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Increases in Alpha Oscillatory Power Reflect an Active Retinotopic Mechanism for Distracter Suppression During Sustained Visuospatial Attention

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Kelly, Simon P., Edmund C. Lalor, Richard B. Reilly, and John J. Foxe. Increases in alpha oscillatory power reflect an active retinotopic mechanism for distracter suppression during sustained visuospatial attention. *J Neurophysiol* 95: 3844–3851, 2006; First published March 29, 2006; doi:10.1152/jn.01234.2005. Human electrophysiological (EEG) studies have demonstrated the involvement of alpha band (8- to 14-Hz) oscillations in the anticipatory biasing of attention. In the context of visual spatial attention within bilateral stimulus arrays, alpha has exhibited greater amplitude over parietooccipital cortex contralateral to the hemifield required to be ignored, relative to that measured when the same hemifield is to be attended. Whether this differential effect arises solely from alpha desynchronization (decreases) over the “attending” hemisphere, from synchronization (increases) over the “ignoring” hemisphere, or both, has not been fully resolved. This is because of the confounding effect of externally evoked desynchronization that occurs involuntarily in response to visual cues. Here, bilateral flickering stimuli were presented simultaneously and continuously over entire trial blocks, such that externally evoked alpha desynchronization is equated in precue baseline and postcue intervals. Equivalent random letter sequences were superimposed on the left and right flicker stimuli. Subjects were required to count the presentations of the target letter “X” at the cued hemifield over an 8-s period and ignore the sequence in the opposite hemifield. The data showed significant increases in alpha power over the ignoring hemisphere relative to the precue baseline, observable for both cue directions. A strong attentional bias necessitated by the subjective difficulty in gating the distracting letter sequence is reflected in a large effect size of 2.1 ($\eta^2 = 0.82$), measured from the attention \times hemisphere interaction. This strongly suggests that alpha synchronization reflects an active attentional suppression mechanism, rather than a passive one reflecting “idling” circuits.

INTRODUCTION

An intuitive principle of brain function asserts that at any instant, the full expanse of sensory input in our environment cannot be processed in its entirety because of limited resources, and therefore attentional *selection* takes place, serving to single out relevant inputs for preferential processing (Broadbent 1958). This can be carried out endogenously (voluntarily) in anticipation of an event, and results in a processing advantage for that event when it occurs (e.g., Posner et al. 1980). Two modulatory mechanisms can be envisioned as the basis for

establishing the “attentional set” that facilitates this processing advantage. The first involves the enhancement of neural excitability in those circuits responsible for processing the attended stimulus (Foxe and Simpson 2005; Foxe et al. 2005; Kastner et al. 1999; Luck et al. 1997; Muller et al. 1998). The second is the suppression of other “unattended” neural circuits, leading to attenuated processing of competing stimuli (e.g., Slotnick et al. 2003; Smith et al. 2000; Vanduffel et al. 2000).

Studies of attention-modulated neuronal response patterns have shown that both mechanisms co-occur in situations where stimulus feature analysis is required at a selected spatial location, in the presence of competing stimuli sharing the same features (e.g., Moore and Armstrong 2003; Motter 1993). However, the attentional bias set in place to facilitate such response modulations (for a review see Hillyard et al. 1998) and, ultimately, behavioral performance (Posner et al. 1980) has received relatively little research attention (Luck et al. 1997; e.g., Kastner et al. 1999; Worden et al. 2000). It is likely that, as in the case of response modulations, mechanisms of both enhancement and suppression are at play in attentional biasing and that the relative contribution of each to effective selection depends on the demands of the task. In the present study, electroencephalographic (EEG) activity was recorded during a visual spatial attention task involving the simultaneous, continuous presentation of bilateral flicker stimuli. Feature content was equated on both sides and sustained, unilateral covert monitoring was required for target discrimination. Subjectively speaking, this sets in place the necessity to actively ignore the distracting influence of the unattended stimulus to perform the task successfully.

It is widely believed that the posterior parietal cortex lies at the root of the shifting and maintenance of spatial attention (Corbetta et al. 1993; Nobre et al. 1997). The influence of the top-down attentional bias originating from such higher-order areas is expressed in early visual areas as shifts in baseline firing rates (Luck et al. 1997). The neurophysiological nature of the intervening control mechanisms, underlying this expression of selective attention, has yet to be determined. By many accounts, structures of the thalamus are involved in exerting attentional bias (e.g., Crick 1984; Laberge 2001). A measure of support for this notion comes from imaging studies reporting

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attentional modulations in the pulvinar nucleus (Lagerbe and Buchsbaum 1990; Petersen et al. 1987) and in the lateral geniculate nucleus (LGN; O'Connor et al. 2002; Vanduffel et al. 2000).¹ However, far less is known regarding the dynamical character of the control mechanisms exerted by such a network.

