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Stimulus-driven attention and cognitive control during encoding: An event related brain potentials study

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ABSTRACT

Stimulus-driven attention drawn to relevant items can improve working memory (WM) whether attentional capture is driven by salient, low level features or by contingent salience from shared features with targets. In the current work, we examined the time course of enhanced attention to contingently salient information in a non-spatial WM task using event related brain potentials (ERPs). In line with previous work, we predicted that the encoding of contingently salient stimuli would be associated with an enhancement of cognitive control processes rather than low-level salience detection. The results of this study supported this hypothesis, evidenced by a posterior P3 component of greater amplitude for contingently salient stimuli relative to stimuli of a control color, which is thought to reflect enhanced attention to information that matches a target held in WM. However, P3 amplitude during encoding was unrelated to subsequent memory accuracy. As an exploratory follow up on these results, we conducted a regression analysis including beliefs about ability to focus attention as a moderator, which interacted with P3 amplitude to predict WM recall of salient letters. Furthermore, source localization analyses implicated a significant contribution of regions in the salience network to the detection of target stimuli, but only frontal control regions showed a greater response to salient than control letters. Thus, the results of this experiment suggest that participants enhance cognitive control during the encoding of contingently salient stimuli, but that the relationship between this neural process during encoding and subsequent benefits to WM recall might depend on individual differences in attentional focus.

1. Introduction

Attention and working memory (WM) allow observers to select and prioritize relevant information, where it can be accessed, recalled, and manipulated to serve current task goals. Both attention and WM are limited capacity processes that can encode and maintain only a finite amount of information from a greater number of potential inputs. Thus, it is of vital interest to understand how information is prioritized during encoding to ensure that only the most relevant items gain access to WM resources. Much of the current understanding of how attention selects items for WM focuses on the undeniably important role of voluntary, top-down, or goal-directed attention in volitionally selecting stimuli that match current task demands (Awh & Jonides, 2001; Awh, Vogel, & Oh, 2006; Gazzaley & Nobre, 2012). Attention, however, is not exclusively under volitional control. Attention can also be "captured" or drawn automatically in a bottom-up manner to information based on external factors such as when a stimulus contains salient or novel features (Yantis, 1993). Other investigators have argued that attentional capture is heavily influenced by internal factors and task goals, such as a distractor item sharing features with a target ("contingent" salience; Folk, Remington, & Johnston, 1992; Folk, Leber, & Egeth, 2002). Here, we refer to the automatic direction of attention, regardless of whether it is drawn to inherently salient or contingently salient aspects of a stimulus, as stimulus-driven attention.

Recent evidence suggests that stimulus-driven attention elicited by task-relevant items can benefit WM (Fine & Minnery, 2009; Gaspelin, Leonard, & Luck, 2015; Ravizza & Hazeltine, 2013; Santangelo & Macaluso, 2013; Schmidt, Vogel, Woodman, & Luck, 2002; Wills et al., 2016). These benefits have been found in a variety of experimental designs where attention is captured by low-level visual features such as color opponency (Fine & Minnery, 2009) and visual salience (Santangelo & Macaluso, 2013). These paradigms typically involve using stimulus-driven attention to prioritize information in space, but our group has likewise found evidence that non-spatial attention "capture" by items that share a feature with a target can also enhance WM (Ravizza & Hazeltine, 2013; Wills et al., 2016). In these experiments, participants memorized lists of letters presented at the center of fixation while performing a secondary target detection task (responding

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to a colored pound sign). Each item in the stream was presented in a different color and some trials included a letter that matched the color of the target. In both experiments, participants showed enhanced memory for letters of the target color (Ravizza & Hazeltine, 2013; Wills et al., 2016). We attributed these results to the engagement of stimulus-driven attention drawn automatically to these letters due to contingent salience.

Relatively little is known about the specific neural and cognitive mechanisms underlying the benefits of stimulus-driven attention to WM, however. Previous work with fMRI has not supported a direct role for salience detection regions and processes in the enhancement of WM for salient stimuli (Santangelo & Macaluso, 2013; Wills et al., 2016). For example, in our previous fMRI study (Wills et al., 2016), we found no evidence that salience detection regions (i.e. anterior insula (AI), temporoparietal junction (TPJ), and anterior cingulate cortex (ACC)) were activated during the encoding of contingently salient stimuli. Instead, we found increased activation in frontoparietal regions (i.e. inferior frontal junction and superior parietal lobe) thought to enhance task representations, trigger cognitive control, and integrate stimulus features and task goals to prioritize information in WM. We attributed WM benefits from contingent salience to the enhancement of cognitive control to maintain task goals rather than a direct benefit of salience per se. Instead, salience was thought to provide additional information about a stimulus and its relative importance that can be utilized by control processes to enhance WM.

In line with these findings, behavioral research with spatial attention has suggested that salience detection processes triggered by the capture of stimulus-driven attention may increase the likelihood that information enters WM, such as by influencing encoding order, but controlled processing is required to enhance the representation of an item in WM (Ravizza, Uitvlugt, & Hazeltine, 2016). Cognitive control processes are thought to be a crucial component of information representation in WM (for a review, see Courtney, 2004), and can even influence how strongly attention is guided to contingently salient features (Han & Kim, 2009). Other researchers have suggested that brain regions implicated in goal-driven control and those involved in salience detection may compete during memory tasks (Majerus et al., 2011; Uncapher, Hutchinson, & Wagner, 2011). Thus, it is likely that in order for stimulus-driven attention to improve WM, cognitive control processes rather than salience detection processes must be enhanced during the encoding of salient stimuli.

The purpose of the present work is to use event-related brain potentials (ERPs) to provide converging evidence that the benefits of stimulus-driven attention to WM are associated with an enhancement in cognitive control processes rather than salience detection processes. In the present experiment, we gave participants a modified version of the task used in these previous experiments (Ravizza & Hazeltine, 2013; Wills et al., 2016), during which continuous electroencephalography (EEG) data were recorded. In this task, participants memorized lists of colored letters presented one by one at the center of fixation while simultaneously monitoring for pound signs of a target color. Consistent with our previous work, we predicted that participants would show enhanced memory for letters that matched the color of the target.

