Neural Dynamics of Conflict Control in Working Memory

Khoi D. Vo[1], Audrey Siqi-Liu[1], Alondra Chaire[2], Sophia Li[1],
Elise Demeter[3], Tobias Egner[1], and Marty G. Woldorff[1]

Abstract

■ Attention and working memory (WM) have classically been considered as two separate cognitive functions, but more recent theories have conceptualized them as operating on shared representations and being distinguished primarily by whether attention is directed internally (WM) or externally (attention, traditionally defined). Supporting this idea, a recent behavioral study documented a "WM Stroop effect," showing that maintaining a color word in WM impacts perceptual color-naming performance to the same degree as presenting the color word externally in the classic Stroop task. Here, we employed ERPs to examine the neural processes underlying this WM Stroop task compared to those in the classic Stroop and in a WM-control task. Based on the assumption that holding a color word in WM would (pre-)activate the same color representation as by externally presenting that color word, we hypothesized that the neural cascade of conflict–control processes would occur more rapidly in the WM Stroop than in the classic Stroop task. Our behavioral results replicated equivalent interference behavioral effects for the WM and classic Stroop tasks. Importantly, however, the ERP signatures of conflict detection and resolution displayed substantially shorter latencies in the WM Stroop task. Moreover, delay-period conflict in the WM Stroop task, but not in the WM control task, impacted the ERP and performance measures for the WM probe stimuli. Together, these findings provide new insights into how the brain processes conflict between internal representations and external stimuli, and they support the view of shared representations between internally held WM content and attentional processing of external stimuli. ■

INTRODUCTION

We often perform tasks that require an externally directed focus of attention (such as driving a car or cooking a meal), while also keeping in mind internal information (working memory [WM]) that may or may not be related to the task at hand (e.g., remembering directions vs. remembering to return a missed call from your in-laws). What we maintain in WM can affect our attention and thus substantially impact the way we interact with stimuli in our environment. Likewise, our interaction with the external world can also influence the information we are endeavoring to maintain in WM. Although the interplay between attention and WM is crucial to successfully navigating everyday life, the nature of their relationship is not well understood.

Attention and WM have classically been considered two separate cognitive functions: Attention refers to the prioritized processing of a subset of information in the environment (Treisman, 1960; Broadbent, 1958), whereas WM has traditionally been thought of as a dedicated cognitive system that acts as a buffer to temporarily process and maintain information internally when such information is no longer present in the environment (Baddeley, 1992; Baddeley & Hitch, 1974). Recent work, however,

has indicated that attention and WM are not as separable as previously believed. Specifically, WM could be conceived as an *internally* directed form of attention, with a common set of representational substrates and attentional control mechanisms that either activate representations endogenously or facilitate their activation by external stimuli by attending to them (Kiyonaga & Egner, 2013; Gazzaley & Nobre, 2012; Postle, 2006; Awh & Jonides, 2001).

A compelling set of behavioral findings to support this notion derives from a modified color-word Stroop task devised by Kiyonaga and Egner (2014). These authors showed that the classic Stroop effect (MacLeod, 1991; Stroop, 1935)—slower and more error-prone responses when participants have to name the font color of a semantically incongruent word (e.g., the word BLUE in red ink) compared to a congruent one (e.g., the word BLUE in blue ink)—could be instantiated when participants were instead asked to hold a color word (e.g., "blue") in mind during a simple perceptual color categorization task (classifying colored swatches as being blue, green, red, or yellow). This "WM Stroop effect" was also subject to modulation by the proportion of incongruent trials just like the classic Stroop effect (e.g., Bugg & Crump, 2012), with smaller Stroop effects under conditions of more frequent incongruent trials (Kiyonaga & Egner, 2014). These findings thus indicated that internally activated representations can interfere with externally

[1]Duke University, Durham, NC, [2]German Centre for Neurodegenerative Diseases, Magdeburg, Germany, [3]University of North Carolina at Charlotte

attended information in a similar way as external distracters, with similar strategic effects on conflict-resolution processes, suggesting that WM shares representation and control processes with external attention.

However, because of the purely behavioral nature of these findings, it is not known to what degree the underlying neural control mechanisms may differ between the circumstances of an internal versus external source of processing conflict. In particular, although many prior studies have investigated the neural mechanisms of detecting and resolving conflict in information processing that stems from external distractors, such as in the classic Stroop task (Appelbaum, Meyerhoff, & Woldorff, 2009; Egner & Hirsch, 2005; Kerns et al., 2004; MacDonald, Cohen, Stenger, & Carter, 2000), it is not known how conflict stemming from an internal WM representation might be detected and resolved. The core assumption of shared representations between WM and attended external stimuli results in a strong prediction regarding the temporal cascade of neural conflict–control processes. Namely, a color word held in WM would result in a "pre-activation" of the corresponding representation, and thus the conflict generation (and resolution) in the WM Stroop task would be expected to occur more rapidly than in the classic Stroop task, where color and color-word information are both presented externally and simultaneously. Given this timing-related prediction, a particularly sensitive way to approach this question would be to leverage the high temporal resolution of EEG.

Accordingly, we addressed this question here by combining an adapted and extended version of the WM Stroop task (Kiyonaga & Egner, 2014) with EEG, along with an additional, specifically directed, control task. Participants performed three variants of the Stroop task (see Methods section). Of the three Stroop variant tasks, two were delayed-match-to-sample WM tasks that integrated the color discrimination into the delay period, with the third being the classic Stroop task. The key commonality across these tasks was that subjects were required to perform a color discrimination on an external stimulus in which the processing of the task-relevant stimulus feature (a color swatch) could be interfered with by other conflicting task-irrelevant information (i.e., the color word). Between the two WM tasks, the key difference was whether the *source* of this conflict (i.e., how task-irrelevant information was introduced) was from a clash with another external stimulus feature (classic Stroop task) or a clash with information being maintained in WM (WM Stroop task). The key difference between the two WM tasks was whether or not the item being held in WM overlapped in domain with the task demands during the delay-period Stroop task. The standard WM Stroop task (keeping color words in WM) involved such an overlap (color representations), whereas the newly devised WM Stroop control task did not (participants were instead asked to remember a number word rather than a color word). Contrasts between these three tasks allowed us

to delineate the neural dynamics—in terms of amplitudes and latencies of ERP measures of brain activity—of processing conflict stemming from a clash between internal information and externally presented stimuli compared to conflict between two features of an externally presented stimulus, while controlling for WM load.

METHODS

Participants

Thirty-three healthy volunteers provided written informed consent to participate in our study in accordance with the Duke University institutional review board. Three participants were excluded because of an excessive level of noise in the EEG data ($n = 2$) or poor behavioral performance ($n = 1$), yielding 30 participants for the final analyses (13 men; ages 18–30 years). All participants passed a screening before the study that ensured they were fluent in English, did not have any color-vision deficiency, and were not taking any attention-enhancing drugs. Participants were compensated \$15 per hour for their participation.

Tasks

Participants performed three variants of the Stroop task, as introduced above and described in detail below.

