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RESEARCH ARTICLE

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Transient increases of synchronized neural activity during movement preparation: influence of cognitive constraints

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Abstract The ability to prepare movement is an essential requirement for the control of goal-directed actions. It allows us to respond in an adaptable and swift manner to environmental conditions. In the present study, we manipulate cognitive context, by means of response probability, to modify the degree of movement preparation in a delayed cueing task performed with the right hand, and evaluate the neural dynamics (EEG coherence) and behavioural output (reaction time). Task-related coherence was stronger over the contralateral hemisphere. In particular, coherence between the left sensorimotor area and frontal (C3-F3, C3-FC3) and parietal (C3-P3) regions was increased during right-hand movement preparation as compared to rest in the alpha frequency band (8–12 Hz). Reducing response probability diminished the degree of functional coupling between C3-F3 and C3-FC3, and was associated with a prolonged reaction time. These findings suggest an association between neural dynamics and behavioural performance and emphasize that response predictability biases information processing in goal-oriented behaviour.

Keywords Transient increases · Synchronized neural activity · Movement preparation · Cognitive constraints · Response probability · Delayed cueing task

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Introduction

When preparing for a voluntary action, the underlying processes incorporate movement-specific as well as cognitive-related factors such as knowledge and expectation. Cognitive aspects impinge on neural activity in motor cortical areas (Georgopoulos 2000), and as such are able to shape the decision to prepare for an efficient action. Particularly important are the readiness to respond and the intention to perform, which together have been termed preparatory set (Evarts et al. 1984). To examine the preparation of voluntary movement, subjects are usually instructed to respond to a stimulus after a delayed time period following a cue. In this case, motor preparation is voluntary and characterized by several phases that translate stimulus information into an appropriate output. These stages involve processes such as attentional control, response planning and a decision to act, and are likely to take place in distributed cortical areas.

Here we use EEG coherence to follow the functional interaction between different cortical areas during movement preparation. In contrast to EEG power, which provides a quantitative measure of the synchrony of relatively local sources for each frequency within the range of an electrode, EEG coherence is a larger-scale measure, which captures dynamic functional interactions between electrodes separated by longer distances. There is considerable evidence to support the assumption that synchronized oscillations reflect a basic form of communication between cortical assemblies during task-related activity (see reviews by Bressler 1995; Klimesch 1999; Singer 1994).

In the current study we focus on how the functional interaction between different cortical areas during movement preparation is modulated by cognitive constraints. Emphasis was placed on the dorsolateral prefrontal area, which has a supervisory role in the planning of behaviour in a top-down manner (Fuster 1993). Accordingly, we investigated EEG-EEG coherence and behavioural responses in a delay reaction time task while manipulating the cognitive context. In particular, the predictive value of the warning cue was reduced in order to modify the degree of movement preparation, as evidenced by a prolonged reaction time. Under these circumstances we predicted that the coherence between EEG signals picked up over the sensorimotor cortex and those over more frontal regions would be lower than with fully predictive cues.

Materials and methods

Task and procedure

Right-handed subjects (n=7, age 35±5 years) as determined by the Edinburgh handedness inventory (Oldfield 1971) gave informed consent to participate in the study, which was approved by the local ethics committee. They were asked to perform a visuo-manual reaction time task during which a cue stimulus would carry the instruction to get ready while a subsequent target stimulus would provide the ’go’ signal for the requested movement. Subjects were seated in front of a desk with a custom-built button press device, and faced a computer screen at a distance of 80 cm. A fixation cross was continuously visible in the centre of the screen. During each trial, an arrow was presented that pointed to the right, and served as a cue for a following target signal that consisted of a figure 0. The cue and target stimuli appeared on the right side of the fixation cross and remained visible on the screen for 500 ms, while a fixed time interval of 3 s occurred between the onsets of cue and target. Both stimuli subtended a visual angle of 2° with the fixation cross. Subjects had to respond to the target signal by pressing the right-sided button as fast as possible with the thumb of the right hand. The predictability of the target signal was set at 75%, and the task required a left-sided button press with the thumb of the left hand, or bimanual button presses with the thumbs of both hands in the remaining trials. In these cases, the figure 0 occurred on the left side or both sides of the fixation cross in the appropriate direction(s), respectively. Therefore, the subjects were made uncertain about the possibility of the upcoming response. The thumbs rested on the button press device at all times. A performance condition in which the predictability of the target stimulus was set at 100% served as control. In the latter case, the certainty of the response along with the fixed temporal interval between cue and target enabled optimal preparation for movement execution. The interval between trials varied between 7–9 s.

EEG recordings

Continuous EEG was recorded from Ag/AgCl surface electrodes mounted on an EEG cap (Easy Cap, Falk Minow Services, Herrsching-Breitbrunn, Germany), according to the 10–20 International system. Left-hemispheric (C3, F3, FC3, P3) and right-hemispheric (C4, F4, FC4, P4) activity was analysed in this study. The activity recorded at these electrodes is likely to overlie the sensorimotor cortex (C3/4), dorsolateral prefrontal (F3/4), premotor (FC3/4) and superior parietal (P3/4) areas (Homan et al. 1987; Steinmetz et al. 1989), although it is possible that activity from neighbouring cortical regions contributed to the EEG. EEG signals were amplified, band-pass filtered 0.15 Hz–100 Hz, and sampled at 500 Hz (NeuroScan Synamps, El Paso, USA). The electro-oculogram was also recorded (band-pass 0.1 Hz–30 Hz) to allow rejection of EEG data contaminated by eye movements. A rest (baseline) condition was included and consisted of fixating a small cross on the screen. Linked binaural electrodes were used as our reference.

