Updating of context in working memory: An event-related potential study

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Flexible control of behavior depends on the representation, maintenance, and updating of context information in working memory, which is thought to rely on the prefrontal cortex (PFC). However, in contrast to maintenance, the dynamics of context activation and updating have not been well studied. To identify neural signals associated with context updating, we compared event-related potentials associated with cues that did or did not provide task-relevant context information. The earliest effect of context was detected 200 msec following cue onset and had a scalp topography consistent with a generator in the PFC. Subsequent effects of context were detected at 400–700 msec following cue onset (P3b), with a broad scalp distribution spanning posterior areas, and during the final 300 msec preceding the target, with a probable generator in the medial frontal cortex. We propose that the effect of context on P2 is consistent with the onset of context updating in the PFC. Subsequent components may be indicative of activation of task-relevant posterior regions and context maintenance.

Cognitive control, the ability to flexibly direct behavior in accordance with a behavioral goal, depends on the brain's ability to represent, maintain, and update the rules that guide behavior in a contextually appropriate manner (Miller & Cohen, 2001). For example, when a telephone ring is heard at home, it is appropriate to answer it. However, the same stimulus at a stranger's house should usually elicit a different response. In this example, external cues contribute context information that can be used to select the appropriate rule and guide behavior accordingly. However, under other circumstances, appropriate behavior must rely more heavily (or even entirely) on internal representations. For example, when one drives in a familiar environment, whether to make a left or a right at an intersection depends entirely on one's goal (e.g., whether one is headed home or to the grocery store). Furthermore, such internal representations must be able to be updated flexibly in accord with behavioral goals (e.g., receiving a request to stop at the grocery store on the way home). We refer to the internally represented information needed to select and guide appropriate behavior as internal representations of context, or more simply, *context representations*. These may include actively represented information about prior or current stimuli, as well as more abstract information, such as instructions, rules, or goals, that are required to guide behavior in accord with current demands. We consider such context representations to be an important form of information that can be maintained in working memory and, thus, rely on similar mechanisms.¹

Once context representations have been activated in response to external stimuli and/or retrieved from episodic

memory, they must be actively maintained in order to exert influence over processing in the service of achieving temporally extended behavioral goals. From this perspective, the active maintenance of context representations can be viewed as a critical function of working memory in executive function and cognitive control. In this regard, the representation of context can be viewed as a critical component of the traditional concept of controlled processing, which relies on the top-down influence of an *attentional template* or *task instruction*, both forms of context representations. Conversely, under conditions in which stimuli in the environment fully determine the necessary response (e.g., when there is a consistent mapping between stimulus and response), performance can proceed relatively independently of the top-down control provided by context representations and come to rely on more direct, automatic processing (e.g., Cohen, Dunbar, & McClelland, 1990; Schneider & Shiffrin, 1977). That is, under such conditions, performance does not rely on the representation of context.

Dynamics of Context Updating

We can define three component processes that must be engaged whenever task context changes: (1) detection of the change in context, (2) activation of a representation of the new context, and (3) use of this information to reconfigure the mechanisms responsible for performing the new task. This analysis closely parallels discussions in the task-switching literature. Indeed, context updating is central to task switching: Context updating is required whenever task instructions change or when subjects' attention

is interrupted by a distraction. The former occurs at least once in all psychological experiments (at the beginning) but is more directly manipulated using task-switching paradigms (Monsell, 2003), in which stimulus-response (S-R) mappings change repeatedly and under the experimenter's control. In such paradigms, a set of stimuli is usually associated with multiple rules for responding, and a change in task context is signaled either explicitly by a cue that precedes stimulus presentation or by trial order. Although context updating must occur whenever the task switches, it may also occur within repetitions of a task—for instance, following lapses of attention.

The Role of the Prefrontal Cortex in Context Updating

There is a large and growing body of evidence that implicates regions of the prefrontal cortex (PFC) in context processing. Traditionally, this research has focused on the role of the PFC in actively maintaining context representations in working memory and on their influence on task performance (Bunge, 2004; D'Esposito, 2007; Passingham & Sakai, 2004; Stoet & Snyder, 2009; Yeung, Nystrom, Aronson, & Cohen, 2006). This was described by Miller and Cohen (2001) in the guided activation theory of PFC function. This theory proposes that patterns of neural activity maintained in the PFC represent context and that this neural activity biases posterior neocortical pathways responsible for task execution by guiding the flow of activity along those pathways that implement task-appropriate S-R mappings. Extensions of this theory have proposed that phasic dopamine responses serve to update context representations in the PFC, by gating new representations into the PFC when cues are detected in the environment that signal a need to change context (Braver & Cohen, 2000; Frank, Loughry, & O'Reilly, 2001). This suggests that a transient electrophysiological signal might be detected over the PFC, associated with the change in context as new inputs arrive and produce a new pattern of neural activity. For example, such a signal would be expected to occur following cues that signal task switches in a task-switching paradigm. Furthermore, because context updating within the PFC should initiate a reconfiguration of processing pathways needed to perform the new task, an additional prediction is that a signal reflecting context updating within the PFC should be followed by activity changes in the posterior cortical pathways responsible for task performance. For instance, during a cued task switch, PFC activation may be followed by reconfiguration of activity in the parietal and/or motor cortex as a new set of S-R mappings are activated for the upcoming task. For clarity, we restrict use of the term *context updating* to refer to the process of updating context representations in the PFC. Following usage in the task-switching literature, we use the term *task reconfiguration* to refer to the updating both of context information in the PFC and of representations in other neural systems required to perform the specified task.

Despite progress in developing theoretical models of the neural mechanisms underlying task reconfiguration

(e.g., Brown, Reynolds, & Braver, 2007; O'Reilly, Noelle, Braver, & Cohen, 2002; Reynolds, Braver, Brown, & Van der Stigchel, 2006), there is relatively little empirical evidence bearing on these mechanisms. The purpose of the present study was to seek electrophysiological evidence for context updating in the PFC, in order to identify the time course and scalp distribution of this process and its relationship to other task reconfiguration processes.

EEG Components Sensitive to Task Switching

Electroencephalography studies of task switching have reported changes in event-related potentials (ERPs) that are consistent with task reconfiguration in posterior regions of the cortex. However, findings with a preceding, frontally generated component consistent with the onset of context updating within the PFC have been inconsistent.

The most reliable effect of task switching in the EEG has been an increase in a posterior positivity (Asthle, Jackson, & Swainson, 2006, 2008a, 2008b; Karayanidis, Coltheart, Michie, & Murphy, 2003; Kieffaber & Hetrick, 2005; Nicholson, Karayanidis, Bumak, Poboka, & Michie, 2006; Nicholson, Karayanidis, Poboka, Heathcote, & Michie, 2005; Rushworth, Passingham, & Nobre, 2002, 2005; Swainson, Jackson, & Jackson, 2006; Wylie, Javitt, & Foxe, 2003). This positive component has been observed to be maximal over centroparietal electrodes with a time range of 300–500 msec. This potential increases in amplitude more in response to cues that signal switch trials than to cues that signal repeat trials and is more reliable when advance information about the upcoming task is available (Nicholson, Karayanidis, Davies, & Michie, 2006; Swainson et al., 2006). This is consistent with the interpretation of this posterior positivity as a component of the P300 and its relationship to context updating as originally proposed by Donchin and Coles (1988). However, it may not reflect context updating in the more specific sense of the term, as we use it here: the updating of context representations in the PFC. Rather, the posterior positivity may reflect task reconfiguration processes in posterior pathways that are subsequent to context updating in the PFC. Findings in the literature are consistent with this view.

