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Dynamics of cognitive control: Theoretical bases, paradigms, and a view for the future

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Abstract

Cognitive control (with the closely related concepts of attention control and executive function) encompasses the collection of processes that are involved in generating and maintaining appropriate task goals and suppressing task goals that are no longer relevant, as well the way in which current goal representations are used to modify attentional biases to improve task performance. Here we provide a comprehensive but non-exhaustive review of this complex literature, with an emphasis on the contributions made by techniques for studying human brain function. The review is divided into five sections: (1) overview and historical perspective of cognitive control, its subcomponent processes, and its neural substrate; (2) most common types of tasks used to assess and/or manipulate the level of control; (3) main research findings obtained with various imaging methodologies, with a focus on ERP data, and briefer overviews of oscillatory (event-related spectral perturbations, ERSPs) and fMRI data; (4) major theories of cognitive control; and (5) discussion of open questions regarding how to integrate the various dimensions of control, as well as the faster vs. slower temporal dynamics informing this complex and multifaceted concept.

Keywords: Cognitive control; executive function; control dynamics; EEG; ERPs; fMRI; neuroimaging

1. Cognitive Control: Overview and Historical Perspective

This paper is intended to provide a comprehensive but non-exhaustive overview of the extant literature on cognitive control. We start with some definitions and a historical perspective on how the idea of cognitive control has developed over the last several decades, including its subcomponent processes, and what is known about its neural substrate. We then review the most common tasks used to assess and/or manipulate the level of control, highlighting their commonalities and differences, which allow researchers to tap onto different aspects of control. Next, we review some of the main research findings obtained with various methodologies used for investigating human brain function, with an emphasis on ERPs, and briefer overviews of oscillatory (event-related spectral perturbations, ERSPs) and functional magnetic resonance imaging (fMRI) data, which provide very different views (from infra-slow to ms-scale) of the temporal dynamics of control processes. We conclude with a review of major theories of control and discuss a series of open questions regarding their integration. We also compare and discuss the different temporal scales provided by different psychophysiological methods and how they inform this complex and multifaceted concept.

Cognitive control is a core concept in modern cognitive neuroscience, which stemmed from the renewed interest in information processing that emanated from the cognitive revolution of the 1950's and 60's. Theorizing about cognitive (or attention) control requires us to explicitly model both the mechanisms connecting environmental stimuli with specific responses (and more generally actions) and the higher order processes that regulate these mechanisms.¹ Early cognitive models of speeded reactions, such as Sternberg's (1966) serial model, postulated a fixed flow of information across a set of

¹ Traditionally, the concept of attention relates to the mechanisms used for selecting environmental information relevant for generating adaptive response (i.e., responses that are appropriate for the subject's context or task). As such attention can be formally considered as a "filter" in which varying weights are given to different types of evidence extracted from the environment, in order to activate responses (hence the terminology "attention weights" describing this filter). Cognitive (or attention) control instead refers to the mechanisms used for setting, changing, or deleting these attention weights. However, it is very difficult to theorize about cognitive/attention control without first generating a theory (at least in broad terms) about how attention might work. Thus most theories of cognitive control imply a theory of attention.

processing stages. However, soon results accumulated that could not be easily accounted for by such models, and new theories emerged (see automaticity theories, e.g., Shiffrin & Schneider, 1977; Schneider & Shiffrin, 1977; Logan, 1988) that considered alternative processing routes leading from perception to action. Still, these theories were dominated by feed-forward rules and could not account for the extensive processing flexibility evident in human cognition. A key concept at the basis of this cognitive flexibility is the distinction between "bottom up" and "top down" processing (Gregory, 1970). This distinction was born out of a critical observation: Our processing system can interpret the same stimulus in different ways, depending on the context in which it is presented. This implies that the human information processing system does not rely only on feed-forward mechanisms – in which stimulus information is processed in an ordered, hierarchical fashion – but also on feedback mechanisms. These feedback mechanisms make it possible for contextual information to lead the system to select only some of several candidate representations for further processing and to initiate one of several possible courses of action (see the concept of attention filters, e.g., Broadbent, 1958; Triesman, 1969).

The view that attention operates through a set of *filters, biases or weights* is now commonly accepted at multiple levels of analysis – from behavioral neuroscience to cognitive psychology and cognitive neuroscience. These filters are deployed to enhance or suppress different perceptual modalities, stimulus features, spatial locations, or object representations. In other words, attentional biases serve to extract information relevant to the current task goals, which are themselves viewed as distributed representations. For example, in the well-known Stroop task, cognitive control is inferred in the process of setting up an attentional bias towards the ink color and away from the prepotent tendency to read the word, in order to reduce interference in naming the ink color of incongruent color words (e.g., responding *'blue'* to the word **red** written in blue ink). Cohen, Dunbar, and McClelland (1990) assumed the existence of parallel distributed processing (PDP), in which a set of *common* (i.e.,

domain general) cognitive and neural mechanisms could be invoked and modeled to account for a diversity of control functions, such as *concurrently* suppressing some processes while enhancing others. For example, a common mechanism for representing contextual information (or "context for responding") could be invoked to account for the implementation of cognitive control across a range of laboratory tasks, including those considered to engage working memory and/or inhibitory processing (Miller & Cohen, 2001).

This way of defining the construct of cognitive control emphasizes its significance within the context of stimulus-response paradigms conducted in the laboratory. However, instantiations of cognitive control are also pervasive in real life, from making simple decisions of varying importance (e.g., opting to respond to a phone call selling insurance you do not care to purchase vs. responding to your crying baby), to more complex decisions whose consequences will only become evident in the future (e.g., choosing a career path, deciding on a graduate school, planning a family). The apparent lack of flexibility in making both simple and more complex decisions in patients with frontal (and parietal) brain lesions sparked the interest of investigators in the neuropsychological tradition (which developed in parallel with the cognitive revolution; Milner, 1963). Evidence from lesioned patients, together with animal studies of frontal lobe function (e.g., Goldman-Rakic 1995; Goldman-Rakic & Leung, 2009; Petrides, 2005; 2015), has provided crucial information about the neural circuitry supporting cognitive control. Current neuroscience research has further identified specific brain networks (reviewed by C. Gratton, Sun & Petersen, 2018) that contribute to distinct aspects of cognitive control. Communication within and across network structures is enabled by oscillatory mechanisms (Fries et al., 2013; Sadaghiani et al., 2012; see G. Gratton, 2018, for a review) and is supported by neurotransmitter systems (e.g., Goa & Goldman-Rakic, 2003; for a review see Cools, 2016) that modulate mechanisms for long-distance transmission and local lateral inhibition. Rapid transmission of information is supported by the integrity of white matter tracts (e.g., Bennett & Madden, 2014). These putative structural and functional

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mechanisms are often significantly impaired in a number of conditions, including normal and pathological aging (e.g., Fabiani, 2012), addiction (Hester et al., 2009), as well as a number of psychopathological diseases, such as schizophrenia, depression, and obsessive-compulsive disorder (e.g., Lesh et al., 2011; Ursu et al., 2003), making cognitive control a critical area of study.

Within this broader historical view, the collection of processes involved in generating, maintaining, and suppressing task goals, as well as the way in which these task goals are used to modify attentional biases, is referred to in multiple ways, including *attention control, cognitive control* and *executive function*. Although these terms are by and large used interchangeably, there are occasionally subtle differences in their intended meaning. Attention control is often used when describing within-trial or trial-by-trial variations in the direction of attention in response to changing task demands. Cognitive control is often used to refer to the set of mechanisms that are deployed in tasks that demand flexibility at one or multiple levels. Executive function may be more broadly construed as also implicating long-term goal representation, and nesting or interleaving of goals set for different time scales (e.g., Koechlin, Ody, & Kouneiher, 2003; Fuster 2008; Nee & D'Esposito, 2016).

Recent theorizing about cognitive control has sought to partition this complex function into a subset of component elements (e.g., Miyake & Friedman, 2000; see also Gardner, Holzman, Klein, Linton, & Spence, 1959, for earlier work with a similar logic). Extant theoretical models propose different, though often partially overlapping, subdivisions, some of which are listed in **Box 1** and briefly reviewed throughout this paper. Although the identification and naming of each subcomponent differ across accounts, the following general "processing pieces" are commonly agreed upon. First, representations of the currently possible task goals must be generated and maintained active or, at least, made easily accessible while they are useful for the task at hand (e.g., see the concept of central executive proposed by Baddeley, 1974; 1996; and the more recent model of working memory proposed by Cowan, 2001; 2016). Second, mechanisms must exist for recognizing the particular contextual cues that lead to the

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preferential selection of one specific goal over other alternatives (goal selection or attention biasing mechanisms). Third, task-sets (e.g., Schneider & Logan, 2010) or specific plans for action must be set up so that stimuli elicit appropriate responses (e.g., Allport's notion of "prepared reflexes," Allport et al., 1994). Fourth, monitoring (and orienting) mechanisms must be present to identify contextual cues signaling that current task goals are no longer relevant, and guide the system to implement newly relevant goals (the need for monitoring processes also arises from cognitive theory, see Lavie, Hirst, de Fockert, & Viding, 2004). Fifth, mechanisms must be postulated for suppressing representations and action plans associated with the no-longer-appropriate task goals, so as to reduce interference and prevent the initiation of inappropriate responses. In this general framework, the *updating, shifting*, and *inhibition* processes proposed by Miyake and Friedman can be construed as domain-general mechanisms that enable the sharpening and maintenance of some representations concurrently with the suppression of others (as per PDP modeling example mentioned earlier).

