

Anticipatory Biasing of Visuospatial Attention Indexed by Retinotopically Specific α -Band Electroencephalography Increases over Occipital Cortex

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α -Band (8–14 Hz) oscillatory EEG activity was examined with high-density scalp electrical recording during the cue–stimulus interval of an endogenous spatial cueing paradigm. In different blocks, cued spatial locations (left or right) were in either the upper or lower visual field, and attended stimuli were either oriented Ts or moving dots. Distractor stimuli were equally likely in the uncued hemifield. Sustained focal increases of α -band

activity were seen over occipital cortex contralateral to the direction of the to-be-ignored location (ipsilateral to the cued direction of attention) before onset of the to-be-attended stimulus. The focus of α -band activity also moved depending on whether cued locations were in the upper or lower field. Results are consistent with active gating of uncued spatial locations.

Key words: alpha; attention; ERP; cueing; oscillations; gating

Without moving their eyes, humans can voluntarily deploy attention to locations in visual space at which a stimulus is expected to appear. This so-called “covert attention” results in improved processing of stimuli occurring at the locus of attention while attenuating processing of stimuli located elsewhere in the visual field (Posner et al., 1980). Although many studies have looked at the effects of such attentional deployment on subsequent processing of visual stimuli at attended and nonattended locations (Parasuraman, 1998), less is known about the biasing mechanisms which are engaged before the onset of a to-be-attended visual stimulus (Harter et al., 1989; Yamaguchi et al., 1994). In studies of voluntary attention, a symbolic cue, such as an arrow, directs subjects to attend to a particular spatial location. An important issue is the extent to which voluntary allocation of attention in response to such a cue differentially modulates visual brain areas in preparation for processing expected stimuli. Recent studies have reported that visual processing areas, retinotopically mapped to the attended region of space, exhibit increased activation in the postcue–prestimulus period (Luck et al., 1997; Kastner et al., 1999), which may prepare them for processing stimuli at corresponding visual locations, perhaps biasing competitive stimulus interactions (Kastner et al., 1999). Most recently, it was shown that an arrow cue used to specify the direction of a subsequent moving stimulus resulted in modulations of motion-sensitive brain areas in the postcue–prestimulus period, relative to a noninformative cue (Shulman et al., 1999). Furthermore, it has been shown that after onset of to-be-attended stimuli, neural responses to nearby distractor stimuli may be suppressed (Moran and Desimone, 1985; Reynolds et al., 1999), and behavioral responses to stimuli at nonattended locations are

slowed relative to those at attended locations (Posner et al., 1980). This raises the question of whether inhibitory processes targeted at locations likely to contain distractor information may be engaged in preparation for attending to specific spatial locations.

Recent evidence suggests that preparatory attentional processes in an intermodal attention task are reflected in α -band (8–14 Hz) oscillatory activity of the scalp electroencephalogram (Foxe et al., 1998). When subjects were cued to attend to the auditory component of an upcoming compound auditory–visual stimulus, focal increased α -band activity was seen over parietal–occipital areas preceding stimulus onset. It was proposed that these increased α levels reflected active gating of visual space when auditory selective attention was engaged. Further support for a suppressive attentional role for α oscillations comes from the finding that parietal–occipital α -band increases are associated with disengagement of visual processing during an object–non-object detection task (Vanni et al., 1997).

We examined α -band oscillatory activity related to voluntary deployment of visuospatial attention in a spatial cueing paradigm. If α -band activity indexes attentive disengagement of visual processing, then topographically specific changes in α would be expected to track anticipatory deployment of attention to discrete areas of visual space. α increases should be greatest over visual areas corresponding to portions of space where distractor stimuli are likely to appear. Furthermore, because different stimulus features are processed in different specialized brain regions, the

