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Working-Memory-Triggered Dynamic Adjustments in Cognitive Control

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Dynamic adjustments in cognitive control are well documented in conflict tasks, wherein competition from irrelevant stimulus attributes intensifies selection demands and leads to subsequent performance benefits. The current study investigated whether mnemonic demands, in a working memory (WM) task, can drive similar online control modifications. Demand levels (high vs. low) of WM maintenance (memory load of 2 items vs. 1 item) and delay-spanning distractor interference (confusable vs. not confusable with memoranda) were manipulated using a factorial design during a WM delayed-recognition task. Performance was best subsequent to trials in which both maintenance and distractor interference demands were high, followed by trials with high demand in either of these 2 control domains, and worst following trials with low demand in both domains. These results suggest that dynamic adjustments in cognitive control are not triggered exclusively by conflict-specific contexts but are also triggered by WM demands, revealing a putative mechanism by which this system configures itself for successful task performance.

Keywords: cognitive control, working memory, conflict adaptation, sequence effects, dynamic control

Working memory (WM) is critical for surviving and thriving in complex, ever-changing, and challenging situations. Stressful environments degrade WM performance (Evans & Schamberg, 2009; Vasterling et al., 2006), and greater performance impairments signal greater risk for psychiatric dysfunction (Unsworth, Heitz, & Engle, 2005). Yet, little is known about how WM operates on a moment-to-moment basis in the face of changing demands and stressors. Rather than implicating a homunculus, who sits patiently deciding if cognitive control should be up- or down-regulated, a comprehensive account of WM should aim to delineate the circumstances under which WM processes are dynamically modified to influence subsequent behavior, as demands are encountered in the environment. As a first step, we investigated the impact of prior mnemonic demands during a WM delayed-recognition task, on subsequent task performance.

Working memory involves maintaining and manipulating relevant information over short intervals without getting distracted by irrelevant information. Maintenance-related cognitive control operations activate dorsolateral prefrontal cortex, whereas control processes protecting against interference activate ventrolateral prefrontal cortex and other structures (Dolcos, Miller, Kragel, Jha, & McCarthy, 2007; Jha, Fabian, & Aguirre, 2004; Jha & McCarthy, 2000). Numerous studies have established that neural activity levels within these structures increase, and behavioral performance levels decrease, with parametric increases in memory load and distractor interference during delayed-recognition tasks (see D'Esposito, Postle, & Rypma, 2000). Thus, the type of cognitive demand, as well as the level of demand, can be tracked with neural and behavioral measures. While studies utilizing such experimental manipulations have been invaluable in elucidating WM's functional neural architecture (D'Esposito et al., 2000), such studies fail to advance understanding of how WM control processes are configured in response to shifting demands.

Computational theories of cognitive control, which emphasize dynamic adjustments in control during response conflict tasks, have successfully demonstrated when control is most likely to be engaged, modulated, or withdrawn (Botvinick, Braver, Barch, Carter, & Cohen, 2001; Brown & Braver, 2008). In these tasks, conflict trials contain distracting stimulus features associated with an incorrect response. Cognitive demands are higher, response times are slower, and accuracy is lower for conflict versus no-conflict trials because these distracting features trigger prepotent response tendencies that must be overcome for successful performance. Many studies have shown that performance on high-conflict trials is better following high- (vs. low-) conflict trials (Botvinick, Nystrom, Fissell, Carter, & Cohen, 1999; Gratton, Coles, & Donchin, 1992; Kerns et al., 2004). This facilitated performance as a function of previous high demand (high conflict) is referred to as *conflict adaptation* and is proposed to result from a conflict-triggered upregulation in cognitive control. Trials immediately following conflict trials, thus, enjoy greater access to control resources to resolve interference from irrelevant stimulus features (Botvinick et al., 2001).

There is some evidence that the engagement of WM control operations at one moment in time has consequent effects on task performance (Persson & Reuter-Lorenz, 2008; Pessoa, Gutierrez, Bandettini, & Ungerleider, 2002; Schmeichel, 2007). Yet, none of these studies have examined the moment-to-moment influence of

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current demand level on subsequent engagement of control during WM tasks. Nonetheless, conflict adaptation provides prima facie support that engagement of cognitive control can be dynamically adjusted based on prior control demands. What remains unclear is whether this important feature of cognitive control is present exclusively during conflict tasks, characterized by the need to overcome prepotency, or whether it is present in other demand contexts.

