Neural correlates of changing intention in the human FEF and IPS

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Abstract:
Previous research demonstrates that our apparent mental flexibility depends largely upon the strength of our prior intention; changing our intention in advance enables a smooth transition from one task to another (e.g. Astle et al. 2008a; Duncan et al. 2006; Husain et al. 2003). However, these necessarily rapid anticipatory mechanisms have been difficult to study in the human brain. We used electroencephalography and magnetoencephalography (EEG and MEG), specifically event-related potentials and fields (ERPs and ERFs), respectively, to explore the neural correlates of this important aspect of mental flexibility. Subjects performed a manual version of a pro/anti-saccade task, using preparatory cues to switch between the pro and anti rules. When subjects switched their intention we observed a positivity over central electrodes, which correlated significantly with our behavioural data; the greater the ERP effect, the stronger the subject’s change of intention. ERFs, alongside subject-specific structural MRIs, were used to project into source space. When subjects switched their intention they showed significantly elevated activity in the right FEF and left IPS; the greater the left IPS activity on switch trials, the stronger the subject’s change of intention. This network has previously been implicated in the top-down control of eye movements but here we demonstrate its role in the top-down control of a task set – in particular, that it is recruited when we change the task that we intend to perform.
Introduction:

Preparation for an upcoming sensory event is essential in order to maximise the efficiency of processing of, and response to, that event. The intention to perform a particular act prior to the onset of an imperative stimulus is referred to as ‘preparatory set’ (Evarts et al. 1984; Connolly et al. 2002). The neural correlates of preparatory set in the oculomotor system have been widely studied using a pro / anti-saccade paradigm. Prior to the imperative stimulus, the intention to perform a reflexive pro-saccade to, or perform a voluntary anti-saccade away from, a peripheral target can be distinguished by activity in the frontal eye fields (FEF; Connolly et al. 2002, 2005; Ettinger et al. 2008; Everling & Munoz, 2000), the intra-parietal sulcus (IPS; Ettinger et al. 2008; O’Driscol et al. 1995), as well as various sub-cortical structures.

Furthermore, this fronto-parietal network is implicated in control processes other than saccade generation per se (Wager et al., 2004). For instance, top-down biasing signals from the FEF are thought critical to the covert orienting of spatial attention in vision (Taylor et al. 2007; Schwartz et al. 2005), as well as various other non-saccadic control processes (see Wager et al. 2004 for a review). We used a manual pro / anti task (with lateral button presses rather than saccades) to explore the mechanisms by which subjects change their intention, in sensor (EEG) and source space (MEG).

We used a task-switching paradigm modelled closely on the well-studied pro / anti-saccade paradigm, because the rapid preparatory processes underpinning the pro and anti rules are relatively well-understood and could thus provide a principled basis for constraining our MEG source reconstruction. In particular we wanted to know whether the anticipatory control processes underpinning task-switching build upon those processes of preparatory set mentioned above. There are a number of further advantages to choosing a manual version of the Pro / Anti-saccade paradigm. Firstly the paradigm is simple and intuitive, requiring minimal training of the subjects. Secondly, because the paradigm involves pre-potent and non-pre-potent tasks, it is particularly demanding. For instance, frontal patients demonstrate particular problems in overriding the Pro response (Husain et al. 2003). Thirdly, there is typically an interesting asymmetry in the size of the behavioural switch cost; the performance difference between switching to the Pro task and repeating the Pro task is larger than for the Anti task. Indeed, in many cases there is little switch cost for the Anti task at all. This asymmetry has been used to draw important conclusions about top-down control (Allport et al. 1994).