Classic Stroop Task

The prototypical Stroop task (Stroop, 1935) consists of a series of color words presented in colored font where participants are tasked to report the font color while ignoring the semantic meaning of the word. However, in order to approximately equate visual stimuli across tasks in this study, our *classic Stroop* task (Figure 1A) consisted of a series of color words (red, blue, green, purple) written in white font (red, green, blue values: 200, 200, 200) and superimposed on rectangular color swatches (red = 255, 0, 0; blue = 0, 0, 255; green = 34, 139, 34; purple = 153, 50, 204). Using one of four designated response keys on a gamepad mapped to the possible colors, participants were asked to report the color of the rectangular swatches and to ignore the accompanying color word (Figure 1A). Previous work from our group has demonstrated that this alternative presentation of Stroop stimuli produces similar behavioral conflict effects as the standard Stroop stimulus (Appelbaum, Boehler, Davis, Won, & Woldorff, 2014; Appelbaum, Boehler, Won, Davis, & Woldorff, 2012; Appelbaum et al., 2009). In this task, participants were given up to 1000 msec to respond. Each color-word swatch stimulus was presented on a black background and separated in time by a jittered intertrial interval of 1100–1300 msec. Equal proportions of congruent trials (semantic meaning and color swatch in agreement) and incongruent trials (semantic meaning and color swatch differing) were
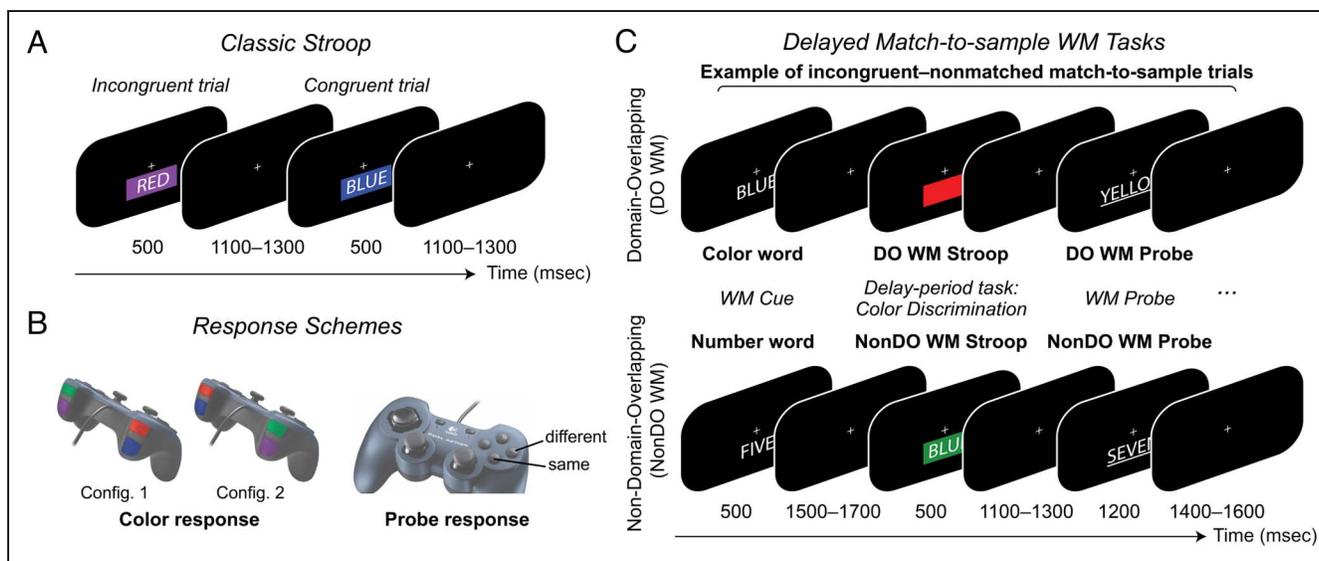
Figure 1. Experimental paradigm with sample trial sequences. Participants completed each task in four independent blocks of 60 trials (240 trials per task), where the common task requirement was to perform a color discrimination on an external stimulus (color patch). (A) Our version of a classic Stroop task where the stimuli have been altered in order to control for visual presentation across the three tasks. (B) Two response schemes for color responses (counterbalanced across participants) and one response scheme for probe responses (constant across participants). (C) Two delayed match-to-sample WM tasks where participants were told that the item held in WM (WM Cue) will be tested (WM probe) after they performed a color discrimination task during the delay period.

presented in randomized order. This task was used to assess typical conflict–control processes outside of the WM domain, where conflict originates from clashing representations triggered by two features of an *external* stimulus, that is, the color of the swatch and the semantic meaning of the printed color word.

Domain-overlapping WM Stroop Task

This delayed match-to-sample task (Figure 1C, top) was patterned after the WM-variant Stroop task from Kiyonaga and Egner (2014). Each trial started with a *color word* WM cue (the words RED, BLUE, GREEN, or PURPLE, printed in white on a black background), which participants were asked to remember for a subsequent WM test at the end of the trial. Following the WM cue, participants were shown a rectangular color swatch (red, blue, green, or purple), with the task to report the color of the swatch using the same button mapping as the classic Stroop task. Because the internally attended stimuli (i.e., the color word memoranda) and perceptual stimuli during the delay-period task had semantic/feature-domain overlap (i.e., color), we refer to it as the domain-overlapping WM Stroop task (*DO WM Stroop*). After the delay period, another color word, now underlined to clarify that it was the WM probe, was shown and participants indicated whether this probe matched the WM cue they had kept in memory. This DO WM task, in particular its delay-period segment, was used to assess conflict–control processes when conflict was caused by incompatibility between an internally represented WM item (the color word) and an external stimulus feature (the color of the swatch).

Participants had up to 1000 msec to respond during the DO WM Stroop task and up to 1200 msec to respond to the DO WM probe. A jittered interstimulus interval (ISI) of 1500–1700 msec separated the WM cue and the color swatch, and a jittered ISI of 1100–1300 msec separated the color swatch and the WM probe. A jittered intertrial interval of 1400–1600 msec separated each compound-event trial. Equal proportions of congruent trials (WM cue meaning and color swatch in agreement) and incongruent trials (WM cue meaning and color swatch differing), as well as equal proportions of trials of matching and nonmatching WM probes, were presented in randomized order.

Non-DO WM Stroop Task

We included an additional dual-task paradigm (Figure 1C, bottom) as a comparison to the DO WM task that was not present in the original Kiyonaga and Egner (2014) study. This dual task was also a delayed match-to-sample WM task, but here the memoranda did not overlap semantically with the relevant external stimulus feature during the delay-period task, thus providing a WM-load control condition with respect to the DO WM task. Specifically, the WM cue item and probe in this condition were *number words* (four, five, six, seven) instead of color words, with the delay-period task using the same structure and stimuli as our classic Stroop task (color word superimposed on a rectangular color swatch). Because the WM item and delay-period Stroop task did not have any feature-domain overlap, we refer to this Stroop as the non-DO WM Stroop task (*NonDO WM Stroop*). Thus, both the NonDO WM Stroop and the classic Stroop

required control over conflict triggered by clashing external stimulus features, rather than triggered by an internal WM representation clashing with an external stimulus as in the DO WM Stroop task. In addition, the fact that participants had to also keep in mind a WM item in this condition allowed us to compare the interplay between external processing and WM maintenance as a function of whether there was or was not domain/semantic overlap between the external item and the internally held one (i.e., comparing the responses to the NonDO WM probe and the DO WM probe).

The trial organization, timing, task requirements, and response mappings of the NonDO WM task were the same as the DO WM task. Likewise, equal proportions of congruent (color word meaning and color swatch in agreement) and incongruent (color word meaning and color swatch differing) Stroop stimuli, as well as equal proportions of matching and nonmatching WM probes, were presented in randomized order. For the purpose of this report, WM probes for the DO and NonDO WM tasks were analyzed based on whether the preceding delay-period color discrimination task was a congruent or incongruent trial, but not as a function of whether they were matching or nonmatching with the memoranda because this contrast was too general and did not specifically highlight the impact of delay-period task conflicts on WM maintenance.

Procedure

All tasks were programmed using the Presentation software package (Neurobehavioral Systems, Inc.) and presented on a 24-in. LCD monitor. Data were collected in a dimly lit, electrically shielded room where participants were seated in a comfortable chair positioned ~60 cm from the screen. To control for eye movement, participants were asked to continuously fixate on a crosshair placed in the center of the screen throughout the session. All stimuli were presented just below this fixation crosshair.

Each participant completed 240 trials per task (classic Stroop, DO WM Stroop, NonDO WM Stroop) for a total of 720 trials. Each task was divided into four blocks of 60 trials. Participants completed two blocks for each task (two DO WM blocks, two NonDO WM blocks, two classic Stroop blocks, randomized) before taking a break (duration ~2–5 min, as needed). After the break, participants completed the remaining six task blocks, which were again randomized. This pseudorandomized block ordering was to ensure that participants were exposed to all three tasks in a fair manner and that no task was inadvertently randomized to mostly occur during the beginning or the end of a testing session. Lastly, for every block of 60 trials, participants were able to take a short break at the midway point or after the block if needed.