INSERT BOX 1 ABOUT HERE

2. Tests and Paradigms Used to Assess or Manipulate Cognitive Control

Neuropsychological tests and experimental paradigms that assess aspects of cognitive control have been derived from different traditions and with distinct purposes.² The primary purpose of neuropsychological tests is to assess performance deficits in clinical groups against norms from typical groups. As a result, they tend to have strong psychometric properties but low process specificity. Experimental paradigms are designed to manipulate the contribution of distinct cognitive control

² In this paper we use the term "neuropsychology" to refer to a research tradition that involves collecting data in a clinical setting on special populations, such as patients suffering from stroke or dementia, often times with a diagnostic and/or classification purpose. Neuropsychology focuses in large part on individual differences, and the ability to differentiate one participant or patient from another (hence the need for standardized and reliable test, with good psychometric properties). We use the term "neurocognitive" to refer to a research tradition in which anatomical or physiological data are collected in an experimental setting, often times on healthy participants (although special populations can also be used), with the purpose of refining our theorizing about brain and cognitive function. Importantly, inferences are not made about particular individuals, but rather about the general theory of how humans process information. Hence the emphasis is on the design of tasks that address general theoretical questions irrespective of their specific psychometric properties.

processes to task performance, while controlling for sensory, memory and/or motor contributions. Typically, these tests have not been bound by specific normalized administration procedures or task parameters: They provide flexibility in design and high process specificity, but at a cost of standardization, because typically they do not have established psychometric properties. However, recent work has sought to standardize and psychometrically characterize some experimental cognitive paradigms to facilitate their use in clinical and translational research (CNTRACS initiative; Gold et al., 2012).

Classic neuropsychological tests of cognitive control target broad constructs such as concept formation and rule-shifting (e.g., Wisconsin Card Sorting Test; Heaton, 1981), action planning (e.g., Tower of London; Shallice, 1982), and cognitive flexibility (e.g., word generation tasks, e.g., Benton & Hamsher, 1989). Many of these tests cannot differentiate between distinct cognitive control processes that contribute to task performance. For instance, in the WCST, a difficulty shifting from one sorting rule to another may be due to a difficulty shifting away from the current rule (i.e., perseveration) or a difficulty shifting to a rule that previously had to be ignored (i.e., learned irrelevance; Owen et al., 1993). The need to differentiate between these alternatives is illustrated by the finding that frontal lesion patients and medicated Parkinson's disease patients show exclusive deficits in perseveration and learned irrelevance, respectively (Owen et al., 1993).

There is now a substantial and well-established toolbox of experimental paradigms that are used to avoid the specificity issues common to neuropsychological tests and to investigate cognitive control processes involved in trial-by-trial variations in task demands. A useful classification of these tasks emanates from the seminal work of Miyake and Friedman (2000), who used factor analyses to examine individual differences in performance across a range of cognitive control tasks. This resulted in three major task groupings: *Updating* tasks that require the continuous updating of information in memory (e.g., the N-back task); *Shifting* tasks that require alternating between two or more stimulus-response

pairings (e.g., task-switching paradigms); and *Inhibition* (or *Conflict*) tasks that require the suppression of a prepotent or prepared response (e.g., the Stroop and stop-signal tasks). This terminology involves an important distinction between updating (i.e., incorporating novel information into working memory) and shifting (i.e., on-line selection of already available attentional settings used in previous trials), which resonates with Cowan's partition of working memory into representations within the focus of attention, outside the focus of attention but readily available, and inactive but retrievable (Cowan, 2001; 2016).

It is important to emphasize that, although this data-driven classification provides a useful reference framework, it does not imply that performance on any of these paradigms involves exclusively one or even a subset of the general elements of cognitive control described above (i.e., access to representations, goal selection, response planning, monitoring/orienting and inhibition/suppression). In fact, in most paradigms, effective cognitive control relies on implementation of all five elements. However, clever experimental design (e.g., tasks that involve processing cues in the absence of response preparation, **Baniqued et al.**, **2018**; **Provost et al.**, **2018** or cues that differ in information value; **Barceló & Cooper**, **2018**; Karayanidis et al., 2009) coupled with high-temporal-resolution imaging, allow us to map different cognitive control processes to distinct conditions and/or time intervals. In other words, we can study individual cognitive control processes by experimental manipulations that amplify (or reduce) the impact of a single element of cognitive control paradigms manipulate the need for control at the level of stimulus processing, stimulus-response mapping and/or response selection and execution, while controlling sensory and motor task requirements. They can be broadly classified under four headings (see **Figure 1** for a pictorial representation of these classes of paradigms).

INSERT FIGURE 1 ABOUT HERE

2.1 Continuous working memory paradigms. These paradigms require processing the properties of the current stimulus and making response-related decisions, while simultaneously maintaining and

updating information held in working memory. A prime example is the N-back task (Fig. 1A). Participants are shown a series of stimuli (e.g., words, numbers) and are required to respond to the current stimulus if it is identical to a stimulus presented one, two or more trials ago. So, in Figure 1A, on 2-back blocks, participants are required to respond to the second occurrence of the number 4, while keeping in working memory the numbers 4 and 7, in preparation for the next trial. Cognitive control load is manipulated by increasing the length of the sequence that needs to be maintained in working memory (e.g., 3-back has a higher load than 2-back and a lower load than 4-back).

2.2 Conflict paradigms. These paradigms introduce interference that results in a conflict between task-relevant and task-irrelevant stimulus properties and/or stimulus-response associations. As such, cognitive control is engaged to monitor this conflict and reduce its impact on performance. The conflict manipulation is achieved by presenting stimuli that contain features associated with different responses. On conflict trials, typically, this results in increased reaction time and error rate. For instance, the Eriksen flanker task (Eriksen & Eriksen 1974; Fig. 1B) requires participants to respond to the central stimulus in an array, which is flanked by stimuli that are mapped to a congruent response, an incongruent response (e.g., < is mapped to left and > to right hand response) or no response (e.g., 'X' is not mapped to a response). Here, while the response requirements are identical across all conditions, neutral stimulus arrays introduce greater perceptual interference, and incongruent arrays also produce greater stimulus-response mapping interference than congruent arrays, resulting in greater need for control. Likewise, in the Simon task (Hommel, 1993; Simon, 1969), conflict is achieved by manipulating the location (left or right) of presentation of stimuli requiring left or right responses. In other types of conflict tasks, such as the Stroop task mentioned earlier (and its variants, such as the spatial Stroop used by Baniqued et al., 2018), interference effects are exacerbated by juxtaposing a prepotent tendency to process some stimulus features (e.g., read words) and/or strong stimulus-response associations (e.g., the tendency to shift eye gaze towards the direction of a sudden-onset stimulus) against task-specific

instructions to focus on a weaker stimulus feature (e.g., ink color) or to respond using a counterintuitive stimulus-response association (e.g., shift gaze *away* from a sudden-onset stimulus, as in the saccade/anti-saccade task). In Miyake and Friedman's view, these tasks are considered tests of inhibitory (or Common-EF) function (Miyake & Friedman, 2012).

2.2.1 Trial by trial modulation of cognitive control. In conflict (and other) paradigms, cognitive control can also be examined in the effects of trial-to-trial variations in performance that arise from changes in the expectation that the irrelevant feature might be associated with the correct response. For instance, in the Eriksen Flanker Task, when trial N is congruent (i.e., there is compatibility between target and noise features, e.g., >>>>), this may reinforce the association between noise features and responses, leading to an increased conflict effect to incongruent stimuli on the subsequent trial (i.e., trial N+1) as compared to when the target and noise features were incongruent at trial N. A similar effect can be obtained by using external, arbitrary cues that are associated with different probabilities of subsequent congruent and incongruent trials. This *conflict adaptation effect* was first reported by Gratton, Coles, and Donchin (1992; see also Botvinick et al 2001; Ghinescu et al., 2010; 2016; Van Gunten, Volpert-Esmond, & Bartholow, 2018), and is generally considered as a classic example of a cognitive control phenomenon, in which the attention weights assigned to different stimulus features are dynamically changed depending on their expected utility. Using Miyake and Friedman's terminology, conflict adaptation can be viewed as a shifting phenomenon, since the relationships between specific cues and responses exist in advance of the trial in which the effect is observed.³ Importantly, the

³ The actual mechanisms leading to the phenomenon of conflict adaptation have been the subject of a large debate. Some authors, such as Ulrich Mayr (e.g., Mayr, Awh, & Laurey, 2003 see also Nieuwenhuis et al., 2006) have argued that sequential conflict adaptation mostly reflects the "hot-hand" phenomenon, by which the repeated use of the same stimulus-response association leads to faster responses – and therefore it is not related to a real attention control mechanism. This, however, does not explain the fact that conflict adaptation may occur even as a function of cues that do not require a response, a finding already present in the original Gratton et al. (1992) paper, first demonstrating the conflict adaptation phenomenon. A number of other studies (such as Ullsperger et al., 2005; Van Steenbergen, et al., 2009, 2010; Weissman et al., 2014) have presented additional evidence against the hot-hand argument. A somewhat different account for conflict adaptation is present in the work of Bernhard Hommel (e.g., Spape & Hommel, 2008), who argued that conflict adaptation involves the re-

changes in attention weights during conflict adaptation occur on both congruent and incongruent trials (albeit in different directions). Note that conflict, *per se*, should only occur on incongruent trials. However, the dynamic adjustments indexed by conflict adaptation show that conflict level is assessed continuously against changing contextual and subjective cues. Note also that the presence of conflict adaptation may tend to mitigate or erase interference effects in conflict paradigms when the congruent and incongruent conditions are blocked – a phenomenon that may be relevant to the interpretation of brain imaging data obtained in this fashion using conflict paradigms.

2.3 Response inhibition paradigms. Like conflict paradigms, these paradigms also involve monitoring conflict, in this instance between a prepotent tendency to emit a response and the need to withhold that response under certain circumstances (for example **Wessel, 2018**). Paradigms such as the go-nogo task (Fig. 1C) involve a primary task that requires a response (e.g., a 2-choice decision task such as "press left for *X* and right for *O*") as well as an infrequent contingency condition that requires this response to be withheld (e.g., do not respond to red stimuli). Here, the properties of the stimulus itself determine whether to implement the S-R association, select and execute a response or, alternatively, to interrupt this process and wait for the next trial. A variant of this is the A-X continuous performance task (AX-CPT; e.g., Gonthier et al., 2016; Lopez-Garcia et al., 2016). In this paradigm, a response needs to be given to X on a trial, but only if the X was preceded by an A on the immediately preceding trial. This paradigm mixes some of the elements of continuous working memory tasks (such as the N-back task) with those of go-nogo tasks, and therefore can be expected to tax multiple aspects of cognitive control. The stop-signal task requires the urgent interruption of a prepared, prepotent response that is already ongoing. Here, the primary *'go'* task is occasionally interrupted by a stop-signal – often a tone or a stop

instantiation of specific episodic links between stimuli and responses, which is considered to be an "automatic" process (similar views are also presented by Verguts & Notabaert, 2009; Schmidt, 2013). This account, however, is still consistent with the idea that conflict adaptation is due to attention/cognitive control mechanisms, since it is mediated by variations of the weights given to particular stimulus features in driving responses (which corresponds to the process of "shifting" in Miyake and Friedman's terms).

sign – that occurs very soon after the target and signals the need to withhold the response to the primary task. Although all these paradigms involve cognitive control processes to suppress a prepotent motor response, they differ in the stage at which the interruption is implemented: response planning for the go/nogo task and response execution for the stop-signal task.

