Fractionating the Cognitive Control Required to Bring About a Change in Task: A Dense-sensor Event-related Potential Study

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Abstract

■ The ability to change our behavior is one that we frequently exert, although determining the mechanisms by which we do so is far from trivial. Task switching is a useful experimental paradigm for studying cognitive control functions. Switching between tasks is associated with a decrement in performance, or "switch-cost," relative to repeating the same task. We have previously demonstrated that this cost is dependent on switching from *performing* one task to performing another; changing only our *intended* performance does not elicit the same performance deficit. Using event-related potentials (ERPs), we dissociated two electrophysiological indices mirroring this behavioral distinction [Astle, D. E., Jackson, G. M., & Swainson, R. Dissociating neural indices of dynamic cognitive control in advance task-set preparation: An ERP study of task switching. *Brain Res, 1125,* 94–103, 2006]. However, what was unclear were the specific aspects of performance that were critical for triggering the neural mechanisms associated specifically with switching from a previously performed task. Two candidate aspects were: (i) that performance required a physical response

and (ii) that the two tasks shared their responses (they had bivalent response mappings). The present study therefore compared three separate groups to explore the effects of these different aspects of performance. Each group completed the same basic task-switching paradigm, but with either an overt response or covert response, and either switching between tasks that shared their responses (bivalent response mappings) or had separate responses (univalent response mappings). When comparing precue-locked ERPs, we observed three separable components: one common to all three groups, one which primarily dissociated overt from covert responding, and one which primarily dissociated bivalent from univalent responding. We therefore concluded that changing our behavior engages at least three dissociable mechanisms. Interestingly, in the overt conditions, residual switch-costs were absent; in addition, therefore, we concluded that it is possible to engage cognitive control in advance, such that the new behavior is as efficient as were the subject to have repeated the old behavior. ■

INTRODUCTION

Human behavior is characterized by our ability to act coherently, yet flexibly, within a frequently changing environment. It is thought that we may employ "cognitive control" mechanisms to enable our patterns of behavior to change appropriately when necessary. The specific mechanisms involved are, as yet, largely unknown; however, they may depend upon the type of behavioral switch required. For example, a switch between purely covert actions, such as attending to what we see versus what we hear, may not involve the same mechanisms as a switch between overt actions, such as making a written note of what we see versus what we hear. And the mechanisms enabling a switch between tasks which share responses, such as pressing digits on a phone keypad versus pressing keys on a calculator, may differ from those enabling a switch between tasks involving entirely different responses, such as typing

versus walking. This study contrasts different types of behavioral switch in order to more clearly define separable aspects of cognitive behavioral control.

When subjects perform a new task, relative to repeating a previously performed task, the efficiency of their behavior is reduced. Studies investigating how this "switch-cost" is affected by a range of task manipulations have been used to explore the cognitive mechanisms by which changes in behavior are instigated (e.g., Mayr & Keele, 2000; Allport, Styles, & Hsieh, 1994). The *neural* mechanisms which underpin control have, to some extent, been revealed by combining this technique with the study of individuals with developmental (Mueller, Jackson, Dhalla, Datsopoulos, & Hollis, 2006) or neurodegenerative (Aron et al., 2003) disorders, or with acquired brain damage (Mayr, Diedrichsen, Ivry, & Keele, 2006), alongside studies using neuroimaging (Brass & von Cramon, 2002, 2004; Swainson et al., 2003) and electrophysiological recording (Swainson, Jackson, & Jackson, 2006; Kieffaber & Hetrick, 2005; Barcelo, 2003). Although its effects are generally limited in extent (i.e., a

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residual part of the switch-cost is usually seen to be immune to preparation; Rogers & Monsell, 1995), it is clear that subjects can, to a large degree, employ cognitive control in advance (such as following a "precue," before the onset of an imperative stimulus), thereby reducing this switch-cost (Meiran, 1996). What is unclear at this point are the specific mechanisms of advance cognitive control, which enable us to change our behavior, and whether they depend upon the particular type of switch required—for example, between tasks with overt versus covert responses, or with shared versus unique responses.

Neural Correlates of Advance Cognitive Control

Neuroimaging

Neuroimaging studies of task switching (primarily using functional magnetic resonance imaging [fMRI]) have revealed that there are a number of processes which may occur when we change our behavior. fMRI, in particular, has provided a useful means for distinguishing different cognitive control mechanisms and their separable neural substrates. For instance, Rushworth and colleagues contrasted "attentional switching" (switching between currently relevant attentional task attributes) and "intentional switching" (switching between alternative stimulus–response rules). Restricting their analyses to the medial prefrontal cortices, Rushworth and colleagues established that the former was associated only with activity in pre-supplementary motor area (pre-SMA)/SMA, whereas the latter demonstrated additional activity in the rostral and caudal cingulate zones (Rushworth, Hadland, Paus, & Sipila, 2002). Rushworth and colleagues therefore demonstrated a distinction within cognitive control between dealing with conflict occurring at a sensory level (incurred by attentional switching) and conflict arising at a motor level (incurred by intentional switching), thereby showing that changing our behavior appears to encompass multiple processes—in this case, switching *sensory processes* and *motor processes*. There are a number of other dissociations between different aspects of control in the fMRI literature (e.g., Crone, Wendelken, Donohue, & Bunge, 2006).

Traditionally, it has been considered difficult to isolate neural activity occurring in advance of the imperative stimulus from that occurring after it (Slagter et al., 2006). Neuroimaging studies of cognitive control tend to implicate a broadly distributed fronto-parietal network; this includes regions such as the medial prefrontal, superior and inferior parietal, medial parietal, and premotor cortices (Wager, Jonides, & Reading, 2004). There has remained some debate as to whether this fronto-parietal network can employ top–down control in an advance fashion (i.e., following the precue, prior to the onset of the target). The fundamental obstacle to establishing neural correlates of *advance* cognitive control using

fMRI is that the blood oxygenation level-dependent signal typically takes a number of seconds to return to baseline; this makes it particularly difficult to capture rapid anticipatory task-switching processes. To overcome this, researchers have either increased the period allowed for preparation (Kimberg, Aguirre, & D'Esposito, 2000), presented a number of precue-only trials (Slagter et al., 2006; Brass & von Cramon, 2002), or contrasted the activity elicited by different types of precue (Forstmann, Brass, Koch, & Cramon, 2005). Although not universally observed, there is now evidence to suggest that this fronto-parietal network is active prior to the onset of the target. For instance, Slagter et al. (2006) recently observed activity in the pre-SMA, dorsal premotor region, right fusiform gyrus, and posterior portion of the intraparietal sulcus (IPS) on precue-only trials.

There is, however, a cautionary note to make about such studies. In order to establish the neural correlates of these rapid, advance, control mechanisms, it is necessary to adapt the paradigm; consequently, the control mechanisms themselves may be altered. For instance, if on a large proportion of trials only a precue is presented without a subsequent target (such that subjects engage in preparation needlessly), then subjects might be less inclined to prepare on subsequent trials. Similarly, if the cue–target interval (CTI) is lengthened, then subjects might delay engaging in preparation or recruit additional cortical regions to assist in task-set maintenance over this extended period. For these methodological reasons, it is important to also use event-related brain potentials (ERPs) to study advance cognitive control.

