

Emerging themes in cognitive control: Commentary on the special issue of *Psychophysiology* entitled “Dynamics of Cognitive Control: A View Across Methodologies”

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1 | INTRODUCTION

This special issue highlights the degree to which psychophysiological approaches can inform us about the neural mechanisms underlying cognitive control (G. Gratton, Cooper, Fabiani, Carter, & Karayanidis, 2018). They range from theoretical to empirical articles and address four important and contemporary topics in the field. The first topic considers how and when cognitive control is engendered proactively as compared to reactively. The second examines how adjustments of control occur, for example, when errors need to be detected. The third addresses the degree to which connectivity between brain regions enables and supports cognitive control. The fourth explores how the nature of control can vary based on interventions or individual differences.

Of note, most of the articles in this special issue utilize methods that are known for their temporal precision, such as ERPs and EEG time-frequency analysis, as compared to fMRI, which is better suited for obtaining information regarding localization of function. As such, the psychophysiological methods used in articles in this issue are well suited to address these four topics, as they provide insight into the sequence and timing by which these control processes occur. In this commentary, I will address each of these four topics and provide some context in which to situate the interesting work presented in this special issue.

2 | MODES OF CONTROL: PROACTIVE VERSUS REACTIVE CONTROL

As argued in the classic article by Miller and Cohen (2001), prefrontal regions are seen as important for modulating

activity in more posterior brain regions so that the correct operations are selected to meet current goals. For example, in the absence of any visual stimulation, activity in the lateral prefrontal cortex increases substantially at the onset of a cue that provides information about task requirements (e.g., the location that will be task relevant), with somewhat smaller increases in activity in posterior brain regions that process the task-relevant information (e.g., visual cortex). The nature of this pattern of activity is thought to reflect a proactive top-down setting by prefrontal regions so as to increase activation in brain regions that are required to process task-relevant information. Once the stimulus appears, activity is still observed over frontal regions, consistent with a continuing role for this region in task biasing. However, larger increases in activity are observed over visual processing regions as they are now engaged by stimulus processing (Kastner, Pinsk, De Weerd, Desimone, & Ungerleider, 1999). As such, cognitive control can be implemented both proactively, before stimulus processing, and reactively, once the information on which control must be exerted becomes manifest.

This distinction between these two “varieties” of control has been articulated by Braver (2012) in his dual-mechanisms framework. That framework posits that lateral prefrontal regions support proactive control by actively maintaining task goals. Reactive control involves a reinstatement of those task goals when the stimulus appears as well as the engagement of other control regions. A number of articles in this issue examine how these two types of control are exerted and their interrelationships.

One question that arises is whether the types of operations being performed during proactive and reactive phases of control are more or less the same process but just applied

at different points in time, or whether they can represent somewhat distinct processes. The article by **Barceló and Cooper (2018)** speaks to this question. In their study, they examined positive ERP components engendered across three tasks carefully designed to have the same types of perceptual displays and stimulus-response (S-R) mapping. The three tasks were (a) one that required a simple perceptual categorization in which oddball items required a response, (b) a go/no-go task in which responses were given to certain items and withheld to others, and (c) a task-switching paradigm in which items were categorized on the basis of two distinct types of features (color, orientation). Their work focused on responses to identical stimuli (gray gratings) that served different purposes in each task: as nontargets in the oddball task, as no-go distractors in the no-go task, and as the cue indicating as to whether the same or different task should be performed on the upcoming trial in the task-switching task. Notice that, while these gray gratings provide information about the task set in the task-switching paradigm, they do not do so for either the oddball or no-go task, as in these tasks, the task remains the same throughout.

A larger P3 amplitude was observed over central and parietal leads for the switch task than the other two tasks, suggesting that this component may be indexing proactive updating of a task set that is more complicated for the switching task, as there are two task sets to be maintained, as compared to the other two tasks, in which only one task set need be maintained. However, within the context of the switch task alone, the size of the P3 amplitude did not differ as a function of switch trials (in which the task performed on the current trial is different from that on the prior trial) versus repeat trials (in which the same task must be performed as on the prior trial). This finding suggests the proactive imposition of a domain-general context signal, applied equally to switch and repeat trials. Following this component was a later positive complex, peaking between 500 and 900 ms, which was observed over parietal regions. Once again, this component was greater for the switch task than for the other two tasks. Importantly, however, this later positive complex was larger in amplitude for switch than repeat trials, which may index the engagement of a revised S-R mapping to enable execution of the new task rules. Hence, this work suggests that proactive control may have two separate components: one that engendered a general task set and one that is involved in setting revised S-R mappings on switch trials (see also Karayanidis, Provost, Brown, Paton, & Heathcote, 2011).