A recent study by Fischer, Dreisbach, and Goschke (2008) found that not only response conflict, but also variations in the difficulty of a number comparison task, generated alterations in subsequent processing. While their results certainly broaden the task contexts in which control adjustments are observed, since they too incorporated a response-conflict component in their task, more studies are required to determine the specific conditions under which dynamic adjustments occur. In the present study we investigated whether parametric manipulations in memory load and distractor interference, which successfully modulate control demands *during* WM delayed-recognition trials (see D'Esposito et al., 2000), may also trigger dynamic adjustments in control *across* trials.

High- and low-demand conditions of memory maintenance (memory load of two items vs. one item) and delay-spanning distractor interference (distractors confusable vs. not confusable with memoranda) were combined in a factorial design. We asked three main questions. First, will current trial performance be sensitive to the level of cognitive demand in the previous trial? In line with conflict adaptation, we predicted that performance would be better on trials preceded by high- (vs. low-) demand trials. Second, will current trial performance differ on the basis of the domain (maintenance-related or interference-related) of cognitive demand in the previous trial? Past research has suggested that WM performance is sensitive to demand levels of maintenance- and interference-related control processes (Jha et al., 2004; Jha & McCarthy, 2000). As such, we had no a priori reason to suspect that these control domains would differ in their ability to provoke dynamic adjustments in subsequent trials. Third, if dynamic adjustments in subsequent trial performance are observed, will their magnitude vary as a function of current trial demand level or domain? Since conflict adaptation occurs only when current trial conflict is high, we predicted that current high-demand trials would be most sensitive to previous trial demand level. We had no a priori reason to suspect that this pattern would differ across the two control domains investigated herein.

Method

Fifty-four (30 female) healthy volunteers provided informed consent prior to entry into this study, which was approved by the University of Pennsylvania Institutional Review Board. All participants sat in a quiet room, 57 cm from a monitor, to perform a delayed-recognition WM task, instructing them to remember images of faces or shoes across individual trials (see Figure 1A).

As shown in Figure 1, each trial began with the presentation of a memory array (S1), consisting of either two memoranda (high mnemonic load) or one memorandum and a noise mask (low mnemonic load), appearing side by side for 3,000 ms. S1 offset was followed by a 3,500-ms delay period, after which a test item (S2) was presented centrally for 2,500 ms. On half of the trials, S2 was a single image from the S1 array (*match trials*), and on the remaining trials, S2 was a novel image that had not appeared at any other point in the experiment (*nonmatch trials*). S2 was always from the same stimulus category as S1 (e.g., if S1 consisted of faces, S2 was a face). Participants were instructed to determine