Event-related Brain Potentials

ERPs have a high temporal resolution that enables the isolation of processes occurring in anticipation of performing the new task from those which occur, say, after target onset (Swainson et al., 2006; Nicholson, Karayanidis, Poboka, Heathcote, & Michie, 2005). There does seem to be a common finding in such studies: a late parietal positivity (LPP) for switch trials (i.e., an increased positivity over parietal electrodes, late in the epoch, on switch trials) is seen following a precue, in anticipation of target onset (e.g., Kieffaber & Hetrick, 2005; Nicholson et al., 2005; Rushworth, Passingham, & Nobre, 2002, 2005). This LPP can occur either precue-locked or target-locked depending upon the amount of time given for preparation (Nicholson et al., 2005). In conditions where the LPP is seen pretarget, there is an associated improvement in task switching (Swainson et al., 2006)—implicating this component as a marker of advance cognitive control. One might, on the basis of the fMRI data, presume that the generator of the LPP is located within the parietal lobes (e.g., Slagter et al., 2006; Rushworth, Hadland, et al., 2002; Kimberg et al.,

2000). However, source analysis has suggested a location within the ventromedial occipito-temporal cortex (Rushworth et al., 2005; Rushworth, Passingham, et al., 2002), a region associated with attentional selection (Nobre, Allison, & McCarthy, 1998).

A less common ERP component observed in advance of the target is a late frontal negativity (LFN) for switch trials. This has been seen in fewer studies than the LPP (Tieges et al., 2006; Lorist et al., 2000), and it has been unclear whether this modulation reflects a distinct process or the same process as the LPP, that is, the LFN and the LPP could be two separate ends of the same dipole. In a recent study, the size of the LFN (but not the LPP) was mediated by caffeine intake (Tieges et al., 2006). The authors speculated that the source of this component might be located within the frontal cortex, as caffeine is thought to boost activity within the dopaminergic pathways (Garrett & Griffiths, 1997) that connect the striatum with the frontal cortex, and this loop has previously been implicated in task switching (Cools, Barker, Sahakian, & Robbins, 2003).

In our previous study, we were able to separate two different mechanisms of advance cognitive control, indexed by an LPP and an LFN, respectively, using a behavioral manipulation. In a combined task-switching "go/no-go" paradigm, subjects prepared to change their behavior (or to repeat it, depending upon the trial type) following a precue on every trial. On some ("no-go") trials, a subsequent target did not appear, such that although subjects prepared to perform the task, they never actually did so. Switch trials following a "no-go" required a change in *prepared*, but not *performed*, task; we reasoned that this equated to a change in *intention* (from intending to perform one task to actually performing another) versus a change in *intention* and *action* (changing between performing alternative tasks), respectively. In terms of behavior, there were no switch-costs following a "no-go," implying that changing one's *intention* does not incur a cost relative to repeating one's intention. Conversely, changing one's *performance* incurred a robust switch-cost. In terms of ERPs, the LPP was associated with a change in intention; that is, it was present both following a "no-go" and following a "go." By contrast, the LFN was only associated with a change in performance; that is, it was only present following a "go." On this basis, we reasoned that the mechanism by which we change our behavior encompasses both changing *intended performance* (indexed by a LPP) and changing *actual performance* (indexed by an LFN) (Astle, Jackson, & Swainson, 2006). The current study sought to further explore the separable roles of the LPP and LFN.

The Current Study

Our previous study demonstrated that changing *actual performance* (as opposed merely to changing our *intended performance*) was critical for producing the characteristic switch-cost, and for distinguishing the LFN from the LPP. However, it is unclear which aspects of performance were important. In continuation from this previous study, then, we explored more thoroughly the contribution of different aspects of performance to the mechanisms by which we switch between tasks. We focus on just two possible aspects: (i) making a physical response and (ii) using responses which are shared between the two tasks. The first of these—making an overt (physical) versus a covert response (a response that is made without physical action)—is rarely manipulated, such that in the vast majority of psychological paradigms, including task-switching paradigms, performance requires a physical response. Yet it may be that the cognitive control mechanisms that bring about a change in *task* performance per se differ from those that control our *physical* performance. For this reason, a condition using a covert response (with subjects responding using mental imagery, which was only physically reported at the end of each block) was included in the current experiment. The second aspect, however—using shared versus unique responses—has already been shown to be an important determinant of how easily we can switch between tasks (Meiran, 2000). Meiran compared conditions in which subjects switched between tasks which had their own unique responses (univalent response mappings) with conditions where the tasks shared responses (bivalent response mappings). Specifically, in the univalent condition, subjects responded to each task with a separate hand, and in the bivalent condition to each task with the same fingers across both hands. In both conditions there were switch-costs but, whereas the bivalent condition produced, as usual, a switch-cost which *was not* fully removed with preparation, the univalent condition produced a switch-cost which *was* removed with preparation. It seems clear that, when changing our behavior, whether or not the old and new tasks have common responses is important.

In the current study, we investigated whether either (or both) of these two factors—making overt versus covert responses and using shared versus unique responses across tasks—were the critical aspects of performance for triggering the behavioral and electrophysiological effects seen in our previous study. We produced three different variants of the same task-switching paradigm, each requiring either overt (Conditions 1 and 3) or covert (Condition 2) responses, and with the tasks either sharing responses (Conditions 1 and 2) or having unique responses (Condition 3). Although in all three conditions subjects had to switch between categorizing the stimuli according to two task-sets (i.e., categorizing a letter as either a vowel/consonant or as lower/uppercase), only in two conditions did this also necessitate a physical response, and only in two conditions did this necessitate performing a task which shared its responses with another task.

Our principal research question was: when changing our behavior from performing one task to performing another, which features of our performance determine the mechanisms which bring about this change? We predicted that we would, once again, observe a precue-locked LPP and a precue-locked LFN. Moreover, we wanted to establish how these separate components would be affected by these manipulations. This, it was hoped, would enable us to specify, more so than in our previous study (Astle et al., 2006), the functional identity of both the LPP and the LFN.

METHODS

Subjects

Subjects were randomly assigned to one of three groups: one performed task switching with an overt bivalent response, another with a covert bivalent response, and a third with a univalent overt response. The overt bivalent group comprised 15 subjects, of which 6 were men, with an average age of 22 ± 3.14 year (*SD*). The covert bivalent group also comprised 15 people, of which 9 were men, with an average age of 24 years 6 months ± 5.1 year (*SD*). The overt univalent group comprised 16 people, of which 6 were men, with an average age of 25 years 8 months ± 2.96 years (*SD*). All 46 participants were naive to the purposes of the experiment and had never performed any task-switching experiments before. In each condition, all subjects contributed to the precue-locked comparison of the ERP data.

