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Mechanisms of selective inhibition in visual spatial attention are indexed by α-band EEG synchronization

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Abstract

Electroencephalographic studies in humans have demonstrated that orienting of visual attention induces a decrease in oscillatory α-band activity (α-desynchronization) over cortical areas tuned to the attended visual space. This is interpreted as reflecting intentionally enhanced excitability of these areas to facilitate upcoming visual processing. However, the inverse mechanism might also apply. Brain areas that process task-irrelevant space might be actively suppressed by increased α-activity (α-synchronization) to protect against input of distracter information. In the present study, we demonstrate that such suppression mechanisms are highly selective and are taking place even without distracters that need to be ignored. During voluntary orienting of attention, we found α-synchronization to dominate over desynchronization, to be topographically specific for each of eight attention positions, and to occur over areas processing unattended space in a retinotopically organized pattern. This indicates that α-synchronization is an important component of selective attention, serving active suppression of unattended positions during visual spatial orienting.

Introduction

Voluntarily directing visual attention to specific positions in space without movements of the eyes or head (covert attention shift) leads to improved processing of visual stimuli appearing at the attended positions (perceptual benefit), at the cost of visual processing at unattended locations. Behaviourally, this benefit is expressed in decreased reaction times and enhanced detection rates (Posner *et al*., 1980). In terms of brain activity, the perceptual benefit is associated with an enhancement of visually evoked responses to stimuli that coincide in space with the attention focus. This has been found in humans and nonhuman primates using single-unit recordings (Luck *et al*., 1997), functional magnetic resonance imaging (fMRI) and electroencephalography (EEG; Hillyard & Anllo-Vento, 1998; Martinez *et al*., 1999; Woldorff *et al*., 2002; Di Russo *et al*., 2003; Yamagishi *et al*., 2003; Sauseng *et al*., 2005). Remarkably, even in the absence of visual stimulation, early visual areas show retinotopically organized activity changes in accordance with the attended position, presumably mediated through top-down control from higher-order attention areas (Luck *et al*., 1997; Kastner *et al*., 1999; Muller *et al*., 2003). These changes have also been termed shifts in visual baseline activity, because they were observed in attention-orienting paradigms before onset of the visual stimulus, as shown by single-unit recordings and fMRI (Luck *et al*., 1997; Kastner *et al*., 1999; Hopfinger *et al*., 2000; Serences *et al*., 2004; Giesbrecht *et al*., 2006).

Studies investigating the EEG and/or magnetoencephalography (MEG) correlates of covert orienting of visual attention found oscillatory α-band activity (8–14 Hz) over posterior sites to be reduced in accordance with the direction of attention (Sauseng *et al*., 2005; Thut *et al*., 2006; Yamagishi *et al*., 2005). This α-desynchronization potentially reflects the visual baseline shifts reported in multiunit recordings and fMRI because it is observed contralateral to the attended positions (Sauseng *et al*., 2005; Yamagishi *et al*., 2005; Thut *et al*., 2006), partially originates from early visual areas (Yamagishi *et al*., 2005) and cannot be explained by an external change in the visual field, i.e. is internally driven (Sauseng *et al*., 2005; Thut *et al*., 2006). This α-desynchronization has thus been interpreted as reflecting enhanced excitability of cortical areas processing the attended part of the visual field (Sauseng *et al*., 2005; Yamagishi *et al*., 2005; Thut *et al*., 2006). Notably, two recent studies have found an increase in α-activity (α-synchronization) over posterior sites contralateral to the unattended location (i.e. ipsilaterally to the attended position), which might serve to actively suppress visual input from task-irrelevant positions (Worden *et al*., 2000; Kelly *et al*., 2006). This would be in line with evidence that α-synchronization reflects active inhibitory processes, previously obtained using cross-modal attention paradigms (Foxe *et al*., 1998; Fu *et al*., 2001), and may imply that excitatory baseline shifts during orienting of attention go along with inhibitory mechanisms to sharpen the focus of visual spatial attention.

However, as pointed out previously (Kelly *et al*., 2006), the divergent EEG findings of α-desynchronization (Sauseng *et al*., 2005; Thut *et al*., 2006) vs. α-synchronization (Worden *et al*., 2000; Kelly *et al*., 2006) may also be explained by variations in the employed paradigms. These paradigms all involve covert orienting of attention towards cued positions in anticipation of an upcoming imperative visual task stimulus, but differ in visual task demands. As suggested, anticipatory α-synchronization might be tied to visual tasks in which active suppression of distracter information is required contralateral to the attended position. Indeed, in the two studies reporting α-synchronization, visual target and distracter stimuli were either bilaterally presented at attended vs. unattended locations (Kelly *et al*.,

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2006) or subjects had to ignore targets when presented at opposite, unattended, positions (Worden *et al*., 2000). Anticipatory α-desynchronization, on the other hand, has been reported to dominate when upcoming visual stimuli have to be processed independently of cued positions in the absence of concurrent distracters, i.e. when no distracter has to be ignored (Sauseng *et al*., 2005; Thut *et al*., 2006). It could therefore be argued that α-synchronization of occipitoparietal origin is only observed in distinct paradigms and does not reflect a general mechanism associated with spatial orienting of visual attention.

