

Modulation of brain activity by selective task sets observed using event-related potentials

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Abstract

We investigated the ability of subjects to shift dynamically between selective task sets, using informative trial-by-trial cues. Two tasks were used which involved non-overlapping neural systems and different hemispheric specialization. In a verbal task, subjects decided whether a letter string was a real word or a non-word. In a spatial task, subjects decided whether an angle was acute or obtuse. A behavioural experiment showed that performance improved when cues predicted the upcoming task (80% validity), compared to when neutral cues did not afford selective task sets. Event-related potentials (ERPs) revealed brain activity related to forming selective task expectations, to switching tasks, and to the modulation of target processing as a function of such expectations and switches. Activity predicting the probable task started over parietal electrodes 160 ms after cue presentation, while activity related to task switching started at frontal electrodes around 280 ms. Both types of activities developed before target onset. Target processing was significantly influenced by the validity of the cue prediction, including strong modulation of language-related potentials. These results show that it is possible to switch dynamically between task sets involving distinct neural systems, even before the appearance of an imperative target stimulus, and that the nature of the task sets can influence neural activity related to task-set reconfiguration. Selective task sets can in turn modulate the processing of target stimuli. The effects also apply to the case of foveally presented words, whose processing has often been hypothesized to be automatic and outside the influence of selective attention.

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1. Introduction

Switching between different aspects of tasks or between tasks is costly. But it is possible to overcome some of the costs, and optimise behaviour, if the task attributes or the tasks themselves are predictable. For example, in the field of attentional orienting, it is well documented that prior knowledge about the spatial location (Posner, 1980) or temporal interval (Griffin, Miniussi, & Nobre, 2001; Nobre, 2001) of an event, can improve task performance. In the task-switching literature, prior knowledge about the relevant task set can at-

tenuate task-switching costs under most conditions (Meiran, 1996; Rogers & Monsell, 1995).

Switching between tasks is clearly a complex cognitive act, which involves several components (Meiran, 2000; Monsell, 1996, 2003). The specific components involved and their interplay are yet to be resolved (see Monsell, 2003), but switching costs probably include processes of task-set reconfiguration (Meiran, 1996; Rogers & Monsell, 1995), transient interference from previous stimulus–response mappings (Allport, Styles, & Hsieh, 1994; Allport & Wylie, 1999), and long-term task interference effects (Kray & Lindenberger, 2000; Mayr, 2002; Mayr & Keele, 2000). Each of these processes, in turn, may end up being defined by several constituent operations. For example, Meiran (2000) has suggested that there may be differential contributions

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of selecting the stimulus dimensions (attentional set) versus the relevant response rules (intentional set) during the task-reconfiguration phase.

Brain imaging experiments have begun to reveal the network of brain areas that participate in task switching. Of particular interest has been the identification of brain areas involved in controlling the reconfiguration of task sets (e.g., Brass & von Cramon, 2002; Kimberg, Aguirre, & D'Esposito, 2000; MacDonald, Cohen, Stenger, & Carter, 2000; Sohn, Ursu, Anderson, Stenger, & Carter, 2000). Overall, the studies highlight medial and lateral regions of prefrontal cortex and parietal cortex as brain areas of potential relevance to task-switching operations. The specific contribution of participating regions is also beginning to be investigated (Brass & von Cramon, 2002; Luks, Simpson, Feiwell, & Miller, 2002). A study combining functional magnetic resonance imaging (fMRI) and transcranial magnetic stimulation (TMS) has shown that the neural mechanisms of task-set reconfiguration may depend on what aspect of task performance task-switching emphasises (Rushworth, Hadland, Paus, & Sipila, 2002). The pre-supplementary area was critically involved in reconfiguring an intentional set, in which different stimulus–response mappings were required between tasks; but was not critical in reconfiguring an attentional set, in which different stimulus dimensions were relevant to drive responses between tasks.

The excellent temporal resolution of event-related potentials (ERPs) has also begun to be exploited to identify the different components of task switching (Karayanidis, Coltheart, Michie, & Murphy, 2003; Rushworth, Passingham, & Nobre, 2002; Swainson et al., 2003; Wylie, Javitt, & Foxe, 2003). ERPs have clearly revealed cue-related task-set reconfiguration processes that occur prior to the presentation of the imperative target stimuli, and separate target-related activity related to implementing a task switch on the imperative stimulus (Karayanidis et al., 2003; Rushworth, Passingham et al., 2002). Research using ERPs has also begun to reveal the flexibility in the neural mechanisms underlying task switching. The patterns of activity associated with reconfiguring and implementing a switch of tasks are different depending on the aspect of the task emphasised. When tasks require a switch of intentional set, cue-related ERPs during reconfiguration show differences over medial frontal and then parietal regions, and target-related ERPs during task implementation show differences in potentials linked to responses (Rushworth, Passingham et al., 2002). When tasks require a switch of attentional set, cue-related ERPs during reconfiguration show differences over lateral frontal and then parietal regions, and target-related ERPs during task implementation show differences in early potentials linked to visual analysis (Rushworth, Passingham, & Nobre, *in press*).

The present experiment combined ERPs with a task-cueing manipulation (Biederman, 1973; Mascetti, Nicoletti, Carfagna, Cilia, & Marzi, 2001; Sudevan & Taylor, 1987) in order to probe further the flexibility of the neural mechanisms

involved in task switching. The central question is whether the specific nature of the attentional set may also influence the pattern of neural activity linked to task-set reconfiguration and implementation. Specifically, the question was whether task sets involving different types of material and psychological functions rely on the same or different task-set reconfiguration processes. We used probabilistic cues (Dreisbach, Haider, & Kluwe, 2002) that predicted (80% validity) the likely upcoming task. The two competing tasks used non-overlapping stimulus sets and made different cognitive demands. Participants decided whether a letter string constituted a real word or not (verbal, lexical-decision task) or decided whether an angle presented in a pie graph was acute or obtuse (spatial, angle-decision task). These verbal and spatial tasks are thought to involve largely non-overlapping neural systems and different hemispheric dominance (Hellige, 1990). The ERP components elicited by the cues predicting the verbal versus spatial task were compared to reveal any contribution of the specific anticipated task sets. The visual appearance of the cueing stimuli and the proportion of switch trials were equated across the conditions, so that any differences isolated neural activity engaged by the nature of the predicted tasks.

2. Materials and methods

2.1. Participants

Two groups of subjects participated as paid volunteers. All subjects were native English speakers and had normal or corrected to normal visual acuity. Participants reported being free of neurological disorders. All were right handed, mean score on the Edinburgh handedness inventory: +90.6 group a; +90.5 group b (Oldfield, 1971). The experimental methods were non-invasive and had ethical approval from the Department of Experimental Psychology University of Oxford, UK.

Seven native English speakers (five females) took part in the behavioural experimental session, lasting about 1 h (group a). They had an age range of 19–29 years (mean 23.10 years). Twenty-four additional subjects (group b) took part in the ERP experimental session, lasting about 2.5 h. Four were subsequently excluded from the analyses because of excessive artifacts during EEG recording (see below). The remaining 20 subjects (10 females) had an age range of 19–29 years (mean 23.14 years).

2.2. Experimental tasks

In both, the behavioural and the ERP experiments, subjects made a discrimination response to a verbal or spatial target stimulus that followed a centrally placed symbolic cueing stimulus. The experimental variables and procedures were the same for both task versions unless otherwise noted. Fig. 1 illustrates the task version used for ERP recording.

