Pre-stimulus EEG effects related to response speed, task switching and upcoming response hand

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Abstract

The task-switching paradigm provides an opportunity to study whether oscillatory relations in neuronal activity are involved in switching between and maintaining task sets. The EEG of subjects performing an alternating runs [Rogers, R.D., Monsell, S., 1995. Costs of a predictable switch between simple cognitive tasks. Journal of Experimental Psychology: General 124, 207–231] task-switching task was analyzed using event-related potentials, the lateralized readiness potential, instantaneous amplitude and the phase-locking value [Lachaux, J.P., Rodriguez, E., Martinirie, J., Varela, F.J., 1999. Measuring phase synchrony in brain signals. Human Brain Mapping 8, 194–208]. The two tasks differed in the relevant modality (visual versus auditory) and the hand with which responses were to be given. The mixture model [de Jong, R., 2000. An intention driven account of residual switch costs. In: Monsell, S., Driver, J. (Eds.), Attention and Performance XVII: Cognitive Control. MIT Press, Cambridge] was used to assign pre-stimulus switch probabilities to switch trials based on reaction time; these probabilities were used to create a fast–slow distinction between trials on both switch and hold trials. Results showed both time- and time–frequency-domain effects, during the intervals preceding stimuli, of switching versus maintenance, response speed of the upcoming stimulus, and response hand. Of potential importance for task-switching theory were interactions between reaction time by switch–hold trial type that were found for a frontal slow negative potential and the lateralized readiness potential during the response–stimulus interval, indicating that effective preparation for switch trial s involves different anticipatory activity than for hold trials. Theta-band oscillatory activity during the pre-stimulus period was found to be higher when subsequent reaction times were shorter, but this response speed effect did not interact with trial type. The response hand of the upcoming task was associated with lateralization of pre-stimulus mu- and beta-band amplitude and, specifically for switch trials, beta-band phase locking.

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1. Introduction

Voluntary actions are characterized by a combination of flexibility and persistence (Goschke, 2003): responses to similar stimuli may change, as new intentions are formed, and responses to changing stimuli may remain constant, as goals are maintained over time and situations. The state of the brain that determines its response to different stimuli is described by the task set (Monsell, 2003), defined as the mapping of stimuli to responses. Under changing circumstances, either switching between different task sets or holding a task set may be required. Patients with prefrontal damage show a lack of control of flexibility in response to environmental demands (Barcelo and Knight, 2002; Milner, 1963). Such patients are able to set up stimulus–response mappings, but may fail to keep the task set active when confronted with distractions, or persevere in a task set when a switch is required, as in the Wisconsin card sorting test (Grant and Berg, 1948). The task-switching paradigm provides an opportunity to study the control of task sets.

The task-switching paradigm involves the presentation of sequences of trials that require either changing or maintaining task sets. The mean reaction time of trials for which subjects have to change task set is higher than that of trials requiring the same task set as the previous trial (Allport et al., 1994; Rogers and Monsell, 1995; Meiran, 1996). These switch costs can be reduced by increasing the length of the preparation interval, but they are still present at long intervals (Monsell, 2003). The
important part in anticipatory processing (Koch, 2003; Mayr goals, as opposed to subsequent reconfiguration, may play an reaction time distributions (de Jong, 2000). One is the short- long-interval switch trials is described as a mixture of two other model of task switching, the distribution of the reaction times of response associations (Wylie and Allport, 2000), is one way bias of the previous task set (Allport et al., 1994), or the previously realized task set, such as task set inertia, a persisting residual switch costs. Some form of interference due to a persistent switch costs at long preparation intervals are called switch costs. The decay of the effect of previous task sets over time could explain the reduction of switch costs by increased preparation interval. Even if preparation for switch and hold trials involves the same mechanisms for preparation, the effect of decaying interference on these mechanisms could lead to an interaction of trial type and preparation interval on reaction time (Gilbert and Shallice, 2002). Another hypothesis explaining switch costs is that a time-consuming task set reconfiguration process is necessary to switch task sets, and that this process can be only partially completed prior to stimulus presentation (Rogers and Monsell, 1995). Decreased switch costs for longer preparation intervals would then reflect the completion of the initial, endogenous part of the reconfiguration process. Arguments for an anticipatory contribution to switch costs were provided by the findings that switch costs could be restricted to the first trial after a switch (Rogers and Monsell, 1995) and that when inter-trial interval (i.e., decay time) and cue–stimulus interval (preparation time) were disentangled, an increase in cue–stimulus interval was still found to reduce switch costs (Meiran, 1996). Even though by definition some kind of change in stimulus–response mapping must be initiated to allow a switch to occur, whether a switch-specific reconfiguration process must be assumed to underlie this switch would be hard to infer from data on switch costs (Gilbert and Shallice, 2002). Further, the retrieval of task-set goals, as opposed to subsequent reconfiguration, may play an important part in anticipatory processing (Koch, 2003; Mayr and Kliegl, 2003).

The distributions of reaction times supply further information on residual switch costs than only the means. In the mixture model of task switching, the distribution of the reaction times of long-interval switch trials is described as a mixture of two other reaction time distributions (de Jong, 2000). One is the short-interval switch distribution, which contains the longest reaction times: the influence of the previous task set is greatest in this condition, whether this is best described by strong inertia or the lack of time to initiate reconfiguration. The other is the long-interval hold condition, which contains generally fast responses. In this condition, the previous task set was already correct. A mixture of these two conditions’ distributions can be used to model the condition containing residual switch costs, in the simplest case using a single parameter that specifies the proportion of trials from the fast, “no switch necessary” distribution. The residual switch cost is then due to the subset of trials from the slow distribution in which a switch is necessary but not made pre-stimulus. That is, in the mixture model, a subset of reaction times when subjects have to switch has the same, fast distribution of reaction times when switching is unnecessary.

The mixture model has been shown to provide good fits to data (de Jong et al., 1999; de Jong, 2000, 2001; Nieuwenhuis and Monsell, 2002). One explanation of the characteristic pattern of reaction time distributions is the failure to engage hypothesis (de Jong, 2000), which states that subjects intend to switch on most trials, but sometimes fail to engage the intention during the pre-stimulus interval, that is, to reconfigure their task set prior to stimulus presentation. In that case, their state at stimulus presentation is no better than when they were given only a short interval between trials. If they do successfully switch, on the other hand, they are as fast as when no switch was necessary at all at stimulus presentation, that is, as fast as hold trials under the same further conditions. Other explanations are of course possible: for instance, some form of proactive interference could be hypothesized to only occur on a certain proportion of trials. The mixture model does, nevertheless, open the possibility that despite persistent switch costs, full task-set reconfiguration may still be possible, pre-stimulus, on a subset of trials. Taking physiological data into account may help clarify the underlying causes of switch costs, and provide starting points to reduce the concepts of switching and holding tasks to specific physical and computational processes.

Psychophysiological studies of task switching have measured various aspects of the brain’s behavior during cognitive control and task switching. fMRI studies have found prefrontal and parietal areas with increased activity during preparation for a switch (e.g. Sohn and Carlson, 2000; Braver et al., 2003; Derfuss et al., 2004). The event-related potential (ERP) has also been shown to be sensitive to brain activity associated with switching task sets. The ERP components that were of most interest to the present study were the contingent negative variation and lateralized readiness potential.