Changing our intentions prior to performing a new cognitive task, reduces the difficulty of switching between tasks and enables a smoother transition into the new task (e.g. Husain et al. 2003; Lavric et al. 2008). When subjects switch from performing one task to performing another, their RTs slow and/or error rates increase relative to had they repeated that task. This difference is typically referred to as the ‘switch cost’. Throughout this manuscript the ‘switch cost for the Pro task’ refers to the difference between Pro trials following an Anti trial on trial N-1 (i.e. switching to the Pro task), and Pro trials following a Pro trial on
trial N-1 (i.e. repeating the Pro task); likewise, the ‘switch cost for the Anti task’ refers to the difference between Anti trials following a Pro trial on trial N-1 (i.e. switching to the Anti task), and Anti trials following an Anti trial on trial N-1 (i.e. repeating the Anti task). Importantly this switch cost reduces with increased preparation; if subjects are given advance warning of the upcoming task, for instance in the form of a cue, then they can initiate the new task-set in anticipation of the imperative stimulus and thus reduce the cost of switching (e.g. Rogers and Monsell, 1995; Astle et al 2008a). Using cues also enables the researcher to separate task-set control from any additional control processes that might occur as subjects select responses to targets. That said, because it is particularly effortful, it can be difficult to get subjects to use the cue to engage fully in this advance task-set control (Mizon and Monsell, 2006). In our study we used various design features to try and encourage cue use. Sometimes subjects would have little time to use the cue (short cue-target interval (CTI) trails), encouraging them to engage in preparation immediately upon cue presentation. Comparing these short and long CTI trials would also provide us with a behavioural measure of how much benefit subjects were gaining from using the cue to prepare. A second characteristic of our paradigm designed to encourage preparation was to manipulate the amount of information present with the target. Randomly, on some trials the target would be white, with their being no colour information with the target to tell subjects whether to perform the Pro or Anti task. In short, we sometimes gave subjects a preparatory cue, instructing them to switch or repeat task, but no action cue to instruct them which task to perform. Responses on these white arrow trials will inevitably be slower and more error prone, but the fact that subjects know that any trial could subsequently transpire to be a white arrow trial will provide strong incentive to use the preparatory cue – if they don’t, and it is a white arrow trial, they will not know which task to perform. In short, we are not interested in these design features per se, but they are included in order to maximise subjects’ use of the cue to prepare.

In addition to the problem of subjects not preparing, anticipatory changes of intention are technically difficult to study in the human brain, because they are necessarily rapid. There have been numerous attempts to capture the neural correlates of this preparatory activity using fMRI. The temporal resolution of fMRI is such that it is difficult to attribute activity to the preparation period alone without substantially changing the paradigm and thus possibly changing the control processes themselves. For instance, some fMRI studies have extended the gap between the cue and the imperative stimulus (Kimberg et al. 2000), used partial cue designs such that the cue is not always predictive of the upcoming stimulus (Brass et al. 2004), or have needed to combine the fMRI with measures with real-time temporal resolution (e.g. Transcranial Magnetic Stimulation, Rushworth et al. 2002). Because of relatively large differences in the paradigms and tasks used, the results of these studies have been mixed.

In parallel to this fMRI literature, there have been a number of ERP studies that have attempted to capture cue-locked activity by capitalising on the high temporal resolution of this technique. Following the
cue there is typically a switch-related positivity over the central and posterior channels, from ~300 ms until around 1000 ms (e.g. Astle et al. 2008a, 2008b, 2009; Lavric et al. 2008; Nicholson et al. 2005; Rushworth et al. 2002); in some cases this is accompanied by a negativity over the frontal channels (e.g. Astle et al. 2008a, 2008b, 2009; Lavric et al. 2008). We know of only one ERP study of task-set control using pro-saccade and anti-saccade tasks, and this showed a broadly similar pattern of results (Mueller et al. 2009). Across the vast majority of studies the occurrence and timing of these cue-locked switch-repeat differences coincides with the reduction in switch costs with preparation in the behavioural data. Thus, many have argued that these ERP effects are markers of those processes that bring about a change in task-set, although the exact nature of this control remains unclear (e.g. Lavric et al. 2008; Astle et al. 2009).

Our aim here was to use ERPs and ERFs to isolate these anticipatory task-switching mechanisms. With the ERPs we firstly wanted to replicate the switch-related parietal positivity mentioned above, and provide evidence (in addition to the behavioural data) of subjects preparing differentially for switch and repeat trials. Furthermore we wanted to know whether this anticipatory marker was sensitive to how well subjects had used the cue to anticipate a change of task. With the ERFs we wanted to identify the cortical correlates of this anticipatory task-switching process; to our knowledge this is the first MEG study of anticipatory task-set control, and using the well-studied pro/anti paradigm provides a possible means of constraining our source reconstruction. One possibility is that subjects engage generic mechanisms, such as those anticipatory mechanisms used in preparatory set (e.g. Connolly et al. 2002), but to a greater extent on switch trials. The differential deployment of these generic mechanisms would result in subjects making a smoother transition from one task to the next. In short, anticipatory task-set control might be a special case of preparatory set, and thus might engage a similar fronto-parietal network, but to a greater extent when subjects prepare for a switch of task.