A phenomenon that has repeatedly been linked with thalamo-cortical interplay is the human alpha rhythm, an oscillation within the 8- to 14-Hz frequency band observable in the scalp EEG (Lopes da Silva 1991). On a fine-grained level, single thalamo-cortical relay cells have been found to exhibit periodic bursting in the alpha range during hyperpolarization of the membrane potential, a state associated with decreased sensory transmission, most notably during EEG-synchronized sleep (Llinas 1988; Steriade 2000; Steriade et al. 1990). As a consequence, it was hypothesized that oscillations in this range embody the mechanism by which gating might occur in the thalamus (Lopes da Silva 1991). Perhaps not surprisingly given these findings, effects of alpha power have been observed during selective attention tasks that require the gating of distracting information (Foxe et al. 1998; Fu et al. 2001; Worden et al. 2000). In Foxe et al. (1998), alpha power was found to be greater over visual cortex while preparing to attend to the auditory part of a compound auditory-visual stimulus, than when preparing for the visual part. In a later study (Worden et al. 2000), involving a visual spatial attention task, it was found that alpha power was greater over the hemisphere contralateral to the hemifield to be ignored, than contralateral to the hemifield to be attended in preparation for an imperative stimulus. In both of these studies a visual cue ("S1") indicated the modality or hemifield to be attended, so that an attentional bias is deployed before the presentation of the imperative stimulus ("S2").

A quite separate body of research has focused on the phenomenon of event-related desynchronization (ERD) and synchronization (ERS) of alpha (Pfurtscheller and Lopes da Silva 1999). This refers to the phasic (i.e., short-lasting) decrease (ERD) or increase (ERS) of alpha power after an event, relative to a baseline level measured preceding the event. ERD/ERS may be considered a more specific version of the traditional contention that alpha is increased during periods of mental inactivity or "idling" and is decreased during active cognition (Mulholland 1965; Pfurtscheller 1992). Pfurtscheller and colleagues demonstrated that the ERD is focal, occurring predominantly over activated areas of cortex, and in early work showed that it occurs over visual cortex in response to photic stimulation even in the absence of task instructions, with eyes closed (Pfurtscheller and Aranibar 1977). This essentially indicates the existence of *externally evoked* desynchronization, as distinct from changes in alpha driven by endogenous attention deployment. In a series of studies of anticipatory attention using measurements of ERD, Baastiaansen and Brunia (2001) consistently found that alpha desynchronizes in the period preceding an imperative visual stimulus containing "knowledge of results" (KR), indicating the achieved accuracy on a time estimation trial. Further, in a visuospatial attention task

similar to that of Worden et al. (2000) but without the requirement to ignore competing stimuli, alpha desynchronization was found over parietooccipital scalp, and was greater over the hemisphere contralateral to the hemifield to be attended (Sauseng et al. 2005). Thus it appears that in the visual domain, alpha ERD can occur both in relation to anticipatory attention deployment and also in relation to earlier, more involuntary processes.

The incidence of anticipatory alpha-band ERD warrants caution in the interpretation of alpha-based suppression effects, a fact duly considered in the earlier reports (Foxe et al. 1998; Worden et al. 2000). In Worden et al. (2000), although an interaction between hemisphere and attention demonstrates that alpha plays a role in selection mechanisms, it is not fully clear whether the interaction arises entirely from desynchronization (activation) over the attending hemisphere, entirely from synchronization (deactivation) over the ignoring hemisphere, or from both. The traditional view of alpha as an idling rhythm would suggest that synchronization occurs only during passive states in the absence of stimulation, which would favor the interpretation of pure desynchronization. However, the retinotopic scalp distribution of alpha power observed in the study of Worden et al. (2000), which was dependent on the location of the stimulus to be ignored, suggested the presence of an active mechanism.

One reason that this issue has not been fully resolvable in S1-S2-type paradigms using visual cues is that the attentional modulations of alpha within the cue-stimulus interval are superimposed on the externally evoked desynchronization resulting from the presentation of the cue stimulus. This rules out the direct comparison of postcue and precue alpha power, as is often carried out in studies of ERD (see Pfurtscheller and Lopes da Silva 1999). An intersensory selective attention study using auditory cues (Fu et al. 2001) enabled such a comparison, which revealed greater alpha in the postcue than that in the precue period when preparing to ignore visual input. However, the issue has yet to be addressed within the context of visual spatial attention.

In the present paper we demonstrate that by presenting bilateral stimuli simultaneously and continuously over entire trial blocks, externally evoked alpha desynchronization is equated in the precue and postcue intervals, allowing separate observation of synchronization and/or desynchronization relative to a valid reference period. The data examined are from a recent spatial attention-based brain computer interface (BCI) study (Kelly et al. 2005), previously aimed at classifying left/right spatial attention based on single trials using steady-state visual evoked potentials (SSVEPs). In addition to a pre- vs. postcue comparison, a within-subjects statistical analysis of alpha power in these data enable the investigation of the sustainability of alpha-based attentional deployment over time owing to the considerable length (8 s) of trials. Further, the effects of task difficulty and/or the frequency of stimulation, giving rise to *evoked* oscillations, are amenable to investigation in these data through the use of two stimulus settings, one involving flicker frequencies inside, and the other outside, the alpha band. Our principal hypothesis was that strong event-related synchronization would occur over parietooccipital scalp contralateral to the ignored stimulus, corroborating evidence for active suppression reflected in alpha oscillations measured

¹ Whether these modulations occur early in processing during initial afference or later as a result of feedback cannot be determined through hemodynamic studies given the limited temporal resolution inherent in the techniques currently used.

in a previous study using an intersensory paradigm (Fu et al. 2001).