If preparation for a task switch involves an anticipatory switching process, and if this process can either occur or not as the failure to engage hypothesis suggests, then a reaction time by switch versus hold interaction would be expected to occur on slow negative potentials, as such potentials (i.e., the late contingent negative variation (CNV) (Leuthold et al., 2004; Mnatsakanian and Tarkka, 2002; Rosahl and Knight, 1995), readiness potential (Cui et al., 2000) and the stimulus-preceding negativity (SPN; Brunia, 1999)) appear to reflect processes that occur between a cue that indicates some form of cognitive action that must be performed in the future, and the point at which the action is expected to occur. Such future actions may involve either stimulus processing or motor responses (Brunia, 1999), and may be complex, e.g. the selection and maintenance of a cued part of a stimulus to be compared with another stimulus to be presented later (Mnatsakanian and Tarkka, 2002). A frontocentral increase in the CNV has also been found to increase with effort (Falkenstein et al., 2003). The term CNV will be used in the present paper to refer to such slow, pre-stimulus negative potentials. The lateralized readiness potential (LRP) (Coles, 1989; Leuthold et al., 2004) may also measure preparation of task sets, when the sets differ on which hand must be used to respond with. The LRP is a measure of the lateralization of the slow negative potential preceding a response, the contralateral motor cortex showing increased negativity. A pre-stimulus LRP occurs when specific muscle movements can be prepared
(Leuthold et al., 2004). So, if task sets differ on response hand, so that a set of left- or right-hand finger movements could be prepared, the LRP may reflect differences in switching between and holding those task sets. If switching between tasks involves switching between hands, the fast switches may show a greater pre-stimulus shift in LRP than slow switches. That is, the lateralization for the response on the previous trial would have a different sign from that on the next trial, and preparation may involve a shift in lateralization towards the correct sign. If hold trials show a reversed fast–slow LRP pattern, such a preparatory LRP effect on reaction time would seem to be due to post-response variability of left-hand versus right-hand bias. However, if no such fast–slow differences are found during preparation for hold trials, then the presence of an LRP effect for switch trials would seem to reflect variability due to a switch-specific preparatory process that occurs only, or to a greater extent, preceding stimuli followed by fast responses.

A number of studies have used the ERP to study brain activity related to task switching. Wylie et al. (2003) used sequences of three trials with the same task set, providing switch, nested and pre-switch trials for the first, second and third trials in each sequence. Tasks were cued by the stimulus color, as well as by the AAABBB… sequence. The data showed effects on sustained positivities occurring late in the trials, that is, preceding the upcoming stimulus. It was found that the ERP level preceding switch, nested and pre-switch trials was, at parietal sites, most positive for pre-switch trials, while at frontal sites nested trials showed the greatest positivity. These sustained positivities were interpreted to reflect sustained activity. Based on this interpretation, it was argued that it would be unexpected, from an assumption of frontal areas playing a controlling role in preparing for switch trials, that frontal sites did not show the greatest sustained positivity on pre-switch trials. However, as described above, negative shifts, such as the CNV, may reflect anticipatory processing, so that the interpretation of a relatively positive ERP level as more sustained activity may not be valid. Other studies have reported frontal effects related to changing task set. Lorist et al. (2000) found frontal and parietal negative shifts prior to switch and holding those task sets. If switching between tasks involves switching between hands, the fast switches may show a greater pre-stimulus shift in LRP than slow switches. That is, the lateralization for the response on the previous trial would have a different sign from that on the next trial, and preparation may involve a shift in lateralization towards the correct sign. If hold trials show a reversed fast–slow LRP pattern, such a preparatory LRP effect on reaction time would seem to be due to post-response variability of left-hand versus right-hand bias. However, if no such fast–slow differences are found during preparation for hold trials, then the presence of an LRP effect for switch trials would seem to reflect variability due to a switch-specific preparatory process that occurs only, or to a greater extent, preceding stimuli followed by fast responses.

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been done for fMRI by Braver et al. (2003). Preparatory task switching was expected to occur preceding fast switch trials but not slow switch trials or either fast or slow hold trials. The fast and slow groups were defined in terms of the mixture model and failure to engage hypothesis, as described in detail in Section 2. The basic idea of this approach is that each switch trial belongs to either the (endogenously) switched or the not switched subset. While it is in principle unknown to which subset a specific trial belongs, it can be reasoned that the faster the reaction time on a trial, the more likely it is to belong to the switched subset, as opposed to being an outlier of the unprepared subset. Using the mixture model, Bayes’ theorem and estimations for the switched and non-switched reaction time distributions, the odds that a specific switch trial belongs to the switched and non-switched can be calculated based on that trials reaction time. These odds could then be used to define groups of fast and slow trials which could be interpreted as having high probabilities of belonging to the switched versus the not switched group. Differences in physiological measures could then be determined between these groups. If effective preparation for switch trials involves different anticipatory processes than for hold trials, a fast–slow by switch–hold interaction should be found during the response–stimulus interval on one or more psychophysiological measures.

Note that within each subset of fast and slow trials, there is still variance, and this may be due to other forms of preparation than a specifically switching-related process, such as endogenous task-set reconfiguration or some form of goal replacement. These other forms of preparation, in the general sense of any pre-stimulus changes in the state of the brain that bias it to perform a certain task with heightened efficiency, were also of interest.

Oscillatory EEG characteristics (Tallon-Baudry and Bertrand, 1999) were also measured in the present study. Rhythmic behavior can easily arise in neuronal systems: for example, populations of coupled excitatory and inhibitory neurons can respond to afferent activation with synchronized oscillations (Wang, 1999; Azouz and Gray, 2000; Sukov and Barth, 2001), and oscillations can also be caused by intracellular dynamics (e.g., chattering cells; Gray and McCormick, 1996) or wave propagation (Nunez, 2000). Rhythmic behavior may play a role in assembly coding (Roelfsema et al., 1996). Assembly coding, the distribution of information over specialized neuronal populations, has been argued to be an important coding strategy for the brain (Singer et al., 1997; Roelfsema et al., 1996). The phase of oscillations of neuronal activity can be seen as a way to create space for spatially and temporally overlapping patterns of activity. Letting the activity of members of assemblies oscillate in phase with each other and out of phase with members of other assemblies provides a mechanism to achieve this. Experimental evidence for such a role for phase locking has been found by Engel et al. (1991). The relevance of assembly coding for task switching is that a task set can be seen as a set of assemblies of stimulus and response representations which must be simultaneously active and yet separated into the correct pairs. A number of frequency bands are of potential interest in studying preparation in a task-switching context: the theta, alpha and beta frequency bands. Each band may reveal part of the neuronal changes that occur during preparation for different tasks.

The 5–7 Hz, or theta frequency band, has been associated with working memory (Raghavachari et al., 2001), memory encoding (Klimesch, 1996) and retrieval (Klimesch, 1999) and sensorimotor integration (Bland and Oddie, 2001). Areas related to functions that are involved in distributed processing have been shown to have increased theta-band activity, e.g. for language areas following syntactic violations (Bastiaansen et al., 2002). In a recent study using an alternating runs task, it was found that switching to a visual task was associated with a transient increase in occipital theta-band amplitude during the response–stimulus interval (Gladwin and de Jong, 2005). The present study involved task sets which mapped right and left-hand responses to visual and auditory stimuli, respectively. These task sets involve separable neuronal areas (the left and right motor, the visual and the auditory cortices), so that switching between tasks might show shifts in patterns of theta amplitude depending on which task is relevant.