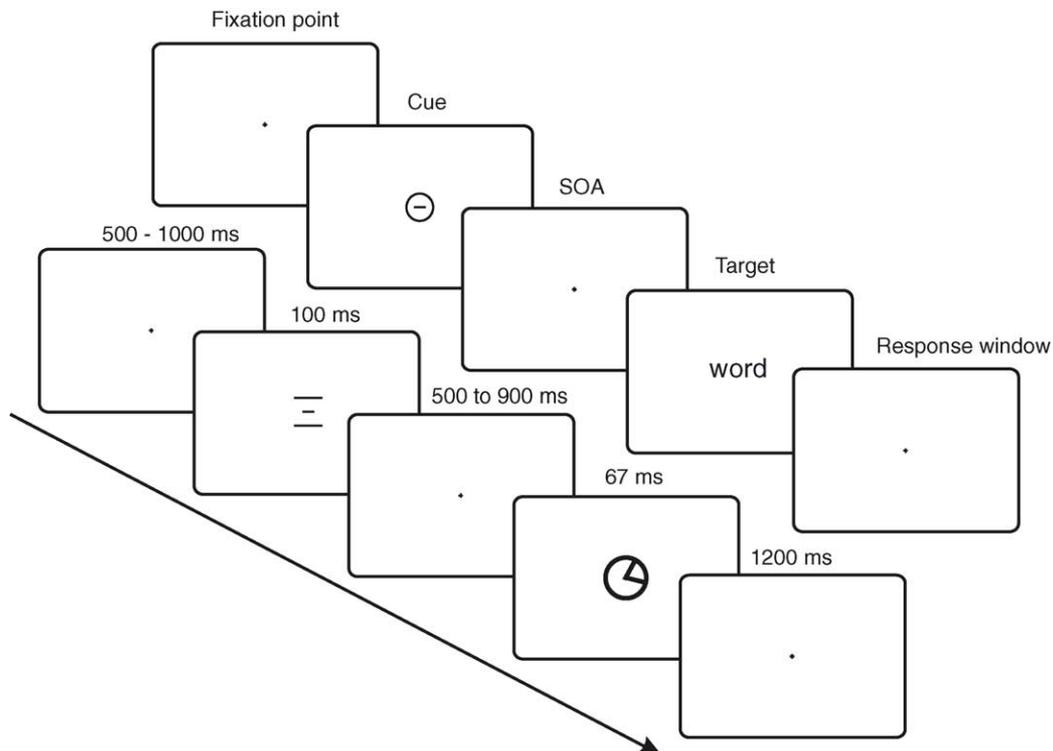


Fig. 1. Time course of the experimental conditions. Subjects fixated on the central cross (0.3° width). A brief (100 ms) cue (80% validity) indicated the target to follow (verbal or spatial). After a random interval of 500–900 ms the target appeared (67 ms). Subjects were instructed to make a discrimination response to the target, which was a lexical decision for verbal target (word or pseudo-word) and angle judgement for the spatial target (acute or obtuse angle).

The main difference between the two versions of the task was in the nature of the cueing stimuli. In the behavioural task (group a), three cues were used. Two cues (\ominus , \oplus , but see Fig. 1 for the exact appearances of stimuli) were informative and predicted (80% probability) the type of target stimulus to follow. A third cue was a neutral question-mark (?) and was followed by verbal or spatial targets with an equal (50%) probability. Informative cues occurred on approximately two-thirds (62.5%) of the trials, and neutral cues occurred on the remaining 37.5% of trials. In the ERP task (group b), only informative cues (80% probability) were presented.

The cue was presented for 100 ms, and was followed by a blank period for a random interval between 500 and 900 ms. The target appeared for 67 ms followed by a 1200 ms window during which subjects responded. A blank screen with a random interval between 500 and 1000 ms was interspersed between trials.

Cues were arbitrary symbolic stimuli. Shapes of the informative cues (\ominus and \oplus) were selected to avoid easy or consistent verbalization and to avoid the appearance of angles. The designation of which cue predicted a verbal or spatial target was counterbalanced across subjects. Targets were imperative stimuli. Verbal targets were letter strings that required a lexical (word/non-word) decision. Spatial targets were angles and required an acute/obtuse decision.

All stimuli were presented centrally, in white colour on a black background. The verbal stimuli were 250 real

words and 250 orthographically and phonologically legal non-words (pseudo words). Words were concrete nouns (4–6 letters) with low ratings of frequency (1–50, mean 13.32); and high ratings of concreteness (mean = 564), imageability (mean = 477), and familiarity (mean = 545) (Oxford Psycholinguistic Database, 1991). Pseudo words were constructed by permuting the letters from the real words, and by replacing single letters when necessary. Verbal stimuli had a height of 7 mm and a width between 17 and 28 mm. Spatial stimuli were acute or obtuse angles presented in a pie-graph format (see Fig. 1). Acute angles used were 70° , 75° , and 80° . Obtuse angles used were 100° , 105° , and 110° . The pie-graph, in which the angles appeared, had a diameter of 24 mm.

2.3. Procedure

Subjects sat in a dimly illuminated room facing a computer monitor placed 100 cm in front of them. They were informed at the beginning of the experiment about the relationship between cue and target type. They were required to maintain visual fixation on a small cross that was continuously present at the centre of the monitor. Subjects made a speeded lexical decision or angle decision using a two-choice button press. Subjects used their right and left hands alternately for half of the task. The hand used for response was assigned randomly at the beginning of each block. Subjects used the first

and second fingers of the same hand to identify the specific verbal (word/pseudo) and spatial (acute/obtuse) stimuli. The finger assigned to each specific target was counterbalanced across subjects.

In the purely behavioural task, subjects performed 11 blocks of 96 trials, including an initial practice block. For the ERP task, subjects sat in an electrically shielded room. They performed 11 blocks of 100 trials, including an initial practice block. We asked subjects to suppress saccades and to avoid blinking during the active portions of the task. Within blocks, short pauses occurred after every 20 trials to enable subjects to blink and move their eyes. Additional pauses occurred between blocks, and subjects indicated when they were ready to proceed.

In the ERP session, the electroencephalographic (EEG) activity was recorded continuously from 54 scalp sites using tin electrodes mounted on an elastic cap (Electro-cap Inc.) and positioned according to the 10–20 International System (AEEGS, 1991). The montage included 8 midline sites (FPZ, FZ, FCZ, CZ, CPZ, PZ, POZ, and OZ) and 23 sites over each hemisphere (FP1/2, AF3/4, AF7/8, F3/4, F5/6, F7/8, FC1/2, FC3/4, FC5/6, FT7/8, C3/4, C5/6, T7/8, CP1/2, CP3/4, CP5/6, TP7/8, P3/4, P5/6, P7/8, PO3/4, PO7/8, and O1/2). Additional electrodes were used as ground and reference sites. The ground electrode was positioned between FPZ and FZ along the midline. The right mastoid served as the active reference for all electrodes. Recordings obtained from the left mastoid electrode were used off-line to re-reference the scalp recordings to the average of the left and right mastoids. Electrode impedance was less than 5 k Ω . The signal was amplified 20,000 times and digitized at a sampling rate of 250 Hz. Data were recorded with a band-pass filter of 0.03–100 Hz.

Horizontal and vertical eye movements were detected by recording the electrooculogram (EOG). The voltage difference between two electrodes located to the left and right of the external canthi recorded horizontal eye movements. The voltage difference between electrodes located above and beneath the right eye recorded vertical eye movements and blinks.

The epoching of the ERPs was performed off-line. Epochs started 200 ms before and ended 1824 ms after stimulus onset. Epochs with excessively noisy EEG, eye-movement artifacts (blinks or saccades) or incorrect behavioural responses were rejected. Cue- and target-related epochs were discarded if the voltage exceeded $\pm 150 \mu\text{V}$ between -200 and 800 ms at any electrode site. Epochs where voltage exceeded $\pm 50 \mu\text{V}$ at the VEOG or HEOG electrodes between -200 and 800 ms were also discarded. Trials with reaction times (RTs) faster than 130 ms or slower than 1100 ms were regarded as errors, and were also excluded. To maintain an acceptable signal-to-noise ratio, a lower limit of 30 artifact-free trials per subject per condition was set. Four subjects failed to meet this criterion and were excluded from further analysis.

Separate averaged ERP waveforms were constructed for four types of cues according to the predicted *task* (verbal, spa-

tial) and the *switching* requirement (switch, stay). Four types of ERPs elicited by targets were also constructed, according to the *target type* (verbal, spatial) and the *validity* of the preceding cue (valid, invalid). In the cue analyses, the actual mean number of trials contributing to the averages ranged between 175 and 179. In the target analyses, the number of trials contributing to the averages was 85 in both invalid conditions and 350 in both valid conditions. In addition, separate target waveforms were constructed for the two types of verbal stimuli (word, pseudo) in valid and invalid trials. For the two types of verbal stimuli, 176 trials contribute to valid trials and 43 to invalid trials.