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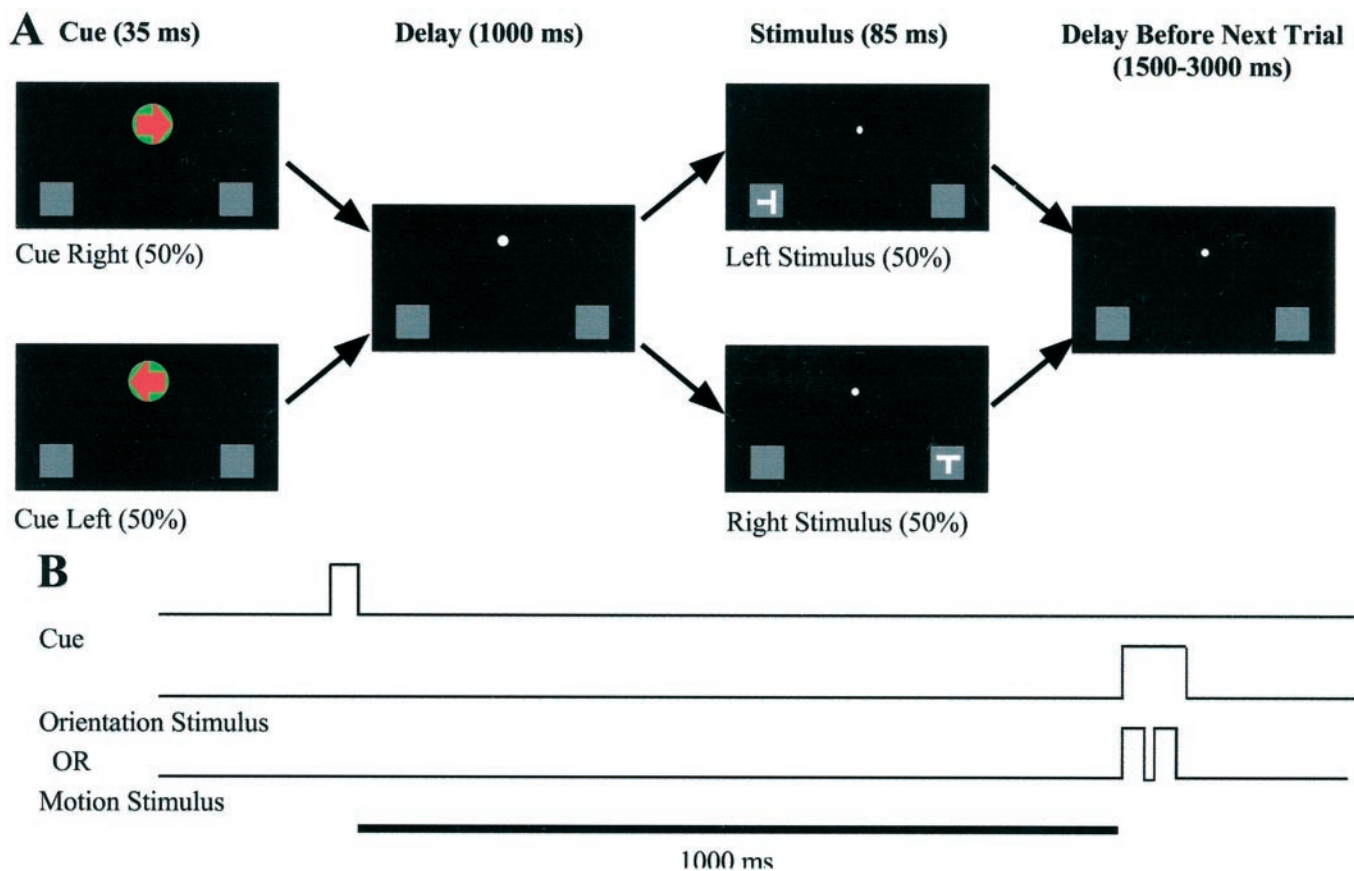


Figure 1. Schematic illustration of stimulus configuration. *A*, Stimulus configuration for a lower visual field trial. On each trial, the arrow cue could point right or left with equal probability. A delay period followed the cue, after which one of four stimuli would appear at either the left or right location marker with equal probability. One stimulus was designated as the target stimulus at the beginning of each block of trials. Subjects were required to respond with a button press only when a target stimulus was detected at the cued location. *B*, Time course of each trial. The fixation point was replaced by the cue stimulus for 35 msec followed by a 1000 msec delay period. After the delay, a stimulus would appear briefly at one of the marked locations. Orientation stimuli were presented for 85 msec. Motion stimuli consisted of a 30 msec presentation of a dot at one location followed by a 15 msec delay and 30 msec presentation of a dot at a second location producing an apparent motion effect. After the stimulus was a variable (1500–3000 msec) period before the start of the next trial.

location of preparatory brain activity, either excitatory or inhibitory, may vary in accordance with the expected features of the impending stimuli. This was examined using two classes of target-distractor stimuli.

MATERIALS AND METHODS

Subjects. Ten right-handed, neurologically normal, paid volunteers (five male and five female) participated (mean age, 27.1 years; SD, 6.7 years). Three additional subjects were excluded because of excessive eye movements. Informed consent was obtained from all subjects.

