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The impact of salience and visual working memory on the monitoring and control of saccadic behavior: An eye-tracking and EEG study

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Abstract

In a concurrent eye-tracking and EEG study, we investigated the impact of salience on the monitoring and control of eye movement behavior and the role of visual working memory (VWM) capacity in mediating this effect. Participants made eye movements to a unique line-segment target embedded in a search display also containing a unique distractor. Target and distractor salience was manipulated by varying degree of orientation offset from a homogenous background. VWM capacity was measured using a change-detection task. Results showed greater likelihood of incorrect saccades when the distractor was relatively more salient than when the target was salient. Misdirected saccades to salient distractors were strongly represented in the error-monitoring system by rapid and robust errorrelated negativity (ERN), which predicted a significant adjustment of oculomotor behavior. Misdirected saccades to less-salient distractors, while arguably representing larger errors, were not as well detected or utilized by the error/ performance-monitoring system. This system was instead better engaged in tasks requiring greater cognitive control and by individuals with higher VWM capacity. Our findings show that relative salience of task-relevant and taskirrelevant stimuli can define situations where an increase in cognitive control is necessary, with individual differences in VWM capacity explaining significant variance in the degree of monitoring and control of goal-directed eye movement behavior. The present study supports a conflict-monitoring interpretation of the ERN, whereby the level of competition between different responses, and the stimuli that define these responses, was more important in the generation of an enhanced ERN than the error commission itself.

Descriptors: Attention, Error processing, Working memory, EEG, Eye movements

Perceptually salient stimuli can capture the eyes despite task goals, thereby disrupting task-relevant performance (Theeuwes, Kramer, Hahn, & Irwin, 1998). Accordingly such saccades are treated as an error in the brain (Belopolsky & Kramer, 2006). This automatic capture is an important aspect of a flexible saccadic control system, which allows temporary interruption of task-driven behavior in order to process and respond to potentially informative salient events in the visual environment. However, the eyes are also often misdeployed to distractors that are less salient than the target (e.g., Weaver, Paoletti, & van Zoest, 2014; Zehetleitner, Koch, Goschy, & Müller, 2013). This constitutes a stranger error: the target is both salient and the strategic behavioral goal, yet the eyes are deployed elsewhere.

Why do people make this type of mistake? One possibility is that this error is not strongly or efficiently recognized by the performance-monitoring system, and thus the underlying visual schemas driving the behavior are not corrected. Here, we test this idea by investigating how the error-monitoring system responds to different types of saccadic error and how this predicts subsequent oculomotor behavior.

Current Study

Participants completed a visual search task designed to induce a high error rate (van Zoest, Donk, & Theeuwes, 2004) while we concurrently recorded EEG from electrodes on the scalp surface and eye movements via an infrared eye tracker. The participants' goal was to make speeded eye movements to a unique line-segment target embedded in a search display also containing a unique distractor either more or less salient than the target (see Figure 1A). The relative saliency of targets and distractors was varied so that differing degrees of control would be required to successfully select the target. Salient distractors create greater competition for oculomotor selection because the stimulus-driven prioritization of physical salience competes against goal-directed prioritization of the less-salient but task-relevant target. When the target is instead more salient than the distractor, both stimulus-driven and

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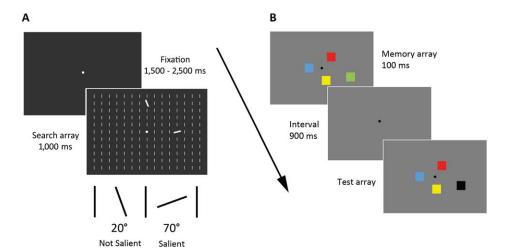


Figure 1. Trial sequence. A: Primary task, where participants made a speeded saccade to a uniquely oriented target line element while attempting to ignore a uniquely oriented distractor line element. The target was the relatively more-salient element for half the experiment and the less-salient element for the other half. Unique elements were defined by their opposing orientations (left- vs. right-tilted) and could appear in one of four equidistant locations. All line elements were the same size. B: Color change-detection task used to calculate VWM capacity estimate. Participants indicated whether any squares changed color from the memory to test array.

goal-directed processes should theoretically work in concert to assist target selection. Accordingly, we expected a greater proportion of saccade errors in the salient distractor condition than the salient target condition. The concurrent use of eye-tracking techniques allowed us to accurately measure the outcome of this competition for oculomotor selection on a trial-by-trial basis and so directly link selection performance to underlying neural mechanisms involved in error processing as indexed in EEG.

Error Monitoring

Research into error processing over the last 25 years has been facilitated by the discovery of the error-related negativity (ERN; Gehring, Goss, Coles, Meyer, & Donchin, 1993; also known as error-negativity/Ne; Falkenstein, Hohnsbein, & Hoormann, 1991), an ERP component that accompanies response errors (for reviews, see Falkenstein, Hoormann, Christ, & Hohnsbein, 2000; Gehring, Liu, Orr, & Carp, 2012). The ERN is characterized as a negative potential with a frontocentral maximum that occurs soon after execution of an incorrect response and has been linked to activity in the anterior cingulate cortex (ACC; Dehaene, Posner, & Tucker, 1994; Luu & Tucker, 2001; Ridderinkhof, Ullsperger, Crone, & Nieuwenhuis, 2004) and observed across a range of tasks, stimuli, and response modalities.