The alpha (8–12 Hz) frequency band (called mu when related to motor cortex activity) has been considered to be an idling rhythm (Pfurtscheller et al., 1996), because it is reduced occipitally during visual stimulation (Berger, 1930) and at motor regions during movements (Pfurtscheller and Berghold, 1989). Alpha-band oscillations have been proposed to play a more specific role within the coordination of neuronal activity as a localized inhibitory mechanism (Cooper et al., 2003). Cooper et al. suggest the interpretation that “increased alpha power may index the active inhibition of non-task relevant cortical areas.” The anticipatory suppression of distracters in the visual modality has been shown to be associated with increases in parietal and occipital alpha-band oscillations (Fu et al., 2001; Worden et al., 2000; Foxe et al., 1998). Such a mechanism may then play a role in the control of irrelevant task sets during task switching. Evidence for the existence of inhibition at the level of task sets has been found in behavioral studies by Mayr and Keele (2000). For the task used in the present study, task sets differed on modality, so that the irrelevant sensory cortex could be repressed to choose, by elimination, the correct task set. Similarly, the hand to be used for responses had to be switched, so that alpha-band waves might influence competition between hands and in that way specify the relevant task set. Such an effect could be studied in the present task, when preparing for left and right-hand responses in the context of switching and holding task sets.

Each task set in the present experiment contained two responses that were restricted to one hand. So, the response on switch trials was always made with the other hand than that
used for the previous trial, while hold trials required a response with the same hand. This allowed the LRP formula to be applied to amplitude time courses, to provide a measure of motor-related amplitude asymmetry (MRAA) defined as L-R(prepare for left-hand task) – L-R(prepare for right-hand task). Here, L-R(condition) refers to the difference in amplitude between the left and right motor regions for the specified condition. A positive MRAA during the pre-stimulus period, calculated for a given frequency band, would for instance occur if the amplitude over the motor region to be used for the upcoming response showed a decrease relative to the opposite motor region.

Beta-band (14–30 Hz) oscillations decrease over the contralateral motor cortex when a movement is made (Pfurtscheller et al., 2000). This effect was interpreted similarly to the idling of alpha waves described above. Recently, beta waves have been argued to be related, not to idling, but to an active maintenance of stable positions (Brown, 2000). If foreknowledge is available about the hand to be responded with, these ideas lead to the same prediction. If preparatory processes are allowed to determine that hand’s motor cortex’s activity, its beta amplitude, as well as mu amplitude, is expected to decrease relative to the irrelevant motor cortex. Alternatively, holding the irrelevant hand in check, and so leaving only the unrestrained hand able to respond, would increase the beta power over the irrelevant cortex relative to the relevant cortex. In both cases, lateralization of beta amplitude would be expected to measure motor preparation, similarly to the MRAA described above.

A further frequency band that has been related to psychological states and processes (e.g. Tallon-Baudry and Bertrand, 1999) is the gamma band (30–70 Hz). This band will influence of muscular activity.

In summary, a number of questions concerning ERP’s and oscillatory EEG activity were of interest in this explorative study. Perhaps most importantly for hypotheses concerning task switching, it was studied whether effective preparation, as determined by subsequent reaction time, was different for switch and hold trials. Trial type by reaction time interactions was looked for on various measures. A fast–slow difference in the CNV or LRP occurring only or more strongly for switch trials would suggest anticipatory behavior related specifically to switching between task sets. Theta-band activity might show differences in memory retrieval, for instance if switching to a new task requires the re-triggering the task memory to a greater extent than when preparing for a hold trial. Inhibitory processes involved in successful anticipatory switching would be expected to be related to alpha-band activity. An effective anticipatory switch might involve stronger pre-stimulus inhibition of previous-task areas than that occurs preceding slow switch trials. If pre-stimulus switching involves motor processes, lateralization of oscillatory beta-band activity would be expected to occur during response–stimulus intervals (due to the restriction of each task’s response set to either the right or the left hand). Some more general questions concerning oscillatory EEG activity were also of interest. First, could increases of theta activity be found that were related to task-relevant cortical areas? Second, could increases of alpha activity be found that were related to task-irrelevant areas? Third, what motor-related asymmetries could be found over motor cortices in the mu and beta frequency bands? Fourth, were there task-related changes in phase locking between stimulus- and response-related areas?

2. Method

2.1. Subjects

Seventeen right-handed, young (age 18–25 years) females with normal or corrected to normal eyesight were tested. Subjects were paid for participation and were informed of the experimental goals and procedures.

2.2. Task

The task was a variation of Rogers and Monsell’s (1995) alternating runs paradigm. In this paradigm two tasks A and B are performed in an AABBAABB... sequence. On each trial a letter (an X or an O) and a 1200 or 400 Hz tone were presented simultaneously. Subjects responded to the letters with the index and middle finger of one hand, and to the tones with the fingers of the other hand. Which hand was initially assigned to which task was counterbalanced over subjects. All subjects switched task–hand assignments twice during the experiment, after the first and third set of blocks (see below). A 2 × 2 matrix was continuously present on the screen and the letters were presented in a clockwise sequence in the four cells of the matrix. Each cell of the matrix was associated with one of the two tasks. The assignment was randomized, but consistent per subject and was always such that the AABB... sequence was followed during the clockwise rotation of the relevant cell. Subjects were trained on the day prior to the experiment, and performed a short refresher session prior to the EEG measurements.

Besides the mixed-task blocks in which the sequence is AABBAABB... (‘switch-blocks’) subjects also performed ‘pure-task’ blocks. The pure-task blocks resemble the mixed-task blocks in terms of presentation of the stimuli, but in these blocks the subject only has to perform one of the tasks. These blocks were not of interest in the EEG analysis presented here.

The experiment consisted of four sets of six blocks, each block consisting of 100 trials. Each set contained four mixed-task blocks and one pure block for each task. The assignment of the hands to the tasks was switched twice during the experiment: after the first and the third group of six blocks. This was done to be able to calculate the LRP and MRAA per subject, per task, without each subject having hand confounded with modality. Three response–stimulus intervals (RSI’s) were used in this experiment: 150, 750 and 1500 ms. These RSI’s were randomly distributed over the trials, but because only the long intervals would be analyzed in the EEG trials preceded by long intervals were presented more often. Because only the shortest and longest intervals were relevant for the distribu-
tional reaction time analysis described below, the middle RSI was set to the lowest probability. The odds of occurrence of the short, medium and long-LSI’s were 2:1:3.

2.3. Procedure

Subjects were seated in a comfortable chair in front of a table on which their forearms could rest. The distance between the subject and the computer screen was approximately 60 cm. Subjects were instructed to keep as still as possible during the execution of the task.

The day before the actual experiment a practice session was held to reduce learning effects during the experiment. During this practice session subjects performed sets of blocks as described above until they reached an accuracy of at least 90% and reported that they were familiar with the task. A short warm-up session was held before the actual experiment. Halfway through the experiment subjects were allowed to take a break to reduce the effects of fatigue.

2.4. Measurements

The EEG was recorded using a 125-electrode cap (Electrocap International Inc., Eaton, OH, USA). REFA-128 amplifiers (TMS International) were used. Two earlobe electrodes were used as reference electrodes and a chest electrode was used for the common signal. EOG was measured using four electrodes (HEOGL+, HEOGR+, VEOGL+ and VEOGL−). The data were sampled at 500 Hz using the data acquisition program Onyx (Version 1.02, Silicon Biomedical Instruments BV, The Netherlands). The data were filtered online, with a time constant of 10 s and a low-pass stop frequency of 250 Hz. Impedance was kept below 5 kΩ for all electrodes during the experiment. A five-button response box was used for response collection.