Our previous fMRI results suggested that stimulus-driven attention drawn to relevant stimuli can benefit WM and that this benefit is attributed to an enhancement of cognitive control regions (Wills et al., 2016). Thus, we likewise predicted that our ERP results would reflect the enhancement of controlled target detection processes during the encoding of contingently salient letters. Specifically, we predicted the presence of a clear posterior P3 component showing greater amplitude during the encoding of contingently salient letters relative to letters presented in a control, irrelevant color (Donchin, 1981; Dong, Reder, Yao, Liu, & Chen, 2015; Polich, 2007). The P3 component is thought to reflect the encoding of targets into WM, matching target information to templates held in WM, and processes relevant to the selection of an appropriate response (Brouwer, Reuderink, Vincent, van Gerven, & van Erp, 2013; Polich, 2003, 2007; Vogel & Luck, 2002; Devillez, Guyader, & Guérin-Dugué, 2015). These cognitive control processes provide a likely explanation for our previous findings using non-spatial contingent capture: participants may show enhanced encoding of contingently salient, task relevant information that matches a target template held in WM. Furthermore, we followed up on the ERP results using standardized low resolution electromagnetic tomography analysis (sLORETA; Pascual-Marqui, 2002) to estimate neural generators of the P3 potential. We hypothesized that these results would corroborate our fMRI findings and reveal frontal and parietal sources of greater activation for salient relative to control letters.

Additionally, if there are differences in activation related to salience detection, the temporal resolution of ERP should make this method more robust than fMRI to detect these differences and they will likely be revealed in the source localization analysis. This method allowed us to examine potential neural generators of differential activity for targets and contingently salient letters and their respective control conditions during a smaller time window than our previous fMRI work. Furthermore, this time window was locked ERPs, which are not subjected to the same temporal delay between the presentation of a stimulus and the measured changes in brain activity. However, because source localization does not provide a direct measure of brain activation, but models activations based on mathematical parameters and assumptions, this analysis was largely exploratory and designed to drive future hypotheses about the neural mechanisms of the benefits of stimulus-driven attention via contingent salience.

Finally, we collected additional self-report measures, including the Attentional Control Scale (ACS; Derryberry & Reed, 2002), to conduct exploratory analyses examining the potential moderating role of individual differences in one's perceptions of his/her own attentional focus in the relationship between ERPs and memory in this task. In our previous experiments (Wills et al., 2016), although we found a significant behavioral accuracy benefit for salient relative to control letter, there was substantial variability in the data and a clear brain-behavior relationship was not established. Thus, examining individual differences may clarify the relationship between brain activity related to cognitive control during encoding and subsequent WM accuracy. Specifically, the ACS provides measures of perceived ability to control and shift attention (Judah, Grant, Mills, & Lechner, 2014; Quigley, Wright, Dobson, & Sears, 2017; Williams, Rau, Suchy, Thorgusen, & Smith, 2017). Previous work has suggested that beliefs about one's abilities can interact with ERP measurements to predict behavioral outcomes. For example, Schroder et al. (2017) found that the relationship between growth mindset of intelligence – i.e., the belief that intelligence is changeable (Dweck, 2013) – and behavioral post-error accuracy in a go/no-go task differed significantly in children with larger relative to smaller error positivity (Pe) amplitude, considered an index of attention to error. The authors interpreted this result to suggest that growth mindset and neural mechanisms of attention interacted to predict ability to recover after failure. Thus, we predicted that participants' beliefs about their ability to control attention, as indexed by scores on the ACS, might interact with P3 amplitude to predict WM benefits to the contingently salient letters.

2. Method

2.1. Participants

Thirty-five right-handed Michigan State University undergraduate and graduate students (ages 18–24, 7 male, 28 female) with normal or corrected-to-normal vision participated in the ERP experiment. Three participants were excluded from analysis – one for poor quality EEG data (more than half of trials excluded in artifact rejection) and two because of poor behavioral performance on the task (more than 3 median average deviations below the mean; Leys, Ley, Klein, Bernard, & Licata, 2013). Participation was voluntary and participants were

compensated $10 per hour. All procedures were approved by the Human Research Protection Program at Michigan State University, and written informed consent was obtained from all participants before beginning the experiment.

2.2. Stimuli

Stimuli were eight phonologically similar letters (B, C, D, G, P, T, V, and Z) and pound signs (#) presented in one of nine colors (red, yellow, lime, magenta, silver, teal, cyan, blue, and purple) at the center of fixation and on a black background. Participants responded to the stimuli using the number pad on a standard keyboard, and all behavioral responses were collected using E-Prime software.

2.3. Procedure

Fig. 1 illustrates the experimental design. At the start of the experiment, participants were assigned a target color and were instructed to monitor for a pound sign of that color throughout the experiment. Participants received a reminder of the target color at the start of each block, and this screen was followed by the pseudo-random presentation of 18 trials. Each trial began with an encoding period during which six letters, each presented in a different color from the nine possible colors, and one colored pound sign were presented serially for 500 ms each and separated by fixation crosses that were also presented for 500 ms. Participants were instructed to memorize the letters in order while monitoring for pound signs of the target color and ignoring pound signs of the irrelevant color. The target pound sign occurred twice in each block and could occur in any position in the list chosen at random. Participants were to respond to this target as soon as it was detected. In half of the trials, one letter in the sequence was presented in the target color (salient color condition), and in the other half, a letter was presented in a non-target color but was matched for frequency (control color condition). Both the target and control color were selected and counterbalanced between red, yellow, and lime, and could occur as the third, fourth, fifth, or sixth letter in the list. The colors of the remaining letters and non-target pound signs were drawn randomly from the remaining colors in the color list such that each item in a given trial was presented in a unique color.

Following the encoding period was a 2000 ms retention interval. This interval was followed by the presentation of a prompt including one letter within a set of five dashed lines for 4000 ms. Participants were asked to indicate whether the given letter was the correct letter in the correct position as presented during the encoding trial (a yes/no response). The letter presented in the prompt could be the letter presented in the salient, control, or a random color from the previous list. Although every trial presented either a salient or control colored letter during encoding, the salient and control letters were probed for retrieval in only one-third of trials each (six salient retrieval trials, six control retrieval trials, out of 18 trials per block). Out of the remaining third (six trials), four trials asked about a randomly colored letter to minimize the likelihood that participants would attend only to the salient and control letters, and the other two trials, which contained the target pound sign, were excluded from analysis. In total, participants completed two practice blocks of the experiment and eight blocks during which continuous EEG data were recorded. There were 144 trials in total – 72 salient trials and 72 control trials including those with target pound signs (16 trials). The removal of target pound trials resulted in 64 encoding trials used in the analysis for both the salient and control conditions, and 48 retrieval trials for each condition (excluding the 16 target pound trials and 32 trials that tested randomly colored letters). Following the completion of the WM task, participants were given a packet of self-report questionnaires, which included demographic information and the Attentional Control Scale (Derryberry & Reed, 2002).[1]

2.4. ERP data acquisition

Continuous EEG activity was recorded throughout the task using BioSemi's Active-Two system (BioSemi, Amsterdam, The Netherlands). Participants were fitted with a flexible cap including 64 Ag-AgCl electrodes placed using the 10/20 system. Two electrodes were placed on the left and right mastoids and served as the reference for offline processing Electrooculogram (EOG) activity was recorded using three additional electrodes: one inferior to the left pupil and the remaining two on the outer canthi of each eye. The common mode sense active electrode and the driven right leg passive electrode served as online references for the other electrodes. The EEG signal was digitized using ActiView software (BioSemi) at a sampling rate of 1024 Hz.