While the ERN is broadly thought to be caused by the execution of an error and involved in signaling the need for compensatory processing, there are several theories regarding its exact computational purpose. Error-detection theory posits that the ERN reflects the outcome of a comparison process that signals the degree of mismatch between representations of the executed versus correct response (Falkenstein, Hohnsbein, Hoorman, & Blanke, 1990). The latter representation itself is considered the result of mapping a stimulus to an appropriate response (e.g., a saccade directed toward a target). Deviations between the executed response and the actual response generate a mismatch/error signal. In contrast, conflict-monitoring theory considers the ERN to be blind to the "correctness" of the executed response, and to instead reflect the overall degree of conflict between response schemas activated by stimuli in the environment (Botvinick, Braver, Barch, Carter, &

Cohen, 2001). According to this perspective, the relationship between ERN and overt errors simply reflects the fact that such errors become more likely when conflict increases. Finally, reinforcement-learning interpretations of ERN (e.g., Alexander & Brown, 2010; Holroyd & Coles, 2002) suggest that the component is independent of response processing and rather reflects the degree to which any outcome event varies from expectations.

As noted above, the deployment of the eyes to a less-salient distractor is a striking mistake that occurs with relatively high frequency. Thus, we approached the study with uncertainty about how this error might be recognized by the brain. Conflict monitoring theory appears to predict a larger/earlier ERN for the salient distractor condition, because directly pitching stimulus-driven processes against goal-directed processes of selection should produce greater response conflict. However, error-detection and reinforcement-learning theories of the ERN predict a larger/earlier ERN in the salient target condition: the greater salience of the target either strengthens the representation of the correct response, resulting in a larger mismatch/error signal when individuals make an error, or reduces the probability of errors, rendering them more unexpected.

Control and Visual Working Memory

A second focus of the present work was to explore whether an individual's ability to maintain task goals in the face of distraction impacts the processing of saccadic errors. Visual working memory (VWM) capacity is considered to index the ability of an individual to implement cognitive control by actively maintaining task goals (e.g., visual representation or template of the target) while filtering out task-irrelevant visual distractors (Vogel, McCullough, & Machizawa, 2005; see Luck & Vogel, 2013, for a recent review). Research has shown individual differences in VWM capacity predict higher-order cognitive functioning in healthy individuals (Cowan et al., 2005; Fukuda, Vogel, Mayer, & Awh, 2010; Johnson et al., 2013) and performance in tasks requiring cognitive control (Fukuda & Vogel, 2009; Weaver et al., 2014). Given its critical role in implementing effective cognitive control, error processing may reflect a mechanism via which VWM operates to establish, maintain, and optimize performance. If this were the case, an

individual with higher VWM capacity would be expected to process errors more efficiently and effectively.

Working memory (WM) capacity, as measured by an operation span task, is in fact known to predict the amplitude of ERN, for example, when errors are made in a Simon task (Miller, Watson, & Strayer, 2012). But visual WM is distinct from the broader WM indexed in this situation: the operation span task measures memory for semantic and verbal rather than sensory information (Luck & Vogel, 2013). However, both VWM capacity (as measured by change-detection paradigms) and WM capacity (as measured by complex span tasks) are considered to reflect the ability to exert attentional control via active maintenance of information relevant to the ongoing task. One possibility is that it is this shared underpinning that underlies existing observations of a relationship between WM capacity and ERN. Consistent with this idea, individual differences in WM capacity determined by operation-span scores have also been observed to account for performance variance in lower-level cognitive tasks (e.g., antisaccade tasks, Unsworth, Schrock, & Engle, 2004). However, because operation span tasks recruit a number of cognitive processes, they not only measure a domain-free "executive function," but also domain-specific rehearsal and storage processes (Kane, Conway, Hambrick, & Engle, 2007). If VWM capacity also predicts ERN amplitude, this would argue for the idea that it is domain-general attentional control processes that specifically drive the relationship between WM and ERN.

We estimated VWM capacity for each participant in a separate experimental session using Luck and Vogel's (1997) color change-detection task. Our expectation was that participants with high VWM capacity should be able to better maintain task goals, thus better recognizing a conflict/mismatch between these goals and actual performance. This should express as an increase in error processing—a bigger ERN—particularly in the salient distractor condition, when competition for selection is strong.

Post-Error Performance

Finally, we approached the data with interest in the outcome of error processing. In order to optimize performance, an effective performance-monitoring system must not only detect an error, but also use this information to then implement greater behavioral control to minimize subsequent errors. Increased control might involve subsequent changes in strategy, attentional focus, and response bias. One instantiation of such an adjustment is post-error slowing (PES; Rabbitt, 1966). This is broadly thought to reflect a strategic adjustment aimed at reducing future errors (see Dutilh et al., 2012, for alternative explanations).

Importantly, all theories of the ERN predict that greater ERN will result in greater compensatory behavior on subsequent trials. However, experimental evidence is in fact rather mixed, with some research supporting a relationship between the ERN and behavioral adjustment (Debener et al., 2005; Gehring et al., 1993; Holroyd, Yeung, Coles, & Cohen, 2005; Ladouceur, Dahl, & Carter, 2007; Rodriguez-Fornells, Kurzbuch, & Münte, 2002), and other research not (Dudschig & Jentzsch, 2009; Gehring & Fencsik, 2001; Hajcak, McDonald, & Simons, 2003; Nieuwenhuis, Ridderinkhof, Blom, Band, & Kok, 2001; Reinhart, Carlisle, Kang, & Woodman, 2012; van Meel, Heslenfeld, Oosterlaan, & Sergeant, 2007). Here, we measured PES and post-error accuracy in saccadic responses in order to determine how error monitoring impacted subsequent behavior, and whether this varied as a function of the type of saccadic error that was made.