With regard to reactive control, a larger frontal P3/late positivity complex from 300–1,200 ms poststimulus presentation was observed to targets, which was greater for switch than repeat trials. This pattern suggests a reinstatement of both of these types of control mechanisms: one related to task set and one related to S-R mappings. This work highlights that proactive control may involve separate mechanisms,

these mechanisms may be reinstated in a reactive manner, and proactive mechanisms may somewhat “meld” into reactive ones. As such, while the distinction of control processes into proactive and reactive processes has been a useful heuristic, it likely needs additional elaboration.

Another article in this issue (**Provost, Jamadar, Heathcote, Brown, & Karayanidis, 2018**) examines the limitations of proactive control, and those aspects of control that must occur reactively. As discussed above, in a standard task-switching paradigm, a cue indicates which task should be performed on a given trial. This cue provides time to set the system for the relevant task before the actual stimulus appears. The longer the time between the cue and the stimulus, the more time there is for task-set preparation. As such, ERPs recorded during the cue-target interval can index this proactive process. Nonetheless, even with long cue-stimulus intervals, there is almost always a residual switch cost; that is, proactive control can only get you so far. Even with advanced preparation, responses are faster on repeat trials as compared to switch trials. Hence, this residual switch cost reflects processes that are handled by reactive mechanisms and can be indexed by ERPs locked to the target (Karayanidis & Jamadar, 2014).

Provost et al. (2018) explore the nature of this reactive mechanism through target-locked ERPs that are examined in relation to the response time distribution via orthogonal polynomial trend analysis. This approach allows them to differentiate the nature of ERP components according to the speed of the response, in a graded manner from fast responses to slower ones. The assumption here is that slower responses are likely to be associated with less efficient proactive processes and thus rely more on reactive control compared to faster ones. To examine particular operations that might contribute to this differential processing between fast and slow trials, they examined how reaction time (RT) influences three ERP components in a task-switching paradigm for switch versus repeat trials. The components examined were the early N2, taken as sensitive to interference at the level of target identification (Gehring, Gratton, Coles, & Donchin, 1992), the late N2 as an index of interference during target processing (West, 2003), and the P3b as an index of the decision difficulty, particularly with regard to target-response transformations (Donchin, Karis, Bashore, Coles, & Gratton, 1986).

What they observed, consistent with prior studies, was that switch trials produced larger later N2 and smaller P3b components than repeat trials. What was of interest is how these effects varied across the RT distribution. The difference in the N2 amplitude for switch versus repeat trials did not vary as a function of RT, suggesting that task preparation does not influence interference during target processing. In contrast, as RT increased, so did the difference in the amplitude of the P3b between switch and repeat trials. For the fastest trials, there was no difference in the P3b amplitude

between switch and repeat trials, but there was a difference in the P3b latency, likely reflecting the residual switch cost, which could potentially reflect the basic need to reconfigure task sets. However, past that point, switch costs appear to reflect not only this basic effect but also decision difficulty, as indexed by P3b amplitude. Such a finding suggests that for faster trials there is a carryover of proactive control that minimizes decision difficulty, but this carryover is reduced for trials with increasing RT. This article complements that by **Barceló and Cooper (2018)** in suggesting that reactive processes may not be a unitary set either. And also consistent with Barceló and Cooper, these results indicate that control processes likely to be invoked proactively (e.g., configuring of a task set) may also need to be invoked reactively.

3 | ADJUSTMENTS OF CONTROL

Another conceptual issue addressed by numerous articles in this special issue is how control can be adjusted. One of the more prominent models that addresses this issue is the conflict monitoring/control loop theory. The main idea of this theory is that when there is a high degree of conflict in the system, as often occurs when errors are emitted, some adjustment needs to be made to control to preclude further errors (Botvinick, Braver, Barch, Carter, & Cohen, 2001; Botvinick, Cohen, & Carter, 2004). In its classic form, the model suggests that, when the anterior cingulate detects conflict, it sends a signal to the dorsolateral prefrontal cortex (DLPFC) to increase control. Thus, conflict sends a signal that forms a closed loop to increase control.