For example, the scalp topography of a component commonly observed in task-switching paradigms, the P3b, is typically centered over central and posterior electrodes, and its estimated sources are broad (Bledowski et al., 2004; Halgren, Marinkovic, & Chauvel, 1998; Linden, 2005; Mulert et al., 2004). They include the inferior parietal lobe (temporoparietal junction), the supplementary motor cortex, the anterior cingulate, the inferior and superior temporal gyrus, as well as the insula, and, in some cases, the hippocampus, in addition to the lateral PFC. Furthermore, the onset of the P3b (300–400 msec) lags behind reported effects of attention in the PFC. These observations are consistent with the interpretation of the posterior positivity as reflecting the effects of task reconfiguration within posterior pathways in response to context updating in the PFC. This is supported by findings from a number of recent studies that have reported more anterior electrophysiological signals that precede the posterior positivity.

For example, differential activity for task-relevant versus task-irrelevant stimuli has been detected in frontal regions within 200 msec of stimulus onset in neuronal recordings (Halgren et al., 1994; Rainer, Asaad, & Miller, 1998), as well as measurements of scalp electrical activity (Foxe, Simpson, Ahlfors, & Saron, 2005; Luck & Hillyard, 1994) and scalp magnetic fields (Bar, 2003; Bar et al., 2006; Perianez et al., 2004). More specifically, a switch-related ERP component following cues was reported by Astle et al. (2008a, 2008b), who observed an *early anterior positivity* that started between 150 and 200 msec following cue onset, and by Nicholson et al. (2005; see their Figure 4 and Table 1), who found a component within 100 msec of cue onset. Astle et al. (2008b) related this effect to “some aspect of cue-processing” that was reflective of “detecting the switch pre-cues as being particularly important” (p. 1414; see also Kieffaber & Hetrick, 2005). Karayanidis et al. (2003), using an alternating-runs paradigm, detected similar effects 100–200 msec following events (see also Barcelo, Escera, Corral, & Perianez, 2006; Lavric, Mizon, & Monsell, 2008). These findings are consistent with the prediction that context updating should be associated with a frontally distributed electrophysiological signal and that this should precede more posteriorly distributed signals associated with subsequent task reconfiguration processes. However, such findings have not been consistent in the task-switching literature. In some studies, no switch-related differences were observed prior to P3b (Wylie et al., 2003; Wylie, Murray, Javitt, & Foxe, 2009). It has also been difficult to determine whether the anterior distribution of the potentials discussed above reflects a frontal source.

In summary, although potentials have been reported that have spatiotemporal characteristics consistent with context updating in the PFC, these findings have not been consistent across studies, and their cortical generators have not been confirmed. To our knowledge, no previous studies have sought specifically to identify electrophysiological correlates of context updating in the PFC. This was the purpose of the present study.

The Present Study

We sought to test directly the prediction that frontally distributed potentials should precede the P3b and be systematically related to context updating. To do so, we used the simplest task that requires context updating, a variant of the continuous performance task (CPT; Rosvold, Mirsky, Sarason, Bransome, & Beck, 1956) that is closely related to but simpler than most task-switching paradigms. In the standard version of the CPT, subjects view a continuous stream of letters and respond to specified targets with a buttonpress. In AX-CPT variants of the task, however, the response to the target is contingent on the previous stimulus. For example, in one version, subjects are instructed to respond with a buttonpress whenever a target is detected (e.g., the letter “X”), but only when it follows a particular cue (e.g., the letter “A”). Thus, the response to a target (e.g., buttonpress to X) is contingent on the context provided by a preceding cue (e.g., A or

non-A), and each appearance of a cue should elicit context updating. Typically, such cue–target sequences are embedded within a stream of stimuli that carry no contextual information and do not require a response. Like cues, these *control* stimuli must be encoded (in order to know whether or not they are a cue), but unlike cues, they do not provide any information needed for processing subsequent stimuli. Accordingly, these control stimuli should not elicit context updating (since there is no context to represent). Thus, a comparison between cues and control stimuli should provide a useful contrast for identifying signals related to context updating.

Such a contrast may be more reliable than the ones that have been used in previous task-switching studies. As was noted above, contrasting switch and repeat trials has produced inconsistent results with regard to potentials preceding the posterior positivity (Brass, Ullsperger, Knoesche, von Cramon, & Phillips, 2005; Rushworth, Passingham, & Nobre, 2002, 2005; Wylie et al., 2003). This inconsistency may be due to the assumption that, in task-switching paradigms, context is updated only on switch trials and is simply maintained (from the previous trial) on repeats. However, this may not always be so. Depending on task conditions (e.g., trial sequence, intertrial interval, emphasis on accuracy), subjects might choose to (re)activate context on some or all repetition trials as a strategy to avoid maintenance costs or maximize accuracy, or they may be forced to do so because of a distraction following the previous trial (Rushworth, Hadland, Paus, & Sipila, 2002; Todd, Niv, & Cohen, 2009; Wylie & Allport, 2000). Consequently, context updating could occur on repeat as well as switch trials, minimizing the switch–repeat differential and compromising its reliability across studies. In contrast, the comparison between cues and control stimuli in the AX-CPT task should be more reliable, because cues always require context updating, whereas control stimuli neither require a response nor provide information that bears on any subsequent response. Accordingly, in the present study, we used the AX-CPT to explicitly control the conditions under which context updating was required.

We used a version of the AX-CPT in which cue–target pairs were imbedded in sequences of control stimuli and varied the dependency of target response on the preceding cue in order to manipulate the likelihood that subjects would engage in context updating. To make the task more consistent with task-switching paradigms, we used a two-alternative forced choice design for responses.² On context-dependent trials, the cue played the same role as the instructions in an exogenously cued task-switching paradigm, specifying the response rule for the upcoming target. For instance, following an “A,” the subjects were required to press the right button for an “X” and the left button for a “Y,” and following a “B,” these rules were reversed. Thus, on such trials, cues should have triggered context updating to ensure that the correct rules were applied in responding to the subsequent target. In these respects, context-dependent trials were comparable to trials in an instructed (exogenously cued) task-switching paradigm; cue switches (e.g., A–X

followed by B–X or B–Y) were analogous to switch trials, and cue repetitions (e.g., A–X followed by A–X or A–Y) were analogous to repeat trials.

These context-dependent trials were compared with two other types of trials. Context-independent trials paralleled context-dependent trials in all respects, except that response to the target was *not* contingent on the preceding cue. For instance, following a “C” or “D” cue, the subjects would see a “W” or “Z” target but would always be required to press left for a “W” and right for a “Z.” Thus, on these trials, the target–response contingency was the same, irrespective of the preceding cue. In other words, the subjects could make the correct response on the basis of target identity only, without relying on the preceding context. It should be noted that the subjects could still use the context provided by the cue to prepare for the upcoming target, by reminding themselves of the target–response rule. However, with practice, we would expect the subjects to learn these simple and consistently mapped target–response associations and come to respond automatically to the target, without relying on the context provided by the cue (Cohen et al., 1990; Schneider & Shiffrin, 1977). Therefore, we expected that these trials would be associated with substantially less context updating than would context-dependent trials.

Finally, we included a set of control trials, in which stimuli were random single letters interleaved among the cue–target pairs of the context-dependent and context-independent trials. These stimuli did not require any response. The subjects had to visually and semantically encode these stimuli in order to determine their identity, in order to know not to respond; however, they were not associated with any future response rule. It was possible that during early performance, the subjects might activate a context representation indicating that they were not to respond to these stimuli. However, again, as with the context-independent targets, we expect that with practice, the subjects would come to automatically recognize that they did not need to respond to these stimuli. Thus, we did not expect control stimuli to trigger context updating.