In the present EEG study, we aimed to gain further insight into oscillatory α-band increases (synchronization) during endogenous visual spatial attention deployment. If α-synchronization is indeed a suppressive mechanism only used for ignoring or blocking irrelevant information, it should not generalize to visual tasks in which nothing has to be ignored. If it reflects a general mechanism that goes along with enhancement, achieving a sharpened attention focus by suppressing unattended space (whether relevant or not), then it would be expected to be present even in the absence of distracter information and to be retinotopically organized, i.e. showing different topographic patterns for different attended locations. This was tested by studying scalp topography of α-band changes as a function of eight attended positions and using a visual task design with targets but no concurrent distracters.

Materials and methods

Participants

Twelve healthy volunteers (five female) aged 23–39 years (mean 29.9 years) participated in this study, carried out in accordance with the principles laid down in the Declaration of Helsinki and approved by the Ethical Committee of the University Hospital of Geneva. All subjects provided written informed consent, were right-handed (Oldfield, 1971) and reported normal or corrected-to-normal vision.

Task and stimuli

Participants viewed a central fixation cross surrounded by eight light-grey squares indicating possible target locations (Fig. 1). The squares were placed in a clock-face arrangement at a radius of 7.5° from the cross at equidistant positions (12.00, 1.30, 3.00, 4.30, 6.00, 7.30, 9.00 and 10.30 h). The central cross and all eight squares were continuously displayed to mark possible target positions and to serve as spatial guides for orienting of attention to reduce between-trial variability per condition and participant. A symbolic spatial cue (green central arrow, flashed for 80 ms) pointed to the to-be-attended position, which varied randomly across trials. After 1300 ms a visual stimulus appeared, more often at cued than noncued locations (88 vs. 12% of all trials), in the centre of a grey square. The visual stimuli (presented for 80 ms) consisted of go (×) or nogo (+) targets, which were randomized across trials with 1 : 1 probability of appearance. There was a 1600 ms delay between the disappearance of the target and the next cue. Participants were asked to keep central fixation, to covertly direct and maintain attention to the cued position, to respond to go-stimuli at cued and noncued locations and to minimize eye blinks. Responses were given with the right index finger. A go–nogo paradigm was adopted based on pilot experiments to reduce the risk of motor preparatory activity (α-desynchronization over left central leads) contaminating the scalp topography of attention-related processes in the cue–target interval.

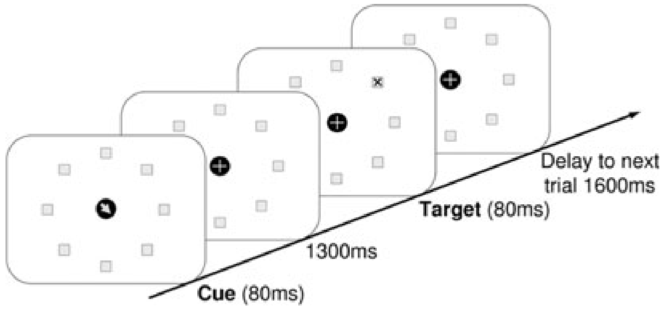

FIG. 1. Visual display and task. A central green arrow (symbolic cue) indicating the to-be-attended position was followed by a peripheral go (×) or nogo (+) stimulus (target), more likely to appear at cued than uncued positions (88 vs. 12%). The white '+' on black background shows the central fixation cross. Cue direction was randomly intermixed within experimental blocks.

Behavioural data were recorded via a response box (E-Prime 1.1; Psychology Software Tools, Pittsburgh, PA, USA). Each subject practiced the task for 1 h the day before the EEG recording. During the experimental session, 126 trials were presented for each of the eight cue conditions (randomly intermixed within blocks of ∼5 min duration each), resulting in a total of 1008 trials.

EEG recording

EEG was recorded continuously with a 128-channel EEG system (Electrical Geodesics Inc., Eugene, USA) at 500 Hz sampling rate (bandpass filter 0.01–200 Hz), with impedances < 50 kΩ and a vertex reference. Vertical and horizontal eye movements were monitored with separate EOG leads. The data were visually inspected to reject epochs with eye movements or artefacts. Epochs started 400 ms before cue onset (pre-cue) and covered the whole cue–target interval (1300 ms after cue onset). The average epoch acceptance rate was 77.7 ± 6.9% (SEM). Epoch acceptance rate did not differ significantly between cue conditions.

EEG analysis

The evolution of α (8–14Hz) band activity over the entire epoch was computed using a modified temporal spectral evolution algorithm (Salmelin & Hari, 1994; Worden *et al*., 2000), related to the event-related (de)synchronization procedure (Pfurtscheller & Lopes da Silva, 1999). Single epochs were: (i) 8–14 Hz band-pass filtered, ii) rectified, iii) smoothed by averaging over time samples within a moving averaging window of 100 ms, and (iv) averaged across all trials per electrode, condition and participant.

This provides information on the spatial scalp distribution and time-course of the oscillatory α-band activity in its absolute form. For a better assessment of cue-related changes, temporal spectral evolution amplitudes were also baseline-corrected to the pre-cue interval (400 ms) by either subtraction (α-activity in cue–target interval minus pre-cue α-activity) or normalization (α-activity in cue–target interval divided by pre-cue α-activity, followed by log transformation, i.e. $\log_{10}$).