Method

Participants

Twenty-three volunteers participated in exchange for payment or course credit. The University of Trento Ethics Committee approved the study, and informed consent was gained prior to participation. Three participants were excluded from primary analyses due to poor task performance (< 25% target selection for salient distractor condition). The remaining 20 participants (all female with normal or corrected-to-normal vision, 19 right-handed) had a mean age of 22.60 years.

Independent analyses of this dataset—investigating mechanisms of attentional selection rather than error processing—have been reported in Weaver, van Zoest, and Hickey (2016).

Stimulus Presentation

The experiment was programmed using MATLAB (version 8.0.0.783, The MathWorks, Inc., Natick, MA) and run on a Dell Precision T3400 computer (Core 2 Quad CPU at 2.40 GHz). A Dell 1907FPT 19" LCD monitor ($1,024 \times 768$ pixel resolution; 60 Hz refresh rate) displayed stimuli at an approximate viewing distance of 57 cm.

A stimuli array of 15×15 white line elements (subtending $27^{\circ} \times 27^{\circ}$ of visual angle; each element $\sim 0.1^{\circ} \times 1^{\circ}$) with a central fixation circle was centrally presented on a black background. Each array consisted of a target and distractor line element defined by their unique orientations in opposing directions (i.e., angularly oriented 20° or 70° to the left or right of vertical) embedded among vertically oriented nontargets. The target and distractor could be presented at any one of four possible equidistant locations 7.72° above, below, left, or right of fixation on a given trial.

Procedure and Design

Visual search task. The stimuli and procedure are shown in Figure 1. Participants performed an eye-tracker drift correction and initiated each trial by pressing a button while fixating a central fixation circle. The fixation point remained on screen for a further 1,500–2,500 ms, after which it was replaced by the stimuli array for 1,000 ms. Participants were instructed to maintain fixation until the array appeared and to then make a speeded saccade toward the target (e.g., left-tilted) element while ignoring the distractor (e.g., right-tilted) element. Performance feedback was provided by online tones indicating anticipative (< 80 ms) or late saccades (> 600 ms) and presenting average saccade reaction times (SRTs) at the end of each trial block. Following 24 practice trials, participants completed 12 blocks of 64 experimental trials.

Relative salience of the unique elements was manipulated by varying the degree of orientation offset from the surrounding homogenous vertical nontargets. The target was the more-salient element (70° offset) for half of the experiment (salient target condition) and the less-salient element (20° offset) for the other half (salient distractor condition). Salience condition and target orientation (left- vs. right-tilted) orders were counterbalanced across participants. Target and distractor location were counterbalanced within participants and presented in a random sequence.

Visual working memory capacity task. Participants also completed a color change-detection task in a prior session to provide a measure of VWM capacity. Using the same design as Luck and Vogel (1997), in each of 24 practice and 192 experimental trials,

participants were presented with a memory array of four, six, or eight colored squares (each subtending $0.65^{\circ} \times 0.65^{\circ}$) on a gray background for 100 ms. A test array was presented after a 900-ms delay, and participants were asked to indicate with a button press whether the memory array was identical to the test array (50% of trials) or whether one square had changed color (50% of trials). The test array remained until a response was made. Squares could appear anywhere within a $9.8^{\circ} \times 7.8^{\circ}$ region, at least 2° (center to center) apart from each other. One of seven possible colors was randomly assigned to each square, although no more than two squares could be the same color on any given array. For change trials, the specific square and its new color were randomly determined. A measure of VWM capacity, K, was derived for each of the three array sizes using Cowan's (2001) formula: $K = \text{set size} \times$ (hit rate + false alarm rate), and then averaged together to give a single estimate of VWM capacity per participant.

Data Recording

EEG and eye movement data were recorded concurrently. A desk-mounted EyeLink 1000 (SR Research, Ltd., Mississauga, ON, Canada) recorded the position of the right eye at 1000 Hz. EEG was recorded from the scalp using 62 Ag/AgCl electrodes arranged according to the 10/20 system (Jasper, 1958). Impedance was kept below 20 KΩ for all electrodes. EEG was amplified online using a BrainAmp amplifier (Brain Products GmbH, Munich, Germany), digitized at a sampling rate of 1000 Hz, referenced online to an additional electrode on the right mastoid, and rereferenced offline to the algebraic average of electrodes on both left and right mastoids. An antialiasing filter with band-pass of 0.016–250 Hz was applied during recording, and data were subsequently digitally low-pass filtered at 46 Hz (noncausal 63-point least-squares FIR filter; -3 dB at 44 Hz; -6 dB at 48 Hz).

Analysis

Analyses were completed using MATLAB with the EEGLAB toolbox (v13.1.1; Delorme & Makeig, 2004) and EYE-EEG extension (v0.41; Dimigen, Sommer, Hohlfeld, Jacobs, & Kliegl, 2011).

Behavioral analysis. A saccade was defined when eye movement velocity surpassed 30°/s or acceleration surpassed 8000°/s², and amplitude exceeded 3°. The SRT was defined as the time taken to initiate the first saccade following stimulus onset. Selection of the target and distractor were defined if the first saccade landed within 4° of the respective locations of these stimuli. Trials were rejected if first saccades were initiated more than 3° from central fixation point (1.02% of trials), did not land at either target or distractor locations (1.99%), or if they were anticipative (< 60 ms; 0.03%) or late (> 2.5 standard deviations later than participant mean SRT; 2.23%). A further 0.20% of trials were rejected due to a computer error. Combined, these criteria led to the overall exclusion of 5.46% of trials from the 20 participants included in the primary analyses.