METHODS

Subjects and task

Ten subjects, ages between 22 and 30 yr, participated in the study. All subjects reported normal or corrected-to-normal vision. The Ethics Committee of St. Vincent's Hospital approved the experimental procedures and each subject provided written informed consent. Subjects were seated 60 cm from a CRT monitor on which was displayed two white square flicker stimuli ($4.2 \times 4.2^\circ$ of visual angle) centered 5° bilateral to a central fixation cross on the horizontal meridian, on a black background (see Fig. 1). Each flash lasted for a single frame of the monitor refresh, set at 85 Hz. Two stimulus settings were used in separate experimental blocks, allowing investigation of the effects of evoked oscillations inside and outside the alpha band.

- *Setting 1.* The left square flickered at 9.45 Hz and the right at 10.63 Hz (inside the alpha band).
- *Setting 2.* The left flickered at 14.17 Hz and the right at 17.01 Hz (outside the alpha band).

In the center of each of the white squares, letters from "A" through "H" ($1 \times 1^\circ$) were presented in a random sequence, similar to the spatial attention paradigm used by Morgan et al. (1996). Embedded in the sequence of letters was the target letter "X" that occurred with equal probability (about 0.11). Subjects were instructed to maintain central fixation and keep count of target presentations in the cued hemifield during each trial and report this number on completion of the trial. The letter in each hemifield switched after every three flashes of the white square on which it was superimposed.

EEG data from 72 channels were recorded during the task, filtered over the range 0–134 Hz, and digitized at a rate of 512 Hz using the BioSemi Active Two system. These data were rereferenced offline to a midline frontopolar electrode site (FPz). In addition, horizontal electrooculographic (EOG) data were recorded using two electrodes placed at the outer canthi of the eyes, allowing measurement of eye movements during testing. To map EOG amplitude to visual angle, preliminary calibration runs were carried out, wherein subjects performed brief cued eye movements to four displacement angles between the fixation cross and the cued stimulus: 0.5 , 2.9 , 5 , and 7.1° corresponding to the end of the horizontal leg of the fixation cross, the inner edge, the center, and the outer edge of the cued stimulus, respectively. Trial rejection resulting from eye movements was subsequently based on a linear mapping determined from these data (Barea et al. 2002; Murray et al. 2001).

Each subject underwent a total of ten sessions, each lasting <5 min. For five of the sessions Setting 1 was used and for the other five sessions Setting 2, ordered alternately with the beginning setting

counterbalanced across subjects. Each trial started with a warning stimulus (red fixation cross) lasting 0.5 s, followed by a cue stimulus consisting of a white fixation cross of the same size with a small arrow on the left or right arm, lasting 0.5 s. The subject was instructed to covertly attend to the cued square while strictly maintaining fixation on the central fixation cross for 8 s (the "attend period"). After the attend period the fixation cross changed to green for 5 s, signifying a rest period. Each session consisted of 20 trials, with an equal number cued-left as cued-right, in random order. The white flicker stimuli and superimposed letter sequences were continuously presented throughout the experimental block, remaining for the rest periods as well as attend periods.

Analysis strategy

Two separate analyses were performed on the data. The first analysis was carried out to investigate the effect of stimulus setting on the attentional modulations of alpha, and to examine the sustainability of these modulations over time on the order of several seconds. For this analysis, Fourier spectral estimation was used to measure alpha power at several time points over the 8-s attend period for both stimulation settings. This method provided high-frequency resolution, such that the frequencies containing SSVEP power could be isolated and omitted from the measurement of alpha power. The second analysis examined the time course of alpha power over prestimulus and poststimulus periods. To achieve high temporal resolution, a modified temporal spectral evolution (TSE; see Foxe et al. 1998) analysis was carried out on the blocks for Setting 2 only.

FOURIER ANALYSIS ACROSS STIMULATION SETTINGS AND OVER DURATION OF SUSTAINED SPATIAL SELECTION. Data were epoched from the onset of the cue stimulus (0 s) to the end of the attend period (8.5 s). Artifact rejection was based on a threshold of $60 \mu\text{V}$ applied to electrodes posterior to Cz, filtered between 2 and 30 Hz (fourth-order Butterworth). Trials containing eye movements of $>2^\circ$ were also rejected. This resulted in acceptance of <20 sweeps per cue direction for one subject, and thus this subject was excluded from the analysis. For the remaining nine subjects, an average (\pm SD) of 88 ± 13 sweeps were retained for Setting 1 and 83 ± 14 for Setting 2.