Based on previous work (Foxe *et al*., 1998; Worden *et al*., 2000; Sauseng *et al*., 2005), we focused on the last 250 ms of the cue–target interval (pre-target activity), during which sustained α-changes and anticipatory bias in spatial attention are expected to be at their highest levels. The spatial distribution of α-activity across the entire electrode array (pre-target α-map topography) was examined in terms of relatedness across the eight (cued and attended) positions. To this end, we determined the intercorrelations between the α-maps for each individual ($n = 8$ maps, one for each condition) using computations of spatial correlation coefficients (Michel *et al.*, 1999; Michel *et al.*, 2001; Blanke *et al.*, 2005; Murray *et al.*, 2006). These spatial correlation coefficients were then subjected to an ANOVA with the within-subject factor Angular Distance between contrasted maps (conditions: +45°, +90°, +135°, ±180°, −135°, −90°, −45°). Where appropriate, polynomial quadratic contrasts were performed to probe for a U-shaped function of correlation coefficients over angular distances.

Similarly to Worden *et al.* (2000), we also compared pre-target α-map topography between conditions with regard to the locus of maximum α-decrease and -increase in the 3-D sensor array (spherical, normalized radius) to probe for a retinotopic organization over occipitoparietal electrodes. We tested for differences in the x, y and z coordinates of the α-maxima and -minima across cue conditions using repeated-measure ANOVAs and subsequent paired t-tests or one-sample t-tests, where appropriate.

Finally, pre-target α-activity was tested for significant deviation from pre-cue (baseline) activity over occipitoparietal recording sites using repeated-measure ANOVA on absolute α-values and one-sample t-tests on baseline-corrected data (testing against baseline values that have been adjusted to 0), to assess the direction of the α-changes (increases vs. decreases). The ANOVA was performed on the lateral cue conditions (1.30, 3.00, 4.30, 7.30, 9.00 and 10.30 h) with the factors Time Period (baseline vs. pre-target), Region of Interest (ROI; ipsilateral vs. contralateral to cued position), Cueing Direction (left vs. right side) and Cueing Elevation [(10.30 and 1.30 h) vs. (9.00 and 3.00 h) vs. (7.30 and 4.30 h)].

Results

Behaviour

In the spatially cued target discrimination task (go- vs. nogo-stimuli) involving spatial cueing to one of eight possible target positions, participants responded faster to go-stimuli at validly cued than at invalidly cued locations (main effect of Validity: $F_{1,11} = 80.2$, $P < 0.0001$; 389.9 ± 12.6 vs. 525.6 ± 17.4 ms; mean ± SEM) showing that they were correctly attending to the cued position. This effect was independent of attended location (interaction Validity × Position: $F_{7,77} = 1.6$, n.s.). Within invalid conditions ($n = 7$), reaction times changed systematically as a function of distance from the attended position ($F_{6,66} = 5.7$, $P < 0.0001$) following an inverted U-shaped function (polynomial quadratic contrast: $F_{1,11} = 24.3$, $P < 0.001$) with slowest responses occurring around maximum distances of 135–225° (Fig. 2).

The hit rates for go-stimuli were 99.3 ± 0.3% vs. 96.4 ± 1.7%, and the false alarm rates for nogo-stimuli 9.9 ± 3.1% vs. 2.8 ± 0.9%, for validly cued vs. invalidly cued positions (mean ± SEM). Breaking down these measures in terms of position relative to cued location (0°, 45°, 90°, 135°, 180°, 225°, 270° and 315°) did not reveal significant differences (hit rate, range: 94.8 ± 3.8% to 99.3 ± 0.3%, $F_{7,77} = 0.8$, n.s.; false-alarm rate, range: 2.1 ± 1.5% to 9.9 ± 3.1%, $F_{7,77} = 1.9$, n.s.).

EEG measurement of anticipatory α-activity

Absolute α-activity

At posterior, occipitoparietal ROIs, α-activity (8–14 Hz) showed sustained changes that started at ~400 ms following cue-onset and slowly evolved over the remaining 900 ms of the cue–target interval to reach maximal values towards target onset (Fig. 3A). This timing is in agreement with previous results showing that the sustained, attention-related changes develop at ~400–600 ms following cue onset (e.g. Worden *et al.*, 2000; Yamagishi *et al.*, 2005; Thut *et al.*, 2006). These changes were preceded by an early short-lasting burst of α-activity, peaking at ~180 ms after cue onset, which occurred independently of cued position and most probably reflected a phase-locked response to the foveally presented cue. The sustained changes consisted of increases (synchronization) in α-activity (Fig. 3A). Sustained anticipatory α-decreases (desynchronization) were absent or small (Fig. 3A).

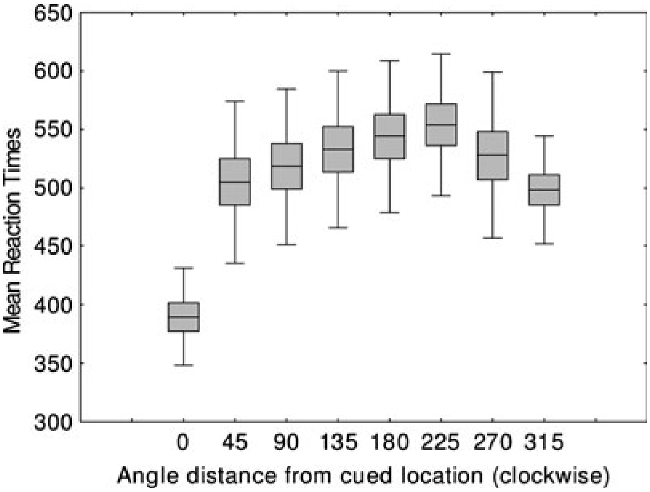

FIG. 2. Reaction times (ms) to go-stimuli as a function of angular distance (clockwise) from attended location. The boxplot depicts the mean reaction times (black bars), SEM (box) and standard deviations (whiskers). Note the inverted U-shaped function, with slowest responses at maximal distances from attended position (135–225°).