Offline data processing and analyses were conducted using EEGLab (Delorme & Makeig, 2004) and ERPLab (Lopez-Calderon & Luck, 2014). First, data were resampled to 512 Hz. The raw data were then filtered using a bandpass filter with cutoffs of .1 and 30 Hz (12 dB/oct rolloff). The data were then visually inspected and segments containing gross artifacts and noise were removed in preparation for blink correction using Independent Components Analysis (ICA; Jung et al., 2000). The blink-corrected data were then re-referenced to the average signal of the two mastoid electrodes. Next, the time-locked data were separated into individual epochs for each encoding trial beginning 100 ms before stimulus presentation and extending 900 ms post-stimulus. A computer-based algorithm was then employed to detect physiological artifacts and reject trials meeting any of the following criteria: a voltage step greater than 50 μV between contiguous sampling points, a voltage difference of more than 200 μV within a trial, or a maximum voltage difference of less than .5 μV within a trial.

Finally, time-locked averages were computed separately for each stimulus type. The following values are the number of trials retained after artifact rejection: salient letter ($M = 61.82$ trials, $SD = 2.21$, range: 53–64), control letter ($M = 61.94$ trials, $SD = 2.34$, range: 55–64), random letter ($M = 684.62$ trials, $SD = 34.29$, range: 589–718), target pound sign ($M = 15.23$ trials, $SD = .96$, range: 12–16) and non-target pound sign ($M = 122.38$, $SD = 5.61$, range: 105–128). From the resulting waveforms, we calculated P3 amplitude using a time window of 300–800 ms (Ergen, Marbach, Brand, Başar-Eroğlu, & Demiralp, 2008). Due to the inflated risk of Type 1 error when making comparisons across a large number of electrode sites (Lage-Castellanos, Martínez-Montes, Hernández-Cabrera, & Galán, 2010), we limited our analyses to three midline sites: Fz, Cz, and Pz. These electrodes were chosen based on previous literature defining P3 as the amplitude change over midline electrode sites (Fz, Cz, and Pz) (Johnson, 1993; Polich, 2007). Our main analyses compared the resulting P3 amplitudes in the salient and control letter conditions.

Following the ERP analysis, source localization analysis was conducted using sLORETA (Pascual-Marqui, 2002), a functional imaging method that computes the three-dimensional distribution of current density that is modeled as volume elements (voxels) in the Montreal Neurological Institute (MNI) coordinates. This method assumes similar activation of neighboring neuronal sources and has been validated by studies combining sLORETA with other functional neuroimaging methods including fMRI (Mulert et al., 2004; Vitacco, Brandeis, Pascual-Marqui, & Martin, 2002). First, sLORETA solutions were computed for each individual subject for the salient and control letter

[1] The questionnaire packet given to participants after completing the ERP experiment also included the State-Trait Anxiety Inventory (STAI-T; Spielberger & Gorsuch, 1983), the Implicit Theories of Anxiety Scale (TOA; Schroder, Dawood, Yalch, Donnellan, & Moser, 2015), the Penn State Worry Questionnaire (PSWQ; Meyer, Miller, Metzger, & Borkovec, 1990), and the Mood and Anxiety Symptom Questionnaire (MASQ; Watson & Clark, 1991). However, we focused our analyses on the WM task, and with the exception of some exploratory analyses looking at the attentional control scale (ACS), these data were not analyzed for the current work.

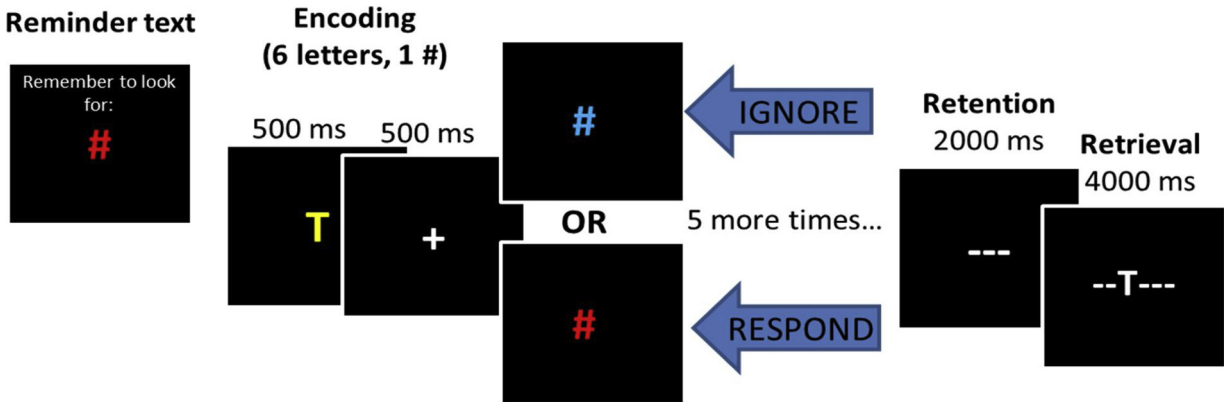

Fig. 1. Illustration of the behavioral task. Participants were instructed to monitor for a pound sign of a target color while memorizing colored letters and ignoring pound signs of the non-target color. In each trial, seven items (6 letters and a pound sign) were presented one at a time, each in a different color, with some trials including a letter of the target color. Following this encoding list, participants were prompted with one letter and asked to report whether the prompt showed the correct letter in the correct position from the previous list.