Fifteen segments of length 1.7 s were extracted using rectangular windows centered at 1-, 1.5-, ..., 8-s postcue onset. The segment length contains an integral number of cycles of the SSVEP frequencies in Setting 1 (9.45 and 10.63 Hz), so that SSVEP power is confined to single frequency bins (Regan 1989). For each segment the Fast Fourier Transform was computed, and all amplitude values inside the range 8–13.5 Hz, except at precisely 9.45 and 10.63 Hz, were averaged to provide a measure of alpha power (carried out for both stimulation settings, although no SSVEPs existed in the alpha range in Setting 2). The exclusion of SSVEP frequencies allowed the measurement of endogenously induced alpha power without the confound of evoked oscillations. Alpha measures were averaged across trials for each subject.

A five-way ANOVA was used for statistical testing, with the factors of setting (1 vs. 2), attention (Left vs. Right), hemisphere (Left vs. Right), time interval (three periods, averaged across the first, second, and third set of five segments), and electrode (three locations over each hemisphere, PO7/PO8, PO3/PO4, and O1/O2).

MODIFIED TSE ANALYSIS OF POSTCUE ALPHA RELATIVE TO PRECUE BASELINE. In this analysis, the data for each subject from the five blocks at Setting 2 were epoched from -0.5 to 2.5 s relative to cue onset. Artifact and eye movement rejection were carried out using the same criteria as above, resulting in exclusion of the same subject. The modified TSE analysis is set out in the following steps.

1) The epochs are band-pass filtered in the range 8–13.5 Hz (fourth-order Butterworth).

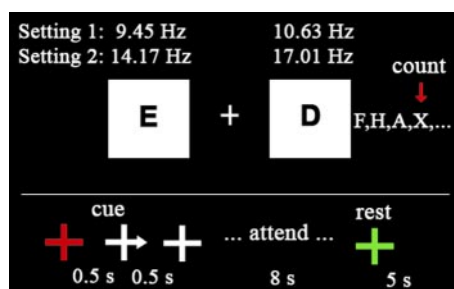


FIG. 1. Bilateral flickering stimuli were presented simultaneously with superimposed letter sequences changing about 3.5 (Setting 1) or about 5 (Setting 2) times/s (*top*). Subjects were required to attend to the cued stimulus and count presentations of the target "X" over an 8-s period, while ignoring the letters on the opposite side. Between trials there was a rest period of 5 s (*bottom*).

- 2) Each epoch is rectified (negative potential becomes positive).
 - 3) Envelope detection is carried out on each epoch. This involves the locating of local maxima in the rectified waveform and linear interpolation between these points.
 - 4) Epochs are averaged across trials.
- A four-way ANOVA was used in this case, with factors of attention, hemisphere, electrode (as above), and time interval (two levels: -0.5 to 0 s reference period, and 1 to 2 s postcue period).

RESULTS

Behavioral performance was assessed by comparing target counts reported by the subject with the number of targets actually presented in the cued hemifield. The number of targets presented over the attend period ranged from 0 to 8 for Setting 1 (median 3), and ranged from 0 to 10 for Setting 2 (median 5). The histograms shown in Fig. 2 plot the distribution of counting errors made for each stimulation setting, with data pooled from all nine subjects. Trials for which the subject did not count targets because of a momentary lapse in concentration were excluded—this occurred not more than once for all subjects except one, for whom it occurred ten times in total. Counting errors were made on $30.7 \pm 13.1\%$ of trials (average \pm SD across subjects) for Setting 1 and on $56.3 \pm 18.9\%$ of trials for Setting 2, demonstrating the difficulty of the task and thus the necessity to attend only to the cued stream of letters, while ignoring the uncued stream.

In statistical testing for differences in difficulty between settings, normalization of counting errors was required to account for differences in the number of targets actually presented, detailed above. This arises from faster flicker rates (and thus letter sequences) in Setting 2. First, the absolute difference between the subject-reported target count and actual target count was computed for each trial. This difference was then averaged across trials for each stimulus setting and for each cue direction, and then normalized by dividing by the mean of the actual counts for that setting and cued hemifield. A two-way ANOVA on this index of counting error revealed greater counting errors for Setting 2 than for Setting 1 [$F(1,8) = 18.3, P < 0.005$]. Although the flicker rate was slightly faster in the right hemifield than the left in both settings, no effect of cue direction was found ($P = 0.32$).

