Cortical Representations of Cognitive Control and Working Memory Are Dependent Yet Non-Interacting

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Cognitive control (CC) and working memory (WM) are concurrently necessary for adaptive human behavior. These processes are thought to rely on similar neural mechanisms, yet little is known of the potential competitive or cooperative brain dynamics that support their concurrent engagement during complex behavioral tasks. Here, statistical interactions (synergy/competition) and dependencies (correlations) in brain function related to CC and WM were measured using functional magnetic resonance imaging. Twenty-five healthy adults performed a novel factorial cognitive paradigm, in which a 2-back verbal WM task was combined with the multisource interference task. Overlapping main effects in neural activation were evident in all regions of the “cognitive control network,” together with robust behavioral main effects. However, no significant behavioral or cortical interaction effects were apparent. Conversely, robust positive correlations between the 2 main effects were evident within many components of the network. The results offer robust evidence that the neural representations of WM and CC are statistically dependent, but do not compete. These findings support the notion that CC and WM demands may be dynamically and flexibly encoded within a common brain network to support the efficient production of adaptive behavior across diverse task contexts.

Keywords: cognitive control, dual task, fMRI, frontoparietal, working memory

Introduction

Cognitive control (CC) and working memory (WM) processes are necessary for the efficient production of goal-directed human behavior. CC operations serve to bias perception, information processing, and motor behavior in the brain in favor of stimuli and responses relevant to current goals (Miller and Cohen 2001). These processes include the ability to adaptively focus and shift attention, to inhibit inappropriate behavioral responses, and to manage stimulus–response conflict. WM provides the means to maintain, manipulate, and update behavioral goals and goal-relevant information in mind (Baddeley 1992).

To date, behavioral and neurobiological investigations have largely considered these constructs in isolation. However, many of the same mechanisms that underlie the biasing of perceptual processes during CC are thought to also support, or possibly even drive, the encoding and maintenance of goal-relevant information in WM (Awh et al. 2006; Rutman et al. 2010; Zanto et al. 2011; Gazzaley and Nobre 2012). For example, WM performance has been linked to attention-mediated top-down modulation of neural activity in perceptual cortices (Zanto and Gazzaley 2009; Rutman et al. 2010; Gazzaley 2011; Zanto et al. 2011), while selective attention is known to be influenced by information concurrently held in mind (Postle et al. 2004; Soto et al. 2005, 2008; Kumar et al. 2009). While, to date, the interplay between WM and CC has been most comprehensively considered with respect to selective attention, this relationship also extends to other facets of behavioral control (e.g., cognitive conflict resolution; Redick and Engle 2011; Unsworth et al. 2012). Indeed, the conceptual boundaries between different CC constructs (e.g., selective attention and conflict resolution) remain a matter of considerable debate (Friedman and Miyake 2004; Freitas and Clark 2014). Functional neuroimaging studies also reveal a consistent spatial correspondence in the cortical representations of a range of CC and WM processes within the “cognitive control network” of the brain (Cole and Schneider 2007; Niendam et al. 2012; Fedorenko et al. 2013). These findings together suggest a fundamental reliance on shared neural resources and overlapping mechanisms facilitating WM and CC.

In line with this assertion, behavioral investigations that employ factorial designs have revealed significant interactions between WM load and CC task performance (Kim et al. 2005; Park et al. 2007; Gil-Gomez de Liano et al. 2010; Zhao et al. 2010; Wuhr and Biebl 2011). Updating of WM representations has also been reported to disrupt concurrent adaptive adjustments of control (i.e., conflict-adaptation; Soutschek et al. 2013). Only a small number of investigations have assessed the neural basis of these competitive interactions. Lavie and colleagues (de Fockert et al. 2001; Kelley and Lavie 2011) report functional interactions in visual perceptual areas when CC tasks were undertaken during the maintenance period of delayed-recognition WM paradigms. The factorial integration of visual search and WM demands has also been reported to elicit competitive behavioral and neurobiological interactions within the CC network (Mayer et al. 2007; Silk et al. 2010; Fusser et al. 2011). These findings, alongside associated electrophysiological and behavioral work (Lavie et al. 2004; Schmeichel 2007; Jongen and Jonkman 2011; Pratt et al. 2011; Zhao et al. 2014), suggest that CC and WM may depend on, and compete for, a common neural substrate.