Behavioral Task

A single letter was presented on each trial, to which two task-sets could be implemented: (1) to discriminate the letter as either vowel or consonant, or (2) to discriminate the letter as upper- or lowercase. The set of possible stimuli was a series of vowels and consonants in uppercase and lowercase (A, E, I, U, a, e, i, u, G, B, T, D, g, b, t, d). Each trial was precued by a "transition cue": either "=," indicating that subjects should perform the same task as previously, or "<>," indicating that they should change task and perform the alternative task to last time. No task information was given with the target; subjects were told which task to start with and, subsequently, the precue was the only source of task information, instructing them to either switch or repeat. This basic structure was the same for each of the three groups.

The overt bivalent group responded with a two-button mouse, with right for uppercase and consonant, and left for lowercase and vowel (such that the two tasks shared responses). The subjects assigned to the covert bivalent response group were instructed to imagine themselves moving up and down a mental number line in response to the letters that appear, in the vowel/consonant task moving +1 for consonants and −1 for vowels, and in the upper/lowercase task, moving +1 for uppercase and −1 for lowercase. Subjects were instructed to start each block at 10 on their mental number line; at the end of the block they were asked to shout out the number that they finished on. Feedback was given on the screen as to whether this was correct or incorrect. In this condition, although the tasks shared responses (i.e., +1 or −1), the response was made covertly. The overt univalent group used two hands (with a separate hand corresponding to each task), with the middle and index fingers on each hand responding to each task. The leftmost finger on each hand corresponded to lowercase and vowel, and the rightmost to uppercase and consonant, such that although the response was physical, the two tasks did not share responses. The hand-to-task mapping was counterbalanced across participants. Importantly, the judgements required were common across the three groups (i.e., vowel/consonant or lower/uppercase); however, the output was specifically either overt (Groups 1 and 3) or covert (Group 2), and the two tasks either shared responses (Groups 1 and 2) or had unique responses (Group 3).

Experimental Design

After performing practice of each task separately and then of switching between the two, subjects proceeded to the experimental blocks. Of these there were 39; each was 10 trials long and started with subjects being instructed as to which task to start the block with. Each block contained two to three short (200 msec) CTI (the period allowed for preparation following the precue, prior to target onset) trials as well as seven to eight long (1200 msec) CTI trials, to provide incentive to engage in preparation immediately upon precue presentation. The run of short trials occurred randomly at either the start, middle, or end of the block. Each precue was on the screen for the full duration of the CTI. Each target was on the screen for 200 msec. Following each target there was a variable interval, such that each trial independent of preparation time lasted 3000 msec (including reaction time [RT]). This was the same for all three experiments.

Electroencephalogram Recording and ERP Formation

Electroencephalogram was recorded throughout each block using a 128-channel electrical geodesic net (Electrical Geodesics; Tucker, Liotti, Potts, Russell, & Posner, 1994), digitized at 250 Hz. The recording was performed with a hardware bandpass filter of 0.01 to 100 Hz. Before recording, impedance on each of the 128 electrodes was reduced to <50 kΩ.

Precue-locked epochs were created, with each epoch starting 100 msec before precue onset and ending 1200 msec afterward. Segments were rejected if contaminated by eye-blinks/movements (indicated by electrooculogram activity greater that 70 μV), an error of response (incorrect response or omission of response), or if the trial followed an error on the previous trial. Trials containing voltage amplitudes greater than 200 μV or a change greater than 100 μV were also removed. Channels that were bad for more than 20% of trials were rejected.

ERPs were only formed from long CTI trials. In the overt conditions, only trials which were accurate and were preceded by an accurate trial were included; in the covert condition, only trials from blocks in which the subject reached the correct number on the mental number line at the end of the block were included. Following this rationale, in the overt bivalent condition, 15 subjects contributed individual averages to the overall cue-locked data (on average, each subject having 85 repeat and 83 switch trials waveforms), 15 in the covert condition (on average, each subject having 84 repeat and 79 switch waveforms), and 16 subjects in the univalent overt condition (on average, each having 96 repeat and 95 switch waveforms). Following the artifact rejection criteria outlined above, 11% of the cue-locked epochs were rejected in the bivalent condition, 12% in the univalent, and 7% in the covert.

Waveform Comparisons

Segments were average-referenced to a standard adult 128-electrode montage. Epochs were baseline-corrected for the first 100 msec before the onset of the precue; all switch and repeat waveforms were explicitly compared (all statistics conducted using MATLAB v5, scripts developed in-house) by means of a t test for every 4-msec sample. Two waveforms were counted as significantly different if significance persisted for more than nine samples. Two temporal regions of consecutive significance were counted as a continuation of the same difference if the gap between them was less than 10 samples. This approach was based upon those used by Astle et al. (2006), Swainson et al. (2003), and Rugg, Doyle, and Melan (1993).

The primary method of comparison was between switch and repeat waveforms within each condition. In addition, we produced difference waves (Switch − Repeat) for each condition and compared these across the three conditions using repeated one-way analyses of variance (ANOVAs). Difference waves have been used to compare across conditions in a number of other ERP studies of task switching (e.g., Nicholson, Karayanidis, Bumak, Poboka, & Michie, 2006; Tieges et al., 2006; Nicholson et al., 2005; Karayanidis, Coltheart, Michie, & Murphy, 2003). Where this analysis revealed consecutively significant differences (>9 consecutive samples)

between conditions, we submitted the mean voltage for this time window to post hoc Scheffé tests. However, the use of difference waves has a principal limitation: They do not tell us whether any differences are primarily the result of an effect on switch trials or repeat trials. For this reason, we also compared switch and repeat trials separately across this window, using one-way ANOVAs. Again, post hoc Scheffé tests were also used to further specify the results of these one-way ANOVAs. All precue-locked ERP comparisons that reached consecutive significance are reported.

RESULTS

Behavioral Results

The behavioral data were divided into repeat (rp) and switch (sw) trials, for both errors and RTs (these data are displayed in Figure 1)—only trials correct for trial n and trial $n − 1$ were included in the RT data. The RT data from the two physical response conditions were compared directly using a repeated measures ANOVA, with switch and CTI as within-subjects factors, and univalent/bivalent as a between-subjects factor. This revealed a significant three-way interaction [$F(1, 29) = 4.819, p = .036$], which appears to be the result of a larger reduction in switch-costs with preparation in the bivalent condition [$F(1, 14) = 23.01, p < .001$] than in the univalent condition [$F(1, 15) = 6.773, p = .02$]. In both
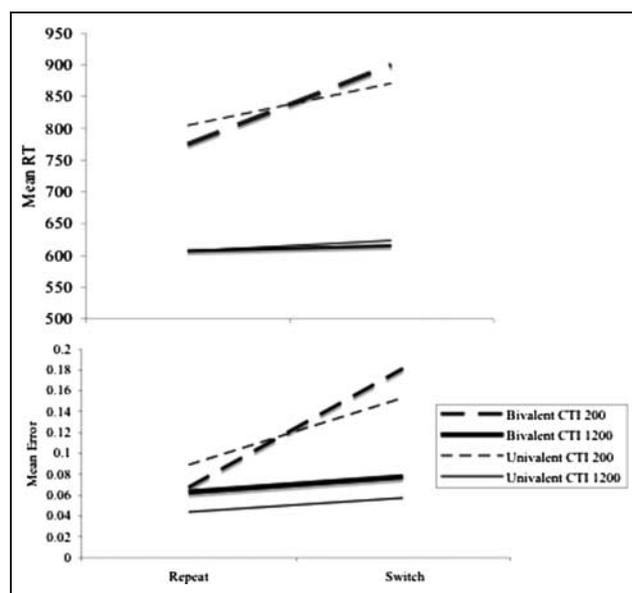