2.5. Reaction time analysis

Reaction times were analyzed according to the mixture model (de Jong, 2000). This model describes the cumulative distribution function (CDF) of the reaction time of long-LSI switch trials ($F_{\text{switch}}$) as a weighted mixture of the CDF’s of “switched” and “not switched” switch trials (termed “prepared” and “unprepared” in de Jong, 2000); that is, the population of reaction times in this category is modeled as a mixture of two other populations:

$$F_{\text{mixed}}(t) = \alpha F_{\text{switch}}(t) + (1 - \alpha) F_{\text{not switched}}(t)$$

The CDF maps reaction time to cumulative distribution, given two basis distributions $F_{\text{switch}}$ and $F_{\text{not switched}}$. “Switched” refers here to having the correct stimulus–response mappings prior to stimulus presentation, that is, full pre-stimulus task-set reconfiguration. Note that the switched and not-switched conditions still contain any other preparatory source of reaction time variance apart from the switch of task sets. The model formalizes the statement that the condition in which residual switch costs are found contains two subpopulations of trials: those when the subject has already switched task sets at stimulus presentation and those when he or she has not. This condition is therefore termed the mixture distribution. The $\alpha$ parameter stands for the proportion of switched trials. The switched and not-switched CDF’s are estimated from long-LSI hold trials and short-LSI switch trials, respectively. It is possible, as suggested by the hypothesis of an endogenous and an exogenous reconfiguration, that even switch trials which were preceded by a switch are not just as fast as the fastest subset of hold trials. An extension of the model including this possibility shifts the estimated switched distribution by $\delta$ ms:

$$F_{\text{switch}}(t) = F_{\text{long-LSI hold}}(t - \delta)$$

The $\alpha$ and $\delta$ parameters can be estimated from reaction time data using the multinomial maximum likelihood method (Yantis et al., 1991; see de Jong, 2000).

Once the $\alpha$ and $\delta$ parameters are known, and if the model fit is satisfactory, Bayes’ theorem can be used to assign odds to trials on the basis of their reaction times. Bayes’ theorem provides the following equation:

$$P(\text{switched}|t) = \frac{P(t|\text{switched})P(\text{switched})}{P(t|\text{switched})P(\text{switched}) + P(t|\text{not switched})P(\text{not switched})}$$

where $P(\text{switched}|t)$ stands for the chance that the subject was prepared given a reaction time of $t$ and $P(t|\text{switched})$ for the chance of the reaction time given the switched state. The a priori chances $P(\text{switched})$ and $P(\text{not switched})$ are $\alpha$ and $(1 - \alpha)$ and $P(t|\text{switched})$ and $P(t|\text{not switched})$ can be estimated using the long-LSI hold and short-LSI switch cumulative density functions.

Ideally, this procedure would provide two extreme subsets of long-LSI switch trials, with the probability of successful preparation of the switch being either very high or very low. In practice, given the limited total number of trials and the need to retain a sufficient number of trials in each category for psychophysiological analyses, a compromise had to be made. The decision to assign trials to prepared and unprepared groups was therefore taken in two steps. First, the fastest third of the trials were assigned to the switch-prepared group and the slowest third of the trials were assigned to the switch-unprepared group, regardless of probabilities. Second, if the preparation probability of any remaining trials was above 0.9 or below 0.1, those trials were assigned to the prepared or the unprepared group, respectively.

To study switch- or hold-specific parts of preparatory activity, a similar fast–slow split was made for the hold trials. Since the mixture model does not specify subsets of hold trials, the same proportion of trials were assigned to fast and slow hold categories. That is, for each subject, if the fastest $x\%$ of the switch trials were assigned to the fast switch category, then the fastest $x\%$ of the hold trials were also assigned to the fast hold category. This leads to fast and slow categories that are similar in a relative sense: e.g. fast switch trials may be slower than fast hold trials, but both categories contain trials from the same part of the reaction time distributions they are drawn from.
2.6. Preprocessing of the EEG-data

Only the trials with a RSI of 1500 ms were analyzed. EEG-data were low-pass filtered (cut-off 124.5 Hz, pass 93.375 Hz) and downsamped to 250 Hz (in the interests of disk space and the time required to run programs). Brain Vision Analyzer (Version 1.03, Brain Products GMBH, München, Germany) was used for preprocessing. The average of the two ear electrodes was used as the new reference for the data. Segments containing artefacts were removed based on visual inspection. Blinks were removed using the ocular correction algorithm of Gratton et al. (1983).

2.7. Cluster analysis

A simple semi-data-driven cluster analysis was used to define the regions for the frequency-domain analysis. Correlations were calculated between all combinations of electrodes. This was done per condition per subject. A number of anchor electrodes were selected around which a cluster was to be formed. For each anchor the optimal cluster of electrodes was calculated by seeking the correlation cut-off for cluster membership that maximized the mean ratio of the correlation between EEG signals with the anchor within the group and to the mean ratio outside the group. The segments of EEG signals that were to be analyzed (the response–stimulus period, with 1 s before response and 2.5 s afterward stimulus) were used to calculate correlations. Consistency of ROI membership was calculated as a value between 0 and 1, indicating the fraction of cases an electrode was appointed to a certain cluster (0 = never, 1 = for all subjects for every condition). Electrodes were assigned to the cluster with which they were the most consistent, provided that their consistency was above 0.5; that is, that they were at least more likely to be included than they were not to be included in the cluster. The cluster analysis was performed with the following 11 anchor electrodes: Fz, F3, F4, C3, C4, Pz, P3, P4, Oz, T3 and T4. Anchors were chosen to provide a reasonable coverage of the scalp and to roughly correspond with underlying brain regions—frontal, parietal and occipital cortex, and left and right motor cortex. The spatial resolution seemed to be sufficient to capture the topography of the expected effects (i.e., occipital and parietal regions for effects of modality, or left and right motor regions for effects of hand preparation), and greatly reduced the number of statistical tests to be performed relative to using individual electrodes. The use of the data-driven component in determining clusters was hoped to reduce the pooling of dissimilar signals. The amplitude signals were averaged over the electrodes in the region. In the case of phase locking between regions, the average was taken over all the inter-region electrode pairs.

2.8. Transformation to the frequency domain

Considering a signal as a sum of oscillating component signals with varying phase and amplitude, wavelet analysis can be used to determine the time course of amplitude and phase of the component signals. Wavelet analysis is based on the convolution of signals with wavelets: oscillatory functions which have finite energy and are therefore localized in time. Wavelets have a mean and standard deviation in time and frequency, specifying their location and the uncertainty of their localization. In this study, the complex Morlet wavelet was used, which is based on the product of Gaussian curve with a real cosine and an imaginary sine. The Morley wavelet has a Gaussian distribution both in the time domain (standard deviation $\sigma_t$) and in the frequency domain (standard deviation $\sigma_f = 1/(2\pi\sigma_t)$), around the center time and frequency of the wavelet. By convolving a signal with the wavelet, the time course of the amplitude of the signal around the frequency mean of the wavelet (the instantaneous amplitude IA) can be found. Formally:

$\text{IA}(t, f) = |w(t, f)s(t)|$

where $w(t, f)$ is a normalized, complex form of the Morlet wavelet:

$w(t, f) = \frac{1}{\text{sqrt}(\sigma_t \text{sqrt}(\pi))} \exp\left(-0.5 \left(\frac{t}{\sigma_t}\right)^2\right)\exp(i2\pi ft),$

where $f$ is the frequency around which the signal is to be analyzed. The complex form can be interpreted as a mathematical way to separate the cosine- and sine-based wavelets, as $\exp(2i\pi ft) = \cos(2\pi ft) + i \sin(2\pi ft)$. The respective convolutions measure the similarity of the signal to a cosine and a sine; using these measures as Cartesian coordinates defines a vector of which the length abstracts amplitude from phase. The convolutions are performed for each frequency around which the signal is to be analyzed. The vectors over time of amplitude for each trial were averaged per time point relative to the time of the response of the previous trial. This provided the typical amplitude time courses during the response–stimulus interval. Note that amplitude and power are directly related, power being 0.5 times the square of the amplitude.

