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A shift of visual spatial attention is selectively associated with human EEG alpha activity

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Abstract

Event-related potentials and ongoing oscillatory electroencephalogram (EEG) activity were measured while subjects performed a cued visual spatial attention task. They were instructed to shift their attention to either the left or right visual hemifield according to a cue, which could be valid or invalid. Thereafter, a peripheral target had to be evaluated. At posterior parietal brain areas early components of the event-related potential (P1 and N1) were higher when the cue had been valid compared with invalid. An anticipatory attention effect was found in EEG alpha magnitude at parieto-occipital electrode sites. Starting 200 ms before target onset alpha amplitudes were significantly stronger suppressed at sites contralateral to the attended visual hemifield than ipsilateral to it. In addition, phase coupling between prefrontal and posterior parietal electrode sites was calculated. It was found that prefrontal cortex shows stronger phase coupling with posterior sites that are contralateral to the attended hemifield than ipsilateral sites. The results suggest that a shift of attention selectively modulates excitability of the contralateral posterior parietal cortex and that this posterior modulation of alpha activity is controlled by prefrontal regions.

Introduction

By directing an attentional ‘spotlight’ to a part of the visual field it is possible to facilitate perception of an attended stimulus while suppressing the processing of other competing stimuli (see Posner & Petersen, 1990). These covert shifts of attention can be done without moving the eyes. In a series of experiments, Hillyard and co-workers have demonstrated that peripheral visual stimuli elicit higher early brain potentials if attention is directed towards them than when they are unattended (for a review, see Hillyard *et al*., 1998a,b). These differences appear as early as 100 ms after stimulus presentation onset and are most pronounced over posterior (extrastriate) brain areas (LaBerge, 1997; Mangun *et al*., 1997; Woldorff *et al*., 1997; Hillyard & Anllo-Vento, 1998; Hopfinger *et al*., 2000). Increased activity contralateral to the attended stimulus was found in neuroimaging studies as well as in animal studies using single-cell recordings (e.g. Luck *et al*., 1997; Kastner *et al*., 1999). Moreover, oscillatory brain activity reflects effects of spatial selective attention. It was found that human electroencephalogram (EEG) alpha (about 10 Hz) and low beta (about 15 Hz) oscillations differentiate between attended and unattended stimuli (Vázquez Marrufo *et al*., 2001; Yamagishi *et al*., 2003). Alpha shows stronger amplitude suppression but beta responds with an increase in power for attended stimuli.

When a subject’s attention is directed to a spatial position in the visual field or to a sensory modality, attentional shifts can be investigated even before a visual target is presented. In precedence to target presentation, event-related potentials (ERPs) reveal a more negative slow cortical potential contralateral to the cued hemifield compared with control conditions (Worden *et al*., 2000). Similar effects are found within the respective association cortices when the sensory modality is cued (Foxe *et al*., 1998). However, even more striking are the differences of ongoing oscillatory brain activity between 8 and 13 Hz. This frequency band is known as EEG alpha and represents the dominant rhythm in the attentive and awake human. Its amplitudes are pronounced during the absence of visual stimulation and decrease during cognitive activity (see Klimesch, 1999 for review). It was shown that alpha amplitudes can decrease before visual stimulation when a target is expected (Klimesch *et al*., 1998). This alpha suppression preceding target presentation was found to react on shifts in attention. Foxe *et al*. (1998) found smaller parieto-occipital alpha amplitudes in an interval between a cue and a visual target compared with the time period prior to an auditory target. In visual spatial attention tasks it was shown that parietal alpha power was decreased over contralateral sites preceding target presentation when attention was selectively directed to one visual hemifield (Worden *et al*., 2000; Yamagishi *et al*., 2003). EEG alpha activity can be interpreted as an indicator of cortical inhibition (Klimesch *et al*., 1999; Hummel *et al*., 2002; Jensen *et al*., 2002). Thus, when spatial attention is directed to one hemifield, the contralateral decrease of alpha power may indicate the release from inhibition for the relevant visual association cortex. Similar effects are reported in anticipatory attention paradigms in which targets of different sensory modalities are expected. Dependent on whether the stimulus is auditory, visual or somatosensory, an anticipatory alpha power decrease can be obtained at the respective sensory association cortices (e.g. Bastiaansen & Brunia, 2001; Bastiaansen *et al*., 2001). Similar electrophysiological reactivity can be found in a somewhat higher frequency band at

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sensorimotor cortex for preparation of motor responses (Kaiser *et al.*, 2001, 2003). Though the temporal incidence of these anticipatory modulations of ongoing oscillations is like the contingent negative variation, it was shown that these two phenomena are not related to each other (Filipovic *et al.*, 2001).

Although most consistent findings related to visual spatial attention are reported for posterior extrastriate cortices, prefrontal brain areas are also considered to play an important role in selective attention. The prefrontal cortex might be the neuronal correlate of executive control, together with posterior brain regions building an attention-related network (see, e.g. LaBerge, 1997; Gitelman *et al.*, 1999; Rosen *et al.*, 1999; Nobre, 2001; Griffin & Nobre, 2003; Small *et al.*, 2003; Nobre *et al.*, 2004; Gonzalez Andino *et al.*, 2005). An important question is how local effects of alpha activity are related to this attention network, and whether this network oscillates at alpha frequency. There is evidence that fronto-parietal alpha coupling is influenced by expectancy (von Stein *et al.*, 2000; Serrien *et al.*, 2004; Sauseng *et al.*, in press), and that posterior EEG alpha power modulations are governed by prefrontal brain areas (Sauseng *et al.*, 2005). But also connectivity in the lower beta range (about 15 Hz) between prefrontal and posterior cortices is reported to be strongly related to attention processes (Gross *et al.*, 2004; Schnitzler & Gross, 2005).