Figure 1. Behavioral data for task switching in the two overt conditions, with bivalent shown in thick lines, and univalent shown in thin lines. Data taken from short CTI (200 msec) trials are shown with a dashed line and data taken from long CTI (1200 msec) trials are shown with a solid line. Upper panel shows RT data, lower panel shows mean proportion error data. Note that residual switch costs (i.e., switch–repeat differences at 1200 msec CTI) are absent for both the univalent and bivalent conditions in both RT and error data.

the bivalent and univalent groups, these interactions between CTI and switch were the result of there being significant switch-costs at the short CTI [bivalent (sw = 897 msec, rp = 781 msec): $F(1, 14) = 20.998, p < .001$; univalent (sw = 871 msec, rp = 804 msec): $F(1, 15) = 11.990, p = .003$], but not at the long CTI [bivalent (sw = 614 msec, rp = 607 msec): $F(1, 14) = 1.148, p = .302$; univalent (sw = 623 msec, rp = 607 msec): $F(1, 15) = 3.544, p = .078$].

The same comparison was run with the error data, which revealed no three-way interaction [$F(1, 29) = 1.739, p = .198$]. However, there was a significant two-way interaction between switch and CTI [$F(1, 30) = 16.323, p < .001$], which was the result of significant switch costs at the short CTI [$F(1, 30) = 25.069, p < .001$], but not at the long CTI [$F(1, 30) = 2.559, p = .120$]. The bivalent/univalent variable did not interact with any other factor. In both conditions (as in the RTs), with preparation (i.e., at the long CTI) there were no significant residual switch-costs [bivalent (sw = 0.08, rp = 0.06): $F(1, 14) = 0.974, p = .340$; univalent (sw = 0.06, rp = 0.04): $F(1, 15) = 1.756, p = .205$]. In summary: in both the univalent and bivalent groups, subjects were making use of the precue to prepare and more so

on switch than repeat trials. This occurred to such an extent that in both groups switch costs were absent at the long CTI, both in terms of errors and RTs.

ERP Results

Only the precue-locked ERPs are discussed here, as the target-locked data from the three response conditions differed greatly, making any direct comparison difficult. It is important to note that none of the components we observed precue-locked were seen target-locked (in the same condition or in any of the other conditions), that is, all of the components we report here were apparently uniquely associated with the precue–target period. Therefore, components which we show to be absent in the precue-locked period were, indeed, genuinely absent for that condition, rather than simply delayed in time.

Precue-locked

Early Anterior Positivity

This component is displayed in Figure 2. An increased positivity for switches relative to repeats was observed
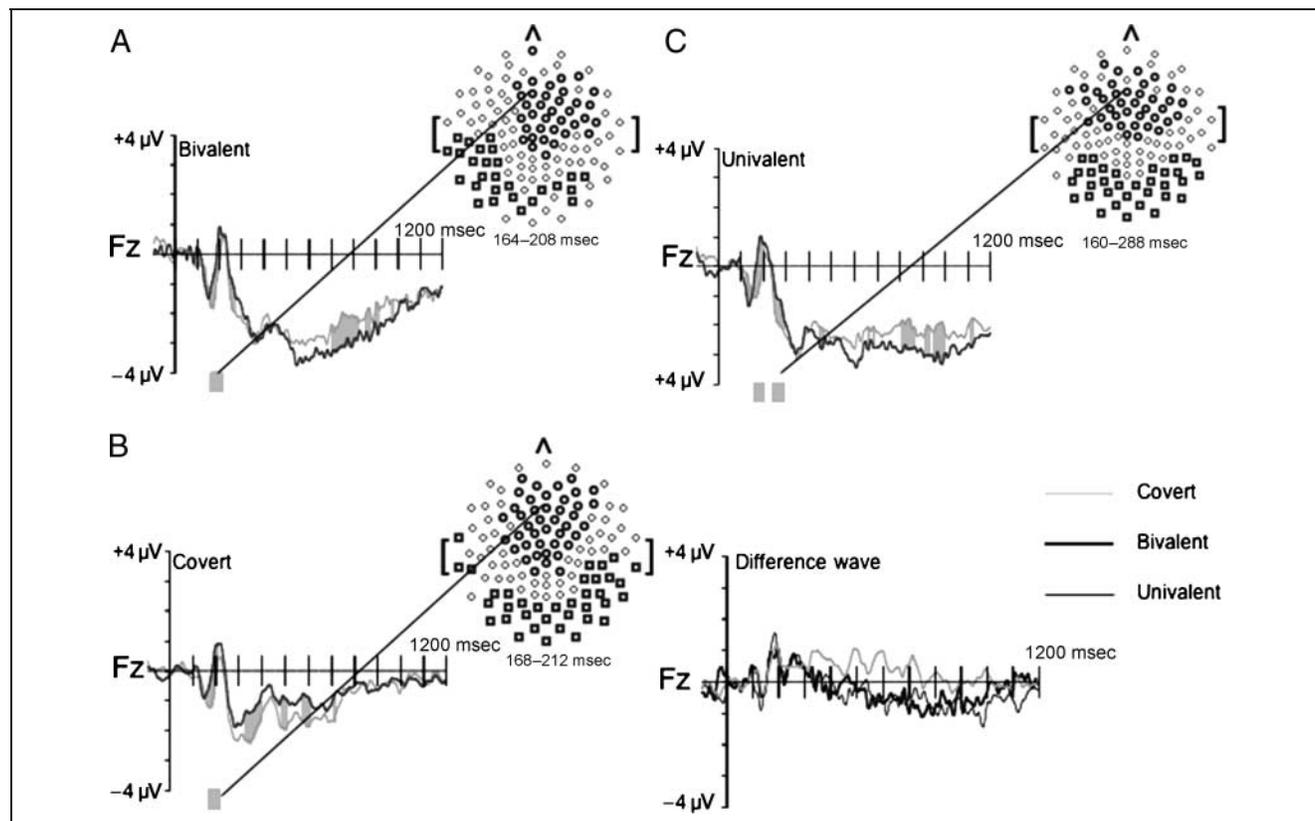