Methods:

Participants:

17 subjects completed an EEG session (mean age 26.3, st.dev. 3.08, 9 female) and 10 subjects completed the MEG session (mean age 25.8, st.dev. 2.78, 7 female). 7 subjects completed both sessions. Approval was given by the ethical review board at the School of Psychology, University of Nottingham, UK. 2 subjects were removed from the EEG data analysis because of excessive oculomotor artifacts.

Behavioural task:

The same paradigm was used for both the EEG and MEG sessions. An arrow, pointing either leftward or
rightward, was presented on every trial (see Figure 1). If the arrow was green then participants responded by pressing the button corresponding to the arrow direction (‘Pro’ task). If the arrow was red then participants responded by pressing the button on the side opposite to the arrow direction (the ‘Anti’ task). Each trial was cued by a ‘transition cue’ (e.g. Astle et al. 2008; Rushworth et al. 2002): either an ‘=’, indicating that subjects should perform the same task as on the previous trial, or an ‘<>’ indicating that they should change task and perform the alternative task to that which they performed previously. Some researchers have found that much of the ‘switch cost’ might actually be a ‘cue change cost’ (Logan and Bundesen, 2003). We used these transitions cues to avoid any such confound between cue-switches and task-switches: with transition cues a change of task is as likely to result from a repeat of cue as from a change of cue. Subjects were told which task to start each block with, and subsequently the cue instructed them to either switch or stay.

**Insert Figure 1 about here**

Experimental design:

Subjects practised each task (10 trials per task) and practised switching between the two tasks (40 trials), then proceeded to the experimental blocks (39 blocks of 10 trials). These blocks were short because it has previously been demonstrated that subjects are less inclined to engage in preparation for a change in task if they expect that this effort will need to be maintained for a long block (De Jong, 2000; see also Astle et al. 2008a). There were 50% Pro and 50% Anti trials and 50% switch and 50% stay trials, and these two variables of task and transition, respectively, were fully orthogonal. We varied the cue-target interval (CTI), including a few trials upon which subjects had very little preparation time. Whilst these short CTI trials could not be used for analyzing the neural correlates of task-set preparation, when compared with long CTI trials, they would provide a good behavioural measure of how well subjects had used the cue to prepare for a change of task. The reduction in switch costs from the short CTI to the long CTI is an important marker of how well subjects had engaged anticipatory control processes in advance of a change of task (see also Monsell and Mizon, 2006). Each block contained 2 or 3 short (200 ms) CTI (cue-target interval) trials as well as 7 or 8 long (1200 ms) CTI trials. The run of short CTI trials occurred randomly at the beginning, middle or end of the block (Astle et al. 2008a, 2008b). This design, rather than simply interleaving trials with different CTIs, was chosen to minimize the number of trials upon which subjects switched from one CTI to another, as this may interact with switches of task. Each cue was presented for the duration of the CTI. Each target was on the screen for 200 ms. Following each target there was a variable interval, such that each trial lasted 3000ms irrespective of CTI (including RT). Only long CTI trials were analysed in the ERP/ERF analyses.

On half of the trials participants were presented with a white, rather than a red or green, arrow. This was to encourage participants to use the preparatory cue; on white arrow trials the preparatory cue was the only means of determining which task to perform, making its use essential. We did not make all the arrows white; if all the arrows were white and subjects performed the incorrect task on a trial, all
subsequent trials would also be incorrect and the entire block would need discarding. This mixture of
coloured and white arrows enabled us to keep subjects on track, whilst encouraging them to prepare.

**EEG recording, ERP formation and analysis:**

EEG was recorded using a 128-channel electrical geodesic net (Electrical Geodesics, Inc. (EGI), Tucker et al., 1994), digitised at 250 Hz, and bandpass filtered at 0.01 Hz to 100 Hz. Impedance on each electrode was reduced to <50 kΩ; the EGI system provides an excellent signal-to-noise ratio, despite these relatively high electrode impedances (Ferree et al. 2001). The vertex was used as an acquisition reference, and the average reference was used as an offline reference. After recording we applied a 40 Hz low-pass filter.

Cue-locked epochs were from -100 to 1200 ms, relative to cue onset. Baseline correction was performed using the -100 to 0 ms window. Segments were rejected if contaminated by eye-blinks/movements (electro-oculogram activity greater than 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.