Boudewyn and Carter (2018) use a time-frequency approach to examine this issue. Based on data and theoretical arguments summarized by Cavanagh and Frank (2014), they argue that theta band activity (i.e., oscillatory EEG signals in the 4–7 Hz range) recorded from midfrontal regions reflects a neural mechanism utilized to increase control. To investigate when and how this mechanism gets invoked, they had individuals perform a standard color-word Stroop task in which individuals identify the ink color in which a word is presented while ignoring the meaning of the word itself. This task requires control because our extensive experience with word reading makes that process more automatic than color naming.

Of most relevance to the current discussion, Boudewyn and Carter examined electrophysiological responses in this frequency range after the commission of an error as compared to a correct response. More specifically, they used theta power during the prestimulus period of trials that followed errors as a metric of post-error adjustment. Theta was increased in the time period after an error but prior to the next trial, suggesting that theta is indexing a proactive engagement of control. Supporting this conclusion was an

analysis in which they took the set of trials subsequent to an error, and divided them based on whether the prestimulus theta was high or was low. The error rate on trials following high prestimulus theta was lower than that observed for trials following low prestimulus theta. Consistent with reports of difficulties in cognitive control in individuals with schizophrenia (Lesh, Niendam, Minzenberg, & Carter, 2011), they found that both of these effects were reduced in individuals with schizophrenia as compared to controls.

Another approach used to examine the need for adjustment is to employ the conflict adaptation effect, which was the focus of the article by **Von Gunten, Volpert-Esmond, and Bartholow (2018)**. Consistent with what we have just discussed, this approach examines the impact of the prior trial on the current trial. However, rather than focusing on whether or not an error was made on the prior trial, this approach examines the degree of control engendered by the prior trial. Generally, trials with distracting or incongruent information (in this study, instantiated by flanking arrows that pointed in the opposite direction of the central arrow on which the response should be based) require more control than those in which there is no conflict (in this case, because the flanking arrows provided compatible information).

Typically, the conflict adaptation effect entails the observation of longer RT on incongruent trials preceded by congruent trials than by incongruent trials. Or, said differently, there is less of a difference between incongruent and congruent trials when preceded by incongruent trials as compared to congruent trials. The explanation for this effect is as follows. Processing of information on an incongruent trial requires a higher level of cognitive control. This high state of control then bleeds over into the next trial. In contrast, because less control is required for congruent trials, control must be ramped up when the subsequent trial is incongruent. Thought of differently, having to process an incongruent trial in some sense automatically engenders proactive control.

The goal of the article by Von Gunten and colleagues was to examine how such control mechanisms might vary over the extent of trials during an experimental session and how different aspects of processing as indexed by ERPs contribute to these effects. First, to index how much conflict had been detected, they used the frontocentral N2 component, generally occurring 200–350 ms postpresentation and thought to be generated by the anterior cingulate cortex (ACC; Van Veen & Carter, 2002). Second, to index the degree of top-down control engendered, they used the frontal slow wave (FSW), generally observed 600–1,000 ms postpresentation over frontal and central leads (West & Bailey, 2012).

They found that, on any given trial, the larger the N2, which signals the detection of conflict, the larger was the FSW, which indexes the implementation of increased control. Moreover, consistent with the conflict adaptation effect, they found a larger N2 and FSW for incongruent than

congruent trials, and that this effect was greater when those incongruent trials were preceded by congruent trials.