Figure 2. The early anterior positivity (EAP), time-locked to precue onset at 0 msec, with switch waveforms shown as a dark line and repeat waveforms shown as a gray line. The effect is present in the bivalent (A), covert (B), and univalent (C) conditions. Panel D shows a switch–repeat difference for each of these conditions. Waveforms are shown from electrode Fz, and topographical plots apply to the time period of consecutive significance at Fz. In the topographical plots, dark circles indicate significantly greater positivity for switch than repeat trials, and vice versa for dark squares. Lines to topographical plots indicate the electrode site at which the accompanying waveforms were recorded.

over frontal electrodes early in the epoch in each of the three conditions. It is unclear whether this effect stemmed primarily from a shift in amplitude of switch relative to repeat trials over a period including both the frontal N1 and P2 or from a delayed latency of these early negative and positive peaks on repeat trials relative to switch. In all three conditions, the effect can clearly be seen at Fz, reaching consecutive significance in the bivalent overt (164–208 msec), the bivalent covert (168–212 msec), and the univalent overt (160–200, 244–288 msec) conditions (Panels A, B, and C, respectively). In each condition, the anterior positivity was accompanied by an occipital negativity, which can be seen on each of the topographical plots. Difference waves were compared for the three conditions (Panel D), which revealed no period of consecutive significance at this electrode between the conditions within a 0–320 msec window. For this reason, it was concluded that the early anterior positivity (EAP) was not modulated by either of the overt/covert or bivalent/univalent response manipulations.

Late Parietal Positivity

This component is displayed in Figure 3. An increased positivity for switch relative to repeat trials was observed over parietal electrodes (clustered about Pz) in each of the three conditions. This reached consecutive signifi-cance in the bivalent overt (188–960 msec), bivalent co-vert (268–1196 msec), and univalent overt (384–744 msec) conditions (Panels A, B and C, respectively). Each con-dition showed a similar topography, but the duration of this component seems to differ slightly across the three conditions: Switch and repeat waveforms con-verged again earliest in the univalent condition, followed by the bivalent overt condition, with the waveforms still differing in the covert condition at the onset of the target. This is most clearly illustrated by the difference wave (Panel D). Although the difference waves might appear to differ earlier in the epoch, a direct comparison only revealed a significant effect of condition from 752 to 812 msec. Although the resulting Scheffé test results for this window did not reach significance, they do (as the difference waveforms indicate) suggest that the overall significant difference is driven by a difference in the univalent condition relative to the bivalent covert ($p = .054$), and, to some extent, relative to the bivalent overt ($p = .151$), but not by the difference between the two bivalent conditions ($p = .876$). We therefore con-cluded that this component was modulated by the overlap between stimulus–response mappings, but not by the physical nature of the response. To further explore the origins of this change in switch–repeat voltage difference across the three conditions between 752 and 812 msec, the voltages across this window were
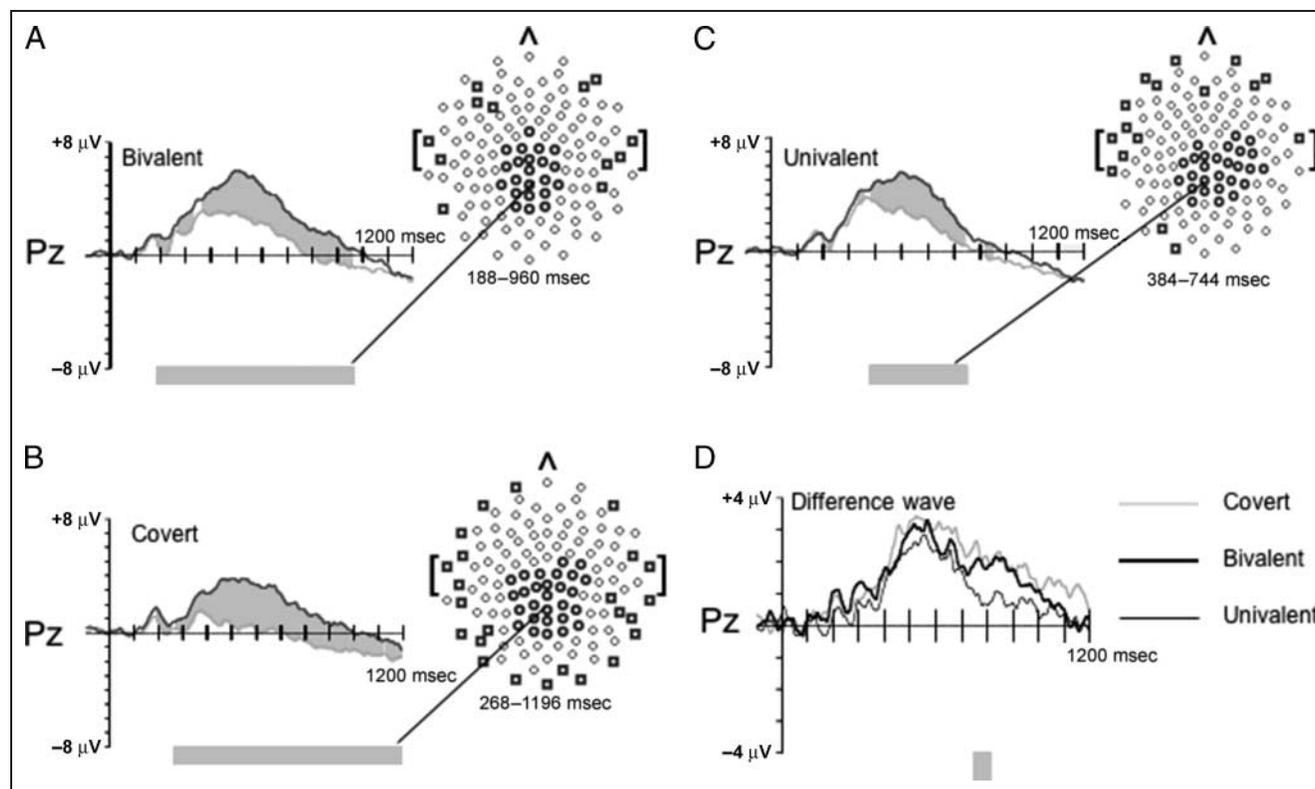

Figure 3. The late parietal positivity (LPP), time-locked to precue onset at 0 msec, with switch waveforms shown as a dark line and repeat waveforms shown as a gray line. The effect is present in each of the three conditions (shown in A, B, and C), shown at electrode Pz. Other plotting conventions as for Figure 2. Panel D shows a switch–repeat difference wave for each condition, demonstrating that this component is foreshortened in the univalent condition relative to the other two conditions.

compared separately for repeat and switch trials. This established that the difference could not be specifically attributed to a significant change in voltage on repeat trials [$F(2, 42) = 0.744$, $p = .481$] or switch trials [$F(2, 42) = 0.894$, $p = .417$].