In the present study a visual attention task was run. A central cue indicated in which hemifield a peripheral target would be presented a few hundred milliseconds following the cue. The cue was only valid in 75% of the trials. Participants directed their attention to the cued target location without moving their eyes even before presentation of the target. We hypothesized that after target presentation early ERP components (P1–N1) would show higher amplitudes in the valid than in the invalid conditions. In respect to the ongoing EEG (in particular alpha oscillations), attention-related differences were expected already before a target was presented, when attention was shifted to a specific location. In particular, we expected EEG alpha to show smaller magnitudes contralateral to the attended hemifield. Such attention-related effects should also be manifested in alpha phase synchronization between prefrontal and posterior electrode sites, i.e. phase synchronization between prefrontal areas and brain regions contralateral to the attended visual hemifield should be stronger than synchronization between frontal and ipsilateral sites.

Materials and methods

Participants

Twenty-nine healthy volunteers participated in the study after giving written informed consent. Data of seven participants could not be used for analysis due to artefacts caused by eye blinks and/or horizontal eye movements. Three of the remaining 22 participants were male. With the exception of two volunteers all subjects were right-handed. Mean age was 23.6 years (SD ± 2.8).

Task

Participants performed a cued visual attention task. They had to fixate the centre of a computer monitor (indicated by a fixation cross) throughout the whole experiment. At the beginning of each trial an arrow (1.2 × 0.6 °) either pointing to the right or to the left was foveally presented for 34 ms. The direction of the arrow indicated in which visual hemifield a target stimulus would appear subsequently and subjects were instructed to focus their attention to the cued hemifield without moving their eyes to the target location. After an interval with a duration ranging between 600 and 800 ms (jittered between trials) a target was presented for 50 ms. Targets were white bars on black background and were shown 6.5 ° either right or left from the centre of the computer monitor. Subjects had to indicate by button press whether the bar was small (1 × 1.9 °) or large (1 × 2.2 °). Frequencies for small and large targets were 50% and were equally distributed to the different experimental conditions. The inter-trial interval was 2300 ms. A total of 1024 trials was run. In half of them attention was cued to the right and in the other half attention was cued to the left hemifield. In 75% of the trials cue and target location were congruent (valid condition), and the remaining 25% were incongruent (invalid condition).

EEG recordings

EEG was recorded from 30 Ag/AgCl electrodes positioned according to the extended 10–20-system against a linked earlobe reference. Vertical and horizontal electrooculogram was recorded from two additional channels to control for eye movements. The EEG was acquired with a Synamps 32-channel amplifier (Neuroscan). Sampling rate was 250 Hz, and signals between 0.16 and 45 Hz were amplified. A notch filter at 50 Hz was applied. Impedances of the recorded channels were kept below 15 kOhm.

Data analysis and statistical designs

Data were visually inspected for artefacts and thereafter segmented into 2000-ms epochs (ranging from 1000 ms preceding target presentation to 1000 ms after target onset). ERPs for four experimental conditions (right hemifield presentation valid, left hemifield presentation valid, right hemifield presentation invalid, left hemifield presentation invalid) were obtained by averaging over trials. Five regions of interest (ROI) were defined and respective electrode sites were pooled: left posterior parietal (PL: electrodes P3, Po1, Po3), right posterior parietal (PR: electrodes P4, Po2, Po4), left prefrontal (FL: electrodes F3, F5), right prefrontal (FR: electrodes F4, F6), and a fronto-medial region (FM: electrodes Fz, Fc1, Fc2). To test for differences of early evoked components between the valid and invalid conditions, point-to-point *t*-tests were run between 0 and 200 ms after onset of the target (this interval covers the time window in which P1 and N1 components were elicited). Additionally, the same analysis was run for a 200-ms time window preceding stimulus onset to investigate differences in the slow negative component in the prestimulus interval (contingent negative variation). Differences were considered as reliable when $P < 0.01$ for at least three consecutive sample points.

Temporal spectral analysis of the single trials was run by applying complex Morlet wavelets (2–45 Hz, 14 frequency steps, c = 5) implemented in BrainVision Analyser 1.05 (Brain Products). Thereby the temporal resolution is superior to methods based on Fourier transformation at still good frequency resolution. Instantaneous amplitude estimates were calculated for the theta (4.25–6.37 Hz), lower alpha (6.89–10.34 Hz), upper alpha (9.54–14.31 Hz), beta (17.48–26.22 Hz) and gamma (33.35–50.03 Hz) band (note that the complex Morlet transformation results in broader bands the higher the centre frequency is). The mean magnitude of the respective frequency bands was calculated for six time windows: three time windows with 200 ms duration preceding target presentation (−600 to −400 ms, −400 to −200 ms and −200 to 0 ms) and three windows of 200 ms duration following target presentation (0–200 ms, 200–400 ms, 400–600 ms). Four-way ANOVAs with factors VALIDITY (valid, invalid), HEMIFIELD (right, left), ROI (left, right) and TIME (the six time windows) were run for each frequency band and posterior parietal as well as prefrontal ROIs separately. Greenhouse-Geisser correction was applied where necessary. *Post-hoc* Scheffé tests were calculated to evaluate significant interactions.

To control for baseline differences of spectral amplitude already occurring before the start of a trial, mean magnitude of a baseline interval (600–400 ms preceding presentation of the cue) was compared between the different experimental conditions. Two-way ANOVAs with factors CONDITION (valid left, valid right, invalid left, invalid right) and ROI (FL, FR, FM, PL, PR) were calculated for each frequency band separately. In addition to that, the reactivity of the lower and upper alpha bands during the prestimulus interval was investigated. Therefore, *t*-tests were calculated between mean spectral amplitude during the baseline interval (600–400 ms preceding start of the trial) and the time window immediately preceding presentation of the target (−200–0 ms prestimulus). This was done to clarify whether a shift of attention leads to less alpha power *decrease* at ipsilateral posterior sites or rather to a power *increase* as suggested by Worden *et al.* (2000) and Yamagishi *et al.* (2003).