In summary, to identify the onset of context updating, we compared the effects of cue processing during context-dependent trials with those of cue processing during context-independent trials and with those of processing of control stimuli. We predicted that these comparisons would reflect a progressive decrease in the likelihood of context updating during cue processing and that a parallel effect in voltage potentials would index the engagement of this process. More specifically, we predicted that the onset of such changes would indicate the onset of context updating and that its scalp distribution would be maximal over frontal electrodes. We show that the first effect of context updating occurred at approximately 200 msec following cue onset and preceding cue offset. It occurred over frontal electrodes, and its scalp distribution was consistent with a source in the PFC. Additional effects were observed 400–700 msec after cue onset, distributed over posterior electrodes (P3b), and from 700 msec until response onset, distributed over frontal electrodes. We interpret these ef-

fects as reflecting the influence that context updating in the PFC has on reconfiguring posterior mechanisms responsible for task execution.

METHOD

Subjects

Sixteen students (age: $M = 23$ years, $SD = 4.8$; 7 women) participated in the study and were reimbursed \$30 for their time. This study was approved by the Institutional Review Panel for Human Subjects at Princeton University. All the subjects provided written, informed consent prior to participation.

Behavioral Task

The subjects performed a variant of the AX–CPT, in which they viewed a continuous stream of letters and responded to selected targets with a specified buttonpress. There were three types of trials embedded within the letter stream: context dependent (c-dep) and context independent (c-ind), both of which involved cue–target pairs (cued trials), and control trials, which involved a single letter.

Letter stimuli for cued trials (sampled from the set: “A,” “B,” “X,” “Y,” “C,” “D,” “W,” and “Z”) were randomly assigned across subjects as cues or targets. In c-dep trials, as in standard versions of the AX–CPT, the cue letter (e.g., an “A” or a “B”) served as a context that determined how the subject should respond to the subsequent target. For example, if “A” and “B” were assigned as cues and “X” and “Y” as targets, an “A” followed by an “X” might have required a left buttonpress, in which case a “B” followed by an “X” would require a right buttonpress, and the converse set of rules applied to the “Y” target. Thus, for c-dep trials, the response to the target letter was undetermined (e.g., whether to respond left or right to an “X”). Accurate performance required that the subject encode the cue and use this to actively update and maintain a representation of the context it provided, in order to respond correctly to the target.

Context-independent trials also involved a specified (but different) set of letters as cues (e.g., “C” or “D”) and targets (e.g., “W” or “Z”). However, on these trials, each target letter was always associated with the same response (e.g., a left buttonpress for the letter “W” and a right buttonpress for the letter “Z”), irrespective of the preceding cue. Thus, the cue provided the information that a “W” or “Z” would appear next, which could be used to prepare for the ensuing target (i.e., configure the S–R mappings for the two possible targets). However, this was not required for accurate performance, since the correct response was fully determined by the target itself when it appeared. We expected that once the subjects were practiced in the task, responding to these targets would become automatic, relying less on advance preparation and, therefore, context updating.

Control trials comprised a single letter (sampled from the set: “M,” “K,” “H,” or “L”)³ and did not require any response. The subjects simply had to identify the letter and determine that it was not part of a c-dep or c-ind trial. As with c-ind trials, we expected that as the subjects became practiced in the task, these processes would become relatively automatic and, therefore, would not engage context updating.

A sample trial sequence is presented in Figure 1. Stimuli were displayed one at a time in Courier New 28-point boldface, white on a black background, on a monitor at an approximately 1-m viewing distance (subtending about 0.5° of visual angle). On cued (c-dep and c-ind) trials, the cue was presented for 250 msec, followed by a blank interstimulus interval (ISI) and then a target letter that remained on the screen for 1,000 msec or until a response was made. The target was followed by another ISI. The ISI averaged 1,000 msec across trials but was varied between 750 and 1,250 msec to prevent the subjects from anticipating the timing of the next stimulus. Responses were made using a two-button response mouse (Model Series 2-7S; Logitech, Fremont, CA). Feedback was displayed beneath the target

Figure 1. Subjects were presented with sequences of letters in which two types of cued trials, composed of a cue (i.e., context) and a target, were embedded within control stimuli. During context-dependent (c-dep) trials, response selection was dependent on cue identity. During context-independent (c-ind) trials, response selection was independent of cue identity. To evaluate context updating, event-related potential responses to context cues were compared with one another and those to control stimuli, which neither required a response nor predicted the next stimulus. ISI, interstimulus interval.

stimulus for 200 msec in the case of errors (“Too Slow” or “Wrong Key”). On control trials, a cue letter appeared for 250 msec and was followed by a blank ISI.

The session was composed of a total of 1,920 trials: 50% cued trials and 50% control trials, to keep the likelihood of a cue–target sequence at chance.⁴ However, this produced twice as many control trials as each type of cued trial (c-dep and c-ind). To correct for this imbalance, analyses were conducted by randomly splitting the control trials into two equivalent groups and treating the design as a one-factor design with four levels (c-dep, c-ind, Control 1, and Control 2). Trials were presented in 40 blocks of 48 trials, with trial type varied in a pseudorandom, balanced fashion within each block. Only correct trials were analyzed. Trials at the beginning of a block and following incorrect responses were also excluded, as were trials contaminated by transient activity artifacts (see the EEG Recording and Data Processing section). An average of 380 trials (80%) per condition was retained across subjects. All the subjects were retained for analysis.

Procedure

Experiment presentation was controlled by E-Prime (Version 1.1 SP3, Psychology Software Tools, Pittsburgh, PA). The session started with three blocks of practice: The subjects first trained on each of the context conditions separately and then practiced the combined se-

quence. The latter was repeated as necessary to achieve proficiency (>80% accuracy). Behavioral and EEG data were recorded during the subsequent testing session. To control fatigue, breaks of 1 min were mandatory every five blocks. The testing session lasted approximately 80 min.

EEG Recording and Data Processing

EEG data were recorded via Ag–AgCl scalp electrodes embedded in an 87-electrode fabric cap (Electro-Cap International, Eaton, OH) arranged according to the extended 10–20 system. Data were digitized at 1000 Hz (band-pass filtered from 0.02 to 300 Hz; impedances, <40 k Ω) and were amplified by a gain of 10,000 with a 12-bit processor using Sensorium (Model EPA-6, Charlotte, VT) amplifiers, with 1-G Ω input impedance. Acquisition was controlled by Cogniscan (Version 2.22, EJC Systems, Newfoundland, NJ) software. Additional electrodes (impedances, <10 k Ω) included the electrode common placed on the chin, physical reference on the right mastoid, and vertical electrooculogram below the left eye. All electrode recordings were originally referenced offline to an electrode placed on the left mastoid but were subsequently rereferenced to a common average to facilitate source localization. Digital tags were obtained for cue and target stimuli. ERP epochs were constructed offline. For data screening and visualization (EMSE Suite Version 5.0, Source Signal Imaging, San Diego, CA), on cued trials, event epochs were defined as lasting from 250 msec before the cue stimulus to 2,750 msec following, in order to capture cue and targets. On control trials, recording began 250 msec before and ended 1,000 msec following the stimulus. However, in both cases, analyses were conducted only up to 1,000 msec following cue or control stimulus onset. Trials with blinks, eye or muscle movements, and signal drift were removed offline. The remaining epochs were low-pass filtered (20 Hz), normalized to the 250-msec precue baseline, and averaged across subjects for each of the context and control conditions.

ERP Analysis

The averaged epochs, or ERPs, were analyzed for the 10–20 system electrodes (FP1, FP2, F7, F3, Fz, F4, F8, T7, C3, Cz, C4, T8, P7, P3, Pz, P4, P8, O1, O2), as well as for AFz and Oz to complete the midline, for a total of 21 electrodes. We analyzed all time points from 250 msec preceding the cue onset to 1,000 msec following the cue (cue epochs), using partial least squares (PLS) analysis implemented in MATLAB (Version 7.4, The MathWorks, Natick, MA), a multivariate analysis that allowed us to simultaneously evaluate the spatial and temporal distribution of ERP differences, relative to experimental manipulations (for a full description, see Lobaugh, West, & McIntosh, 2001).