The angle of the cosine and sine similarity vectors provides the phase of the signal, with 0 rad being the phase of the cosine component of the wavelet. Phases can be used to calculate phase locking between two signals, that is, the consistency of their phase difference. Synchrony is a special case, with a phase difference of zero, but a finding of any consistent phase locking between two signals, that is, the consistency of their phase difference. Synchrony is a special case, with a phase locking value (PLV, Lachaux et al., 1999) is a measure for phase locking between two signals that will be used in this study. It is calculated as the length of the mean phase-difference vector over $N$ trials as follows:

$\text{PLV}(t) = \frac{1}{N} |\text{SUM}(n = 1 \ldots N) \exp(i(\phi_1(t,n) - \phi_2(t,n)))|$

The phase-difference vector, $\exp(i(\phi_1(t,n) - \phi_2(t,n)))$, is a complex number with length 1 and an angle equal to the phase difference between two signals, at a given time–frequency point. The more this phase difference remains constant over trials, the longer the sum of the vectors over trials will be as they will extend the summed vector in one direction, maximally away from zero, instead of making it crooked. If the phase-difference
is random over trials, the vectors to be summed will cancel each other’s directions and the length will tend to zero. The PLV is calculated for all time–frequency points of interest, for all combinations of signals.

In the present study, a wavelet-based analysis approach was used in which a set of wavelets were chosen, together with an associated set of uncertainties. The wavelets were chosen so that the frequency range of interest (theta to beta frequency bands) was sampled with a 1–2 Hz resolution, and with temporal variance small enough to detect changes in oscillatory characteristics that arise over a period of at least 100–200 ms. The chosen frequencies were 5–25 Hz, in steps of 1 Hz from 5 to 15 Hz and of 2 Hz from 15 to 25 Hz. The \( f \)'s were equal to the step size. The frequencies 30, 40 and 70 Hz were also analyzed, with \( f \)'s of 4, 5 and 5 Hz. These frequencies were analyzed to determine the possible influence of EMG artefacts.

2.9. Statistical procedures

The false discovery rate procedure (FDR) (Benjamini and Hochberg, 1995; Genovese et al., 2002) was used to correct for the chance capitalization involved in multiple tests. The FDR controls the proportion of false positives among all tests for which the null hypotheses is rejected, in contrast to Bonferroni correction, which controls the chance of any false positive among all tests. The procedure works for any statistical test that generates a \( P \)-value and consists of the following steps:

1. Let \( q \) be the desired FDR between 0 and 1. This is the expected proportion of false discoveries.
2. Order the \( P \)-values form smallest to largest: \( P(1) \leq P(2) \leq \cdots \leq P(V) \), where \( V \) is the total of simultaneous performed tests.
3. Compare each \( P(i) \) sequentially with \( (qi)/V \), starting with the largest \( P \)-value. Let \( k \) be the largest \( i \) for which \( P(i) \leq (qi)/V \).
4. The threshold for all test statistics is \( P(k) \). Reject all null hypotheses \( H(i) \), \( i = 1, 2, \ldots, k \).

The value of the \( q \)-parameter was set to 0.05 in this study. This means that all of the rejected null hypotheses, no more than 5% is expected to be a false positive. The FDR procedure is far less conservative than Bonferroni correction, which controls the chance of any false positives at all.

The logarithm of instantaneous amplitudes was taken to normalize their distribution and so that differences between conditions reflected relative changes in amplitude. The PLV was normalized by taking the artanh transform of the square root of the PLV values.

For the time–frequency-domain measures, a number of contrasts were tested, using the FDR procedure separately per contrast. Conditions belonging to a category to be compared were pooled. For instance, in the comparison “visual versus auditory, given switch and prepared”, the left- and right-hand response trials were pooled, and unprepared and hold trials were excluded. This example compares the data found when successfully switching to a visual versus an auditory task set.

2.10. Lateralization

The LRP is derived from EEG (usually measured at C3 and C4) by means of the double subtraction described in the introduction. For the LRP, the double subtraction is subsequently multiplied by 0.5. This allows the LRP to be interpreted as the mean effect on the contralateral, relative to the ipsilateral, motor area, averaged over the left and right hand. Having instantaneous amplitudes for several frequency bands available for the C3- and C4-regions, analogous LRP-type measures can be derived using IA instead of raw EEG (Kaiser et al., 2003). These motor-related amplitude asymmetries (MRAA) were calculated using the log-normalized IA, as the double difference (IA, C3 – IA, C4, left hand) – (IA, C3 – IA, C4, right hand). The hand used for determining conditions was considered to be the hand to be used for the upcoming task.

3. Results

The data of six subjects were lost: five to technical problems and one due to the use of medication. This left 14 subjects for behavioral analysis and 11 subjects for EEG analyses.

3.1. Behavioral data

Mean reaction time and accuracy results are shown in Fig. 1 (data for the pure-task conditions are shown for sake of completeness and will not be analyzed). Switch costs decreased as the RSI increased, suggesting that subjects were on average benefiting from opportunities for advance preparation. The accuracy and reaction times were analyzed using repeated measures MANOVA with factors task (visual versus auditory), trial type (switch versus hold) and RSI. Accuracy showed a significant effect of trial type \( F(1, 9) = 12.9, P = 0.005 \). For reaction time, the analysis yielded significant main effects of trial type \( F(1, 10) = 53.9, P = 0.000 \) and RSI \( F(2, 9) = 30.8, P = 0.000 \), and significant interactions of trial type by RSI \( F(2, 9) = 38.1, P = 0.000 \) and task by RSI \( F(2, 9) = 9.5, P = 0.006 \).

V incented cumulative density functions of reaction times are shown in Fig. 2, for hold, long-RSI, switch, short-RSI, and switch, long-RSI trials. Note that the switch, long-RSI distributions have a smaller mean but a substantially larger variance than switch, short-RSI distributions. This unusual feature, together with the fact that the fast parts of the switch, long-RSI distributions approach that of the hold, long-RSI distributions whereas their slow parts approach that of the switch, short-RSI distributions, suggests that the condition in which residual switch costs are found may consist of a mixture of two subsets of trials: one with a fast, “no switch necessary at stimulus presentation” distribution, one with a slow, “not switched at stimulus presentation” distribution.

The fit of the switch, long-RSI distribution as produced by the mixture model is also shown in Fig. 2. The overall impression of a reasonable fit was confirmed by goodness-of-fit tests focused on the fast part of the distributions as in de Jong (2000). For the visual task, the fit was \( G2(11) = 12.85, P > 0.1 \),
with mean estimated $a = 0.61$ (S.E. = 0.05) and mean estimated $\delta = -1.6$ ms (S.E. = 6.7). For the auditory task, the fit was $G^2(11) = 12.47$, $P > 0.1$, with mean estimated $a = 0.69$ (S.E. = 0.05) and mean estimated $\delta = 9$ ms (S.E. = 8.2). Thus, the present results are in accordance with previous suggestions that occasional failures to effectively engage in advance preparation may, at least under some circumstances, be the predominant cause of residual switch costs (de Jong, 2000).