To investigate phase coupling between frontal and posterior areas, a method suggested by Lachaux *et al.* (1999; termed phase-locking value or PLV) – implemented in BESA 5.1 – was calculated. The advantage of this method over spectral coherence is that it is insensitive against power modulations that were expected in the present experiment. The phase coupling between frontal ROIs (FL, FR, FM) with left and right parieto-occipital brain areas (PL, PR) was investigated. Thus, the relevant ROI pairings for analysis were FL–PL, FL–PR, FR–PL, FR–PR, FM–PL and FM–PR. This analysis was run for theta, lower alpha, upper alpha, beta and gamma, and for valid as well as invalid trials. For statistical comparisons four-way ANOVAs with factors VALIDITY (valid, invalid), HEMIFIELD (left, right), ROI PAIR (respective anterior ROI to PL, respective anterior ROI to PR) and TIME WINDOW (the six time windows as used in the analysis of amplitude estimates). Separate ANOVAs were run for each respective anterior ROI (FL, FR, FM). We expected to find stronger phase coupling between the posterior site contralateral to the attended hemifield and anterior ROIs in the alpha band. The lateralization pattern was expected to be reversed in the invalid compared with the valid conditions in the prestimulus interval because in the invalid conditions attention was cued to the hemifield opposite to that where the target occurred. In contrast, fronto-parietal connectivity was expected to be similar between valid and invalid conditions in the post-stimulus interval.

For statistical analysis of spectral amplitude estimates as well as phase coupling Bonferroni correction was applied when multiple ANOVAs were run.

Results

Response accuracy was not significantly better in the valid condition compared with invalid ($t_{21} = 1.07$, $P > 0.05$); 71.2% (SE = 1.84) of the valid trials were correctly responded to and 70.2% of invalid targets were correctly recognized (SE = 1.89). In contrast to accuracy, response time showed a significant attention-related effect ($t_{21} = 4.01$, $P < 0.01$). The invalid condition (615.7 ms, SE = 11.9) resulted in slower response times compared with the valid trials (600.4 ms, SE = 12.5).

At the posterior parietal ROIs early ERP components were larger in the valid compared with the invalid conditions (Fig. 1). When the target was presented to the left hemifield differences between the valid and the invalid condition were reliable ($t_{21} > 2.83$, $P < 0.01$ for at least three consecutive sample points) between 100 and 128 ms (P1) and 152 and 176 ms (N1) at left parietal sites, and from 100 to 132 ms (P1 component) and 152 to 184 ms (N1) at the right posterior parietal ROI. Similarly, the left posterior parietal brain region showed significant differences ($t_{21} > 2.83$, $P < 0.01$ for at least three consecutive sample points) between valid and invalid around the P1 and N1 component (112–132 ms and 152–184 ms, respectively) when the target was presented to the right visual hemispace. At the right parietal ROI the differences were significant between 112 and 124 ms as well as 152 and 176 ms. There were no reliable effects of cue validity on early ERP components at frontal ROIs ($t_{21} < 2.83$, $P > 0.01$ for at least three consecutive sample points).

A slow negative component preceded target presentation. But this negativity did not differentiate between the conditions at parietal as well as frontal ROIs.

Figure 2 depicts the results from time–frequency analyses for the lower alpha frequency band and the posterior parietal ROIs. The four-way interaction VALIDITY*HEMIFIELD*ROI*TIME was significant ($F_{5/105} = 9.09$, $P < 0.01$). *Post-hoc* Scheffé tests indicate that stronger amplitude suppression was found for the ROI contralateral to the attended hemifield from 200 ms preceding target presentation to 600 ms post-stimulus in the valid condition ($P < 0.05$). The invalid condition, on the other hand, elicited smaller lower alpha magnitude ipsilateral to the target location during the 200 ms preceding stimulus onset ($P < 0.05$; note that in the invalid conditions the subjects had directed their attention to the hemifield opposite the target location). From 200 to 600 ms post-stimulus alpha suppression was reliably stronger contralateral to the stimulated visual hemifield ($P < 0.05$).

For the prefrontal ROIs no significant four-way interaction was found ($F_{5/105} = 0.32$, $P > 0.05$).

Very similar results were obtained for the upper alpha frequency band (Fig. 3). The ANOVA with factors VALIDITY, HEMIFIELD, ROI and TIME yielded a significant four-way interaction ($F_{5/105} = 17.64$, $P < 0.01$). Equivalently to the lower alpha band, upper alpha magnitude was suppressed at the contralateral posterior parietal ROIs in the valid and at the ipsilateral parietal ROIs in the invalid condition during the 200 ms prestimulus interval as revealed by *post-hoc* Scheffé tests ($P < 0.05$). In the post-stimulus period in both conditions upper alpha magnitude was smaller at posterior ROIs contralateral to the hemifield where the target was presented. This was significant between 0 and 600 ms post-stimulus and from 200 to 600 ms for the valid and the invalid condition, respectively ($P < 0.05$). The four-way interaction did not reach significance for prefrontal ROIs ($F_{5/105} = 1.21$, $P > 0.05$).

In the theta, beta and gamma band there was no interaction between factors VALIDITY, HEMIFIELD, ROI and TIME significant ($F_{5/105} < 1.66$, $P > 0.05$). This was the case for prefrontal as well as posterior parietal brain regions.

The control analysis performed to compare magnitude estimates in a baseline interval preceding the beginning of single trials revealed no significant main effect for factor CONDITION ($F_{3/63} < 1.88$, $P > 0.05$), nor any interaction between factors CONDITION and ROI ($F_{12/252} < 1.82$, $P > 0.05$) in any of the five frequency bands. *T*-tests comparing posterior alpha amplitude in the pretrial baseline with alpha magnitude immediately preceding presentation of the target showed that in any condition and at any posterior parietal ROI lower as well as upper alpha band activity decreased under attentional demand ($t_{21} > 3.05$, $P < 0.01$). This indicates that also ipsilateral posterior brain regions exhibit alpha power suppression instead of increase during directed attention.