The voltages were submitted to 40 ms bins (as in Astle et al. 2008b, 2009). For each bin we produced a repeated-measures ANOVA, with the four-way within-subjects factors of task, switching, and two electrode factors. We produced 5 clusters of electrodes, including a midline frontal cluster, a midline central cluster, a midline posterior cluster, a left-hemisphere cluster and a right-hemisphere cluster. Each cluster comprised 16 electrodes, these were entered separately into the ANOVA, resulting in a 2x2x5x16 way ANOVA. There were no interactions with electrode, just at the cluster-level. This clustering approach is a good means of data reduction and spatial smoothing, often used in the literature (e.g. Astle et al. 2008b, 2009; Lavric et al. 2008). We did not perform source reconstruction on the ERP waveforms for various reasons: i) without structural scans we could not form an accurate model of source space; ii) without an accurate recording of the locations of the electrodes we could not compute an accurate lead-field. We did however look for correlations between our sensor-level effect (defined as the peak switch-repeat difference at Cz, between 180 and 800 ms) and our behavioural preparation effect.

**MEG data acquisition and analysis:**

MEG data were recorded using the third-order synthetic gradiometer configuration of a 275-channel CTF whole-head MEG scanner, with a sampling rate of 600 Hz. EOG was recorded throughout. Head-localising coils were placed at the nasion and left and right pre-auricular points. Head position was monitored throughout. The data were processed in the same way as the EEG data, to produce ERFs.

We projected into 3D voxel space and then performed a General Linear Model-based statistical analysis (GLM). All of the MEG pre-processing and analysis procedures were performed using SPM 8 (Wellcome Trust Centre for Neuroimaging, London). For all participants a structural MRI was acquired using a Philips
3T scanner, to produce a cortical mesh, containing 5124 vertices. Each structural scan was co-registered with each subject’s head position, using fiducial markers and head digitisation (Polhemus Isotrack). Next, a forward computation was produced, using this co-registered model of source space. With this lead field matrix a source reconstruction was then performed, using a Multiple Sparse Priors approach to establish the generators of the evoked response. This is an implementation of hierarchical and empirical Bayes modelling that automatically selects cortical sources by allowing the data to drive the selection of a sparse or distributed solution without the need to specify priors (e.g. Minimum Norm, Friston et al. 2008).

Sources were weighted using a Gaussian distribution with an 8 ms full width half maximum, favouring those sources active between 300 and 700 ms post cue. This was in part motivated by the ERP data, and also by examining subjects’ individual ERFs. The data were not spatially smoothed. These images were then converted to voxel space, with each voxel measuring 2 x 2 x 2 mm, and compared using a second-level analysis, as implemented in SPM8. We applied a cortical mask to our statistical analysis (created using “wfu_pickatlas” Maldjian et al, 2003), placing 5mm spheres within bilateral FEF (LH: -32, 3, 48; RH: 32, 3, 48) and IPS (LH: -28,-46, 42; RG: 28, -46, 42) (Connelly et al. 2002; Schwartz et al. 2005; Taylor et al. 2007). A small volume correction was used reporting areas with p[FWE]<= 0.05.

**Results:**

**Insert Figure 2 around here**

**Behavioural results**

For the reaction time (RT) and error rate analyses, we removed all trials following an error. For the RT analyses we also removed trials upon which an error had occurred. We particularly focus on two important effects: i) the cost of switching tasks reduced with preparation; and ii) the relative cost of switching to the Pro task was larger than the cost of switching to the Anti task. In each case we included session (EEG versus MEG) as a between-subjects factor but these effects did not differ significantly across the two sessions.

The size of the RT switch cost (switch minus stay trials) was reduced from 66 ms [F(1,25)=19.458, p<0.001] at the short CTI to 22 ms [F(1,25)=14.507, p=0.001] at the long CTI [see Figure 2A, interaction between CTI and Switching: F(1,24)=9.476, p=0.005]. The reduction in switch costs did not differ significantly across the two sessions: in the EEG session switch costs were reduced from 66 ms to 30 ms for the Pro task, and from 34 ms to 8 ms for the Anti task; in the MEG session, switch costs were reduced from 132 ms to 36 ms for the Pro task and from 40 ms to 14 ms for the Anti task. Overall, the error rate switch cost (switch minus stay trials) did not reduce significantly with preparation, being 4% on both the short and long CTI trials. Again this did not differ across the two sessions.