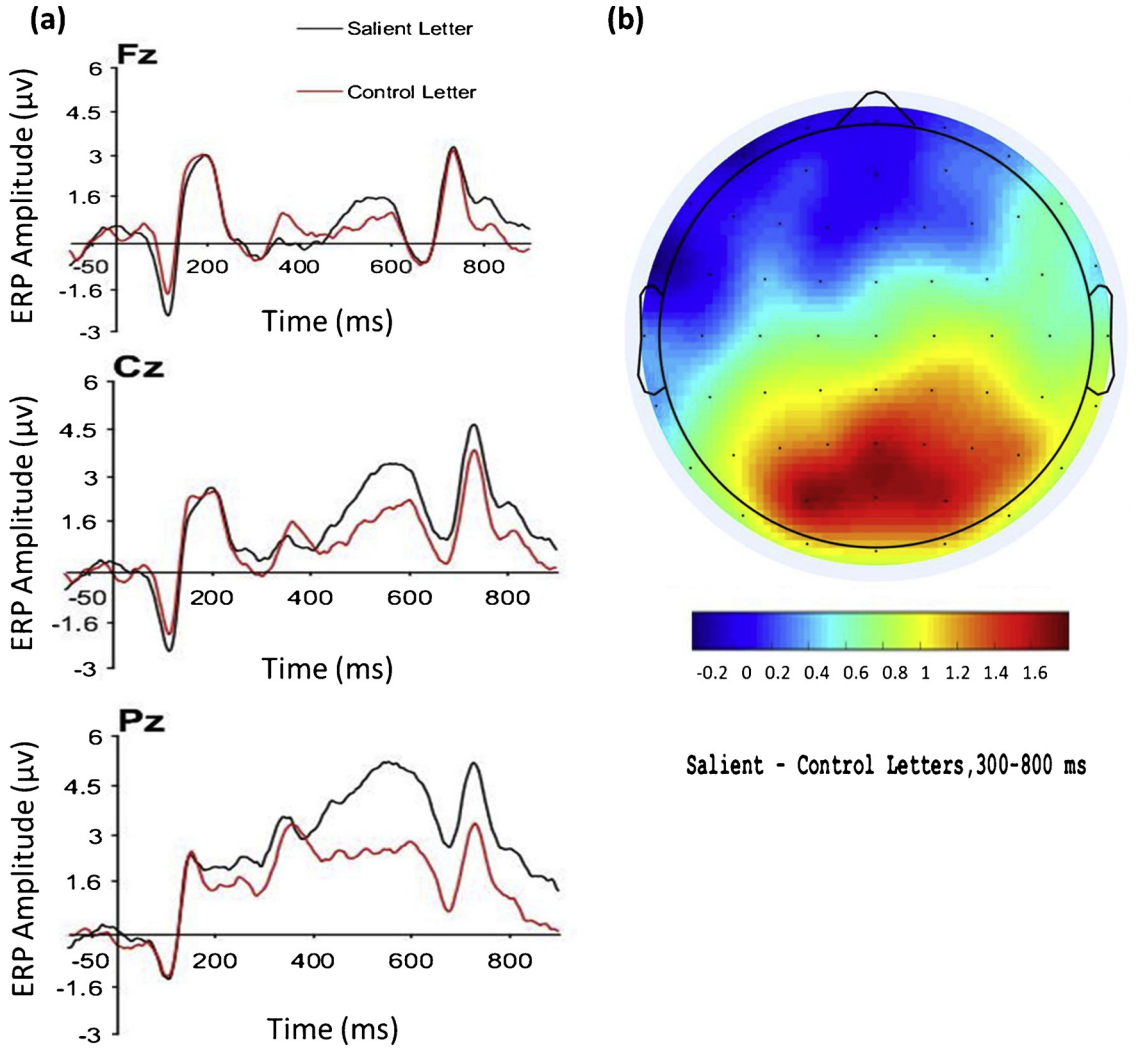

Fig. 2. (A) ERPs for electrode sites Fz, Cz, and Pz during the encoding of salient and control letters. Time 0 is stimulus onset. (B) Head map showing the average topographical distribution of the salient minus control difference wave from 300 to 800 ms post stimulus (P3).

conditions. Then, single sample *t*-tests were computed for each condition of interest (salient letters, control letters, target pound signs, non-target pound signs) to examine potential neural sources of the P3 potential. Finally, to identify source differences between salient and control letter conditions and target and non-target pound sign conditions, a paired-samples *t*-test (log of ratio of averages) was conducted for the time window of 300–800 ms with 5000 random permutations (Lorenzo-López, Amenedo, Pascual-Marqui, & Cadaveira, 2008; Pandey et al., 2012). Levels of significance were corrected for multiple comparisons ($p < .05$).

3. Results

3.1. Behavioral data

As expected, accuracy for the target pound sign was high (M = .96, SD = .04). Accuracy scores for letter probes in the salient and control conditions were calculated by subtracting hits minus false alarms to correct for guessing. Unlike in our previous work (Ravizza & Hazeltine, 2013; Wills et al., 2016), there was no significant difference in memory accuracy for salient (M = .65, SD = .17) relative to control (M = .61, SD = .16) letters, $t(31) = 1.22$, $p = .23$. However, on correct trials, participants responded consistently faster to salient (M = 1458.87, SD = 235.74) relative to control probes (M = 1535.20, SD = 243.01), $t(31) = -2.13$, $p = .04$. Thus, although accuracy differences did not reach significance, the RT data suggest that participants were able to access the salient letters more quickly and thus provide some evidence of enhancement of salient letters in WM.

3.2. ERP data

To examine whether P3 amplitude was greater during encoding of salient relative to control letters, we conducted a Site (Fz, Cz, Pz) by Condition (Salient vs. Control) repeated-measures ANOVA. This analysis revealed main effects of Site, $F(2,62) = 25.10$, $p < .001$, $\eta_p^2 = .45$, and Condition, $F(1,31) = 5.58$, $p = .025$, $\eta_p^2 = .15$. There was also a significant interaction between the two factors, $F(2,62) = 11.54$, $p < .001$, $\eta_p^2 = .271$. As a follow-up to this analysis, we conducted multiple paired-sample t-tests using a Bonferroni correction. To be considered significant under this correction, the p value could not exceed .016. These tests revealed no differences in P3 amplitude for the two conditions at Fz, $t(31) = .41$, $p = .69$, or Cz, $t(31) = 1.82$, $p = .079$, but P3 amplitude was significantly greater during the encoding of salient relative to control letters at Pz, $t(31) = 4.25$, $p < .001$. Grand averaged waveforms and corresponding topographical distribution of the difference in P3 amplitude between salient and control letters from 300 to 800 ms are shown in Fig. 2. The topographical distribution of this potential is consistent with a target P3b (Bledowski, Prvulovic, Goebel, Zanella, & Linden, 2004; Polich, 2007). No evidence of a novelty-driven P3 was observed during the encoding of salient relative to control letters.