Over the posterior recording sites, α-activity was differentially modulated in the cue–target interval depending on cued (attended) position (Fig. 3A). However, mapping the absolute α-values onto the entire electrode array did not adequately illustrate the topography of attention-related changes in α-activity (Fig. 3B). This was because the absolute α-map topography was dominated by a left–right asymmetry over posterior recording sites (α_left > α_right) which was already present in the baseline interval prior to cue onset independently of cue condition (Fig. 3B, pre-cue maps; in line with Thut *et al.*, 2006) and which was more important (in terms of strength) than the subsequent cue-related changes. These were masked by the pre-existing topography even in the last 250 ms of the cue–target interval where the anticipatory attention bias is expected to be maximal (Fig. 3B, pre-target maps; time window marked in Fig. 3A by shaded boxes). For better assessment of the effects of cued position on spatial α-distribution, we therefore focused on α-changes in the cue–target relative to the pre-cue (baseline) interval rather than on absolute α-values.

Baseline-corrected (relative) α-activity

Figure 4 illustrates the spatial distribution of relative changes in α-activity in the last 250 ms before target onset (pre-target α-map topography) for each cued (attended) position. Relative changes that are corrected for pre-cue (baseline) activity were obtained by either normalization to the pre-cue interval (division and log-transformation; Fig. 4A) or subtraction of the pre-cue values (Fig. 4B). The figure shows that pre-target α-map topography varied systematically with the locus of attention. Maps were dominated by α-increases (highlighted in red) over

