

A neural microcircuit for cognitive conflict detection and signaling

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During human response conflict – competition between multiple conflicting actions when a mistake could be made – a specific pattern of brain electrical activity occurs over the medial frontal cortex (MFC), characterized by modulations of ongoing theta-band (~6 Hz) oscillations and synchronization with task-relevant brain regions. Despite the replicable and robust findings linking MFC theta to conflict processing, the significance of MFC theta for how neural microcircuits actually detect conflict and broadcast that signal is unknown. A neural MFC microcircuit model is proposed for processing conflict and generating theta oscillations. The model makes several novel predictions for the causes and consequences of MFC theta and conflict processing, and may be relevant for understanding the neural implementations of related cognitive processes.

It is a law of nature we overlook, that intellectual versatility is the compensation for change, danger, and trouble... Nature never appeals to intelligence until habit and instinct are useless. H.G. Wells, *The Time Machine*.

Cognitive control, conflict processing, and the need for biologically inspired theories

Cognitive control refers to the ability to monitor one's actions and the external environment for mistakes, conflicts, and negative performance feedback, and to initiate rapid but flexible action adjustments to optimize goal-directed behavior [1,2]. It is one of the most important sets of cognitive functions for success in a complex and rapidly changing world, and individual differences in these abilities predict real-world outcomes including academic success and career choices [3,4].

The need for cognitive control is perhaps strongest in situations of response conflict, in which multiple competing actions are activated but only one is appropriate and should be selected. Response conflict is epitomized by the well-known Stroop task [5], in which one responds to the color of a font rather than the meaning of the word (e.g., say 'red' when reading the word 'blue'). It is becoming increasingly clear that impaired cognitive control is a hallmark of several disorders ranging from attention

deficit hyperactivity disorder (ADHD) to schizophrenia to obsessive-compulsive disorder [6–8].

Psychological and cognitive neuroscience theories of cognitive control abound [9,10], but most extant models are built on abstracted assumptions rather than on neurobiologically plausible foundations. This gap between model assumptions and neurobiology hinders progress in understanding the neural mechanisms underlying (as opposed to correlates of) conflict processing. Many current models that claim to be neurobiological or neurobiologically informed are so in name only, and are better characterized as 'box-and-arrow' models. For example, many cognitive control models have a box labeled 'anterior cingulate cortex,' but there are no neurobiological constraints that make that box resemble the cingulate any more than it could resemble lateral prefrontal cortex, thalamus, or retina. Furthermore, equations of the form $c = wa_1a_2$, which are used in some cognitive control models [11], to compute the amount of conflict as a weighted combination of the activation of two responses cannot be considered biologically informed or constrained any more than a linear regression ($y = mx + b$) is biologically constrained. Other models that include biologically constrained neurons [12] lack sufficient specificity to account for the empirical neurophysiology data described later in this paper.

The box-and-arrow approach of cognitive modeling was an important first step that was necessary to begin integrating cognitive psychology with neuroscience, and this approach has taken us a long way. However, as neuroscientific knowledge has increased over the past decade it has become apparent that the neophrenological 'brain region X performs cognitive process Y' approach is too simplistic to provide deep insights into the neurophysiological mechanisms of cognition. 'Biologically inspired' models that contain little or no biological plausibility may be useful as descriptive models for characterizing task performance or functional magnetic resonance imaging (fMRI) activations, but provide limited insights into the neurophysiological mechanisms of cognitive computations, and cannot easily be integrated into advances in the neuroscientific understanding of how the brain represents, processes, and transmits information. In part this is because many cognitive control theories were developed to fit patterns of behavioral task data or fMRI activations; they were not developed to account for functional, cytoarchitectonic, or physiological properties of the brain [13].

The purpose of this paper is to review recent findings that provide insights into putative neurophysiological mechanisms underlying conflict processing, and to propose

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a model that can account for key features of conflict processing and its neural manifestations in humans, while relying solely on known neurophysiological and biophysical mechanisms. This new model generates precise and testable (and, in a few cases, surprising) hypotheses that may help understand how high-level cognitive processes can be implemented at the level of neural microcircuits and dendritic computations, and what implications those neural microcircuit dynamics might have for the timing of behavior.

Behavioral manifestations of conflict

Response conflict occurs when one response is automatically activated by a task-irrelevant feature (such as the physical location of the stimulus) whereas a different response is activated by the task instructions that often entail arbitrary stimulus–response mappings such as pressing the left-hand button for a purple stimulus. The competition between the fast automatic response and the slow task-relevant response [14] generates conflict, particularly when subjects are encouraged to respond quickly [15]. At a conceptual level, this process can be reasonably approximated as a weighted multiplication of motor activation magnitudes [16]. There are several tasks to manipulate response conflict and measure its effects on behavior, including the Stroop task described above, and the ‘Simon task’ [17,18] (Figure 1A).

The effects of conflict on behavior depend on the recent trial history of conflict, a phenomenon known as the congruency sequence effect [19]. Though highly replicable, the

nature of congruency sequence effects depends on several variables, including the type of task, the duration of the intertrial interval, and instructions such as a speed–accuracy trade-off. In the flankers task, for example, current-trial behavior is less strongly influenced by conflict when the previous trial contained conflict. In spatial conflict tasks such as the Simon task, the conflict effect may even reverse after incongruent trials (Figure 1B). In the Stroop task, negative priming can occur, which means that the response to a stimulus is impaired when that stimulus was ignored in the previous trial. The common theme across these effects is that behavior and brain activity on the current trial are strongly influenced by the congruency of the previous trial.