To do so, a matrix was constructed containing a baseline-normalized voltage signal in each cell, with electrodes at all time points in columns and the four experimental conditions in rows. A deviation matrix, reflecting covariation between voltage and condition, was computed by subtracting the grand mean in each column from the task mean in each condition (i.e., row). The deviation matrix was analyzed by singular value decomposition to produce four orthogonal latent variables (LVs) that described spatiotemporal profiles (electrodes and time points) that best distinguished between the experimental conditions (c-dep, c-ind, control). Each LV was composed of a set of weights (salience) for each electrode and condition (i.e., identifying the combination of electrodes and time points that showed similar effects across some combination of conditions), as well as a scalar (singular value) proportional to the amount of covariation accounted for by that LV. In the present work, we sought to identify those voxels at the time points at which voltage signal increased as a function of the context provided by the cue. A context effect would show the strongest signal (and salience in the LV) for c-dep cues, followed by c-ind cues and then control stimuli.

Statistical assessment of these results was conducted by first establishing a statistical threshold to decide how many LVs to re-

tain for interpretation. The LVs were tested for significance, using permutation testing (Nichols & Holmes, 2001), by calculating the probability of obtaining their observed singular value (percentage of covariation they accounted for) by chance. Second, within significant LVs, the standard error for each salience was estimated by bootstrap resampling (Efron & Tibshirani, 1986) and was compared with the magnitude of the salience to obtain a bootstrap ratio (BR, salience divided by its standard error). Unless otherwise indicated, saliences that were three times greater in magnitude than their standard error were considered reliable and, thus, retained for interpretation (Lobaugh et al., 2001). The number of permutation samples was set at 500, and the number of bootstrap samples was set at 100 (Lobaugh et al., 2001).

Univariate post hoc analyses were conducted on the mean amplitude of ERPs within those intervals showing significant effects as identified by the multivariate analysis.

Scalp current density and distributed source analysis. Two methods were employed to examine the intracranial signal generators: scalp current density (SCD) and distributed source analysis as implemented in EMSE Suite (Version 5.0, Source Signal Imaging, San Diego, CA). SCD maps were calculated from the spherical spline interpolation of the surface voltage recordings. These provided an estimate of the local radial current (A/m^2) while simultaneously eliminating (by spatially filtering) the contribution of the tangential current spread due to volume conduction (Nunez et al., 1994) and were used for improved topographical visualization and as a reference for the source analysis.

For the distributed source analysis, we used a template-based realistic head model to constrain the forward solution and standardized low-resolution brain electromagnetic tomography (sLORETA; Pascual-Marqui, 2002) to generate the transformation matrix. The head model was created from a T1-weighted MNI152 average brain (www.bic.mni.mcgill.ca). This image was coregistered to match electrode locations, digitized (Fastrak, Polhemus, 5DT, Colchester, VT) for 1 subject using a least-squares fit to electrode (scalp) positions and three fiducial points (left and right preauricular points, nasion). A finite element model, modeling CSF, gray and white matter, skull (bone), and head (muscle) (conductivities: 1.79, 0.33, 0.2, 0.0132, and 0.35 S/m), was then constructed from segmented regions of this coregistered anatomical image. The transformation matrix was then generated using sLORETA. Source localization was performed for each condition within each subject, at the peak of each time interval identified as significantly distinguishing context versus control in the previous PLS analysis. Note that because sLORETA standardizes current density estimates by measurement noise, as well as by prior source variances, the resultant source maps contain arbitrary scores rather than estimates of current density per unit volume ($A\cdot m/m^3$) as does LORETA. We would also like to emphasize that the sLORETA merely provides a model of the internal distribution of current, and the margin of error is unknown. Thus, the source localization results should be interpreted in the context of other literature.

Statistical analysis of the source solutions (for each condition within each subject, at each interval of interest) was based on the protocol of Park et al. (2002). The source maps were converted into the original space of the T1 image (2-mm resolution) for voxel-based image analysis (AFNI, <http://afni.nimh.nih.gov/afni/>; see Cox, 1996). The images were convolved with a 6-mm full-width half-maximum isotropic Gaussian filter to accommodate variations in source coordinates across subjects and were transformed into a standard stereotactic anatomical space (Talairach & Tournoux, 1988). Global signal variation between subjects and conditions was eliminated by grand mean scaling within each subject. These maps were analyzed using a mixed-effects ANOVA with task (c-dep, c-ind, control) as a fixed variable and subject as a random variable. To correct for multiple comparisons, the statistical threshold was divided by the number of measurements. A p value of .00065 (i.e., 77 channels used for sLORETA) was used as threshold to ensure a familywise error

rate of .05 (Grave de Peralta Menendez, Murray, Michel, Martuzzi, & Gonzalez Andino, 2004).

RESULTS

Behavior

Response time (RT) was comparable across cued trial targets [c-dep, 477 msec vs. c-ind, 476 msec; $t(15) < 1$]. However, accuracy was lower for c-dep than for c-ind trials [89% vs. 94%, respectively; $t(15) = 3.32$, $p < .01$, two-tailed]. This differential may have reflected occasional failure to maintain context during preparation on c-dep trials (de Jong, 2000), which would compromise response selection on these, but not c-ind, trials.

ERP Analysis

PLS components. The PLS analysis produced one significant LV ($p < .01$) accounting for 96% of the cova-

Figure 2. Saliencies (see the text for details) are shown for both trial condition and electrodes across time on the first and only significant latent variable (LV) produced by the partial least squares analysis of the cue epoch. The condition saliencies (top) show the experimental effect captured by this LV. Electrode and time saliencies corresponding to this effect are shown below for four midline electrodes (Fz frontal, Cz central, Pz posterior, Oz occipital). The gray bars indicate the intervals in which the bootstrap ratio (saliency/standard error) was greater than three. The black bars indicate cue duration and target onset. ERPs showing these effects are shown in Figure 3.

Figure 3. Event-related potentials for midline electrodes (see the Appendix for laterality effects) during the cue epoch confirm the effects described by the saliences in Latent Variable 1 (Figure 2). Black horizontal bars indicate onset and duration of cue (0–250 msec) and target (1,000+ msec). Note that since the interstimulus interval was variable (750–1,000 msec), the waveform is contaminated by noise at time points greater than 1,000 msec following cue onset. Shading indicates intervals showing reliable differences between saliences, as assessed through bootstrap resampling and confirmed by univariate analyses. Three time windows show the effects of context: Frontal electrodes show this effect at a peak around 200 msec and, again, as a late slow negativity; posterior electrodes show the same effect midway through the interval, at P3b.

riation in the deviation matrix. This component identified electrodes and time points showing a significant effect of context (Figure 2), suggesting that our manipulation was effective. The ERPs for selected electrodes showing the identified experimental effect are shown in Figure 3. This component captured both a difference between cued and control trials and a difference between c-dep and c-ind trials. More specifically, the condition saliences (Figure 2) showed a gradient of decreasing values from the c-dep to the c-ind condition to the control trials. This effect was reliable (i.e., $BR > 3.0$; Figure 2) at three different time intervals following cue onset, each with a distinct spatial distribution (Figure 2; see Figure 3 for ERPs).

These statistical effects can be qualified as follows. The first detectable difference between cued and control trials occurred at frontal electrodes in the interval of 200–288 msec following cue onset. This positive peak (P2) difference was reliable (i.e., $BR > 3.0$; Figure 2) in frontopolar, frontal, and central electrodes and was strongest at the midline. A second positive peak, corresponding to the P3b potential, was detected at posterior and occipital electrodes. The difference between cued and control trials was reliable (i.e., $BR > 3.0$; Figure 2) at 400–700 msec post-cue-onset. Finally, a late slow negative potential (SW_{neg}) was detected following 700 msec and lasted until target/response onset. As at the P2, this effect was reliable (i.e., $BR > 3.0$; Figure 2) across frontal and central electrodes, but not at parietal or occipital electrodes.