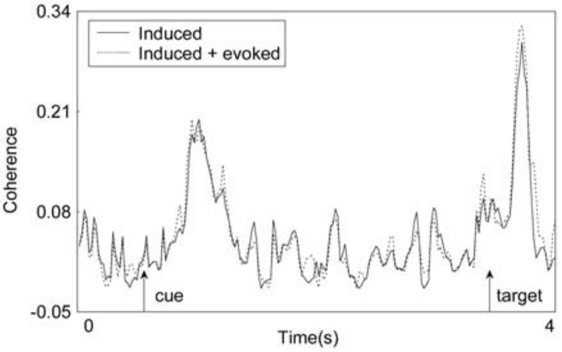

Fig. 1 Event-related coherence using the method of complex demodulation. A comparison between the computation of induced (not phase-locked to the stimulus) and induced + evoked (phase-locked to the stimulus) EEG coherence. The time interval shows 4 s: a pre-cue and post-target epoch of 500 ms and an epoch of 3 s between cue and target. The *arrows* denote the onset of the cue and target signals

Analysis

Behavioural data

Mean reaction times of the button presses to the target stimuli were calculated in both performance conditions and analysed by means of a paired t-test. Times shorter than 150 ms or in excess of 1000 ms were considered outliers and excluded from data analysis.

EEG data

EEG records were visually inspected and those with prominent artefact from eye-movement or scalp muscle contraction rejected. A total of 24 trials were set aside for analysis in each condition. Trials were segmented into epochs that were aligned to the target signal. These epochs comprised intervals of 4 s; from 500 ms pre-cue until 500 ms post-target and included the 3 s delay period. Event-related coherence was used to assess functional coupling between the sensorimotor area and more frontal (C3-F3, C4-F4, C3-FC3 and C4-FC4) and parietal (C3-P3 and C4-P4) areas in the frequency domain. The frontal regions (prefrontal, premotor) were chosen due to their direct involvement in cognitive aspects of goal-directed behaviour, whereas the parietal area was included as a control region as it has largely been implicated in visuo-motor processing regardless of motor performance (Thoenissen et al. 2002). EEG coherence was estimated by means of complex demodulation (Thatcher 1995), using NeuroScan software. Complex demodulation converts the broadband source activities to a narrowband series of complex numbers for a center frequency of interest, plus or minus some half-bandwidth. It derives real and imaginary time series from the original time series. As such, the modulus of the resulting complex time series is the envelope of the original time series at the selected frequency, which was set in the present study at 10 Hz, with a half-bandwidth of 2 Hz and roll-off of 12 dB, allowing for the evaluation of alpha activity (8–12 Hz). The method of complex demodulation permits the computation of induced (internally generated, not phase-locked to the stimulus) and induced + evoked (phase-locked to the stimulus) EEG coherence. Induced activity uses the variance for a given point across sweeps whereas evoked activity is computed on the time-locked average. In other words, the phase-locked mean activity is removed in the induced option, but maintained in the induced + evoked option and therefore includes both types of activity. Figure 1 illustrates an individual example that shows the computation of event-related coherence according to both options for the C3-F3 connection. It can be observed that the computational difference is small, which suggests that the internally generated EEG activity contributed predominantly to the coherence scores. The similarity between the values obtained in both computational options is in line with the hypothesis that it is unlikely that processing stages beyond primary visual cortex distinguish between internally generated and externally evoked synchrony (Singer 1998). In the present study, we focussed on spectral changes in the alpha band as a discrete spectral peak was a consistent finding and it has been suggested that frequency interactions in the low-frequency range <12 Hz might mediate top-down activity that reflects internal processes such as planning (von Stein et al. 2000). In particular, coherence in the alpha band between the EEG signals from frontal regions has been associated with movement-related decisions (Shibata et al. 1998). We evaluated the whole alpha band (8–12 Hz), as preliminary spectral analysis failed to show any consistent clustering of peak frequency within the lower and upper ranges of the alpha band. Neither was any clear spectral peak observed in the beta (12–30 Hz) or theta (4–8 Hz) frequency bands. In addition, both the theta and beta bands were evaluated by means of complex demodulation using centre frequencies of 6 Hz, 15 Hz, 20 Hz and 25 Hz and half-band widths of 2 Hz, as for the alpha band and no consistent task-related activity pattern was found. The estimated coherences were transformed using the inverse hyperbolic tangent.

There is considerable debate over which is the most appropriate way to avoid overestimated coherence values due to volume conduction and common references (Nunez 2000). We opted not to make use of Laplacian algorithms, as the emergent measurements may lead to underestimations of EEG coherence in lower frequency bands due to excessive spatial filtering. We used linked binaural electrodes as our reference. This procedure introduces a common signal to all channels, leading to inflated coherence estimates. We limited this by using a subtractive approach. Therefore, in order to separate the task-related coherence from the background coherence, the values of the resting state were subtracted from those of the active state. This reduces any contribution from volume conduction of signals between active electrodes. Coherence increments are expressed as positive values and can be interpreted as indicating greater interregional coupling, whereas coherence decrements are depicted as negative values and denote a state of relative functional disconnection.