Interestingly, however, this effect was only observed for the beginning third of trials but not the middle or last, despite robust RT effects across the entire experiment. However, the pattern for the N2 and the FSW diverged. More specifically, across trials, the amplitude of the N2 stayed stable but the amplitude of the FSW lessened for incongruent trials preceded by congruent trials. These incongruent trials are those on which reactive control is more likely, as only low levels of control were needed to respond correctly on the prior congruent trial. This pattern suggests that conflict is being detected, but with time, the degree of engagement of the neural mechanisms for reactive control change. Conversely, they found that for incongruent trials preceded by incongruent trials, in which proactive control is more likely, the N2 actually increased over trials. While the FSW also reduced with time, the effect was heightened compared to incongruent trials preceded by the congruent trial. While a more fine-grained interpretation of this pattern of results is beyond the scope of this commentary, it does show that the degree to which proactive and reactive control mechanisms are invoked may vary as the individual gets more familiar with, practiced, efficient, or even potentially fatigued during a task. Hence, the relative contribution of proactive to reactive control may vary in a given individual over time.

In the work discussed so far, the response of the system to variations in the nature of prior events is generally adaptive, leading to increases in control and better performance. However, in the case of errors, processing can also be disrupted, leading to momentary cessations or alterations in behavior, including the elongation of RT (e.g., Notebaert et al., 2009). From this perspective, errors might be considered maladaptive, as they derail ongoing behaviors. While these two strands of the literature—those focusing on adaptive responses and those focusing on maladaptive responses—have proceeded relatively independently, **Wessel (2018a)** proposes a theory designed to integrate the two. He argues that errors cause a disruption or halting of ongoing behavior, consistent with the maladaptive theories. This disruption occurs relatively automatically, and is followed by an orienting response designed to discern the source of the error. This mechanism, it is argued, is not specifically engendered by errors per se, but rather is a more general automatic mechanism that is engaged by unexpected or low probability events. The result of this mechanism is to interrupt ongoing processing so as to divert attention to discern the source of the unanticipated information.

With regard to the neural underpinnings, **Wessel (2018a)** cites work suggesting that an inhibition network consisting of regions of the presupplementary motor area, right inferior frontal gyrus, and subthalamic nucleus of the basal ganglia are involved in the disruption of behavior. **Van Campen,**

Kunert, van den Wildenberg, & Ridderinkof (2018) present evidence using transcranial magnetic stimulation (TMS) of the critical role of right inferior frontal gyrus in the suppression of such action tendencies. The associated orienting response is thought to occur via locus coeruleus–noradrenergic input to right ventrolateral regions (Corbetta & Shulman, 2002) as well as the right anterior insular cortex. (For task designs that are optimized to detect such inhibitory processes, see **Wessel, 2018b**).

In the case of errors, however, a specific control mechanism is invoked to increase control so as to avoid potential future errors. This control mechanism, thought to be guided by frontal regions, can adjust behavior through a variety of mechanisms, including adaptive tuning of perceptual systems, changes in the motor threshold, and/or tuning of top-down attentional systems (e.g., Danielmeier, Eichele, Forstmann, Tittgemeyer, & Ullsperger, 2011). Hence, the theory proposed by **Wessel (2018a)** suggests that actually what has been treated as a unitary phenomenon, post-error slowing, may arise either from the interrupt associated with the reorienting process or from later adjustments in control. It is argued that the former is more likely to be associated with poorer or unchanged performance compared to accurate trials, while the latter is associated with improved performance. This idea that at least some errors lead to increased control meshes well with the conflict monitoring/closed loop theory of cognitive control discussed earlier (Botvinick et al., 2001, 2004).

What is common across all of these articles is that they highlight the adaptive, and complicated, nature of how control can be implemented.

4 | BRAIN CONNECTIVITY AS A MECHANISM FOR COGNITIVE CONTROL

A third topic addressed by numerous articles in this issue is the degree to which connectivity between brain regions enables cognitive control. While connectivity appears to be an obvious requirement for such control, the means and methods by which such control occurs is not well explained or modeled. Yet, it is a critical issue that must be addressed if a full and valid model of the neural bases of cognitive control is to be articulated. Some of the articles in this special issue tackle this issue head on, and this portion of the commentary will focus on this topic.

4.1 | Interregional connectivity

As discussed above, most contemporary models (e.g., Miller & Cohen, 2001) assume that frontal regions, or regions in the frontoparietal network, modulate or otherwise affect

processing in distant brain regions. To do so requires, on the face of it, a functional or anatomical relationship between what are typically referred to as “sources” (i.e., frontal regions) as compared to “sites” of control (i.e., posterior regions).