The RT switch cost was larger for Pro (61 ms) than Anti (28 ms) trials (See Figure 2B) [interaction between Switching and Task: F(1,24)=10.067, p=0.004], because the RT difference between switch and stay trials was larger for Pro trials [F(1,25) = 37.838, p<0.001] than it was for Anti trials [F(1,25)= 3.866, p=0.060]. This asymmetric switch cost did not differ across the two sessions: in the EEG session the
switch cost was 48 ms and 21 ms, for the Pro and Anti tasks respectively; in the MEG session, switch
costs were 84 ms and 27 ms, for the Pro and Anti tasks respectively. The same effect was present for the
error rate switch costs [interaction between Switching and Task: F(1,24)=12.653, p=0.002]; switching to
the Pro task incurred the greatest cost [F(1,25)=25.416, p<0.001] with there being no overall cost of
switching to the Anti task [F(1,25)=0.001, p=0.999]. Again, these effects did not differ across the two
sessions.

**Summary of the behavioural results:**

Subjects used the cue to prepare for a switch of task: the RT cost of switching was reduced with
preparation, and the error rate cost of switching to the Pro task was reduced with preparation. We also
replicated the typically observed asymmetric RT and error rate switch cost, with the cost of switching
tasks being greatest for switching to the easier Pro task than to the more difficult Anti task. Finally we
compared error rates for trials upon which the arrow was white and trials upon which the arrow was
coloured. On white arrow trials subjects' only means of knowing which task to perform was the
preparatory cue. When subjects had the opportunity to use the preparatory cue (on long CTI trials) error
rates were 8% for white and 6% for coloured arrow trials; whilst this is significant [F(1,24)=9.471,
p=0.005], we think that the small 2% difference indicates that on the vast majority of trials subjects did
indeed use the cue and knew which task to perform. This effect of arrow colour on prepared trials was
most marked on Pro trials [coloured: 5%; white: 9%, F(1,24)=9.757, p=0.005] relative to Anti trials
[coloured: 6; white: 7%, F(1,24)=2.261, p=0.119; interaction between task and arrow colour:
F(1,24)=4.756, p=0.039].

**Insert Figure 3 around here**

**ERP results**

The grand-average waveforms can be seen in Figure 3A. In the cue-locked period there was a substantial
effect of switching task on the ERP voltage, on both Pro and Anti trials, between 160 and 800 ms,
primarily driven by switch trials being more positive than stay trials over the over the Midline-Central
cluster (Figure 3A, middle panel). The topographical distribution of this effect can be seen in Figure 2E,
for both Pro and Anti trials; the ERF topographical distributions for the same window can be seen below
the ERP distributions. Early in the epoch (280-340 ms) the effect of switching task on the ERPs differed
depending upon whether the subjects were switching from the Pro to the Anti task, or vice versa: when
switching to the Anti task there was a significant switch-related positivity over the Midline-Frontal
electrodes and a switch-related negativity over the Midline-Posterior electrodes, which were not present
when switching to the Pro task. The topographical distribution of this effect, as well as the ERFs, can be
seen in Figure 2F. This summary was confirmed by our statistical analyses, the results of which are
described as follows:

**Main effects of Switching and interactions between Switching and Electrode:**
In the cue-locked period, between 440 and 800 ms, voltages were significantly more positive for task-switch than task-stay trials [main effect of Switching: $F > 5.124$, $p < 0.040$]. Between 160 and 280, and from 320 to 640 ms, this switch-stay difference was not the same size across all electrode clusters [interaction between Switching and Electrode Cluster: $F > 2.640$, $p < 0.07$]. Across all of these time bins this was the result of a significant effect of Switching task on voltages recorded at the Midline-Central cluster [$p < 0.06$]. From 160-200, 240-280, and 320-440 ms, there was also an effect of Switching task on voltages recorded over the Midline-Frontal cluster [$p < 0.05$], and from 160-200 and 240-280 over the Midline-Posterior cluster also [$p < 0.016$].