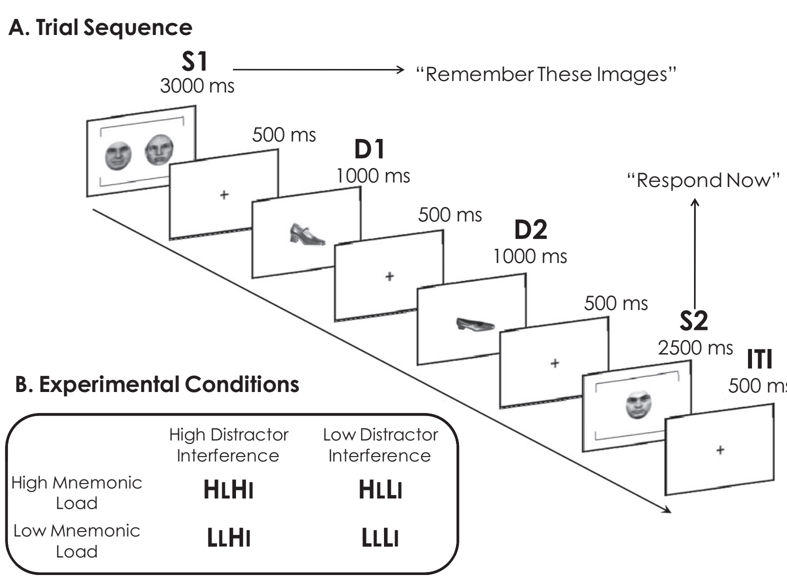

Figure 1. A: Time course of one trial of delayed recognition working memory task. Face and shoe working memory trials were intermixed. After a series of practice trials, participants began the experiment, which consisted of two experimental blocks of 30 trials each, totaling 60 trials. B: Examples of each of the distinct manipulations of mnemonic load and distractor interference, and the labeling system used to describe these specific conditions.

whether S2 matched either S1 memorandum and to indicate a match or nonmatch response by pressing a designated button. Before beginning the experiment, participants were instructed to respond in a manner that would ensure that they made accurate responses without being unduly slow. Half of the trials required working memory for faces, whereas the other half required working memory for shoes, and these trial types were intermixed.

On all trials, two task-irrelevant distractors, consisting of either faces or shoes, were presented sequentially during the delay interval. Both distractor images within a trial were always of the same category (e.g., two faces or two shoes), were never repeated across trials, and were never identical to any S1 or S2 items. Participants were instructed to keep their gaze focused at fixation and to disregard these distractors. Both S1 and S2 featured brackets above and below the images to distinguish them from distractors, which appeared without brackets. On half of the trials the distractors were from the same stimulus category as the memory items (high distractor interference), whereas on the other half the distractors were from the other stimulus category (low distractor interference). These trial types were randomly intermixed. After a series of practice trials, participants began the experiment, which consisted of two experimental blocks of 30 trials each, totaling 60 trials.

Thus, control demands were manipulated along the two domains of mnemonic load and distractor interference, yielding four distinct trial types that occurred equally often and were pseudorandomly intermixed (Figure 1B). We chose these levels of load and interference on the basis of previous studies (Jha et al., 2004; Jha & McCarthy, 2000) indicating that manipulations along both dimensions should affect performance comparably. Furthermore, although a load difference of only one item may seem small, we had several specific reasons for choosing load levels of one and two. First, our prior results (see Jha & McCarthy, 2000) suggested that the differences in activation level within prefrontal regions, during fMRI studies of working memory maintenance, show a large activation difference between one and two items and a much smaller difference between two and three items. These activity profiles were consistent with the behavioral differences in accuracy as a function of load level. Thus, on the basis of our previous results, we did not suspect that the functional differences would be as pronounced if the high load level was three instead of two. Beyond three faces, as reported in Jha and McCarthy (2000), performance begins to drop closer to chance levels. In addition, when load levels are very high, the strategy used to perform the task may shift. Braver and colleagues (Braver, Gray, & Burgess, 2007) suggested that when load is low, a proactive strategy of actively maintaining memory items over the course of the delay interval may be used. When the load level is too great, however, individuals may shift to a reactive or familiarity-based strategy in which they do not actively maintain the items—rather they simply wait until the S2 test item appears to actively recall the encoding episode. Thus, we chose load levels of one and two to maximize our chances of promoting an active perceptual maintenance strategy, while not overtaxing participants to the point of chance performance.

Results

Because the instructions to participants emphasized ensuring accuracy more than speed, the primary analyses were conducted using participants' accuracy (percentage correct) for identifying S2 as a match or nonmatch. To ensure that the results were not driven by speed–accuracy tradeoff, and for the sake of completion, response times (RT, in milliseconds) on correct trials were also investigated. Accuracy and RT scores were examined according to the specific conditions of the current trial (trial *N*), as seen in Figure 2. In addition, current trial performance, collapsed across current trial condition, was examined as a function of the previous trial type (trial $N - 1$), as seen in Figure 3. In this analysis, only trials on which trial $N - 1$ responses were correct were included.

We conducted repeated measures analyses of variance (ANOVA) separately for the effects of current (trial *N*) and previous trial (trial $N - 1$) control demands, each with two factors and two levels within each factor (Control Domain: Mnemonic Load and Distractor Interference × Demand Level: High and Low).