Effects of stimulation setting and time

Figure 3 shows the time courses of alpha power from 1 to 8 s postcue onset within the attend period, for the left and right

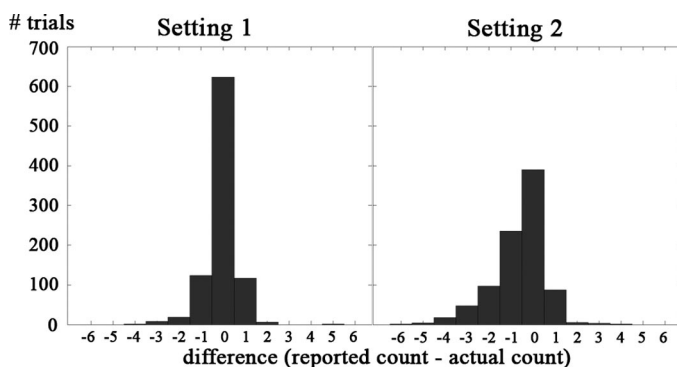


FIG. 2. Histograms of the distribution of counting errors for each setting, measured as the subject-reported count minus the actual number of targets. Trials are pooled for all 9 subjects included in the analysis.

hemisphere, averaged over the three selected electrodes. Topographic maps further illustrate the increase of alpha power over the “nonattending” hemisphere.

The ANOVA revealed a main effect of setting [$F(1,8) = 5.36, P < 0.05$], with overall alpha amplitude greater for Setting 2. Note that this attests the assertion that SSVEP power is isolated to the two excluded frequency bins; that alpha amplitude is artificially enhanced by the SSVEPs within the alpha range in Setting 1 is assuredly unlikely, given that the difference is in the opposite direction.

There was also a main effect of time [$F(2,16) = 4.51, P < 0.05$]. Bonferroni-corrected pairwise comparisons suggested that this was driven by a marginally significant drop in overall alpha from the first time frame to the second ($P = 0.074$). A further drop from the second to the third time frame did not prove significant ($P > 0.1$).

A strong attention \times hemisphere interaction [$F(1,8) = 35.5, P < 0.0001$] confirmed the presence of alpha-based suppression/enhancement effects, replicating the principal results of Worden et al. (2000). This was topographically specific, as suggested by an attention \times hemisphere \times electrode interaction [$F(2,16) = 12.79, P < 0.0001$]. There was also a setting \times attention \times time interaction [$F(2,16) = 5.65, P < 0.05$]. In the absence of prior hypotheses related to such an interaction, this multifactor interaction was not pursued further through post hoc comparisons. However, from inspection of Fig. 3, it appears that the drop in alpha over time may be more pronounced for the attend-right condition in Setting 1, but more for the attend-left condition in Setting 2. More readily apparent in Fig. 3 is the hemispheric asymmetry of the alpha differential, which was stronger over the right hemisphere. Although flicker frequencies in the right hemifield were faster than those in the left for both settings, the absence of a significant difference in counting error renders unclear the possible influence of this asymmetry. In any case, further investigation of hemispheric differences in the expression of alpha-based selection mechanisms may be of interest in light of accounts of right-hemisphere specialization of attention function (Foxe et al. 2003; Heilman and Van Den Abell 1980; Vallar and Perani 1986).

On the basis of previous work (Worden et al. 2000), our hypotheses at the outset of this study, regarding oscillatory phenomena related to spatial attention, were restricted to the alpha band. Nevertheless, it was of interest to investigate how specific these effects are to the alpha band. To this end, attentional modulation was quantified for all frequencies and time points within the attend period by dividing spectral power calculated in this Fourier analysis for the attend-left condition by that for the attend-right condition, and log-transforming the result so that the absence of modulation is represented by a value of zero. Figure 4 shows a representative time–frequency surface plot quantifying attentional modulation for the left hemisphere electrodes for Setting 2. Modulation appears to be localized to the alpha band, with additional nonzero modulations observable at the SSVEP frequencies (about 14 and 17 Hz) and harmonics thereof (e.g., about 34 Hz).

Postcue alpha versus precue baseline

Figure 5 shows the modified TSE time courses over a time frame encompassing pre- and postcue intervals. Note the peak at about 250 ms after both the change of color of the crosshair