In these paradigms, however, WM and CC demands are generally independent to each other. That is, CC must be performed under task-“irrelevant” WM load, or WM must be maintained during task-“irrelevant” CC operations. Moreover, 2 discrete sets of task demands, perceptual stimuli, and motor responses must be concurrently managed. Consequently, it remains tenuous whether competitive interactions are the result of coincident cognitive operations, or competition...
between mutually exclusive behavioral goals. To address this gap in knowledge, we designed a novel factorial experiment by integrating canonical CC and WM paradigms into a common task framework. CC manipulations were based on the multisource interference task (MSIT; Bush and Shin 2006), in which both stimulus-based (Flanker effect) and response-based (Simon effect) CC is introduced, and prepotent response tendencies must be inhibited. WM demands were introduced using a verbal n-back WM paradigm (Kirchner 1958; Owen et al. 2005), which requires continual encoding, maintenance, and updating of WM representations. Critically, each task trial consisted of a single perceptual stimulus, a single motor response, and a unified behavioral goal, allowing us to assess the hypothesis that competitive interactions between CC and WM in behavioral performance and task-related cortical dynamics would arise as a consequence of reliance on shared neural mechanisms.

If a common neural substrate (i.e., neuronal population/pathway) was indeed required for both operations, this common resource would need to be preferentially allocated to one process over the other, resulting in subadditive interactions within the shared network. Alternatively, supraadditive interactions would manifest if additional resources were brought online to mediate concurrent demands. Efficient behavioral output in the face of competition for resources would therefore likely result in spatially distinct regions of both supra- and subadditive effects within cortical regions. However, should these cognitive systems operate via independent pathways than the activation profiles related to CC and WM would be independent (i.e., uncorrelated) across the population, despite macroscopic spatial overlap.

Materials and Methods

Participants

Twenty-five right-handed adults (14 males; mean age ± SD = 25.5 ± 4.4 years) were recruited from the general community through advertisements in local electronic media. Exclusion criteria included a history of psychiatric or neurologic illness, substance dependence, significant head injury, current use of psychotropic medications, or MRI incompatibility (e.g., cardiac pace-maker), as assessed using the Structured Clinical Interview for DSM-IV Axis-I Disorders (First et al. 2002) and self-report. Participants had completed an average of 14.8 ± 2.2 years of education and had a mean estimated full-scale IQ of 110 ± 10 (Wechsler Abbreviated Scale of Intelligence; Wechsler 1999). The study was approved by local Research and Ethics Committee and all participants provided written informed consent prior to participation.

Behavioral Paradigm

Stimuli were composed of 3 single-digit numbers, ranging from “0” to “3,” centered on a visual display; one of these numbers (the target) was always distinct from the other 2 (the “distracters”; e.g., “2 1 1”; Fig. 1A). Participants identified the value of the target number as quickly and accurately as possible by pressing a button under the index finger for “1,” the middle finger for “2,” and the ring finger for “3,” using their right hand. CC demands were manipulated by altering the composition of the presented triplets (Fig. 1A). “Congruent” trials featured the target number spatially aligned with the corresponding response finger (e.g., a “1” target, corresponding to the leftmost response finger, is always presented as the leftmost digit), paired with distracters having a value of “0,” which do not represent a response alternative. This condition served as an active baseline task. Conversely, “incongruent” trials introduced response-based conflict by presenting the target digit spatially discordant to the corresponding response finger (Simon and Berbaum 1990), and stimulus-based conflict by including alternate response possibilities as distracters (Eriksen and Eriksen 1974). These task demands and stimulus characteristics replicate those of a conventional MSIT design (Bush et al. 2003; Bush and Shin 2006; Yucel et al. 2007).

WM demands were manipulated by requiring participants to compare the target number of the current stimulus with that of the stimulus presented “n” trials previously (n = 0, 1, or 2; Fig. 1A). Participants were instructed to withhold any response should this condition be satisfied. This procedure conforms to conventional verbal n-back paradigms (Baddeley 2003), with the caveat that traditional response rules were reversed; in this case, an n-back match required a nonresponse, while all other trials followed MSIT response rules. By including all combinations of WM load and CC, a 2 × 3 (CC × WM) full factorial experiment was implemented (Fig. 1A).