2.4 Task-switching paradigms. These paradigms (Allport, Styles & Hsieh, 1994; Rogers & Monsell, 1995; Meiran, Chorev & Sapir, 2000; Rubinstein, Meyer, & Evan, 2001; Monsell, 2003) target cognitive control mechanisms required to shift between goals or "task sets" (e.g., classifying the number 3 based on parity [odd vs. even] or magnitude [<5 or >5], see Figure 1D; for overview of paradigms see Kiesel et al., 2010, and Jamadar, Thienel & Karayanidis, 2015; see also Baniqued et al., 2018; Provost et al., 2018). Here, cognitive control processes are required to implement the information provided by external cues (e.g., the letters P or M, to indicate parity or magnitude, presented prior to the stimulus, see Fig. 1D) or internal cues (e.g., implement an instruction to change task every two trials) on the current target. These paradigms produce robust switch costs (i.e., increases in response time on switch trials [e.g., AB] compared to repeat trials [e.g., AA]), as well as mixing costs (i.e., increased response times on repeat trials in a mixed-task [e.g., ABAAA...] compared to a single-task block [e.g., AAAAA...]. One can conceptualize mixing costs as resulting from a sustained increase in control under conditions of increased conflict, and switch costs from transient increases in control in response to trial-to-trial variability in conflict. These effects have been shown to be differentially sensitive to manipulations of memory load and post-target conflict (for reviews see Kiesel et al., 2010; Vandierendonck et al., 2010). Seminal work by Rogers and Monsell (1995) showed that switch costs (a) diminish when the paradigm provides advance information about an impending switch trial, and (b) remain significant even with very long preparation intervals. Hence, variations of the task-switching paradigm are used to manipulate both proactive control processes involved in trial-to-trial shifts in task-set in anticipation of target onset, and reactive control processes involved in implementing the updated task-set on the target (see below

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for discussion of Braver's [2012] dual mechanisms of cognitive control framework). By modeling the RT distributions for switch and repeat trials, de Jong (2000) showed that control processes involved in preparation to switch are not necessarily engaged on every trial, but can be variably employed across trials. Moreover, analyses modeling ERPs as a function of RT showed that trial-by-trial variability in preparation to switch task is associated with reduced RT switch cost (Karayanidis et al., 2011, see also **Provost et al., 2018** for effects of trial-by-trial variability in conflict processing). A particular strength of the task-switching paradigm is that variations in task and timing parameters can introduce manipulations of working memory, stimulus and/or response level interference and response inhibition demands within the same base paradigm (e.g., Meiran, 2000).

2.5 Error processing. In all paradigms reviewed above, adaptive control of behavior can also be assessed by examining processes associated with feedback information and/or with adapting performance following an error (e.g., Falkenstein, Hohnsbein, Hoorman, & Blanke et al., 1991; Gehring et al., 1993; see also **Grammer et al., 2018**). Error processing mechanisms involve using internal or external feedback to identify having committed an error, as well as adjusting behavior to avoid further errors. For example, after an error, response control processes are engaged to correct behavior, which manifests as slower reaction time on the next trial. These feedback and error processing mechanisms are implemented in varying degrees in all above paradigms, allowing for performance monitoring and adjustment to be dissociated from other cognitive control processes (Cho et al., 2009; Van Veen & Carter, 2006).

In this brief overview, we have shown how, by fractionating cognitive control mechanisms, these experimental paradigms enable the study of the neural substrates of distinct subcomponents in a way that neuropsychological tasks cannot achieve. In the next section, we briefly review the main neurocognitive findings that have informed extant theories of cognitive control.

3. Brain Mechanisms in Support of Cognitive Control

Studies of patients with brain lesions as well as studies of individual differences across task conditions and over the lifespan have provided crucial evidence for neurocognitive models of cognitive control (see empirical papers in this special issue focusing on differences across groups, e.g., **Boudewyn & Carter, 2018**; **Grammer, Gehring, & Morrison, 2018**; **Baniqued et al., 2018**, and across conditions or trials in the same individuals, e.g., **Barceló & Cooper, 2018**; **Provost et al., 2018**). Each of these topics has been the subject of recent in-depth reviews (e.g., development: Hughes, 2013; aging: Fabiani, 2012; schizophrenia: Lesh et al., 2011). Here we provide a brief synopsis.

3.1 Lesions studies. As noted earlier, the systematic examination of the symptomatology and neuropsychological performance of patients with frontal lobe lesions (e.g., Milner, 1963) led to a hypothesized link between the structural integrity of the frontal lobes and the set of processing abilities that is now referred to as the executive/cognitive control system. Patients with frontal dysfunction or lesions often exhibit apathy and perseveration, or, at the other end of the spectrum, disinhibition and inappropriate behaviors (Rosen et al., 2004; Stuss & Alexander, 2007). More generally, frontal lobe patients often display behaviors that suggest a difficulty in monitoring and interpreting contextual cues so as to adapt task goals and suppress inappropriate actions. For instance, they often show utilization behaviors, responding in a stereotyped manner to proximal stimuli irrespective of context (e.g., massaging the shoulders of a stranger seated in the pew in front of them in church; Lhermitte 1983). These behaviors are taken to index lack of flexible goal adaptation and perseveration of responses in the face of a changing environment, all hallmarks of failing cognitive control. These studies have helped to identify the prefrontal cortex as a key player in the circuitry supporting control processes.

Lesions of the anterior cingulate cortex (ACC) and parietal cortex can also affect cognitive control processes. For example, Bush, Luu, and Posner (2000) described the effects of ACC lesions as producing

a "host of symptoms, which include apathy, inattention, dysregulation of autonomic functions, akinetic mutism and emotional instability," as well as specific deficits in conflict tasks (e.g., Stroop), all consistent with deficits in cognitive control. Lesions in the parietal cortex, and particularly the right hemisphere, also often elicit hemineglect, a failure to actively shift attention toward external stimuli in (typically the left) half of the visual field (Corbetta & Shulman, 2011). It is important to consider, however, that most investigators consider the parietal cortex as the "recipient", rather the "actor" of cognitive control operations (see e.g., Requin et al., 1990; Fuster, 2008). That is, parietal regions are assumed to be the target of control, i.e., the areas that hold the spatial attention weights used for biasing the processing of incoming information, rather than the areas where cognitive control operations are selected (prefrontal regions).

3.2 Lifespan development studies. Cognitive control processes are also known to change over the lifespan. In children and adolescents, development of control processes (Hommel, Kray & Lindenberger, 2011; Kray, Schmitt, Heintz & Blaye, 2015; see also Crone & Steinbeis, 2017) appears to mirror that of the prefrontal cortex, which does not reach structural and functional maturity until the early-mid 20's (Lenroot & Giedd, 2006; see also Bunge, 2002; Tamnes, Hertingm Goddings, Meuwesem et al., 2017). Changes in control processes are also known to occur at the other end of the age spectrum, which is typically characterized by moderate reduction in some aspects of cognitive control. For instance, older adults typically perform more poorly than younger adults in neuropsychological tests tapping into control functions, such as the WCST (e.g., Fabiani & Friedman, 1995; for reviews see Salthouse, 2010; West, 1996; Moscowitch & Winocur, 1992), as well as in typical laboratory control tasks (e.g., Hsieh et al., 2012; Kray & Lindenberger, 2000; Meiran, Gotler & Perlman 2001; Whitson et al., 2011; for review see Ruthruff & Lien, 2016). These findings, coupled with evidence of disproportionate age-related volumetric reductions in prefrontal regions (Raz et al.; 2010; Gordon et al., 2008) suggest that prefrontal dysfunction significantly contributes to age-related cognitive decline.

Some theories of cognitive aging emphasize the impact of a specific cognitive control process (e.g., inhibition, Hasher & Zacks, 1988; working memory capacity, Craik & Byrd, 1982; see also Gordon et al., 2014; for a review see Fabiani, Zimmerman & Gratton, 2015) or a specific mechanism (e.g., speed of processing, Salthouse 2000). Others attempt to integrate the complex picture of behavioral and neural changes that emerge with increasing age into a broader theoretical framework that can account for the vast individual variability in cognitive profiles across the lifespan and, more so, at the older end of the age spectrum. For instance, reduced efficiency of top-down control mechanisms (e.g., CRUNCH, Reuter-Lorenz, 2008) can incorporate both reduced structural/functional connectivity, and increased frontal and bilateral cortical recruitment at lower levels of cognitive load in older adults (see Schneider-Garces et al., 2010). Importantly, declines in prefrontal cortex tissue and cognitive control performance in older adults are increasingly shown to vary with the presence of modifiable cardiovascular and cerebrovascular factors (e.g., Jolly et al., 2016; Chiarelli et al., in press; Fabiani et al., 2014a, 2014b; Tan et al., 2016; 2017; Zimmerman et al., 2014) and to be, at least partly, mitigated by cardiorespiratory fitness (Kramer et al., 1999; Gordon et al., 2008; Fletcher et al., 2016). Exercise intervention programs appear to stave off, if not reverse, some of the declines in cognitive control found in older adults (Colcombe & Kramer, 2003; Heyn et al., 2004; Smith et al., 2010; Bherer et al., 2013; Gajewski & Falkenstein, 2016) and more recently in inactive children (Hillman et al., 2008; Chaddock et al., 2012). These findings highlight the complex interactions between lifestyle and neural influences on the development of cognitive control processes across the lifespan, that are encapsulated in Reuter-Lorenz's and Park's (2014) STAC-r theory of aging, and in Fabiani's (2012) GOLDEN aging framework.