Response Mapping and Practice

Behavioral responses for this study were collected from both hands using a Logitech Dual Action gamepad

(Figure 1C). To respond during the color discrimination stage in each task, participants had to push one of the four bumper buttons on the top of the gamepad using their index and middle fingers. Each button was associated with one color (e.g., red-left index, blue-left middle, green-right index, purple-right middle). Two sets of button-color mappings (Figure 1B) were counterbalanced across participants. To respond to the WM probe, participants used their right thumb to press button 2 when they judged the WM probe and memoranda to be the same, and button 3 when they thought they were different. Before starting the study, participants were given time to practice using the gamepad, completing eight practice color discrimination trials to learn the button-color mapping and eight practice WM probe trials to learn the match and nonmatch button mapping. Participants also practiced the two WM tasks in full for eight trials in order to familiarize themselves with the organization and timing of these delayed match-to-sample trials (e.g., encode WM cue, perform color discrimination, and respond to WM probe). Participants were asked to repeat the practices until comfortable with the tasks and familiar with the button mappings to meet the required criteria for moving forward with the study (i.e., high accuracy [> 90%] and below-threshold response times (RTs) [color discrimination: < 1000 msec, WM probe: < 1200 msec]). The practice trial data were not analyzed further.

EEG Data Acquisition and Preprocessing

EEG data (500-Hz sample rate per channel; online low-pass anti-aliasing filter with a half-amplitude cutoff equivalent of 130 Hz) were recorded using a 64-channel, custom-designed, equidistant, extended-coverage cap (Woldorff et al., 2002) with active electrodes (ActiCAP) and a Brain Products actiCHamp amplifier (Brain Products GmbH). Data were recorded referenced to the right mastoid and rereferenced off-line to the algebraic average of the left and right mastoids. Channel impedances were kept below 15 kOhms.

Off-line data analysis was performed using EEGLAB (Delorme & Makeig, 2004) and FieldTrip (Oostenveld, Fries, Maris, & Schoffelen, 2011) software packages. Data were filtered off-line with a 0.05–30 Hz bandpass, causal, finite impulse response filter and then downsampled to 250 Hz. Noisy channels were replaced using an interpolation of surrounding channels before running an independent component analysis, where the number of interpolated channels were accounted for because of independence considerations (principal components = 63 minus the number of interpolated channels). Independent components were extracted using the extended infomax algorithm in EEGLAB. Components that reflected eye blinks and horizontal eye movement were removed. This meant one or two components were removed for each participant, with the exception of four participants who had three components removed. All time-locked epochs were extracted from −1000 to 2500 msec

Table 1. Number of Epochs Per Condition: Mean (*SD*)

	DO WM	NonDO WM	Classic Stroop
Color discrimination (Stroop)			
Congruent	103 (10)	103 (12)	114 (4)
Incongruent	100 (12)	102 (11)	112 (5)
WM probe			
Prior Stroop Congruent	101 (10)	100 (13)	–
Prior Stroop Incongruent	99 (12)	99 (11)	–

and were baseline corrected from −200 to 0 msec, relative to stimulus onset. Any artifacts remaining in the epochs were detected using a threshold ranging between ±90 mV over the time period between −500 and 1500 msec. Epochs that were detected to have artifacts in no more than five channels were kept and corrected by interpolating the noisy channels. Remaining epochs with uncorrectable artifacts were excluded from further analyses. For ERP plotting and statistical analyses, another low-pass filter (20 Hz, second-order Butterworth) and baseline correction from −200 to 0 msec was applied to the averaged ERP data. Only epochs related to the color discrimination or to the WM probe were analyzed (Table 1). All ROIs used to analyze the ERP components described below were defined based on where these components were greatest collapsed across all relevant conditions.

ERP Components of Interest

In order to assess how conflict processing may differ as a function of whether the conflict arises from a clash between external stimulus features or from a clash between an external stimulus feature and a representation held in WM, we focused on two hallmark conflict-related ERP components. These ERP components are elicited time-locked to the color discrimination stimulus in each task (i.e., DO WM Stroop, NonDO WM Stroop, and classic Stroop) and are best visualized as the difference between incongruent and congruent trials. Here, for each task, we show both the raw waves as a function of congruency, as well as the difference waves (incongruency *minus* congruent).

Negative Incongruency Effect

The first conflict-related processing component is an early, centrally distributed, negative-polarity wave peaking around 300 to 500 msec, in which activity during incongruent trials are more negative compared to activity during congruent trials (herein referred to as the negative incongruency component or N_{inc}). The N_{inc} is observed in many conflict tasks with similar spatial distribution but with varying latencies depending on the nature of the conflict and task parameters thought to affect the timing of such conflict processing (Donohue, Appelbaum, McKay, & Woldorff, 2016; Appelbaum et al., 2014; Donohue, Liotti, Perez, & Woldorff, 2012; Coderre, Conklin, & van Heuven, 2011). In general, the N_{inc} is thought to capture the generation of conflict (e.g., detection) as it unfolds during information processing before a behavioral response. In a classic Stroop task, this negative incongruency usually peaks around 450 msec poststimulus onset and is often referred to as the N450 (West & Alain, 1999, 2000). However, because the timing of this incongruency effect might vary across conditions in our study (West & Alain, 2000), we will refer to such conflict-related negativity as a N_{inc} to avoid specific latency assumptions (Donohue et al., 2016). Specifically, we expected that conflict generation/detection would occur earlier during the DO WM Stroop compared to the other two tasks because of the cognitive pre-instantiation of color processing from having to maintain a color word in WM. We also expected a later onset latency for the N_{inc} during the delay-period NonDO WM Stroop as compared to the classic Stroop, based on the assumption that the (unrelated) WM load of the NonDO Stroop task would delay stimulus processing (de Fockert, Rees, Frith, & Lavie, 2001). For this study, we focused our analysis of the N_{inc} at a cluster of centroparietal channels (Cz, CPz, C1p, C2p) typically activated by this neural response, and that also had the greatest level of such activity across participants here, irrespective of task.

Late Positive Complex

The second conflict-related processing component is the posteriorly distributed late positive complex (LPC), also known as the conflict slow potential. LPC activity is more positive for incongruent relative to congruent trials, typically occurring immediately after the N_{inc} within the neural cascade of conflict–control processes during Stroop tasks, with an onset latency of ∼500 msec and lasting up to 900- to 1000-msec poststimulus onset (e.g., Donohue et al., 2016; Larson, Clayson, & Clawson, 2014; Appelbaum et al., 2009). The LPC has been implicated as an index of conflict resolution and adaptation processes (Larson et al., 2014; McKay, van den Berg, & Woldorff, 2017), that is, the up-regulation of controlled attention in response to conflict, as demonstrated in studies of the congruency sequence effect (or "conflict adaptation"), where interference effects are reduced following an incongruent as compared to a congruent trial (Donohue et al., 2012; Larson, Kaufman, & Perlstein, 2009; Egner, 2007; Gratton, Coles, & Donchin, 1992). In other words, larger LPC during high conflict, incongruent trials (vs. low conflict, congruent trials) reflects this up-regulation, which would ramify in enhanced selective attention following such an event. We leveraged the LPC to better understand the similarities

and differences in this later stage of conflict processing during the DO WM Stroop as compared to the other two tasks. Specifically, based on the same logic as our N_{inc} predictions, we expected an earlier LPC during the DO WM Stroop as compared to the other two tasks and a later LPC during the NonDO WM Stroop as compared to the classic Stroop. The ROI for analyzing the LPC was composed of channels (CPz, Pz, POz, P1, P2, PO1, PO2), again chosen to be consistent with previous studies and because these sites showed the strongest LPC activity here across the different conflict tasks.

P300 to the WM Probe

Besides the conflict-related processing components during the Stroop tasks, we also examined the classic P300 component elicited by the WM probe in the two delayed match-to-sample tasks. The positive-polarity P300, which peaks within a typical time window between 250 and 500 msec, is a widely studied ERP component that has often been implicated for its role as an index of cognitive control during attention and memory-related operations (Polich, 2007, 2011). Our specific interest here was to examine how the cognitive-control processes that occurred during the delay period affected the processing of the memoranda during WM retrieval. More explicitly, we expected greater P300 amplitude when the item held in WM had been better maintained because of less interference from the delay-period Stroop task (i.e., WM probes following congruent vs. incongruent Stroop trials; Polich, 2007). The cluster of interest for the P300 analysis focused on the classic parietal channels typically used for such activity (Cp1, P1, P2, Pz).