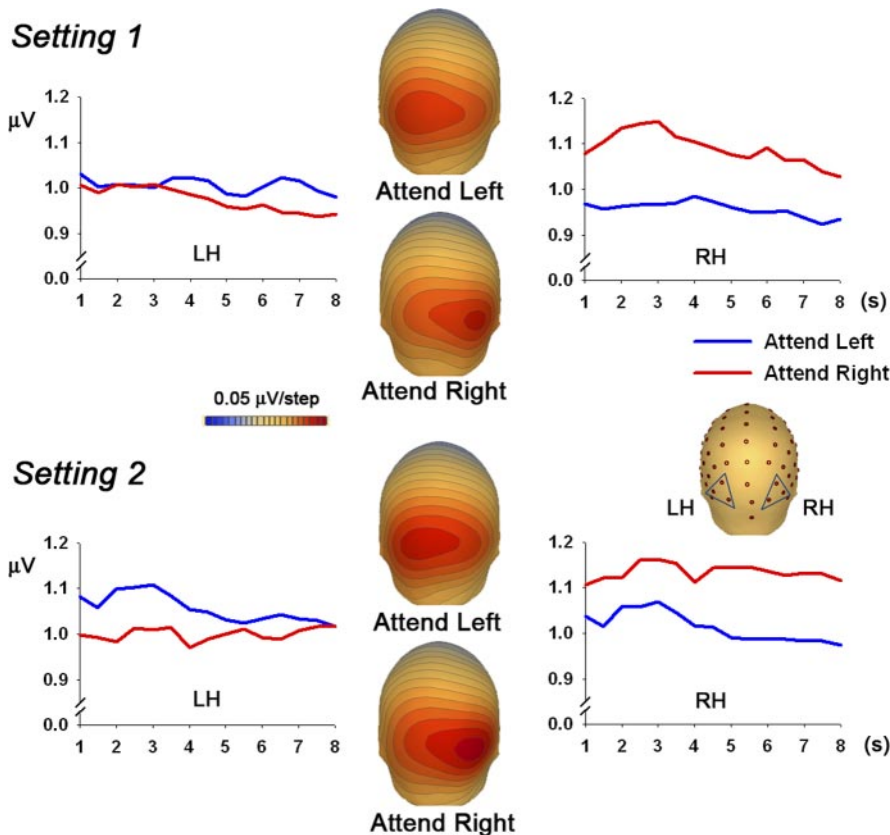


FIG. 3. Time courses of alpha amplitude derived from short-time Fourier analysis for attention deployments toward the left and right stimulus. Traces are averaged over the 3 selected electrodes over each hemisphere, marked on the electrode montage shown. Scalp maps were generated using BESA software (<http://www.besa.de>). Focus of increased alpha can be seen over parietooccipital scalp contralateral to the ignored hemifield.

to green and after the cue stimulus. These are likely effects of evoked activity resulting from the centrally presented stimulus changes.

An attention \times hemisphere interaction was found once again [$F(1,8) = 34.16, P < 0.0001$], again specific to electrode [attention \times hemisphere \times electrode, $F(2,16) = 7.48, P < 0.01$], but also varying as a function of time interval [attention \times hemisphere \times time, $F(1,8) = 8.76, P < 0.05$]. A four-way interaction between all factors [$F(2,16) = 4.26, P < 0.05$] called for post hoc comparisons at each electrode. Of primary interest was the difference between prestimulus and poststimulus alpha. At electrode O1 (LH) there was a significant

increase of $0.35 \mu\text{V}$ in alpha amplitude when cued to attend left [$F(1,8) = 6.12, P < 0.05$]; at PO8 and O2 (RH) a significant increase (0.5 and $0.4 \mu\text{V}$, respectively) when cued to attend right [PO8: $F(1,8) = 6.79, P < 0.05$; O2: $F(1,8) = 7.09, P < 0.05$]. No event-related decreases in alpha amplitude reached significance at any electrode (all $P > 0.2$).

DISCUSSION

Our results contribute to mounting evidence that alpha oscillations are actively involved in the biasing of visual attention (Foxe et al. 1998; Fu et al. 2001; Rihs et al. 2005; Worden et al. 2000). By circumventing the occurrence of externally evoked alpha desynchronization normally seen after the onset of intermittent visual stimulation (Pfurtscheller and Aranibar 1977), such as that caused by visual cues, we found clear increases of alpha power relative to a precue baseline, over visual cortex contralateral to the ignored hemifield.

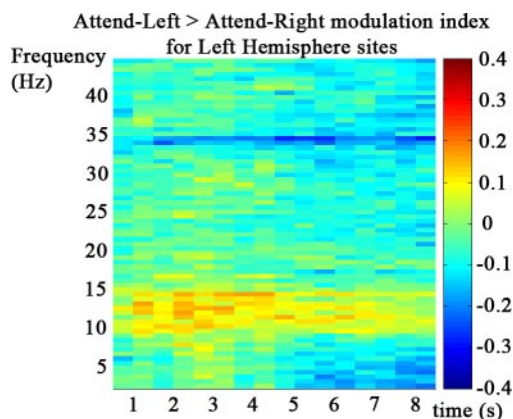


FIG. 4. Time–frequency surface plot for all time points within the attend period and for frequencies between 2 and 45 Hz, showing the attentional modulation {measured as $\log [\text{Power}(\text{attend-Left})/\text{Power}(\text{attend-Right})]$ } for the left hemisphere parietooccipital electrodes (O1, PO3, and PO7) for Setting 2. Modulation is localized to the alpha band (8–14 Hz) with additional modulations seen at stimulation frequencies and harmonics.