**Interactions between Task, Switching and Electrode:**

Between 280 and 360 ms the effect of Switching task differed, depending upon whether subjects were switching from the Pro task to the Anti to task, or vice versa [3 way interactions between Task, Switching and Electrode Cluster: $F < 3.380$, $p < 0.018$]. This was because when subjects switched to the Anti task the voltages were more positive over the Midline-Frontal electrodes and more negative over the Midline-Posterior electrodes, relative to when they the repeated the Anti task [$F > 3.540$, $p < 0.081$]. This was not the case for the Pro task [$F < 2.188$, $p > 0.169$] [interaction between Task and Switching over the Midline-Frontal and Posterior clusters between 280 and 360 ms: $F > 7.279$, $p < 0.018$]. (These interactions can most clearly be seen in the grand-average waveforms).

**Correlations between ERPs and behaviour**

The extent to which subjects used the cue to anticipate a switch of tasks (i.e. the reduction in switch costs with preparation) was correlated with the size of the switch-related ERP effect (the voltage peak in difference between switch and stay trials), as measured at Cz, across subjects. We expressed the voltage difference as a z-score before performing the correlations. In the RT data (Figure 3B) there was no significant correlation on Pro trials [$r = -0.208$, $p = 0.456$], however, there was on Anti trials [$r = 0.622$, $p = 0.017$]; those subjects who showed the greatest cue-locked switch-related ERP effect also showed the greatest reduction in switch-costs with preparation. There were no significant correlations with the error data.

**MEG results**

When subjects switched task, following the cue, our analysis revealed significant increases in neural activity in the right FEF and in the left IPS (e.g. Connolly et al. 2002; Ettinger et al. 2008) – these can be seen in Figure 4A. We observed significant peaks for switching task in the right hemisphere FEF [peak MNI: 30, 6, 50; $F = 9.54$, $p[FWE]=0.047$] and two peaks in the left hemisphere IPS [(peak MNI: -26, -48, 42; $F = 10.82$, $p[FWE]=0.029$); (peak MNI: -30, -45, 44; $F = 8.90$, $p[FWE]=0.050$)]. These effects match very closely with previous studies of the FEFs and IPS (e.g. Asari et al. 2005; Connolly et al. 2002; Corbetta et al. 1998; Paus, 1996; Prime et al. 2010; Schwartz et al. 2005; Taylor et al. 2007). There were no significant main effects of task and or significant interactions between task and switching. The fitted normalized responses can be seen in Figure 4B.
Correlations between source activity and behavioural measures

We correlated the reduction in switch cost with preparation with normalized source activity on switch trials (Figure 4C). There were no significant correlations with activity in the right FEF. For the left IPS, we combined the activity measures from the two close peaks, and whilst this did not correlate with the behavioural measure on Pro trials \( r = -0.006, p = 0.987 \), it did on Anti trials \( r = 0.783, p = 0.007 \); activity in the left IPS on task-switch trials significantly predicted the extent to which subjects used the cue to prepare for a switch of task (this is also the case for each IPS peak individually).

Discussion:

Being able to shift our intention, prior to performing a new task, is essential for achieving our apparent mental flexibility (Monsell and Mizon, 2006); it has however proven difficult to identify the neural correlates of anticipatory control, for numerous reasons: (i) the temporal resolution of fMRI is such that it is difficult to capture neural activity uniquely associated with the cue (e.g. Kimberg et al. 2000); (ii) there is little non-human primate electrophysiology work on task-set control (although see Yamada et al. 2010); (iii) the tasks are often more complex than the well-studied pro and anti-saccade tasks, tend to differ widely across different studies, making it difficult for consensus to emerge. We used techniques with real-time resolution, alongside tasks with well-documented neural correlates, to explore the mechanisms by which subjects switch between these tasks.

We designed our paradigm in an attempt to maximise subjects’ use of advance cues. Accordingly, in our behavioural data we observed a significant reduction in the RT cost of switching task. Furthermore, whilst subjects were more error prone when there was no information with the target (i.e. on white arrow trials), when subjects had time to prepare this effect was small. In the ERP data, mirroring the behavioural preparation effect we observed a significant cue-locked positive voltage increase for switch trials relative to stays trials. Furthermore, those subjects who showed the greatest behavioural preparation effect for switching to the Anti task also showed the greatest cue-locked switch-stay voltage difference whilst preparing for the Anti task. With good evidence from the behavioural and ERP data for cue-locked preparation, we also analysed the ERFs to explore the cortical correlates of this effect. In the MEG data there was a significant increase in activity in the right FEF and left IPS when subjects anticipated a switch in task. Furthermore, those subjects who showed the greatest behavioural preparation effect for switching to the Anti task also showed the greatest left IPS activity on Anti trials.