Two additional conditions were included which were not of interest to the present investigation: One condition presented only response-based “Simon” conflict (e.g., “3 0 0”), and the other only stimulus-based “Flanker” conflict demands (e.g., “1 2 1”). These conditions were not crossed with WM demands.

fMRI Experimental Design

The experiment consisted of 4 task blocks per condition (32 total), presented such that no 2 consecutive blocks called upon the same CC or

![Figure 1](https://example.com/figure1.png)

**Figure 1.** Experimental design. [A] A 2 × 3 factorial structure of the cognitive paradigm with examples of visual stimuli corresponding to low-demand (congruent) and high-demand (incongruent) CC presented at the top. Given a sequential presentation, the appropriate response option to each stimulus is indicated for the 3 levels of WM demand. [B] Example time course of experimental presentation, including rest periods (grey fixation) followed by an instruction screen and stimulus presentation with jittered interstimulus interval.
WM demands and clustered in an A-B-A-B-C-B-C-D-C-D fashion to prevent task-related variability in the measured functional time series from occurring at noise-dominated frequencies (i.e., >1/128 s). Each task block contained 8 + n stimuli presented for 2 s each, with a jittered inter-stimulus interval of between 3.6 and 7.2 s (mean = 4.8 s), varied in steps of 1.2 s (Fig. 1B), and optimized using the optseq2 algorithm (Dale 1999). The first stimulus in 1-back blocks and the first 2 stimuli in 2-back blocks were discarded during analysis to allow for ramping up of memory load. Each of these blocks contained 2 n-back match trials (i.e., non-response contingencies).

An instruction screen indicating the WM level of the subsequent block was displayed for 4.8 s prior to the first stimulus of each block, and every second task block was followed by a 19.2-s rest period. White and grey fixation crosses were presented during inter-stimulus intervals and rest periods, respectively (Fig. 1B). The total experimental time was 28 min 20 s, split evenly between 2 equal runs that were counterbalanced in order across participants. A practise session consisting of two 0-back, two 1-back, and two 2-back blocks preceded scanning to ensure that participants had a complete understanding of the task requirements.

Stimuli were generated and responses recorded using the Presentation software (version 14.4, Neurobehavioural Systems) and a 3-button MR-compatible response box connected to the response computer via a fiber optic cable. Stimuli were backprojected onto a semitransparent display at the foot of the scanner bed and viewed through a head coil-mounted mirror.

Image Acquisition
Images were obtained on a 3-T Siemens Trio scanner equipped with a 32-channel head coil. Each functional run consisted of 354 whole-brain, gradient-echo planar images (GRE-EPIs) comprising 36 interleaved, contiguous axial slices [time repetition (TR) = 2400 ms; time echo (TE) = 32 ms; flip angle = 90°; slice thickness = 3 mm; in-plane resolution (matrix) = 3.3 × 3.3 mm (64 × 64); field of view = 210 × 210 mm]. Three additional whole-brain volumes were acquired and discarded prior to each functional acquisition to allow magnetization to reach steady state. High-resolution T1-weighted magnetization-prepared rapid gradient-echo structural images were also acquired (176 sagittal slices, 0.9 mm isotropic voxels; TR = 1900 ms; TE = 2.24 ms; field of view = 230 × 230 mm; matrix = 256 × 256).

Behavioral Results
Analysis of reaction times from all correct responses in each individual was entered into a 2 × 3 repeated-measures ANOVA with factors “CC” and “WM.” Post hoc pair-wise comparisons were undertaken to disambiguate significant main effects and interaction effects. Mean error rates (and their log-transformed equivalents) failed to meet assumptions of normality. Mean reaction times from all correct responses in each individual were resampled to 2 mm isotropic during normalization, and the images were spatially smoothed using a Gaussian kernel of 8 mm (full-width at half-maximum, FWHM).