As the mixture model produced adequate fits to the data, it was possible to associate individual reaction times on switch,
long-RSI trials with estimated probabilities of pre-stimulus switching, using the Bayesian procedure described above. The mean estimated probabilities of successful preparation were 0.92 and 0.97 for the fast subgroups of trials in the visual and auditory tasks, respectively; the associated mean reaction times were 405 ms (S.E. = 9) and 400 ms (S.E. = 8). The probabilities for the slow subgroups were 0.21 and 0.24 for the visual and auditory task, respectively, with corresponding mean reaction times of 967 ms (S.E. = 46) and 1009 ms (S.E. = 54). Though the mean probabilities for the slow subgroups are somewhat higher than we might have wished for, the very substantial difference in mean probability between the fast and slow subgroups should provide a solid basis for subsequent analyses.

As described above, hold, long-RSI trials were also subcategorized into fast and slow groups. The associated mean reaction times were 365 ms (S.E. = 8 ms) for the fast visual group, 679 ms (S.E. = 27 ms) for the slow visual group, 353 ms (S.E. = 9 ms) for the fast auditory group and 749 ms (S.E. = 44 ms) for the slow auditory group.

As noted by a reviewer, the reaction time of trials may have been partly caused by the switches in hand mapping that occurred twice during the experiment. This would confound the preparatory interpretation of the fast and slow subsets. However, reaction times did not show a learning effect following the switches of hand mapping. This was tested by comparing the average number of trials since a change in mapping for the fastest and slowest 30 trials, separately for switch and hold trials. No significant effect was found, suggesting that it was not the case that the slower trials occurred sooner after a mapping switch.

3.2. EEG time-domain measures

3.2.1. Pre-stimulus: CNV and LRP

For the CNV the 100 ms preceding the previous response was used as the baseline. For this and some subsequent analyses, it should be noted that, due to the alternating runs paradigm used in this study, this baseline is confounded by the

![Fig. 3. The ERP, locked to and baselined (from −100 to 0 ms) at the response of the previous task, for switch and non-switch trials, separated for trials which will have fast and slow responses.](image_url)
previous trial type (i.e., hold trials are always preceded by switch trials, and vice versa). Therefore, some care must be taken in interpreting the results (see below). Fig. 3 shows the grand-average CNV’s for fast and slow switch and hold trials. The differences between fast and slow trials seem maximal at frontal and central areas, and seem to be generally larger for switch trials. The differences between CNV’s were tested, using the mean values over the second half of the RSI, with repeated measures MANOVA. Besides the factors trial type (switch/hold), speed (fast/slow) and modality (visual/auditory), the five midline channels Fpz, Fz, Cz, Pz and Oz were included as a factor in the analysis. The significant main effects at the 0.05 level were channel \((F(4, 7) = 23.6, P < 0.0005)\) and speed \((F(1, 10) = 10.0, P < 0.01)\). The interaction between trial type and speed was significant \((F(1, 10) = 8.8, P < 0.02)\), as was the interaction of channel and trial type \((F(4, 7) = 5.0, P < 0.05)\). No effects involving modality approached significance. The trial type by speed interaction was studied further. It was significant only for electrodes Fz \((F(1, 10) = 9.0, P = 0.013)\), Cz \((10.2, .01)\) and Pz \((5.2, .046)\). At Fz and Pz, the fast–slow difference was only significant for the switch condition, while it was significant for both switch and hold at Cz.

Fig. 4 shows the grand-average lateralized readiness potentials of the fast and slow switch and hold trials. The LRP’s were computed based on the identity (left hand/right hand) of the previous response, so the LRP associated with the upcoming response changes sign for switch but not for hold trials. Recall the formula \(\text{LRP} = L-R(\text{previous response left-handed}) - L-R(\text{previous response right-handed})\), where \(L-R(X)\) refers to the difference between the C3 and C4 electrodes in condition \(X\). The LRP will always be positive for the previous response. For hold trials, the next response, following the response–stimulus interval, will again show a positive LRP, as the same hand is used again. So, at that time, the \(L-R(\text{left}) - L-R(\text{right})\) form is preserved during the current response, even though the “left” and “right” qualifiers are based on the previous response. For switch trials, however, the LRP at response becomes negative, as when the previous response was right (or left), the next response must be left (or right). The formula written in terms of the second response thus reads \(L-R(\text{current response right-handed}) - L-R(\text{current response left-handed})\) for switch trials, and so the LRP is reversed for the switch responses.

The LRP for both fast and slow hold trials can be seen to gradually decay during the RSI towards a relatively low but significant level of lateralization in the direction of the upcoming response hand. The LRP for switch trials exhibits a similar time course during the RSI, with the LRP for slow switch trials remaining lateralized in the direction of the previous instead of the upcoming response hand, and the LRP for fast trials exhibiting a somewhat stronger decay but falling short of reaching a significant level of lateralization in the direction of the upcoming response hand by the end of the RSI. The differences between mean LRP amplitude during the second half of the RSI (750 ms interval before stimulus onset) were tested using repeated measures MANOVA, with trial type, response speed and task modality as factors. The analysis yielded a significant interaction of trial type and response speed \((F(1, 10) = 11.62, P < 0.01)\). The interaction was due to the effect only occurring prior to switch trials \((t(10) = 2.8, P < 0.05)\).

A further aspect of the waveforms in Fig. 4 can be noted. Within 150 ms after stimulus onset, all waveforms exhibit a steep increase of lateralization towards the upcoming response hand. For fast trials, this increase could be thought to be associated with response execution, as such an acceleration of LRP amplitude is commonly observed to precede actual response execution (i.e., reaction time) by 200–300 ms. For slow trials, however, with mean reaction times of 714 and 968 ms for hold and switch trials, respectively, the steep increase seems to occur too early to be tied to response execution proper, and therefore suggests that even on slow trials, the upcoming response hand is prepared: not in such a way as to lead to pre-stimulus lateralization, but so that lateralization can occur quickly post-stimulus.

3.2.2. Post-stimulus ERPs

Fig. 5 shows grand-average post-stimulus ERPs for fast and slow switch and hold trials, with the 100 ms interval before stimulus onset serving as baseline. The P300 is larger for fast than for slow trials; this difference is found both for switch and hold trials and is maximal at central and parietal areas. Also, P300 amplitude for hold trials exceeds that for switch trials, for both fast and slow trials. These differences were tested using
repeated measures MANOVA with the same factors used in the analysis of the pre-stimulus effects. The mean amplitude in the interval from 275 to 375 ms post-stimulus was analyzed. Trial type (F(1, 10) = 50.4, P < 0.001), speed (F(1, 10) = 17.3, P < 0.005) and channel (F(4, 7) = 10.9, P < 0.005) showed main effects. Channel interacted with trial type (F(4, 7) = 15.3, P < 0.001) and speed (F(4, 7) = 13.0, P < 0.002).

It should be noted that post-stimulus effects may be related to the baseline period, at which time sizable CNV effects were found. In these data, fast trials showed a greater pre-stimulus negative deflection relative to slow trials. Their greater post-stimulus P300 may be related to negating this baseline shift. The effect of trial type on P300 amplitude was not accompanied by a differential CNV effect.

We analyzed early post-stimulus ERPs (50–200 ms post-stimulus) for possible effects of modality that might indicate a dependence on relevant modality of perceptual processing of the compound stimulus. No significant effects were found.