2.4. Analysis

2.4.1. Behavioural data

Behavioural effects of cues predicting the nature of the upcoming task were analysed using repeated-measures analyses of variance (ANOVAs). Separate ANOVAs tested for effects on % correct responses and mean reaction times for correct responses. For the purely behavioural experiment, the dependent variables were subjected to a two-factor ANOVA, which assessed the effects of *target type* (verbal, spatial) and cue *validity* (valid, neutral, and invalid). Because of the way the task was coded, it was not possible to test for effects of the requirement to switch task from the previous trial. For the ERP experiment, a three-factor ANOVA was used, testing the effects of *target type* (verbal, spatial) and cue *validity* (valid, invalid), and task *switching* from the previous trial (switch, stay).

2.4.2. ERPs elicited by cues

Significant effects of task factors upon the ERPs elicited by verbal and spatial task cues were evaluated using repeated-measures analyses of variance. The factors typically tested for cue stimuli were: the *task* predicted (verbal, spatial), the *switching* requirement (switch, stay), electrode *hemisphere* (left, right), and *electrode* site.

Because there were no a priori hypotheses for how the specific task sets predicted would affect the ERPs, we employed an analysis strategy that tested for effects of task and switching factors over successive time bins at distinct scalp regions. Five region-specific sets of analyses were performed for both cue and target stimuli. Successive time bins in steps of 40 ms between 0 and 600 ms were used for analyses over midline, frontal, temporal, central, and posterior regions of the scalp. The midline region included electrodes FPZ, FZ, CZ, PZ, and OZ. The frontal region included electrodes FP1/2, AF3/4, AF7/8, F5/6, and F7/8. The central region included electrodes FC1/2, CP1/2, FC3/4, C3/4, and CP3/4. The temporal region included electrodes FC5/6, CP5/6, FC7/8, T7/8, and TP7/8. The posterior region included electrodes P5/6, P7/8, PO3/4, PO7/8, and O1/2. The factor hemisphere did not apply to the midline analysis.

In order to test for differences in the topographical distributions of successive cue-related ERP effects an additional

series of analyses using normalised data were also performed (McCarthy & Wood, 1985). The effect of predicted task was isolated by subtracting waveforms elicited by spatial cues from waveforms elicited by verbal cues. The effect of switching requirement was isolated by subtracting the waveform elicited in the stay condition from the waveform in the switch condition. Topographies were compared over the time bins where effects were identified, over the 20 electrode pairs used for the lateral region analyses (i.e., excluding midline electrodes). The factors in the topographical analyses were time bins, hemisphere, and electrode.

2.4.3. ERPs elicited by targets

Analyses directed at testing modulations of specific ERP components were performed for the target stimuli. Verbal and spatial targets were analysed separately, because of the marked differences in the physical characteristics of the stimuli used (letter strings versus angles, see Section 2 and Fig. 1). Factors tested were: validity of preceding cue (valid, invalid), electrode hemisphere (where relevant), and electrode location. In the case of verbal stimuli, the additional factor of letter string type (word, pseudo) was also tested.

Electrode locations and time windows for measurements were determined from inspection of the group grand-average waveforms. Identifiable visual ERP components (P1 and N1) were analyzed for both types of target stimuli (verbal, spatial). P1 and N1 were analyzed at the three lateral occipital electrode pairs where they were maximal. Mean amplitude of P1 was analyzed at PO3/4, PO7/8, and O1/2 between 80 and 130 ms. Mean amplitude of N1 was analyzed at P5/6, P7/8, and PO7/8 between 140 and 190 ms. The P300 potential (P3) was analyzed at F3/Z/4, C3/Z/4, and P3/Z/4. Different time intervals were used for different target types. Mean amplitude of the P3 was calculated between 450 and 650 ms for verbal stimuli, and between 400 and 600 ms for spatial stimuli. In addition, the N330 and N400 language-related ERP components (N3 and N4, respectively) were measured for verbal stimuli only. The electrodes used were the same as those for the P3 component. Mean amplitude of the N3 was obtained between 280 and 360 ms. Mean amplitude of the N4 was obtained between 380 and 460 ms. All mean amplitude values were calculated with reference to the 200 ms pre-stimulus baseline.

Regional analyses were also carried out to identify other possible unpredicted effects of target modulation. As for cue stimuli, the experimental factors were tested over successive time bins at midline, frontal, central, temporal, and posterior scalp regions.

The Greenhouse–Geisser epsilon correction for non-sphericity was used where appropriate (Jennings & Wood, 1976). Only the corrected probability values (and degrees of freedom) are reported. To avoid false-positive results, in light of the multiple tests performed in the regional analyses, only effects that occurred simultaneously in two regions or over two successive time bins were considered reliable.

3. Results

3.1. Behavioural results

Fig. 2a shows the results for the purely behavioural experiment. Subjects performed the spatial and verbal tasks with an equally high level of accuracy—98% correct in each case (range, 97–99%). The results showed that cues predicting the probable upcoming task significantly influenced performance, by both speeding responses to expected predicted targets and by slowing responses to unexpected, unpredicted targets. The main factor of target validity was significant ($F(2,6) = 11.96$; $p = .001$). Post hoc contrasts of means using Helmoltz Comparisons showed that RTs to validly cued targets (605 ms) were significantly faster than RTs to both neutral (629 ms) and invalid targets (667 ms) ($F = 15.23$; $p = .002$). Reaction times during invalid trials were also significantly slower than during neutral trials ($F = 8.68$; $p = .012$).

Fig. 2b shows the pattern of behavioural findings during the ERP experiment. Accuracy of task performance was again high 89.3% (range, 80–97%) and did not differentiate between the spatial and verbal tasks. However, overall, subjects were faster to respond to spatial targets (650 ms) than to verbal targets (656 ms) ($F(1,19) = 14.47$; $p = .001$). The analysis confirmed the significant effects of predictive

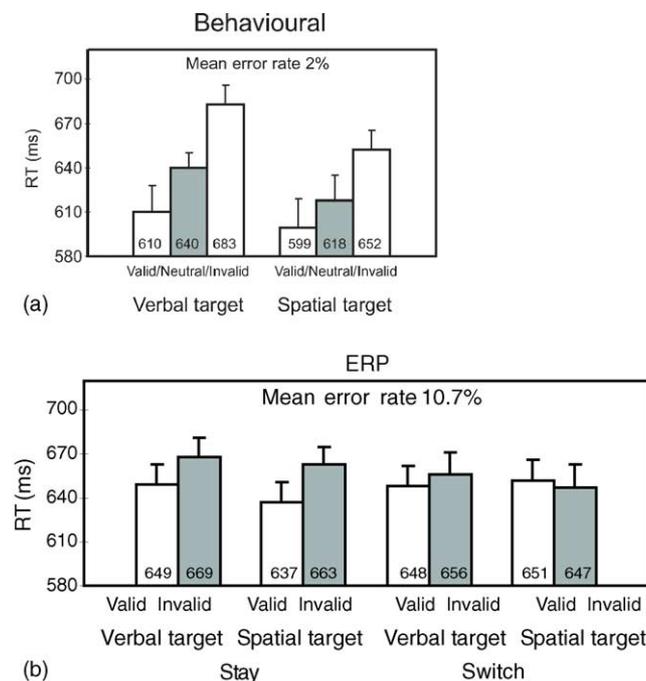


Fig. 2. Mean RT for verbal and spatial targets for both experiments. (a) For the behavioural experiment, results are plotted according to the factor of cue validity (valid, neutral, and invalid). (b) For the ERP experiment, results are plotted according to the factors of cue validity (valid and invalid) and the requirement to switch task from the previous trial (switch and stay). In both experiments, reaction times for validly cued targets were significantly faster, compared to invalidly cued targets.

cues upon performance. Mean RTs to validly cued targets (647 ms) were significantly faster than RTs to invalidly cued targets (659 ms) ($F(1,19) = 30.31$; $p < .001$). The main effect of switching task from the previous trial did not reach significance ($F(1,19) = 1.17$; $p = .290$). However, cue validity and switching interacted strongly ($F(1,19) = 19.50$; $p < .001$). Subsidiary ANOVAs showed that validity effects were significant for trials in which the task was repeated (23 ms) ($F(1,19) = 14.47$; $p = .001$), but were negligible when the task switched from the previous trial (1 ms) ($F(1,19) = .54$; $p = ns$). There were no further interactions between the factors.