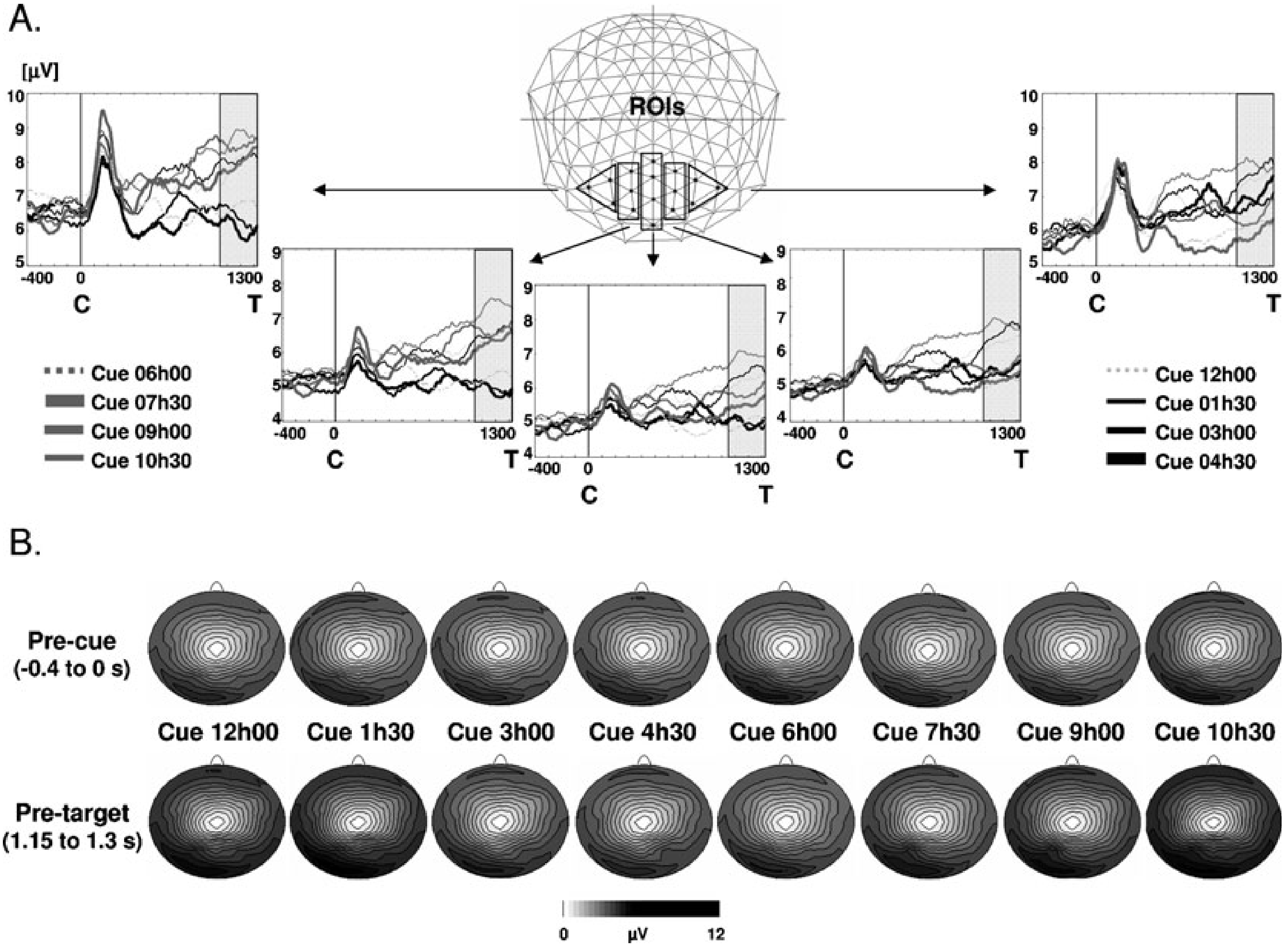

FIG. 3. (A) Temporal spectral evolution of oscillatory α-band (8–14 Hz) activity (absolute values, grand-averaged) over five regions of interest (ROIs) through parieto-occipital areas (see top panel) and for each of the eight cued and attended positions (12.00, 1.30, 3.00, 4.30, 6.00, 7.30, 9.00 and 10.30 h). Waveforms are shown from 400 ms before the cue (C) to appearance of the target (T); the shaded band is the 250 ms pre-target period. Note the steady α-increase from 400 ms postcue towards target onset. (B) Absolute α-map topography over the entire electrode array per cued and attended position before cue onset (pre-cue maps, upper panels) and in the last 250 ms of the cue–target interval (pre-target maps, lower panels). Absolute α-maps were dominated by a left–right asymmetry in α-activity (left > right) that was already present in the pre-cue (baseline) period (see pre-cue maps) and that masked subsequent attention-related changes in the cue–target interval (see pre-target maps and Fig. 4).

posterior sites ipsilateral to the attended location and were symmetrical for corresponding positions of the attended right (1.30, 3.00 and 4.30 h) vs. left (10.30, 9.00 and 7.30 h) hemifield. In addition, ipsilateral α-increases were located more laterally when attention was directed to the lower visual field or horizontal midline (3.00, 4.30, 7.30 and 9.00 h) and more medially for upper visual field conditions (1.30 and 10.30 h). α-Decreases (highlighted in blue) were less important, and mostly observed for attention directed to position 4.30 h. Weakest changes in α-activity were found for attention directed to the most inferior, central position (6.00 h). Furthermore, equivalent results were obtained independently of whether data were baseline-corrected by normalization or subtraction (Fig. 4A vs. B; see also statistical results below). This corroborates our finding of α-increases dominating over -decreases, the latter being absent or small with both corrections. In fact, using the common subtraction method for baseline correction, relative α-decreases may be more difficult to trace than relative α-increases because deviations from baseline α-activity could be positively skewed (as it is physically impossible for α-activity to pass below zero). Using division and log-transformation for normalization, on the other hand, eliminates this bias.

Analysis of spatial intercorrelations between pre-target α-map topographies revealed a systematic pattern (Fig. 4, box plots) with spatial correlation coefficients decreasing steadily with angular distance between cue conditions (main effect of Distance: normalization (norm), $F_{6,66} = 6.9$, $P = 0.00001$; subtraction (sub), $F_{6,66} = 6.7$, $P = 0.00001$), again following a U-shaped function (polynomial quadratic contrast: norm, $F_{1,11} = 7.8$, $P = 0.017$; sub, $F_{1,11} = 8.2$, $P = 0.015$). The α-map topographies of neighbouring attention positions (±45°) showed the highest spatial similarity (spatial correlation coefficients). The smallest spatial correlations between scalp topographies were observed at maximal distances of 180°.

Analysis of the x, y and z coordinates of the α-maps' maxima and minima across the different cue conditions confirmed that the location of maximum α-increases along the left–right dimension (x-axis) depended on the direction of attention (leftward vs. rightward cueing conditions: norm, $F_{1,11} = 48.8$; $P < 0.0001$; sub, $F_{1,11} = 27.8$, $P < 0.001$). Maximum α-increases occurred ipsilaterally to the cued (attended) position (leftward cueing: norm and sub, $x = -0.15 \pm 0.06$ and -0.20 ± 0.07, respectively; rightward cueing: norm and sub, $x = +0.38 \pm 0.09$ and $+0.27 \pm 0.06$, respectively) deviating

