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Working memory capacity and task goals modulate error-related ERPs

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Abstract

The present study investigated individual differences in information processing following errant behavior. Participants were initially classified as high or as low working memory capacity using the Operation Span Task. In a subsequent session, they then performed a high congruency version of the flanker task under both speed and accuracy stress. We recorded ERPs and behavioral measures of accuracy and response time in the flanker task with a primary focus on processing following an error. The error-related negativity was larger for the high working memory capacity group than for the low working memory capacity group. The positivity following an error (Pe) was modulated to a greater extent by speed-accuracy instruction for the high working memory capacity group than for the low working memory capacity group. These data help to explicate the neural bases of individual differences in working memory capacity and cognitive control.

KEYWORDS

cognitive control, error-related negativity, individual differences, post-error slowing, working memory capacity

1 | INTRODUCTION

Two-process models of cognitive control suggest that the prefrontal cortex (PFC) supports goal maintenance, enabling ontask behavior, whereas the anterior cingulate cortex (ACC) plays a critical role in providing negative feedback to errors and strategically adjusting off-task behavior as necessary (see Botvinick, Cohen, & Carter, 2004; Braver, Gray, & Burgess, 2007; Cohen, Botvinick, & Carter, 2000; Simons, 2010). To help elucidate these dual mechanisms of control, the overwhelming majority of the research conducted on cognitive control has focused on exerting limited-capacity attentional resources to regulate automatic behaviors that conflict with task goals. In doing so, cognitive science has relied heavily on oppositional logic, pitting automatic and controlled processes against one another, often measuring response speed, accuracy, and/or neural activity to stimuli that call for incongruent automatic and controlled responses. Consistent with two-process models of attentional control, when using a Stroop task in combination with event-related brain imaging, MacDonald,

Cohen, Stenger, and Carter (2000) observed dissociable roles for dorsolateral PFC and ACC in implementing task goals and monitoring performance, respectively. This finding converges with a much larger body of evidence supporting the notion that PFC is responsible for actively maintaining task goals, and ACC is responsible for monitoring the environment for potential sources of interference that conflict with those goals (for a review, see Watson, Lambert, Miller, & Strayer, 2011).

1.1 | Individual differences in cognitive control

The delineating of these two brain regions with their distinct roles in attentional control is now fairly well understood; what remains unclear is how PFC (goal maintenance) and ACC (action monitoring) interact to coordinate these dual mechanisms of control. One possibility is that PFC actively maintains task goals, thereby biasing corresponding neural activity in the ACC in a top-down manner (Miller & Cohen, 2001). An alternative possibility is that conflict monitoring

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in the ACC may dynamically influence the updating of task goals in PFC, especially if one is off task and has committed an error (Cohen et al., 2000; Kerns et al., 2004). Although both possibilities may be true, additional insight into answering this PFC-ACC interaction question may come from research on individual differences in working memory capacity (Engle, 2002), which is thought to reflect the ability to maintain task goals in interference-rich contexts.

In an influential review, Kane and Engle (2002; see also Engle, 2010) synthesized a wealth of evidence from single-cell brain imaging and neuropsychological research to argue that the PFC and networked brain regions are necessary for effective working memory capacity. Over 25 years of empirical research has demonstrated a beneficial role of greater working memory capacity in situations requiring individuals to exert cognitive control to maintain task goals and to avoid distraction (Engle, 2002; Watson et al., 2011). Because of this, Engle (2002) defined working memory as short-term memory plus controlled attention. Consistent with this reasoning, individuals with lower working memory capacity perform more poorly than individuals with higher working memory capacity in situations where successful performance is dependent on topdown controlled attention, including but not limited to Stroop color naming, regulation of false memories in the Deese-Roediger-McDermott (DRM) paradigm, Simon task response conflict, the antisaccade task, the flanker task, multitasking, and susceptibility to inattentional blindness (Heitz & Engle, 2007; Kane, Bleckley, Conway, & Engle, 2001; Kane & Engle, 2002, 2003; Miller, Watson, & Strayer, 2012; Sanbonmatsu, Strayer, Medeiros-Ward, & Watson, 2013; Seegmiller, Watson, & Strayer, 2011; Watson, Bunting, Poole, & Conway, 2005). Individuals with higher working memory capacity also adopt a more proactive strategy toward information processing in order to limit interference when tasks make interference manipulations explicit (Braver et al., 2007; Burgess, Gray, Conway, & Braver, 2011; Cowan & Saults, 2013). Taken together, these findings strongly support the notion that the increased cognitive control afforded by those with greater working memory capacity can be used to effectively maintain task goals, to be cognitively flexible, and to manage potential sources of interference to those goals (e.g., habitual responses) in a variety of different task domains.