3.2. ERP results

3.2.1. Cues

Fig. 3a and Fig. 4a show representative ERP waveforms elicited by the predictive cue stimuli. Waveforms were characterized by pronounced visual evoked responses with lateral posterior maxima (P1 and N1) followed by a positive peak anteriorly around 200 ms and a sustained positivity during the remaining of the epoch over the posterior electrode sites. Analyses revealed that information predicting the type of upcoming task and the requirement to switch tasks from

the previous trial exerted significant effects on brain activity before the imperative target stimuli. Waveforms elicited by cues predicting verbal targets elicited a larger N1 component than for spatial cues over the left posterior sites, and showed greater sustained positivity over central and posterior sites, especially over the midline and right hemisphere, starting around 280 ms. Waveforms elicited by cues predicting task switching relative to task repetition were more negative over frontal and central regions of the scalp between 280 and 440 ms, and more positive over parietal and posterior regions of the scalp during the later parts of the waveforms.

3.2.1.1. Effects of predicted task. The nature of the predicted task influenced brain activity elicited by the cue before the requirement to switch task from the previous trial. The first reliable effects of the task factor (verbal, spatial) were observed at 160–200 ms at the posterior and temporal regions as cue \times hemisphere ($F(1.0,19.0) = 8.55$; $p = .009$) and cue \times hemisphere \times electrode ($F(2.2,41.0) = 3.54$; $p = .03$) interactions. During this time, the N1 component elicited by verbal cues was more negative than those elicited by spatial cues, primarily over posterior electrodes in the left hemisphere (maximal at PO7, see Fig. 3).

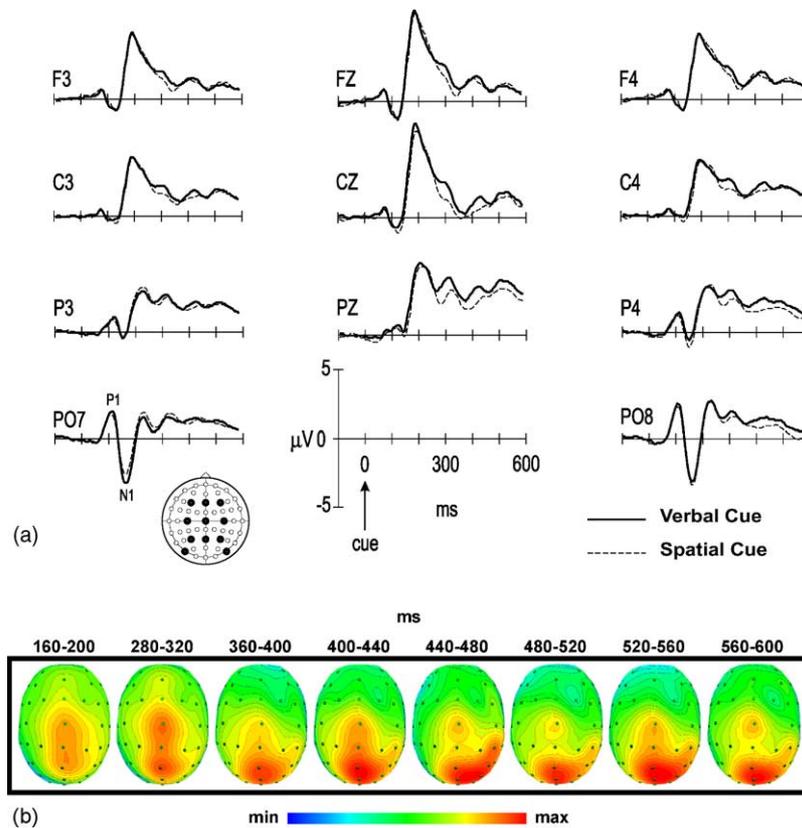


Fig. 3. (a) Grand-averaged waveforms ($n = 20$ subjects) elicited by the predictive cues for the verbal (solid lines) and spatial (dashed lines) condition. The onset of the cue stimulus (at 0 ms) is labelled. Main ERP features, such as P1 and N1, are marked in these sample waveforms for orientation. The electrode montage used for the experiment is shown at the bottom. The locations of the electrode sites for the sample waveforms are shaded black. Polarity of the waveforms is plotted with positive values upward in this and subsequent figures. (b) Topographies of the significant effects of predicted task using normalised data. Red colour represents maximum relative positive voltage difference and blue represents maximum relative negative voltage difference. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of the article.)

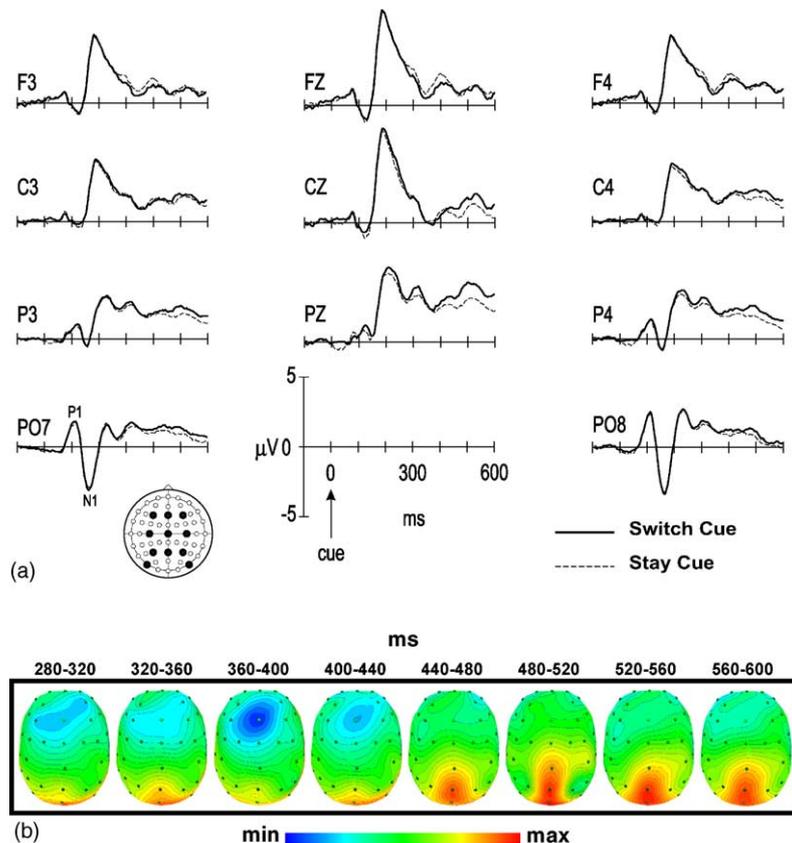


Fig. 4. (a) Grand-averaged waveforms elicited by the predictive cues indicating the requirement to switch task (solid lines) and to stay with the previous task set (dashed lines). (b) Topographies of the significant effects of predicted switching requirement using normalised data. Waveform polarity and topography colour scheme as in Fig. 3. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of the article.)

