paper, we suggest that the resolution of interference in a task that requires cognitive control relies on the activity of the basal ganglia, a subcortical circuit believed to be responsible for selecting which sensory information is ultimately transmitted to the prefrontal cortex (PFC). We then present an empirical test of this hypothesis and a computational model that accounts for the data presented herein.

The remainder of this paper is structured in four parts. First, we provide a brief overview of the problem of cognitive control in response selection interference. Second, we introduce the basal ganglia circuit, its role in response selection, and a behavioral task that measures the competitive basal ganglia dynamics to resolve conflict. Third, we present an experiment that demonstrates the existence of a significant (and hitherto unsuspected) correlation between performance on a cognitive control task (the Simon task: Craft & Simon, 1970; Simon, 1990) and a task that measures com-

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petitive basal ganglia dynamics (the Probabilistic Stimulus Selection task: Frank, Seeberger, & O'Reilly, 2004). Lastly, we present a computational model that provides an explicit and mechanistic account of interference in the Simon task in terms of basal ganglia dynamics, which accounts for our results.

1.1. Cognitive control

Cognitive control is typically studied through tasks that require managing interference between competing responses. For example, in the Stroop task, participants are asked to say out loud the name of the color a word is presented in while ignoring the word itself. When the word is the name of a different color (e.g., RED printed in blue), interference arises because of the tendency to name the word. This interference is manifested in longer reaction times to such incongruent trials, as opposed to congruent ones where no interference exists (e.g., RED printed in red). Another example is the Simon task (Craft & Simon, 1970; Lu & Proctor, 1995; Proctor & Lu, 1999; Simon, 1990), in which participants are asked to respond with their left and right hand to specific visual features (e.g., shape or color) of a stimulus that appears on a screen. For example, they might be asked to respond with their left hand when the stimulus is a square, and with their right hand if the stimulus is a circle (Fig. 1). Interference occurs when a stimulus is presented on the side of the screen that is contralateral to the desired response. As a result, these “incongruent” trials (Fig. 1C and D) are less accurate and take longer than “congruent” trials in which the stimulus appears on the side of the desired response (Fig. 1A and B). This extra time is supposed to reflect the additional cost necessary to resolve conflict generated by the activation of two competing responses (one for the shape, one for the position).

The precise source of interference in these tasks has been much debated and might vary across different paradigms (Liu, Banich, Jacobson, & Tanabe, 2004; Nee, Wager, & Jonides, 2007; van Veen & Carter, 2005). In the specific case of the Simon task, interference likely occurs early on, at the moment in which the relevant and irrelevant features of the stimuli are being processed, as evidenced from both a review of the behavioral data (Lu & Proctor, 1995) and from the onset of brain oscillations in the fronto-parietal network that reliably indicate individual differences in working memory encoding (Gulbinaite, van Rijn, & Cohen, 2014).

While different authors might disagree on the source of interference for specific tasks, they tend to agree that, at the neural

level, interference is resolved through mechanisms underpinned by the prefrontal cortex (PFC: Miller, 2000; Miller & Cohen, 2001). More specifically, by holding a representation of the intended goal (for instance, paying attention to the shape of the stimulus, rather than its position), PFC exerts a top-down influence that ultimately counters the prepotency of unwanted responses. The role of PFC in exerting this form of control has been verified in numerous imaging studies (Cole, Laurent, & Stocco, 2013; Cole & Schneider, 2007; Kane & Engle, 2002; Koechlin, Ody, & Kouneiher, 2003; MacDonald, Cohen, Stenger, & Carter, 2000; Miller, 2000; Ridderinkhof, van den Wildenberg, Segalowitz, & Carter, 2004), proposed for both proactive and reactive control (Braver, 2012; Braver, Paxton, Locke, & Barch, 2009) and implemented in numerous neurocomputational models (Botvinick & Plaut, 2004; Cohen, Braver, & O'Reilly, 1996; Cohen, Dunbar, & McClelland, 1990; Herd, Banich, & O'Reilly, 2006). Within neural network models, this mechanism is typically implemented by adding specific “task” or “goal” representational units at the top of the network hierarchy. The activation spreading from these units ultimately provides the necessary boost to overcome the interference caused by irrelevant stimuli that are encoded by units whose synaptic weights are normally much stronger. For example, in the early influential model of the Stroop task by Cohen et al. (1990), different sets of units encode the stimulus' word and the stimulus' color, and both are connected to the output layer of the network, whose units represent color names. Stroop interference originates because the connectivity between input *word* units and output color names is much stronger than that between input *color* units and output color names. The model can successfully overcome interference, however, when additional input units are added that encode the task goal (that is, whether to name the color or read the word).

For such a mechanism to function properly, PFC must be able to maintain active representations of the relevant information, while at the same time discarding irrelevant information that would lead to a top-down activation of the irrelevant or incorrect responses. Indeed, single-cell recordings show that PFC neurons exhibit precisely this type of selectivity. For example, PFC neurons were found to encode only the relevant information of the stimulus (the location of a target) and not other aspects (i.e., the location of distractors; Rainer, Asaad, & Miller, 1998). Conversely, accidental encoding of irrelevant information in PFC is associated with poor performance in cognitive control tasks. For instance, compared to individuals with lower cognitive capacity (as indexed by working

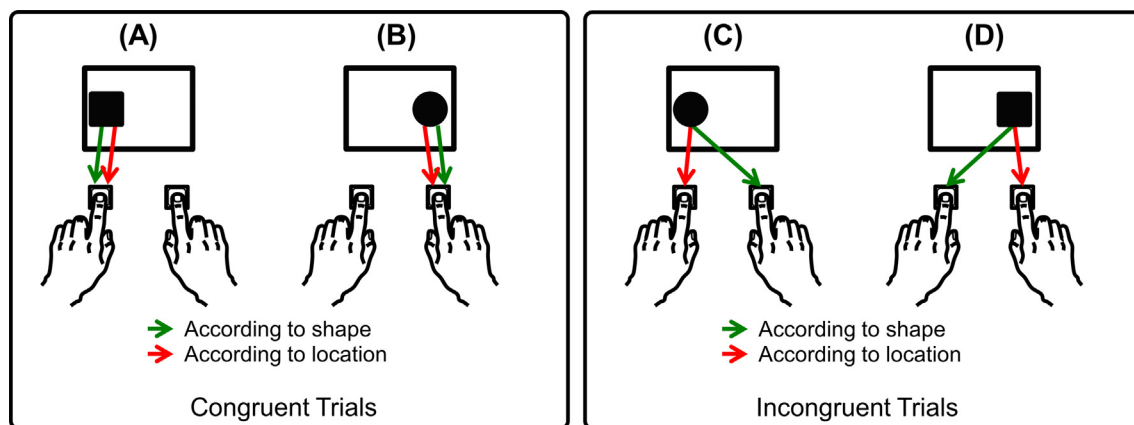


Fig. 1. Overview of the Simon task. In the case illustrated here, participants are instructed to respond with their left hand if the stimulus is a square, and with their right hand if it is a circle. Additionally, the stimulus can appear on the left or the right side of the screen. During congruent trials (A and B), the stimuli appear on the same side as their associated response. During incongruent trials (C and D), on the other hand, the stimuli appear on the opposite side, thus creating a competition between the correct response associated with the shape of the stimulus and the incorrect response associated with the location of the stimulus. Incongruent trials are typically associated with more errors and longer response times (Fig. 4).

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