Analysing phase coupling revealed a significant four-way interaction VALIDITY*HEMIFIELD*ELECTRODE PAIR*TIME WINDOW

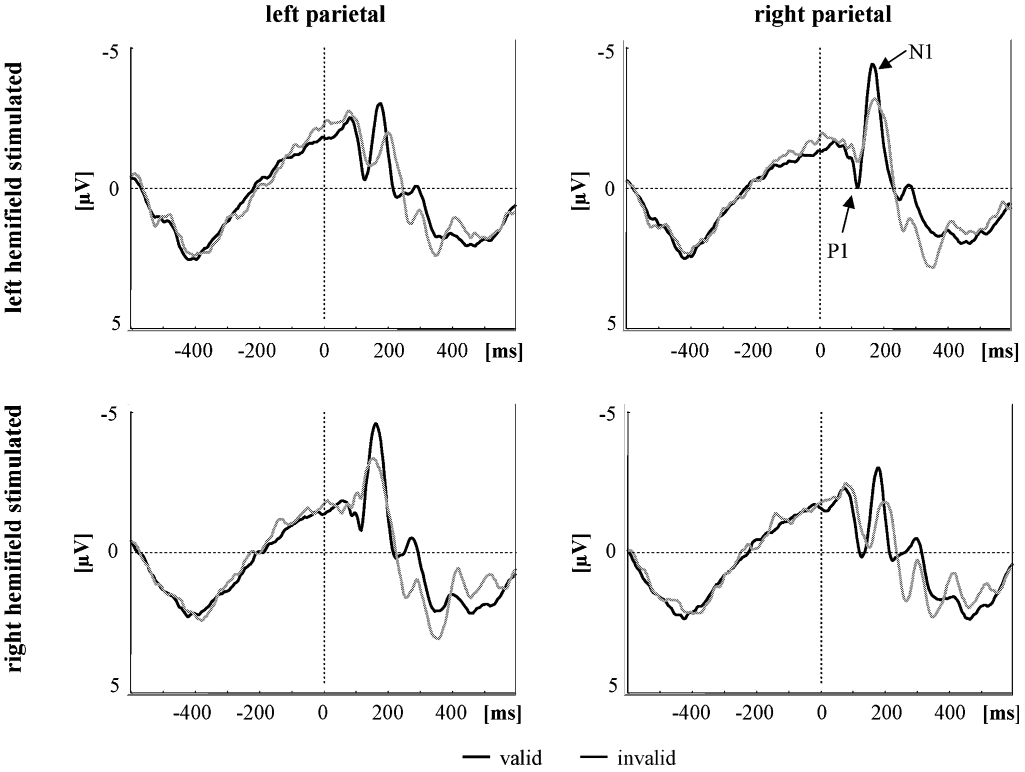

FIG. 1. ERPs from a left and right posterior parietal ROI for valid and invalid cued conditions are depicted. Valid conditions elicit higher P1 and N1 amplitudes than invalidly cued conditions. In the prestimulus interval a slow negative potential was elicited, but this did also not differentiate between the conditions.

in the upper alpha band for the coupling between the fronto-medial brain region (FM) and posterior parietal cortex left (PL) and right (PR), respectively ($F_{5/105} = 3.01$, $P < 0.05$). As shown in Fig. 4 and revealed by *post-hoc* Scheffé tests, in the 200 ms preceding target presentation, phase coupling was always higher between FM and the parieto-occipital ROI, which was contralateral to the attended hemifield ($P < 0.05$). This means that in the valid conditions phase coupling was stronger between FM and PL when attention was directed to the right hemifield. When the left hemifield was attended coupling was higher between FM and PR. As in the invalid conditions the hemifield opposite the later target presentation was attended, the synchronization patterns are reversed between valid and invalid conditions. In the post-stimulus time window (200–600 ms), on the other hand, valid as well as invalid conditions elicited higher PLVs between FM and the parieto-occipital region contralateral to the stimulated hemifield ($P < 0.05$; for the valid condition this effect was significant for the whole post-stimulus interval from 0 to 600 ms).

Phase coupling between dorsolateral prefrontal ROIs and posterior parietal cortices and other frequency bands than upper alpha did not reveal any significant four-way interaction ($F_{5/105} < 1.70$, $P > 0.05$).

Discussion

It is well documented that the P1–N1 complex of the visual event-related potential responds to shifts of attention (see above, and for reviews Hillyard *et al.*, 1998a,b). In accordance with these findings we observed enhanced P1 and N1 components in the valid compared with the invalid condition at posterior parietal brain regions. This was elicited by targets presented in the left as well as in the right visual hemifield. The effect, however, did not show any lateralization. For the prefrontal ROIs no significant differences of early evoked components (within the first 200 ms after target presentation) were found. Preceding target presentation slow negative potentials were found. These, however, did not differ between conditions, as was reported by Foxe *et al.* (1998) and Worden *et al.* (2000).