Statistical Analysis of ERPs

Statistical significance tests for the ERPs of interest were conducted using permutation statistics for all experimental contrasts (Maris & Oostenveld, 2007). In these permutation tests, a null distribution was derived by assigning labels for the specific conditions (color discrimination: congruent and incongruent) randomly to the data extracted for each task from the predefined ROIs. A difference wave (i.e., incongruent *minus* congruent) based on the new data labels was calculated, and each time point in this difference wave was tested against a null hypothesis that the difference should be zero. This permutation procedure was repeated 10,000 times to create a bootstrap distribution of the t statistic of the null hypothesis for each time point. The t values obtained from the real difference wave data (i.e., difference waves calculated using the original, true data labels) were compared to the bootstrapped t distributions and were considered significant if they fell within the top or bottom 2.5% of the null distribution on a timepoint-by-timepoint basis (corresponding to a two-tailed test at $p <$ .05). An additional cluster-based correction (maximum cluster-level statistic) was applied to the final results over

prespecified broad time periods (based on prior reports for the associated ERP) for each ERP of interest. The Stroop-stimulus N_{inc} effects were examined from 200 to 600 msec, the Stroop-stimulus LPC effects from 400 up to 1600 msec, and the WM Probe P300 effects from 200 to 700 msec. The significant maximal cluster that survived the correction provided critical information about the onset, offset, and duration of a given ERP of interest that was significantly different from the null hypothesis based on a corrected critical alpha value of .05. Thus, reported p values for all ERP analyses are cluster-based corrected p values.

In addition to deriving the onsets and durations of all ERPs of interest using permutation statistics, we also conducted repeated-measures analyses of variance (rmANOVAs) to test for latency and amplitude differences across tasks and congruency. To test for amplitude differences, averaged voltages were extracted from across task-specific time windows that contained the peak amplitudes (100-msec windows for N_{inc} and 200-msec windows for LPC) and a 3 × 2 rmANOVA (Task × Congruency) was conducted. To test for latency differences, an additional factor of Time was included, where ERPs extracted from five consecutive time windows (100-msec windows for N_{inc} [0–500 msec] and 200-msec windows for LPC [200–1200 msec]) were analyzed in consideration of task and congruency. All analyses were corrected for sphericity violations when necessary using the Greenhouse–Geisser correction.

RESULTS
Color Discrimination (Stroop) Behavioral Results

To examine how color discrimination performance was impacted by conflicting information that was either externally presented or held internally in WM, we conducted a 3 (Task: DO WM Stroop, NonDO WM Stroop, classic Stroop) × 2 (Congruency: congruent vs. incongruent) rmANOVA on RT (Figure 2A) and mean accuracy (Figure 2B). Participants were slower to respond during incongruent Stroop trials than during congruent ones, demonstrating a main effect of Congruency, $F(1, 29) =$ 147.2, $p <$ .001, $\eta^2 =$ .84. There was also a main effect of Task on RT, $F(2, 29) =$ 104.9, $p <$ .001, $\eta^2 =$ .78, with responses being quickest during the classic Stroop and slowest during the NonDO WM Stroop (p_{bonf}'s < .001). These main effects were qualified by a marginally significant Task × Congruency interaction effect after correcting for violations of sphericity, $F(1.5, 29) = 3.5, p =$ .052, $\eta^2 =$ .12. While congruency effects were comparable between the DO WM Stroop and classic Stroop ($p_{bonf} =$ .29), as well as between the DO WM and NonDO WM Stroop tasks ($p_{bonf} =$ 1), this effect was significantly greater in the NonDO WM Stroop compared to classic Stroop ($p_{bonf} =$ .002). Given that the stimuli and task demand for the color discrimination in the NonDO WM Stroop task were identical to the classic Stroop task, this finding indicates that the additional WM load in the NonDO WM Stroop
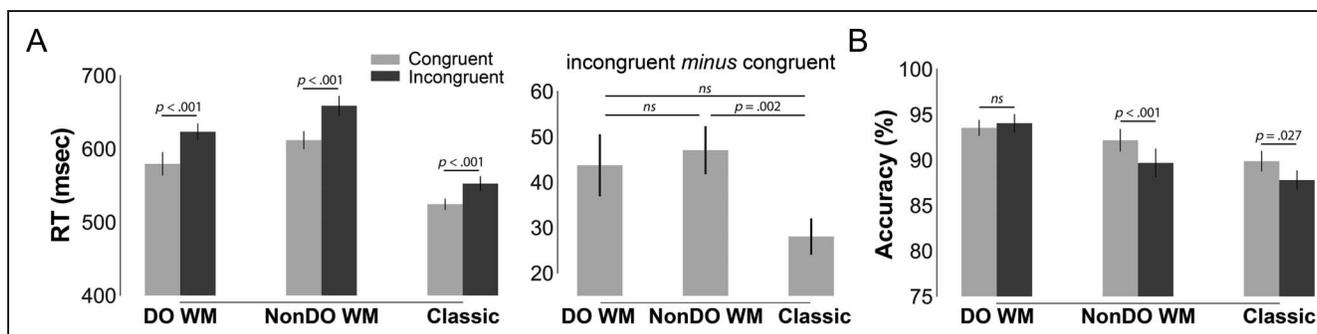
Figure 2. Behavioral results (mean ± standard errors) for the color discrimination (Stroop) responses across the three tasks. (A) Across all tasks, participants were slower to respond during incongruent trials than congruent trials and slower to respond during the WM tasks than during the standalone classic Stroop (left). However, this incongruency effect (incongruent *minus* congruent) was only significantly different between the NonDO WM and classic tasks (middle). (B) Aside from the DO WM task, participants were more accurate in their responses during congruent trials relative to incongruent trials.

led to greater RT Stroop interference in that task as compared to its classic Stroop counterpart.

With respect to accuracy, we observed the classic main effect of Congruency, $F(1, 29) = 6.8, p = .015, \eta^2 = .19$, because of a greater number of errors on incongruent than congruent trials, and a main effect of Task, $F(2, 29) = 20.8, p < .001, \eta^2 = .42$; pairwise comparisons indicated that overall accuracy was lowest during the classic Stroop and highest during the DO WM Stroop (p_{bonf}'s < .05). These main effects were qualified by a Task × Congruency interaction, $F(1.4, 29) = 4.2, p = .034, \eta^2 = .126$. This interaction was because of the fact that congruency effects on accuracy were observed in the classic Stroop (congruent: 89.9 ± 6.1%; incongruent: 87.8 ± 5.9%; $t(29) = -2.3, p = .027, d = -0.42$) and the NonDO WM Stroop (congruent: 92.2 ± 6.8%; incongruent: 89.7 ± 8.6%; $t(29) = -3.9, p < .001, d = -0.71$), but not in the DO WM Stroop (congruent: 93.5 ± 4.8%; incongruent: 94.0 ± 5.5%; $t(29) = 0.55, p = .588, d = 0.10$).

In summary, we replicated prior behavioral results from Kiyonaga and Egner (2014), namely, that the classic Stroop RT interference effect was emulated during the DO WM Stroop task. Although participants were generally slower to respond during the delay-period Stroop tasks compared to the classic Stroop task (Figure 2A left), the relative Stroop interference effect was only significantly different between the NonDO WM Stroop and the classic Stroop (Figure 2A middle). Controlling for the effect of WM load, there were comparable Stroop interference effects between the two delay-period Stroop tasks.

Neural Conflict-detection Processes during Delay-period Color Discrimination

Time-locked to the onset of the color discrimination (Stroop) stimulus, a N_{inc} (negative-polarity incongruency effect) was observed in all three tasks. The individual traces for congruent and incongruent trials and the corresponding difference waves are depicted in Figure 3, along with the corresponding topographic maps and

onset/offset latencies defined by nonparametric permutation testing (see Methods section). The N_{inc} during the NonDO WM Stroop (onset: 356 msec; offset: 624 msec) resembled a prototypical Stroop N450 effect and was visually comparable with the N_{inc} from the classic Stroop (onset: 372 msec; offset: 552 msec). However, as hypothesized, the N_{inc} during the DO WM Stroop had a substantially earlier latency (onset: 264 msec; offset: 412 msec) as compared to the other two Stroop tasks.