Consistent with prior work (Jha & McCarthy, 2000), the ANOVA for current trial effects revealed a main effect of mnemonic load: Participants were more accurate (93% vs. 85%), $F(1, 53) = 37.85$, $MSE = .008$, $\eta_p^2 = .42$, $p < .001$, and faster (936 ms vs. 1,111 ms), $F(1, 53) = 109.42$, $MSE = 14532.088$, $\eta_p^2 = .67$,

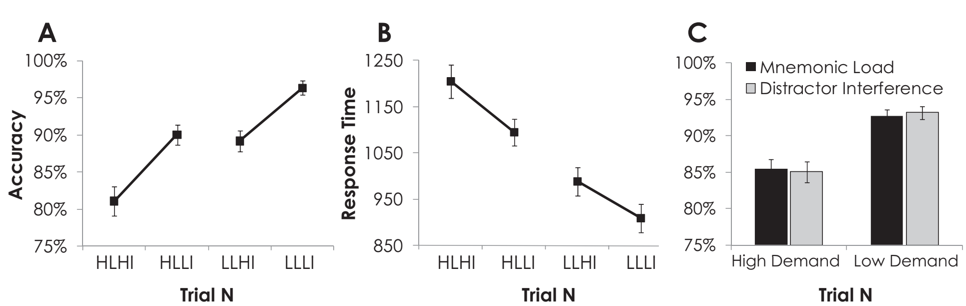

Figure 2. A: Participants' average accuracy (percentage correct) for each of the specific current trial conditions. B: Participants' average response time (in milliseconds) for each of the indicated current trial conditions. C: Average accuracy as a function of high versus low current trial control demand, in the domains of mnemonic load and distractor interference, separately, while collapsed across levels of the alternate domain. HLHI = high mnemonic load, high distractor interference; HLLI = high mnemonic load, low distractor interference; LLHI = low mnemonic load, high distractor interference; LLLI = low mnemonic load, low distractor interference. Error bars represent one standard error above and below the mean.

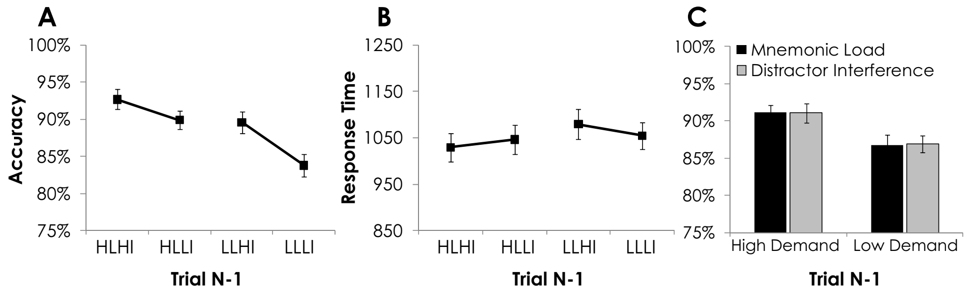

Figure 3. A: Participants' average accuracy on the current trial, when the immediately preceding trial (trial $N - 1$) was the specific condition indicated. B: Average response time on the current trial, when the preceding trial (trial $N - 1$) was the condition indicated. C: Average accuracy as a function of high versus low previous trial control demand, in the domains of mnemonic load and distractor interference, separately, while collapsed across levels of the alternate domain. HLHI = high mnemonic load, high distractor interference; HLLI = high mnemonic load, low distractor interference; LLHI = low mnemonic load, high distractor interference; LLLI = low mnemonic load, low distractor interference. Error bars represent one standard error above and below the mean.

$p < .001$, when the current trial was low mnemonic load (vs. high load). Also in keeping with prior findings (Jha et al., 2004; Sreenivasan & Jha, 2007), there was a main effect of distractor interference: Participants were more accurate (93% vs. 85%), $F(1, 53) = 37.96$, $MSE = .009$, $\eta_p^2 = .42$, $p < .001$, and faster (984 ms vs. 1,060 ms), $F(1, 53) = 40.40$, $MSE = 8715.212$, $\eta_p^2 = .43$, $p < .001$, when the current trial had low distractor interference (vs. high interference). There was no interaction between the mnemonic load and distractor interference effects on either accuracy ($p > .42$) or RT ($p > .58$). The magnitude of the effects of mnemonic and interference demands on accuracy did not differ ($p > .52$; see Figure 2C), though the magnitude of the effect of current trial mnemonic load on RT was greater than that of distractor interference, $t(1, 53) = 4.20$, $p > .001$.