Paired *t* tests (two-tailed) on mean ERP amplitude during each of the three intervals at the specified electrodes confirmed that the signal was strongest for c-dep trials, followed by c-ind trials [c-dep > c-ind; $t(15) > 1.85$, $p < .04$] and finally control trials [c-ind > control; $t(15) > 2.19$, $p < .05$]. No differences were detected between control conditions [$t(15) < 1.36$, $p > .19$]. A confirmatory repeated measures ANOVA on ERP amplitude, which included a test on laterality effects, is presented in the Appendix.

Sequence effects on P2. The results reported above focused on the contrast between c-dep and c-ind trials, on the assumption that the former more reliably engaged the updating of context than did the latter. This contrast revealed a frontal distributed positivity (P2) during cue processing that was greater in c-dep than in c-ind trials, consistent with the hypothesis that this signal reflects context updating in the PFC. However, the design of our experiment permits a more detailed test of this hypothesis, paralleling the analysis of sequence effects in task-switching experiments.

In our design, sequences of c-dep trials most closely paralleled those of a task-switching experiment: Sequences in which the cue switched from one trial to the next (e.g., A–X/Y followed by B–X/Y or vice versa) involved a change in the S–R mapping, paralleling switch trials in a task-switching experiment. Similarly, sequences in which the cue was the same (e.g., A–X/Y followed by A–X/Y, and similarly for the B cue) were akin to repeat trials. In contrast, in sequences of c-ind trials, cue switches (e.g., between C and D) did not involve a change in S–R map-

ping and, thus, should not elicit context updating. Thus, comparing switches within sequences of c-dep versus c-ind trials should isolate the effects of context updating from the effects of a switch in cue (without a change in context).

To test for these effects, we conducted a repeated measures ANOVA on responses to the cue in the second trial of sequences of either c-dep or c-ind trials, involving either a switch or a repeat of the cue; this reduced the number of trials in each condition to 47, on average. We included three factors: trial type (c-dep vs. c-ind), sequence type (switch vs. repeat), and electrode (Fz vs. Cz). For the dependent measure, we first identified the latency of the peak amplitude in the P2 waveform averaged separately for each cell in the design. The amplitude at this latency was then identified for each subject, and these data were entered into the analysis. If context updating occurs for c-dep but not c-ind trials, and, among c-dep trials, for switch but not repeat sequences, we would expect an interaction between the trial type and sequence type factors, with c-dep switch trials associated with a greater P2 than the other three conditions. The results of this analysis are presented in Table A1 and Figure 4. It revealed a trend for the main effect of context [$F(1,15) = 2.1$, $p = .17$], with P2 peak amplitude being greater during c-dep trials ($3.35 \mu V$) than during c-ind trials ($2.59 \mu V$). This echoes the finding of our primary analysis comparing all c-dep and c-ind trials, albeit with reduced power. The only other significant effect was the three-way interaction [$F(1,15) = 5.0$, $p = .04$], which occurred because the switch–repeat difference was reversed (P2 was greater for repeat trials) during the c-dep trials at electrode Fz (see Figure 4).

One possible reason that we did not observe the predicted interaction (i.e., a switch effect for c-dep vs. c-ind trials) is that repeat c-dep trials may also have elicited context updating. As was noted earlier, in context-dependent tasks, subjects may choose to update context even on repeat trials (e.g., if they have become distracted or have traded preparation for reduced costs of maintenance, especially when there is a high likelihood of switching; Todd et al., 2009). The significant three-way interaction suggests that such an effect was numerically apparent in our data, with c-dep repeat trials being associated with a greater P2 amplitude than were c-ind repeat trials, which was near significance in Fz (3.66 vs. $2.39 \mu V$, $p < .07$). Thus, context updating may have occurred even during repeated c-dep trials.

If the purpose of examining sequential effects is to identify signals associated with task reconfiguration (i.e., updating of both context information in the PFC and representations in other neural systems required to perform the specified task), the most appropriate analysis to conduct on our data would be to compare those trials involving a switch in S–R mapping with those involving no change in S–R mapping, while controlling for the effects of cue repetition. Our design affords this analysis by directly comparing c-dep switch trials (involving a change in S–R mapping) with c-ind switch trials (involving a cue switch but no change in S–R mapping). This

Figure 4. Event-related potentials for midline electrodes Fz and Cz during the cue epoch, split by sequence within c-dep and c-ind transitions. The black horizontal bar indicates onset and duration of the cue (0–250 msec). Shading indicates intervals showing significant effects in the main analysis (see Figure 3) and is retained for reference. A repeated measures ANOVA on the peak amplitude in these intervals revealed a trend effect of trial type (c-dep > c-ind) during P2 and during SW_{neg}, but not an effect of transition (switch > repeat), indicating that the subjects updated context even when stimulus–response rules remained the same across trials (see Tables A1 and A3).

comprises a subset of the main effect of trial type in the ANOVA described above, confined to the switch trials in the c-dep and c-ind conditions. This comparison shows a near-significant effect in Cz, with P2 amplitude greater for c-dep than for c-ind switch trials (3.66 vs. 2.29 μV , $p < .06$). Thus, the frontally distributed P2 shows evidence of being selectively sensitive to conditions that require context updating, independently of changes in the identity of the cue.

Sequence effects on P3b. Paralleling our analysis of the P2, we conducted the same three-way ANOVA (trial type $\times$ sequence $\times$ electrode) on the P3b at electrodes Pz versus Oz (see Figure 3). As before, we predicted an interaction between trial type and sequence type, with c-dep switch trials being associated with a greater P2 than the other three conditions would be. Table A2 shows the results of this analysis (see also Figure 5). Whereas the two-way interaction between trial type and sequence was not reliable [$F(1,15) < 1$], the three-way interaction that

included electrode as a factor showed a trend toward significance [$F(1,15) = 2.96$, $p = .11$]. As can be seen in Figure 5, the interaction between trial type and sequence was more pronounced at electrode Oz than at Pz. These findings suggest that S–R transitions modulated the P3b. Interestingly, the main effect of cue transition was significant in this analysis [$F(1,15) = 13.14$, $p = .002$]. This suggests that at these electrodes, the P3b was sensitive to cue switches irrespective of changes in S–R mappings. We will return to this observation below in discussing the effects of cue repetition and priming.

Sequence effects on SW_{neg}. Finally, the same analyses were applied to the SW_{neg} potential at electrodes Fz versus Cz (see Figure 3). The results are presented in Table A3 (see Figure 4). There was a trend for a main effect of trial type [c-dep, $-5.41 \mu\text{V}$ vs. c-ind, $-4.18 \mu\text{V}$; $F(1,15) = 2.54$, $p = .13$] and a significant main effect of electrode [Fz, $-4.09 \mu\text{V}$ vs. Cz, $-5.52 \mu\text{V}$; $F(1,15) = 8.49$, $p = .01$]. In addition, the two-way interaction showed a trend

Figure 5. Event-related potentials for midline electrodes Pz and Oz during the cue epoch, split by sequence within c-dep and c-ind transitions. The black horizontal bar indicates onset and duration of cue (0–250 msec). Shading indicates the interval showing significant effects in the main analysis (see Figure 3) and is retained for reference. A repeated measures ANOVA on the peak amplitude in this interval revealed a trend effect of trial type (c-dep > c-ind) during P3b, as well as an effect of transition (switch > repeat) (see Table A2 for full ANOVA results). The effect of switching, however, occurred even within c-ind trials (dotted solid line > dotted broken line), within which the stimulus-response mapping stayed the same across trials, and thus suggests a contribution from cue priming to this effect (see the text).