The EEG epochs of the transformed coherence values were separated into four time intervals that consisted of 500 ms: (1) pre-stimulus immediately before the cue, (2) post-stimulus immediately after the cue, (3) pre-stimulus midway in the delay period before the target, (4) post-stimulus immediately after the target. Intervals of 500 ms were chosen as preliminary examination of the coherence data showed that the principal activity changes occurred within this time frame. However, in the case of the post-stimulus period we also analysed an interval of 250 ms immediately after the target. The pre-stimulus intervals before cue and target were taken as a reference for the post-stimulus intervals after cue and target. Thereafter, separate percentage scores were calculated as $(Px-Pr)\times100/Pr$, where Px referred to the post-values and Pr indicated the pre-values. Normality of the values was verified by the Shapiro-Wilk's W test ($P>0.05$).

An initial analysis was conducted for the left hemisphere and the percentage coherence scores were analysed by means of a 3×2×2 (region × probability × moment) ANOVA. The first factor represented the three combinations of cortical regions: C3-F3, C3-FC3, C3-P3; the second factor indicated the 75% and 100% probability conditions of the target signal, whereas the third factor referred to the events of cue and target. Additional analyses of the absolute peak coherences for C3-F3 and C3-FC3 after the target were made by means of paired *t*-tests. Also, to establish that changes in the relative coherence were due to modulations of post-cue and post-target, and not to changes in the reference periods, the coherence values of the three regions were subjected to separate 2×2 (probability × moment) ANOVA's. The first factor referred to the 75% and 100% probability conditions, whereas the second factor indicated the intervals of pre-cue and pre-target. In order to establish that power changes were not responsible for modulations in coherence at the warning cue and target, the event-related power was examined for the electrodes (C3, F3, FC3, P3) and correlated with the corresponding coherence values of C3-F3, C3-FC3 and C3-P3 over the 500 ms post-target intervals. This measure was used to ensure that changes in coherence were not due to modulations in non-linearly related frequency components (Florian et al. 1998). The correlation coefficients were transformed into Fisher's *z*-scores and thereafter subjected to separate 2×2 (probability × site) ANOVA's for each connection. The first factor represented the 75% and 100% probability conditions of the target signal, and the second factor referred to the correlation between C3 power and C3-F3 coherence vs. F3 power and C3-F3 coherence for the prefrontal connection; C3 power and C3-FC3 coherence vs. FC3 power and C3-FC3 coherence for the premotor connection; C3 power and C3-P3 coherence vs. P3 power and C3-P3 coherence for the parietal connection.

To evaluate differences in coherence with the target signal in the left vs. right hemisphere, the percentage scores were analysed by means of 2×2 (probability × hemisphere) ANOVAs for the three different couplings: prefrontal (C3-F3 vs. C4-F4), premotor (C3-FC3 vs. C4-FC4) and parietal (C3-P3 vs. C4-P4). The first factor referred to the 75% and 100% probability conditions, whereas the second factor included the left vs. right hemispheric couplings. This analysis would demonstrate whether the effect of response predictability is confined to the left hemisphere, which is taken to be the side from which the right-handed action is directed (Serrien et al. 2003), or is found across distributed cortical regions in both hemispheres.

Results

Behavioural data

The subjects' reaction times were slower in the 75% than in the 100% condition [$t_6=3.9$, $P<0.01$] and were 297±14 ms and 250±11 ms, respectively (mean ± SE). This result indicates that response uncertainty affected behavioural performance.

Relative increases in EEG-EEG coherence depend on response probability. The event-related coherence in percentage scores data showed significant main effects of region [$F_{2,12}=11.1$, $P<0.01$], probability [$F_{1,6}=70.2$, $P<0.01$] and moment [$F_{1,6}=6.1$, $P<0.05$]. All two-way interactions were significant; region × probability [$F_{2,12}=16.3$, $P<0.01$], region × moment [$F_{2,12}=77.3$, $P<0.01$] and probability × moment [$F_{1,6}=10.3$, $P<0.02$]. The region × probability × moment interaction was also significant [$F_{2,12}=3.9$, $P<0.05$]. Tukey post hoc analysis revealed that the increase in coherence at the target for C3-F3 and C3-FC3 was less in the 75% as compared to the 100% probability condition ($P<0.05$, for both). This is illustrated in Fig. 2, which also shows the C3-P3 coherence was low and relatively unmodulated, and that modifications in coherence at the cue were less marked than with the target. These data suggest that response uncertainty limited increases in functional coupling of the sensorimotor region with the frontal areas, particularly following the target stimulus.