The next effects occurred between 280 and 320 ms in the midline and central analyses (task \times electrode interaction, $F_s > 3.24$; $p < .05$). During this time bin, verbal cues elicited a relatively more positive response compared to spatial cues over the central lateral region of the scalp. Significant effects re-emerged at 360–600 ms at central, temporal, and midline regions (task \times electrode: central, 360–600 interval— $F_s > 4.93$; $p < .030$; temporal, 360–560 interval— $F_s > 4.83$; $p < .018$; midline, 360–440 and 480–560— $F_s > 4.38$; $p < .026$). Effects developed later over the posterior region, starting at 400 ms (main effect of task— $F_s > 4.19$; $p < .05$; task \times hemisphere, 440–580 and 520–560 intervals— $F_s > 5.82$; $p < .026$; task \times electrode, 520–600 interval— $F_s > 3.46$; $p < .042$). The pattern indicated a relative positivity for verbal cues, primarily over posterior sites, including the more posterior electrodes in the central and temporal regions. The effect had a right-hemisphere bias.

Comparison of the topographies using normalised data suggested at least two separate effects of the predicted task upon the ERP waveforms (Fig. 3b). Difference waveforms (verbal minus spatial) were compared over successive time bins with significant effects. Differences in the distribution of the effects during the N1 time period (160–200) and the next significant effects (280–320) approached significance

(bins \times hemisphere— $F(1.0,19.0) = 3.49$; $p = .080$). Between 280 and 600 ms the distribution of the effect changed gradually from a widespread positive effect centred over the parietal scalp to a more focused posterior effect centred over occipital scalp and accompanied by a negative effect over frontal electrodes. Between successive time bins, the difference in topographies approached significance between 440–480 and 480–520 ms ($F(4.28,81.31) = 2.38$; $p = .06$).

3.2.1.2. Effects of switching task. Brain activity following cues indicating a required task switch, compared to cues signalling a task repetition, differed from 280 ms to the end of the analysed waveform. Switch cues were associated with more negative voltage over frontal and central scalp regions (280–440 ms), followed by more positive voltage over parietal and posterior regions in the later part of the waveform (440–600 ms). The first effects occurred over the frontal region (switching \times electrode, 280–400 ms— $F_s > 2.54$; $p < .05$). Effects over central and midline regions started at 280 ms and persisted until 600 ms (switching \times electrode, 280–400 ms— $F_s > 3.27$; $p < .05$). The posterior effects occurred during the later part of the waveform (main effect of switching, 400–600 ms— $F_s > 5.52$; $p < .05$).

Topographical analysis confirmed the existence of two separate effects with different distribution over the scalp (Fig. 4b). Comparisons of significant switching effects (switch minus stay) over successive time bins showed a significant discontinuity in the distribution of the switching effects at 440 ms (bin \times electrode pair, $F(2.90,55.03) = 3.40$; $p < .05$).

3.2.1.3. Relative effects of task type and task switching. The effects of predicted task type and the requirement to switch were qualitatively different. Comparison of the topographies of the two effects using normalised data at time bins, when both effects were significant, showed that the scalp distributions of the effects were significantly different throughout (280–320, 360–600 in 40 ms bins, condition \times electrode pair interaction, $F_s > 3.55$; $p < .05$).

3.2.1.4. Interactions between task type and task switching. The effects of task switching depended to some extent on the nature of the task predicted, as revealed by interactions between the task-type and task switching factors. Interactions between the two factors occurred between 320 and 520 ms over midline and central regions (task \times switching \times electrode interaction, midline and central regions, 320–520 ms, $F_s > 3.95$; $p < .045$)

and between 320 and 560 ms over the temporal region (task \times switching \times electrode interaction, temporal region, 320–560, $F_s > 3.41$; $p < .032$). During this period, the negative midline frontal and central modulation and the positive parietal modulation associated with switching cues were larger when the verbal task was predicted than when the spatial task was predicted.

3.2.2. Spatial targets

Fig. 5 shows grand-averaged ERP waveforms elicited by valid and invalid spatial targets from representative electrodes.

3.2.2.1. Visual-evoked components. Target validity did not modulate the P1 or N1 visual components. The P1 was maximal over electrodes PO7/8, as revealed by a main effect of electrode ($F(1.9,35.3) = 10.40$; $p = .001$). The N1 was largest over electrodes P5/6 with a right hemisphere bias, as indicated by a main effect of electrode ($F(1.5,28.1) = 5.29$; $p = .018$) and an interaction between electrode and hemisphere ($F(1.2,22.0) = 12.14$; $p = .001$).

3.2.2.2. P300 component. The P3 was significantly larger for the invalid condition when compared with the valid condition (8.69 μ V versus 7.99 μ V) ($F(1.0,19.0) = 5.15$; $p = .035$).

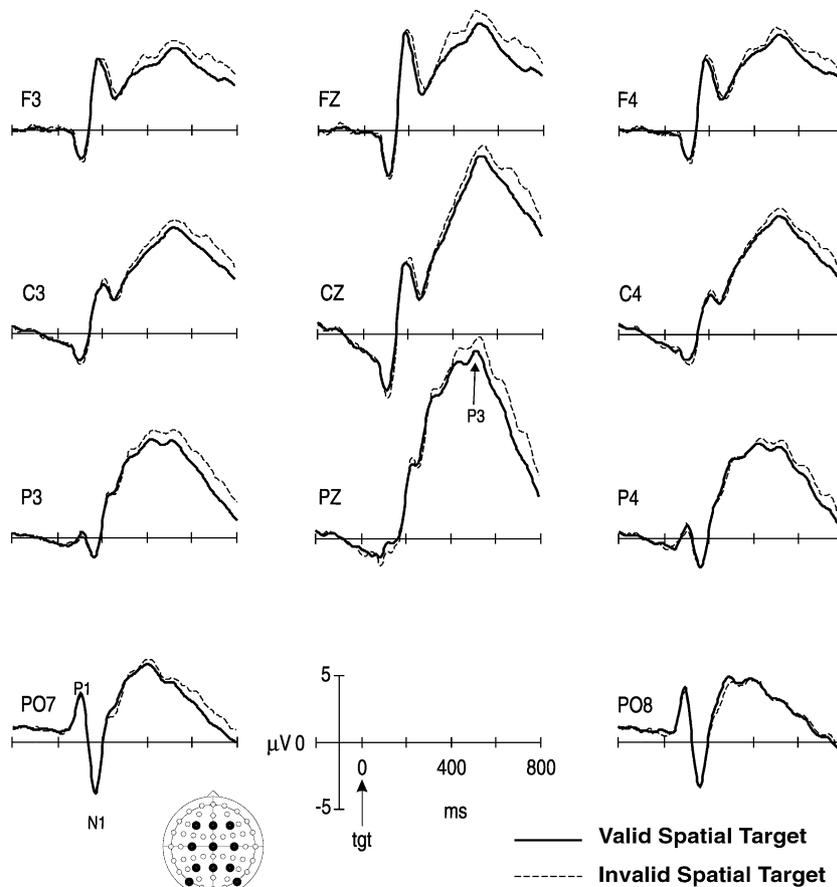


Fig. 5. ERPs elicited by valid (solid lines) and invalid (dashed lines) spatial targets from representative electrodes. The onset of target (Tgt) stimuli is labelled.

The interaction between target validity and hemisphere indicated that the biggest difference occurred at the midline electrodes ($F(1.6,29.9) = 3.84; p = .042$).

3.2.2.3. Regional analyses. The first effects involving target validity occurred at 240–280 ms in all regional analyses as an interaction between target validity and electrode ($F_s > 3.50; p < .05$). During this time, ERPs elicited in valid trials were more negative than those elicited by invalid trials over the frontal sites, while the reverse occurred over posterior sites (see Fig. 5). Significant effects involving target validity continued as an interaction with electrode over the frontal region throughout all the time epochs (240–600 ms; $F_s > 5.00; p < .05$). Target validity also exerted a main effect during the 400–520 ms interval at this region ($F_s > 5.00; p < .05$). The frontal-region effects reflected the relative focal positivity of the potentials elicited by invalid targets, which was larger over more anterior electrodes. In the central region, a target validity \times electrode interaction at 360–400 ms ($F(1.8,33.7) = 3.54; p = .046$) indicated a similar effect, at the more anterior electrodes in this region.

Starting at 440 ms, target validity had additional significant effects at midline, temporal and posterior regions, mainly reflecting the larger P3 component elicited by invalid targets.