The ANOVA for previous trial control demands revealed a main effect of previous mnemonic load (mnemonic load on trial $N - 1$): Participants were more accurate (91% vs. 87%), $F(1, 53) = 17.98$, $MSE = .006$, $\eta_p^2 = .25$, $p < .001$, and faster (1,004 ms vs. 1,039 ms), $F(1, 53) = 5.93$, $MSE = 7144.808$, $\eta_p^2 = .10$, $p < .02$, when the preceding trial was high mnemonic load (vs. low mnemonic load). There was also a main effect of previous distractor interference (interference level on trial $N - 1$) on accuracy (91% vs. 86%), $F(1, 53) = 9.20$, $MSE = .009$, $\eta_p^2 = .15$, $p < .01$, but not on RT, $p > .10$. Participants were more accurate when the previous trial was high interference (vs. low interference). There were no significant interactions between previous trial mnemonic and interference demands for either accuracy, $p > .20$, or RT, $p > .12$, and current trial performance benefits as a function of high versus low previous trial demand levels were comparable across both previous trial control domains (see Figure 3C).

We also conducted a series of ANOVAs to examine the impact of previous control demands at each current trial demand level. As there were no significant interactions between mnemonic and interference demands on performance as a function of either current or previous trial type, we examined the Current Trial × Previous Trial interactions by entering only one current trial and one previous trial demand category at a time. In addition, because the task instructions emphasized accuracy and no evidence of speed–accuracy tradeoffs was observed, this analysis explored task accuracy exclusively.

Each ANOVA had one current trial factor and one previous trial factor with two levels of demand for each factor (high and low). The four resulting ANOVAs were as follows: (a) current mnemonic load, previous mnemonic load; (b) current distractor interference, previous mnemonic load; (c) current mnemonic load, previous distractor interference; and (d) current distractor interference, previous distractor interference.

In all four ANOVAs, the main effects for current trial and previous trial were significant, $p < .05$, and replicated the patterns reported above. Briefly, current trial accuracy (collapsed across *previous* trial demand level) was higher when the current trial demand level was low (vs. high) for both mnemonic load and distractor interference. Current trial accuracy (collapsed across *current* trial load level) was higher when previous trial demand level was high (vs. low) for both control domains as well. Based on the prior conflict adaptation results (see Egner, 2007, for a summary), we anticipated that the interactions between current and previous trial demand level would be significant. Specifically, we predicted that the benefits of previous high versus low demand would be more robust when the current demand levels were high (vs. low).

The results as a function of current trial mnemonic load were not consistent with this prediction. The magnitudes of performance benefits resulting from previous high (vs. low) mnemonic demand were comparable when the current trial mnemonic load level was low (vs. high), resulting in a nonsignificant interaction between current trial mnemonic load and previous trial mnemonic load, $p > .32$ (Figure 4A). The magnitude of performance benefits resulting from previous high (vs. low) interference demands was greater when the current trial load level was low (vs. high), corresponding with a significant Current Trial Mnemonic Load × Previous Trial Distractor Interference interaction, $F(1, 53) = 5.69$, $MSE = .009$, $\eta_p^2 = .10$, $p < .05$ (Figure 4C). Thus, neither of the previous trial domains produced greater benefits for current high (vs. low) mnemonic load trials.