The alpha bands exhibited reliable attention-related effects. Both lower and upper alpha were found to be more suppressed at sites contralateral to the attended hemifield. This effect started 200 ms preceding target presentation supporting the assumption that alpha suppression marked the shift of attention to the cued location. In the valid conditions it continued until 600 ms post-stimulus. The late post-stimulus effect might simply reflect the processing of the visual target and not directed attention per se, as also in the invalid conditions alpha

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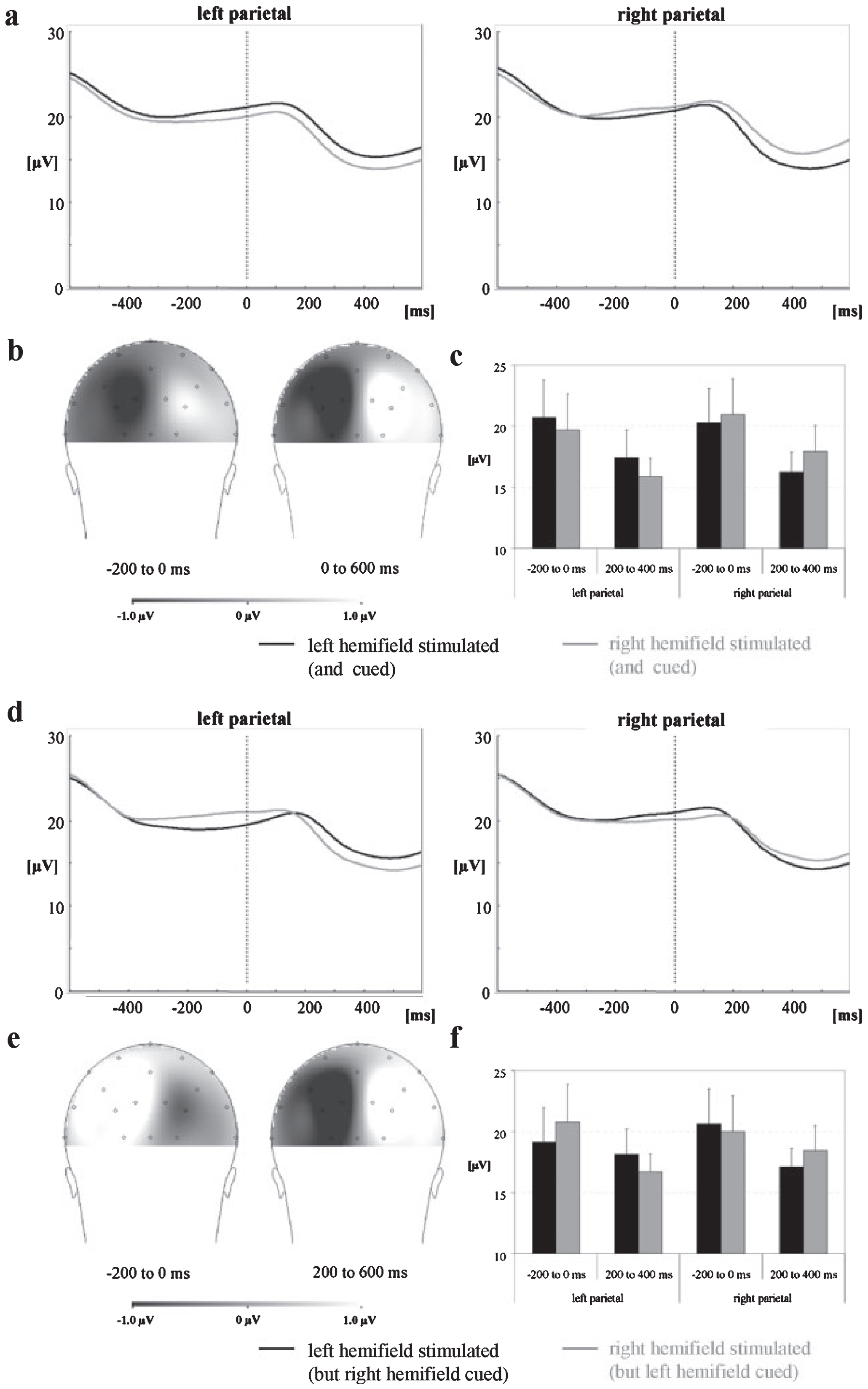
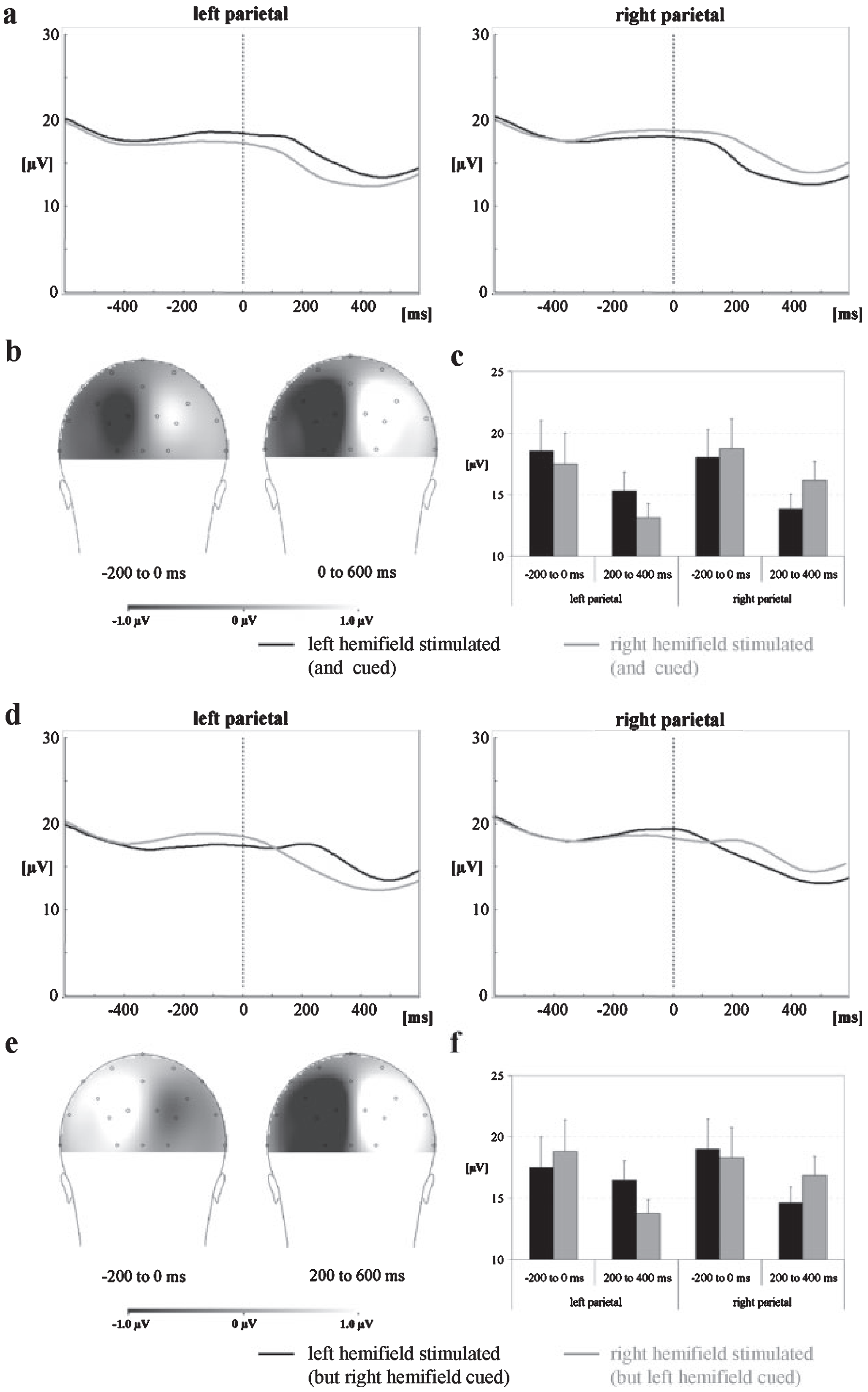
FIG. 2. Temporal evolution of *lower* alpha magnitude is shown for the valid (a) and invalid (d) conditions. The lower alpha band reacts with stronger power suppression contralateral to the stimulated hemifield. In the valid condition this effect starts 200 ms before target onset and is continued in the post-stimulus interval. The invalid conditions elicit reversed activation patterns compared with the valid conditions in the prestimulus interval. This is due to the fact that in the invalid condition the hemispace opposite to later target presentation was attended in the prestimulus interval. The spatial distribution of the effect is mapped in (b) and (e) for the valid and invalid conditions, respectively. Maps (back view of the head) represent difference of alpha activity between conditions right hemifield stimulated and left hemifield stimulated (right minus left). Thus, negative values (dark grey) show that there is higher alpha magnitude when the left hemifield was stimulated and positive differences (white) indicate stronger alpha power for right hemifield stimulation. Maps correspond to time windows with significant lateralization effects. In (c) and (f) means and standard errors of one prestimulus (− 200–0 ms) and one post-stimulus (200–400 ms) time window are depicted. Note the inversion of the lateralization effect between the valid and invalid conditions in the prestimulus interval.