Behavioural switch cost:
In addition to demonstrating that subjects were indeed preparing following the cue, we also wanted to use the behavioural data to replicate an effect often seen in Pro / Antisaccade paradigms – the asymmetric switch cost. Across various task-switching paradigms in which the two tasks are not equally easy, it is common to observe the largest switch cost for the easiest task (e.g. Allport et al. 1994; Mueller et al. 2009). It is thought that when performing the hardest task, the easiest or most ‘prepotent’ task needs suppressing. Thus, when subjects switch back to the easier task they have to overcome this inhibition and therefore incur a greater switch cost. It is however also worth noting that much of this difference is often driven by subjects being much faster at repeating the easy task than they are at repeating the difficult task (e.g. Mueller et al. 2009); often there is little difference in performance of the two tasks on switch trials (see Figure 2B). Our asymmetric effect was present in both the RT and error data.

Cue-locked ERP correlates of task-set control:

We observed an early ERP effect that distinguished switching to the Pro task and switching to the Anti task (280-340 ms). However, this does not mirror the asymmetric switch cost, since the ERP effect is present for switching to the Anti task rather than for switching to the Pro task. Indeed we have previously observed this ERP effect for tasks that are equally difficult (Astle et al. 2008a, 2008b) and we think that this early ERP effect reflects some aspect of cue processing: The effect resembles closely the well-documented ‘frontal selection positivity’ and ‘occipital selection negativity’, which are revealed by comparing the ERPs elicited by attended-to targets with unattended-to distracters in non-spatial attention tasks (Hillyard and Munte 1984). Subjects could have processed cues indicting a switch to the Anti task like ‘targets’, and stay cues like ‘distracters’, because of their relative importance; the switch cues may take on greater importance when they instruct subjects to prepare to perform the most difficult (Anti) task. Indeed, when we compared the proportion of errors that subjects made, we found that there was no significant difference between coloured and white arrow trials when the cue had indicated that subjects should prepare for an Anti trial, whereas there was when subjects prepared for a Pro trial. This implies that subjects rely heavily on the preparatory cue when it tells them to prepare to perform the Anti task, because their accuracy is not influenced by the information with the subsequent target (or lack thereof).

The largest ERP effect that we observed was common to switching to the Pro and Anti tasks, and we think that this effect indexes the process that resulted in the reduction in behavioural switch costs with preparation. We observed a large centro-parietal switch-related positivity regardless of whether subjects were switching to the Pro task or to the Anti task. This has been observed many times previously, and in all cases has mirrored a reduction in switch costs (e.g. Astle et al. 2008a, 2008b, 2009; Lavric et al. 2008; Mueller et al. 2009; Nicholson et al. 2005; Rushworth et al. 2002), although it remains unclear what the ERP effect indexes exactly. In our data it does not just mirror this process, on Anti trials it correlates significantly with it across subjects. We do not think that this ERP effect indexes an obligatory task-switching process. If the switch-stay ERP difference was driven by an additional task-set reconfiguration
process we might expect it to be present on switch trials but not on stay trials (since the task-set is already configured on a stay trial). However, separate analysis of the topographical distribution versus amplitude of the ERP effect indicates that the difference between switch and stay trials is primarily quantitative rather than qualitative (Astle et al. 2009; Wylie et al. 2009). Furthermore there are some demonstrations of subjects reducing their switch cost, in the absence of this cue-locked ERP effect (Astle et al. 2008b), implying that it is does not reflect an obligatory process. We think that this ERP effect indexes the selective biasing of the to-be-used stimulus-response mapping, prior to its use (Duncan and Desimone, 1995). Such a process would be nonessential but nonetheless beneficial if it could be performed in advance of target onset, furthermore it would be less necessary if the two sets of stimulus-response mappings were more readily separable (as in Astle et al. 2008b). Of course this advance biasing would be most beneficial for an Anti trial, because the stimulus-response mapping that the arrow naturally affords is incorrect on these trials. This may be why we observed the significant correlation between the size of this ERP preparation effect and the reduction in switch costs in the behavioural data on Anti and not Pro trials; the quality of subjects’ preparation really counts when they have to perform the counter-intuitive Anti task.