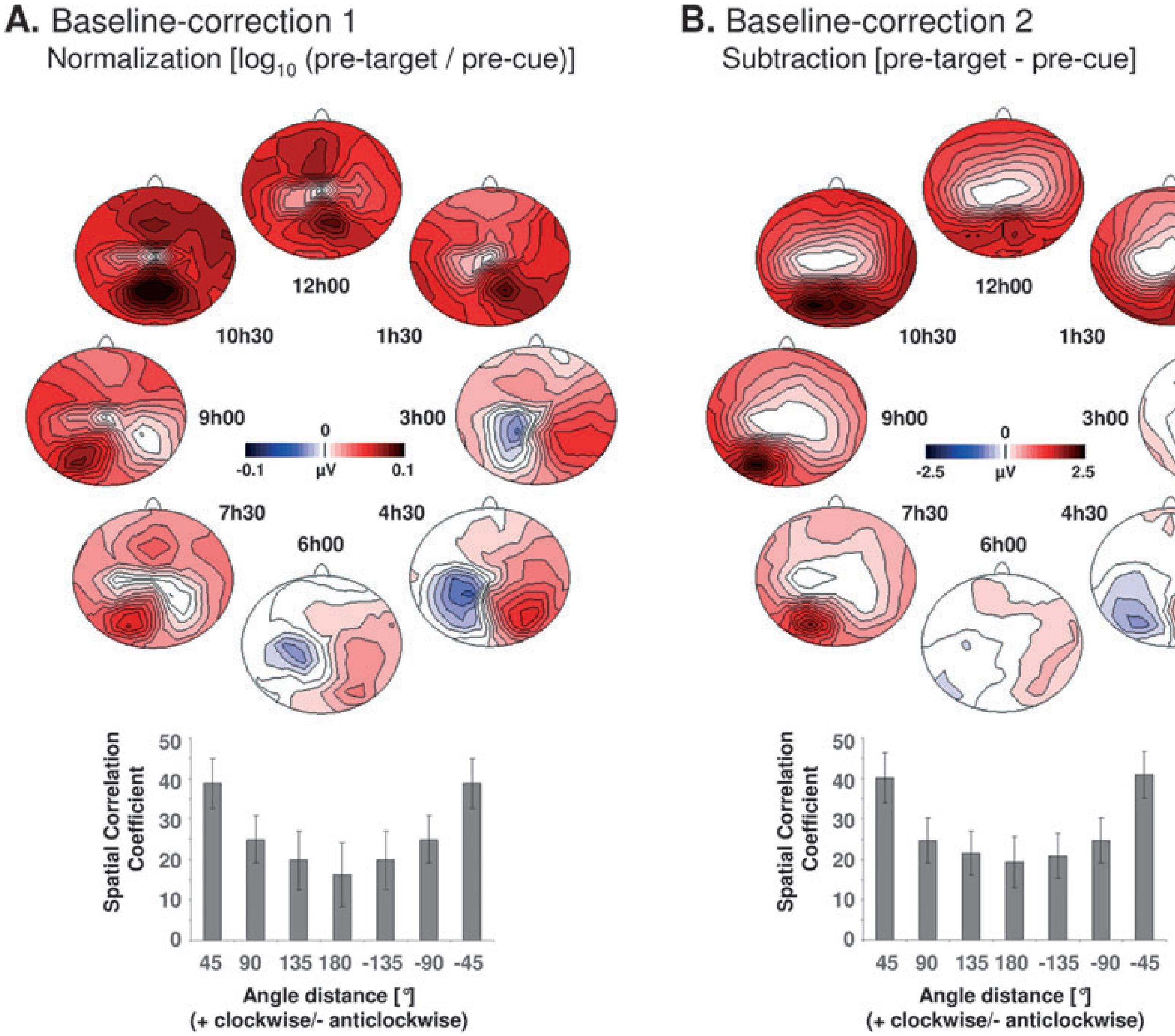

FIG. 4. Spatial distribution of relative (baseline-corrected) changes in α-band activity over the entire electrode array for each of the eight cued and attended positions and two baseline-correction algorithms (A vs. B). Data represent the last 250 ms of the cue–target interval (pre-target map topography). Box plots depict spatial correlation coefficients of the pre-target maps fitted to their own or increasingly distant cue conditions (0–315° angular distance) for evaluation of their intercorrelations. Map topographies were defined by posterior α-increases (synchronization) that depended in location on side (left vs. right) and elevation (upper vs. lower) of the attended position. Each pre-target map showed close resemblance with its neighbours and increasing dissimilarity with maps of more distant positions. Bars indicate SEM.

significantly from the midline (one-sample *t*-tests against $x = 0$; norm and sub, respectively, $t = -2.4$ and -2.8, $P = 0.033$ and 0.016 for leftward and $t = 4.2$ and 4.8, $P = 0.002$ and 0.0001 for rightward cueing). In addition, the *x*-coordinates of maximum α-increases depended on the horizontal offset of the attention focus from the vertical meridian [0° vs. 5.3° vs. 7.5°; (12.00 and 6.00 h) vs. (1.30, 4.30, 7.30 and 10.30 h) vs. (9.00 and 3.00 h)]. With increasing horizontal offset of attended positions, the locus of maximum α-increase shifted gradually outwards [norm: $x(\text{abs}) = 0.14 \pm 0.11$ vs. 0.23 ± 0.05 vs. 0.40 ± 0.08; $F_{2,22} = 3.2$, $P = 0.061$; sub: $x(\text{abs}) = 0.07 \pm 0.12$ vs. 0.18 ± 0.08 vs. 0.39 ± 0.07; $F_{2,22} = 7.9$, $P = 0.003$; x-values are absolute values (abs)]. Moreover, when attention was directed to the upper visual field, maximum α-increases were found more medially than with lower visual field conditions [norm: $x(\text{abs}) = 0.02 \pm 0.05$ vs. 0.34 ± 0.08; $F_{1,11} = 8.65$, $P = 0.013$; sub: $x(\text{abs}) = 0.05 \pm 0.09$ vs. 0.43 ± 0.07; $F_{1,11} = 29.38$, $P = 0.0002$]. No significant differences for maximum α-increases across conditions were found on the anterior–posterior (*y*) or caudal–rostral (*z*) axes, nor was there a consistent spatial distribution of α-minima (maximal α-decreases).