Main effects of target validity were obtained between 440 and 600 ms at midline and temporal regions, and at 520–600 ms over the posterior region. Target validity \times electrode interactions were obtained between 440 and 560 ms over the posterior region, and target validity \times hemisphere interactions were obtained between 560 and 600 ms over posterior and temporal regions. All F_s were greater than 3.00, $p < .05$. The interaction terms reflected the larger magnitude of these effects over left and central parietal sites (see Fig. 5).

3.2.3. Verbal targets

Fig. 6 shows grand-averaged ERP waveforms elicited by valid and invalid verbal targets from representative electrodes.

3.2.3.1. Visual-evoked components. The P1 and N1 had a similar distribution as for spatial targets, and again showed no significant modulation by target validity.

3.2.3.2. P300 component. No significant differences in the P3 component involving target validity were obtained.

3.2.3.3. Language-related components. Two language-related components were identified with distinct scalp

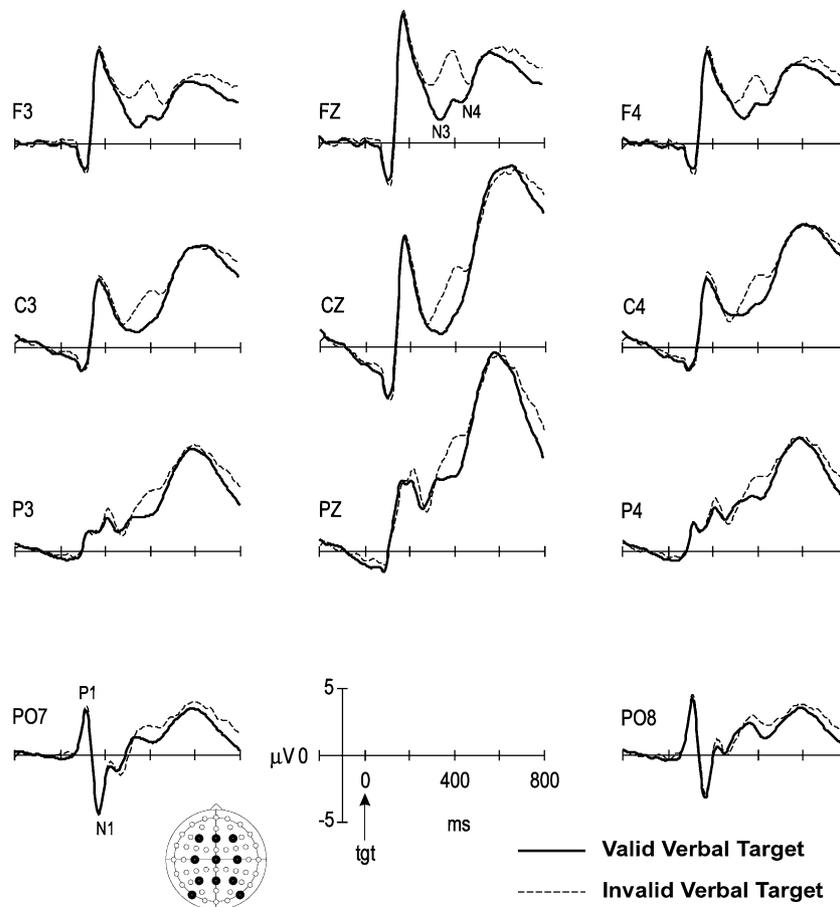


Fig. 6. ERPs elicited by valid (solid lines) and invalid (dashed lines) verbal targets from representative electrodes.

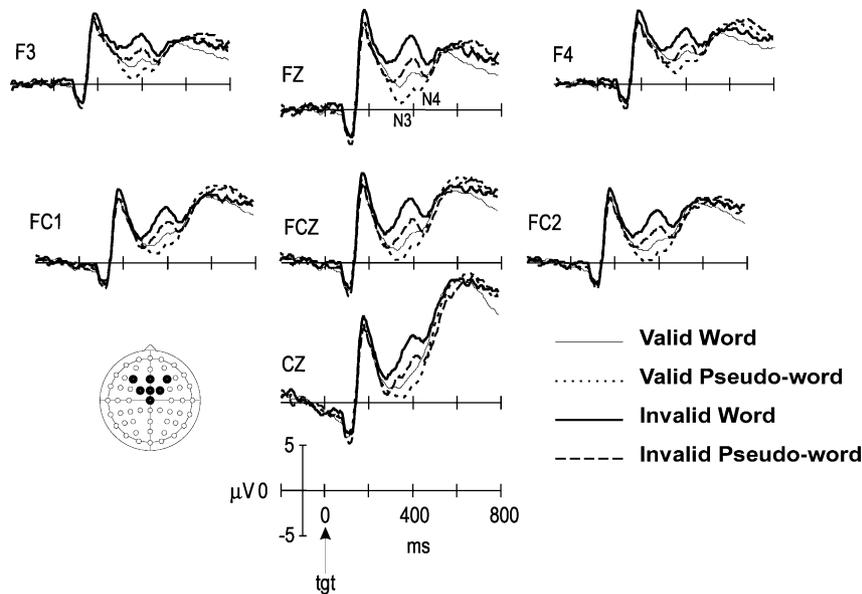


Fig. 7. Grand-averaged ERPs to valid and invalid verbal targets divided according to words (solid lines) and pseudo words (dashed lines), for clusters of significant central and frontal electrode sites.

distributions. Both words and pseudo words elicited a large negative component broadly distributed over the central–posterior region of the scalp, identified as the N400 component (N4) (Kutas & Hillyard, 1980), which has been linked to lexical/semantic analysis or integration of verbal or conceptual material (Rossell, Price, & Nobre, 2003). In addition, verbal stimuli also elicited an earlier broad negative potential more focally distributed over the left frontal scalp region, identified as the N330 (N3) (Nobre & McCarthy, 1994). Both of these components were significantly affected by the predictive cues.

Analysis during the earlier N3 time-window, showed a modulation of the N3 component over the electrodes where it had a maximal distribution. The N3 was enhanced by the expectation of verbal targets. Target validity interacted with both hemisphere ($F(1.7,31.6) = 7.56; p = .003$) and electrode ($F(1.1,21.4) = 7.89; p = .009$). The target validity effects were largest over the midline and left areas, and over the more frontal electrodes. This was also reflected in the three-way interaction between target validity, hemisphere and electrode ($F(2.6,48.5) = 3.03; p = .046$). The maximal effects were observed at F3 and FZ.

Analysis over the N4 time period also showed enhancement of this component by the expectation of verbal targets. N4 enhancement was revealed by a main effect of target validity ($F(1.0,19.0) = 16.60; p = .001$) and by the interaction between target validity and hemisphere ($F(1.3,25.1) = 7.28; p = .008$). The interaction with hemisphere indicated that the effects were largest over the midline electrodes (FZ, CZ, and PZ), and not lateralised.

The N3 and the N4 components were similarly modulated for both real words and for pseudo words (see Fig. 7). In general, pseudo words elicited larger language-related

potentials in this lexical-decision task (see also Bentin, McCarthy, & Wood, 1985). In agreement with the focal left anterior distribution of the N3, there were interactions between letter string and hemisphere ($F(1.7,31.5) = 7.44; p = .004$), between letter string and electrode ($F(1.1,21.4) = 7.75; p = .004$), and between letter string, hemisphere and electrode ($F(2.6,48.9) = 3.11; p = .042$). The type of letter string exerted a main effect upon the N4 ($F(1.0,19.0) = 16.12; p = .001$). The N4 was more negative for pseudo words, especially over midline sites, as revealed by a significant letter string by hemisphere interaction ($F(1.3,24.9) = 7.17; p = .008$). In both cases, the language-related potentials were larger when attention was directed toward the verbal task. Target validity exerted main effects upon the mean amplitudes of the N3 ($F(1.0,19.0) = 5.46; p = .031$) and the N4 ($F(1.0,19.0) = 8.19; p = .010$). Modulation of the N3 was again more focally distributed over midline (FZ) and left frontal (F3) electrodes. Target validity interacted with electrode ($F(1.4,27.5) = 13.69; p < .001$).