1.2 | Electrophysiological markers of cognitive control

In related literature, the error-related negativity (ERN, which has also been referred to in the literature as the negativity following an error, or the Ne) is a response-locked electrophysiological signature—ERP—associated with the commission of errors and thought to arise because of conflict or action monitoring in the ACC (Falkenstein, Hohnsbein, & Hoor-

mann, 1991; Gehring, Goss, Coles, Meyer, & Donchin, 1993; Holroyd & Coles, 2002). The ERN is a manifestation of a preconscious process that occurs before awareness of an error is established (Nieuwenhuis, Ridderinkhof, Blom, Band, & Kok, 2001) and peaks around 50 ms after an error response. With respect to individual differences, when recording neural activity from patients with lateral PFC damage, Gehring and Knight (2000) provided clear evidence of altered action monitoring and management of a source of interference tracked by ACC. More specifically, the ERN for the patients was equal for correct and error trials, suggesting possible loss of task goals in PFC that could have appropriately biased information processing and corresponding activity in ACC. In contrast, errors for age-matched controls elicited greater ERN activity than correct trials-the typical pattern in this literature. Importantly, these results support two-process models of attentional control where ERN activity and conflict monitoring in the ACC can be modulated top down through the active maintenance of task goals by the PFC (Botvinick, Braver, Barch, Carter, & Cohen, 2001; Botvinick et al., 2004; Cohen et al., 2000; Kane & Engle, 2002; Miller & Cohen, 2001). Other research has linked the ERN to the mesencephalic dopamine system, suggesting that a negative reinforcement signal disinhibits motor neurons in the ACC, which generates the ERN. This signal allows the ACC to "learn" and relinquish control when necessary (Holroyd & Coles, 2002). Furthermore, the authors suggest that the ERN is the first indication that an action has produced an error response and that this signal is used to train the ACC into avoiding future errors in similar contexts.

In a similar experiment on electrophysiological markers of cognitive control, Gehring et al. (1993) directly manipulated accuracy versus speed task goals that were given to participants during a flanker task (Eriksen & Eriksen, 1974). They found that accuracy stress produced a larger amplitude ERN, whereas speed stress muted the magnitude of the ERN. To explain these findings, Gehring et al. (1993) argued that it was more important to make correct responses under accuracy stress than under speed stress, yielding a task-goal-specific regulation of the ERN. That is, under accuracy stress, a larger ERN might be a manifestation of the need to update task goals. In contrast, under speed stress, participants had to quickly respond, yielding more errors in the flanker task. However, given that errors were acceptable in the context of the speeded response task goal, the ERN was diminished. Whereas the ERN is a manifestation of error detection and conflict monitoring, the Pe is associated with error recognition and occurs anywhere from 200 to 500 ms after an error response (Falkenstein, Hoormann, Christ, & Hohnsbein, 2000). The Pe, or positivity following an error, originates within the posterior cingulate cortex (PCC; Falkenstein et al., 2000; Overbeek,

Nieuwenhuis, & Ridderinkhof, 2005). The Pe is an ERP component believed to be a manifestation of conscious awareness of an error.

1.3 | Electrophysiological markers of individual differences in cognitive control

Returning to our earlier discussion, although there is considerable evidence of individual differences in frontally mediated working memory capacity influencing outward behavior in interference-rich contexts (Engle, 2002; Kane & Engle, 2002; Watson et al., 2011), it has only recently been demonstrated that there are corresponding differences in neural activity and electrophysiological markers of cognitive control arising out of the ACC. More specifically, we recently reported an electrophysiological study using a variant of the Simon task, recording ERPs in healthy normal individuals with varying working memory capacity (see Miller et al., 2012). Consistent with two-process models of cognitive control, our results revealed individual differences in working memory capacity that bias neural activity and alter error monitoring in frontal-executive networks, where those with high capacity showed a greater ERN than those with low capacity. These individual differences in attentional control were also observed in the post-error positivity (Pe), a response-locked ERP component associated with updating cognitive strategies (Falkenstein et al., 2000), suggesting greater awareness of errors with increased working memory capacity. The ERN and Pe are thought to reflect independent aspects of post-error processing, with the former linked to error or conflict monitoring and the latter associated with conscious error recognition and remedial action (Nieuwenhuis et al., 2001). Most importantly for the purposes of the present study, the combination of these ERN/Pe signatures observed by Miller et al. (2012) suggests individuals with greater working memory capacity have a more finely tuned attentional control network and, therefore, are more likely to spontaneously monitor potential sources of interference in their actions and to consciously refresh task goals following the loss of cognitive set.

1.4 | Present study

With respect to cognitive control and underlying frontalexecutive attentional networks, both direct manipulations of task goals (Gehring et al., 1993) and individual differences in working memory capacity (Miller et al., 2012) have been shown to modulate the magnitude of the ERN in a top-down fashion. However, it is noteworthy that these two experimental-behavioral factors—speed versus accuracy task goals, and high versus low working memory capacity—have yet to be combined in the attentional control literature, particPSYCHOPHYSIOLOGY

ularly in tandem with the concurrent collection of errorrelated ERP signatures. This gap in the literature is noteworthy as we believe that the factorial crossing of task instructions (speed vs. accuracy) and individual differences in working memory capacity (high vs. low) yields a number of interesting empirical comparisons that could prove theoretically useful in elucidating and dissociating various mechanisms of cognitive control.

To this end, the present study has two aims. First, we will assess the extent to which the increased ERN/Pe signatures with increased working memory capacity reported by Miller et al. (2012) can be modulated by experimenterprovided task goals while using a flanker task. For instance, although those with greater capacity spontaneously monitor their actions/errors and consciously update task goals as indexed by a larger ERN and Pe, respectively, it is unclear whether task instructions might have a similar impact on those with lower working memory capacity. That is, one might predict that those with less working memory capacity may be better able to upregulate their cognitive control and their corresponding ERP signatures with the enhanced cognitive scaffolding afforded by the accuracy task instructions.