3.3 Psychopathological studies. Cognitive control deficits are also central symptoms in many psychopathological conditions, including schizophrenia (e.g., Boudewyn & Carter, 2018), depression (for review see Paulus, 2015) and addiction (e.g., Hester et al., 2009; Fleming & Bartholow, 2014). In fact, under the Research Domain Criteria (RDoC) framework, cognitive control deficits are considered

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defining characteristics for some psychopathologies (Kozak & Cuthbert, 2016). Importantly, disruption of the same cognitive mechanism (e.g., the ability to inhibit actions or thoughts) may lead to different maladaptive behaviors in different conditions. For instance, difficulties with response inhibition are central to ADHD, whereas difficulties inhibiting emotionally negative representations and memories are associated with rumination in depression and with difficulties in emotion control in anxiety disorders.

3.4 Electrophysiological data. As cognitive control is typically implemented in rapidly transitioning environments, the excellent temporal resolution of EEG is particularly suited to capture its *temporal scale*. Time-locking the EEG signal to temporally distinct significant events (e.g., preparatory cues, imperative stimuli, correct or incorrect responses) facilitates teasing apart the relative contributions of cognitive control processes with markedly distinct temporal and neural signatures.

A considerable body of work has focused on ERP components elicited during typical experimental paradigms associated with conflict detection and monitoring, such as the conflict tasks described earlier. Work with these paradigms typically focuses on ERP components associated with conflict detection and interference management processes that emerge in stimulus-locked ERP waveforms, and with error detection and adaptation processes that can be measured in response-locked waveforms.

3.4.1 N2 and N2-like components (including the error-related negativity, ERN). In stimulus-locked ERP waveforms, conflict paradigms elicit an N2 component, peaking around 200-400 ms and maximal over frontocentral electrodes (e.g., Folstein & Van Petten, 2008; Fig. 2, left column). This N2 is significantly larger for stimuli associated with greater conflict (e.g., incongruent color words, stimuli masked by incongruent flankers or mapped to an incongruent response). Evidence from source modeling (e.g., Bocquillon et al., 2014; Huster, Westerhausen, Pantev, & Konrad, 2010; Ladouceur, Dahl, & Carter, 2007; Nieuwenhuis, Yeung, Van Den Wildenberg, & Ridderinkhof, 2003), and direct recording from the cortex (Wang, Ulbert, Schomer, Marinkovic, & Halgren, 2005; Yeung, Botvinick, & Cohen, 2004; Yeung, Cohen, & Botvinick, 2011) suggest that the N2 is generated within the anterior-central cingulate

cortex - a key node within conflict monitoring loops (MacDonald, Cohen, Stenger, & Carter, 2000; Botvinick, Braver, Barch, Carter, & Cohen, 2001; see also Shackman et al., 2011 for a more general view of the cingulate cortex).

Response-locked ERPs show N2-like ERP components, such as the ERN, which are generated specifically when response conflict is explicitly signaled (Fig. 2, middle and right columns). Like the N2, the ERN appears to originate from the ACC (Herrmann, Rommler, Ehlis, Heidrich, & Fallgatter, 2004; lannaccone et al., 2015; Luu, Tucker, & Makeig, 2004; van Veen & Carter, 2002), and hence is likely to index early conflict detection similar to that of the N2 proper. Both negativities are thought to manifest a process of signaling the need for activation of goal-appropriate networks and therefore to be strongly involved with cognitive control operations. Together they capture early, transient and rapid adjustments of the cognitive control system on a 'needs' basis, providing a correlate of reactive cognitive control associated with conflict-related adjustments of behavior.

INSERT FIGURE 2 ABOUT HERE

3.4.2 P300 complex. Whereas frontal negativities appear to be especially sensitive to the *reactive* control processes required to deal with stimulus-driven or response-driven interference, the ubiquitous P300 complex appears to be sensitive to both proactive and reactive control adjustments. A major distinction is made between the frontal P3a, which is often associated with orienting and novelty (e.g., Knight, 1984; Fabiani & Friedman, 1995; Fabiani et al., 1998), and the parietal P3b, which is linked to "context updating" (including the updating of stimulus-response associations) and task complexity (see Donchin, 1981; Donchin & Coles, 1988; Johnson, 1993; Polich, 2007; Verleger, Jaśkowski, & Wascher, 2005).

Within the context of experimental paradigms manipulating cognitive control, a large parietally maximal P300 is sensitive to both goal and task demands, and is modulated by perceptual, motor and contextual task complexity and the consequent need for increased proactive control. For example, in

task-switching paradigms, ERPs time-locked to the onset of *cues* that herald the need to change the task to be performed on the upcoming target elicit a larger parietal positivity than cues that herald a task repeat (for a review see Karayanidis et al., 2010; Karayanidis & Jamadar, 2015; see also Gratton, Low & Fabiani, 2008; Baniqued et al., 2013, for a similar phenomenon shown with optical imaging). The finding that, on switch (but not repeat) trials, faster responses are associated with larger amplitude of this cuelocked parietal positivity has been interpreted as suggesting that this positivity indexes switch preparation processes, such as task-set updating (Karayanidis, Provost et al., 2011). Moreover, cuelocked parietal positivities measured within a similar latency are larger for repeat trials in mixed-task than single-task blocks (Jost, Mayr, & Rösler, 2008; Karayanidis, Whitson et al., 2011), and for cues that indicate with certainty that the task *will* change vs. that the task *may* change, even when the task identity is not specified by either cue (Karayanidis et al., 2009; see Figure 3). There is less clear consensus regarding whether this cue-locked index of proactive control represents a pure modulation of the parietal P3b or a distinct ERP component superimposed on a P3b (Karayanidis et al., 2010). Recent suggestions that the P300 complex may represent goal-specific modulations of control networks dependent on context (see **Barceló & Cooper, 2018)** would argue in favor of the former option.

INSERT FIGURE 3 ABOUT HERE

A P300 is also observed for *target* stimuli. In this case, the P3b is *smaller* for a task switch than for a task repeat (Karayanidis, Coltheart, Michie, & Murphy, 2003) and for targets associated with slower than with faster responses (**Provost et al., 2018**). These target-locked switch effects are generally accepted as modulations of the posterior P3b under conditions that require reactive control to facilitate accurate decision-making⁴.

⁴ The criteria for establishing whether differential modulation of a parietal positivity by any given task manipulation qualifies as a P3b effect remain poorly specified. For instance, the amplitude of a stimulus-locked parietal positivity has been shown to be smaller in conditions that increase task complexity or decision difficulty, such as incongruent vs. neutral targets (Hsieh & Liu, 2008), dual vs. single task performance (Tieges, Snel, Kok, Plat,

3.4.3 Oscillations. The above ERP components are clearly temporally sensitive to goal- and/or context-specific modulations of control networks that dynamically process contextual information. It is increasingly recognized that these ERP components emerge at the endpoint of oscillatory communications across control networks, characterized by distinct frequencies, with slow frequency theta oscillations (4-8 Hz), in particular, been championed as the lingua franca of cognitive control (see Cohen, Elger, & Ranganth, 2007; Cavanagh, Cohen, & Allen, 2009; Cohen & Cavanagh, 2011; Cohen, 2011; Cavanagh & Frank, 2014; Sauseng, Griesmayr, Freunberger, & Klimesch, 2010). During conditions that require cognitive control, theta oscillations, particularly over midfrontal cortex, show increased power in transient bursts as short as 300 ms or sustained trains that can exceed 10 sec (Mitchell, McNaughton, Flanagan, & Kirk, 2008). Transient bursts of frontal theta have been associated with need for moment-to-moment reactive adjustment of control. For instance, midfrontal theta power increases when updating working memory (Jacobs, Hwang, Curran, & Kahana, 2006; Jensen & Tesche, 2002; Klimesch et al., 2005), inhibiting a response (Funderud et al., 2012; Kamarajan et al., 2004) or identifying/correcting an error (Cavanagh, Cohen, & Allen, 2009; Luu et al., 2004; Trujillo & Allen, 2007). In contrast, sustained theta coherence between frontal and posterior sites has been reported in contexts that require updating or maintaining a task goal (Moore, Gale, Morris, & Forrester, 2006; Moore, Mills, Marshman, & Corr, 2012; Sauseng, Klimesch, Schabus, & Doppelmayr, 2005) across a range of contexts, including switching tasks (Cooper et al., 2015; Sauseng et al., 2006) and internally guiding attention (Aftanas & Golocheikine, 2001; Cahn & Polich, 2006). Given the range of contexts that show modulation in theta oscillatory activity, it has been suggested that theta oscillations may facilitate complex, flexible adjustments of frontal control circuits based on current contextual demands (Voytek et al., 2015). That is, theta oscillations may facilitate distinct goal-directed processing via a common

[&]amp; Ridderinkhof, 2007). (But see Sirevaag et al., 1989; Low et al. 2009, for evidence of P3 amplitude crossover across primary and secondary tasks).

mechanism – establishing transient functional assemblies through dynamic communication between task relevant cortical regions.

Despite the broad time course of theta oscillations, most studies have examined the association between theta activity and reactive control processes. However, there is increasing evidence that proactive or anticipatory control dynamics are also sensitive to modulations in multiple frequency bands, including theta. For instance, high frequency gamma (>30 Hz) is increased during working memory maintenance periods (Jokisch & Jensen, 2007; Kaiser, Ripper, Birbaumer, & Lutzenberger, 2003) and is uniquely tied to specific information that is encoded in working memory (Howard, 2003; Lundqvist et al., 2016). Blocking of alpha band activity is a common signature of working memory encoding for future retrieval (Jensen, Gelfand, Kounios, & Lisman, 2002; Klimesch et al., 2005; Sauseng et al., 2005). Selective attention and proactive inhibition are associated with changes in alpha power over posterior sites (e.g., Foxe & Snyder, 2011; Fu et al., 2001; Hanslmayr, Gross, Klimesch, & Shapiro, 2011; Ikkai, Dandekar, & Curtis, 2016). Moreover, activity in posterior alpha (Foxe, Murphy, & De Sanctis, 2014; Mansfield, Karayanidis, & Cohen, 2012), theta (Cooper et al., 2015; Cunillera et al., 2012; Sauseng et al., 2006) and central beta (Gladwin, Lindsen, & de Jong, 2006) has been linked to advance preparation for switching tasks in task-switching paradigms. Recently, Cooper, Darriba, Karayanidis, and Barceló (2016) showed evidence of a frequency hierarchy that appears to map onto the hierarchical structure of cognitive control proposed by recent models (e.g., Koechlin & Summerfield, 2007): Simple S-R processes were associated with activity in lower frequencies, whereas abstract, future-oriented control processes were linked to activity in higher theta and alpha bands. These findings suggest that control networks engage a complex interplay across multiple frequency bands and multiple time scales to facilitate contextually appropriate cognition.