Late Frontal Negativity

This component is displayed in Figure 4. The bivalent overt condition demonstrated a clear slow negative wave for switch relative to repeat trials, which we labeled the LFN. This can be clearly seen at AFz, reaching consecutive significance from 548 to 936 msec (Panel A). [N.B. the topography of the LFN in our previous study (Astle et al., 2006) is slightly different to the LFN we observed in the current study, perhaps because this component is shifted earlier in time in the current example.] This switch–repeat modulation, in the current study, was, however, completely absent in the bivalent covert condition (the same electrode and topographical plot are shown for comparison, Panel B). In the overt univalent condition, the overall shape of the waveform was similar to that in the bivalent overt condition, but with a critical switch–repeat difference only for shorter periods within the epoch, reaching consecutive significance at 560–620 msec, 828–868 msec, and 972–1012 msec (a topo-

graphical plot for this whole period is shown: 560–1012 msec, Panel C). The difference wave demonstrates that the covert condition is easily distinguishable from the overt conditions (panel D). To investigate these differences between the conditions further, we submitted these difference voltages to a series of repeated one-way ANOVAs, which revealed a consecutively significant effect of condition at 484–832 msec. This window was further examined by submitting the mean voltages for the three conditions to post hoc Scheffé tests. As the difference waveforms suggest, the effect of condition was driven mainly by a difference between the covert condition and both the bivalent ($p = .009$) and univalent ($p = .049$) overt conditions, rather than between the two overt conditions ($p = .772$). We therefore concluded that this component was principally modulated by the physical nature of the response. To further explore the origins of this change in voltage difference across the three conditions between 484 and 832 msec, the voltages across this window were compared separately for repeat and switch trials. This established that the difference was not the result of a change in voltage on repeat trials [$F(2, 42) = 1.105$, $p = .341$], but a change in voltage on switch trials [$F(2, 42) = 3.422$, $p = .042$]. Post hoc Scheffé test revealed that this significant effect on switch trials was primarily the result
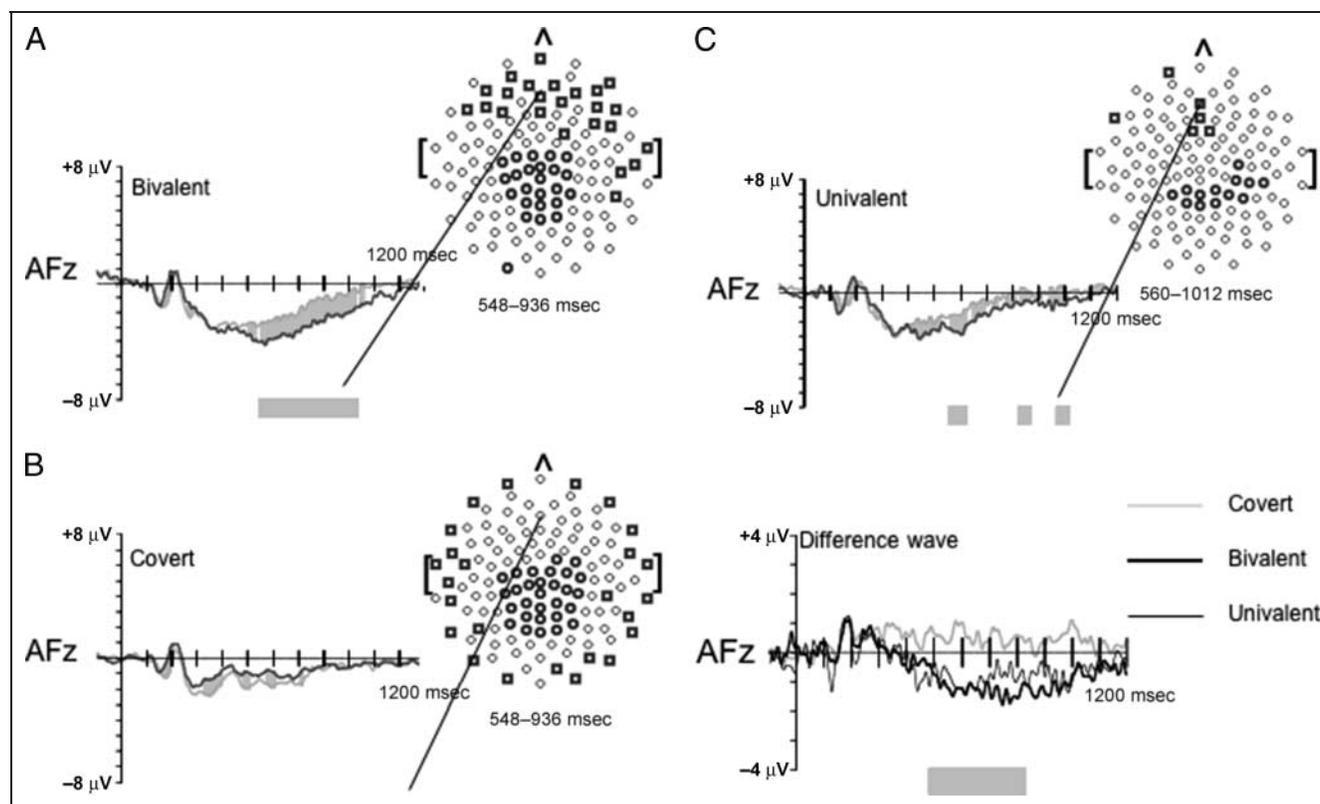

Figure 4. The late frontal negativity (LFN), time-locked to precue onset at 0 msec, with switch waveforms shown as a dark line and repeat waveforms shown as a gray line. The effect is present only in the bivalent (A) and univalent (C) conditions, shown at electrode AFz. The appropriate electrode and topography are also shown for the covert condition (B). Other plotting conventions as for Figure 2. Panel D shows a switch–repeat difference wave for each condition, which demonstrates that this component is absent in the covert condition.

of a difference between the overt and covert bivalent conditions ($p = .042$), with the overt univalent condition not significantly differing from either the overt bivalent condition ($p = .358$) or the covert bivalent condition ($p = .503$).

DISCUSSION

This study explored the relationship between different aspects of performance and neural correlates of cognitive control in a precued task-switching paradigm. Subjects switched between judging letters as vowel/consonant and as lower/uppercase; they responded either with a manual button press or a covert mental count, and with either shared (bivalent) response meanings between tasks or unique (univalent) response meanings. In previous studies using the precued task-switching paradigm, subjects, on average have not fully prepared in advance of the target, as evidenced by the presence of residual switch-costs (Nicholson et al., 2005; Rushworth et al., 2005; Rushworth, Passingham, et al., 2002); ERPs of this period have, therefore, yet to reveal fully all those components that might constitute subjects' adoption of a new task. In contrast, subjects in the present study were apparently able to prepare fully for a switch trial on the long CTI trials. Importantly, this implies that performance of a new task can, given appropriate conditions, be as efficient as the repeated performance of an old task. Such a finding is in support of the "failure to engage" explanation of residual switch-costs—that is, the residual cost does not reflect the need for a discrete posttarget process but rather incomplete preparation on a subset of trials (De Jong, 2000). Because the residual switch-cost was entirely eliminated in the current study, it is likely that pretarget control processes were compressed within the precue–target period, and therefore, potentially fully captured by the precue-locked ERPs shown here.