[$F(1,15) = 3.24, p = .09$], which occurred because the switch effect was significant during c-ind trials (repeat, $-3.10 \mu\text{V}$ vs. switch, $-5.27 \mu\text{V}$, $p < .02$), but not during c-dep trials (repeat, $-5.88 \mu\text{V}$ vs. switch, $-4.93 \mu\text{V}$, $p = .4$). However, since S–R rules stayed constant across c-ind transitions, the former is unlikely to reflect task reconfiguration but may be indexing changes in cue identity (see also below). In sum, a weak effect of trial type was observed in SW_{neg} , and this potential was greatest at the Cz electrode.

Effects of cue priming on P2, P3b, and SW_{neg} . Our analyses of S–R rule switches within cued trials revealed that such transitions had the greatest impact on the P3b. On the surface, this is consistent with the hypothesis that the P3b reflects task reconfiguration processes in posterior cortical pathways. However, a puzzling finding is that switch trials in the c-ind condition, in which S–R rules

stayed the same, produced a P3b that was comparable to that in c-dep switch trials, in which S–R rules changed (see Figure 5; compare solid smooth and dotted lines). One possible explanation for this pattern of results is that the P3b is sensitive to changes in cue identity independently of whether S–R rules changed. Such an effect has previously been described in the task-switching literature (Logan & Bundesen, 2003; Mayr & Kliegl, 2003) and has been attributed to visual priming that facilitates cue encoding during cue repetitions, but not during cue switches. If present, this effect would increase P3b during cue switches even when S–R rules stayed the same across trials (i.e., in c-ind trials).

To test for this effect, we compared c-ind switch trials with c-ind repeats; the S–R rule was the same for all of these trials, and only cue identity changed on switch trials. We ran a repeated measures ANOVA on peak amplitude at

Figure 6. Scalp current density (SCD) maps are shown across conditions (rows) at four intervals (columns): at 120 msec following cue onset (column 1, for comparison) and at each of the intervals showing a reliable effect in the partial least squares (PLS) analysis (P2, P3b, SW_{neg}). Contour lines represent steps of 5 $\mu A/m^2$. Scale is reversed in polarity to match voltage maps. The P2 (columns 2–4) is shown in three views (left, dorsal, and right) to show the complete distribution of SCD across the scalp. The boxes indicate locations and time points at which a significant effect of context was detected in the PLS analysis (see the text for details).

P3b, with two factors: sequence type (switch vs. repeat) and electrode (Pz vs. Oz). The effect of sequence was significant [$F(1,15) = 13.02, p = .003$]: Switches produced a greater P3b (4.18 μV) than did repetitions (2.21 μV). Both the effect of electrode and the interaction showed a trend [$F(1,15) > 3.44, p < .08$]. The potential and the switch effect were more pronounced at electrode Pz than at Oz (Figure 5). These results indicate that cue priming may have contributed to P3b peak amplitude.

For completeness, we also evaluated whether such effects were present during P2 and SW_{neg}. For P2, there were no significant effects [$F(1,15) < 1$]. For SW_{neg}, there was a significant effect of cue switching [$F(1,15) = 0.02$]. This potential was more negative for switches ($-5.27 \mu V$) than for repetitions ($-3.10 \mu V$). In aggregate, these findings suggest that cue priming had an effect on both P3b and SW_{neg}, but not on the preceding P2. The attenuation of these potentials during cue repetitions suggest that the subjects were potentially less likely to engage in task preparation during these trials, which is consistent with the cue-priming account.

Scalp Current Density and Distributed Source Analysis

The six columns in Figure 6 show the SCD estimates of sources corresponding to the three significant peaks, as well as during early visual evoked potentials (~120 msec postcue) for comparison. The leftmost column shows a condition-invariant right-lateralized peak

along the posterior scalp, over the parieto-occipital cortex and consistent with visual processing of the stimulus (Di Russo, Martinez, Sereno, Pitzalis, & Hillyard, 2002). At P2 (columns 2–4), four density clusters were observed: two peaks along the frontocentral midline, accompanied by two additional maxima across the lateral aspects of the frontal scalp. The left frontal and posterior midline maxima (columns 2 and 3) showed no change across conditions. In contrast, the anterior midline peak (column 3) decreased in strength with increasing context, whereas the right frontal peak (column 4) appeared to strengthen with context demand, suggesting that these two maxima may have reflected a single source shifting from the superior to the lateral cortex as context demand increased. The P3b (column 5) showed a single source distributed across the parietal midline increasing in strength with context demand. The SW_{neg} (column 6) showed a negative minimum over the frontal midline and, potentially, a second density cluster, a positive maximum, over occipital electrodes, and both increased in strength with context demand.

To evaluate the source generators for these effects, we conducted a source analysis for each of the three components, either at peak (P2, P3b) or at maximum amplitude before target (SW_{neg}). sLORETA was calculated separately for each subject and for each condition.⁵ A mixed-effects ANOVA with subject as a random variable was conducted at P2, P3b, and SW_{neg}. An additional analysis was conducted on the source maps at 120 msec

Figure 7. Statistical analysis of condition effects on normalized current density per volume (units are arbitrary scores) at sources shown in Figure 5. The top image shows the statistical results from a mixed-effects ANOVA on the sources identified in the full-volume standardized low-resolution brain electromagnetic tomography ($p < .0000065$). The P2 (column 2) sources were estimated to include the right dorsolateral prefrontal cortex and also the left premotor cortex (not shown). The P3b (column 3) was estimated to include the unlikely location of the striatum (see the text), and the SW_{neg} (column 4) was associated with a frontal midline source. The bottom image shows *cortical* current density maps in the c-dep condition (i.e., not task differences), for comparison with the full-volume analysis.

post-cue-onset as a baseline comparison. The source regions of interest are shown in Figure 7 and are reported in x , y , and z coordinates (in millimeters) of the Talairach coordinate system (Talairach & Tournoux, 1988) and with references to approximate Brodmann areas (BAs).

P120. Neither the main effect of task nor pairwise contrasts showed any significant sources, as was expected. The mean source map across conditions showed intensity values greater than zero in the right cingulate cortex (BA30, [21 –51 10]) and the precuneus [18 –45 41].

P2. No differences were found between the c-ind and control conditions. However, the c-dep condition showed two regions that had greater signal strength than either the c-ind or the control condition: the right middle frontal gyrus (BA8/9, [41 18 41]) and the left precentral gyrus (BA6, [–55 –4 25]; only the former is visible in Figure 7). Comparing these source locations with the SCD maps (Figure 6), we see a correspondence between the right middle frontal gyrus and the right SCD peak. The left precentral gyrus source did not have an obvious corresponding peak in the SCD maps. It may have been masked by or contributed to the SCD maximum over left frontal electrodes (column 2 in Figure 6). The broad frontocentral midline peak is unrepresented in our source solution. This is not unexpected, considering the similarity of the SCD in this region across trials. We did not find any regions reliably greater for the control than for the context conditions.

P3b. At the peak of the P3b potential, we found a broadly distributed source localized to midline around the striatum. The validity of this solution is dubious, because the cytoarchitecture of the striatum, composed largely of unaligned, short-process, spiny cells (Nambu & Llinas, 1997), is unlikely to produce potentials detectable at the scalp surface. It is more likely that the result reflects depth indeterminacy, the inability of source solutions to distinguish between a deep point dipole and a diffuse surface generator (Dien, Spencer, & Donchin, 2003; Scherg & Picton, 1991; Wagner, Fuchs, & Kastner, 2004). Therefore, we recalculated the sLORETA, restricting the analysis to the cortex. The resulting map (Figure 7, bottom row) confirms that an alternative source was diffusely distributed across the cortex and included the inferior and posterior parietal cortex as well as the temporoparietal junction, in line with previous literature (Bledowski et al., 2004; Mulert et al., 2004).⁶

SW_{neg} . Finally, sources at 1,000 msec postcue spanned the frontal midline, including the anterior cingulate cortex (BA24, [–5 9 31]; BA30, [–6 26 31]) and the medial frontal gyrus (BA 9, [–6 29 31]). Similar to the P3b, the SW_{neg} showed a distributed scalp map, and the source solution was in accord with the cortex-restricted solution (Figure 7, bottom row), as well as with previous literature (Hamano et al., 1997).