Some evidence in the literature for this relationship between sources and sites of control comes from work performed with TMS, which disrupts ongoing neural processing. For example, TMS over the right inferior frontal junction perturbs performance on a working memory task in which individuals have to pay attention to one of two features of a stimulus (color, motion) of two sequentially presented items and then decide if a probe item matched either on the relevant dimension (Zanto, Rubens, Thangavel, & Gazzaley, 2011). Suggesting a direct effect of perturbations of prefrontal region was the finding that TMS applied to this region altered a P1 ERP component recorded over posterior regions involved in color (V4) and motion (V5) regions, respectively (depending on condition). TMS reduced the size of this component when the attribute was task relevant, and increased it when the attribute was task irrelevant. Moreover, the more an individual exhibited disruption of the posterior P1 component after frontal TMS, the larger was his/her decline in working memory performance after stimulation. Similar disruptive effects of TMS, but over left DLPFC, are observed in a modified N-back task on activity in the fusiform face area and parahippocampal place area, when faces versus places are attended, respectively (Lee & D’Esposito, 2012).

Such control from prefrontal regions likely relies on functional and anatomical (i.e., white matter) connectivity. For example, inhibiting the retrieval of visual emotional memories from the hippocampus appears to rely on the interaction of right prefrontal regions with areas of visual cortex and the hippocampus that would support such memories (Depue, Curran, & Banich, 2007), as a more negative relationship between activity in the right DLPFC and the hippocampus predicts better memory suppression (Depue, Burgess, Willcott, Ruzic, & Banich, 2010). Subsequent work showed that activity in this region of right DLPFC has a negative relationship with different target sites depending on the inhibitory domain. A greater negative relationship with orbitofrontal/amygdala regions predicts individual differences in the ability to suppress emotional reactions while a greater negative relationship with right inferior regions and the subthalamic nucleus predicts the ability to inhibit motor responses. Moreover, these effects are partially mediated by the integrity of the white matter tracts connecting right DLPFC to these target regions (Depue, Orr, Smolker, Naaz, & Banich, 2015).

While most of the work performed to date focuses on frontal-posterior connectivity, the article by **Baniqued, Low, Fletcher, Gratton, and Fabiani (2018)** reminds us that connectivity between other brain regions can also be related to

control, especially as one ages. They examined those factors that influence the ability for older adults aged 55–87 to perform well when switching between tasks using spatial word-spatial position Stroop stimuli. In this task, the attended dimension was indicated by a cue that varied on a trial-by-trial basis. On some trials, the word’s meaning was the relevant dimension and, on other trials, it was the word’s position relative to a fixation cross. By intermingling these two types of trial, the ability to task switch was investigated. The authors found that the greater the connectivity between time-linked brain activation between left middle frontal gyrus (MFG) and right MFG, as measured via the event-related optical signal (EROS), when switching from the word to the position task, the better was the ability to task switch. Moreover, this ability was also predicted by the volume of the anterior section of the corpus callosum, which connects these two regions. The authors suggested that this pattern may represent a coupling between the engagement of an early domain general mechanism in the left middle frontal gyrus for engaging a task set, followed by a more domain-specific mechanism in the right middle frontal gyrus required for the position task.

Another potential explanation for this finding that might be worth considering is the degree to which the coupling between homologous regions, in and of itself, may be driving the effect. Much research has found that coordination across the hemispheres is especially advantageous under more demanding conditions (see Banich, 1998, for review) allowing for additional resources to be brought to bear. Compared to younger adults, older adults exhibit this coupling at lower levels of processing load (Reuter-Lorenz, Stanczak, & Miller, 1999) and, in general, exhibit a more bilateral pattern of brain activation (Dennis & Cabeza, 2008). Furthermore, the ability of the load to be divided across the hemispheres with aging has been linked to the structural integrity of the corpus callosum (Davis, Kragel, Madden, & Cabeza, 2012). Regardless of which explanation turns out to be most valid, this work highlights how connectivity can aid in control of processing.

4.2 | The effect of top-down modulation

While sites and sources of control may be interconnected, one important question is the means by which top-down modulation works to alter activity at the sites of control. One way this question has been looked at is to investigate whether top-down control enhances activity related to the task-relevant information or whether it reduces activity related to task-irrelevant information. This issue was examined in the article by **Janssens, De Loof, Boehler, Pourtois, and Verguts (2018)** by examining alpha band activity as an index of the attention given to information. Increased alpha activity is thought to be associated with an inhibition of attention and stimulus processing, whereas decreased alpha

(sometimes referred to as alpha suppression) is thought to reflect increased attention and/or processing.