The 6 conditions-of-interest were coded as individual predictors of the fMRI time series within a general linear model (GLM) by specifying the onset of each stimulus for which there was a correct response as a delta (i.e., stick) function. Additional regressors were included to account for variance associated with error trials, instruction periods, and WM ramping effects (first stimulus in 1-Back, and first 2 stimuli in 2-Back blocks); the resulting model was convolved with a canonical hemodynamic response function. A high-pass filter (1/128 s) was additionally included to account for low-frequency noise, while temporal autocorrelations were estimated using a first-order autoregressive model [AR(1)]. Regression coefficient estimates (betas) were calculated using a restricted maximum likelihood approach. The resulting parameter estimates from each individual were used as summary statistics for group-level analysis (i.e., hierarchical mixed-effects statistical modeling).

Group-level inference proceeded in an analogous manner to the behavioral analysis described above. The parameter estimates corresponding to the 6 task conditions formed the dependent variable of a second GLM, from which the average group effect of each task condition was estimated. Contrasts between the resulting parameter estimates were used for statistical inference within a repeated-measures ANOVA framework. Voxel-wise statistical parametric maps (SPMs; i.e., T or F-statistic maps) were calculated for each of the positive main effects and the interaction effect across the whole-brain volume. In addition to whole-brain analysis, the null conjunction (i.e., intersection; Friston et al. 2005) of the 2 positive main effects was used as a functional mask to further constrain assessment of interaction effects to spatially coincident task-relevant brain regions.

Penetration maps were additionally calculated to highlight interaction effects that may characterize a subset of participants, but fail to manifest at the group level due to between-subject variability (e.g., Mbwana et al. 2009). To perform the penetration analysis, the within-subject CC × WM interaction effect was first assessed in each individual. The resulting SPMs were then binarized and summed across participants. Voxels in which an interaction effect was present in more than one (n > 5) of the sample were reported.

Voxel-wise contrast estimates from the individual level also served in the assessment of group-level Pearson correlations between the magnitude of the main CC effect (i.e., incongruent > congruent) and the main WM effect (2-Back > 0-Back) across subjects (Wake Forest University Biological Parametric Mapping toolbox; http://fmri.wfubmc.edu/software/bpm/). Where outliers (>3 SD) were detected in either variable, they were removed and the analysis was re-run for that cluster. Only clusters that met corrected statistical thresholds (see below) following removal of outlier(s) were reported. Post hoc, the WM effect was separated into “engagement” (1-Back > 0-Back) and “load” (2-Back > 1-Back) components for all significant effect.

All results are presented at statistical thresholds corrected for multiple comparisons (cluster-based family-wise error-corrected P < 0.05) either at the whole-brain level or within functional masks defined by orthogonal contrasts. Cluster-extent threshold requirements at a given voxel-height threshold were estimated based on the shape and volume of each mask, and the spatial smoothness of the data, using Monte Carlo simulations as implemented in the AlphaSim toolbox (AFNI; National Institutes of Mental Health, Bethesda, MD, USA). Null probability distributions were estimated based on 1000 permutations of simulated noise data having a spatial smoothness (FWHM) of 13 mm (estimated using SPM8). Contiguous clusters in the noise field were defined by edge- or diagonally-connected voxels whose magnitude surpassed the specified voxel-wise threshold.

Results
Behavioral Results
Analysis of reaction times revealed robust main effects of both CC (F(1, 24 = 194.5, P < 0.001) and WM (F(2, 49 = 120.9, P < 0.001),...
but failed to support the presence of an interaction between the two ($F_{2,48} = 1.51, P = 0.23$; Fig. 2A). Post hoc comparisons indicated significant main WM effects related to both engagement (1- vs. 0-back; $F_{1,24} = 68.1, P < 0.001$) and load (2- vs. 1-back; $F_{1,24} = 96.5, P < 0.001$).

Comparable results were apparent with respect to error rates (Fig. 2B); both CC ($Z = -2.24, P = 0.05$) and WM ($Z = -3.95, P < 0.001$) elicited significant main effects, but no significant interaction was observed ($Z = -0.75, P = 0.45$). Post hoc analysis of the WM factor indicated significant effects at both levels (load: $Z = -2.87, P = 0.004$; engagement: $Z = -3.23, P = 0.001$).