Behavior Correlations

To examine the relationship of the three context-sensitive ERP components to target performance, we computed Pearson correlation coefficients between mean voltage potential at each interval identified in the PLS analysis at peak electrodes Fz (for P2 and SW_{neg}) and Pz (for P3b), with subsequent RT and accuracy across subjects. Correlations were reliable only for the SW_{neg} ($p < .05$). In the c-dep condition, increased negativity of this potential was associated with both higher accuracy ($r = -.49, p = .05$) and a shorter RT ($r = .53, p = .03$). The effect on accuracy is consistent with the interpretation of this potential as reflecting the successful retrieval and maintenance of task context in the PFC. In contrast, in the c-ind condition, increased negativity was associated only with a shorter RT ($r = .59, p = .02$). This finding is consistent with the fact that target identity during c-ind trials provided all the information necessary for a correct response. Thus, advance retrieval of context would be unlikely to benefit accuracy in this condition but could improve preparation and, therefore, RT. The lack of correlations between performance and earlier components may indicate that, on most correct trials, earlier processes (involved in task reconfiguration) were completed before the onset of SW_{neg}.

DISCUSSION

This study sought to identify electrophysiological correlates of context updating. The first effect of context was detected at around 200 msec following cue onset and had a scalp topography consistent with a generator in the PFC. This suggests that the P2 may provide a marker of context updating in the PFC. In the remaining discussion, we consider the relationship of this potential to task switching, to the other components (P3b, SW_{neg}) we observed to be influenced by context, and to working memory more generally.

P2, Context Updating, and Task Switching

In the present study, we manipulated context updating by varying the dependence between cue identity and response selection. In identifying the effects of context, we compared trials in which context was required for accurate performance (c-dep) with those in which it was not (c-ind and control trials). As we have noted, the c-dep trials are closely analogous to those in exogenously instructed task-switching paradigms, in which a cue provides the context necessary for knowing which task to perform next. Insofar as switch costs (differences in performance between switch and repeat trials) are often used to index task reconfiguration (which includes context updating), we might have expected to find similar effects, including an enhanced P2, when comparing switch with repeat trials in the c-dep condition of our experiment. However, we did not observe such effects. We believe that this was because context updating occurred during repeat, as well as switch, trials in the c-dep condition. This is consistent with findings in the task-switching literature, in which RT during repeat trials

increases and switch costs are diminished or absent when switch and repeat trials are intermixed rather than blocked (Braver, Reynolds, & Donaldson, 2003; Rubin & Meiran, 2005). This is especially so when repeat trials are relatively infrequent (Monsell & Mizon, 2006), as was the case in our design (~25%). Under such conditions, subjects may choose not to maintain the prior context, given the low likelihood that it will be useful on the next trial, and thus will need to update (in this case, reactivate) context even on repeat trials, diminishing the contrast between repeats and switches.

This effect may also explain the inconsistency of the findings regarding the P2 in task-switching experiments. Two studies that showed a switching effect on P2 used cues that specifically promoted the use of different strategies for repeat versus switch trials. Astle and colleagues (Astle et al., 2008a, 2008b) used *transition cues* that instructed subjects either to stay or change task, relative to the previous trial, therefore encouraging maintenance of context across trials for repeats and updating of context for switch trials. In contrast, P2 effects were absent in two studies that used standard task-switching cues (Wylie et al., 2003; Wylie et al., 2009), akin to the c-dep trials in the present study. This may explain the absence of switch effects within these trials in our experiment.

Relationship to Other Observations and Interpretations of Anterior P2 Potentials

Anteriorly distributed P2 potentials have been observed in a number of other experiments, most of which have involved attentional manipulations. For example, a frontally distributed P2 has been associated with detection of attended stimuli (Anllo-Vento, Luck, & Hillyard, 1998; Hillyard & Münte, 1984; Makeig et al., 1999), which is attenuated when detection fails (see Vogel, Luck, & Shapiro, 1998, for effects of suppression during attentional blink) and increases parametrically with the degree to which the eliciting stimulus is predictive of a subsequent target (Ruchkin, Johnson, Canoune, Ritter, & Hammer, 1990; Swainson et al., 2006). This anterior P2 potential has been described as a “frontal selection positivity” (e.g., Potts, 2004) that reflects the “selection of task-relevant perceptual representations” (Potts, Martin, Burton, & Montague, 2006, p. 1116). This description is entirely consistent with the hypothesis that such attentional processes rely on the updating of context representations (e.g., attentional templates) in the PFC and that the P2 reflects the operation of these mechanisms.

However, both our findings and those in the literature leave open at least one alternative interpretation: The P2 reflects the detection of conditions that trigger context updating, rather than the process of context updating itself (i.e., the first, rather than the second, of the three components outlined in the introduction). Although our findings cannot rule out this possibility, current theoretical and empirical work suggests that the triggering of context updating may involve mechanisms outside of the frontal cortex. For example, there is a growing corpus of evidence to suggest that neurons within the ventral tegmental area

(VTA) of the midbrain are responsive to unexpected but meaningful events and may signal a need to update context. These neurons are in a position to trigger changes in the activation within the PFC that represents context, either directly or via projections to structures closely interconnected with the PFC, such as the basal ganglia (e.g., Frank et al., 2001). This predicts that VTA activity should respond to the same manipulations of context as and correlate with changes in PFC activity. In support of this, using the same experimental conditions as those in the present study, we have recently observed a context-sensitive fMRI signal in the VTA that correlates closely with one in the PFC. However, the timing of this VTA activity, relative to changes in both PFC activity and the P2, remains to be determined.

Finally, we should note that caution is required in interpreting the PFC as the source of the P2 that we observed. We identified two sources, one in the right dorsolateral PFC and one in the left ventrolateral PFC (motor cortex), that may be critically involved in representing context within the current task. Although we have recently used fMRI to confirm involvement of the right dorsolateral region in distinguishing c-dep trials from c-ind trials (Eshel, Luka, Lenartowicz, Nystrom, & Cohen, 2008), the scalp distribution of the P2 in the present study was distributed over frontal and central electrodes and showed multiple peaks. It is likely that it was generated by multiple loci of neural activity and may even reflect multiple processes or influences, some of which are not directly associated with context updating (e.g., the effects of task difficulty). Nevertheless, our findings are consistent with the prediction, from guided activation theory, that an electrophysiological signature sensitive to conditions requiring context updating should be observed over the frontal cortex and that this should be antecedent to electrophysiological indices of subsequent task reconfiguration processes. In the section that follows, we turn to the evidence in support of the latter prediction.

P3b, SW_{neg} , and Working Memory

In addition to the P2, we observed an effect of context on the P3b and SW_{neg} . The P3b component has been shown to increase with time availability, task relevance and novelty, and motivation for processing of a stimulus and has been interpreted as reflecting stimulus evaluation and categorization (Donchin & Coles, 1988; Polich, 2007). The P3b has also been interpreted by Donchin and Coles as reflecting context updating. Accordingly, like others, we found an increase in the P3b peak amplitude with S–R rule switching, as compared with S–R rule repetitions (e.g., Karayanidis et al., 2003; Kieffaber & Hetrick, 2005; Lavric et al., 2008; Swainson et al., 2006; Wylie et al., 2003). However, it is also possible that these effects could reflect task configuration processes subsequent to context updating, in structures posterior to the PFC that are responsible for implementing the S–R pathways necessary to perform the upcoming task. The posterior distribution that we observed for the P3b is consistent with this interpretation. So, too, is our observation that it was sensitive to stimulus-specific effects, such

as cue priming (also reported by Nicholson, Karayanidis, Bumak, et al., 2006). That is, the P3b responded to changes in cues across trials even when the S–R rule remained the same, which suggests that the P3b reflects processes in addition to context updating.