To substantiate the latency differences across tasks, we conducted a 3 × 5 rmANOVA on the congruency difference waves (i.e., incongruent minus congruent), with the factors of Task (DO WM Stroop, NonDO WM Stroop, classic Stroop) and Time Window (0–100 msec, 100–200, 200–300, 300–400, 400–500). The time window of 0–500 msec was chosen for these sequential time windows to sufficiently capture the temporal characteristics of the N_{inc} across all the task conditions. There was no main effect of Task, $F(2, 58) = 0.85, p = .43, \eta^2 = .03$, but there was a significant main effect of Time, $F(2.96, 85.83) = 17.65, p < .001, \eta^2 = .378$, which was expected because of differences in averaged voltage signal within each time bin driven by the rise and fall of the N_{inc}. Importantly, there was an interaction effect of Task × Time, $F(4.7, 136.4) = 11.74, p < .001, \eta^2 = .29$, indicating that conflict detection processes, as proxied by the N_{inc}, occurred at different latencies across the tasks.

To probe this interaction further, we conducted three follow-up 2 × 5 rmANOVAs comparing different pairs of tasks (DO vs. NonDO, DO vs. classic, NonDO vs. classic) along the same time factor. There was a significant Task × Time interaction when comparing between the DO WM Stroop and NonDO WM Stroop tasks, $F(2.9, 85.2) = 17.5, p < .001, \eta^2 = .15$, and between the DO WM Stroop and classic Stroop tasks, $F(3, 87) = 20.42, p < .001, \eta^2 = .41$. However, this interaction was not significant for the comparison between the NonDO WM Stroop and classic Stroop tasks, $F(2.6, 76.4) = 0.90, p = .44, \eta^2 = .03$. These results indicate that when the conflict during the color categorization task was because of a clash

between an internally held color word and the externally perceived color swatch (in the DO WM Stroop), conflict processing occurred substantially earlier than when conflict was caused from two clashing external stimulus features. In contrast, the conflict-detection onset latencies were comparable between the NonDO WM Stroop and classic Stroop. Notably, this meant that the additional WM load manipulation during the NonDO WM Stroop did not significantly impact the onset of conflict detection processes as compared to its standalone counterpart, the classic Stroop.

Neural Conflict Resolution Processes during Delay-period Color Discrimination

LPC activity was also analyzed time-locked to the onset of the color discrimination Stroop stimulus (Figure 4). LPC activity was detected in all three tasks, with the earliest latency occurring during the DO WM Stroop (onset: 460 msec; offset: 1200 msec) as compared to both the NonDO WM Stroop (onset: 668 msec; offset: 1116 msec) and the classic Stroop (onset: 624 msec; offset: 984 msec). Note that although the LPC was significant for the longest period of time in the DO WM condition, all three LPC components resolved well after average RT to the Stroop stimuli. Thus, it is unlikely that any differences in LPC duration would have affected the observed RTs.

Similar to the analyses for the N_{inc}, the latency differences across tasks for the LPC were substantiated through a 3×4 rmANOVA on the difference waves, with the factors of Task (DO WM Stroop, NonDO WM Stroop, classic Stroop) and Time Window (200–400 msec, 400–600, 600–800, 800–1000). There was no main effect of Task, $F(2, 58) = 2.54$, $p = .087$, $\eta^2 = .081$, but there
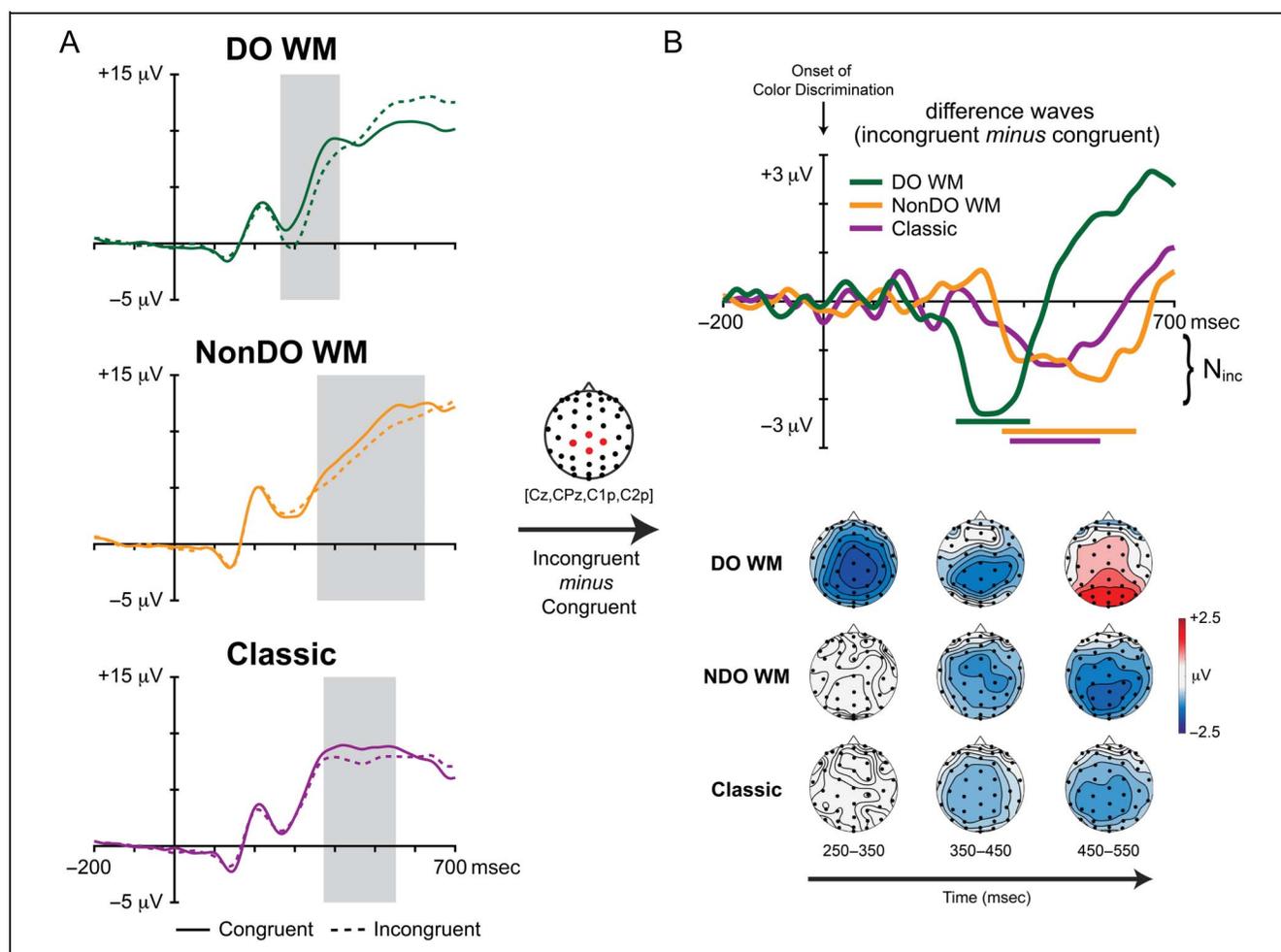