Stimuli. Stimuli were presented against a black background. The central cue was a circle ($\sim 1^\circ$ visual angle) with an embedded arrow and was designed to minimize any sensory effects related to physical differences between the two cue stimuli. The arrow and the circle were presented in red and green, and for each trial, it was equally probable that the arrow would be red on a green background or green on a red background. Red and green values were precalibrated for each subject to be approximately isoluminant by flicker photometry. Dark gray squares ($\sim 1.2^\circ$ visual angle) served as location markers and remained on the screen throughout each block of 16 trials. Location markers were positioned $\sim 3.5^\circ$ lateral to fixation and, in different blocks, $\sim 3.5^\circ$ either above or below the horizontal meridian. In orientation discrimination trials, stimuli were rotated Ts ($\sim 1^\circ$ visual angle) constructed from two orthogonal line segments. Orientation stimuli were presented for 85 msec in one of four orientations (0, 90, 180, and 270°), one of which was designated the “target” stimulus at the beginning of each trial block. In motion discrimination trials, stimuli were a sequential pair of dots (each $\sim 0.25^\circ$ visual angle),

which showed apparent motion in one of four directions (up, down, right, and left), one of which was designated the target at the start of each block. Apparent motion was produced by presenting the first dot for 30 msec, followed by a 15 msec blank period, followed by a 30 msec presentation of the second dot.

Procedure. The sequence of events in each trial is illustrated in Figure 1. One stimulus was designated as the target stimulus at the beginning of each block of 16 trials. Subjects maintained fixation on a small dot at the center of the screen, and two continuously displayed dark gray squares served as markers to indicate the spatial locations at which stimuli could occur. On each trial, a brief (35 msec) arrow cue was presented at the center of the screen that pointed either right or left with equal probability. A 1000 msec delay period ensued, after which a stimulus appeared with equal probability at one of the two location markers. Subjects were instructed to attend to stimuli that occurred at the location cued by the arrow without moving their eyes. If the stimulus appeared at the attended location, subjects had to make a discrimination about the identity of the stimulus and respond with a button press (right hand) only if one stimulus (the target) of four possible stimuli was detected. Stimuli that appeared at the noncued location were to be ignored. Over the 16 trials that constituted a trial block, each combination of motion or orientation, cue side and stimulus side were presented once with the exception that, for each trial there was an additional 0.1 probability of a target being presented at the cued side so that the number of targets per block would not be completely deterministic.

To examine the possibility that preparatory attentional processes occur in retinotopically mapped regions of occipital cortex, the bilateral stimulus locations could be in either the upper or lower visual field in