Considering that the post-target interval of 500 ms included activity related to movement preparation as well as movement execution, additional analyses of the coherence values for the initial 250 ms following the target stimulus were conducted. This time frame would reflect movement preparatory activity only. The paired *t*-

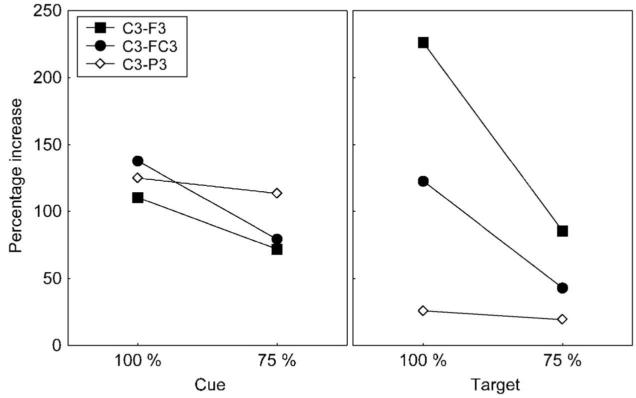

Fig. 2 The percentage increase of coherence during the post-cue and post-target intervals as compared to the pre-cue and pre-target intervals. The event locations of cue and target evoked a proportional increase in EEG coherence for C3-F3, C3-FC3 and C3-P3. A substantial drop in coherence is evident for the C3-F3 and C3-FC3 connections at the target in the 75% as compared to the 100% probability condition

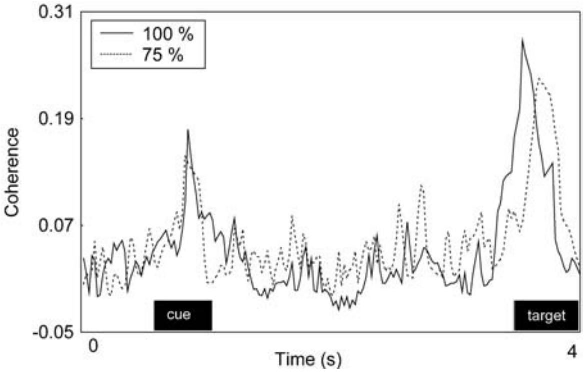

Fig. 3 Time series of the absolute coherence changes as a function of response probability (100% and 75%) for C3-F3 in the alpha band. The time interval shows 4 s: a pre-cue and post-target epoch of 500 ms and an epoch of 3 s between cue and target. The *black-shaded rectangles* indicate the 500 ms duration of the cue and target, and in addition show the time intervals that were used for analysis. It can be noticed that transient increases in coherence in the alpha band occurred in response to the cue and target in both performance conditions. However, peak coherence depended on response certainty, and was lower in the 75% as compared to the 100% probability condition. Individual data

tests showed significant effects for the C3-F3 and C3-FC3 connection, $P<0.05$. The percentage coherence scores for the 75% and 100% conditions were 96% and 263% (C3-F3), 69% and 184% (C3-FC3), 49% and 52% (C3-P3).

A correlation analysis across subjects of the reaction times and the degree of coherence changes in the C3-F3 and C3-FC3 connections at the target for the combined probability conditions ($n=14$) revealed significant scores of −.93 and −.71, respectively ($P<0.05$ for both). This finding indicates that the individual reaction times could be associated with the transient increase in functional coupling between central and frontal areas; the higher the degree of coherence augmentation with the target event, the faster the reaction time albeit with a stronger influence from the prefrontal region.

Absolute increases in EEG-EEG coherence depend on response probability

The cue and target resulted in proportional increases in coherence as compared to reference intervals. The changes were more marked following the target and depended on response probability. In interpreting these proportional changes we established that there was no significant variation in absolute coherence levels between the reference periods with respect to probability or timing ($P>0.05$). The overall mean scores of the 75% and 100% probability conditions were .03 and .04 (C3-F3), .02 and .01 (C3-FC3), .03 and .03 (C3-P3).

Both cue and target also evoked clear peaks in absolute as opposed to relative coherence. These peaks were reduced as a function of response predictability. For example, peak C3-F3 coherence around the target was significantly lowered with response uncertainty [$t_6=2.6$, $P<0.05$], and resulted in coherence values of .13±.03 and .23±.05 for the 75% and 100% probability conditions, respectively. Likewise peak C3-FC3 coherence around the target was significantly reduced in the 75% (.06±.01) as compared to the 100% (.08±.02) probability condition [$t_6=3.5$, $P<0.05$]. The latter results indicate that the absolute degree of coherence in the frontal areas was influenced by response uncertainty. This is further illustrated in Fig. 3, which shows an individual time series of coherence modulations as a function of response probability for the C3-F3 connection. It can be observed that a transient increase in functional coupling occurred with respect to both stimuli, albeit more prominently with the target. In addition, a stronger gradual development of anticipatory activity before onset of the target was evident when response probability was 100% as compared to 75%, and may be attributed to the fixed interval between cue and 'go' target, which engendered temporal expectancy. Event-related changes in coherence were limited to the alpha band (Fig. 4).