Figure 3. ERP activity for conflict detection (N_{inc}) during color discrimination. Plotted ERP waveforms are averaged from a cluster of four centro-parietal channels (Cz, CPz, C1p, C2p). (A) Raw ERP waveforms for congruent and incongruent trials, along with associated windows of significant differences between congruent and incongruent traces, as identified by permutation statistics ($p_{corrected} < .05$). Cluster correction was done between 200 and 600 msec. (B) Difference waves (incongruent minus congruent, top) were calculated for each condition and plotted with the same cluster-corrected windows of significance along with topographic maps of these differences waves (bottom). Conflict detection, as measured by the negative incongruency component (N_{inc}), occurred much earlier for color discrimination during the DO task, but the degree, or strength, of conflict detection did not differ across tasks. Because of the latency shift during the DO task, part of the LPC was also captured in the superior-scalp topographic map associated with this task, although this wave tends to be largest over more posterior sites (see Figure 4).
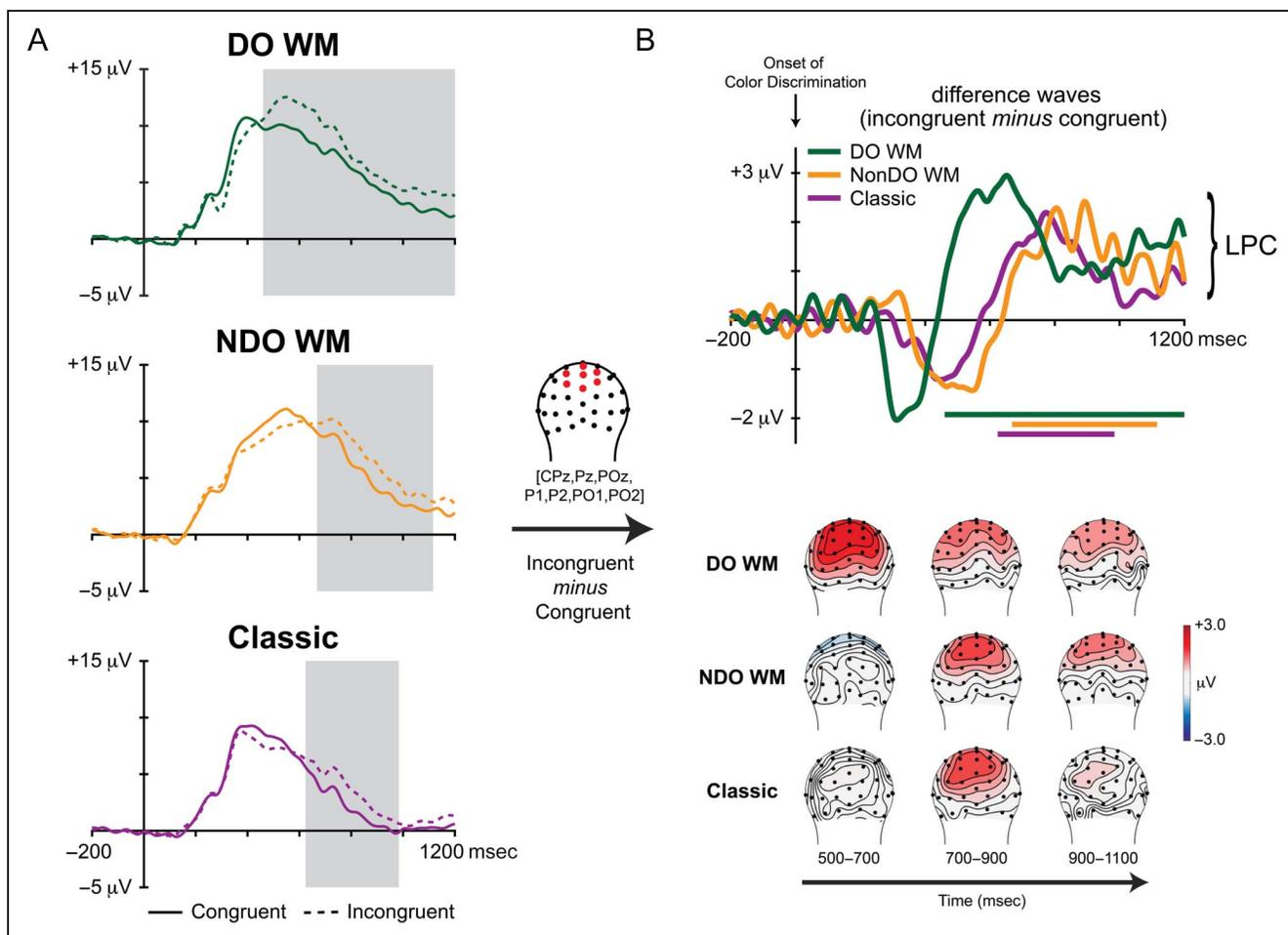
Figure 4. ERP activity for conflict resolution (LPC) during color discrimination. Plotted ERP waveforms are averaged from a cluster of seven posterior channels (CPz, Pz, POz, P1, P2, PO1, and PO2). (A) Raw ERP waveforms for congruent and incongruent trials for each task with associated windows of significant differences between the trial conditions ($p_{corrected} < .05$). Cluster correction for this set of permutation statistics was done between 400 and 1600 msec. (B) Difference waves (incongruent minus congruent) with the same windows of cluster-corrected significance (top) and associated topographic maps for each task (bottom). Conflict resolution following color discrimination, as measured by the late positivity complex (LPC), occurred earliest during the DO WM Stroop and slowest during the NonDO WM Stroop. The degree, or intensity, of this resolution process was greater during the DO WM task only.

was an expected main effect of Time, $F(2.04, 59.12) = 45.95, p < .001, \eta^2 = .61$. Most importantly, we observed a significant interaction of Task × Time, $F(4.45, 129.1) = 22.51, p < .001, \eta^2 = .44$, indicating that LPC onset latencies differed across the tasks. We conducted follow-up tests to further probe the Task × Time interaction, comparing all pairings of tasks along the same time window factor. All three follow-ups yielded significant interaction effects between task and time, namely, that conflict resolution processes started earlier for both DO WM Stroop, $F(3, 87) = 20.41, p < .001, \eta^2 = .41$, and classic Stroop, $F(3, 87) = 5.45, p = .002, \eta^2 = .16$, as compared to the NonDO WM Stroop; and earliest during DO WM Stroop when comparing between the DO and NonDO WM delay-period Stroops, $F(3, 87) = 35.18, p < .001, \eta^2 = .55$. Extra WM load during the NonDO WM Stroop delayed the onset of LPC activity during this task as compared to the classic Stroop, unlike the N_{inc} where this load manipulation had no effect.

WM Probe Behavioral Results

To evaluate how WM maintenance was affected when attentional resources were diverted to the color discrimination task during the delay period, performance measures of RTs and mean accuracy for WM probe responses were analyzed for the DO and NonDO Stroop tasks. For these analyses, only responses following correct color discrimination responses were analyzed to ensure that conflict had been successfully resolved during the delay period. First, we conducted a 2 × 2 rmANOVA ([Task: DO WM probe vs. NonDO WM probe] × [Prior color discrimination (Stroop) Congruency: congruent vs. incongruent]) on the RTs for probe responses (Figure 5A). Main effects of task and prior congruency indicated that responses during DO WM probe were slower than that of NonDO WM probe, $F(1, 29) = 14.04, p < .001, \eta^2 = .326$, as well as during WM probes that followed an incongruent delay-period Stroop stimulus compared to those following a congruent one, $F(1, 29) = 5.76, p = .023, \eta^2 = .166$.
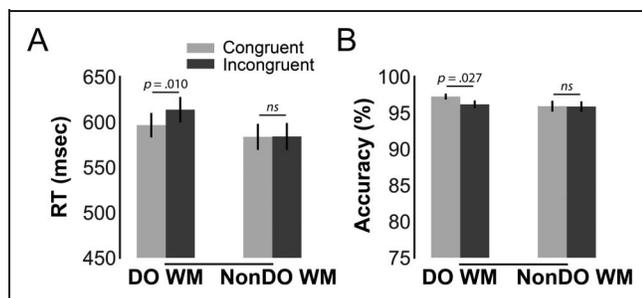
Figure 5. Behavioral results (mean ± standard errors) for WM probe responses during the DO and NonDO WM tasks. (A) Participants were slower to respond during probe trials following delay periods with incongruent color discrimination than with congruent, but only during the DO WM task. (B) Likewise, participants were more accurate in their WM probe responses following congruent color discrimination than following incongruent, but, again, only for the DO WM task.