3.2.3.4. Regional analyses. The regional analyses confirmed the results from the directed analyses on the modulation of the N3 and N4 components. The pattern of results indicated the successive modulation of the overlapping N3 and N4 components. Effects progressed from a frontal-left distribution toward a more central–posterior midline distribution. The earliest significant effects started at 240–280 ms over frontal and central regions, as an interaction between target validity and hemisphere (both F s $> 5.50; p < .05$). In addition a cue \times hemisphere \times electrode interaction occurred at the frontal region ($F(2.5,47.6) = 7.15; p = .001$). The effects indicated a larger, left lateralised N3 component elicited by the valid targets. Target validity exerted a main effect starting at

280 ms over frontal regions, 320 ms over midline and central regions, and 360 ms over temporal and posterior regions; and lasting until 440 at frontal, midline and central regions, and 480 over temporal and posterior regions ($F_s > 4.00$; $p < .05$). In addition, cue \times hemisphere and cue \times electrode interactions co-occurred over most time intervals at frontal, central and temporal analyses ($F_s > 5.00$; $p < .05$). Midline analyses contained target validity \times electrode interactions only ($F_s > 4.00$; $p < .05$).

4. Discussion

4.1. Behavioural effects

The behavioural results showed that people are able to use probabilistic predictive symbolic cues to prepare selectively for different types of cognitive tasks, at least when these involve non-overlapping stimulus and cognitive sets (cf. Dreisbach et al., 2002; Sohn & Carlson, 1998). The results therefore confirm that, in addition, to being able to attend to selective stimulus attributes to optimize behaviour within a given task, people are able to attend selectively toward a likely cognitive task set. These task-reconfiguration effects improved behavioural performance for either the spatial, angle-decision task or the verbal, lexical-decision task. The use of neutral cues in the purely behavioural experiment indicated that these reconfiguration effects involve both facilitatory effects toward the anticipated task set and inhibitory effects toward the other, competing task set. Responses to items in the validly cued task were shortened, whereas responses to items in the invalidly cued task were lengthened. In the ERP experiment, it was possible to subdivide trials into those after task switches versus task repetitions. The validity of the cue predicting the upcoming task interacted strongly with the requirement to switch task. There were no significant switching costs after valid cues predicting the upcoming task, suggesting that the task-reconfiguration was sufficient to overcome reaction-time costs of task-switching in our task.

The two tasks used in the present experiment rely upon highly non-overlapping neural systems and have different postulated hemispheric specialization (Hellige, 1990). The ability to switch voluntarily and dynamically between the two tasks thus suggests the ability to regulate the activity levels between different neural systems that could be called upon alternatively to control action. In this case of non-overlapping tasks, the effects of cue validity outweighed the interference between tasks during switching trials. Our results are compatible with, but do not necessarily invoke the existence of some limited task-independent central resources. Both tasks could compete, for instance, for resources related to decision making or controlling manual responses (Pashler, 1998). It is also possible that activity in distinct neural systems could be optimised by probabilistic cognitive expectations or stimulus associations even in the absence of competition for common

resources. Future tasks that manipulate the decision-making requirements, and the extent of overlap of input modalities and response effectors, are required in order to address this important and interesting issue.

4.2. ERPs to cues

The main question guiding the research was whether the different natures of the predicted task sets could contribute to the pattern of neural activity during the task-reconfiguration phase. Previous research has indicated that brain activity during task-reconfiguration is partly determined by whether the task-switch emphasises changes in perceptual selection or motor decisions. Here, the question was whether neural activity during task configuration is also influenced by the specific neural circuitry involved in tasks of different cognitive domains (in this case verbal versus spatial). To address the question, we compared the ERPs elicited by the task-predicting cues. These symbolic cues predicted with a high probability (80%) the subsequent appearance of a verbal or spatial stimulus on a trial-by-trial basis. The proportion of switch versus non-switch trials was balanced within subjects, and the assignment of a given cue stimulus to the predicted task was counterbalanced across subjects. The resulting brain activity related to task reconfiguration was therefore clear from any possible confounding differences due to general task-switching variables or the physical appearance of the cueing stimuli per se (see Miniussi, Wilding, Coull, & Nobre, 1999; Nobre, Sebestyen, & Miniussi, 2000).

The results showed clear effects of anticipating specific task sets, starting much before the appearance of any imperative task stimulus. The first effects of task set occurred over the left posterior scalp during the time period of the N1 component (160–200 ms), followed by a widespread modulation over central scalp regions, which gradually became more focused over posterior scalp regions. These effects are determined by the nature of the expected tasks. They may reflect activation of brain areas in the neural systems involved in performing the spatial or verbal tasks. Inhibition of brain areas associated with the unanticipated task may also contribute. Activation of brain areas specialized for different tasks (verbal or spatial) engaged by cues that instructed the nature of the task to be performed on the upcoming stimulus set has been observed using fMRI (Sakai & Passingham, 2003). Pre-activation of brain areas involved in coding relevant attributes of stimuli, which are thought to facilitate stimulus-processing within given tasks, has also been commonly noted in attentional orienting studies using fMRI (e.g., Chawla, Rees, & Friston, 1999; Hopfinger, Buonocore, & Mangun, 2000; Kastner, Pinsk, De Weerd, Desimone, & Ungerleider, 1999). To isolate cue- or instruction-related activity, the fMRI studies used long intervals preceding target appearance, which may have introduced additional cognitive variables. The high temporal resolution of ERPs in the present experiment enabled identification of these task-reconfiguration effects online using short cue–target intervals. Our study also specifi-

cally linked neural activity related to the expected task set to attentional modulation of behavioural performance.

In addition to the type of task predicted by cues, the prediction of the requirement to switch task from the previous trial also exerted significant effects on the pattern of brain activity before the appearance of the imperative target stimulus. There were two clearly dissociable effects. Modulation of activity over frontal regions of the scalp occurred earlier (280–440 ms) followed by modulation of activity over parietal and posterior scalp regions (440–600 ms). The anterior-then-posterior distribution of the effects is similar to previous ERP results comparing activity engaged by cues instructing task switches versus task repetition (Rushworth, Passingham, & Nobre, 2002; Rushworth et al., *in press*). However, whereas the later posterior effect appears consistent between this and the previous two studies (see also Wylie et al., 2003), the early effects differ in both distribution and polarity. In the present experiment, the early frontal effect of task-reconfiguration was a relative negative voltage distributed over frontal and central scalps around the midline. Cues instructing reconfiguration of an intentional set (stimulus–response mapping) elicited relative positive-voltage over midline frontal sites (Rushworth, Passingham et al., 2002), whereas cues instructing reconfiguration of an attentional set (relevant perceptual feature for response) elicited relative negative-voltage that was lateralised over frontal regions (Rushworth et al., *in press*). Using an adaptation of the Wisconsin Card Sorting Task, an MEG study also identified an anterior-then-posterior set of activations related to task switching. Anterior sources were localised to the inferior frontal gyrus and anterior cingulate, whereas the posterior source was localised to the supramarginal gyrus of the inferior parietal lobule (Perianéz et al., 2004). Brain-imaging studies using haemodynamic measures have also pointed to the involvement of frontal and parietal circuits in task-set reconfiguration (e.g., Brass & von Cramon, 2002; Kimberg et al., 2000; MacDonald et al., 2000; Sohn et al., 2000).

The poor spatial resolution of ERPs impedes any strong conclusions about the specific neuroanatomical sources for the effects of predicted task or the requirement to switch tasks in the present experiment. The relative nature of the ERP effects and the arbitrariness of their polarity also hinder interpretation of the underlying mechanisms at play. The ERP modulations observed are likely to involve concurrent activation in multiple brain areas. Already by the time of the N1 component, a number of brain areas have been implicated in the processing of visual stimuli, including occipital and parietal sources (Di Russo, Martinez, Sereno, Pitzalis, & Hillyard, 2002). Spatial orienting effects have been identified around this time period (Harter, Miller, Price, LaLonde, & Keyes, 1989; Nobre et al., 2000; Yamaguchi, Tsuchiya, & Kobayashi, 1994), and therefore differential activity in brain areas involved in spatial cognition is a possible functional underpinning of the effect. However, some left-hemisphere language orienting effect cannot be ruled out. Revealing the specific brain areas and mechanisms involved will require ex-

periments with convergent methodologies. The persistence of effects over lateralised posterior regions of the scalp until the time that the imperative spatial or verbal stimuli appeared is suggestive of differential tonic activity levels in posterior brain regions (Chelazzi, Miller, Duncan, & Desimone, 1993; Luck, Chelazzi, Hillyard, & Desimone, 1997) associated with the different tasks predicted.