As an alternative possibility, while individual differences in the magnitude of the ERN as a function of individual differences in working memory capacity may be additive with respect to the speed versus accuracy task instructions, an interaction may emerge in the magnitude of the Pe. More specifically, it has been suggested that, unlike the ERN, the Pe may be more reflective of consciously updating task goals in light of errors or other off-task behaviors (Falkenstein et al., 2000; Nieuwenhuis et al., 2001). If this is the case, those with increased working memory capacity may be especially flexible and well calibrated to the speed versus accuracy task instructions, being both more likely to update task goals under accuracy stress while also being less likely to update task goals under speed stress. Consequently, those with increased working memory capacity may show greater modulation of the Pe in response to the speed versus accuracy instructions, whereas those with reduced working memory capacity may show less flexible, more rigid ERP signatures associated with context updating.

Related to this last point, a second aim of the current study is to link outward behavioral responses, such as posterror slowing, with the ERP signatures obtained across individual differences in working memory capacity and the experimenter-provided task instructions. For example, if those with greater working memory capacity show enhanced sensitivity to the speed versus accuracy task instruction as reflected by more flexible Pe responses, one might expect greater slowing of response times on trials following errors versus correct responses, particularly under accuracy stress.

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Such a pattern would be consistent with those with increased working memory capacity more likely to adjust their response criteria following errors, but selectively so under accuracy versus speed task instructions.

2 | METHOD

2.1 | Participants

We collected data from participants in two sessions. In the first session, approximately 250 University of Utah undergraduates performed *the Operation Span Task (OSPAN task;* see below for details) to assess their working memory capacity. In the second session, we invited back 25 participants in the lowest quartile of working memory capacity scores (20 females, \bar{x} = 24.2 years old) and 25 participants in the highest quartile of working memory capacity scores (16 females, \bar{x} = 23.3 years old). Participants with any neurological diagnosis, head trauma, who were left-handed, or above the age of 40 were excluded from the second session. All participants provided informed consent before starting the experiment and received course credit for participation.

2.2 | Materials and procedures

2.2.1 | Session 1

In the first session, participants were given an automated version of the OSPAN task (Unsworth, Heitz, Schrock, & Engle, 2005) to provide an estimate of their working memory capacity. The OSPAN task consists of a series of math problems and letters. Participants were presented with simple math problems and the participant reported the veracity of the statement as either "true" or "false" (e.g. $(8/2) + 2 = 12 \dots$ "false"). Following each math problem, a letter was presented for later recall. After sets of three to seven math/letter pairs, the participants were prompted to recall the letters in the order in which they were presented. All OSPAN stimuli were presented on a computer screen, and responses were made with a computer mouse. The total number of letters accurately recalled in the presented order determined their absolute OSPAN score out of 75. Those individuals who obtained an absolute OSPAN score at or below 25 were classified as low working memory capacity, and those who obtained an absolute OSPAN score at or above 50 were classified as high working memory capacity. Following Unsworth et al. (2005), we excluded all individuals from the experiment who correctly answered fewer than 85% of the math problems, as the math problems were designed to distract the participant from recalling the correct letters. The cutoff scores for determining low versus high working memory capacity groups were similar to those reported by Unsworth et al. (2005).

2.2.2 | Session 2

In Session 2, 50 participants were tested individually on a version of the Eriksen and Eriksen (1974) flanker task created in E-prime 2.0. We instructed participants to respond based on the centrally presented letter in a series of five letter strings. There were two types of stimuli: congruent and incongruent. A congruent stimulus consisted of all identical letters (e.g., SSSSS or HHHHH) and an incongruent stimulus consisted of "flanking" letters that were associated with the opposite response (e.g., SSHSS or HHSHH). Each stimulus was preceded by a fixation cross, presented for 500 ms in the center of the display followed by a blank screen for 100 ms. Stimuli remained in view until the participant responded or 2,000 ms had elapsed. The five-letter horizontal array subtended 2.60 degrees of visual angle.

Participants were asked to respond to the target letter with the Z and / keys on a keyboard with their left and right index fingers, respectively. The mapping of response keys to the central letter identity was counterbalanced across participants. At the beginning of the second session, participants completed a practice block of 50 trials. The practice was used to familiarize the participant with the task and also to collect baseline accuracy and response time data for the speed-stress and accuracy-stress conditions. Before the speed condition, participants were instructed to perform the task as quickly as possible. Similarly, before the accuracy condition, participants were instructed to perform the task as accurately as possible. The speed-accuracy manipulation was blocked, and the order of presentation was counterbalanced across participants.

We gave feedback and bonuses to the participants relative to their baseline performance obtained during their practice sessions. For each block of 100 trials in the speed-stress condition, participants who responded 15% faster than their baseline reaction time and were at least 75% accurate received 25 cents. For each block of 100 trials in the accuracy-stress condition, participants who were at least as fast as their baseline response time and at least 95% accurate received 25 cents. Participants earned up to an additional \$3.00 based on their average reaction time for the speed-stress condition and their accuracy during the accuracy-stress condition. We used monetary incentives to encourage the participants to adhere to the task instructions (i.e., responding quickly during the speed condition and responding accurately during the accuracy condition). Participants were provided with a 5-min break between speed and accuracy blocks of trials.