Importantly, these main effects were qualified by an interaction between Task and Congruency, $F(1, 29) = 4.93$, $p = .034$, $\eta^2 = .145$: The congruency effect on probe RT was greater for DO WM probes, $t(29) = 2.738$, $p = .010$, $d = 0.500$, than for NonDO WM probes, $t(29) = -0.049$, $p = .961$, $d = -0.009$. In other words, conflict during the delay-period Stroop resulted in a delay in retrieving the memorandum and matching it against the WM probe (cf. Kiyonaga & Egner, 2014), but only when that conflict involved a clash between the external stimulus and the WM representation in the same featural domain (i.e., domain overlapping).

Running the same 2 × 2 rmANOVA on the accuracy of the valid probe responses (Figure 5B) did not yield any significant main or interaction effects of the aforementioned factors (all $ps > .05$). However, there was a simple main effect of Congruency on the amount of errors made during DO WM probes, with greater errors following incongruent versus congruent delay-period Stroop trials ($F = 5.39$, $p = .027$).

In summary, conflict during the delay-period Stroop resulted in poorer WM maintenance, making retrieval harder during WM probe, but *only* when the memoranda

and delay-period perceptual task overlapped domain-wise. Although there was an equivalent WM load maintained during the NonDO WM task, WM maintenance was not affected by conflict during the delay period when there was no domain overlap.

Neural Effect of Delay-period Stroop Conflict on Subsequent WM Probe P300

To understand how conflict during the delay period influenced retrieval during the WM probe, we analyzed EEG data time-locked to the DO and NonDO WM probes based on whether the associated preceding delay-period Stroop trial was congruent versus incongruent. To examine whether there were differences in evoked P300 activity across the four individual contrasts (Figure 6A), we conducted a 2 × 2 × 5 rmANOVA with factors of Task (DO and NonDO) and Prior Stroop Congruency (congruent and incongruent) on averaged ERP data within consecutive 100-msec time windows between 200 and 700 msec (time window: 200–300 msec, 300–400, 400–500, 500–600, 600–700). This time window was chosen to capture the entire duration in which the P300 occurred in the probe response. The difference waves (congruent *minus* incongruent) are displayed in Figure 6B.

These analyses showed that there was a main effect of Task, with P300 amplitude being greater in response to the DO WM probes compared to the NonDO WM probes, $F(1, 29) = 6.77$, $p = .014$, $\eta^2 = .19$. We also observed a main effect of Prior Congruency, as probes that followed congruent delay-period Stroop trials had greater P300 amplitude than probes that followed incongruent Stroop trials, $F(1, 29) = 9.55$, $p = .004$, $\eta^2 = .25$. There was also an expected main effect of Time Window, $F(2.32, 67.33) = 23.86$, $p < .001$, $\eta^2 = .45$, reflecting the rise, peak, and fall in P300 amplitude over time. These main effects were qualified by a significant interaction between Task and Time Window, $F(2.13, 67.76) = 6.77$, $p = .002$, $\eta^2 = .19$, and, most importantly, by a significant interaction between Task and Prior Congruency, $F(1, 29) = 10.92$, $p = .003$,
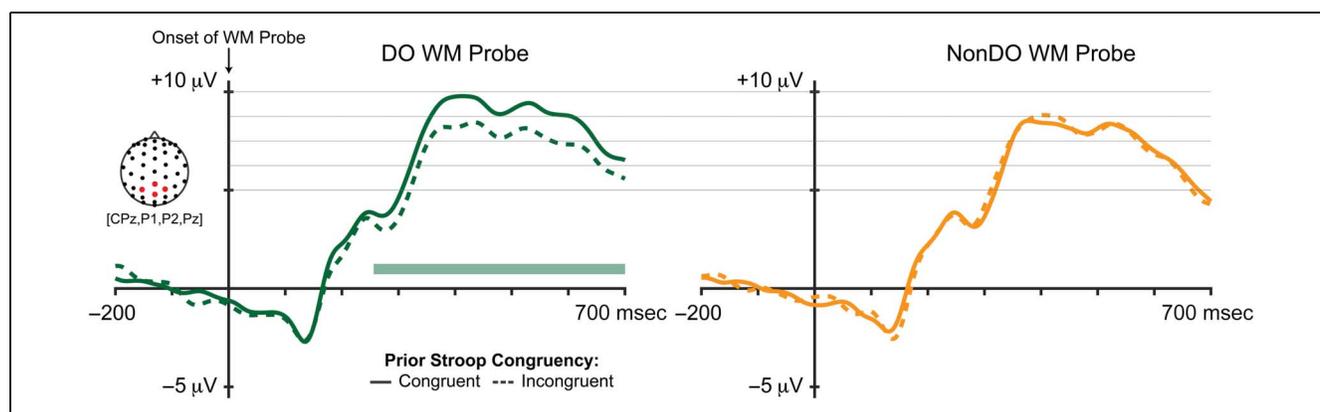

Figure 6. Raw ERP waveforms during WM probe. Modulation by prior Stroop congruency was only significant during the DO WM task (period of significance marked by a green bar, $p_{corr} < .05$). P300 activity was averaged across four centro-posterior channels (CPz, P1, P2, and Pz). Guide lines (light gray) are included to allow for easier comparisons between tasks.

$\eta^2 = .27$. This was because of the fact that the significant effect of prior congruency on probe P300 was driven by large differences for the DO WM probes ($p < .001$), which were not observed in response NonDO WM probes ($p = .89$). There were no other interaction effects. In summary, P300 amplitude was greater during WM probes following congruent (relative to incongruent) Stroop trials, but only when the memoranda overlapped representationally with the delay-period task demands. There was no such facilitation for NonDO WM probes following congruent versus incongruent Stroop trials.

DISCUSSION

In this study, we investigated how conflict stemming from either clashing external stimulus features or between an external stimulus and an item held in WM may differ in terms of the underlying neural cascade of conflict processes. Our behavioral results replicated those of Kiyonaga and Egner (2014), showing that responses during a delay-period color discrimination task are substantially slowed when an incongruent color word is being maintained in WM, and this Stroop effect during the WM-variant Stroop (DO WM Stroop) was comparable to that during the classic Stroop. However, the Stroop interference during the WM-control task (NonDO WM Stroop), a new control condition included in this study, was more pronounced compared to its standalone classic Stroop counterpart. This is presumably because of increased cognitive load from having to maintain a numerical representation in WM while performing the color discrimination. Most importantly, the current demonstrated that behaviorally equivalent effects between the classic Stroop and its WM variant were underpinned by a divergent neural cascade of conflict–control processes, namely, that the onset latencies for conflict detection (N_{inc}) and conflict resolution (LPC) processes occurred substantially earlier when the distractor (i.e., color word) was held in WM before the color discrimination task (DO WM Stroop) as compared to when the distractor was visually perceived at the same time during the color discrimination task (classic Stroop, as well as NonDO WM Stroop). In addition, WM maintenance during the dual-task paradigms was affected only when the delay-period task demands overlapped domain-wise (i.e., semantically) with the memoranda (DO WM task) but not when there was no overlap (NonDO WM task). We further discuss the implications of these results below.

Differences in the Timing of Conflict–Control Processes

By and large, the neural cascades of conflict control processes were very similar during Stroop performance when the color word distractor was visually presented at the same time as the color patch during the NonDO WM Stroop and the classic Stroop. However, there were two notable differences: (1) The durations of conflict detection and resolutions processes, as indexed by the N_{inc} and LPC, respectively, were extended during the NonDO WM Stroop, and (2) although the onset latency of the conflict detection process (reflected by the N_{inc}) did not differ between the NonDO and classic Stroop tasks, the onset latency of the conflict resolution processes (LPC) was slightly, but significantly, delayed in the NonDO WM Stroop. We posit that this pattern of activity differences is attributable to the additional WM load present in the NonDO WM task, in the form of an additional feature dimension to attend to, and that may have resulted in some delay and/or inefficiency in conflict processing during the delay period in the NonDO Stroop task as compared to the classic Stroop task. Notably, however, WM probe performance and associated neural activity (P300) did not differ as a function of delay-period Stroop congruency during the NonDO WM probe despite the increased cognitive demands throughout the NonDO WM task.