Overall, the results highlight the multiple and non-uniform nature of task-switching mechanisms, and support the growing notion that several components are involved in reconfiguring task set prospectively (Meiran, 2000; Monsell, 2003). In our experiment, activity related to the predicted type of task set clearly influenced the neural activity during task-set reconfiguration before the appearance of any imperative stimulus (see also Sakai & Passingham, 2003). Effects related to the predicted task started earlier (160 ms onward) than those related to the requirement to switch task from the previous trial (280 ms onward). Previous studies of task switching have indicated that neural activity during reconfiguration is also affected by whether switching requires changes in the perceptual attributes that are relevant for selection (attentional set) or the response assignments to different stimulus types (intentional set) (Rushworth, Hadland et al., 2002; Rushworth, Passingham et al., *in press*). Taken together, it appears that when two competing possible tasks differ substantially in their underlying functional neural architecture, reconfiguration starts with a biasing of neural activity toward the probable task. Further reconfiguration occurs to bias neural responses toward the relevant perceptual attributes (attentional set) and response rules (intentional set) within the tasks. Electrophysiological experiments so far have found similar modulation of neural activity over posterior scalp regions associated to the later phases of task-set reconfiguration (Rushworth, Passingham et al., 2002; Rushworth et al., *in press*; Wylie et al., 2003; Perianéz et al., 2004). One possibility is that this reflects activity in posterior parietal regions involved in setting up the relevant stimulus–response associations for the predicted or instructed task. Parallel experiments using different types of cues, tasks, stimulus sets, response-mappings, effectors, etc., will be particularly useful to probe the existence of general neural mechanisms of task switching.

4.3. ERPs to targets

In addition to the task-reconfiguration effects triggered by the cues, the ERPs revealed clear additional neural modulation of target processing at the implementation of the specific task set.

It was not possible to compare directly the ERP modulations of verbal and spatial targets, since these were physically different and required different cognitive operations for the task-relevant responses. However, it was clear that target modulation was different depending on the nature of the target and of the specific task set predicted. Early visual processing of the centrally presented targets was not affected for either task. Modulation of verbal targets oc-

curred for potentials that have been linked to language-related lexical and post-lexical processing, over left frontal and central scalp regions (240–480 ms). Modulation of spatial targets involved a potential that reversed polarity between posterior and frontal scalp regions (240–280 ms) followed by a sustained frontal modulation (240–600 ms) and modulation of the central–posterior P3 component (440–600 ms).

The lack of early visual modulation may appear surprising, given the increased reliance upon visual judgements in the spatial task, and the existence of early specialized visual processing for letter strings (Nobre, Allison, & McCarthy 1994; Tarkiainen, Cornelissen, & Salmelin, 2002; Tarkiainen, Helenius, Hansen, Cornelissen, & Salmelin, 1999) that could serve as a substrate for attentional modulation. However, the conditions to unveil potential early perceptual modulations may not have been optimal in the present experiment. Stimuli were presented foveally, using bright suprathreshold parameters. Both angles and letter strings required extensive visual analysis and integration for task performance.

Defining the specific brain areas or functional processes modulated by attention to specific task sets is not straightforward. Interpretations must rely on previous literature defining the cognitive and neural bases of the relevant ERP components. To our knowledge, angle-decision tasks have not been previously investigated using ERPs, and therefore the potentials linked to these spatial representations and transformations are not well documented. The earliest ERP modulation in the angle-decision task (240–280) may have reflected modulation of visuospatial processing. Future studies examining the relationship of this ERP component to spatial cognition will be of direct interest. The later effects appeared to be related to the P3 potentials, which have been linked to stimulus probabilities, decision making, and context updating (Goldstein, Spencer, & Donchin, 2002; McCarthy & Donchin, 1981). The P3 was larger for unexpected spatial targets, starting anteriorly and later over the central and posterior scalp. P3 enhancement for invalid targets has been observed in spatial attention tasks, especially when each stimulus requires a response (Eimer, 1998). The increased P3 to the unexpected stimulus may reflect the more rare probability of its occurrence (20%) or the additional requirement of updating the context.

In contrast, more is known about ERP components in visual lexical-decision tasks. The verbal task therefore provided a framework in which it was possible to evaluate the consequences of directed task expectations upon perceptual and lexico-semantic processing. The most pronounced language-related potential is the N400 (N4) (Kutas & Hillyard, 1980), most likely reflecting the integration of lexical/semantic representations of words with the ongoing context (Rossell et al., 2003). In addition, a preceding focal left anterior potential (N3) has been identified (Nobre & McCarthy, 1994) that overlaps extensively with the N4 but that can be dissociated both functionally and in spatial distribution. Both these potentials, N3 and N4, were substantially and significantly modulated by

selective attention directed to the verbal task. The language-related potentials were significantly larger when verbal stimuli were expected, or greatly diminished when verbal stimuli were not expected. Language-related potentials were similarly modulated for real words and pseudo words.

The extensive modulation of lexical/semantic processing by task-directed attention was remarkable. The processing of words in general, and their semantic content in particular, have often been suggested to be automatic and outside the control of selective attention (e.g., Marcel, 1983). One previous ERP experiment has shown that both visual- and language-related components elicited by words can be significantly influenced by selective spatial attention (McCarthy & Nobre, 1993). In this previous experiment, words were presented vertically and peripherally, which challenges the generalizability of the findings to foveally presented words written in canonical orientation. A previous fMRI experiment showed substantial modulation of activation in language-related areas when attention was directed toward or away from foveally presented words (Rees, Russell, Frith, & Driver, 1999). However, the poor temporal resolution in fMRI precluded interpretation about whether these effects reflected on-line modulation of language processing or later consequences of task performance. In the present experiment, words were presented in the centre of the screen, in normal orientation, and with no competing concomitant stimuli. Nevertheless, the language-related potentials were substantially attenuated on-line when verbal stimuli were not expected. The present findings clearly demonstrate that lexical–semantic analysis or integration of words can be affected by attention, and therefore is not automatic, even when there is no stimulus immediately competing for attention (see also, Posner, Sandson, Dhawan, & Shulman, 1989; Stolz & Besner, 1998). This occurs not only when potential interference is maximized, as when streams of verbal stimuli compete in the dichotic listening task (Cherry, 1953), but also when attention is directed toward and away from verbal material in general. The results do not, however, preclude the occurrence of some implicit semantic processing of the unexpected verbal stimuli.

4.4. Summary of general findings

We demonstrated that it is possible to direct resources differentially toward behavioural tasks involving distinct cognitive and neural systems. Arbitrary symbolic cues were sufficient to engage task-set reconfiguration processes, which improved performance on an anticipated task and hindered the performance of an unexpected task. Modulations of ERPs elicited by the cues showed that the specific nature of the anticipated task set influences the pattern of brain activity involved in task-set reconfiguration. Multiple effects were documented, possibly including selective engagement of specialized neural systems, starting much before the appearance of imperative verbal or spatial stimuli. The nature of the predicted task influenced brain activity before the prediction of

the requirement to switch task from the previous trial. Attention selectively directed toward alternate possible cognitive tasks had strong further consequences upon the specialized processing of imperative stimuli of different kinds. Attention directed to the verbal task strongly modulated the potentials that have been linked to lexical/semantic processing, including the N4 and also the preceding more anterior and left-lateralised N3 potential. The results highlight the dynamic nature of cognitive systems, and show that their level of engagement can be modulated by online expectations. Modulation extends to the language system, which is often thought to be encapsulated, and to operate independently from other cognitive systems and outside the control of selective attention.

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