2.2.3 | Design

The present study utilized a 2 (Group: high vs. low working memory capacity) \times 2 (Condition: speed-stress vs. accuracystress) split-plot factorial design. All participants completed six blocks of the accuracy-based flanker task and six blocks of the speed-based flanker task, resulting in 12 blocks of trials per participant. Each block consisted of 100 randomized trials, resulting in 1,200 trials per participant. The congruent stimuli (e.g., HHHHH) comprised 75% of the trials, while the incongruent stimuli (e.g., SSHSS) comprised 25% of the trials, thereby creating a high-congruency variant of the paradigm. Kane and Engle (2013) used similar trial proportions to observe individual differences in working memory on a Stroop task. After every block of 100 trials, the program presented the participants with feedback on their average accuracy and response time for that block.

2.2.4 | ERP recording

During the second session, which took place between 1 day and 1 month after the first session, participants had electrodes applied to their scalp and face to record EEG and electrooculographic (EOG) signals. For EEG/EOG data collection, we utilized a 36-channel SynAmps cap manufactured by Compumedics Neuroscan and placed the cap according to the International 10-20 placement guidelines (Jasper, 1958). We used a Compumedics Neuroscan NuAmps amplifier to digitize the signal for computer-based recording and processing. The amplifier sampled EOG and EEG signals at a rate of 250 Hz with a notch filter at 60 Hz and a low-pass filter at 50 Hz. All impedances were below 10 kOhms. Horizontal and vertical EOG artifacts were corrected offline using linear regression derivation within Neuroscan's Scan 4.5 software. A band-pass zero phase shift filter from 0.1 Hz to 12 Hz was applied before rejecting artifacts that exceeded above 70 and below -70 microvolts. Trials with artifacts in the EEG signals were not included in the subsequent analysis (this excluded less than 4% of the data). Error response events were epoched from -500 ms before the response to 1,000 ms postresponse.

3 | RESULTS

3.1 | Behavioral data

We generated cumulative accuracy functions (CAFs) as a way of visualizing the data and verifying that participants complied with the speed-accuracy instructions. In addition, the CAFs are useful in examining individual differences of the temporal accumulation of evidence (Heitz & Engle, 2007). CAFs were created for the accuracy-stress condition (see Figure 1, top) and the speed-stress condition (see Figure 1, bottom) by creating Vincentized deciles for participants in each of the experimental conditions. The CAFs reflect the average accuracy at each decile as a function of the average response time (RT) associated with that group (high vs. low working memory capacity), condition (speed vs. accuPSYCHOPHYSIOLOGY SPR

racy), and trial type (congruent vs. incongruent). As shown in Figure 1, both groups complied with speed-accuracy instructions, and the high working memory capacity group exhibited a faster approach to asymptotic performance.

The CAFs are shifted to the left for the high working memory capacity group, indicating a faster accumulation of evidence compared to the low working memory capacity group. In fact, RT at asymptote (i.e., the 10th decile) was significantly faster for the high working memory capacity group, F(1,48) = 5.45, p < .05, $\eta^2 = .02$; however, accuracy levels did not differ by working memory capacity group at asymptote (p > .05). As expected, asymptotic performance under speed stress was faster, F(1,48) = 62.93, p < .01, $\eta^2 = .71$, and less accurate, F(1,48) = 13.69, p < .01, $\eta^2 = .22$, than under accuracy stress. Asymptotic performance was also faster, F(1,48) = 115.65, p < .01, $\eta^2 = .21$, and more accurate, F(1,48) = 5.94, p < .05, $\eta^2 = .11$, for congruent trials than for incongruent trials.

Following Heitz and Engle (2007), a series of paired sample t tests compared the 10th decile, assumed to reflect asymptotic performance, to the preceding deciles to find the earliest point in the sequence that did not significantly differ from asymptote. For congruent trials under accuracy stress, the high working memory capacity group reached asymptote at the 4th decile, and the low working memory capacity group reached asymptote at the 2nd decile. For incongruent trials under accuracy stress, the high working memory capacity group reached asymptote at the 9th decile, and the low working memory capacity group reached asymptote at the 6th decile. For congruent trials under speed stress, the high working memory capacity group reached asymptote at the 7th decile, and the low working memory capacity group reached asymptote at the 6th decile. For incongruent trials under speed stress, the high working memory capacity group reached asymptote at the 9th decile, and the low working memory capacity group reached asymptote at the 8th decile.

The average performance data from the flanker task, presented in Figure 2a,b, were analyzed using a 2 (Group: high vs. low working memory capacity) \times 2 (Condition: speedstress vs. accuracy-stress) \times 2 (Trial Type: congruent vs. incongruent) split-plot analysis of variance (ANOVA). We considered trials outside the range of 200 to 2,000 ms as outliers, and they were excluded from analysis. Additionally, trials where participants responded three standard deviations above or below their mean RT for that condition were also excluded from further analysis (in total, this excluded less than 2% of trials).