Finally, analysis of the α-amplitude in the 250 ms pre-target vs. baseline interval (averaged within left or right ROIs, illustrated in Fig. 3A) revealed that α-changes depended on the location of the ROI relative to the cued hemifield (ipsi- vs. contralateral ROI) and on cueing elevation [(10.30 and 1.30 h) vs. (9.00 and 3.00 h) vs. (7.30 and 4.30 h); three-way interaction Time Period (baseline vs. pre-target) × ROI × Cueing Elevation: $F_{2,22} = 4.29$, $P = 0.027$]. In comparison to baseline, pre-target α-activity was significantly increased ipsilaterally to the cued hemifield but no significant changes were found contralaterally for both horizontal midlines [(9.00 and 3.00); ipsi- and contralateral, respectively: $F_{1,11} = 5.7$ and 2.1, $P = 0.03$ and 0.17; two-way interaction Time Period × ROI: $F_{1,11} = 4.01$, $P = 0.06$] and lower visual field conditions [(7.30 and 4.30); ipsi- and contralateral, respectively: $F_{1,11} = 4.5$ and 0.01, $P = 0.05$ and 0.9; two-way interaction Time Period × ROI:

$F_{1,11} = 3.89$, $P = 0.07$]. For the upper visual field conditions (10.30 and 1.30), α-activity was significantly higher in the pre-target than the baseline interval ($F_{1,11} = 7.1$, $P = 0.02$) independently of ROI two-way interaction Time Period × ROI: $F_{1,11} = 1.43$; n.s.), further indicating more medially located α-increases for these cue conditions. Additional analysis on baseline-corrected α-activity in the pre-target interval (one-sample *t*-tests against 0) confirmed that the anticipatory α-increases ipsilateral to the attended hemifield deviated significantly from the pre-cue values (leftward cueing, left ROIs: norm and sub, respectively, $t = 3.41$ and 2.44, $P = 0.005$ and 0.033; and rightward cueing, right ROIs: norm and sub, respectively, $t = 3.59$ and 2.5, $P = 0.004$ and 0.029). There was no significant decrease in α-activity contralateral to the attended hemifield.

Discussion

The present study on EEG correlates of orienting of visual attention was designed to probe for retinotopically organized changes of α-band activity, when attention is maintained at specific spatial locations in anticipation of an imperative visual task stimulus. In particular, we aimed to focus on anticipatory α-synchronization, thought to originate in visual areas tuned to the unattended position and interpreted as reflecting active inhibition of these locations (Worden *et al*., 2000; Kelly *et al*., 2006). To this end, we employed a visual task paradigm with single targets but without concurrent distracters. Our results indicate that sustained changes in the α-frequency band occur during covert orienting of attention, in line with previous studies (Worden *et al*., 2000; Yamagishi *et al*., 2003, 2005; Sauseng *et al*., 2005; Thut *et al*., 2006). In addition, our data show that the topographic distribution of these α-changes is specific for eight loci of attention. Importantly, the spatial specificity we found applies to α-synchronization, as our visual task design with single targets but without concurrent distracters did not result in marked anticipatory decreases but increases in α-activity. Furthermore, α-increases showed a retinotopically organized pattern. They were observed over posterior recording sites and depended in location on the laterality, horizontal offset and elevation (upper vs. lower visual field) of the attention focus. Finally, maximum α-increases were found contralaterally to the unattended space. These results provide evidence that α-synchronization, most probably serving active suppression of visual input from unattended positions, plays an important role in selective visual attention.

In terms of scalp topography, our results strikingly match those by Worden *et al*. (2000) who demonstrated retinotopic specificity of α-synchronization for orienting of attention towards the four visual field quadrants. Both data sets show that the α-increase during attention orienting has a focal distribution, is maximal over occipitoparietal sensors contralateral to the unattended position, and is located more medially when attention is allocated to upper visual field in contrast to lower visual field locations. This similarity in finding was not necessarily expected, although in our as compared to Worden and colleagues' study four out of the eight attention positions were placed at similar location in the visual field and at a similar distance from the fixation cross (7.5° vs. 5° of visual angle; Worden *et al*., 2000). Based on previous findings that α-desynchronization is observed during visual spatial orienting in anticipation of single targets without distracters (Sauseng *et al*., 2005; Thut *et al*., 2006) and that α-synchronization dominates when additional distracters have to be suppressed at task-irrelevant positions (Worden *et al*., 2000; Kelly *et al*., 2006), one could have expected that α-synchronization would be less important than desynchronization in the present design (Kelly *et al*., 2006). A number of reasons could account for the lack of significant desynchronization found here. There may have been no significant α-desynchronization (decrease) because of unusually low α-activity at baseline prior to the cue. With very low baseline activity, there would be nothing to reduce. However, absolute α-activity at baseline was similar in amplitudes to previous reports, in which a significant reduction of α-activity has been described and in which identical algorithms for calculation of temporal spectral evolution had been used (Thut *et al*., 2006; see also early transient α-suppression in Worden *et al*., 2000). Furthermore, even with normal baseline values, decreases from baseline α-activity might be more difficult to trace than increases because changes from baseline could be positively skewed, given that α-activity cannot physically pass below zero. However, we did not find significant α-decreases, even if the distribution of the attention-related changes in α-activity was normalized (i.e. divided and log-transformed). We thus interpret the predominance of α-synchronization, its retinotopic organization and correspondence to previous findings (Worden *et al*., 2000) to indicate that active inhibitory processes are a generic component of spatial selective attention, rather than being linked to the presence of a distracter stimulus.