In their study, Janssens and colleagues utilized flanker task displays in which a central item was surrounded by two items in each hemifield. Those two items could be either compatible with the target or they could be incompatible with the target. In the condition of most interest, the relationship varied with hemifield, with incompatible items displayed in one hemifield, and compatible items displayed in the other. Alpha recorded over occipital regions was increased over the hemisphere contralateral to the incompatible distractors, as compared to the hemisphere contralateral to the compatible distractors. Because this effect was observed between 300 and 500 ms postpresentation, the authors suggest that cognitive control can act very quickly to inhibit processing of irrelevant material.

Consistent with the study of **Boudewyn and Carter (2018)** discussed above, Janssens and colleagues found that theta activity appears to index the strength of the top-down signal of control. Theta power was greater on trials with incompatible distractors as compared to when all the flanking items were compatible, suggesting an increase in the implementation of control. This effect was observed maximally at 160 ms postpresentation. Interestingly, on a given trial, the greater the theta, the greater was the subsequent alpha, suggesting that this top-down signal was driving the degree of suppression of incompatible distractors. This relationship once again speaks to the role of connectivity in cognitive control.

4.3 | Oscillatory patterns in the service of cognitive control

Another way to think about how connectivity might aid in cognitive control is to consider the nature of oscillatory relationships between brain regions. In a broad-reaching and thought-providing conceptual synthesis, **G. Gratton (2018)** argues that the nature of oscillatory patterns in the brain serves as a mechanism to support various cognitive processes, including cognitive control. Broadly, this framework suggests three distinct types of oscillatory patterns. The first are open feed-forward systems that generally are employed transiently and briefly to allow stimuli to be linked to responses. The second two types of systems are considered closed loop systems: One is considered to be positive feedback systems in which sustained high frequency oscillations are used to help select and maintain representations. The other is considered to be negative feedback systems, in which brief, low-oscillatory burst are associated with the switch of representations. Impressive work done by the author's lab using EROS as well as that from other methods and researchers is brought to bear to support this thesis.

While not discussed in the article per se, the existence of these two distinct types of closed loop systems may help to provide a mechanism that could subserve two requirements for a control system that are seemingly in conflict. As discussed by Goeschke (2000), a fundamental tension in control systems is the need for stability as well as for flexibility. Stability is needed to maintain task goals, especially in the face of distracting information. If control is not exerted in a stable manner, then behavior is random and disorganized. But, at the same time, a control system needs to be flexible, for those situations in which goals need to be updated, when new information becomes task relevant, or under conditions of novelty.

One current dilemma is how the neural architecture of the brain could allow both these types of control to be implemented. Some approaches, for example, have suggested that prefrontal dopamine may influence the stability of representations, while striatal dopamine may influence flexibility (Cools, 2016). However, the framework provided by G. Gratton provides another potential (and not mutually exclusive) solution. It may be that stable aspects of cognitive control are supported by positive closed loop systems, which are designed to maintain representations. In contrast, the flexible aspects of cognitive control may be supported by negative closed loop systems, which allow for switching between representations.

Hence, a central issue for the field will be to continue to explore what types of neural mechanisms allow both stable control, while avoiding the tendency toward preservation or a limited scope of attention (e.g., tunnel vision) and also flexibility, while avoiding inattention and random responding or responding that is not appropriate to the current context.

4.4 | Systems, subsystems, and hubs

Another way to think about connectivity is to think about interactions between subsystems that might be involved in cognitive control. In part, we already have considered such a type of model, as in the conflict monitoring/control loop theory (Botvinick et al., 2001, 2004), in which the detection of conflict by medial prefrontal regions sends a signal to lateral prefrontal regions to increase top-down control, which is then implemented by lateral prefrontal regions via their connectivity to posterior brain regions. And the work on conflict adaptation suggests that the size of those signals may depend on the degree to which cognitive control has been implemented previously.