There was a main effect of working memory capacity group on RT, F(1,48) = 4.27, p < .05, $\eta^2 = .08$. Participants in the high working memory capacity group responded faster under both speed and accuracy conditions and for both congruent and incongruent trial types. Under accuracy stress, RT PSYCHOPHYSIOLOGY SPE

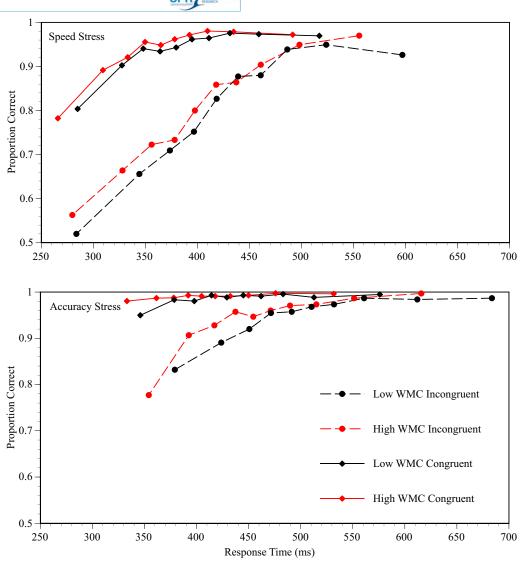


FIGURE 1 Cumulative accuracy functions under speed (top) and accuracy stress (bottom)

was significantly slower than in the speed-stress condition, F (1,48) = 131.27, p < .01, $\eta^2 = .73$. There was also a main effect of trial type on RT. Participants responded slower on incongruent trials than on congruent trials, F(1,48) = 373.09, p < .01, $\eta^2 = .89$. In addition, there was a significant Condition × Trial Type interaction on RT, F(1,48) = 36.48, p < .01, $\eta^2 = .43$, indicating that participants were substantially slower on incongruent trials under accuracy stress. None of the interactions involving working memory capacity were significant (all ps > .05).

Accuracy was higher under accuracy stress than in the speed stress, F(1,48) = 142.84, p < .01, $\eta^2 = .75$. Participants were less accurate on incongruent trials than congruent trials, F(1,48) = 146.06, p < .01, $\eta^2 = .75$. There was also a significant Condition × Trial Type interaction on accuracy, F(1,48) = 130.96, p < .05, $\eta^2 = .73$. Participants were the least accurate on incongruent trials under speed stress and the most accurate on congruent trials under accuracy stress.

There were no working memory capacity group effects on accuracy (all ps > .05).

3.1.1 | Error-related ERPs

The response-locked ERPs are presented in Figure 3a–c. Figure 3a presents the ERPs for trials in which the participant made an error. ERPs for trials in which the participant made a correct response are displayed in Figure 3b. Figure 3c presents the error-correct difference waveforms, which are important because they isolate activity associated with error-related processing. For trials with an error, there was an initial negative component in the ERP that peaked at approximately 50 ms following the errant response, followed by a positive component that peaked at approximately 300 ms following the errant response. By convention, this earlier ERP component has been referred to as the ERN, and the positivity following the ERN is referred to as the Pe.

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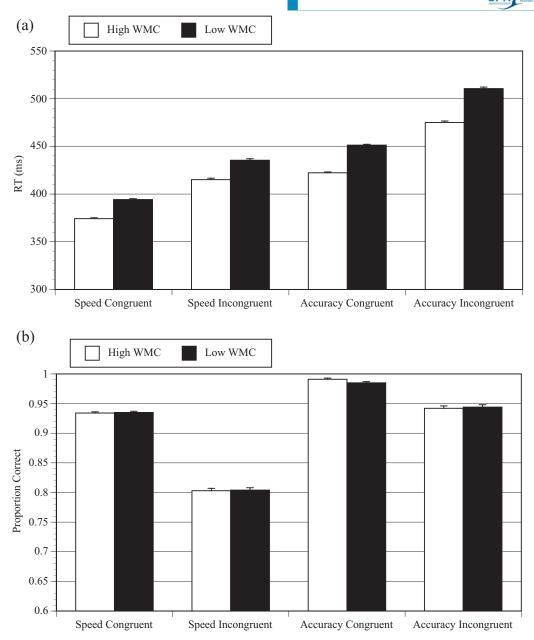


FIGURE 2 (a) Response time. Error bars reflect the standard error of the mean. (b) Response accuracy. Error bars reflect the standard error of the mean

3.1.2 | ERN

To analyze the ERN, the error-correct response-locked difference waveforms for each condition were baseline-corrected using the average of the 500-ms interval prior to the response onset. Three participants in each group were excluded (six participants total) due to the fact that they made fewer than five errors in one or more conditions. Next, we quantified the ERN by computing the average area under the curve at Cz between 0 and 100 ms. Inferential statistics were generated using a 2 (Group: high vs. low working memory capacity) \times 2 (Condition: speed-stress vs. accuracy-stress) split-plot ANOVA. As shown in Figure 4 (top left), there was a significant main effect of working memory capacity group on the ERN, F(1,42) = 13.99, p < .01, $\eta^2 = .25$. However, neither the main effect of condition, nor the interaction between working memory capacity group and condition were significant. These data indicate that the ERN was greater in magnitude for the high working memory capacity group, and this was independent of speed-accuracy stress.

3.1.3 | Positivity following an error

To analyze the P_e , the ERPs at Pz were baseline-corrected using the average postresponse interval between 100 and 200 ms and then quantified by computing the average area under the curve between 200 and 400 ms. A 2 (Group: high vs.