Relative temporal profile of EEG-EEG coherence changes depends on response probability

To underscore that response uncertainty not only influenced the strength of neural activities but also their timing, we used a cross-correlation analysis with distributed lag estimates between the C3-F3 and C3-FC3 coherence patterns in the post-target interval (Fig. 5). The peak cross correlations which were statistically significant were .70 (SE=.17) and .56 (SE=.13) in the 100% and 75% probability condition, respectively. This means that oscillatory activity in both connections was more closely correlated when response certainty was high. Further, the maximal correlation peak was concentrated around 0 ms in the 100% probability condition whereas it was shifted

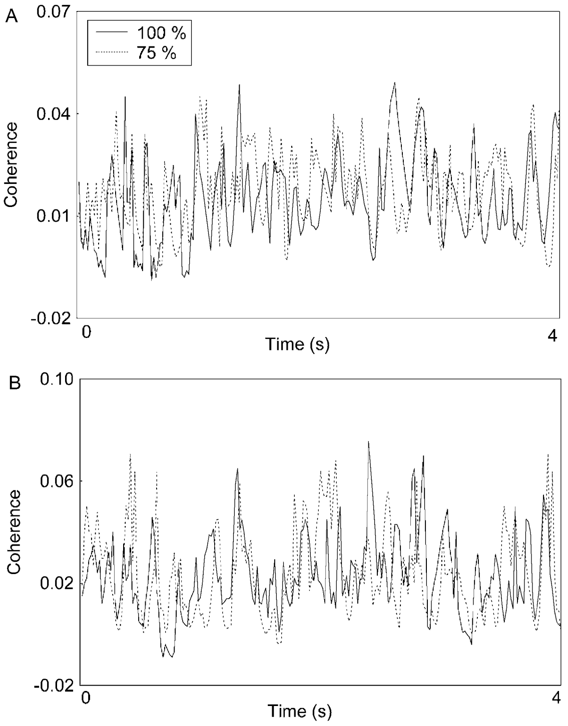

Fig. 4 Time series of the absolute coherence changes as a function of response probability (100% and 75%) for C3-F3 in the theta **(A)** and beta **(B)** frequency bands. The time interval shows 4 s: a pre-cue and post-target epoch of 500 ms and an epoch of 3 s between cue and target. No event-related responses can be observed in either frequency bands. Individual data (same subject as in Fig. 3)

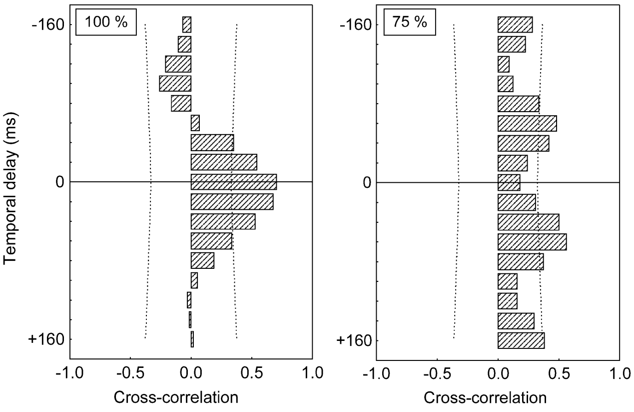

Fig. 5 Distribution of the cross-correlations between the C3-F3 and C3-FC3 coherence patterns as a function of temporal offset in the 75% and 100% probability conditions. *Each bar* corresponds to the maximum correlation at a temporal delay of 20 ms. *Interrupted vertical lines* are 95% confidence levels. Averaged data

in the 75% probability condition, and resulted in an increased lag of the C3-FC3 with respect to the C3-F3 connection. This signifies that the secondary correlation of the coherence between sensorimotor and prefrontal and premotor areas was susceptible to a time delay as a function of reduced response probability. The temporal offset in regional coupling in the 75% probability condition was paralleled by an additional reaction time delay. That the temporal offset was not merely due to an uncertainty associated with stimulus encoding was verified by examining the cross-correlations at the post-cue interval. No time delay was evident at this event location, which suggests that the temporal offset at the target in the 75% probability condition was likely due to a decline in preparatory movement processing with respect to the 100% probability condition. Based on these data, it is hypothesized that both the strength and the temporal synchrony of regional coupling affect the rapidity of the behavioural output. The data further imply that functional synchronization between cortical areas strongly relies on the internal context during movement preparation and is accordingly adapted in a dynamic manner.

Lack of correlation between EEG-EEG coherence and EEG power changes

The correlation analysis between the power and coherence changes for the C3-F3, C3-FC3 and C3-P3 data showed no significant effects ($P>0.05$). The mean correlation coefficients of the C3-F3, C3-FC3 and C3-P3 regions were .01 and .13, .10 and .19, .09 and .15, for the 75% and 100% probability conditions, respectively. These data imply that the observed coherence modulations were independent of power changes, and suggests a primary role for interregional neural synchronization in the alpha frequency band during the preparation of movement. The specific modulations in coherence with response probability were not caused by variation in the occipital alpha activity as was shown by evaluating EEG power at Oz (occipital midline) in the post-target compared to the reference interval. The percentage power changes were equivalent in the 75% and 100% probability condition, and were 18% and 22%, respectively ($P>0.05$).

Differences in coherence changes between left and right hemisphere

The events of cue and target resulted in proportional increases in coherence as compared to reference intervals in a left sided fronto-parietal circuit, with the modulations being more prominent following the target and in the 100% probability condition. To determine whether the effect of response predictability was specific to the left hemisphere, which is taken to be the movement-driving hemisphere for right-handed actions (Serrien et al. 2003), we compared modulations of coherence in both hemispheres. For the prefrontal connection, the main effects of probability [$F_{1,6}=41.2$, $P<0.01$] and hemisphere [$F_{1,6}=167.9$, $P<0.01$] were significant. The probability x hemisphere interaction was also significant [$F_{1,6}=21.1$, $P<0.01$]. The mean percentage scores in the 75% and 100% conditions of the C4-F4 link were 13% and 18% (vs. 86% and 226% for C3-F3). For the premotor connection, the main effects of probability [$F_{1,6}=7.8$,

$P<0.03$] and hemisphere [$F_{1,6}=27.0$, $P<0.01$] were significant. The probability x hemisphere interaction was also significant [$F_{1,6}=10.9$, $P<0.01$]. The mean percentage scores in the 75% and 100% conditions of the right (C4-FC4) hemisphere were 3% and 5% (vs. 43% and 112% for C3-FC3). For the parietal connection, the main effect of hemisphere [$F_{1,6}=13.4$, $P<0.01$] was significant, and indicated lower levels for the right (4%) than left (7%) side.