3.3. Time–frequency analysis

The EEG was recorded using 125 electrodes. Data inspection revealed that some channels picked up an ECG signal. For the frequency-domain analyses (none of the channels used in the ERP analysis were contaminated), a selection of 66 channels was made from the original 128, that contained no evident ECG signal in any subject and gave a complete and evenly distributed representation of the scalp. The selected channels are Fp1, Fp2, F3, Fz, F4, T3, C3, Cz, C4, T4, T5, P3, Pz, P4, T6, O1, Oz, O2, AFz, FC5, FC1, FC2, FC6, CP1, CP2, AF3, AF4, PO3, POz, PO4, F5, F1, F2, F6, P5, P1, P2, P6, FC3, FC4, C5, C1, C2, C6, CP3, CP4, FCz, TP7, CPz, TP8, FT7, FT8, T7, T8, AF1, AF2, T1, T2, CPP7, CPP3, CPP4, CPP8, CPP5, CPP1, CPP2 and CPP6.

The cluster analysis on the selection of electrodes resulted in the following clusters (shown in Fig. 6), with the anchor followed by associated electrodes between brackets: F3 (AF3,
F5); Fz (AFz, FC1, FC2, F1, F2, FCz, AF1, AF2); F4 (AF4, F6, FC4); T3 (TP7, FT7, T7, T1); T4 (TP8, FT8, T8, T2); C3 (C1, C5; C4, C2, C6); P3 (T5, P3, CP1, P5, CP3, CPP3, CPP5, CPP7); Pz (CP2, CPz, CPP1, CPP2); P4 (T6, PO4, P6, CP4, CPP4, CPP6, CPP8) and Oz (O1, O2, Poz).

The remaining electrodes (Fp2, Fp1, FC6, FC5, FC3, Cz, PO3, P1 and P2) failed to be consistently assigned to a cluster and were discarded.

3.3.1. Instantaneous amplitude

FDR was performed on the instantaneous amplitude (IA) data for a number of contrasts: (1) visual versus auditory, for fast switch trials; (2) visual versus auditory, for fast hold trials; (3) fast switch versus fast hold, for the visual and auditory tasks separately; (4) fast versus slow response; (5) the interaction of response speed by trial type.

Of these contrasts, only the response speed factor yielded significant differences (Fig. 7). Theta IA (5–7 Hz) during the preparation interval is higher for fast trials, while post-stimulus theta IA is higher for slow trials. This suggests that this frequency band reflects processes that are necessary for task performance, but can be dealt with adequately prior to stimulus presentation, thereby allowing faster reaction times. Pre- and post-stimulus effects are distributed at anterior and posterior regions, respectively. Fig. 8 shows the time course of theta amplitude for fast and slow trials, revealing these effects of

![Fig. 6. The electrode clusters used for time–frequency analyses. Electrode positions around which a line is drawn were averaged to form a cluster.](image)

![Fig. 7. Significant amplitude differences between fast and slow trials. Amplitude was measured as described in Section 2, using wavelet analysis. Each subplot is a time–frequency plot showing datapoints at which the difference was significant according to the FDR procedure. Time is plotted on the horizontal, frequency on the vertical axis. The gray and black datapoints show positive and negative effects, respectively. The electrode names refer to the anchor-electrode of the cluster. The cut-off t-value for these results, given by the FDR procedure for this contrast, was 3.0.](image)
Fig. 8. The time course of theta-band amplitude for fast and slow trials, from the response of the previous trial past stimulus onset of the upcoming trial.

Fig. 9. The time course of beta-band amplitude for fast and slow trials, from the response of the previous trial past stimulus onset of the upcoming trial.
response speed superimposed on a background time course of theta amplitude increasing after stimulus presentation and following a response.

The time course of the beta-band (20–24 Hz) effect is shown in Fig. 9. Fast trials show lower beta-band amplitude (i.e., more beta-desynchronization) than slow trials in the preparation interval. Given the association of beta-desynchronization with motor preparation, this difference might indicate enhanced advance motor preparation on fast trials. The constant offsets, as found at the temporal and occipital regions that are particularly sensitive to EMG artefacts, seem likely to be due to effects of the lower frequencies of EMG activity.

The high-frequency (>30 Hz) effects of response speed are in the EMG range; when subjects do not prepare, they may be fidgeting in some way.

The FDR-maps for the MRAA for switch and hold trials are given in Fig. 10, showing distinct preparatory effects in the alpha and beta bands. The MRAA shows the lateralization of amplitude according to the relevant hand, changing sign for switch trials but not for hold trials.

The alpha-band (10–14 Hz) MRAA time course is shown in Fig. 11, for fast and slow switch and hold trials. This MRAA can be seen to behave quite differently from the traditional time-domain LRP (Fig. 4). In particular, for both fast and slow switch trials, it clearly reverses sign during the preparation interval to reach levels similar to those found for fast and slow hold trials. Also, its post-stimulus time course is markedly different from that of the LRP, peaking some 200–300 ms post-stimulus and then rapidly declining. The positive sign of the alpha-band MRAA signifies preparation-related alpha desynchronization in the motor cortex contralateral to the response hand or, equivalently, alpha synchronization in the ipsilateral motor cortex.

Fig. 12 shows the beta-band MRAA time course for fast and slow switch and hold trials. As can be seen in the FDR-maps, only switch trials are preceded by significant beta-band lateralization. This lateralization is achieved following a reversal that starts immediately after the previous response. Similar to the alpha-band MRAA, the positive sign of the beta-band MRAA signifies preparation-related beta desynchronization in the motor cortex contralateral to the response hand, or beta synchronization in the ipsilateral motor cortex.

Note that the alpha- and beta-band MRAA’s are not different for fast and slow trials. Thus, whereas both MRAA’s seem to be associated with advance preparation, they do not predict response speed; that is, they do not predict success or failure, or relative effectiveness, of selective task preparation as manifested in reaction time.

3.3.2. Instantaneous phase locking

Because of the large number of tests inherent in testing time by frequency by electrode combination datasets, testing of instantaneous phase-locking effects was restricted to three frequency bands, with FDR applied to each band separately; the three bands are theta (5–7 Hz), alpha (8–14 Hz) and beta (20–24 Hz). It should be noted that this increased the chances of false positives above the nominal 5% rate, but, given the explorative nature of the present study, it seemed appropriate to preserve reasonable power to detect potentially important effects.

No FDR-significant differences in phase locking were found between visual and auditory tasks, or in the interaction between modality and relevant response hand. Thus, no evidence was
found for phasic changes in effective connectivity, expressed in phase locking, of sensory cortices to other areas, e.g. frontal or motor cortices. Also, none of the other contrasts used previously for analysis of instantaneous amplitudes yielded significant results for instantaneous phase locking.

When the factor response hand was taken into account, significant results for instantaneous phase locking in the beta band were obtained, but only for switch trials. These results are schematically depicted in Fig. 13. Fig. 13a shows the pattern of electrode-cluster pairs for which beta-band phase locking was significantly higher during the preparation interval when the upcoming task was associated with the left hand as compared to the right hand. This pattern was centered on the right (i.e., contralateral) centroparietal region and indicates enhanced phase locking of beta-band activity in this region with beta-band activities in bilateral frontal regions. Fig. 13b shows a similar pattern of enhanced beta-band phase locking, but now centered on left centroparietal regions, when the upcoming task was associated with the right hand as compared to the left hand. No such effects were found for hold trials. Indeed, an FDR-based interaction analysis showed the lateralized phase-locking patterns to be significantly stronger for switch as compared to hold trials; the results of this analysis are depicted in Fig. 14. This figure shows the (electrode pair, time) points where the left–right-hand difference was significantly greater for switch than for hold trials. That is, as seen in Fig. 13a, left-hand preparation results in increased right-hemisphere phase locking. Fig. 14a shows that this right-hemisphere increase is significantly greater when the previous response set was on the left hand. The same goes for Figs. 13b and 14b, which show a greater left-hemisphere increase preceding right-hand trials, which is again greater for switch trials. A similar interaction analysis yielded no indication of a possible dependence of these phase-locking results on response speed.