3.5 fMRI data. Over the past decade and a half, a substantial body of fMRI studies has sought to identify brain areas activated during tasks requiring cognitive control, and to define how these areas are

functionally related with each other and co-activated within specific networks. C. Gratton et al. (2018) recently reviewed this literature, so here we only provide a brief summary. Similarly to the subcomponent structure based on performance data proposed by Miyake and Friedman (2012), brain activity related to cognitive control can also be decomposed into three partly dissociable networks: A dorsal fronto-parietal network (DFPN, also called dorsal attention network, DAN), a ventral frontoparietal network (VFPN, also called ventral attention network, VAN), and a mid-frontal (cingular cortex) and anterior insula (operculus) network (cingulo-opercular network, CON)⁵. Interestingly, this structural distinction is evident both in activation patterns during tasks involving cognitive control and in spontaneous brain activity recorded during resting conditions (i.e., when cognitive control is not manipulated). This framework for identifying distinct brain networks that support specific aspects of cognitive control should not necessarily be considered incompatible with meta-analytic and other reports of the existence of a domain general frontal/cingulate/parietal neural system that supports cognitive control across a diverse range of executive functions (Niendam et al., 2012). Rather, what we refer to as domain-general cognitive control (Common-EF or executive function) should be viewed as an emergent property derived from the interplay between these different networks, whose relative roles can be discerned by comparing specific tasks conditions.

A large number of studies have investigated the specific conditions under which different networks are activated. By and large, DAN is activated during conditions in which control is needed to select, maintain or switch between one or more sets of stimulus-response rules that are mapped to different contextually defined task goals. Functional MRI studies have shown that components of this network are activated in task-switching paradigms, and more strongly so for switch than for repeat trials (for reviews

⁵ The distinction between these networks is not always clear. For instance, some studies make distinctions between medial and lateral frontal networks (e.g., Miller & Cohen, 2001), without differentiating between ventral and dorsolateral regions. Other studies emphasize the distinction between dorsal and ventral regions, in the absence of a clear distinction between medial and lateral frontal regions (Corbetta & Shulman, 2002). In particular, the distinction between CON and VAN is not often made (e.g., **C. Gratton et al., 2018**).

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see De Baene, Kuhn & Brass, 2012; Ruge et al., 2013; see Activation Likelihood Estimation [ALE] metaanalyses in Jamadar et al., 2015). This network could therefore be viewed as supporting "shifting" operations in Miyake and Friedman's view. However, the correspondence between the other two networks and the "updating" and "inhibitory" subcomponents of control is less clear. There is certainly evidence for unique circuitry associated with certain forms of response inhibition (e.g., right inferior frontal gyrus and subthalamic nucleus; Aron, Robbins, & Poldrack, 2014; Hampshire & Sharp, 2015), and this may suggest that VAN is associated with inhibitory functions. However, VAN is also clearly activated by novel stimuli, and has therefore been associated with orienting (Corbetta & Shulman, 2002), a construct related, but not identical, to the concept of "updating". Similarly, the specific relationship of CON with any of the components identified by Miyake and Friedman is unclear. CON activation is correlated with a number of independent variables often manipulated in cognitive control studies, including, among others, conflict level and motivation.

This apparent lack of a direct correspondence between cognitive constructs and neural networks raises an important caveat, which we often neglect in our search for brain-behavior correspondence. Psychological constructs *do not need* to bear a one-to-one relationship to the activation of any brain area or set of areas (Sarter, Berntson & Cacioppo, 1996; G. Miller, 1996). In fact, this is an unlikely scenario. Psychological constructs are typically multi-determined and likely to correspond to emergent functions that are born out of the interaction of many different brain regions and networks. For these reasons, looking for a direct correspondence between brain networks and constructs derived from Miyake and Friedman's factor analyses of different tasks, or indeed any other classification of task performance, may be entirely inappropriate or even misleading.

3.6 MEG and fast optical signals. Electrophysiological data provide excellent temporal information and fMRI data provide excellent spatial resolution. However, integrating information across these two domains can be challenging, despite some fruitful attempts to do so using either simultaneously

recorded EEG/fMRI data or data recorded independently using identical task parameters (e.g., Jamadar et al., 2010; Tschentscher & Hauk, 2016; Sadaghiani et al., 2010; Silton et al., 2011). Combining spatial and temporal resolution is especially important when investigating the *dynamics* of the cortical activations that support cognitive control operations. Methodologies such as magnetoencephalography (MEG) and fast optical signals (FOS and event-related optical signals, EROS; Gratton & Fabiani, 2010) provide a good combination of both dimensions and may facilitate the use of Granger causality approaches for modeling the temporal dynamics of processes that characterize cognitive control (e.g., Rykhlevskaia, Fabiani, & Gratton, 2006).

Brass et al. (2005) recorded MEG during task switching and showed that frontal and parietal foci are activated in rapid succession (300-400 ms for frontal and 400-500 ms for parietal, respectively) after cues signaling a task change (see also Steffen, Rocksroh, Wienbruch, & Miller, 2011). This finding is consistent with results obtained with EROS (Baniqued et al., 2018; Gratton et al., 2009; Leaver et al., 2015; for a review see Gratton, Low & Fabiani, 2008). By combining temporal and spatial properties, EROS data can indicate which levels of the network are being activated over time. For instance, in task switching, medial frontal structures (which may be part of CON) showed early activation (≤300ms) in response to preparatory cues signaling a task switch, regardless of the specific task being cued (domaingeneral preparation; see Fig. 4). In contrast, later activations ≥ 600 ms) were specific to the cortical regions associated with the particular task being switched to. These later activation may correspond to the task-specific reprogramming of attention filters in the cortical regions that are used to process taskrelevant information, as predicted by several models of cognitive control. These findings are consistent with ERP evidence of temporally distinct posterior positive components: an early positivity (~250-300ms) associated with preparing to switch (in the absence of information about the identity of the task) and a later one (~500-600ms) elicited only when the switch cue also specified the task to be performed (Karayanidis et al., 2009). Interestingly, a time-frequency analysis of EROS data reported by

Leaver et al. (2015) indicated that some of these activations are associated with theta bursts, again consistent with time-frequency analyses of EEG data (Cooper et al., 2015).

EROS has also been used to investigate the spatio-temporal dynamics of processes leading to alpha activation or suppression prior to or at the moment of stimulus presentation in detection tasks (Mathewson et al., 2014). Mathewson et al. (2009) showed that posterior alpha amplitude and phase at the moment a weak stimulus is presented mediates its detectability – suggesting that alpha might serve as an attention-gating mechanism. Mathewson et al. (2014) used lagged cross-correlation methods to predict the generation of the posterior alpha related to the detection of a weak stimulus. A time-frequency analysis of the EROS data showed that this posterior alpha was generated in the precuneus (a posterior parietal region close to the occipital cortex). Activity in structures within DAN and CON occurring a few hundred milliseconds before stimulus onset predicted (albeit in opposite directions) the amplitude of alpha at the moment of stimulus onset, which, in turn, mediated stimulus detection. These data suggest that both CON and DAN are involved in setting up alpha-based attention-gating mechanisms instrumental to cognitive control.⁶

INSERT FIGURE 4 ABOUT HERE

3.7 Transcranial magnetic stimulation (TMS) and other cortical manipulation data. An important caveat about using brain activation data to inform theories of cognitive control is that these data can only provide correlational rather than causal information. TMS and other methods that can interrupt or otherwise influence cortical activity can provide more specific evidence for causation (see Van Campen et al., 2018). For example, Sauseng, Feldheim, Freunberger, and Hummel (2011) ran a combined EEG/repetitive TMS (rTMS) study that supported the role of DAN in regulating posterior alpha as an information-gating mechanism. They showed that TMS in right prefrontal regions suppressed anticipatory alpha lateralization in a Posner's cueing task, and eliminated the relationship between

⁶ An alternative view of this gating mechanism is that it is based on the transient enhancement of cortical processing for relevant stimuli (e.g., Egner & Hirsch, 2005).

alpha activity and detection rate. This finding is consistent with Mathewson et al.'s (2014) study indicating that structures within DAN may be involved in controlling posterior alpha (see also Romei, Gross, & Thut, 2010; Capotosto, Babiloni, Romani & Corbetta, 2009).

4. Neurocognitive Theories of Cognitive Control

In this section, we provide a brief overview of how evidence from different methodologies has informed several prominent models of cognitive control.

Theories based on analyses of individual differences. There are a number of theories of cognitive control, which, like Miyake and Friedman's framework presented earlier, aim to decompose this complex phenomenon into partially independent functional processes (e.g., updating, shifting, and inhibition or Common-EF in the above framework) that can account for most of the inter-individual and intra-individual (life-span) variability in cognitive control. Most theories of the neural mechanisms in support of cognitive control propose that at least some of these subcomponents have some level of correspondence with specific structures, networks of structures, or physiologically defined events occurring in the brain (e.g., Stuss, 2011). However, as discussed earlier, this correspondence is not necessary, as components identified at the psychological level may be emergent properties of the information processing system as a whole. That being said, seeking some form of correspondence between observable brain phenomena and putative psychological mechanisms may facilitate the process of testing theories of cognitive control.

As noted earlier, clinical observations already available in the 1960's (e.g., Milner, 1963) provided links between frontal lobe lesions and deficits in the executive function/cognitive control system. Based on such evidence, a number of theories emerged in the 1980's, which evoked the existence of a central, top-down system that modulates processing in lower cortical areas. For instance, Mesulam proposed that representational levels of task goals and motivations take place in different cortical regions (such as the parietal, frontal, or cingulate cortex) and influence the bottom-up flow of information (Mesulam.

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1990). Baddeley (1996; see also Baddeley & Hitch, 1974) proposed a view of working memory function in which a central executive – a system that holds current task-goal representations – employs slave systems (i.e., visuo-spatial scratchpad, articulatory loop) to keep specific representations available for addressing task demands. Similarly, Norman and Shallice (1986) proposed a "supervisory attentional system" that controls the implementation of contextually appropriate "schemata" – a concept similar to task-goal representations. While offering a useful framework for conceptualizing the organization of executive control mechanisms and the subservient systems that support them, these theories do not inform our understanding of the operations by which such systems implement top-down control.