Next, we examined P3 amplitude using the same time window for salient relative to non-target pound signs. A second Site (Fz, Cz, Pz) by Condition (Target pound vs. Non-target Pound) repeated-measures ANOVA determined again that there was a main effect of Site, $F(2,62) = 28.73$, $p < .001$, $\eta_p^2 = .48$, and of Condition, $F(1,31) = 84.30$, $p < .001$, $\eta_p^2 = .73$. Again there was also an interaction between these factors, $F(2,62) = 3.98$, $p = .024$, $\eta_p^2 = .11$. We conducted an additional follow-up using t-tests at each electrode site with a Bonferroni correction and found significant differences in P3 amplitude to target relative to non-target pound signs in all three sites (Fz: $t(31) = 7.07$, $p < .001$, Cz: $t(31) = 7.78$, $p < .001$, Pz: $t(31) = 10.44$, $p < .001$). Fig. 3 shows grand averaged waveforms and the corresponding topographical distribution of the difference in P3 amplitude between target and non-target pound signs during the 300–800 ms time window.

3.3. Source localization analysis

Fig. 4 displays the sLORETA brain maps representing the peak cortical areas that showed activation during each condition. Because these analyses revealed significant and widespread cortical activations, only the peak activations are shown. The MNI coordinates of these regions, their corresponding structures, and t-scores are displayed in Table 1. As expected, these analyses show significant frontal and parietal activations in all conditions corresponding to the P3 time window. Of greater interest to this analysis, however, is the difference in P3 sources between the salient and control letter conditions, and the target and non-target pound sign conditions. The results of these analyses are displayed in Fig. 5 and Table 2. The paired test comparing salient and control letter conditions revealed differences in potential P3 sources originating from the frontal cortex; however, these regions failed to survive multiple comparisons corrections (Peak region showing greater activation for salient relative to control letters was found in the middle frontal gyrus; MNI coordinates: −30, 50, 0; *log of ratio of averages* = .117, $p = .67$).

While control regions tended to be implicated as the source of the P3 in the WM task, this component showed a different pattern of results while monitoring for the target-colored pound sign. A paired test comparing target and non-target pound signs revealed robust significant differences in activation corresponding to the P3 time window. These activations were most robust in regions of the salience network such as the anterior insula (MNI coordinates: 40, 20,10; *log of ratio of averages* = .76; $p < .001$), the temporoparietal junction (MNI coordinates: −40, −65, 15; *log of ratio of averages* = .67; $p < .001$), and the inferior frontal gyrus (MNI coordinates: 45, 20, 15; *log of ratio of averages* = .62; $p < .001$). Peak activations for these contrasts are shown in Fig. 5 and Table 2.

3.4. Brain-behavior relationships

To assess whether P3 amplitude was related to behavior, we calculated a difference wave by subtracting each participants' P3 amplitude during the salient trials minus amplitude during control trials. Similarly, we calculated a difference score using the accuracy data, which we will refer to as an index of salience benefit. A greater positive score in this measure indicates that participants showed better WM accuracy for salient letters, and a smaller or more negative value suggests a potential deficit in processing of the salient letters. We first conducted a simple Pearson Correlation analysis to explore whether P3 amplitude difference was related to behavioral salience benefit. This correlation was not significant, $r = .26$, $p = .16$. However, the size and direction suggest that participants who showed higher P3 amplitude for salient relative to control letters might also show enhanced WM for salient letters (Fig. 6).

Given the potential relationship between P3 amplitude and WM, we conducted an exploratory analysis examining the moderating role of individual differences – specifically, beliefs about one's ability to focus attention as measured by the focusing subscale of the ACS (Quigley et al., 2017; Williams et al., 2017). To investigate this relationship, we conducted a moderated regression analysis (Aiken & West, 1991) using the PROCESS macro in SPSS (Hayes, 2018). Prior to this analysis, P3 amplitude difference and ACS focusing scores were centered by subtracting the mean score from each individual's score. An interaction term was computed by multiplying the resulting centered scores. Finally, these values were entered into a regression model with behavioral salience benefit (i.e., salient minus control accuracy) as the dependent variable. The results of this model indicated that neither ACS focusing ($b = -.003$, $SE_b = .007$, $\beta = -.06$, $p = .72$), nor P3 ($b = .02$, $SE_b = .013$, $\beta = .03$, $p = .87$) were reliable predictors of behavioral salience benefit to accuracy. However, the interaction term was significant ($b = -.01$, $SE_b = .003$, $\beta = -.59$, $p = .002$), suggesting that the relationship between P3 amplitude and behavioral salience benefit depended on participants' perceptions of their ability to focus attention. Fig. 5 shows a graph of this interaction. Simple slopes analyses revealed that participants who reported greater ability to focus attention (1 SD above the mean) appeared to showed an increase in WM benefit to salient letters when their P3 amplitude was also greater for salient relative to control letters ($b = .05$, $t(28) = 2.95$, $p = .006$). Conversely, participants who reported lower ability to focus attention (1 SD below the mean) appeared to perform worse on salient trials when P3 amplitude was greater for salient relative to control letters ($b = -.05$, $t(28) = -2.11$, $p = .04$). In participants who reported average (mean) ability to focus attention, there was no effect of attentional focusing on