In the precue-locked period, there were three separable ERP components which could be distinguished by their topography and time course. More importantly, they were dissociated by the three response-type conditions. An EAP was common to all three conditions, an LPP distinguished bivalent from univalent stimulus–response mappings (being prolonged in the bivalent conditions), and an LFN distinguished overt from covert responding (being absent with covert responding). Each of these components is discussed in turn.

Early Anterior Positivity

This early switch-related component encompassed not only the frontal P2, but also the preceding N1 peak; the key feature was its presence in all three conditions. This anterior positivity was accompanied by an occipital negativity. Given that this component has not been seen

in other ERP studies of task switching, we will consider other paradigms which demonstrated a similar component. The EAP observed across these three conditions bares a resemblance to the well-documented "frontal selection positivity" (FSP). In addition to this, the FSP is often accompanied by an "occipital selection negativity" (OSN), which is also apparent on our topographical plots. Interestingly, the FSP and the OSN are revealed by comparing the ERPs elicited by attended-to targets with unattended-to targets in nonspatial attention tasks (Jonkman, Kenemans, Kemner, Verbaten, & van Engeland, 2004; Kenemans, Kok, & Smulders, 1993; Hillyard & Munte, 1984). Using transition precues may have resulted in subjects viewing these precues as targets; perhaps our "switch" precues were equivalent to attended-to targets and our repeat precues were equivalent to unattended-to targets (i.e., distracters).

Potts, Patel, and Azzam (2004) and Potts and Tucker (2001) described the P2a as an example of an FSP. The P2a has been observed across a number of target-detection ("oddball") designs, with an increased positivity for targets relative to distracters. Potts (2004) observed this component both in an overt response (manual response) and a covert response ("mental-count") condition. Although the overt condition produced a larger amplitude contrast between distracter and target stimuli than in the covert condition, the distribution was the same for both conditions, with source analysis suggesting the same location: the bilateral orbitofrontal cortex (Potts, 2004; Potts et al., 2004). Neurons in this region have been closely related to motivational salience (Tremblay & Schultz, 1999). In the current context, because they signaled subjects to overcome the cost of switching tasks, our "switch" precues may have become motivationally salient, relative to our "repeat" precues. This is important given that the behavioral data showed subjects to be maximally using the precue to bring about a change in behavior (with subjects performing the new task as efficiently as the old task); other studies which have not demonstrated the precue-locked EAP have also not demonstrated this behavioral effect (e.g., Astle et al., 2006). Put together, it seems reasonable to suggest that the presence of the EAP indicates that subjects were detecting the switch precues as being particularly important, such that they were then able to prepare fully for the upcoming switch trial.

Early precue-locked switch-related components have not, to our knowledge, been seen in other task-switching studies. The best comparison is perhaps with our previous study (Astle et al., 2006), which employed essentially the same task-switching paradigm (with subjects switching between a vowel/consonant and lower/uppercase judgement). This earlier study used task-precues (i.e., precues that directly instruct subjects as to which task to perform on the subsequent target) as opposed to transition-precues and longer blocks of trials (60 trials per block rather than 10). Notably, subjects still demonstrated a robust residual switch-cost, despite being allowed

1200 msec preparation time. Importantly, the EAP was not present in this earlier study. It seems likely that the EAP seen here reflects processes that are triggered according to motivational conditions affecting the use of the precue prior to target onset, perhaps including the *type* of precue (i.e., transition precues) and/or block length (see also De Jong, 2000). Both of these features differentiate the current from the previous experiment and may explain subjects' maximal preparation during the CTI as well as the presence of the EAP. This issue requires further study, perhaps by exploring the role of these design features upon these early frontal and occipital effects.

Late Parietal Positivity

An LPP has been observed in task switching when subjects switch between the stimulus-attributes that are relevant on each trial (Rushworth et al., 2005), as well as for switching between different stimulus–response mappings (Rushworth, Passingham, et al., 2002). Indeed, given that it has been present in many different task-switching experiments, it has been difficult to assign any specific functional role to the LPP. In our previous study (Astle et al., 2006), we compared switch-related ERPs following a performed task (following a ''go'' trial) and those following a trial upon which the task was only prepared (those following a ''no-go'' trial). Crucially, the same switch-related LPP was observed in both cases. The LPP was interpreted, therefore, not as an index of switching from performing one task to performing an alternative, but rather of switching from simply being *prepared* to perform a task to performing an alternative, regardless of performance. Similar parietal positivities have been described as updating ''attentional set'' (Slagter, Kok, Mol, Talsma, & Kenemans, 2005); Rushworth describes the parietal positivity in task switching as ''defining the stimuli that will later be the determinants of action.'' Source analysis indicated a ventromedial occipito-temporal generator; this region has been commonly active in attentional updating tasks (Nobre et al., 1998). However, we have also observed the LPP in a productive language-switching task (Jackson, Swainson, Cunnington, & Jackson, 2001), in which subjects alternated between naming digits in alternative languages. In this case, the task-relevant stimulus-features themselves were entirely common to the two tasks (i.e., there were no ''task-relevant features'' to be defined), yet the LPP was still present, suggesting that it does not index a process of ''defining stimuli'' that will determine action, per se.

The current data shed light upon the functional identity of this component, with it persisting over a longer duration when responses are bivalent (regardless of whether these are overt or covert), than when they are univalent. We suggest that the LPP is not an index of switching between different goal-relevant visual features, or the preparation of a shift in attention to a different target feature per se, but rather an internal shift in attention to the now relevant stimulus–response mapping. Such a shift may be more easily achieved because the separate responses provide an external cue for easily separating the tasks. This internal shift in attention may be more protracted when the stimulus–response mappings do not readily disentangle (e.g., when the tasks share responses, as with bivalent responses). The implication here is that the LPP indexes an attentional shift to the relevant stimulus–response mapping and that this attentional process is more readily resolved when the responses for the two tasks are easily separable.

To further clarify our position as to the functional identity of the LPP, we designed a subsequent study, which contrasted two between-group conditions. In both conditions, subjects were presented with bivalent targets and used bivalent responses. For both groups, colored targets were present to the left or right of fixation. In both conditions, the tasks competed with each other at both a stimulus and response level. However, in one condition, subjects were able to separate the tasks on the basis of location (with the targets being presented in a specific screen location for each task), whereas in the second condition, the tasks were separable on the basis of color (with targets being presented in a specific color for each task). Those subjects who delineated task on the basis of target color demonstrated a large and persisting precue-locked LPP (this looked much like the bivalent overt condition from the current study). However, those subjects who delineated the tasks by spatial location did not demonstrate an LPP at all. This is, we think, consistent with view that the LPP indexes a mechanism of selective attention; when an external cue (such as response hand, or target location) provides a means for *spatially* separating the tasks, the need for an internal mechanism of selective attention is reduced or redundant—hence, the absence of the LPP.