magnitude was reduced contralateral to the target between 200 and 600 ms post-stimulus. On the other hand, during the last 200 ms of the prestimulus interval a 'real' attention-related alpha effect, not confounded with simple visual processing, was obtained. In the invalid conditions there was stronger alpha suppression at sites contralateral to the cued hemifield, which were ipsilateral to the later actual target location. As there is a reversal of the patterns between the pre- and post-stimulus period in the invalid conditions this effect can



not be explained by a temporal 'smear' because of poor time resolution of the analysis methods.

The attention-related lateralization of EEG power was restricted to the lower and upper alpha bands (approximately 7–14 Hz). Theta did not yield any similar activation patterns as seen in the alpha frequency range, nor did higher frequency bands. From some studies there is evidence also for involvement of beta oscillations in attentional processes (e.g. Vázquez Marrufo *et al*., 2001; Yamagishi *et al*., 2003).



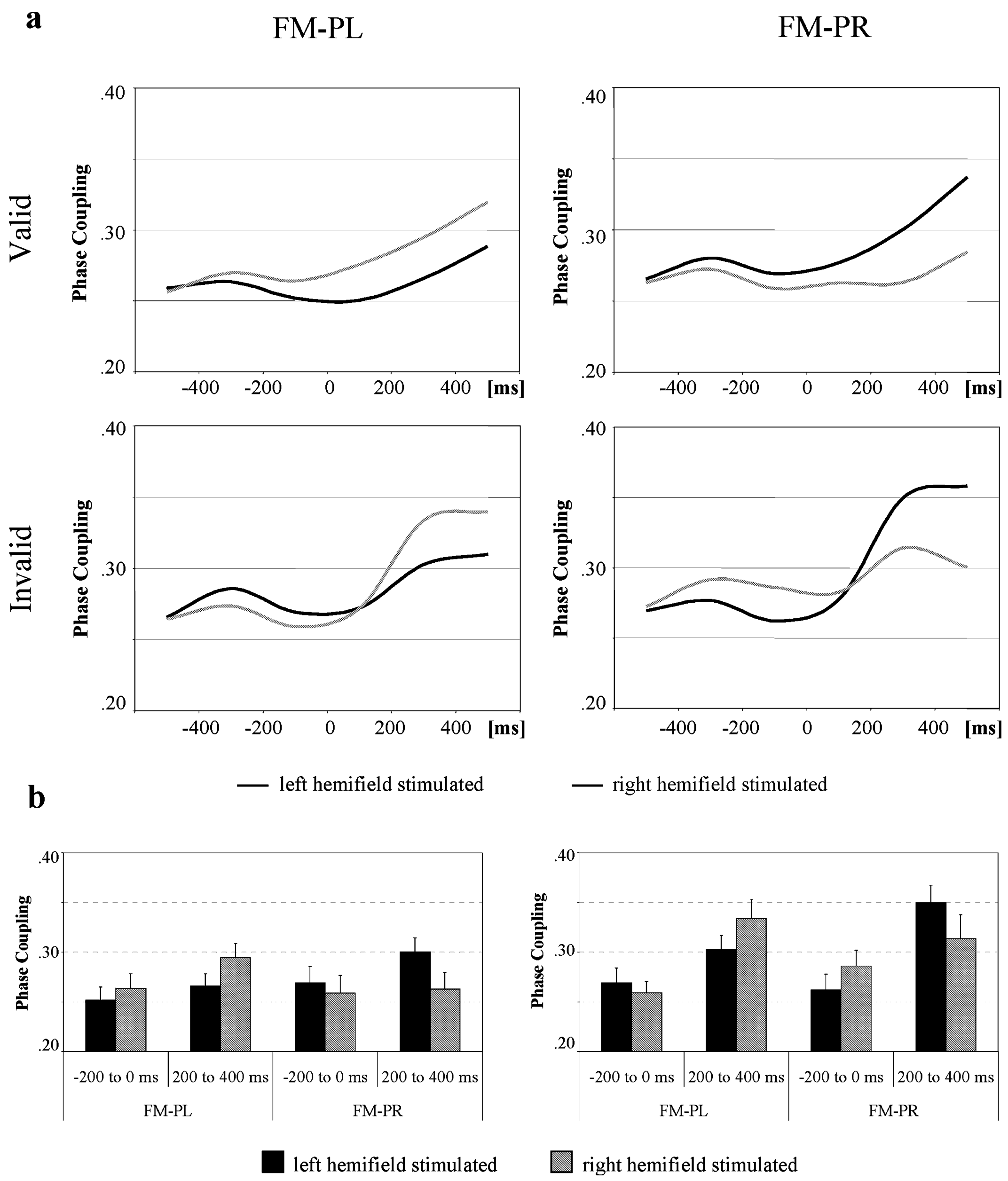


FIG. 4. Temporal evolution of phase coupling between a fronto-medial (FM) and the left (PL) as well as a right posterior parietal (PR) region of interest, respectively (a). In any case there is stronger phase coupling between FM and the brain region contralateral to the attended visual hemifield in the 200-ms time window preceding target onset. Note that in the invalid conditions subjects actually directed their attention to the hemifield opposite to later target presentation. Therefore, prestimulus fronto-parietal phase-locking shows the reverse pattern as in the valid condition. In the post-stimulus interval from 200 ms after target onset in the valid as well as invalid conditions phase coupling was stronger between FM and the brain area contralateral to stimulation than ipsilateral to the target. In (b) means and standard errors of one prestimulus (− 200–0 ms) and one post-stimulus (200–400 ms) time window are depicted. Note the inversion of the lateralization effect between the valid and invalid conditions in the prestimulus interval.

However, the relevance of EEG alpha for selective attention is found more consistently (Foxe *et al.*, 1998; Worden *et al.*, 2000; Vázquez Marrufo *et al.*, 2001; Yamagishi *et al.*, 2003; Babiloni *et al.*, 2004). As also indicated by the present results, directed attention leads to alpha suppression in the relevant brain areas. During spatial attention this effect is strongest over parieto-occipital brain areas (see also Worden

FIG. 3. Temporal evolution of *upper* alpha magnitude is shown for the valid (a) and invalid (d) conditions. Similar to lower alpha, the upper alpha band reacts with stronger power suppression contralateral to the stimulated hemifield. In the valid condition this effect starts 200 ms before target onset and is continued in the post-stimulus interval. The invalid conditions elicit reversed activation patterns compared with the valid conditions in the prestimulus interval. This is due to the fact that in the invalid condition the hemispace opposite to later target presentation was attended in the prestimulus interval. The spatial distribution of the effect is mapped in (b) and (e) for the valid and invalid conditions, respectively. Maps (back view of the head) represent