Of greater interest was the comparison of the neural cascades of conflict–control processes between the WM-variant Stroop and the classic Stroop, to characterize whether and how processing would differ between the case of a clash between a WM representation (i.e., color word) and an external item (i.e., color patch) and the hallmark case of conflict between two clashing external stimulus features in the classic Stroop paradigm. From our results, it is clear that the neural cascades of conflict processing between the WM-variant Stroop and the classic Stroop differed substantially, as reflected by much earlier onset latencies for the N_{inc} (conflict detection) and LPC (conflict resolution) neural processes during the WM-variant Stroop. It is important to note, however, that these earlier onset latencies for conflict detection in the WM-variant Stroop did not always correspond with smaller congruency effects behaviorally. Namely, the DO WM Stroop was associated with smaller (nonsignificant) accuracy congruency effects, but was not associated with smaller RT congruency effects compared to the classic Stroop. Rather, RT congruency effects were only significantly larger in the NonDo WM Stroop compared to the classic Stroop. This pattern of results suggests that, in the current paradigm, RT congruency effects were more strongly affected by WM load differences between tasks, rather than the conflict-detection onset latency.

The most likely explanation for the substantially earlier onset latency for the N_{inc} and subsequently the LPC during WM-variant Stroop falls in line with current theories of WM (D'Esposito & Postle, 2015), where maintaining a color word in WM would be assumed to result in activating the perceptual and semantic long-term memory representation of that color, and that representations activated by the WM process are the same as those that are activated by external, perceptual inputs. Since in the WM-variant Stroop, those representations are already active when the external stimulus is presented (i.e., at the onset of

the delay-period color swatch), conflict will occur more rapidly—and thus be detected and resolved sooner—in this condition compared to conditions where no such color representation was pre-activated (NonDO WM Stroop and classic Stroop).

Alternatively, it is also possible that N_{inc} and LPC activity could reflect different cognitive processes in the DO WM Stroop than in the classic Stroop conditions, rather than reflecting earlier onset of the same or similar conflict detection and resolution processes. That is, maybe these earlier onsetting effects reflect WM maintenance conflict in the face of interference from the Stroop color patch, with that WM conflict occurring only in the DO WM Stroop condition. Although we cannot completely discount this possibility, we consider it to be highly unlikely for several reasons. First, the RT congruency effects were comparable between the DO WM Stroop and classic Stroop tasks, suggesting similar levels of task interference during the Stroop task completion. Second, the N_{inc} and LPC exhibited similar topographies in all three of the tasks, with both just occurring earlier in time in the DO WM Stroop task, suggesting relatively similar underlying neural processes. Thirdly, prior work from our group (Appelbaum et al., 2009) investigating how varying the temporal separation of relevant (e.g., color swatch) and irrelevant (e.g., color word) Stroop stimulus features (by up to ±200 msec), when there was no WM component to the task at all, showed analogous acceleration of the Sroop neural processing of conflict. More specifically, when the irrelevant stimulus in that study came earlier than the relevant one by either 100 or 200 msec (relative to occurring simultaneously), both the N_{inc} and the LPC occurred earlier in time, reflecting earlier incongruency detection and processing, analogous to the current study. Appelbaum et al.'s (2009) results thus show that latency shifts in conflict–control processes can be observed even when the irrelevant stimulus dimension does not need to be stored in WM to be retrieved later on and when it was not associated with an alternate response. Accordingly, it seems fairly unlikely that the earlier N_{inc} and LPC effects observed in the DO WM task in the current study reflect activity associated with different cognitive processes resulting from additional interference from the WM task, and more likely that they reflect an acceleration of the same or similar conflict–control processes observed in the other conditions. Given that the maximum SOA manipulation between Stroop components was only 200 msec in this prior study, however, the color word was not considered to be held in WM but rather held in *sensory* memory, which is still visual attention by nature. As such, by having a color word held in WM in the case of our WM-variant Stroop task, the considerably earlier resultant instantiation of color representation in WM would be expected to lead to a still greater N_{inc} onset latency shift, as observed here (~200 msec earlier).

The topography and amplitudes of the conflict-related ERP components investigated in this study were qualitatively similar across tasks (albeit shifted in onset latencies). At face value, this suggests that the underlying conflict detection and resolution processes may also be equivalent between these conditions, but just occurring at shifted times. However, to draw stronger conclusions regarding this equivalence would require additional research. For instance, one could probe whether conflict adaptation processes would generalize from the classic Stroop task to the WM Stroop task and vice versa (Egner, 2008).

Facilitation of P300 in Response to the WM Probe

The P300 activity in response to the WM probe was facilitated in the DO WM task following congruent compared to incongruent Stroop trials. This pattern of P300 activity differences during the processing of the DO WM probes as a function of prior Stroop congruency mirrored behavioral performance in the WM task, where responses to WM probes were slower following incongruent Stroop trials (which was also observed in Kiyonaga & Egner, 2014). However, the analogous P300 activity in response to the NonDO WM probes was *not* modulated by prior Stroop congruency, and neither were RTs in that task. In fact, following the incongruent delay-period stimuli, the P300 amplitudes were similar for all WM probes for the NonDO WM task as well as for WM probes for the DO task. We speculate that this pattern of neural activity could be explained by an incidental beneficial effect on the memoranda on congruent trials in the DO WM Stroop. Specifically, attending and responding to a congruent external stimulus may have enhanced the activation of the (identical) internally maintained representation of that stimulus (equivalent to attentional "refreshing" of the memorandum; cf. Barrouillet & Camos, 2012). Such refreshing during the delay period would have strengthened the WM representation, thereby leading to faster retrieval and greater P300 responses in response to the WM probe trials that followed congruent color discrimination trials in the DO WM task as compared to the other probe trial conditions. In contrast, in the NonDO WM task, the congruent external stimulus was unrelated to the item being held in WM, thereby not enabling such refreshing and, thus, not learning to any effects on RT or the P300 to the WM probe following congruent versus incongruent trials in that task.

Lastly, it is important to keep in mind that these RT and P300 effects were in response to the WM probe, which occurred substantially later than the N_{inc} and LPC incongruency-reflecting components elicited by the Stroop stimulus. Thus, it is unlikely that probe-related responses were a cause of the differential timing of those earlier Stroop-stimulus incongruency effects as a function of condition.

Conclusions

In summary, this study enhanced our understanding of the interplay between internally attended (WM) information

and the processing of externally presented stimuli. We replicated prior behavioral results from Kiyonaga and Egner (2014)—showing that a mismatch between an activated color word representation in WM and an externally perceived color patch during a WM-variant Stroop task can produce behavioral Stroop interference effects comparable to that of a classic Stroop task. Importantly, however, we demonstrate that the cascade of underlying neural processing differs between these two interference effects. In particular, we show that neural conflict detection and resolution processes occur substantially earlier in the WM Stroop than its classic Stroop counterpart. This finding supports the fundamental assumption that WM representations overlap with representations activated by external stimuli (Kiyonaga & Egner, 2013), such that a pre-activated color representation in WM results in earlier conflict when a mismatching external stimulus is presented than when two incongruent color cues are presented externally. In further support of this conclusion, we also showed that WM probe performance and neural processing were modulated by delay-period conflict only when that conflict involved the WM representation (in the DO WM Stroop) but not when it was unrelated to the information being held in WM (the NonDO Stroop). In summary, by revealing new insights into the timing of conflict–control processes involving WM versus externally activated representations, the present findings support recent theories of shared representations and control processes between WM and perceptual attention.

Acknowledgments

Funding Information

Diversity in Citation Practices

A retrospective analysis of the citations in every article published in this journal from 2010 to 2020 has revealed a persistent pattern of gender imbalance: Although the proportions of authorship teams (categorized by estimated gender identification of first author/last author) publishing in the *Journal of Cognitive Neuroscience (JoCN)* during this period were M(an)/M = .408, W(oman)/M = .335, M/W = .108, and W/W = .149, the comparable proportions for the articles that these authorship teams cited were M/M = .579, W/M = .243, M/W = .102, and W/W = .076 (Fulvio et al., *JoCN*, 33:1, pp. 3–7). Consequently,

JoCN encourages all authors to consider gender balance explicitly when selecting which articles to cite and gives them the opportunity to report their article's gender citation balance.

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