Overall, these data show that even though coherence increases occurred in the right hemisphere due to the target signal, these were small and did not show significant modulations with respect to response probability. Conversely, event-related activity in the left hemisphere was prominent and modulated by response probability.

Discussion

When a cue provides prospective information about an upcoming movement, selective preparation takes place that results in superior reaction times (Deiber et al. 1996). That subjects use advance knowledge was apparent in the present study as a prolonged reaction time in the 75% compared to the 100% probability condition. This suggests that response expectation modulated the nature and timing of the processing preceding and accompanying movement.

The EEG data revealed coherent synchronized oscillations that were part of a neural network activated by the visuo-motor task requirements, in line with recent animal work (Liang et al. 2002). Overall, an increased coherence between the contralateral sensorimotor region and fronto-parietal areas was observed in the alpha frequency band for both cue and target as compared to reference intervals. Task-related coherence varied as a function of the particular event, response probability condition, as well as the cortical connection.

EEG coherence at the event locations of cue and target

With respect to the cue, increases in EEG coherence were observed for all the examined connections with the sensorimotor area, i.e., prefrontal, premotor and parietal. This is in agreement with the hypothesis that these regions are active when subjects orient to a location in the visual field. However, it can be argued that their underlying functions differ. The modulation in the parietal region possibly points to activity related to visuo-motor transformations (Andersen 1997). Coding of the sensory location as such elicited parietal lobe activity, and was accordingly unaffected by response probability. Coherence between C3-F3 and C3-FC3, which tended to be reduced as a function of movement uncertainty, is more likely associated with higher-order task management. In this schema, the degree of functional connectivity of the parietal and frontal regions reflects dissimilar processing demands with the parietal activity being due to stimulus-response association and the prefrontal activity being more closely related to cognitive elements such as knowledge and expectation. This differentiation finds a parallel in the distinct attentional systems involving these regions (Posner and Petersen 1990).

With respect to the target, the increase in functional coupling between the sensorimotor and parietal regions was small and unchanged by response probability, which suggests that it contributed little to the actual motor planning at this particular point in time. This is in line with fMRI data showing that the parietal area does not exhibit specific preparatory activity (Connolly et al. 2002). Conversely, the degree of coherence between the sensorimotor and more frontal cortical areas strongly increased in the 100% probability condition. This observation may reflect the regulating capacities of anterior regions in movement preparation, and their tight coupling with the primary motor cortex in movement execution (Passingham 1993). That the increase in C3-F3 and C3-FC3 coherence was significantly reduced in the 75% probability condition is further evidence that interregional coupling may be important in movement preparation, with the reduction possibly reflecting weakened preparatory set and less influential top-down control. Consistent with this is the temporal asynchrony of the coherence patterns between C3-F3 and C3-FC3 in the 75% probability condition, which may in turn relate to reduced anticipatory processing, or additional decision-related coding. These data corroborate the hypothesis that the strength of the neural network facilitates subsequent processing for motor output (Liang et al. 2002), as also evidenced from a positive association between the amount of interregional coherence and the degree of behavioural success in a tactile discrimination task (Hummel and Gerloff 2001).

These findings point to the significant impact of cognitive factors upon neural interregional synchronization. That the strongest effect was observed for the connections with F3, overlying the prefrontal region, is consistent with the fundamental role of prefrontal cortex in preparatory set by coding the intention and readiness to perform a movement (Connolly et al. 2002; Thoenissen et al. 2002), and also supports its sensitivity to changes in the probability of an event (Casey et al. 2001). Furthermore, cognitive operations that close the perception-action cycle are a crucial function of the prefrontal area (Quintana and Fuster 1999), and incorporate the unique behavioural context by establishing mappings between inputs, internal states, and outputs (Miller 2000). In connections between sensorimotor area and FC3, which overlies the premotor region, set-related activity was also prominent, which supports a significant involvement of the premotor cortex in movement preparation, and corroborates earlier fMRI and TMS studies (Schluter et al. 1999; Toni et al. 1999). Nevertheless, care should be taken in equating the C3-F3 and C3-FC3 coherence with coupling between sensorimotor cortex and prefrontal and premotor cortices, respectively, as pick-up from both the latter areas may contribute to F3 and FC3 EEG. Some discrimination between the activities picked up by these frontal electrodes is however suggested by the fact that the correlation between C3-FC3 and C3-F3 coherence was less than unity and varied in strength and phase according to condition.