difference of alpha activity between conditions right hemifield stimulated and left hemifield stimulated (right minus left). Thus, negative values (dark grey) show that there is higher alpha magnitude when the left hemifield was stimulated and positive differences (white) indicate stronger alpha power for right hemifield stimulation. Maps correspond to time windows with significant lateralization effects. In (c) and (f) means and standard errors of one prestimulus (− 200–0 ms) and one post-stimulus (200–400 ms) time window are depicted. Note the inversion of the lateralization effect between the valid and invalid conditions in the prestimulus interval.

et al., 2000; Yamagishi *et al*., 2003). Yamagishi *et al*. (2003) additionally found the involvement of the primary visual cortex in directed visual attention. But in contrast to the findings at parietal sites they reported an alpha power *increase* contralateral to the attended hemifield in V1. This could be caused by the task used in their study. A small target was embedded into an extensive grating. So the increase of alpha activity in V1 might actually represent inhibition of the grating instead of attention directed to the target. In the presented study the most pronounced effects were centred around parieto-occipital electrode sites, as can be seen from Figs 2 and 3. Interestingly, those sites exhibiting the attention-related prestimulus effect were also the ones showing the largest differences between conditions in the post-stimulus interval. Thus, it appears as if an attentional shift leads to a preparation of those cortical areas that are later involved in the higher sensory processing of the target. It was also demonstrated in an event-related fMRI study that extrastriate regions activated after an attentional shift overlapped with areas responding to a subsequent target (Hopfinger *et al*., 2000). Because alpha oscillations can be interpreted to reflect functional inhibition of cortical activity (Hummel *et al*., 2002), alpha suppression can be seen as release of inhibition leading to increased cortical excitation (Rau *et al*., 2003). Worden *et al*. (2000) discussed a similar phenomenon in terms of 'biased competition'. They reported higher alpha power at electrode sites ipsilateral to the cued location than contralateral to it and interpreted these findings as increased inhibition of process-irrelevant brain regions. However, they did not show that this ipsilateral alpha power exceeded the baseline level. Thus, it is possible that increased ipsilateral compared with contralateral alpha power only reflects a return towards baseline at ipsilateral regions, whereas contralateral brain areas keep being activated exhibiting suppressed alpha activity. From the present study, by comparing attention-related alpha activity with baseline activity, it can be concluded that also sites ipsilateral to the attended hemifield exhibit alpha suppression – although this is weaker than at contralateral areas. When considering that ongoing alpha activity represents a steady state of cortical inhibition, this means that ipsilateral posterior brain regions do not exhibit inhibition going beyond baseline level. Instead, cortical areas contralateral to an attended location are largely released from inhibition, whereas the ipsilateral sites remain slightly more deactivated.