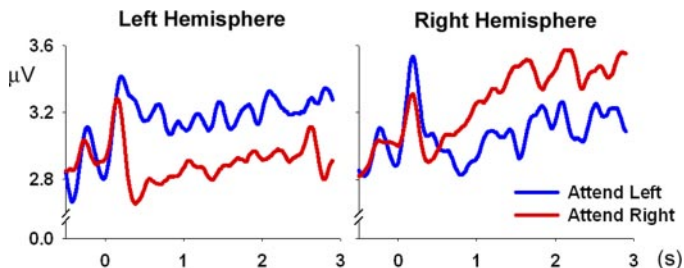


FIG. 5. Time courses of alpha amplitude derived from modified temporal spectral evolution analysis, encompassing precue and postcue intervals. Traces are averaged over the 3 selected electrodes over each hemisphere. A marked increase relative to precue baseline can be seen over each hemisphere when ignoring the contralateral hemifield.

Earlier evidence of alpha reactivity led to the adoption of an activity/idling dichotomy used to describe decreases/increases (ERD/ERS) of power in the alpha band (Mulholland 1965; Pfurtscheller and Lopes da Silva 1999). An antagonistic behavior, whereby ERD cooccurred with ERS, was observed in several situations. For example, during voluntary movement, an ERD of the mu rhythm (8–13 Hz) over central scalp was accompanied by an ERS of visual alpha over visual cortex (Pfurtscheller 1992). Further, focal ERD of mu during voluntary movement of the hand or foot was accompanied by surrounding ERS over central scalp regions, and unilateral motor imagery resulted in both contralateral ERD and ipsilateral ERS (Pfurtscheller and Lopes da Silva 1999). In these contexts ERS was interpreted as reflecting inactivity, or “cortical areas at rest” (Pfurtscheller 1992). However, recent evidence of reactivity to anticipatory attention has indicated that alpha band activity may play a more active role in the deployment of selective attention, both in intersensory attention tasks (Foxe et al. 1998; Fu et al. 2001) and in within-modality visuospatial tasks (Worden et al. 2000). The present results corroborate this view, indicating that a subtle reinterpretation is appropriate, moving from the notion of “idling” or “inactivity” to “active suppression,” at least in attentional contexts. Moreover, the implication of alpha in thalamically mediated gating, as previously hypothesized (Lopes da Silva 1991; Pfurtscheller and Lopes da Silva 1999), is strengthened by the present findings.

Recent studies by Thut and colleagues (Rihs et al. 2005; Thut et al. 2005) lend further support for the involvement of alpha in the biasing of visuospatial attention. In one study, event-related increases in alpha power was shown to be topographically specific for attention to each of eight different spatial locations (Rihs et al. 2005). In another related study using a bilateral stimulus array, a lateralization index measuring the hemispheric differential of alpha power (i.e., RH relative to LH) was found to be deterministic for speed of target detection at the attended hemifield (Thut et al. 2005). In addition to the many EEG studies, monkey intracranial studies have also implicated oscillations in the operations of selective attention. In one study, it was shown that gamma-band (35–90 Hz) oscillations are increased in response to an attended stimulus within the receptive field (RF) of the recorded neuron relative to the same stimulus when attention is directed outside the RF (Fries et al. 2001). Of particular interest in the current discussion is that in the cue-stimulus interval in the latter study, increased low-frequency power (<17 Hz) was observed when preparing to attend to a stimulus outside the RF compared with when attending to a stimulus inside the RF. It is possible that these low-frequency oscillations may represent the monkey homologue of the human alpha rhythm.

Anticipatory desynchronization of alpha relative to the pre-cue baseline was not observed in our data. This is likely the result of continuous bilateral visual stimulation, causing a reduction of alpha power to minimal levels, such that further decreases are not possible. Anticipatory desynchronization has been observed in the absence of stimulation, in anticipation of visual knowledge-of-results (KR) stimuli in time-estimation tasks (Bastiaansen and Brunia 2001) and more recently in spatial-attention tasks (Sauseng et al. 2005; Yamagishi et al. 2005). Of most relevance to the present study is recent work by Sauseng et al. (2005) describing alpha modulations in a visuo-

spatial attention task similar to that used in the study of Worden et al. (2000). An S1–S2-type paradigm involving bilateral stimuli was used in a similar way, but the requirement for the subject to actively ignore the uncued (“invalid”) hemifield was reversed; i.e., the subject was required to discriminate targets appearing in both the valid and invalid hemifield. The absence of any need to suppress the processing of invalid targets was reflected in the finding that only alpha desynchronization, and not synchronization, was observed. Interestingly, desynchronization was greater over the hemisphere contralateral to the attended hemifield. That the task lacked an attentional-suppression component is underlined by the fact that no difference was found in target detection rates for the cued versus uncued hemifield (Sauseng et al. 2005). It is thus likely that antagonistic enhancement and suppression mechanisms together underlie spatial selection of locations at which feature discrimination is required, in the presence of competing stimulation, and that the specific contribution of suppression mechanisms to this antagonism depends on the degree to which distracting stimuli impose competitive interactions in the system. To a large extent, this could be determined by similarity of feature content at attended and unattended locations. In the present paradigm, bilateral stimuli were presented simultaneously with both random letter sequences equivalent in terms of feature content, thereby necessitating sustained deployment of a strong attentional bias. This is reflected in a highly robust alpha-modulation effect size of 2.1 ($\eta^2 = 0.82$), measured from the attention \times hemisphere interaction.