Although the existence of congruency sequence effects is not debated, the underlying causes remain a contentious issue in the cognitive psychology literature. Sequence effects have variously been attributed to conflict adaptation [11,20], expectations of near-future events [21,22], task- or set-switching costs [23], feature binding or response repetitions [24,25], proactive versus reactive control [26,27], negative affect-induced attention [28], and several other accounts [29]. This debate often involves designing increasingly complicated experiments to rule out increasingly detailed potential alternative explanations. Below it will be argued that a neuroscientific perspective may facilitate a concise and parsimonious explanation for at least part of the congruency sequence effects.

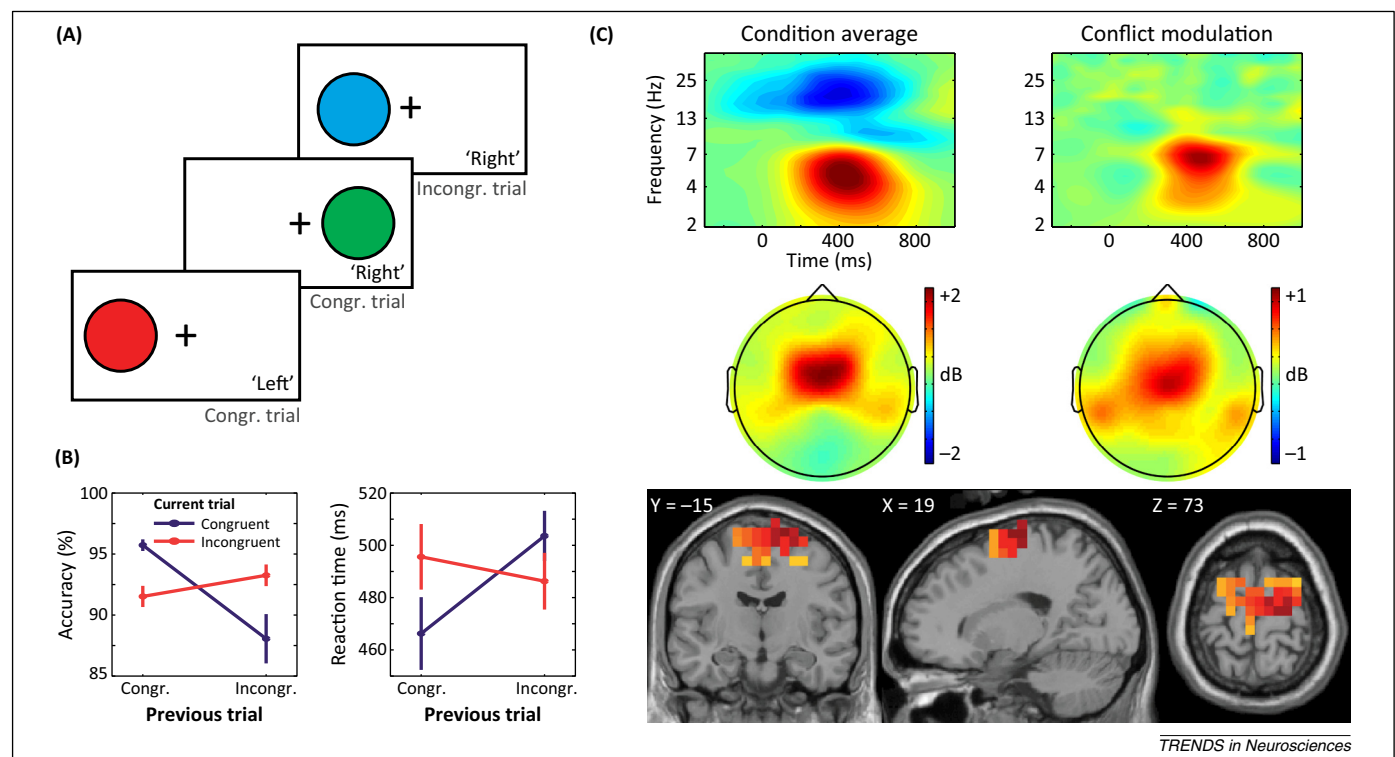


Figure 1. Example conflict task and representative findings. **(A)** The ‘Simon task,’ in which subjects respond as quickly as possible to the color (task-relevant feature) while ignoring the location (task-irrelevant feature). During ‘incongruent’ (i.e., high conflict) trials the stimulus is on the opposite side to the required response. This increases reaction times and error rates. **(B)** Typical behavioral findings from the Simon task. The effect of conflict on the current trial depends on the conflict in the previous trial. **(C)** Typical EEG results from the Simon task, showing modulations in non-phase-locked theta-band power over midfrontal scalp electrodes (‘conflict modulation’ refers to the difference between incongruent and congruent trials). Brain-space estimation algorithms suggest a source of this conflict modulation in or around the supplementary motor area. Panels B and C were adapted, with permission, from [41] and [56], respectively.

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