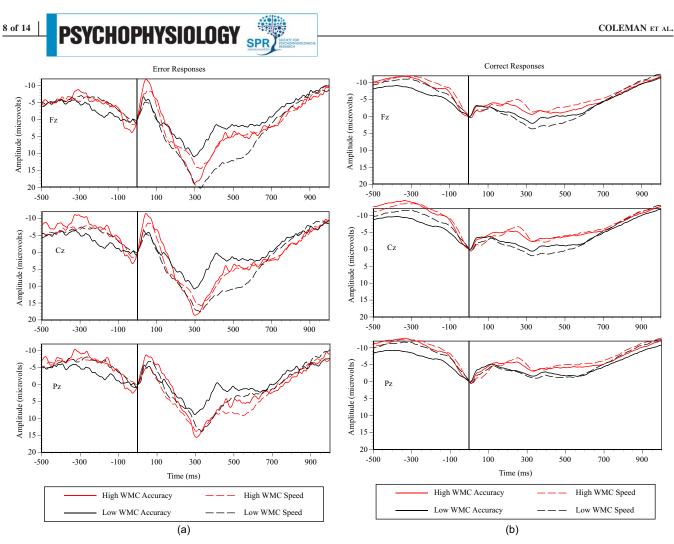


FIGURE 3 (a) Response-locked ERPs on error trials recorded at Fz (top), Cz (middle), and Pz (bottom); (b) Response-locked ERPs on correct trials recorded at Fz (top), Cz (middle), and Pz (bottom)

low working memory capacity) $\times 2$ (Condition: speed-stress vs. accuracy-stress) split-plot ANOVA revealed significant working memory capacity Group \times Condition interaction, *F* (1,42) = 4.39, p < .05, $\eta^2 = .09$. As shown in Figure 4 (top right), working memory capacity differences were greater under accuracy stress than under speed stress, t(1,42) = 2.14, p < .05.

3.1.4 | Post-error slowing

Post-error slowing was calculated by subtracting the average response time of correct trials following a correct response from the average response time of correct trials following an error response (see Figure 4, bottom). We analyzed post-error slowing using a 2 (Group: high vs. low working memory capacity) × 2 (Condition: speed-stress vs. accuracy-stress) split-plot ANOVA. The analysis revealed that responses following an error were slowed to a greater extent under accuracy stress than under speed stress, F(1,38) = 12.81, p < .01, $\eta^2 = .25$. Neither the main effect of working memory capacity group nor the working memory Capacity × Condition interaction was significant (all ps > .05). A fur-

ther analysis examined the relationship between the amount of post-error slowing and the magnitude of the error-related ERPs. Neither for the ERN nor for the Pe were there significant correlations with post-error slowing (all ps > .05).

4 | DISCUSSION

Two-process models of cognitive control suggest PFC supports goal maintenance, enabling on-task behavior, whereas ACC plays a critical role in providing negative feedback to errors and strategically adjusting off-task behavior as necessary (see Botvinick et al., 2004; Braver et al., 2007; Cohen et al., 2000; Simons, 2010). The present study used errorrelated ERP signatures in combination with the experimental manipulations of task goals (i.e., speed vs. accuracy stress) and individual differences in working memory capacity to better understand the regulation of cognitive behavior.

The overt behavioral data indicated that both task instructions and individual differences in working memory capacity modulated task performance. Higher working memory capacity was associated with more rapid responses and a

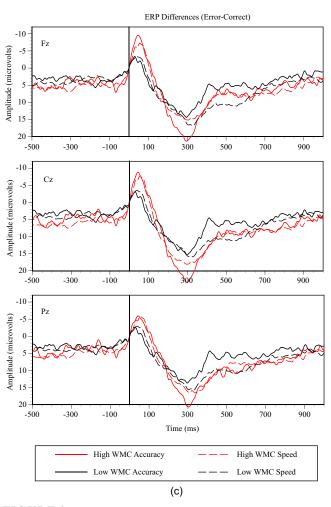


FIGURE 3c Response-locked ERPs for the error-correct difference recorded at Fz (top), Cz (middle), and Pz (bottom)

faster accumulation of evidence when compared to the low working memory capacity group. There was also a greater slowing of responses following an error (i.e., post-error slowing) under accuracy stress than under speed stress. The posterror slowing data are consistent with a course correction to select a more task-appropriate response criterion (i.e., slow down and be more accurate). The ERN was larger for the high working memory capacity group, and this was independent of speed-accuracy instructions—a pattern that differs from the one reported by Gehring et al. (1993).¹ The work-

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ing memory capacity differences in the ERN extend the pattern reported earlier by Miller et al. (2012) and suggest that the ERN reflects an aspect of behavior that is not altered by task instruction. By contrast, working memory capacity differences in the Pe were greater under accuracy stress than under speed stress.

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The ERN and the Pe are thought to reflect functionally independent aspects of error-related processing (Overbeek et al., 2005). One hypothesis regarding the functional significance of the ERN is that it is a manifestation of an error-detection process under the assumption that the errant response is based upon incomplete information processing (Falkenstein et al., 1991). In fact, our study found that errant responses were significantly faster than correct responses (by an average of 40 ms, t(39) = 6.33, p < .01), consistent with the hypothesis that errors may have been based on partial information.

The pattern of data reported in this article is indicative of a more robust error-detection system for the high working memory capacity group. Gehring et al. (1993) suggested that the ERN may be a manifestation of a strategic adjustment process (i.e., slow down after the commission of an error). However, this interpretation is inconsistent with the lack of speed-accuracy differences in our ERN data and the fact that there was no relationship between the magnitude of the ERN and post-error slowing. Other theories of the ERN assume that it reflects an internal feedback mechanism associated with unexpected outcomes (e.g., Holroyd & Coles, 2002). Under this model, working memory capacity differences reflect a stronger feedback signal on error trials.