Another variation on this type of model is one that comes out of investigations in my laboratory and that of my colleagues. The cascade-of-control model (Banich, 2009) focuses, not so much on medial-to-lateral prefrontal connectivity, but rather on connectivity between lateral-to-medial regions. According to this model, the degree of control implemented at one subcomponent of the system has

consequences for how much control is exerted by the other subcomponent of the system. Consistent with Botvinick and colleagues, this model suggests that lateral prefrontal cortex imposes a top-down attentional set (Banich et al., 2000). Rather than detecting errors, medial regions are thought to be engaged in later-stage, typically response-related, aspects of control (Liu, Banich, Jacobson, & Tanabe, 2006; Milham & Banich, 2005; Milham et al., 2001; see also Rushworth, 2008). To the degree that a good top-down set is imposed by lateral prefrontal cortex, there is not much control that must be exerted by midanterior cingulate regions before a response is emitted. Such a situation is observed after a task becomes well practiced (Milham, Banich, Claus, & Cohen, 2003). In contrast, when lateral regions do a poor job of imposing top-down control, more control must be exerted by cingulate regions, as is observed with aging (Milham et al., 2002). A study using ERP signatures of activity in each of these regions as seeded by fMRI analyses indicates that the relationships between the ERP response drawn from the DLPFC in the 300–440 ms poststimulus time and the subsequent response from ACC in the 520–680 ms poststimulus can predict performance on the Stroop task. Interestingly, those individuals with a reduced DLPFC response, but large ACC response show increased RT compared to individuals with a large DLPFC response. This pattern suggests that the ACC can compensate somewhat for the lack of top-down control. However, for individuals with both reduced DLPFC and reduced ACC responses, a higher level of errors is found (Silton et al., 2010).

While we have discussed distinctions between medial and lateral prefrontal regions in cognitive control, another conceptual model is that discussed by **C. Gratton, Sun, and Petersen (2018)**. This model posits a somewhat different division of control regions into subsystems. From this view, a cingulo-opercular network is involved in setting and maintaining an overall task set (e.g., winning the basketball game), while the frontoparietal network is involved in enacting processes that are needed to implement specific configurations of the task (e.g., getting yourself in the correct position to make the next basket). Furthermore, distinctions in the roles played by the right and left frontoparietal network are proposed, with the left frontoparietal network thought to respond to more quickly and more transiently to cues and stimuli in a bottom-up manner, while the right frontoparietal network responds in a more poststimulus, elongated and top-down manner. A somewhat different hemispheric distinction between left and right frontal regions in control has been proposed by Stuss and Alexander (2007), who suggest that the left hemisphere is involved in task setting and the right hemisphere in monitoring. Regardless of which parsing of the control system into subsystems turns out to be most accurate, there remains the issue of how these subsystems are coordinated.

In their contribution, **C. Gratton et al. (2018)** consider how such coordination might occur from a graph theory

perspective. In such an approach, the brain is treated as a series of nodes with varying connection strengths between them. By virtue of having similar patterns of responses either at rest or under specific task conditions, nodes can be organized into networks. C. Gratton and colleagues provide evidence that certain control networks may become more coordinated in their activity as control demands increase.

In addition, not all nodes have similar characteristics. Rather some nodes, which serve as hubs, akin to airline hubs in a transportation network, serve a particularly prominent role. In particular, one way to measure “hubness” is to determine the degree to which a given brain region serves as a connector between distinct networks (often referred to as participation coefficient), much the way certain geographical locations (e.g., Hawaii) can serve as hubs for airline service because they connect to distinct subregions of the globe (e.g., North America, Asia, Australia). In other cases, regions can serve as hubs not between, but within, a network, much as Chicago is a hub in the United States because it connects to regions in the East, the Midwest, and the West.

Evidence is given that the functional connectivity of these hub regions within networks may be stable, but that they are quite malleable and flexible across different task demands. As such, they may play an especially important role in the deployment of control. Such an idea is supported by research performed with my colleagues (Spielberg, Miller, Heller, & Banich, 2015) in which increased control demands, as engendered by incongruent as compared to congruent trials in the color-word Stroop task, are associated with the right inferior frontal sulcus and right anterior insula occupying more central positions as network hubs, and dorsal ACC becoming more tightly coupled with its regional subnetwork.