It is the case that besides a specific change in preparatory set, the attentional requirements were also likely to be different in the 75% as compared to the 100% probability condition. In this respect, it could be argued that response uncertainty would necessitate additional attention, which might have lead to reductions in regional alpha activity (Ray and Cole 1985; Wei et al. 1988). Nevertheless, this is an unlikely explanation for the changes in coherence in the alpha band, as the latter were not correlated with alterations in power. Independent changes in regional EEG power and EEG-EEG coherence have been noted before and it has been suggested that the two measures may relate to different aspects of cortical function that might, to some extent, operate independently of each other (Gerloff et al. 1998; Ohara et al. 2001). Thus, amplitude and coherence may be considered mathematically and functionally independent measures of neocortical dynamics. In particular, it is noteworthy that there is a reduction in intra and interhemispheric coherence with frontal regions in the alpha band with decreasing vigilance level (Cantero et al. 1999) and this, if anything, would bias against the findings presented in this study.

Overall, the data hint at a fronto-parietal network of the movement-driving hemisphere that is implicated in the preparation of a goal-directed task, in which the frontal regions are concerned with movement planning and are strongly influenced by cognitive abilities whereas the parietal region appears to be more involved in the mechanisms of visuo-motor encoding.

Optimal motor preparation and modulations in the alpha frequency band

The present results suggest an association between fronto-central EEG coherence during movement preparation and behavioural performance. In particular, faster reaction times occurred in the setting of a stronger degree of functional coupling. This is in line with data that preparatory activity differs between accurate and inaccurate responses (Gevins et al. 1987).

The modulations in coherence were observed in the alpha frequency band (8–12 Hz). Previously, power changes in this band have been taken to capture cognitive-related processes (Klimesch 1999) and have been related to the speed of information processing as measured by reaction time (Klimesch et al. 1996). Therefore, changes in alpha band activity may reflect dynamic responses to cognitive demands during information processing (González-Hernández et al. 2002). Based on this assumption, it can be hypothesized that in the present experimental design the visual signals triggered an internal state of alertness and readiness that accordingly launched subsequent processes of movement preparation, albeit affected by response uncertainty. In this respect, low-frequency interregional interactions might have mediated the top-down processes that manifest the internal context (Siegel et al. 2000; von Stein et al. 2000), and should be distinguished from independent modulations of local alpha power that have been associated with cortical idling (Pfurtscheller et al. 1996). In particular, low-frequency oscillations might provide a substrate that organizes neural activity over time in order to assimilate distributed information processing in view of future events such as decision-making (Başar et al. 1999; Dinse et al. 1997). Hence, alpha band coupling during movement preparation could be regarded as a general association mechanism that schedules multiple and concurrent brain activities, and as such enables a coherent representational state. Changes in synchronization may also occur within other frequency bands, depending on the task constraints, and perhaps underlying different components of information processing such as memory encoding and perceptual demands. Thus the present observations do not undermine the putative integrative role of the gamma frequency band (Singer 1993), but suggest that synchronization within the alpha band has a significant role in cognitive motor functioning.

Conclusion

Neural synchrony has been suggested to underlie the formation of transient networks that incorporate brain activity into proficient task-related operations (Singer 1993). In agreement with this role, we observed that cognitive constraints altered the degree of EEG-EEG coherence during movement preparation. Thus interregional functional coupling was dynamically modulated as a result of the internal context in which it occurred and modulations were paralleled by changes in behavioural performance.

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References

Andersen RA (1997) Multimodal integration for the representation of space in the posterior parietal cortex. Philos Trans R Soc Lon B Biol Sci 352:1421–1428

Başar E, Başar-Eroglu C, Karakas S, Schürmann M (1999) Are cognitive processes manifested in event-related gamma, alpha, theta and delta oscillations in the EEG? Neurosci Lett 259:165–168

Bressler L (1995) Large-scale cortical networks and cognition. Brain Res Rev 20:288–304

Cantero JL, Atienza M, Salas RM, Gomez CM (1999) Alpha EEG coherence in different brain states: an electrophysiological index of the arousal level in human subjects. Neurosci Lett 271:167–170

Casey BJ, Forman SD, Franzen P, Berkowitz A, Braver TS, Nystrom LE, Thomas KM, Noll DC (2001) Sensitivity of prefrontal cortex to changes in target probability: a functional MRI study. Hum Brain Mapp 13:26–33

Connolly JD, Goodale MA, Menon RS, Munoz DP (2002) Human fMRI evidence for the neural correlates of preparatory set. Nat Neurosci 5:1345–1352

Deiber MP, Ibañez V, Sadato N, Hallett M (1996) Cerebral structures participating in motor preparation in humans: a positron emission tomography study. J Neurophysiol 75:233–247

Dinse HR, Kruger K, Akhavan AC, Spengler F, Schöner G, Schreiner CE (1997) Low-frequency oscillations of visual, auditory and somatosensory cortical neurons evoked by sensory stimulation. Int J Psychophysiol 26:205–227

Evarts EV, ShinodaY, Wise SP (1984) Neurophysiological approaches to higher brain functions. Wiley, New York

Florian G, Andrew C, Pfurtscheller G (1998) Do changes in coherence always reflect changes in functional coupling. Electroencephalogr Clin Neurophysiol 106:87–91

Fuster JM (1993) Frontal lobes. Curr Opin Neurobiol 3:160–165

Georgopoulos AP (2000) Neural aspects of cognitive motor control. Curr Opin Neurobiol 10:238–241