Unlike the above theories, which posit a single executive mechanism that is implemented in the prefrontal cortex and can explain failures in cognitive control across a number of tasks, most neural theories of cognitive control argue that the prefrontal cortex can be segregated into distinct lateral and medial prefrontal regions, which make different contributions to cognitive control. Here, we briefly overview some of the most prominent theories that parse the concept of cognitive control along different lines.

4.1 Theoretical ideas based on the temporal organization of cognitive control. As briefly reviewed earlier, the functional significance of several ERP components has been closely linked to aspects of cognitive control, providing a way to understand the temporal dynamics of control processes on a millisecond scale. Although the theoretical ideas presented in this section do not necessarily have the status of complete/explicit theories of cognitive control, they are highly relevant to this discussion. For example, Donchin (1981; see also Donchin & Coles, 1988) proposed that the P300 (or P3b) manifests the occurrence of updating of working memory representations – clearly linking this ERP component to the "updating" control process. According to Donchin, the fact that the P300 may occur *after* a response is emitted suggests that the P300 itself cannot be part of the feed-forward series of decision processes leading to the response. Rather, P300 is assumed to be related to *future* strategic adjustments, such as

changing how information on the following trials will be processed – a proactive/preparatory function eminently within the realm of cognitive control. Gratton et al. (1992) provided data supporting this view: the size of the conflict adaptation effect occurring *subsequent* to a symbolic cue is related to the amplitude of the P300 elicited by the cue itself (see also Donchin et al., 1988 for a similar predictive effect after an error trial). Brumback et al. (2005; see also Peltz et al., 2011) also provided evidence for a relationship between working memory capacity and the need for updating as a participant processes a sequence of stimuli, with variations occurring on a trial-by-trial basis depending on the nature of the sequence (i.e., how many stimulus repetitions occurred in a row). This, again, reflects the fact that cognitive control processes are engaged continuously with finely tuned variations over very short time scales.

Action monitoring systems within the prefrontal cortex (i.e., lateral PFC – medial PFC; Gehring & Knight, 2000) may also operate in a phasic fashion, generating time-sensitive periods for cognitive control processing. Such a phasic phenomenon may be reflected by the error-related negativity (ERN), where incorrect decisions/responses elicit a negative-going component rapidly following an error (Gehring, Goss, Coles, Meyer, & Donchin, 1993; Gehring, Coles, Meyer, & Donchin, 1995). Here, the rapid occurrence of an ERN underpins a fast set of cortical dynamics that serve to adjust *future* behaviour on the basis of past inappropriate responding. Importantly, these dynamics are top-down in nature (see MacDonald et al., 2000; Botvinick et al., 2001). Source modelling and concurrent fMRI/EEG studies suggest that the ERN is generated in a neural system centered on the anterior cingulate cortex (Hermann, Römmler, Ehlis, Heidrich, & Fallgatter, 2004; Van Veen & Carter, 2002). Given this anatomical and functional evidence, it is likely that the ERN reflects an error detection signal used by performance monitoring mechanisms to strategically adjust behaviour in line with task goals. In this sense, the ERN reflects a transient signature of the cognitive control system that is used to bias future-oriented

decision-making, a crucial step in several models of cognitive control, including the control-loop theory discussed next.

4.2 Theories based on the spatial organization of cognitive control.

4.2.1 Control-conflict loop and related theories. The concept of adaptive cognitive control has been motivated by a well-established literature showing that trial-by-trial variations in performance reflect, in part, adaptation to the context set up by the preceding trial or trials, such as the occurrence of an error or a trial that elicited high levels of conflict. Whether different types of behavioral adaptation reflect a single supporting mechanism (i.e., conflict monitoring) or multiple mechanisms remains an area of very active investigation. The control-conflict loop theory posits a dynamic processing loop involving the ACC/pre-supplementary motor area (pre-SMA) and the dorsolateral prefrontal cortex (DLPFC; MacDonald et al., 2000; Botvinick et al., 2001; Ridderinkhof, Ullsperger, Crone, & Nieuwenhuis, 2004; Botvinick, Cohen, & Carter, 2004; van Veen & Carter, 2002). The ACC/pre-SMA mediates a monitoring function, which identifies brain states indicating an increased need to engage cognitive control. The DLPFC directs control in a task-relevant manner, so that task-relevant circuitry is optimally configured to support ongoing goal-directed behavior. Computational modeling using traditional PDP as well as Bayesian approaches and recent neurostimulation studies support many aspects of this model including the dynamic interactions between ACC/pre-SMA and DLPFC that are predicted to underlie conflict adaptation effects during adaptive cognitive control (MacDonald et al., 2000; Botvinick et al., 2001; Ridderinkhof et al., 2004; Botvinick et al., 2004; Carter, 2015; Reinhart, Zhu, Park, & Woodman, 2015).

Banich and her collaborators (e.g., Banich, 2009; Banich et al., 2009) introduced the *cascade-ofcontrol* model, an extension of the control-conflict loop theory. They proposed that the different sections of DLPFC and ACC are hierarchically organized so as impose top-down biases of selective processing features (e.g., stimulus selection, response selection), which promote task-relevant representations and inhibit automatic biases exhibited by strong pre-existing but task-irrelevant

representations. The level of control cascades, such that, for instance, more efficient early attentional biasing at the posterior DLPFC may reduce the need for later control of response selection processes at the level of posterior dorsal ACC. Interestingly, Banich et al. (2009) illustrate how this type of model can account for both cognitive and emotion control, providing a framework for integrating findings across these fields.

A further development of the dynamic control framework is Braver's *dual mechanisms of cognitive control* model (Braver, 2012). This model distinguishes two sets of control processes, at least partly on a temporal basis. *Proactive control* is implemented in a prospective, anticipatory manner based upon external cues or internal representations of trial history that enable predictions of the likelihood of conflict or other indicators of the need for cognitive control. In contrast, *reactive control* is implemented "on the fly", i.e., in response to encountering conflict during stimulus processing and responding. Both modes of cognitive control are supported by adaptive control mechanisms implemented by interactions between ACC/pre-SMA and the DLPFC as specified in the control-conflict loop theory. However, each mode of control is supported along different time scales by processes that differentially integrate conflict and control. Individual differences related to development, aging or clinical disorders impacting brain functioning may result from changes in one or both of these cognitive control modes (Braver, 2012; Braver & Barch, 2002).

A common feature of all above models is that they invoke a general-purpose prefrontal cognitive control network that consists of two main divisions: the lateral prefrontal cortex and the medial frontal cortex, with "direct" control being implemented by the lateral (primarily dorsolateral) PFC (see **C**. **Gratton et al., this volume**, for a more extended review of research on the different roles of cognitive control networks).

4.2.2 Anterior-posterior organization of control processes. A number of recent models posit further functional specialization of the lateral PFC along its anterior-posterior axis (Koechlin et al., 2003; Badre &

D'Esposito, 2009; Spielberg, Heller, & Miller, 2013; Nee & D'Esposito, 2016). Both Christoff and Gabrieli (2000) and Braver and Bongiolatti (2002) showed evidence that anterior areas of the PFC are specialized for guiding behavior on tasks that require "branching" cognition, or the processing of sub-goals in the context of superordinate goals. Koechlin, Ody, and Kouneiher (2003) proposed a related view where posterior aspects of the PFC support goal-directed responding based on the immediate sensory context, whereas more anterior areas support a broader temporal context, drawing upon information held in episodic memory to enable flexible cognitive control. Finally, based on findings from both fMRI and PFC connectivity studies, Badre and D'Esposito (2009) hypothesized that hierarchical organization within the PFC is based on task complexity, with reducing levels of representation complexity being held along the anterior to posterior PFC gradient (see also Koechlin et al., 2003; Nee & D'Esposito 2016). A detailed discussion regarding the generalizability of these models to more complex aspects of cognition including decision making (e.g., Badre, 2013) and reasoning (Donoso, Collins, & Koechlin, 2014) is beyond the scope of this review. It is important to note, however, that a key element of all these models is that they preserve the functional segregation of lateral and medial prefrontal cortical contributions to cognitive control as proposed by the earlier models. This functional segregation, which capitalizes on the reasonably fine-grained anatomical precision for defining functional circuits yielded by fMRI, has provided an important foundation for our understanding of the neuroscience of human cognitive control.

4.2.3 Network-based views of cognitive control. Largely based on analyses of functional connectivity both in active task conditions and in the resting state paradigm, Petersen and colleagues (Petersen & Posner, 2012, Posner & Petersen, 1990; see also **C. Gratton et al., 2018**) have proposed that at least two distinct networks are involved in cognitive control: a fronto-parietal network (FPN) and a cingulo-opercular network (CON). Analyses of the time-course of task-related activity in these two networks led to the observation that the CON shows sustained activation across the entire period in

which attention control needs to be exerted, whereas the FPN is activated in relatively shorter spurts (within the temporal dynamic ranges that can be ascertained with fMRI). Petersen and colleagues therefore propose that the CON may be involved with the setting up and long-term maintenance of task goals, whereas the FPN may be involved with "rapid," trial-to-trial adjustments in the relative emphasis given to different tasks. This distinction is reminiscent of Braver's differentiation between proactive/sustained vs. reactive/transient modes, as well as Miyake & Friedman's updating (for the CON) and shifting (for the FPN) constructs. It is also reminiscent of Cowan's view of working memory, in which representations that are available but not active may only require *shifting* to be made useable, whereas currently unavailable long-term memory representations may require *updating* to be brought within the focus of attention.

5. Discussion and Conclusions

A recurring theme in this review is that cognitive control should not be viewed as a unitary process, but rather as an emergent function born of the interaction of a number of elementary components. All lines of research, from lesion data to task and individual difference analyses, to spatial and temporal brain imaging data, point at the possibility of titrating cognitive control into a number of component processes and supporting brain structures/networks. In seeking to dissect cognitive control into its core processes and identify their neural correlates, we have now established an extensive toolbox of experimental tasks and neural measures as well as multiple theoretical frameworks to account for the multitude of findings. However, we still are far from consensus about how these different frameworks fit together and what are the fundamental dimensions of cognitive control (see **Box 1**). The challenge that remains is to reconcile these different frameworks into integrated models of the complex dynamics of cognitive control and their network substrate, in a way that can encompass information from multiple tasks, populations, measures and methodologies, as well as different temporal scales.