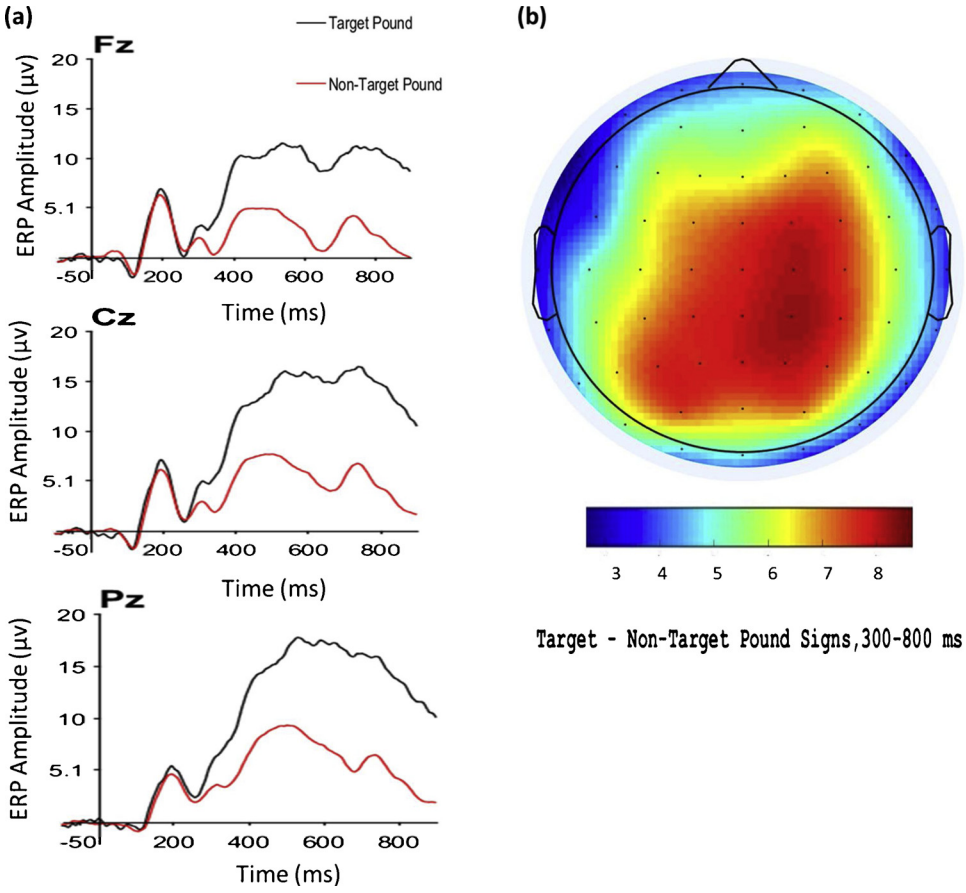

Fig. 3. (A) ERPs for electrode sites Fz, Cz, and Pz during the encoding of target and non-target pound signs. (B) Head map showing the average topographical distribution of the salient minus non-target difference wave from 300 to 800 ms post stimulus (P3).

the relationship between P3 amplitude and behavior (b = .002, t (28) = .16, p = .87).

4. Discussion

The purpose of this experiment was to provide converging evidence using ERP that cognitive control processes, rather than salience detection, underlie the benefits of stimulus-driven attention to WM. Based on previous work investigating other non-spatial attention paradigms (Bledowski et al., 2004; Kranczioch, Debener, & Engel, 2003; Sergent, Baillet, & Dehaene, 2005; Vogel, Luck, & Shapiro, 1998), we predicted that the encoding of contingently salient letters would be accompanied by the enhancement of cognitive control processes evidenced by increased amplitude in the P3 potential. This hypothesis was supported in our data – encoding of salient letters was associated with a larger P3 amplitude than encoding of letters in the control color.

The finding of a larger P3 for salient relative to control letters supports our previous fMRI results, which suggested that the neural mechanisms for the benefits of stimulus-driven attention to contingently salient stimuli were more driven by cognitive control than salience processing (Wills et al., 2016). The parietal P3 potential has been associated with a variety of cognitive control processes related to attention and WM (Azizian & Polich, 2007; Barceló, Periáñez, & Knight, 2002; Debener, Kranczioch, Herrmann, & Engel, 2002; Donchin, 1981; Fabiani, Karis, & Donchin, 1986; Isreal, Chesney, Wickens, & Donchin, 1980). Azizian and Polich (2007) found that higher amplitude in late positive ERPs during encoding was associated with items that were later recalled compared to items that were not. Similarly, Curran (2004) found that devoting full attention to a stimulus during encoding is related to greater memory for that item and increased amplitude in parietal P3 ERP components. P3 amplitude may likewise reflect a measure of resource allocation, with increased amplitude associated with greater task effort and less efficient allocation of attention (Isreal et al., 1980; Kok, 2001; Moore, Gruber, Derose, & Malinowski, 2012).

For the letter conditions in our experiment, the P3 was maximal at parietal electrode sites and is thus consistent with the P3b subcomponent (Bledowski et al., 2004; Polich, 2007). P3b has been associated with successful recognition of target information, top-down attention, response selection, and memory processing including matching stimuli in the environment to memory representations (Bledowski et al., 2004; Brouwer et al., 2013; Devillez et al., 2015; Kok, 2001; Kranczioch et al., 2003; Polich, 2007). We suggest that the enhancement of P3 to contingently salient letters in this paradigm is an index of feature-based target processing, indicating that participants are matching the salient letters to the internal representation of the assigned target for the secondary detection task. It is therefore likely that items presented in the target color receive more attention during encoding as control processes are employed to determine whether the participant should make a target response.

Conversely, during the encoding of target pound signs, P3 amplitude was substantially greater than in any of the other experiment conditions and showed a more widespread topographical distribution. Again, this result is consistent with our previous fMRI work, which demonstrated robust and widespread activation during the encoding of target pound signs (Wills et al., 2016). Taken with the letter results and our previous fMRI results, the current results support a robust target effect for the rare target pound signs. It is unclear whether this effect is indicative of both stimulus-driven attention and cognitive control effects, as we posited in our previous work. However, the current results support the conclusion that the enhancement of attention to the salient