The final component showing a context effect was the SW_{neg} . The timing and distribution of this potential was consistent with its identification as a contingent negative variation (Walter, Aldridge, McCallum, & Cooper, 1964), a negative slow wave observed preceding the latter of two sequentially contingent stimuli. In our design, a contingency was present only between cues and targets. Accordingly, the SW_{neg} was present only following cues in cued trials and was absent following control stimuli. This SW_{neg} is also distinct from the motor preparation Bereitschaftspotential (Deecke, Scheid, & Kornhuber, 1969), because responses were ambiguous prior to target onset. The effect of context on SW_{neg} suggests that this anticipatory potential was more than just expectation of a target based on a learned contingency, because the contingency between the cue and target was similar across cued trials, whereas the SW_{neg} was observed for c-dep, but not c-ind, trials.

One interpretation of the SW_{neg} is that it reflects preparatory resolution of response interference from response selection on a previous trial, which is expected to increase when tasks are switched (Astle et al., 2006, 2008a; Mueller, Swainson, & Jackson, 2007; see also Mueller, Swainson, & Jackson, 2009). In the present study, however, we found an effect of context on this potential but not the expected switch effect. During c-dep trials, the switch effect was not significant, and, to the contrary, the potential was qualitatively greater for S–R rule repetitions than for switches (Figure 4), which should present less, rather than more, response interference. An alternative explanation for the observed effects is that the SW_{neg} represents processes that support maintenance of context (e.g., S–R rules). This is consistent with the finding of a more negative potential during c-dep trials than during c-ind trials, since only the former require context maintenance. It is also supported by the estimated source of this potential falling within the medial frontal cortex, a region that has been implicated in the selection and maintenance of action sets (Rushworth, Buckley, Behrens, Walton, & Bannerman, 2007; Rushworth, Walton, Kennerley, & Bannerman, 2004). Finally, like the P3b, this potential was attenuated with cue repetitions. This is consistent with the idea that context maintenance would be less likely to occur when subjects' performance was facilitated by cue priming.

Conclusion

In the present study, we sought to test the prediction that there should be an electrophysiological signal over the frontal cortex associated with the updating of context in working memory within the PFC and that there should be a subsequent signal distributed more posteriorly that reflects the reconfiguration of task processes within structures responsible for execution of the upcoming task.

Our findings were largely consistent with these predictions. Although the present methods preclude definitive interpretations regarding the precise source of the electrophysiological signals or their unique association with the proposed mechanisms, the findings provide provisional support for the guided activation theory of PFC function and offer encouragement that, with additional work, the P2 may be established as an index of context updating within this structure and prove useful in future studies of the dynamics underlying context updating and cognitive control more generally.

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NOTES

1. Contrast this with a working memory representation in the sense of a phonological buffer, in which information stored is only one component of a larger context representation (e.g., grocery address) or is maintained for recall only (e.g., rote repetition of a street in the address).
2. The traditional AX-CPT requires a single response during targets and no response otherwise.
3. Only four stimuli were used for control trials in order to keep stimulus frequency constant across the entire sequence. This ensured that the cued trial stimuli did not elicit a surprise response, which is associated with a novelty effect in the scalp potential (Friedman, Cycowicz, & Gaeta, 2001).
4. This design component departs from the typical AX-CPT task, in which the frequency of cue-target pairs is manipulated, rather than the dependency in cue-target pairs. Although both manipulate the need for context updating, the latter allowed us to examine the effect more simply, without having to consider variability in strategy associated with differences in task expectancy (see also the Discussion section).
5. Given no differences in the PLS analysis, only one control group was tested.
6. A potential concern with this finding is that the variability in the P3b solution casts doubt on the other source solutions, particularly the P2. We offer four considerations that mitigate this concern. First, the problem of depth indeterminacy has been well described and applies only to broadly distributed sources, not the case for the P2 (which had multiple local maxima) and SW_{neg} . Second, the SCD maps and sLORETA volume and surface solutions are all in agreement for both of the latter components, suggesting consistency in the solutions. Third, the identified sources are in agreement with previously reported sources for both P3b and SW_{neg} . Finally, the P2 PFC source has been confirmed recently in an fMRI adaptation of this task within our laboratory (Eshel, Luka, Lenartowicz, Nystrom, & Cohen, unpublished observations; see the Discussion section).

APPENDIX

The results of the PLS analysis results were corroborated by conducting a repeated measures ANOVA that also examined laterality. We tested effects of context (c-dep, c-ind, Controls 1 and 2) and electrode (left vs. right hemisphere) on mean amplitude during each of the three intervals identified by the PLS analysis (see Figure 2 and main text). We compared electrodes F3, F4, C3, and C4 for P2 and SW_{neg} and electrodes P3 and P4 for P3b. During all three intervals, the main effect of context was significant [$F(3,45) > 9.98, p < .001$]. Paired t tests are as reported in the main text.

Table A1
ANOVA for Task-Switching Effects on Peak Amplitude During P2

	F	df	η_p^2
Trial type (c-dep, c-ind)	2.10 [†]	1, 15	.12
Sequence type (switch, repeat)	0.18	1, 15	.01
Electrode (Fz, Cz)	0.63	1, 15	.04
Trial type $\times$ sequence type	0.00	1, 15	.00
Trial type $\times$ electrode	0.04	1, 15	.00
Sequence type $\times$ electrode	0.06	1, 15	.00
Trial type $\times$ sequence type $\times$ electrode	5.00**	1, 15	.25

[†] $p = .17$. ** $p < .01$.

Table A2
ANOVA for Task-Switching Effects on Peak Amplitude During P3b

	F	df	η_p^2
Trial type (c-dep, c-ind)	2.45 [†]	1, 15	.14
Sequence type (switch, repeat)	13.14**	1, 15	.47
Electrode (Fz, Cz)	3.41 ^{††}	1, 15	.19
Trial type $\times$ sequence type	0.40	1, 15	.03
Trial type $\times$ electrode	0.08	1, 15	.00
Sequence type $\times$ electrode	0.16	1, 15	.00
Trial type $\times$ sequence type $\times$ electrode	2.96 ^{††}	1, 15	.17

[†] $p = .14$. ^{††} $p < .10$. ** $p < .01$.

Table A3
ANOVA for Task-Switching Effects on Peak Amplitude During SW_{neg}

	F	df	η_p^2
Trial type (c-dep, c-ind)	2.54 [†]	1, 15	.15
Sequence type (switch, repeat)	1.45	1, 15	.09
Electrode (Fz, Cz)	8.49**	1, 15	.36
Trial type $\times$ sequence type	3.24 ^{††}	1, 15	.18
Trial type $\times$ electrode	0.27	1, 15	.02
Sequence type $\times$ electrode	0.93	1, 15	.06
Trial type $\times$ sequence type $\times$ electrode	1.20	1, 15	.07

[†] $p = .13$. ^{††} $p < .10$. ** $p < .01$.

In addition, the main effect of electrode was significant during P2 and SW_{neg} . The overall potential was greater at central electrodes ($2.44 \mu V$) than at frontal electrodes ($1.72 \mu V$) [$F(1,15) > 8.14, p < .01$]. No laterality effects were significant during P2 or P3b [$F(1,15) < 1.94, p > .19$], but the potential was more negative over the right hemisphere during SW_{neg} [$F(1,15) = 6.99, p = .018$; -8.25 vs. $-3.85 \mu V$]. No other main effects or interactions were significant.