The positive linear correlation between main CC and main WM reaction time reached trend-level significance ($r_{25} = 0.30, P = 0.072$). Further disambiguation revealed a significant correlation specific to WM engagement (1-back vs. 0-back; $r_{25} = 0.42, P = 0.018$). Although a comparable dependency did not manifest with respect to the load effect (2-back vs. 1-back; $r_{25} = 0.16, P = 0.22$), the point estimate defining the relationship (i.e., slope of the linear regression line) was similar across levels of the WM factor, indicating a similar effect size but greater reaction time variability in response to the load manipulation across participants (Fig. 2C).

**fMRI Results**

Significant positive main effects common to both WM and CC ($t_{24} > 3.1$, cluster extent $|K_6| > 182$) recapitulated the CC network (Niendam et al. 2012); activations included bilateral regions of the dorsomedial prefrontal cortex (i.e., presupplementary motor area and anterior cingulate cortex); lateral prefrontal cortices (i.e., inferior frontal junction and dorsolateral prefrontal cortex); dorsal premotor cortex (i.e., frontal eye fields); anterior insula; intraparietal sulci (superior and inferior parietal lobules); thalamus; and putamen (Fig. 3 and Table 1). Post hoc analysis of the WM effect indicated that activations were significantly responsive to both engagement and load manipulations in all regions exhibiting a main effect, although the load effect generally predominated.

Within the functional mask defined by the null conjunction of the positive main effects, a significant interaction effect was isolated to a small area of the right thalamus in the approximate area of the ventrolateral nucleus ($x, y, z = 18, -12, 10$; $F_{2,48} > 7.2$ [$F_{peak} = 9.4$]; $K_E = 16$; $P_{FWE} = 0.043$; Fig. 3). Post hoc investigation suggested that this region became increasingly sensitive to CC effects as WM demands increased (Fig. 3F; CC effect during 0-back: $t_{24} = 4.88, P < 0.001$; 1-back: $t_{24} = 1.88, P = 0.072$; 2-back: $t_{24} = 0.25, P = 0.81$).

Interaction effects were absent in all cortical regions, both across the whole brain and within the functional mask (Table 1), and penetrance maps similarly failed to indicate reliable within-subject interactions in any brain region. Subcortical interaction effects also failed to manifest in penetrance maps, suggesting that the interaction reported above was generalizable, yet small in magnitude.

Positive correlations between the CC and the WM fMRI main effects were observed within most brain regions encompassed by the conjunction of the 2 main effects, most extensively within the intraparietal sulci and including regions of the dorsomedial prefrontal cortex, left dorsal and lateral prefrontal cortex, right inferior frontal junction, and right anterior insula (Fig. 4 and Table 2). Post hoc analyses indicated significant dependencies with CC at both levels of WM in all regions, with a consistently greater magnitude of correlation related to the load effect.

Finally, the requirement to withhold a response during n-back task performance has the potential to introduce a response inhibition effect (itself a canonical CC demand) into the WM manipulation, particularly given that a prepotent response tendency is likely conditioned by the predominance of response trials in the experiment. To account for this potential confound, an additional covariate coding for all successful non-response trials in the experiment. To account for this potential confound, an additional covariate coding for all successful non-responses was included in the individual-level GLMs. Despite this inclusion, the group-level results reported above were not meaningfully altered.

This non-response effect was more thoroughly explored by subsequently splitting each of the WM regressors into separate predictors of “Response” and “Non-response” trials. As illustrated in Supplementary Figure 1, the non-response effect (all non-response > all response trials) recruited a set of cortical regions approximating the cingulo-opercular network (Supplementary Table 1), and as such did not considerably overlap with the fronto-parietal control network identified above. This finding helps to explain why accounting for the additional variance associated with the non-response effect did not influence the CC and WM findings.
Discussion

In this experiment, concurrent WM and CC resolution was found to engage largely overlapping cortical and subcortical components of the so-called “cognitive control network,” consistent with previous research (Niendam et al. 2012; Fedorenko et al. 2013). While correlations in the brain activations governing CC and WM were identified across many regions of this network, significant cortical or behavioral interactions were not apparent.