EEG analysis. Continuous EEG was segmented into epochs beginning 1,500 ms before fixation onset and ending 1,000 ms after. Independent components (Bell & Sejnowski, 1995) were extracted from the data, and artifactual components associated with eye movements were rejected based on their covariance with simultaneously recorded eye movement data (using saccade-to-fixation variance ratio criterion of 1.1; Plöchl, Ossandon, & König,

2012, within a 10-ms pre- and postsaccade interval). Mean activity from -200 to -100 ms relative to fixation onset was used for ERP baseline correction.

All ERPs were time-locked to fixation onset following the first saccade and derived from activity recorded at the FCz electrode site. Fixation-locked ERPs were used to avoid residual saccadic activity in measurement of the frontocentral ERN. While we did use an independent component analysis procedure to correct for saccade-related activity, we wanted to exercise caution.¹

ERPs were computed for each Salience (salient target vs. salient distractor) \times Selection Outcome condition (saccade to target vs. distractor; henceforth referred to as correct vs. error, respectively). For VWM capacity analyses, ERPs were further split into high-and low-capacity groups based on a median split of their K scores.

ERN amplitude was calculated as the mean difference between correct and error waveforms taken across the first 100 ms following fixation onset, when we expected the ERN to occur. The latency of the ERN component was calculated with a jackknife-based scoring approach using a fractional area measure, which defines latency as the point in time at which 50% of the total ERN component area had been reached (Hansen & Hillyard, 1980; Kiesel, Miller, Jolicoeur, & Brisson, 2008; Luck, 2005, 2014; Ulrich & Miller, 2001). The ERN area for this purpose was calculated as the total negative area under the error minus correct difference waveform 0–400 ms postfixation onset.

Results

Behavior

Behavioral results are shown in Figure 2. Correct selection of the target was less likely when the distractor was salient (M_{Salient Dis-} $t_{ractor} = 0.55$ vs. $M_{Salient\ Target} = 0.77$), t(19) = 5.88, SE = 0.04, p < .001, d = 1.63. A two-way repeated measures analysis of variance (rANOVA) was conducted on SRTs using stimulus salience (salient target vs. salient distractor) and selection outcome (correct vs. error) as within-participant factors. Analyses revealed a significant Salience \times Selection Outcome interaction, F(1,19) = 339.19, $MSE = 86.32, \ p < .001, \ \eta_{\rm p}^2 = .95, \ {\rm and \ a \ main \ effect \ of \ selection}, \ F(1,19) = 38.92, \ MSE = 270.38, \ p < .001, \ \eta_{\rm p}^2 = .67. \ {\rm The \ main}$ effect of salience was not significant (F < 4.26). Planned t tests showed that correct SRTs were on average 15 ms faster than error SRTs when the target was salient, t(19) = -4.12, SE = 3.72, p < .001, d = -0.36, but 61 ms slower when the distractor was salient, t(19) = 13.09, SE = 4.68, p < .001, d = 1.28. These results demonstrate that the stimulus salience manipulation resulted in critical performance differences.

ERPs

A two-way rANOVA was performed on ERP amplitude using within-subject factors of stimulus salience (salient target vs. salient distractor) and selection outcome (correct vs. error). A main effect of selection outcome indicated the presence of an ERN, F(1,19) = 21.28, MSE = 10.51, p < .001, $\eta_p^2 = .53$, which significantly interacted with stimulus salience, F(1,19) = 9.15,

^{1.} All principal findings were replicated when analyzing saccade-locked ERPs using the same parameters adopted by Belopolsky and Kramer (2006): ERPs time-locked to saccade onset, a baseline correction interval of -100 to -50 ms, and measurement of the ERN as mean amplitude in a fixed 90–150 ms postsaccade onset measurement window.

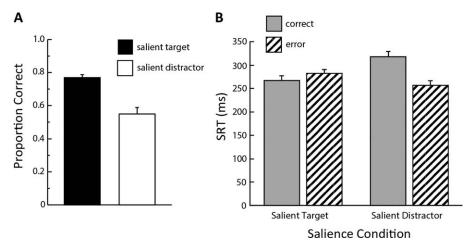


Figure 2. A: Mean proportion of trials where target was correctly selected by the first saccade, as a function of salience condition. B: Mean saccadic reaction times (SRTs; in ms) as a function of salience condition and selection outcome. Error bars reflect standard errors.

MSE = 3.51, p = .007, $\eta_p^2 = .33$. As shown in Figure 3B, the ERN for the salient distractor condition (-4.61 μ V) was larger than for the salient target condition (-2.08 μ V) over the first 100 ms following fixation onset. There was no significant main effect of salience (F < 2.19).

A paired-samples t test on ERN latency showed that the ERN occurred 69 ms earlier, on average, when the distractor (vs. target) was salient, $t_C(19) = 3.71$, $p_C = .001$. Thus, the ERN is larger and/or earlier when distractors are more salient than the target.