Gerloff C, Richard J, Hadley J, Schulman AE, Honda M, Hallett M (1998) Functional coupling and regional activation of human cortical motor areas during simple, internally paced and externally paced finger movements. Brain 121:1513–1531

Gevins AS, Morgan NH, Bressler SL, Cutillo BA, White RM, Illes J, Greer DS, Doyle JC, Zeitlin GM (1987) Human neuroelectric patterns predict performance accuracy. Science 235:580–585

González-Hernández JA, Pita-Alcorta C, Cedeño I, Bosch-Bayard J, Galán-Garcia L, Scherbaum WA, Figueredo-Rodriguez P (2002) Wisconsin Card Sorting Test synchronizes the prefrontal, temporal and posterior association cortex in different frequency ranges and extensions. Hum Brain Mapp 17:37–47

Homan RW, Herman J, Purdy P (1987) Cerebral location of international 10–20 system electrode placement. Electroencephalogr Clin Neurophysiol 66:376–382

Hummel F, Gerloff C (2001) Better swing together. Soc Neurosci Abstr

Klimesch W (1996) Memory processes, brain oscillations and EEG synchronization. Int J Psychophysiol 24:61–100

Klimesch W (1999) EEG alpha and theta oscillations reflect cognitive and memory performance: a review and analysis. Brain Res Rev 29:169–195

Klimesch W, Doppelmayr M, Schimke H, Pachinger T (1996) Alpha frequency, reaction time, and the speed of processing information. J Clin Neurophysiol 13:511–518

Liang H, Bressler SL, Ding M, Truccolo WA, Nakamura R (2002) Synchronized activity in prefrontal cortex during anticipation of visuomotor processing. Neuroreport 13:2011–2015

Miller EK (2000) The prefrontal cortex and cognitive control. Nat Rev Neurosci 1:59–65

Nunez PL (2000) Toward a quantitative description of large-scale neocortical dynamic function and EEG. Behav Brain Sci 23:371–437

Ohara S, Mima T, Baba K, Ikeda A, Kunieda T, Matsumoto R, Yamamoto J, Matsuhashi M, Nagamine T, Hirasawa K, Hori T, Mihara T, Hashimoto N, Salenius S, Shibasaki H (2001) Increased synchronization of cortical oscillatory activities between human supplementary motor and primary sensorimotor areas during voluntary movements. J Neurosci 21:9377–9386

Oldfield RC (1971) The assessment and analysis of handedness. The Edinburgh inventory. Neuropsychologia 9:97–113

Passingham RE (1993) The frontal lobes and voluntary action. Oxford University Press, Oxford

Pfurtscheller G, Stančák A Jr, Neuper C (1996) Event-related synchronization (ERS) in the alpha band—an electrophysiological correlate of cortical idling: a review. Int J Psychophysiol 24:39–46

Posner MI, Petersen S (1990) The attention system of the human brain. Annu Rev Neurosci 13:25–42

Quintana J, Fuster JM (1999) From perception to action: temporal integrative functions of prefrontal and parietal neurons. Cereb Cortex 9:213–221

Ray WJ, Cole HW (1985) EEG alpha activity reflects attentional demands, and beta activity reflects emotional and cognitive processes. Science 228:750–752

Schluter ND, Rushworth MF, Mills KR, Passingham RE (1999) Signal-, set-, and movement-related activity in the human premotor cortex. Neuropsychologia 37:233–243

Serrien DJ, Cassidy MJ, Brown P (2003) The importance of the dominant hemisphere in the organization of bimanual movements. Hum Brain Mapp 18:296–305

Shibata T, Shimoyama I, Ito T, Abla D, Iwasa H, Koseki K, Yamanouchi N, Sato T, Nakajima Y (1998) The synchronization between brain areas under motor inhibition process in humans estimated by event-related EEG coherence. Neurosci Res 31:265–271

Siegel M, Körding KP, König P (2000) Integrating top-down and bottom-up sensory processing by somato-dendritic interactions. J Comput Neurosci 8:161–173

Singer W (1993) Synchronization of cortical activity and its putative role in information processing and learning. Ann Rev Neurosci 18:555–586

Singer W (1994) Coherence as an organizing principle of cortical functions. Int Rev Neurobiol 37:153–183

Singer W (1998) Consciousness and the structure of neuronal representations. Phil Trans R Soc Lond B 353:1829–1840

Steinmetz H, Furst G, Meyer B-U (1989) Craniocerebral topography within the international 10-20 system. Electroencephalogr Clin Neurophysiol 72:499–506

Thatcher RW (1995) Tomographic electroencephalography/magnetoencephalography. Dynamics of human neural network switching. J Neuroimaging 5:35–45

Thoenissen D, Zilles K, Toni I (2002) Differential involvement of parietal and precentral regions in movement preparation and motor intention. J Neurosci 22:9024–9034

Toni I, Schluter ND, Josephs O, Friston K, Passingham RE (1999) Signal-, set- and movement-related activity in the human brain: an event-related fMRI study. Cereb Cortex 9:35–49

Von Stein A, Chiang C, König P (2000) Top-down processing mediated by interareal synchronization. Proc Natl Acad Sci U S A 97:14748–14753

Wei J, Zhao L, Yan G, Duan R, Li D (1988) The temporal and spatial features of event-related EEG spectral changes in 4 mental conditions. Electroencephalogr Clin Neurophysiol 106:416–423