![Fig. 11. The time course of the MRAA in the alpha band, plotted for the fast and slow switch and non-switch conditions.](image1.png)

![Fig. 12. The time course of the MRAA in the beta band, plotted for the fast and slow switch and non-switch conditions.](image2.png)
4. Discussion

This study aimed to explore ERP’s, oscillations and phase locking in the EEG during the preparation interval in a task-switching task, and to determine whether dividing trials into subsets on the basis of reaction time is relevant for psychophysiological studies of task switching. An interaction between reaction time and switch versus hold trials was of interest in testing the idea that anticipatory preparation may be different for switch and hold trials. The lateralization of activity (the LRP, MRAA and lateralized phase locking) was used as an index for motor-related preparation. The theta, alpha and beta frequency bands were studied to find evidence for, respectively, task-related amplitude topography, the inhibition of irrelevant modality and the frequency-domain aspects of lateralization due to hand preparation. Phase locking was studied to determine whether task-related shifts in coupling could be measured using the PLV. As discussed below, various effects on phase locking and oscillatory amplitude were found, as well as differences related to response speed and interactions of response speed and switching versus holding a task set.

The speed of the upcoming response was associated with both time- and frequency-domain effects. Both the CNV and pre-stimulus theta amplitude predicted whether a subject’s response to a stimulus would be fast or slow. Pre- and post-stimulus theta amplitude was reversed for fast and slow trials. While fast trials showed increased anterior theta activity during the preparation interval, slow trials showed posterior theta activity post-stimulus. However, no fast–slow by switch–hold interaction was found on theta-band amplitude. In contrast, the CNV did show a fast–slow by switch–hold interaction. Fast switch trials showed increased frontal negativity pre-stimulus, relative to all other conditions. More centrally, fast trials were preceded by increased negativity, for both switch and hold trials. A frontal pre-stimulus negativity preceding switch trials was also found by Lorist et al. (2000) and also seemed similar to an aspect of Wylie et al.’s (2003) data (Fig. 4), in which the frontal negative slope between responses and stimuli was greatest between pre-switch and switch trials. Taken together with the present results, these effects could be interpreted to have been due to the fast subset of switch trials.

The LRP showed a pre-stimulus fast–slow by switch–hold interaction that seems to be best interpreted as preparation by release. When the same hand was to be used, post-response
lateralization did not decay to a neutral baseline; the previous hand would then appear to retain an increased response tendency. The response–stimulus interval LRP was similar for the fast and slow subsets of hold trials. In contrast, when subjects were to switch hand, this pre-stimulus decay predicted response speed: if the level stayed with that for hold trials, subjects were slower than if the lateralization reached baseline. This loss of lateralization may index the release of the tendency to respond with the previously used hand. Motor preparation was also reflected in the time–frequency-domain measures, but with qualitatively different time courses. The motor cortex associated with the responses that are part of the upcoming task set showed a decrease in mu and beta amplitude and, specifically preceding switch trials, participation in a pattern of increased beta-band phase locking also involving frontal areas.

The timing of the frequency-domain effects (MRAA and lateralized phase locking) is notably different from that of the time-domain LRP, which is strongest around response, showing only rather subtle effects, in terms of differences in rate and asymptote of decay, during preparation. In contrast, the frequency-domain measures, especially phase locking, seem to have a strong preparatory role. The switch-specificity of preparatory beta-MRAA lateralization may be related to the modulation of an automatic post-response amplitude rebound, which is either reduced when the same hand must be used or enhanced when the other hand must be used. This may be an example of cognitive control working through the modulation of automatic processes. The interaction of lateralized phase locking with the switch–hold factor but not with reaction time suggests that this phase locking reflects an anticipatory switching process, but one that does not seem to fail, under the present experimental conditions.

No EEG effects were found that could be related to activation of task-specific brain areas in the theta-band, or to preparation via the selection of modality involving the alpha band. These null findings could be due to a problem of measurability: by no means all brain processes were measured in this study. The way subjects performed this specific task may also have played a role. Because each response hand was uniquely associated with a modality, choosing a hand could remove the need to select modality: incorrect responses could be blocked at response, and correct responses allowed, even if both responses would have been equally evoked by stimulation. A follow-up study (Gladwin and de Jong, 2005) has been done to determine if modality-related oscillatory activity could be found when subjects were to perform tasks that differed only on relevant modality. In that study, two effects of modality over occipital regions were found. Switching to a visual task involved increased occipital theta-band amplitude during the preparation interval, while repeating an auditory task was associated with increased occipital alpha-band amplitude. So, the absence of those effects in the present study suggests that subjects did not prepare via biasing the relevant modality.

No evidence was found for a “remapping” type of preparation involving differences in phase locking between sensory and motor cortices relevant to the current task set. Again, various possible factors weaken the significance of this finding. The specific phase-locking measure used here is insensitive to varying phase differences over trials and cannot detect non-linear coupling. Statistical power is also a problem due to the large number of tests and the explorative nature of the study. The generation of more specific hypotheses and associated measures may yet lead to the discovery of EEG effects reflecting changes in the interactions between sensory, motor and controlling cortex in future studies. One characteristic of the design used here may be especially relevant to such studies. Because stimuli were uniquely mapped to responses, the individual stimulus–response mappings did not have to be changed on a trial-to-trial basis. It is conceivable that precisely that kind of switching could be associated with changing phase relations. So, while the task set did change – the response to the same total tone + letter stimulus could be different following a switch – the correct response per object only changed in terms of its being given or not (cf. the distinction between intentional and attentional set switching; Rushworth et al., 2002). The shifting trial-by-trial intention could then simply be an intention to not move one or the other hand, as opposed to an intention of which the activation must result in changes within the communication pathways from stimuli to responses.

The combination of the motor-related effects and the null findings in the present study could be tentatively interpreted as an effect of the task context that led to preparation based on the motor component of the task. Further studies may reveal whether this is due to a conscious, strategic choice of subjects, if, for example, it is subjectively less effortful to bias response hand than perception, or that this kind of preparation arises more or less automatically in this task context. Similar motor-related effects as in the present study have been found in a follow-up study (in preparation) in which tasks differed only on response hand, without associated modality differences.

In summary, while the brain did show preparatory frequency-domain behavior in this task, fundamental questions remain as to what this behavior is accomplishing. No evidence was found for the idea that phase locking, as measured by the PLV, binds together stimuli and responses. However, this may be due to the task, which subjects may have performed by concentrating on which hand to use. The potential importance of selecting trials on the basis of subjects’ behavior was underscored by strong effects found by comparing fast and slow trials. Fast–slow by switch–hold interactions were found in the preparation interval, suggesting that preparation for switch trials differs from that for hold trials. Such interactions may help understand the mechanisms of voluntary/goal-directed behavior, and may be of interest in complementing post-stimulus results on task switching (e.g. Hsieh and Liu, 2005). It seems that further study using the classification of trials on the basis of reaction time would be useful.

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