ERN and VWM capacity. To assess the relationship between ERN amplitude and participants' individual VWM capacity estimates, we performed two-tailed correlation analyses for each of salient distractor and salient target conditions (see Figure 4). Estimates of VWM capacity (*K*) ranged from 3.10 to 5.31, with a mean

of 3.98. We detected a reliable relationship for salient distractors, r(18) = .57, p = .009, bootstrapped 95% CI [.33, .80], whereby higher VWM capacity estimates predicted a larger ERN response. This effect was not detected for salient targets (p = .137). This, coupled with existing research (Miller et al., 2012), motivated a median-split based on VWM capacity scores to divide participants into high and low K groups (see Figure 5).

A three-way mixed ANOVA on amplitude was conducted using stimulus salience (salient target vs. salient distractor) and selection outcome (correct vs. error) as within-subject factors, and VWM capacity (high K vs. low K) as a between-subjects factor. This analysis revealed significant main effects of selection and VWM capacity, and significant interactions of VWM Capacity \times Selection and Salience \times Selection (Fs > 8.07). A significant three-way interaction, F(1,18) = 7.35, MSE = 2.63, p = .014, η_p^2 = .29, indicates that

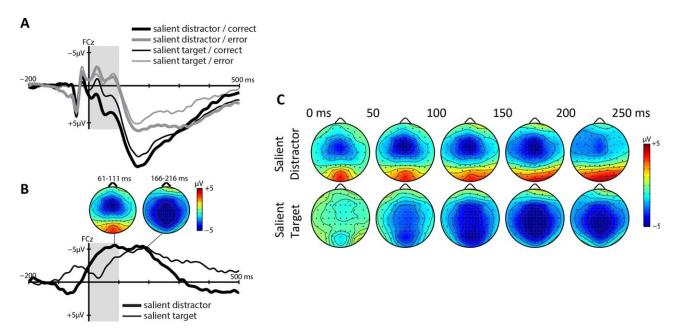


Figure 3. A: Fixation-locked ERPs plotted separately according to salience and selection outcome conditions. Negative voltages are plotted upward. The gray box indicates the time window used to calculate ERN amplitude. B: Difference waveforms, derived by subtracting relevant correct from error waveforms, plotted for each salience condition. Maps highlight peak ERN scalp topography. C: Series of scalp topography maps averaged over 50-ms intervals following fixation onset for salient distractor (upper row) and salient target (lower row) conditions (error minus correct selection voltage).

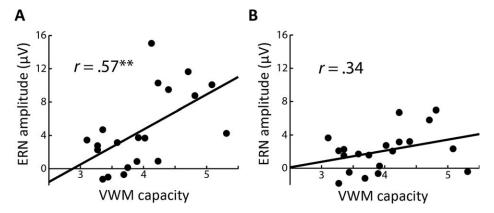


Figure 4. Correlation across participants between VWM capacity scores and ERN amplitude for (A) salient distractor, and (B) salient target conditions. **p < .01.

the ERN was significantly larger for participants with higher VWM capacity when distractors were salient ($M_{High}=-7.79~\mu V$ vs. $M_{Low}=-1.43~\mu V$) than when targets were salient ($M_{High}=-3.29~\mu V$ vs. $M_{Low}=-0.87~\mu V$), all other Fs<2.08.

A two-way mixed ANOVA was conducted on ERN latency with salience as the within-participant factor and VWM capacity as the between-participants factor. We observed significant main effects of stimulus salience, F_C (1,18) = 6.50, p_C = .020

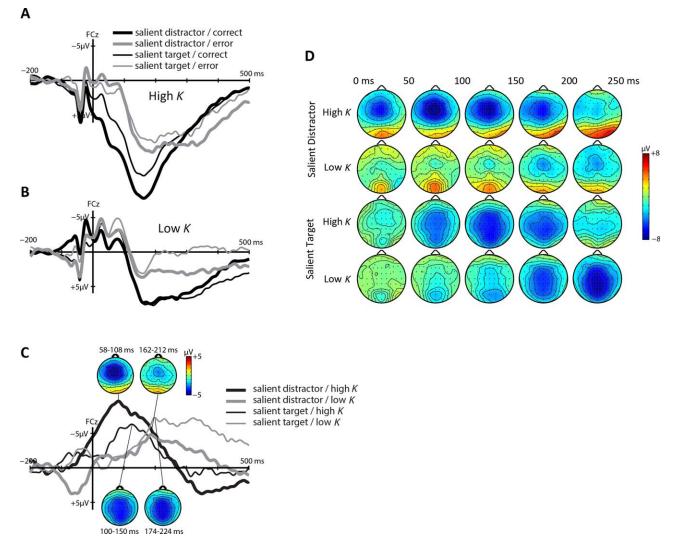


Figure 5. Fixation-locked ERPs plotted separately according to salience and selection outcome conditions for (A) high *K*, and (B) low *K* participants. Negative voltages are plotted upward. C: Difference waveforms, derived by subtracting relevant correct from error waveforms, plotted for each VWM capacity and salience condition. Maps highlight peak ERN scalp topography for each condition. D: Series of scalp topography maps averaged over 50-ms intervals following fixation onset for each VWM capacity and salience condition (error minus correct selection voltage).