The observation of overlapping, statistically dependent neural correlates is consistent with the current weight of evidence proposing that WM and CC are, to some degree, mechanistically related (Courtney 2004; Awh et al. 2006; Gazzaley and Nobre 2012) and possibly represent manifestations of the same underlying cognitive–neural processes (e.g., internal vs. external sustained attention; Soto et al. 2008; Chun 2011). We hypothesized that dependent activations between CC and WM, alongside subadditive interactions, may result from competition for, or exhaustion of, shared neural substrates. Conversely, supraadditive interactions would likely represent compensatory activations. However, the statistically dependent yet additive results reported here point instead to a flexible mechanism of task representation within this shared neural system. Such flexibility may manifest through dynamic tuning of neuronal activity profiles within the CC network in response to changing behavioral goals; that is, neurons in these areas may respond differentially to comparable contexts as a function of differing objectives (Woolgar et al. 2011; Kadohisa et al. 2013; Stokes et al. 2013). As such, complex cognitive processing may not occur as the sum of modularized cognitive operations, but rather as a unified task representation that is dynamically updated. Alternatively, neural populations within the CC network may simultaneously encode multiple representations related to the current goal set (Rigotti et al. 2013; Sreenivasan et al. 2014). For example, a neuron may respond maximally to a specific conjunction of conditions, as opposed to one feature of a task rule or stimulus (Rigotti et al. 2013). Further research will be necessary to disentangle the relative contributions of “adaptive coding” and “mixed selectivity” to cortical flexibility.

In general, greater covariance with CC effects was observed with respect to the WM load effect (i.e., 2-back – 1-back),
when compared with the engagement of encoding and retrieval mechanisms (i.e., 1-back − 0-back). This result is consistent with evidence that the online maintenance of information may result from sustained top-down biasing of perceptual regions (Curtis and D’Esposito 2003; Gazzaley et al. 2004; D’Esposito 2007; Zanto et al. 2011), in a comparable manner to the operation of selective attention and interference resolution processes (Egner and Hirsch 2005; Hwang et al. 2010; Nelissen et al. 2013). Conversely, manipulation of information in mind is thought to rely on a more independent neural mechanism constrained to major association cortices (Spitzer et al. 2014). The neural mechanisms governing CC may therefore be more closely aligned with those supporting maintenance of perceptual representations in mind relative to performing cognitive operations on that information.
It is important to note that the significant correlations observed between the 2 task contexts characterized only subregions of the shared cortical network, with greater sparsity in prefrontal when compared with parietal regions. In line with recent work (Fedorenko et al. 2013), brain regions eliciting additive and independent activations may represent task-specific mechanisms that operate alongside more superordinate or common neural processes.

The lack of interaction effects characterized here is at odds with a number of other behavioral (Kim et al. 2005; Park et al. 2007; Schmeichel 2007; Gil-Gomez de Liano et al. 2010; Zhao et al. 2010; Wuhr and Biebl 2011) and functional imaging studies (de Fockert et al. 2001; Lavie et al. 2004; Silk et al. 2010; Kelley and Lavie 2011; Pratt et al. 2011). This discrepancy may relate to a key distinction between many previous study designs, which interleave CC demands into the maintenance period of delayed-recognition paradigms, versus the current paradigm, whereby control and memory demands were concurrently relevant to task performance. Moreover, perceptual processing and stimulus–response mappings were held constant in this experiment, with each trial consisting of a single stimulus and single response. It is therefore possible that previously reported interaction effects may be accounted for by task-switching, meta-control, or sensorimotor effects.

It is important to acknowledge that WM and CC abilities are also known to be capacity limited (Marois and Ivanoff 2005; Lavie 2010; Logie 2011). If these limitations result from finite shared resources, interactions may result as cognitive capacity becomes overburdened. Differing cognitive demands may therefore account for distinctions across conceptually similar investigations (e.g., Hester et al. 2004; Hester and Garavan 2005). The current experiment was purposefully restricted to investigation of the neural mechanisms underpinning efficacious cognitive processing in response to complex demands. As such, while robust cognitive demands were introduced, (as evidenced by considerable behavioral slowing), errors remained minimal and error trials were discarded from analyses. Increasing task demands beyond the limitations of available cognitive resources will be key to determining how the brain prioritizes resources and encodes contextual information as behavioral objectives are no longer effectively achieved.