Lastly, we consider an interpretation that the ERN is a manifestation of conflict monitoring (Botvinick et al., 2001, 2004), whereby concurrent activation of multiple competing responses indicates a response conflict and the need for increased cognitive control. Consistent with this interpretation, we found that errors were more common on incongruent trials (i.e., trials with stimuli that call for competing responses). Accordingly, the high working memory capacity group exerts greater cognitive control to resolve response conflict (given the larger ERNs for this group and the fact that the majority of errors for both groups was on incongruent trials).

A further test of the hypothesis that the ERN associated with response conflict (as opposed to the commission of an error) can be performed by examining the ERPs obtained when the participant responded correctly on congruent trials (with little response conflict) and incongruent trials (with stimuli that call for competing responses). Figure 5 plots the congruent and incongruent trials in which the participant was correct along with the congruent-incongruent difference waveform. There is, in fact, no ERN (or Pe) for either trial type. This indicates that it is the generation of an error and not response competition by itself that leads to the production of an ERN.

¹Our analysis of the ERN was based upon the error-correct difference waveforms that localized any differences to error-related processes. In this analysis, the ERN did not differ as a function of speed-accuracy instruction. However, inspection of the error waveforms (i.e., Figure 3a) suggests that the ERN was larger for the high working memory capacity group than for the low working memory capacity group, F(1,42) = 8.06, p < .01, and that the ERN was somewhat larger under accuracy stress than under speed stress, F(1,42) = 4.17, p < .05. Gehring et al. (1993) performed their analysis on the error waveforms; however, we believe that the error-correct difference waveforms provide a more precise measure of error-related processing.

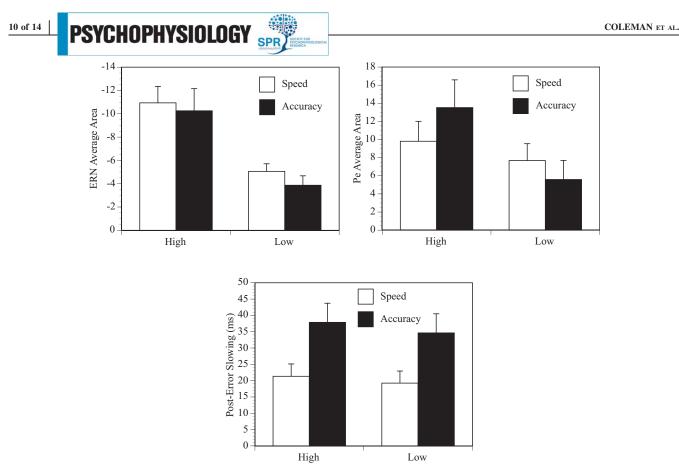


FIGURE 4 ERN area (top-left), Pe area (top-right), and post-error slowing (bottom). Error bars reflect the standard error of the mean

Several accounts have been proposed for the functional significance of the Pe (Falkenstein et al., 2000; Overbeck et al., 2005). According to the affective-processing hypothesis, the Pe is a manifestation of the emotional appraisal of an error (e.g., those who care more would have a larger Pe). According to the error-awareness hypothesis, the Pe reflects the conscious recognition of an error. Finally, according to the behavioral adaption hypothesis, the Pe is an indicator of the process associated with adjusting the response criteria (e.g., slow down following an error). These different accounts are not mutually exclusive (i.e., one could care more about making an error, be aware of the errant behavior, and adjust their response criterion following the error). In the current study, the working memory capacity \times Condition (speed-accuracy) interaction observed in the Pe could reflect differential affect associated with errors when they matter most (i.e., under accuracy stress). According to this interpretation, making an error matters more to the high working memory capacity group under accuracy stress than under speed stress, whereas errors are of equal importance for the low working memory capacity group. However, this interpretation would seem to be weakened by the fact that overall error rates for high and low working memory capacity groups did not differ (i.e., if errors mattered less to the low working memory capacity group, one would expect lower overall accuracy, but this was not observed in the data). The

working memory capacity \times Condition (speed-accuracy) interaction in the Pe could also reflect a greater awareness of errors for the high working memory capacity group under accuracy stress, whereas awareness of errors was equivalent for accuracy and speed stress for the low working memory capacity group. It is also possible that the Pe reflects the updating of a mental model of the environment (i.e., context updating, Donchin & Coles, 1988) in a manner similar to that of the P300 (or P3a) component of the ERP. Unfortunately, there is no independent verification of any differential awareness on context updating in the current data set. We failed to observe a relationship between the magnitude of the Pe and post-error slowing, which would seem to be inconsistent with the behavioral adaption hypothesis. However, we were only able to assess the relationship between the Pe and post-error slowing on a between-subjects basis, so variation on a within-subject basis is still a possibility (cf. Overbeek et al., 2005).

4.1 | What does this tell us about cognitive control?