Cue-locked MEG comparisons:

In our MEG data we observed significant switch-stay differences in the FEF and IPS, a network traditionally implicated in the top-down control of eye movements (Ettinger et al. 2008; Connolly et al. 2002). Firstly, our MEG data implicate this network in tasks that do not require eye movements per se. This is consistent with previous reports that the temporary deactivation of the FEF using transcranial magnetic stimulation techniques impairs attentional orienting (Smith, Jackson and Rorden, 2006; Smith, Jackson and Rorden, 2009), and that the covert orienting of attention is critically dependent upon the ability to execute eye movements (Smith, Rorden and Jackson, 2004). It is important to note that this network is not active in our data because subjects are preparing eye-movements per se. There are various reasons for this: i) the response does not require eye-movements; ii) the imperative stimulus was central rather than peripheral; and, iii) most importantly, the cue does not provide information as to the correct direction, just that subjects should switch or repeat the task-set – i.e. the cue does not provide the information necessary to prepare an eye-movement. Secondly, and more importantly, our data implicate this network in the effective preparation for a switch of task. We do not suggest that these mechanisms are switch-specific, rather that this network subserves a domain-general function useful for various top-down control processes. The FEFs are often active in delay periods, whether preparing to saccade (e.g. Connolly et al. 2002; Prime et al. 2010), maintaining information in visual short term memory (VSTM) (e.g. Prime et al. 2010; Offen et al. 2010), or orienting attention prior to the appearance of a target (e.g. Offen et al. 2010). Likewise, the IPS has been implicated in various types of delay activity, such as that involved in VSTM maintenance (e.g. Xu and Chun, 2006), and anticipatory sensorimotor transformations (e.g. Moon et al. 2007). We suggest that the aforementioned regions are active when we change our intentions, because they are critically involved in biasing a spatial sensorimotor mapping, and hence their
role is very beneficial in anticipatory task-set switching process. Previous research has demonstrated that
activity in the FEF and IPS is capable of biasing the allocation of spatial attention (e.g. Smith et al. 2006,
2008; Taylor et al. 2007), one possibility is that similar biasing signals underpin anticipatory task-set
control. In essence, a task-switching paradigm is much like many other attentional paradigms which
introduce competition; top-down biasing, in this case of a stimulus-response mapping relative to an
alternative, is necessary in order for subjects to achieve their goal. The strength of this preparatory bias
would be particularly important on an Anti trial, because the mapping that is needed is not afforded
naturally by the target. This maybe why, as was the case in the ERP data, activity in the left IPS only
correlated with the behavioural reduction in switch costs on Anti trials.

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Figure Legend:

Figure 1: A trial order schematic of the task, showing a repeat trial followed by a switch trial.

Figure 2: A) The reduction in RT switch costs with preparation. B) The asymmetric RT switch cost. C) The RT data from both the EEG and MEG sessions. D) The error rate data from both the EEG and MEG sessions. E) Topographical plots for switch minus stay trials, averaged across 160 to 800 ms post cue, the upper two plots show the ERPs for the Pro and Anti task, the lower two plots show the ERFs for the same window. F) Topographical plots for switch minus stay trials, averaged across 280 to 360 ms post cue, plotted as in ‘E’.

Figure 3: A) Grand-average cue-locked ERPs, with red lines representing Anti and green lines representing Pro trials, solid lines show switch and dashed lines show repeat trials. The grand-averages show the mean amplitude for the Midline-Frontal, Central and Posterior clusters. B) Correlations between the size of the switch minus repeat difference at Cz and the reduction in RT switch costs with preparation.

Figure 4: A) The Switch>Stay contrast overlaid on a standard MNI template brain. B) The fitted responses from each of the significant peaks, showing the values used by SPM 8 in the statistical comparison, which are normalized across all conditions and all subjects. C) Correlations between the size of the switch effect at the left IPS (left) and right FEF (right) and the reduction in switch costs with preparation (RT).
References:


Connolly JD, Goodale MA, Goltz HC, Munoz DP (2005) FMRI activation in the human frontal eye field is correlated with saccadic reaction time. J Neurophysiol 94(1) 605-11


Trial sequence schematic

- First frame: 200/1200 ms
- Second frame: 200 ms
- Third frame: 2600/1600 ms
- Fourth frame: 200/1200 ms
- Fifth frame: 200 ms