Furthermore, both CC and WM are multifaceted constructs, within which a variety of cognitive processes can be defined (Miller and Cohen 2001; Baddeley 2003). Examples of CC include selective attention toward goal-relevant stimuli (Yantis 2008), inhibition of maladaptive motor responses (Verbruggen and Logan 2008), and resolution of stimulus–response conflict (Botvinick et al. 2001). Similarly, WM encompasses the ability to maintain, manipulate, and update behavioral goals and goal-relevant information in mind (Baddeley 1992). Although the relative independence of, and categorical boundaries between, these processes remain a matter of debate (Hommel et al. 2002; Friedman and Miyake 2004), generalization beyond specific task constructs must be undertaken tenuously. However, here, we employ a WM task that requires continuous maintenance, executive manipulation, and updating of information across multiple levels of load. Similarly, multiple CC demands are concurrently manipulated during task presentation, namely the resolution of “Flanker” interference arising between 2 stimulus characteristics (Eriksen and Eriksen 1974) and “Simon” interference resulting from spatial discordance between the stimulus dimension and the response dimension (Hommel 2011); see also (Kornblum et al. 1990). Critically, both manipulations are thought to invoke a measure of selective attention, prepotent response inhibition, and conflict detection/resolution (e.g., Takezawa and Miyatani 2005; Freitas and Clark 2014). Taken together, the generalization of the results reported here to broader CC and WM domains can be reasonably justified.

Although evidence points toward non-interacting neural activations within cortical regions of a priori interest, a significant subadditive interaction effect was present in the ventrolateral nucleus of the right thalamus. This region displayed decreasing sensitivity to task demands as cognitive load increased, such that maximal control-related responses occurred under no WM load, and maximal WM-related responses occurred in the absence of conflict resolution demands. The ventrolateral nucleus acts as a relay center within the cerebello-dentato-thalamocortical tract of the brain, receiving inputs from the cerebellum and basal ganglia, and projecting to premotor and motor cortices, including the supplementary motor area (Purzner et al. 2007; Marzinik et al. 2008). In relation to CC, the ventrolateral nucleus has been implicated in priming task-relevant motor pathways and inhibiting task-irrelevant
movement during goal-directed behavior (Aron et al. 2003; Marzinzik et al. 2008). To be clear, this region does not directly stimulate (pre-)motor activity, but serves to (dis)inhibit its function. As stimulus–response pathways remain constant throughout this experiment, the priming of relevant motor circuits remains the same across the WM and CC contexts. Accordingly, an increase in behavioral demand while already under load (control or memory) may result in a smaller increment of increased activation in this region than would be observed in isolation.

In summary, this work has shown that competitive interference is not a mandated outcome of concurrent cognitive demands that rely on shared neural resources. This outcome supports a mechanism by which behavioral goals and contextual demands are dynamically and flexibly represented within the so-called CC brain network. These findings corroborate adaptive coding theories of task representation within this network (Duncan 2001; Stokes et al. 2013). Comparably, from a psychological perspective, these results are consistent with the notion that CC and WM are potentially emergent properties of a common higher-order system that serves to regulate perceptual and motor function, as opposed to engendering a set of unique behavioral control processes (Duncan 2001; Hommel et al. 2002; Courtney 2004; Postle 2006). That is, WM may be a temporally extended instantiation of CC, or CC may result from maintaining context-relevant representations in WM. From this perspective, the current experiment may be viewed as the integration of 2 CC (or 2 WM) demands, with implications for generalization of these results to broader contexts. Taken together, the concurrent processing of CC and WM demands would not be the combination of the 2 (thus engendering potential interactions), but rather a qualitatively unique third context. It would therefore appear that, within the limits of this flexible and adaptive system, the brain is able to effectively maintain efficient goal-directed behavioral output without the need to prioritize some cognitive operations over others.

Supplementary Material

Supplementary material can be found at: http://www.cercor.oxfordjournals.org/.

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Notes

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