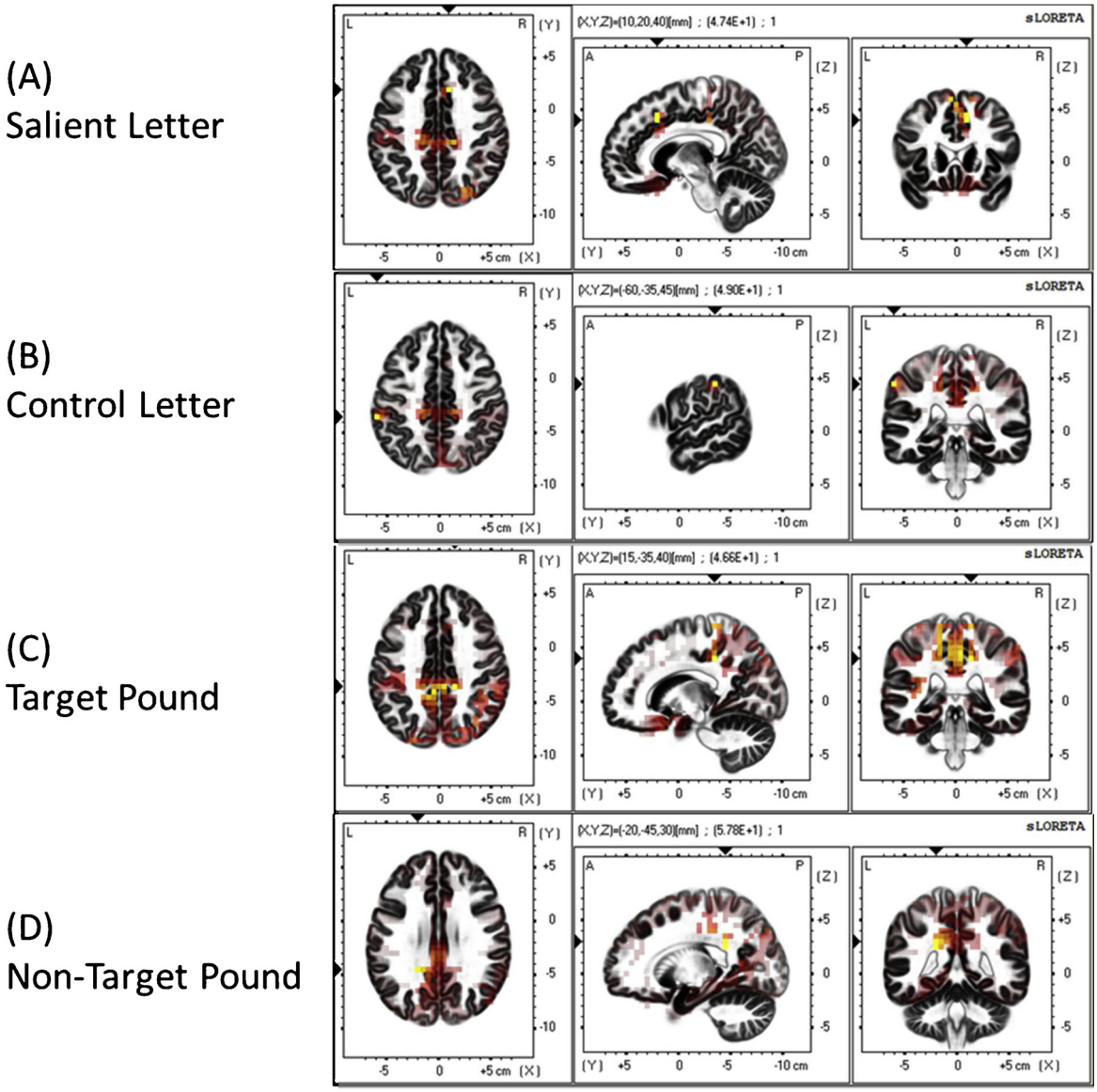

Fig. 4. Separate sLORETA maps for each task condition. Individual analyses revealed widespread activations in each condition, and thus these images are thresholded to display only the peak regions with the greatest sLORETA activations.

letters occurs because of controlled processing from maintaining and matching to the target template held in WM.

Paired tests comparing sLORETA activations for the salient and control letters suggested that the differences in P3 between these conditions might originate from frontal sources, but these results failed to reach significance following multiple comparisons correction. On the other hand, there were robust differences in sLORETA activations for target relative to non-target pound signs. These differences were most pronounced in the anterior insula, which has been associated with the detection of salient information and in initiating appropriate responses to such information (Menon & Uddin, 2010). Furthermore, the temporoparietal junction, a region also implicated in the detection of potentially relevant salient information and subsequent orienting of attention (Corbetta & Shulman, 2002) was also more active for target

Table 1
Peak sLORETA activations in each individual condition.

Condition	MNI Coordinates (X, Y, Z)	Structure	t value
Salient Letter	10, 20, 40	Anterior cingulate gyrus	47.40
	−5, 20, 45	Superior frontal gyrus	46.12
Control Letter	−60, −35, 45	Inferior parietal lobule	49.05
	−15, −30, 60	Precentral gyrus	45.76
	15, −30, 40	Posterior cingulate gyrus	45.62
Target Pound	−20, −45, 25	Posterior cingulate gyrus	58.54
	−20, −45, 30	Precuneus	57.83
Non-Target Pound	15, −35, 40	Posterior cingulate gyrus	46.59
	5, −35, 45	Precuneus	45.83

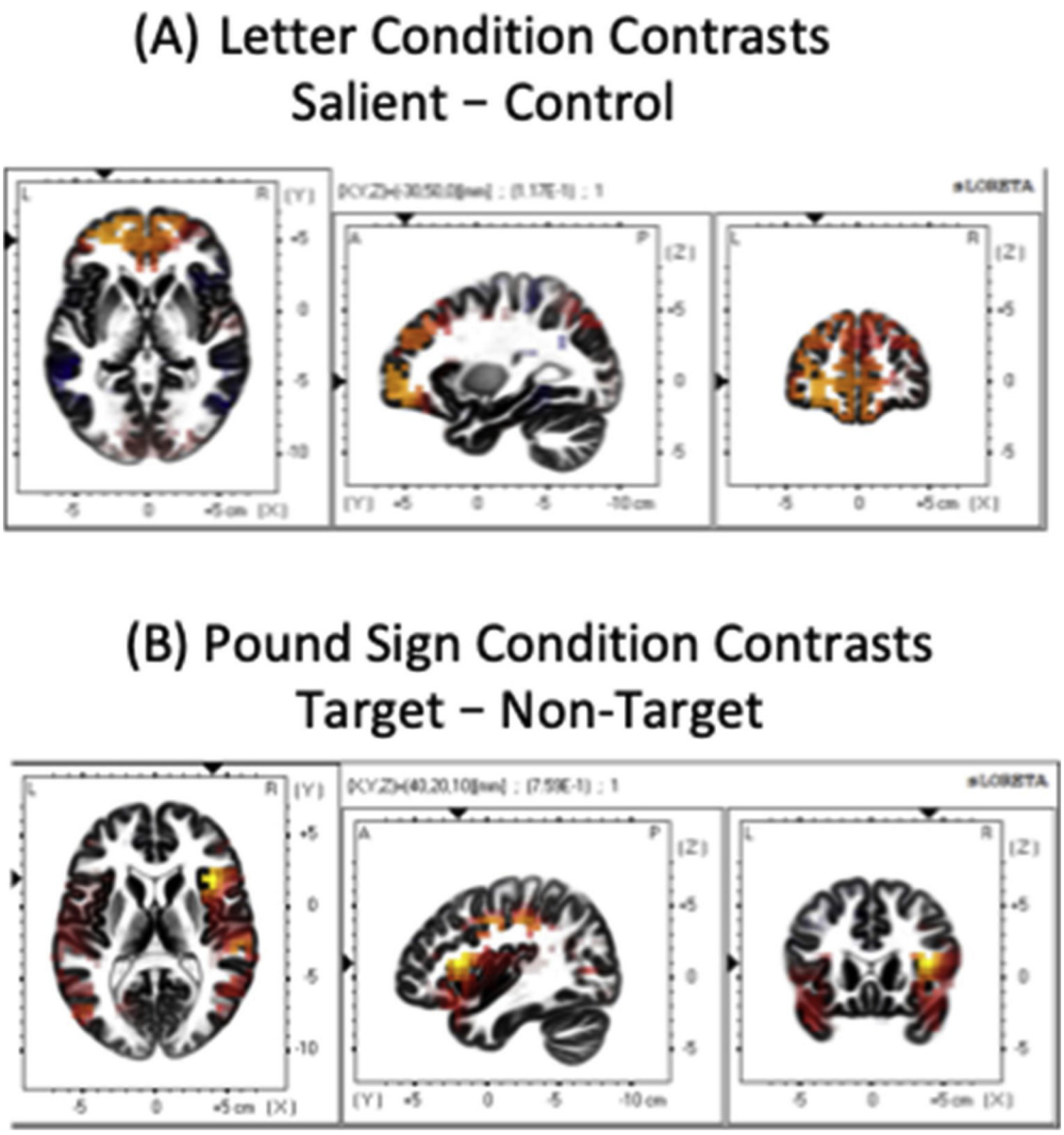

Fig. 5. (A) sLORETA maps of the paired *t*-test comparing salient and control letters. Activations were concentrated in frontal regions but did not reach statistical significance when corrected for multiple comparisons. (B) sLORETA maps of the paired *t*-test comparing target and non-target pound signs. Significant activations were found primarily in the right anterior insula (yellow). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2
Peak coordinates of sLORETA activations corresponding to the paired tests for each contrast of interest.