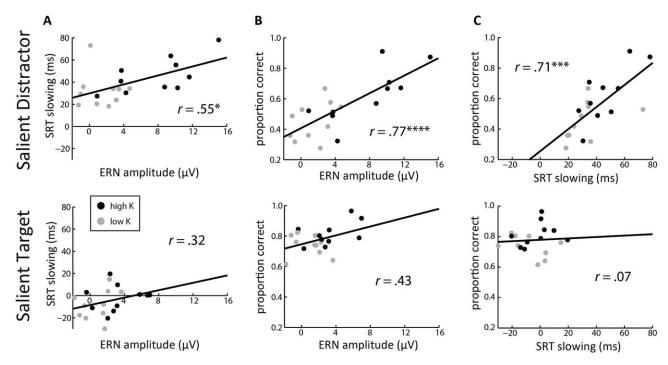


Figure 6. Correlation across participants between ERN amplitude and (A) post-error SRT slowing, and (B) post-error accuracy. Correlation across participants between post-error SRT slowing and accuracy (C). Correlations presented separately for salient distractor (upper panels) and salient target (lower panels) conditions. High K participants are colored black; low K participants are colored gray. Asterisks denote those analyses surviving Holm-Bonferonni correction for multiple comparisons: *p < .05, ***p < .001, ****p < .0001.

 $(M_{Salient\ Target}-M_{Salient\ Distractor}=34\ ms)$, and VWM capacity, F_C (1,18) = 32.37, p_C <.001, but no significant interaction (F_C <0.92). Participants with high VWM capacity scores generated an ERN 119 ms earlier, on average, than participants with low scores.

As further illustrated in Figure 5D, these findings demonstrate that the ERN differed as a function of a participant's VWM capacity such that individuals with a higher *K* generated an earlier and, for salient distractors, a larger ERN.

ERN and post-error performance. To determine the impact of the ERN on post-error behavior, we conducted two-tailed correlation analyses between ERN amplitude on the one hand, and speed and accuracy measures on the other, across participants for each salience condition (see Figure 6). Accuracy was calculated as the likelihood that a correct selection would be made on the trial (E+1) following an error trial (E). Speed was calculated as the relative slowing of the saccadic response on the subsequent trial ($tri-al_{E+1}$ $SRT - trial_E SRT$).

For salient distractors, larger mean ERN amplitude significantly predicted more slowing, r(18) = .55, p = .011, bootstrapped 95% CI [.04, .88], and greater accuracy, r(18) = .77, p < .001, bootstrapped 95% CI [.56, .90], of the saccadic response on the trial following an error. These relationships did not emerge within the salient target condition (speed: p = .164; accuracy: p = .056). However, as shown in the lower panels of Figure 6A,B, participants in this condition showed little evidence of PES, while still maintaining a high level of accuracy. To determine whether speed-accuracy tradeoffs occurred following an error, we additionally analyzed the relationship between PES and post-error accuracy. As demonstrated in Figure 6C, a post-error speed-accuracy tradeoff only occurred when distractors were salient, r(18) = .71, p < .001, bootstrapped 95% CI [.38, .90], and not when targets were salient (p = .77).

Further subdivided into the low and high *K* groups, it seems that the significant correlations were primarily driven by the high *K* group. The Holm-Bonferroni method was used to control for multiple comparisons (Holm, 1979).

In order to assess the reliability of our measures, we calculated split-half correlations for each of the measures (odd vs. even trials). High correlations indicate that effects were of similar magnitude in both partitions of the data. In the salient distractor condition, split-half correlation for the ERN was significant, r(18) = .87, p < .001, as was correlation for speed, r(18) = .75, p < .001, and accuracy, r(18) = .92, p < .001. However, in the salient target condition, split-half correlation for accuracy was significant, r(18) = .63, p = .003, but was not for ERN, r(18) = .38, p = .010, or speed, r(18) = .05, p = .821. This suggests that perhaps the reason why no relationship was observed between ERN and post-error behavior in the salient target condition was because participants did not generate a reliable ERN or engage in a post-error slowing strategy in response to errors for this condition.

These findings indicate that, for salient distractors, the degree of error processing indexed in ERN latency and amplitude predicts the degree to which participants alter their response criterion following commission of an error, resulting in a speed-accuracy tradeoff. When the target was the most salient element in the display, our findings suggest that there was little strategic incentive to slow responding in order to increase accuracy following an error. These latter errors appear to be treated as a "blip" by the error-monitoring system that can otherwise be ignored.

VWM capacity and post-error performance. Higher VWM-capacity participants generated a greater ERN in the salient distractor condition and, in turn, a greater ERN was associated with greater adjustment to post-error behavior only in the salient distractor condition. This suggests that the participants with high VWM

capacity were better able to exert cognitive control to adjust their behavior following such errors. We tested this directly by conducting a two-way mixed ANOVA with salience as the withinparticipant factor and VWM capacity as the between-participants factor. We observed a main effect of VWM capacity on both posterror speed, F(1,18) = 4.63, MSE = 215.17, p = .045, $\eta_p^2 = .21$, and accuracy, F(1,18) = 9.60, MSE = 0.02, p = .006, $\eta_p^2 = .35$. These data indicate that participants with higher VWM capacity scores exhibited greater post-error slowing ($M_{High} = 22$ ms vs. $M_{Low} = 12$ ms) and increased post-error accuracy $(M_{High} = .72 \text{ vs.})$ $M_{Low} = .60$). A significant main effect of salience on post-error speed confirmed that post-error slowing only occurred for the salient distractor condition ($M_{Salient\ Distractor} = 39$ ms vs. $M_{Salient\ Distractor} = 39$ $T_{arget} = -5$ ms), F(1.18) = 98.20, MSE = 199.02, p < .001, $\eta_{\rm p}^2 = .85$. A main effect of salience on post-error accuracy verified the generally higher accuracy observed following an error in the salient target condition, F(1,18) = 40.91, MSE = .01, p < .001, $\eta_p^2 = .69$. No interactions were significant for either post-error performance measures (Fs < 1.63). The lack of significant interactions here means that we did not find evidence supporting the assertion of a stronger relationship between VWM capacity and post-error behavioral adjustment for the salient distractor (vs. salient target) condition.