Cognitive control involves the ability to adopt and deploy dynamic task goals, maintaining goal-directed performance in the face of distractions, and strategically adjusting off-task behavior as necessary to match the task goals. The current



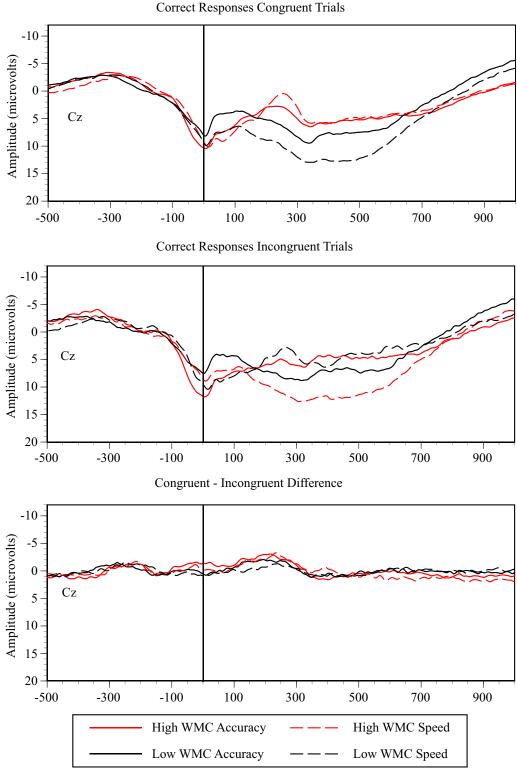


FIGURE 5 Response-locked ERPs for correct trials recorded at Cz for congruent trials (top), incongruent trials (middle), and the congruentincongruent difference (bottom)

research identifies a subset of the neural mechanisms of cognitive control, particularly those related to the regulation of off-task or error-prone behavior. Specifically, the ERN and the Pe provide neural signatures of error-related processing; present after an error was made and absent otherwise (see Figure 3a,b,c). Effects of working memory capacity group were obtained with the ERN, an error-related ERP component that is thought to arise because of conflict or action monitoring (Gehring et al., 1993; Holroyd & Coles, 2002). By contrast, an interactive pattern of working memory

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capacity group and speed-accuracy stress was obtained with the Pe, an error-related ERP component associated with updating cognitive strategies (Falkenstein et al., 2000; Overbeek et al., 2005), suggesting greater awareness of errors with increased working memory capacity. The differential pattern obtained with the ERN and Pe is consistent with the interpretation that these two components reflect distinct cognitive control processes (Sternberg, 1969). Prior research using dipole modeling indicates that the ERN and the Pe originate in different neural structures, with the former localized in the ACC and the latter localized in the PCC (Herrmann, Römmler, Ehlis, Heidrich, & Fallgatter, 2004; Vocat, Pourtois, & Vuilleumier, 2008). These distinct informationprocessing operations associated with the ACC and PCC are essential for effective cognitive control, at least when it comes to dynamically updating the task goals when one is off task and has committed an error (Cohen et al., 2000; Kerns et al., 2004).

4.2 What does this tell us about individual differences in working memory capacity?

The working memory capacity differences in the errorrelated ERPs provide clear evidence of a more robust and flexible error-monitoring network for the high working memory capacity participants. In particular, the ERN was systematically larger for the high working memory capacity group, a pattern that replicates the findings reported by Miller et al., 2012. The Pe was also more sensitive to speed-accuracy instructions for the high working memory capacity group larger when the task goal emphasized accuracy and smaller when the task goal emphasized speed. Given that an important aspect of cognitive control is the ability to detect errant behavior when it occurs and to strategically adjust the parameters of cognitive control to match the task goals, it suggests that the high working memory capacity group is better calibrated in this adaptive form of control.

It is noteworthy that the working memory capacity differences were based on a behavioral classification using the OSPAN task, an assessment that was performed 1 to 30 days prior to the ERP recording session. Given that the error-related ERPs were elicited in a different context (i.e., a different day on a different task), the patterns suggest that the differences reflect relatively stable differences in information processing. These error-related ERPs reveal a more robust error detection network for the high working memory capacity group that is flexible and well calibrated to the task instructions. By contrast, the low working memory capacity group exhibited a more rigid cognitive bias that was less sensitive to changes in task goals.

4.3 Conclusions and theoretical implications

Our research combined behavioral, electrophysiological, and individual difference approaches to understand cognitive control, with a primary focus on the ability to detect and correct errant behavior when it occurs. One of the key findings was that there are two separate error-related ERP components that are associated with individual differences in working memory capacity. The ERN, a component thought to originate in the ACC, was larger for the high working memory capacity group, but the ERN was not modulated by speed-accuracy instructions. The ERN appears to be a manifestation of the relatively automatic registration of the commission of an error-a nonstrategic process that is more robust for the high working memory capacity group. By contrast, the Pe, a component thought to originate in the PCC, was more sensitive to individual differences under accuracy stress than under speed stress. The Pe appears to reflect a more strategic aspect of error-related processing, especially for the high working memory capacity group where the Pe was modulated by speed-accuracy instruction. Together, the ERP data provide evidence for a robust error detection network modulated by individual differences in the working memory capacity and task goals.

Whereas the error-related ERPs were sensitive to individual differences in working memory capacity, the behavioral measures of error-related processing were relatively insensitive to working memory capacity differences. Both groups exhibited virtually identical patterns of post-error slowing-greater under accuracy stress than under speed stress. Aside from working memory capacity differences in the rate of evidence accumulation (cf. Figure 1), the behavioral data were remarkably similar for the two working memory capacity groups. Thus, there is a decoupling of the error-related ERPs and overt behavior. The ERP data provide evidence of a more finely tuned error detection network for the high working memory capacity group; however, this did not directly translate into differences in overt behavior. One possibility is that post-error slowing may not be the key aspect of dynamically adapting one's behavior to the situation.² This is a conundrum that bears further investigation.

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