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Here we want to emphasize that, despite differences in terminology and specific theoretical structures, these various frameworks are not necessarily mutually exclusive. Indeed, it is possible for a particular component of cognitive control to vary along any, or all, of these proposed dimensions in some form of multidimensional space, although the exact set of dimensions that should be used to define this space and the labels used to describe them may vary. This brief overview of the field highlights considerable overlap across dimensions. For example, both proactive and reactive control may include tonic and phasic phenomena. In addition, there is some level of overlap between dimensions contrasting internally vs. externally driven control, and proactive vs. reactive control processes. Similarly, one could argue for partial overlap between the theoretical constructs of conflict monitoring and updating, and the constructs of attention reprogramming and shifting (with similar overlaps with tonic vs. phasic control, respectively).

Multimodal studies have also highlighted specific relationships between cognitive control dimensions (or components) and neural measures taken from distinct brain regions and/or with specific temporal dynamics. For instance, ERP data suggest that the P3a (or frontal P3), which was originally identified in response to novel stimuli (i.e., stimuli for which a previous representation either does not exist or is currently inactive) may be consistent with concepts such as updating (in Miyake and Friedman's model), external control (in Corbetta and Shulman's terms), and reactive processing (in Braver's terminology). Likewise, within these same frameworks, the P3b may be more closely related to shifting, internal control, and proactive processing, respectively. Moreover, these dimensions may map onto the ventral vs. dorsal attention networks, respectively, as proposed earlier by Polich (2007). However, although these analogies are tempting, and can definitely help simplify a relatively complex literature, a number of theoretical points still need to be reconciled, and, more importantly, a number of findings remain unexplained. Below, we discuss a few examples of these hard-to-reconcile findings, and

suggest that integrative work taking into account the distinct properties of different measures and tasks may help bring together seemingly conflicting views.

(1) Disparate views regarding the spatial and functional properties of neural networks that support cognitive control. At first glance, theories of the role of CON appear to differ sharply. In Petersen's view, CON is responsible for tonically holding task goals for the duration of the task (Petersen & Posner, 2012; C. Gratton et al., 2018); Cohen argues that the ACC (part of CON) monitors conflict during a particular task (Carter et al., 2000), whereas Braver et al. (2009) and Corbetta and Shulman (2002) argue that ventral frontal regions (another component of CON) are associated with reactive and external control processing. However, this apparent sharp contrast may actually arise from basic differences in the evidence that is used to support each model. First, each model relies on data from different tasks that involve only partially overlapping processes (e.g., conflict vs. task-switching paradigms). Second, the models refer to brain regions that only partly overlap (e.g., anterior cingulate, inferior frontal gyrus, anterior insula). Third, the temporal properties of the processes being considered are not necessarily commensurable across models (e.g., the 100-ms immediately after an error vs. the entire interval over which a particular task-goal needs to be maintained). Finally, these theoretical discrepancies are exacerbated by the persistent lack of clarity regarding the degree of overlap or separation between the ventral attention network (VAN, emanating from Corbetta & Shulman's work) and CON, an important network in a number of subsequent theories.

(2) Need for understanding interactions between components of cognitive control in complex paradigms. The three dimensions of conflict, inhibition, and interruption are considered essential for cognitive control and executive function. In Miyake and Friedman's factor-analytic approach, they are strongly correlated, and Stroop and stop-signal tasks are grouped under the same umbrella of *inhibition* (more recently referred to as Common-EF, Miyake & Friedman, 2012). In both types of tasks, a fronto-central negativity is observed (e.g., Huster et al., 2010), which resembles in latency and scalp

distribution the N2 family of components (which includes also the ERN, CRN, and FRN; e.g., Folstein & Van Petten, 2008; Larson et al., 2014; see Fig. 2). In a recent view (**Wessel, 2018**), these phenomena are subsumed under the general heading of interruption processes, related to the phasic activation of a dopaminergic circuit after the appearance of a rare, unexpected stimulus. Interestingly, this is reminiscent of the orienting reflex (OR), first described by Sokolov and others in the 1960's (e.g., Sokolov 1960) as including a "freezing response" component. In Wessel's view, this process may be followed by an "updating" event, symbolized by a late positive component (Pe on error trials, or P3a/P3b on trials requiring other types of rare event processing). Indeed, it is this second component, rather than the first, which is associated with slowing after errors (or the eliciting event in general). Hence the three components of control identified by Miyake and Friedman may refer to two hierarchically ordered steps in Wessel's view: Interruption (typically the result of conflict or change in context monitoring), followed by either within- or outside-context re-starting (involving an updating or shifting of attention weights). For each of these operations, a set of brain phenomena involving both ERP responses and fMRI brain activations can be observed. This example, therefore, shows the possible dynamic interplays that can occur between components of control.

(3) Reconciling activations obtained at different temporal scales. There is a pressing need to reconcile activations obtained at different temporal scales and from methods that support different levels of temporal resolution. For example, the three components of cognitive control extracted by Miyake and Friedman may be triggered by the same event, or by different events within the same task context. The relative impact of each of these constructs on performance will therefore vary not only across different tasks but *within the same task*, depending on seemingly more subtle variations in specific task parameters and related timelines. For instance, task-switching paradigms allow us to differentially manipulate the need for updating and the need for interference control and differentiate their impact on shifting efficiency (for reviews see Karayanidis et al., 2010; Kiesel et al., 2010;

Vandierendonck et al., 2010). Variants of the task-switching paradigm also offer the opportunity to differentially manipulate and measure the relative effects of sustained vs. transient proactive control, proactive vs. reactive control, goal updating vs. task-set updating, variations in working memory load, internal vs. external cueing, stimulus and/or response level interference, as well as error processing and response adaptation on both performance and electrophysiological measures of task-switching at different points across the cue-target-response timeline (Jamadar et al., 2015; Karayanidis & Jamadar, 2014).

In addition to differential results emanating from the use of separate task variants, our ability to detect the differential effects of each component construct will change depending on the types of brain measures we analyze. For example, in conflict tasks, monitoring and interruption processes can be revealed by the presence of differences between incongruent and congruent trials in reaction time as well as in fronto-central ERP negativities. In the same task, shifting processes can be examined by analyzing the congruency effect on reaction time on the subsequent trial, as well as the consequences (in terms of prediction of performance for the following trial) on the late positivities occurring after an error or an incongruent trial (e.g., Donchin et al., 1988). In these contexts, a procedure with low temporal resolution, such as fMRI, may indicate that activation consistent with monitoring processes occurs on every trial, thereby suggesting that these processes are *tonically* engaged across the whole duration of the task. This conclusion would be inconsistent with the expectation that occasional shifts across attention settings should generate phasic, short-lived spurts of activity, an expectation supported by the ERP findings⁷. This example illustrates how methods with different temporal and spatial resolution may provide divergent views of the functional significance of different brain networks, and

⁷ One could argue that the tonic presence of monitoring processes should be the other side of the coin of having to maintain a particular set of task goals. In this sense, it is possible to conceive that the same structure (or network) that has to tonically maintain task goals may also be equipped with mechanisms for initiating their interruption, even though these may not necessarily be implemented by the same neurons within the structure or by the same exact regions within the network.

helps highlight the need for theories that encompass these different temporal dynamics and may reconcile seemingly inconsistent results (see **G. Gratton, 2018**).

Within this framework, oscillatory brain activities, and especially theta and alpha rhythms, could play a significant role in helping to propagate or limit activation across brain regions. For example, posterior alpha has been shown to allow for intermittent blocking of sensory input so as to enable the enhancement of other task-relevant activities, while still leaving the possibility for some of this information to come through. This is made possible by the fact that different alpha phases represent different levels of cortical excitability (e.g., Mathewson et al. 2009; 2011), so that, within a very short period of time, our visual cortex may oscillate between microstates characterized by high and low excitability (see also Popov & Popova, 2015). Further, alpha may be regulated (at least to some extent) locally. This mechanism of "local partial gating" of sensory input enables monitoring to occur, while still maintaining selection for particular input information. **G. Gratton (2018)** presents a more detailed description of how brain oscillatory activity may play such a critical control role in the flexible organization of information processing.

In conclusion, cognitive control relies on the dynamic integration of multiple sources of information, so as to support a broad repertoire of behaviors that allow us to select, implement or suppress goals in rapidly changing contexts. Multiple electrophysiological signatures of such information integration are readily observed during laboratory cognitive control tasks, whereas intrinsic and task-related brain networks emerge with phasic and tonic activations when the same tasks are imaged with hemodynamic methods. A framework integrating these different time scales may enable us to more precisely describe goal-directed behavior, characterize the functional consequences of cognitive control deficits in the course of life span development and pathology, and, ultimately, pave the way for effective interventions to counteract control failures.

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Box 1. Definition of main constructs used by major theories of cognitive control

Different theoretical models of cognitive control have sought to fractionate this complex process into elemental cognitive constructs. Despite differences between the specific subcomponents present in taxonomies of control, it is commonly assumed that there is a "core" cognitive control component that can be parcellated. Here, we present the terminology used in some of the most prominent models.

Unity vs. diversity of cognitive control (Miyake et al., 2000; Miyake & Friedman, 2012)

Cognitive control comprises a common mechanism (unity) that arises from independent (but partially correlated) subcomponents (diversity). Using factor analyses, Miyake and colleagues identified three factors that grouped different experimental tasks: *updating* (monitoring and changes to working memory contents), *shifting* (flexible changes between task-sets or goals) and *inhibition* (overriding habitual or prepotent responses). More recently, inhibition was relabeled *common-EF*, which is shown to impact performance on all cognitive control tasks.

Internal vs. external control networks (Corbetta, Patel, & Shulman, 2008; Corbetta & Shulman, 2002)

Cognitive control is said to arise from the interaction between two major frontoparietal networks that flexibly direct our attention towards internal goals or external stimulation. The *dorsal frontoparietal network (DAN)* is believed to support goal-oriented, internally driven attention, by biasing the system towards goal-relevant stimuli and linking them to appropriate responses. The ventral frontoparietal network (VAN) was originally conceptualized as redirecting attention between different objects, i.e., a reorienting system. However, recent evidence suggests that VAN has a broader role in switching between states – a type of network-reset function that reorients attention between different internally-driven or externally-driven task states.