Discussion

The present experiment provides several important lines of evidence that highlight how visual salience impacts error monitoring and adaption in oculomotor control. Results showed greater likelihood of incorrect saccades when the distractor was relatively more salient than when the target was salient. The ERN occurred earlier and/or was larger when the distractor was more (vs. less) salient than the target, demonstrating that stimulus salience affected the degree of error processing. The ERN was further modulated by VWM capacity, whereby participants with higher VWM capacity experienced an earlier onset and, for salient distractors, a larger ERN. A greater ERN, in turn, predicted greater post-error saccadic response slowing and increased post-error accuracy. We can draw three primary conclusions from these results. First, misdirected saccades to salient distractors are strongly represented in the errormonitoring system by a rapid and robust ERN, which leads to a significant adjustment of oculomotor behavior. Second, misdirected saccades to less-salient distractors, while arguably representing larger errors, are not as well detected or utilized by the error/performance-monitoring system. Third, the error/performance-monitoring system is better engaged in tasks requiring greater cognitive control and by individuals with higher VWM capacity.

Our salience manipulation appears to have impacted the degree to which cognitive control was required to select the target. When the target was already the most salient element, the prepotent influence of perceptual salience also prioritized target selection, thereby reducing the need for additional goal-directed guidance. In contrast, having a distractor of greater salience necessitates greater goal-driven influence to override a stimulus-driven priority for distractor selection in order to correctly execute a saccade to the less-salient target. The higher error rate in this condition may have signaled the need for increased cognitive control. One possibility is that this difference in the degree of cognitive control may reflect the use of different search strategies in the two conditions. For example, participants may have adopted a singleton detection mode (Bacon & Egeth, 1994; Leber & Egeth, 2006) for the salient target condition when they could rely on salience to guide search to the target,

but a more effortful feature search mode for the salient distractor condition when search was not accurately guided by salience.

An integral aspect of cognitive control and the implementation of goal-directed guidance is the ability to monitor ongoing performance and adjust behavior accordingly. Increased cognitive control will result in more efficient monitoring and detection of errors, which in turn would provide critical strategic information for subsequent trials. Strategic information would include the need to delay saccade execution until more visual evidence is accumulated, so that goal-directed processes can have sufficient opportunity to influence selection. When it is known that the target is already the most salient element, it appears less necessary to engage in error processing or to utilize any resulting error signal to make strategic adjustments. The reduced necessity is likely because correct oculomotor response decisions can be based primarily on salience. Misdirected saccades to less-salient distractors could be considered to represent a greater deviation from correct performance as they prevail over a correct response strengthened by both goal-directed and low-level processes. It should be an indication that effective performance has broken down. However, our study shows either that the performance-monitoring system is less engaged under these circumstances or that these saccades reflect a type of error that is not processed or utilized to the same extent as misdirected saccades to more-salient distractors.

Saliency and Error Monitoring

Our findings support a conflict-monitoring interpretation of the ERN, whereby the level of competition between the different responses, and the stimuli that define these different responses, was more important in the generation of an enhanced ERN than the error commission itself. Because the salient distractor condition pitched top-down processes against low-level processes, conflict was higher than in the salient target condition, thus predicting the larger/earlier ERN that we observed for the salient distractor. Our ERN results do not support an error-detection theory account, which would have predicted a larger ERN for the salient target condition, because this condition has the greater degree of mismatch between target- and distractor-directed saccadic response representations. Our ERN results were similarly opposite to that predicted by reinforcement-learning theory, which relates an enhanced ERN to greater violation of expectancies when committing errors—a violation that was larger in the salient target condition due to a lower probability of errors.

Finding an ERN difference as a function of distractor salience conflicts with Belopolsky and Kramer (2006), who failed to find a difference in their antisaccade/oculomotor capture paradigm despite observing an effect in the same direction. We speculate that their study may not have been sufficiently powerful (N=9 participants) or sensitive (they did not measure from the FCz electrode, considered most sensitive to the ERN) to detect such a difference. Additionally, they did not manipulate salience to the same extent as in the present study, insofar as their less-salient distractor was still as equally salient as the target, rather than being less salient as in our paradigm.

One limitation of our design was that target and distractor salience levels were yoked to one another: when the target was high salience, the distractor was low salience and vice versa. We adopted this design to limit the length of the experiment—a fully crossed design would have required twice as many trials—but it means that we cannot distinguish if it was the relative salience between target and distractor that drove our results, or whether

similar results would have been observed had the distractor been equally salient to the target. This is an issue we will return to in future studies.

Error Monitoring and Post-Error Performance

Following an erroneous saccade, we observed a slower and more accurate response predicted by ERN magnitude, but only when the saccade was made to distractors more salient than the target. We consider these findings to indicate a strategic adjustment and reflect increased implementation of control for this condition. We interpret the speed-accuracy tradeoff nature of this behavioral adaptation as indicating a conservative shift in the response decision criterion, which allows for increased accumulation of perceptual evidence before a response decision is made (Botvinick et al., 2001; Cohen, Botvinick, & Carter, 2000; Dutilh et al., 2012; Rabbitt & Rodgers, 1977). We speculate that the correlational relationship between ERN and post-error performance measures is likely to be bidirectional, whereby a high error rate signals the need for increased cognitive control expressed both in the implementation of strategic adjustments in oculomotor behavior and in the allocation of more resources to error monitoring as the participants seek to find the right speed-accuracy balance to optimize ongoing performance.