For the present design, we suggest that the reason for the predominance of α-synchronization is to be found in the continuous static display of multiple squares marking potential target positions. This approximates a natural visual scene in which the probable position of future, behaviourally relevant, visual events is often linked to the objects constituting the scene, and contrasts with the designs used in previous EEG studies displaying blank screens (Yamagishi *et al*., 2003, 2005; Sauseng *et al*., 2005) or a limited number of attention markers ($n = 2$) during attention orienting (Worden *et al*., 2000; Kelly *et al*., 2006; Thut *et al*., 2006). As with the exploration of natural scenes, maintaining attention to one particular grey square (object) is expected to require active suppression of all other, continuously displayed, 'opponent' squares (objects), because these are likely to eventually become concurrent, exogenous attention attractors. In this sense, 'opponent' squares (objects) may be considered to represent a sort of covert distracter, although not producing a visual transient on their own. The attraction of attention towards currently unattended salient objects, which are potentially relevant for upcoming behaviour, would be consistent with the phenomenon of inhibition of return, the natural tendency not to return attention to previously explored locations (Posner, 1985). Because in the present study, subjects had to maintain spatial attention on one square or object during a relatively long cue–target interval, attraction of attention towards unattended, 'opponent' squares and thus the need to actively inhibit these locations might even be amplified. In this context, the present finding of a retinotopic organization of α-synchronization, despite the presence of seven broadly scattered 'opponent' squares, is of particular interest. It would suggest that the need for active suppression is inhomogeneously distributed across unattended space. This is conceivable as attention attraction to previously unexplored space would be expected to be strongest for the square that is most remote (diagonal) from the currently attended position. Note that this interpretation would also fit the scalp topography of α-synchronization across the eight attended positions we observed. Attending to the right visual field (e.g. positions 1.30 and 4.30 h) resulted in α-increases over the right hemisphere, i.e. contralateral to the unattended space, and idem for leftward orienting (e.g. positions 7.30 and 10.30 h). Furthermore, attending to the lower visual field (positions 4.30 and 7.30 h) produced a more ventrolateral α-enhancement, whereas attending to the upper visual field (positions 1.30 and 10.30 h) led to a more dorsomedial increase in α-activity. Because the cortical representation of the visual fields in visual areas is left–right reversed over the two hemispheres and the lower visual field is mapped more dorsally than the upper visual field, these results would suggest that α-increases occurred in areas tuned to the visual field quadrant diagonal to the attended position. That is, when attending laterally upwards, α-increases appear to occur in areas tuned to the lower portion of the unattended hemifield (dorsomedial α-distribution) while, when attending laterally downwards, these increases occur in areas processing the upper portion of the unattended hemifield (ventrolateral α-distribution).

Alternatively, 'opponent' positions in the present study might have been disproportionally inhibited because they were very unlikely to be associated with a forthcoming visual event, i.e. were almost irrelevant; this contrasts with previous studies where distracters were not present (Sauseng *et al*., 2005; Thut *et al*., 2006). In fact, the probability of stimuli appearing at one given, noncued location was < 2% in the present study (88% appearing at cued positions). Therefore, inhibiting noncued locations might have constituted an advantage rather than a disadvantage for task execution. This compares to 25–33% probability of targets appearing at noncued positions in previous studies with no visual task distracters (Sauseng *et al*., 2005; Thut *et al*., 2006). Although conceivable, this account is incompatible with a retinotopic organization of α-synchronization, as all seven noncued locations were equally unlikely to be associated with a future visual event.

Evidence for a retinotopic organization of visual spatial attention has also been found in fMRI studies, which showed enhanced haemodynamic responses at the occipital sites representing the attended position and a concomitant suppression of response in areas corresponding to unattended locations (Tootell *et al*., 1998; Somers *et al*., 1999). Further fMRI or MEG studies on the spatial distribution of attentional enhancement and suppression of visual responses (i) have found that these processes occur in a relatively narrow centre–surround profile that is anchored on the attended position and that recovers at more distant locations (Muller & Kleinschmidt, 2004; Schwartz *et al*., 2005; Hopf *et al*., 2006), or (ii) have reported focal enhancement of neuronal activity in areas representing the attended position and more widespread suppression that extends to the representation of unattended quadrants in extrastriate more than striate cortex (Slotnick *et al*., 2003) or even to all other unattended locations (Smith *et al*., 2000). It is important to note that the present and previous EEG results differ from fMRI findings. While the EEG studies have begun to reveal the spatial organization of inhibitory or excitatory oscillatory activity in anticipation of future visual events, fMRI has uncovered the spatial pattern of neuronal response enhancement or suppression in response to these visual stimuli.

In conclusion, our findings demonstrate that α-synchronization is an important component of spatial selective attention. Its spatial distribution, retinotopic organization and occurrence even in the absence of overt distracters indicates that it reflects an active inhibitory process suppressing visual input from unattended positions to sharpen the current focus of attention during visual spatial orienting.

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Abbreviations

abs, absolute values; EEG, electroencephalography; fMRI, functional magnetic resonance imaging; MEG, magnetoencephalography; norm, normalization; ROI, region of interest; sub, subtraction.

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