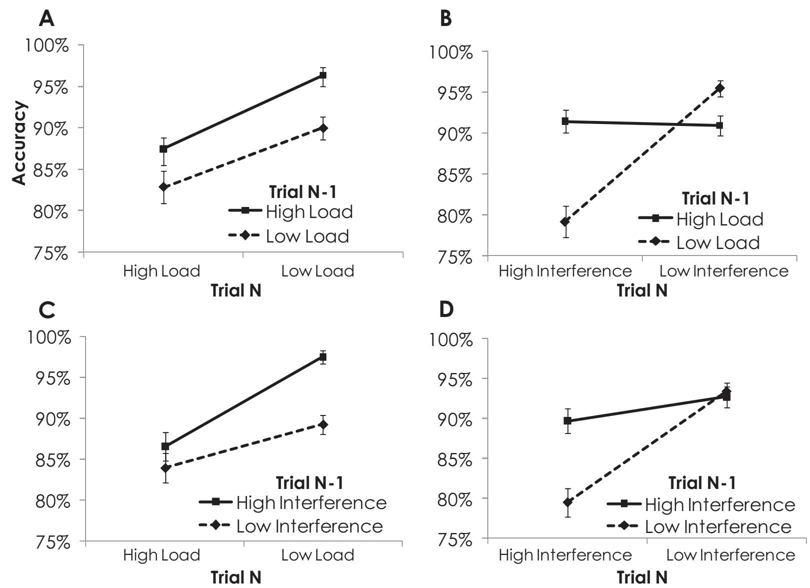

Figure 4. A: Accuracy for current high versus low mnemonic load trials as a function of the mnemonic load of the previous trial. B: Accuracy for current high versus low distractor interference trials as a function of the mnemonic load of the previous trial. C: Accuracy for current high versus low mnemonic load trials as a function of the distractor interference of the previous trial. D: Accuracy for current high versus low distractor interference trials as a function of the distractor interference of the previous trial. Error bars represent one standard error above and below the mean.

An examination of current trial distractor interference revealed patterns consistent with previous studies of conflict adaptation. Previous trial benefits were observed when current trial interference demand levels were high but not low. Indeed, significant interactions with previous trial mnemonic load, $F(1, 53) = 50.08$, $MSE = .008$, $\eta_p^2 = .47$, $p < .001$ (Figure 4B) and previous trial distractor interference, $F(1, 53) = 24.38$, $MSE = .006$, $\eta_p^2 = .32$, $p < .001$ (Figure 4D) were observed.

Discussion

We investigated whether mnemonic demands in a delayed recognition WM task would trigger performance benefits on subsequent trials, similar to effects demonstrated in conflict tasks in the form of conflict adaptation (Egner, 2008). We found that increasing WM demands on current trials corresponded to parametric decreases in current trial accuracy (Figure 2A, collapsed across previous trial type) as predicted by numerous previous studies of WM (see D'Esposito et al., 2000, for an overview). It is important that increasing previous trial WM demands corresponded to commensurate increases in current trial accuracy (Figure 3A, collapsed across all current trial types). Thus, these results give positive support for working-memory-triggered dynamic adjustments in cognitive control.

Although the proposal that conflict adaptation results from conflict-triggered upregulation in cognitive control motivated many of our hypotheses, there have been recent challenges to this proposal. Mayr, Awh, and Laurey (2003) argued that the performance patterns observed in conflict adaptation result from repetition priming. They noted that the conditions demonstrating facilitated performance are also those in which priming of perceptual and response features of stimuli over subsequent trials could reduce task demands. However, several studies have now confirmed that conflict adaptation persists when controlling for stimulus and response repetitions (see Ullsperger, Bylsma, & Botvinick, 2005). In the current study, no memory items were repeated across trials. The only time a memory item was seen more than once, over the course of the entire experiment, was if it appeared as a match stimulus at S2. None of the distractor images were repeated across trials either. In addition to controlling for stimulus repetitions, we pseudorandomly varied the type of response that was required across consecutive trials (match or nonmatch), as well as the stimulus category (face or shoe) that might appear on subsequent trials as memoranda or distractors. Thus, our results cannot be explained by repetition priming associated with repetition of specific exemplars, category of stimuli, or responses made over consecutive trials.