An alternative interpretation of post-error slowing is that it merely reflects the same lapse of attention responsible for the error (Gehring et al., 1993, 2012). However, we measured post-error slowing relative to the error trial SRT itself, and any variations in the SRT difference from trial to trial would not be explained by a lapse of attention spanning multiple trials. Our observed increase in post-error accuracy as a function of ERN magnitude may even suggest an increased attentional focus on these trials. Indeed, because performance in our oculomotor selection task did not reach ceiling in any of our conditions, we were able to measure accuracy of post-error saccades in addition to the traditional post-error measure of response slowing, allowing greater insight to the compensatory process following an error.

Why was a similar relationship not observed for the salient target condition, despite the presence of an ERN (albeit smaller and later)? We argue that there was no strategic benefit to performance accuracy by slowing responses in this condition. Previous studies (Donk & van Zoest, 2008; van Zoest & Donk, 2008; Weaver et al., 2014) demonstrate that, as the latency of saccade execution (i.e., SRT) increases, saccades to the most salient element in a search display, whether the target or distractor, become less likely. Though not reported above, this pattern replicates in the current data. This is presumably due to the short-lived influence of saliency on selection (Cheal & Lyon, 1991; Donk & van Zoest, 2008; Nakayama & Mackeben, 1989; Nothdurft, 2002). For salient targets, this rapidly decaying benefit of salience to performance accuracy more than offsets the slower developing benefit of goaldirected processes, which also prioritize target selection. Consequently, the lack of post-error slowing when it is known in advance that the target is the most salient element in the display (Figure 6A, lower) may reflect adoption of a good strategy, as slowing subsequent responses would serve only to sacrifice both performance speed and accuracy. Alternatively, this approach to task completion may be the inadvertent consequence of reduced performancemonitoring system engagement in the easier salient target condition. Finally, we may not have observed a relationship between ERN and post-error behavior because participants did not reliably generate an ERN signal in this condition. In any case, our study demonstrates the critical importance of visual salience in whether a link between the ERN and post-error compensatory behavior is observed. In this way, our findings move toward a reconciliation of conflicting extant evidence of this relationship.

In addition to the ERN, error processing is also associated with the later-occurring error positivity (Pe; Falkenstein et al., 1990; Overbeek, Nieuwenhuis, & Ridderinkhof, 2005), which some have suggested is also involved in strategic response adaptation. We did not examine the Pe in the current study due to concerns that it would be difficult to isolate from the P300 (Sutton, Braren, Zubin, & John, 1965)—a larger ERP component that might also be expected to differ across salience conditions (Arbel & Donchin, 2009; Davies, Segalowitz, Dywan, & Pailing, 2001; Leuthold & Sommer, 1999; Overbeek et al., 2005).

Error Monitoring and Visual Working Memory

The present study establishes a link between higher VWM capacity and better error monitoring. Finding a larger and/or earlier ERN for individuals with high VWM capacity estimates is consistent with Miller et al. (2012), where higher WM capacity participants were observed to have a larger ERN. It is also consistent with recent neuroimaging evidence demonstrating increased ACC activity as a function of better WM task performance (Faraco et al., 2011). The present study extends this research by linking visual WM capacity with neural measures of oculomotor error processing and by demonstrating how this relationship varies as a function of the relative visual salience of distractor stimuli. That an analogous relationship is found using both visual (K) and verbal (operation span) measures of working memory capacity strongly implicates the critical involvement of the domain-general, but limited-capacity, attention control processes in error monitoring.

We consider the larger ERN for the high VWM capacity group in the salient distractor condition to indicate greater engagement in error monitoring. Greater engagement may be reflected by either better maintenance of task goals and/or greater sensitivity to detecting errors or conflict. Observing a VWM capacity difference in ERN magnitude only for the salient distractor condition was expected, given that this condition required greater top-down control that recruits many of the processes indexed by VWM. Such processes include the ability to maintain a task-defined but less-salient target template, while filtering out and inhibiting responses to highly salient distractors.

The high VWM capacity group also generated the ERN much faster than the low VWM capacity group across saliency conditions. This may again indicate a greater sensitivity to the commission of errors. However, it is also conceivable that the earlier ERN may merely reflect faster processing due to increased motivation by high VWM capacity participants. Because increased motivation likely contributed in some degree to performance on the change-detection task used to estimate VWM capacity, these factors might also explain differences in ERN latency observed as a function of these individual estimates. Taken together, our study shows that the link between VWM capacity and neural mechanisms of error monitoring depends on the degree to which the task recruits those processes that VWM is purported to index.

While the present findings suggest that higher VWM capacity individuals were better able to exert control in order to adjust behavior following an error, VWM capacity impacted post-error behavioral adjustment generally— and not selectively for the salient distractor condition. However, because we had low power for this particular analysis (N=10 participants), such a relationship may become evident in future experiments with larger sample sizes.

Conclusion

Efficient and effective cognitive control relies on the ability to monitor ongoing performance toward task goals, and to implement strategic behavioral adjustments when errors are committed. The present study demonstrates that relative salience of task-relevant and task-irrelevant stimuli can define situations where such an increase in cognitive control is necessary, with individual differences in VWM capacity explaining significant variance in the degree to which cognitive control is applied.

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