Recent evidence emphasizes the role of an inhibitory filter during visual perception for alpha oscillations. Flashed visual stimuli presented at threshold level are perceived with a higher probability when prestimulus alpha power is low (Ergenoglu *et al*., 2004) and, similarly, subjects exhibiting low prestimulus alpha magnitude perform better in a visual perception task (Hanslmayr *et al*., 2005). Hence, a suppression of alpha amplitudes facilitates the perception of a target. This could be the reason for the tendency of (lower) EEG alpha to desynchronize already prior to presentation of highly expected targets (Klimesch *et al*., 1998; Bastiaansen & Brunia, 2001; Bastiaansen *et al*., 2001; Babiloni *et al*., 2004; Harris, 2005). The present results demonstrate that by directing attention to a part of the visual field it is possible to selectively enhance excitability at cortical sites representing the attended part of the visual field. It is well established that a high level of prestimulus alpha activity is associated with good cognitive performance (see Klimesch, 1999 for a review). The present findings seem contradictory as prestimulus alpha magnitude is suppressed when attention is directed to a target. However, Hanslmayr *et al*. (2005) could show that this positive relation between performance and alpha power primarily holds true for memory tasks, whereas low prestimulus alpha enhances perceptual or attentional processing.

Although attention-related lateralization effects of EEG power modulation were restricted to parieto-occipital sites, this does not mean that only posterior cortical regions play a role in directed visual attention. There is clear evidence for a 'controlling' involvement of prefrontal brain areas (for a review, see LaBerge, 1997). It was repetitively shown that frontal eye fields, the supplementary motor area (including the supplementary eye field) and the anterior cingulated gyrus are involved in covert attention (Kodaka *et al*., 1997; Gitelman *et al*., 1999; Nobre *et al*., 2000; see Nobre, 2001 for a review). Nobre *et al*. (2000) reported that largely overlapping brain structures were activated by covert shifts of attention as well as during performance of saccadic eye movements. This indicates that cortical areas responsible for the control of eye movements might also direct covert visual attention. Strong evidence for the role of the frontal eye fields in covert attention is provided by a study by Moore & Fallah (2001) who subthreshold microstimulated the frontal eye fields of monkeys, which resulted in modulation of covert spatial attention performance. In a study run by Rosen *et al*. (1999), also dorsolateral prefrontal cortices were found relevant in visuospatial attention tasks. This was interpreted as neural substrate of a working memory component, because in Posner tasks the cue has to be held in working memory for a few hundred milliseconds. There is strong evidence for the relevance of fronto-parietal EEG alpha networks in working memory tasks, but also during top-down processing (e.g. Weiss & Rappelsberger, 2000; Schack *et al*., 2003, 2005; Haarmann & Cameron, 2005; Sauseng *et al*., 2005). Therefore, it seems unclear whether the effects on phase coupling in the present study are really reflecting attention or rather related to working memory processes. Although the spatial resolution of the EEG is poor, it is more likely that the present results on phase coupling reflect attentional processes. This is because we did not find any involvement of dorsolateral prefrontal electrode sites in the current experiment.

Recently, it was shown that during top-down processing the prefrontal cortex might modulate alpha activity of posterior parts of the brain (Sauseng *et al*., 2005). However, this prefrontal activity does not need to show such a strict lateralization as it was found for the posterior sites in the present study. To clarify the role of fronto-parietal connectivity in directed visual spatial attention, phase coupling was calculated between anterior and parieto-occipital electrode sites. Attention-related effects were found in the upper alpha band between a fronto-medial (FM) and left and right posterior brain regions (PL and PR). When attention was directed to a visual hemifield phase coupling between FM and the posterior region contralateral to the attended hemifield was higher than to the ipsilateral parieto-occipital ROI (Fig. 4). With the methods used here it remains unclear whether the prefrontal cortex is driving or trailing posterior activation. However, recent findings suggest that prefrontal brain areas might control the level of occipital EEG alpha suppression (Sauseng *et al*., 2005), and also findings by Serrien *et al*. (2004) indicate that prefrontal sites might drive parietal sites at alpha frequency. So it seems plausible that in the present study the prefrontal cortex might reflect monitoring functions of attention and that posterior alpha activity is operated by phase coupling with frontal areas.

Based on our findings it remains an open question whether frequencies higher than alpha are involved in selective attention. There, however, is electrophysiological evidence from different spatial scales that beta and gamma oscillations are relevant for attentional processes (Tiitinen *et al*., 1993; Gruber *et al*., 1999; Herrmann & Mecklinger, 1999; Herrmann *et al*., 1999; Fries *et al*., 2001; Herrmann & Knight, 2001; Vázquez Marrufo *et al*., 2001; Yamagishi *et al*., 2003; Gross *et al*., 2004; Gonzalez Andino *et al*., 2005; Senkowski *et al*., 2004). The fact that we did not find attention-related effects in higher frequency bands may be due to the influence of spatial filtering of the EEG (see Nunez *et al*., 2001), which means that the scalp EEG is biased towards slow oscillations. Approaches in which the sources of oscillatory scalp activity are localized might bring more consistent results.

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Abbreviations

EEG, electroencephalogram; ERP, event-related potential; FL, prefrontal left region of interest; FM, fronto-medial region of interest; FR, prefrontal right region of interest; PL, posterior parietal left region of interest; PLV, phase-locking value; PR, posterior parietal right region of interest; ROI, region of interest.

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