Late Frontal Negativity

The final precue-locked component was an LFN which largely discriminated overt from covert responding. We suggest that the LFN relates to the competition, between two tasks, for a single motor output. Firstly, it was absent in the covert condition, which has no *motor* output; secondly, it was somewhat (although not significantly) reduced in the univalent condition, where the two tasks do not compete directly for the same motor output. A similar LFN has been observed elsewhere in a bivalent-response condition, with a complete absence in univalent-response conditions (Mueller, Swainson, & Jackson, 2007). Combining the results of this study with the results of the current study, we conclude that this component is maximal when subjects select a physical response which also maps to a separate judgement in a different task.

One possibility is that where two tasks compete for a single motor output, it is necessary to suppress one of the tasks; this suppression will then be encountered on a subsequent switch trial, when the suppressed task is required. Where two tasks compete but not for *motor* output per se, however, the same type of suppression might not be necessary, hence, the absence of this component in the covert condition. It might also be the case that where responses are overt, if it is possible to "gate-out" one of the competing response-sets—for instance, when the task-sets map to separate effectors (Yeung & Monsell, 2003; Klein, 1964)—this need for suppression might again be reduced, hence, the reduction of this component in the univalent condition (see also Mueller et al., 2007). We suggest that the LFN reflects the recruitment of resources to overcome this persisting inhibition (Rösler, Heil, & Roder, 1997). There is a similarity between the current LFN and a particular slow negative waveform, the contingent negative variation (CNV); the CNV is typically seen between a precue and a subsequent imperative stimulus, provided that, as in the current study, the onset of the subsequent stimulus is, to some extent, predictable and that it requires a physical response (Walter, Cooper, Aldridge, McCallum, & Winter, 1964). Specifically, the CNV has been shown to be increased on trials for which subjects made a particular "effort" (Falkenstein, Hoorman, Hohnsbein, & Kleinsorge, 2003). The LFN seen in the current study could reflect the increased recruitment of resources required to make a physical response to a difficult type of target, that is, one which is known to require the overcoming of persisting inhibition. Notably, switching from an antisaccade task to a prosaccade task demonstrates a similar precue-locked LFN (Mueller, 2006). Producing an antisaccade likely requires the suppression of the more dominant prosaccade task. Therefore, when subjects switch to this prosaccade task, it is likely that the persisting inhibition will be encountered (Mayr & Keele, 2000; Meuter & Allport, 1999), hence, the LFN. Elsewhere in the task-switching literature, it is also apparent that switch-costs are absent following a trial on which a particular task was prepared but not performed (Wylie, Javitt, & Foxe, 2004; Schuch & Koch, 2003); we have previously proposed that this situation of encountering persisting suppression, following the *performance* of the alternative task, is associated with an LFN (Astle et al., 2006). This is also consistent with our observation in the current study that the difference in the LFN across the conditions was primarily the result of a change on switch trials, and that this was driven primarily by a difference between the bivalent overt condition and the bivalent covert condition. That is, the LFN is largest when switching to a task that shares physical responses with the previously used task.

Using Cognitive Control to Change Task

There now exists a large literature on task switching, comprising a number of behavioral studies which have

established key processes involved in changing tasks (Monsell, 2003). A consistent finding, to date, has been that, despite subjects being given apparently ample time and incentive for advance preparation of the new task, a switch-cost remains, implying that it is not possible to prepare fully in advance of a target stimulus for the upcoming new task (Nieuwenhuis & Monsell, 2002). An exception is the study of Tornay and Milan (2001), which showed elimination of the cost in the RT data, but somewhat ambiguous effects in the error data. Meiran (2000) also eliminated the cost of switching, but only by using univalent responses. This "residual switch-cost" has been crucial to a number of theoretical accounts of task switching (Rogers & Monsell, 1995; Allport et al., 1994). However, an important feature of the current study is that the behavioral data (both RTs and errors) suggest that there were no residual switch-costs in either the bivalent or univalent conditions. We suggest that the most parsimonious explanation for the observed effect is that it is possible to employ cognitive control to such an extent that subjects can perform the new task as efficiently as the old task. The notion that subjects *can* fully prepare for a switch is in line with the theory of De Jong (2000), according to which residual switch costs are the result of a mixture between both fully prepared and fully unprepared trials (rather than reflecting the need for any specific "switch" process that can only be performed upon target onset). Shortening the block lengths enabled De Jong to increase the proportion of prepared trials; by increasing the proportion of trials upon which subjects engaged in advance preparation, the overall residual switch-cost was reduced. De Jong argued that although subjects were capable of fully disengaging a prior task during the preparatory period, they do not fully exercise this capability. He established that block length was an important feature in determining the extent to which subjects prepare; when block lengths were reliably short, subjects achieved a reduced residual switch-cost by comparison to that achieved during long blocks. Importantly, this contrast was only apparent when block length was manipulated between subjects, not within subjects. Thus, it seemed that the between-subjects effect of block length was not the result of fatigue, but rather a strategic difference; when subjects know in advance that their efforts will only need to be maintained for a short period, they will consistently employ advance cognitive control on each trial. The current study, as well as demonstrating that fully effective task switching in advance of a target stimulus is possible, also begins to indicate (via the ERP data) the neural processes by which this is made possible. In particular, the EAP may be the critical marker of subjects' increased motivation to engage in preparing for the new task, given that it has been absent in previous experiments in which there has always been a residual switch-cost.

There are a number of other aspects of cognitive control that require further discussion. For instance, the use of transition precues in the current study may have led

to a more endogenously generated task-set than the use of task precues (Forstmann et al., 2005). Using transition precues to change tasks is known to recruit the fronto-parietal network to a greater extent than using task precues. This increased activity for transition precues relative to task precues included regions such as the prefrontal cortex, pre-SMA, and the IPS (Forstmann et al., 2005). Thus, the mechanisms of *advance* cognitive control might also be affected by the way subjects are precued; perhaps advance cognitive control is more complete when transition precues are used. A more thorough exploration of the relationship between advance cognitive control and precue type would be an interesting avenue of future research. This article has focused somewhat exclusively on the advance cognitive control required to bring about a change in task, however, this study also raised broader questions regarding executive function. The transition precues may require greater recruitment of working memory; that is, subjects must retain the identity of the just-performed task in order to determine the to-be-performed task. Similarly, those subjects in the covert response group were also required to maintain their position on the mental number line. A broader question, then, is how does a flexible cognitive system meet different requirements of maintenance (of, say, task or location on a mental number line) and switching tasks? Moreover, are these different requirements subserved by the same or different neural systems? This issue is not tested by the current study but should be addressed in future studies.

Conclusion

When changing tasks, the different aspects of performance determined the mechanisms by which subjects brought about this change. This was revealed by comparing the precue-locked ERPs across three response-type conditions. An EAP was common to all three conditions, an LPP distinguished bivalent from univalent stimulus–response mappings (being prolonged in the bivalent conditions), and an LFN distinguished overt from covert responding (being absent with covert responding). Interestingly, this change in task was particularly efficient; performance of the new task was as quick and accurate as the repeated performance of the old task.

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