A topic of active investigation within the conflict adaptation literature concerns the nature of conflict-triggered upregulation of control processes. In the context of conflict tasks, the domain of control is determined by the specific stimulus and task requirements that produce conflict. For example, conflict could occur at the perceptual/representational level or at the response level. Several studies have suggested that the conflict-driven upregulation of control is domain general (see Botvinick et al., 2001; Freitas, Bahar, Yang, & Banai, 2007), so that conflict resolution improves subsequent to high-conflict trials even if conflict domains differ across trials. Cross-conflict adaptation is proposed to result from conflict on trial $N - 1$, triggering enhancement of all top-down selection mechanisms necessary to resolve conflict in the overall task set.

Maintenance and distractor interference resolution were the two WM control domains examined herein. In the context of our delayed-recognition task, maintenance processes keep representations of memoranda active over the delay interval, and distractor interference resolution protects memory representations from degradation due to competing, task-irrelevant information. At the neural level, maintenance processes for visual stimuli are instantiated as tonic delay-spanning activity within prefrontal and perceptual cortices biased in favor of the perceptual features of memoranda (see Chelazzi, Miller, Duncan, & Desimone, 1993; Fuster & Jervey, 1982). Distractor interference resolution has been proposed to be supported by phasic, gain-control mechanisms that selectively amplify neural activity evoked by memoranda and selectively suppress distractors, with the magnitude of signal modulation commensurate with the level of interference (Sreenivasan & Jha, 2007). Thus, extant evidence suggests that these two control domains are supported by distinct neural mechanisms when they are employed within current trials. Might neural signaling of upregulation of control, triggered by high demand in each of these domains, also be distinct? Or might upregulation be domain general, such that *both* types of selection mechanism (tonic biasing and phasic gain-control modulation) are enhanced subsequent to high demands for either domain?

Because we did not investigate neural activity in the current study, we are unable to answer this question. Although our behavioral results revealed, when collapsed across all current trial types, that performance benefits as a function of previous high (vs. low) demand level were comparable across both domains (see Figure 3C), interaction patterns between current and previous domains were not comparable across both current trial domains. Although performance benefits were exclusively observed for current high interference trials for both previous control domains (see Figures 4B and 4D), performance benefits were not exclusive to current high mnemonic load trials. In addition, current mnemonic load did not show comparable patterns across both control domains (see Figures 4A and 4C). These results challenge the proposal of a domain-general mechanism.

Recent results from the conflict adaptation literature also challenge a domain-general mechanism. When a conflict task is designed so that conflict domains are independent, combined in a factorial design, and methodologically unconfounded, cross-conflict adaptation is not observed. Egner and others (see Egner, 2008) have suggested that dynamic upregulation of control processes may be domain specific. From this point of view, a particular conflict domain would trigger upregulation of only the subset of top-down selection processes necessary to resolve that instantiation of conflict. Control processes tied to other domains of conflict, which may be present within the task set, would not be upregulated. Thus, in a task context that included multiple independent conflict domains, conflict adaptation would be observed only when the conflict domain in trials $N - 1$ and N were identical.

In the current study, we found that performance accuracy was comparably modulated by both previous domains for current high interference trials (Figures 4B and 4D). Yet, it is possible that distinct, control-specific neural mechanisms lead to these performance improvements. For instance, when previous mnemonic load was high, there may have been upregulation in the form of tonic increases in neural representations of trial N memoranda, whereas high previous interference demands may have improved trial N distractor suppression in a gain-control fashion. Both of these mechanisms, while distinct, may lead to similar modulations in performance. Thus, strong evidence in support of domain-specific mechanisms would require neural measures to uncover dynamic effects at multiple processing stages.

In summary, the current results suggest that dynamic control adjustments can be found during WM tasks as they are in conflict tasks. Nonetheless, many more studies must be conducted to fully understand the specific mechanisms supporting our behavioral results. Future studies should examine neural measures to help illuminate the nature of the signal(s) passed along from one trial to the next. Additionally, WM is known to be influenced by many factors, such as age (Bunge & Crone, 2009; Cabeza et al., 2004) and stress (Evans & Schamberg, 2009), so future studies should examine how the dynamic properties of WM interact with these and other factors. Since the WM system is critical for everyday survival as well as lifelong flourishing, a better understanding of how WM dynamically configures itself for best task performance may, one day, inform development of training programs to protect against, or even prevent, age-related or stress-related vulnerabilities.

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