Dual mechanisms of cognitive control (DMC; Braver, 2012; Braver, Gray, & Burgess, 2007)

The DMC model focuses on the timescale of implementation of cognitive control, making a distinction between proactive and reactive control processes. *Reactive control processes* are engaged after the occurrence of an imperative stimulus. They are employed on a 'needs' basis to guide responding, and prevent or correct an error. As such, reactive control processes are activated in a transient, context-dependent manner. In contrast, proactive control refers to processes that are engaged in anticipation of the need to engage in difficult decision-making. For instance, this may include anticipation of a change in task goal, or of increased conflict or ambiguity. This proactive control is conceptualized as a sustained change in attentional weights when preparing to undertake a more difficult task (i.e., proactive maintenance of goal-relevant information). However, it can also involve trial-by-trial shifts in attentional bias and/or response threshold in anticipation of target onset, as for instance, when using cue information to prepare to implement different S-R change on the upcoming target.

Conflict monitoring, detection and adjustment

(Botvinick, Braver, Barch, Carter, & Cohen, 2001; Botvinick, Cohen & Carter, 2004, Kerns et al 2004)

Ongoing monitoring for conflict (e.g., mismatch between incompatible responses, or between current goals and outcomes) is associated with dedicated medial prefrontal circuitry. Once conflict is detected, compensatory mechanisms are recruited to adjust behavior. In doing so, task-sets/actions are dynamically updated and reprogrammed to facilitate goal-appropriate responding. This is associated with increased engagement of attentional control mechanisms in the DLPFC.

Sustained maintenance of information vs. implementations

(Curtis & D'Esposito, 2003; D'Esposito, 2007; see also Nee & D'Esposito 2016)

Sustained maintenance of information in working memory facilitates numerous operations (e.g., short-term exploitation of the information or longer-term memory storage/integration). Here, the architecture of the prefrontal cortex serves as a functional bridge between information held in working memory and the required implementation. That is, depending on the temporal contingencies (i.e., transient or sustained) between information in working memory and desired implementations, the prefrontal cortex will facilitate time-appropriate integration.

Alerting, orienting and executive networks (Petersen & Posner, 2012; Posner & Petersen, 1990)

This framework proposes three core functional networks that subserve distinct components of attention. The alerting network supports arousal for vigilance and performance maintenance. The orienting network prioritizes sensory information for feature selection. The executive network corresponds to the detection of targets that allow information to be introduced into awareness.

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FIGURE LEGENDS

Figure 1. Exemplars of typical cognitive control paradigms. **(A)** N-back task: Participants decide whether the current stimulus matches the stimulus presented N trials earlier. For example, 2-back instructions would require a response to the second occurrence of 4, whereas 3-back instructions would require a response to the second 7. **(B)** Eriksen Flanker task: Participants respond left or right, consistent with the direction of a central 'target' stimulus that is flanked by distractors. These distractors may be congruent (i.e., be associated with the same response as the target), incongruent (i.e., be associated with the other response) or neutral (i.e., not be linked to any response). **(C)** Go-Nogo task: Participants perform a simple choice-reaction time task (e.g., press left for X and right for O), but must withhold their response to occasional nogo stimuli (here designated by red font). **(D)** Task switching paradigm: Participants alternate between two or more simple choice-reaction time tasks (e.g., magnitude vs. parity of a digit). Here we depict a cued-trials paradigm, where the cues (M for magnitude, P for parity) indicate the task to be completed on the next target stimulus. When trial N+1 requires the same task as trial N, it is a repeat trial. When trial N+1 requires a different task than trial N, it is a switch trial.

Figure 2. Reactive cognitive control processes are associated with similar electrophysiological signatures. **(A)** Both stimulus-locked (N2) and response-locked (correct-related negativity: CRN; error-related negativity: ERN) negativities recorded at frontocentral electrodes are modulated by reactive control processes. The N2 is elicited in response to novelty or stimulus–response conflict. The CRN is evoked by motor responses and is modulated by response conflict. The ERN is evoked by incorrect motor responses. **(B)** Time-frequency deconvolutions of these frontal negativities highlight the presence of a common, low-frequency theta (~4-8 Hz) response during cognitive control. Black outlines within the time-frequency plots depict significant increases/decreases in power from a pre-event baseline. **(C)** Topographical distribution of this theta response shows a common enhancement at frontocentral regions of the scalp. This midfrontal theta is thought to index the need for control. Figure adapted from Cavanagh & Frank (2014). (**Reprinted with authors' and publisher's permission**).

Figure 3. Temporal dynamics of proactive cognitive control. Time-domain and frequency-domain analyses of EEG activity within the preparation interval, in a cued-trials task-switching paradigm involving switching between color, digit and letter classification tasks (Karayanidis et al., 2009). This allowed five types of cues to be defined. In single-task blocks, all trials were repeat (A-Rpt). Mixed-task blocks included: repeat (Rpt) cues indicating that the participant must repeat the same task as that

completed on the preceding trial (e.g., AA), switch-to (S-T) cues indicating that the task will change and identified the task that must be completed on the next target (e.g., AB), switch-away (S-A) cues indicating that the task will change, but the relevant task was only indicated by target position (e.g., AB or AC), and non-informative cues (NI) indicating that the task may repeat or switch, depending on the target position (e.g., AA or AB). Therefore, cues allowed different levels of preparation before target onset. (A) Cue-locked ERPs (Karayanidis et al., 2009, reprinted with permission by Springer). An early differential switch positivity emerges for switch-to and switch-away, which validly indicate that the task will change. A second later positivity is present only for switch-to cues, which also specify the task that needs to be uploaded. Just prior to target onset, cues that identify the task to be performed to the target (i.e., repeat and switch-to) show a larger pre-target negativity than cues that do not (i.e., switchaway and non-informative). (B) Theta band imaginary coherence (a measure of phase similarity between electrodes) during the early cueing period. An early theta frontoparietal network (max 100-300 ms post-cue) is activated only for the cues that provide certainty that the task will switch (i.e., switch-to and switch-away) within the timeframe of the switch positivity (Cooper et al., 2015; reprinted with permission by Elsevier). (C & D) Statistical F-maps (FDR corrected, p<.001) depict a significant main effect of cue type for power (dB: decibel) and inter-trial phase clustering measures, respectively, peaking around 250-300ms over midline central-parietal and lateral temporal-parietal sites. Theta band power and phase clustering was enhanced for cue types that provided goal information (i.e., prepare to repeat (Rpt) or to switch (S-T, S-A); Cooper, Wong et al., in review; reprinted with permission from Elsevier).

Figure 4. Statistical parametric maps (Z scores) of the event-related optical signal (EROS) response during different versions of a cued-trials task-switching paradigm. In all studies, a visual cue was presented 2 s before the target and defined the stimulus (study 1–3) or response (study 4) dimensions according to which the participant must respond. The cue was randomized across trials, thus generating conditions in which the same rule was used on consecutive trials (no-switch or repeat conditions) and conditions in which the rule changed (switch conditions). Each column in the figure refers to a different study (N=16 per study). Study 1 involved responding to either the visual or the auditory feature of a bimodal stimulus (e.g., see 'I' and hear 'O'). Study 2 involved responding to global or local stimulus features (e.g., the letter S, written out of H's). Study 3 involved responding to the stimulus presented in the left or the right hemifield, with a compatible or incompatible hand (e.g., the left stimulus was mapped to a response with the right hand). Study 4 involved responding 'left' or 'right' with either a

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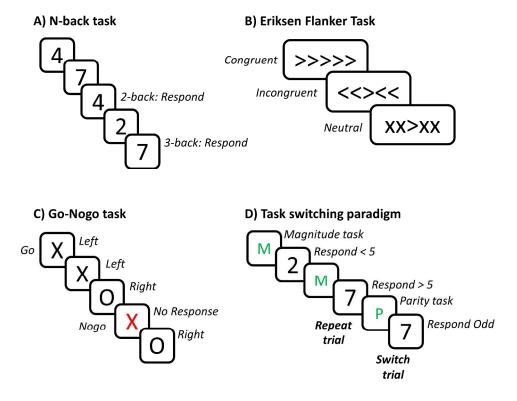


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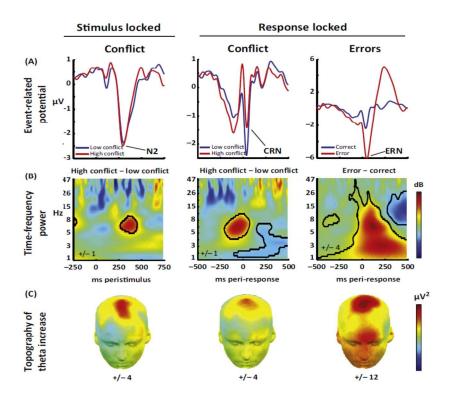


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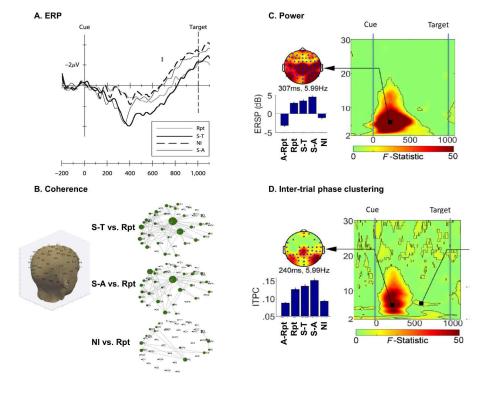


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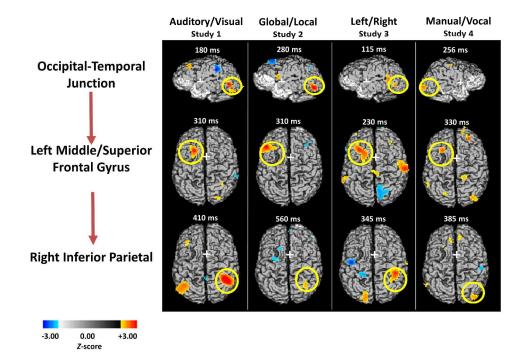


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