5 | MODULATION OF COGNITIVE CONTROL BY EXPERIENCE AND INDIVIDUAL DIFFERENCES

A final issue to be considered, which adds to the complexity to issues regarding cognitive control, is the degree to which control can be modulated by experience and/or individual differences. Articles in this special issue address this point from the perspective of the event-related negativity (ERN) that is observed in response to errors.

In their article, **Drollette et al. (2018)** demonstrated that the amplitude of the ERN can be modulated by experience. More specifically, they enrolled close to 140 8- to 9-year-olds, the majority of whom met criteria for being overweight or obese, into a relatively intense 9-month intervention program designed to improve cardiorespiratory fitness. Children in the program engaged in 70 min of moderate to vigorous physical activity after each school day. The intervention was successful in that the increase in VO₂ max, a measure of

cardiorespiratory fitness, was 5.4% for the intervention group and just 2.1% for a wait list group of approximately equal size. Drollette and colleagues found that behavioral performance on a modified flanker test improved more for the intervention group than for the wait list control group. While the ERN amplitude stayed constant for the intervention group, the ERN actually increased for the control group. Importantly, the more fit a child in the intervention group became, the more reduced was the difference in the ERN post- to pre-test. Whether these improvements in fitness are specific to executive control or are observed across most all cognitive domains remains to be seen. Yet, these results provide evidence that a relatively simple, albeit intense, fitness intervention may help to improve cognitive control, at least in children in whose body mass index is less than optimal (for another developmental investigation of the ERN, see **Grammer, Gehring, & Morrison, 2018**).

Yet, sometimes individuals bring differences to the table that influence cognitive control. In their article, **Coleman, Watson, and Strayer (2018)** discuss how individual differences in working memory operation span can influence levels of cognitive control. Prior work has shown that working memory operation span influences the ability to maintain a task goal in the context of the color-word Stroop task (Kane & Engle, 2003). Here, working memory operation span was investigated in relation to the ability to detect errors during performance of a flanker task. Control demands were varied by the contrast of trials with incongruent versus congruent flankers, and task conditions were manipulated so that in one condition accuracy of responding was emphasized and in another accuracy of responding was.

Their results showed that the amplitude of the ERN was greater for the higher working memory group, but was not affected by the speed/accuracy manipulations. The error positivity (Pe), thought to measure updating of cognitive strategies in response to errors (Overbeek, Nieuwenhuis, & Ridderinkhof, 2005), yielded larger differences between the high and low working memory group when accuracy was stressed as compared to speed. These findings suggest that high working memory individuals may not only be better at detecting errors but also at adjusting control strategies, for example, under conditions that require higher accuracy as compared to faster speed.

The mechanisms of these effects, however, are still not clear. For example, it might be that a higher working memory operation span essentially provides individuals with more “chunks” or “slots” in working memory that can be used to actively process the outcome (successful, unsuccessful) of their control operations, in addition to, say, the chunks or slots required for maintaining task goals. Another nonmutually exclusive possibility is that a high working memory operation span is associated with an overall ability to flexibly reconfigure the relationships between information actively

being maintained in working memory, which in turn facilitates the reconfiguration of control processes.

These findings complement other approaches in the literature that demonstrate that aspects of individual differences in brain organization as indexed by anatomical and functional neuroimaging measures can influence the ability to exert cognitive control. These metrics include cortical thickness, local gyrification index, and fractional anisotropy of white matter tracts (Smolker, Depue, Reineberg, Orr, & Banich, 2015), the composition of intrinsic connectivity networks (Reineberg, Andrews-Hanna, Depue, Friedman, & Banich, 2015), graph theory characteristics of network node organization (Reineberg & Banich, 2016), and systematic changes in patterns of connectivity between intrinsic connectivity networks that vary over time (Nomi et al., 2017). The degree to which these characteristics can be influenced by interventions or experiences and the degree to which such changes might alter the efficiency or effectiveness of control networks, and their translation into alterations in behavior, remains to be seen.

6 | SUMMARY

The articles in this special issue address a number of important topics with regard to cognitive control, highlighting the degree to which it depends on dynamic interactions between processes and systems. These contributions, both theoretical and empirical, provide examples of how the complexity of understanding of cognitive control may be approached and tackled.

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