The present effects of prestimulus attentional biasing may be considered in the context of the broader literature reporting attentional modulation of poststimulus responses. Single-unit studies in nonhuman primates have demonstrated the cooccurrence of both enhancement and suppression effects in visual responses during spatial selective attention. In a recent study, the responses of neurons in V4 were found to be enhanced by stimulation of retinotopically coincident frontal eye field (FEF) neurons but suppressed by stimulation of retinotopically disparate FEF neurons, when stimuli were presented simultaneously within and outside the RF (Moore and Armstrong 2003). This antagonistic modulation was observed only for preferred stimuli, suggesting that the effects of distracter stimulation are contingent on equated feature content. This is supported by the finding that spatial selection across neurons with nonoverlapping RFs in V4 does not occur when the competing stimuli consist of effectively orthogonal feature content (Moran and Desimone 1985). In contrast, Motter (1993) showed that orientation discrimination of a bar at a cued location, in the presence of simultaneously presented competing bars sharing feature content, results in spatial selectivity patterns of both enhancement and suppression, and these patterns were evenly balanced across attention-modulated neurons in areas V1, V2, and V4.

Further evidence of enhancement and suppression mechanisms in selective attention has been found in imaging studies, some of which even report the involvement of the thalamus. In an early PET study, it was found that the pulvinar nucleus was more engaged in a spatial attention task when multiple distracters were present, requiring filtering of visual information, than when target stimuli were presented alone (Lalberge and Buchsbaum 1990). It was shown more recently that activity in the lateral geniculate nucleus (LGN) is also modulated by

spatial attention (O'Connor et al. 2002). In the latter study, both attentional response enhancement and response suppression were found in separate experiments, with suppression effects dependent on the attentional load in the task performed at fixation. Attentional bias was also observed in the LGN, manifest as increased baseline activation in anticipation of a peripheral stimulus. Metabolic activity in the LGN of macaques was also found to be modulated by selective attention (Vanduffel et al. 2000), interpreted by the authors as reflecting a gating mechanism. The possible involvement of alpha oscillations in such functionality is underscored by simultaneous EEG-PET (Lindgren et al. 1999) and EEG-fMRI (Feige et al. 2005) studies, finding that alpha power is inversely correlated with activation in thalamic structures.

A significant main effect of setting was also found in the present data, with overall alpha power found to be higher in Setting 2 (stimulation at 14.17 and 17.01 Hz) than in Setting 1 (9.45 and 10.63 Hz). One possible explanation relates simply to neural hardware: a volume of neural circuitry that would otherwise contribute to overall alpha power across a broader spectral band may be recruited in the generation of narrow-band evoked SSVEPs at discrete frequencies that are contiguous in the spectrum. In Setting 1, this would result in reduced power at alpha-band frequencies other than the flicker-stimulation frequencies. Another explanation relates to task difficulty. It was found in the behavioral data that Setting 2 produces more counting errors than Setting 1. This is most probably a result of the faster letter sequences in Setting 2 (recall that the letter switches on every three cycles of the flicker stimulus). It is possible that elevated tonic alpha power was required to perform the more difficult task, in line with evidence relating alpha with cognitive performance (Doppelmayr et al. 2005; Klimesch 1999). It is important to note, however, that although overall alpha varied with setting, there was no interaction between the alpha-based suppression effect (attention \times hemisphere) and setting (three-way interaction; $P = 0.38$), suggesting that the phasic attentional mechanisms mainly implicated in this study were robust to this manipulation. Further experiments are required to dissociate the effects of stimulation frequency and task difficulty so that these issues can be resolved.

A significant drop in overall alpha power over time within the 8-s attend period was also found. Interpretation of this effect is difficult in the absence of behavioral measures extractable from different points in time over the attend period (target counts were representative of the entire 8-s period). However, intuitively, attentional bias mechanisms may wane over an extended period of time. It is important to note here that the observed effects of time did not interact with attention. Thus the drop of overall alpha could be explained by a gradual decline in suppressive mechanisms reflected in alpha synchronization, which is accompanied by greater event-related desynchronization over the attending hemisphere, possibly in compensation for the decline. Again, further studies are required to fully elucidate the nature of these effects.

In conclusion, the present results demonstrate that endogenous shifts of attention toward the cued stimulus in a continuously presented bilateral flicker-stimulus array are expressed as an event-related increase of alpha power over parietooccipital scalp contralateral to the ignored stimulus. The increased alpha over "unattending" relative to "attending" hemisphere is

then maintained during ongoing feature discrimination over an 8-s trial period. We interpret this increase as an active suppression mechanism, facilitating attentional gating of a competing stimulus sharing the same feature content as the attended stimulus.

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