Contrast	MNI Coordinates (X, Y, Z)	Structure	Log of ratio of averages	P value
Target - Non-Target Pound	40, 20, 10	Anterior insula	.76	< .001
	−40, −65, 15	Temporoparietal junction	.67	< .001
	45, 20, 15	Inferior frontal gyrus	.62	< .001
Salient - Control Letters	−30, 50, 0	Middle frontal gyrus	.117	.67 (n.s)

relative to control pound signs. Greater activation in these regions for target relative to non-target pound signs suggests that there is stimulus-driven attentional capture from salient pound signs. Thus, the large P3 amplitude for target pound signs might be reflective of attentional capture in addition to subsequent evaluative processes stemming from cognitive control. Interestingly, however, this analysis suggested different neural sources for the WM benefit of salience.

These results should be interpreted with caution, however, as there are a number of challenges associated with the localization of ERPs. The use of source localization in EEG and ERP, regardless of the technique chosen, has limitations (for example, localization estimates are modeled based on a number of mathematical parameters and not directly measured like EEG/ERPs; for a detailed discussion of considerations for source localization analysis, see Luck, 2014). Thus, these results reflect one method of estimates for potential generators underlying the P3 potential and should be confirmed using methods with more spatial

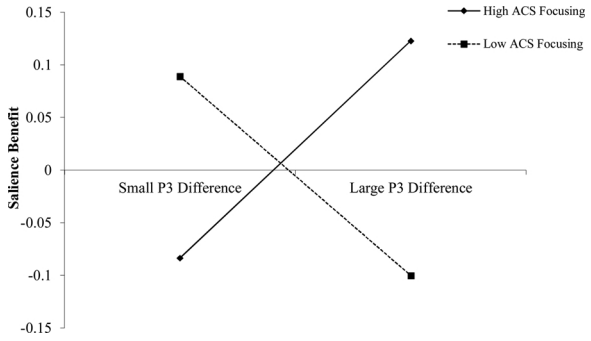

Fig. 6. A figure illustrating the interaction between P3 amplitude difference and ACS focusing in predicting behavioral salience benefit. Large P3 difference means greater P3 amplitude for salient letters, and small P3 difference means greater P3 amplitude for control letters. Positive salience benefit indicates greater memory for salient letters, and negative salience benefit indicates greater memory for control letters. Participants who reported greater ability to focus attention performed better on salient trials when they also had greater P3 amplitude for the salient conditions, whereas participants who reported poor ability to focus performed worse on these trials when P3 was greater for salient letters.

precision. Furthermore, although these analyses imply a role of salience detection regions in detecting targets, paired analyses failed to reveal any differences in these regions or in cognitive control regions that might contribute to the P3 amplitude difference observed during the encoding of contingently salient letters compared to control letters.

Of note, the behavioral data in the current work did not replicate the results of our previous study. We were unable to find evidence that participants remembered the contingently salient letters more accurately than the control colored letters. This result may indicate, as Ravizza et al. (2016) suggested, that the capture of stimulus-driven attention did not improve the quality WM representations for the salient letters, and thus participants were no better at distinguishing the phonologically similar letters despite the additional color cue during encoding. However, we did find evidence in correct trials that participants responded more quickly to the salient trials. The interpretation of reaction time differences in WM retrieval is less clear than accuracy differences, particularly in non-spatial tasks. In spatial WM, faster RT to probes presented in memorized locations is interpreted as evidence that spatial attention has been allocated to these locations during maintenance and processing is thus more efficient (Awh, Jonidies, & Reuter-Lorenz, 1998). In the current non-spatial paradigm, all stimuli were presented in the same location, and thus the enhancement of attention to salient letters during encoding might not reflect increased attention allocation during maintenance and retrieval processes.

Interestingly, only approximately half of our participants responded more accurately to salient relative to control probes. We posit that these results suggest a potential role for individual differences in moderating participants' ability to use contingent salience to improve memory. We made a preliminary attempt to test this hypothesis in our exploratory individual differences analysis examining the potential moderating role of perceived ability to focus attention on the relationship between P3 and WM. This analysis revealed a significant interaction between P3 amplitude differences and focusing in predicting behavioral salience benefits, such that P3 only predicts a benefit to WM for salient stimuli when participants also perceive greater control of attentional focus. This result sheds light on the apparent lack of relationship between P3 during encoding and subsequent WM retrieval by providing preliminary evidence that individual differences may moderate the relationships between brain activity and behavior in this task. However, this result should be interpreted cautiously, as the ACS is thought to reflect beliefs about attention alone and has generally not been related to behavioral measures of attentional control (Quigley et al., 2017; Williams et al., 2017). Future work should seek to clarify the role of individual differences, including perceptions about one's ability to focus and control attention, in the potential benefits of stimulus-driven attention to WM.

In conclusion, the results of the present work indicate that the encoding of contingently salient letters is associated with greater enhancement of cognitive control processes relative to letters of the control color. This is evidenced by a larger parietal P3 wave during the encoding of salient letters, which is thought to reflect control processes such as WM updating, enhanced attention to target information, and response selection. Our findings are consistent with ERP studies of other non-spatial attention paradigms and provide additional evidence that P3 reflects differences in the allocation of attention during encoding that reflect target processing and may be related to WM processing. Although source localization analyses suggested contributions from salience detection regions such as the anterior insula and the temporoparietal junction to the detection of targets, we found no evidence that these regions contribute to the differences in P3 amplitude during the encoding of contingently salient relative to control letters. Exploratory analyses indicated the association between these neural cognitive control mechanisms and WM benefits from stimulus-driven attention may be moderated by individual differences in participants' beliefs about their ability to focus attention. Overall, these results corroborate our previous fMRI work and suggest that the enhancement of processes related to cognitive control and matching of information to targets maintained in WM may underlie any benefits to WM from stimulus-driven attention drawn to contingently salient information.

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