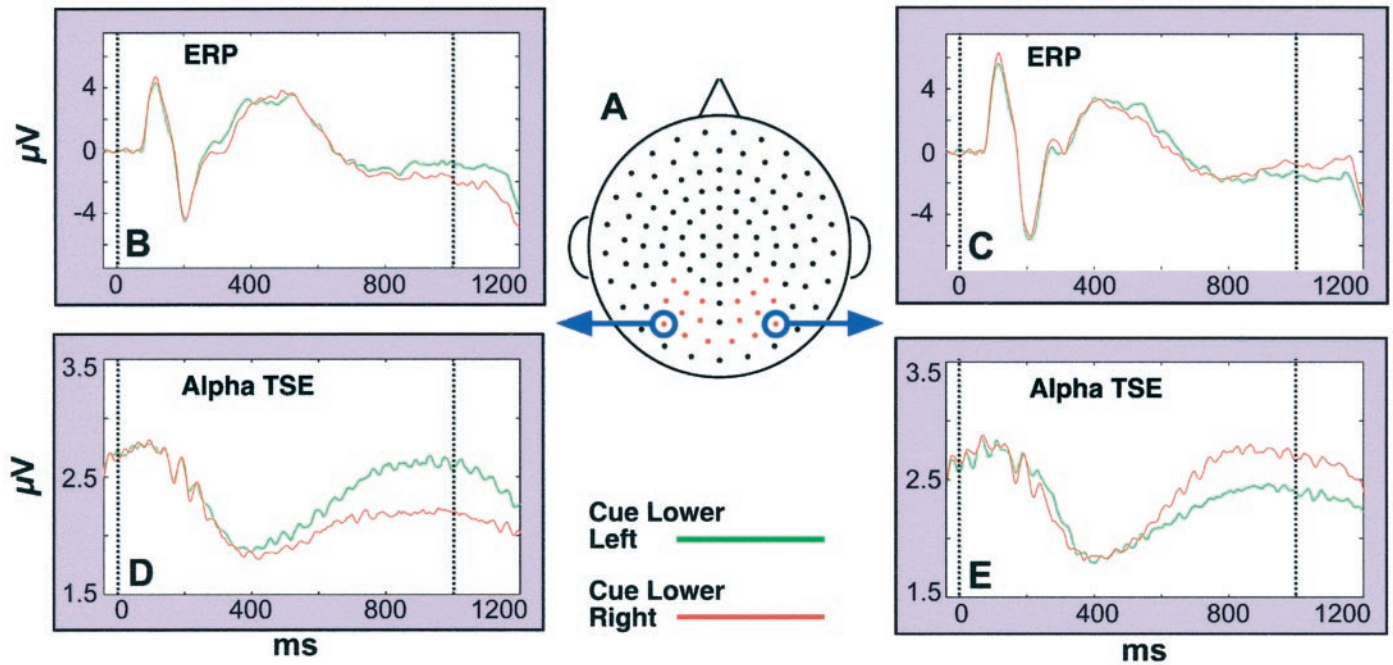


Figure 2. α -Band oscillatory activity is selectively modulated by spatially directing visual attention. *A*, Top view (nose at the top) of the concentric layout of the electrodes that are used to plot the topographic maps in Figure 3. Electrodes used for statistical analysis are shown in red. *B*, *C*, ERPs to the lower left and right cues (collapsed across motion and orientation trials) for two occipital electrode sites, averaged over 10 subjects. Data for attend lower left are plotted in green, and data for attend lower right are plotted in red. *D*, *E*, Corresponding α -band (8–14 Hz) TSE waveforms for the same electrodes. A sustained divergence in TSE amplitude is seen starting at \sim 500 msec, which depends on both the cued direction of attention and the side of recording. TSE amplitudes are larger over occipital cortex ipsilateral to the direction of attention.

different blocks. To investigate whether these processes might be differentially allocated depending on the nature of the expected stimulus, two types of stimuli were used: in orientation–discrimination blocks the stimuli were rotated Ts, which could be in any one of four orientations; in motion–discrimination blocks the stimuli were moving dots, which could move in one of four directions. At the beginning of each block, subjects were instructed which type of discrimination they were to perform (motion or orientation), where the stimulus locations would be (upper or lower visual field), and which of the four stimuli was the target for that block.

Recording. EEG recordings were from 128 tin electrodes, referenced to the nose. Data were digitally acquired at 500 Hz (pass band of DC, 100 Hz), impedances <10 K Ω , and interelectrode spacing \sim 2.4 cm. Eye position was monitored with electro-oculographic recordings from the external canthi. Trials with eye movements and large artifacts were rejected off-line.

Analysis. α -Band oscillatory activity was characterized in the cue–stimulus interval by the temporal spectral evolution (TSE) technique (Salmelin and Hari, 1994). TSE waveforms are computed by bandpass filtering (Butterworth zero phase, 8–14 Hz, 24 dB/octave) individual stimulus-locked epochs after artifact rejection, full-wave rectifying these filtered epochs, and then averaging. TSE provides a measure of α -band amplitude as a function of time. Filtering the data introduces a small degree of temporal spread (<100 msec), so the timing of α -related effects must be taken as approximate. Our electrode montage was constructed as a series of concentric rings centered at the vertex (see Fig. 2*A*). To assess topographic differences between conditions, a grid of electrodes was selected over posterior scalp regions, and “elevation” values were assigned to each electrode based on distance from the vertex, and “eccentricity” values were assigned based on distance from the posterior midline. A repeated measures ANOVA was performed on 18 electrodes located over the posterior scalp, which included these eccentricity and elevation values as independent factors.

RESULTS

Figure 2 illustrates the time course of scalp electrical activity at two posterior scalp sites when the direction of the arrow cue pointed left versus right and stimuli were presented in the lower

hemifield. For comparison, standard event-related potentials are shown in Figure 2, *B* and *C*. Initial activity to the cue is bilateral and unaffected by the direction of the cue. This is followed by a late sustained difference that is more negative contralateral to the cued direction that will not be discussed further here. Corresponding TSE waveforms, showing average α amplitude as a function of time for the same two electrodes, are shown in Figure 2, *D* and *E*. After a transient decrease in α -band activity lasting until \sim 400 msec, a large, sustained, cue-related difference in α -band activity is seen in the later portion of the epoch. This differential activity builds throughout a 400–500 msec period before the presentation of the stimulus, with α amplitude substantially larger over the scalp region contralateral to the to-be-ignored visual field. Additionally, well documented (Hillyard and Anllo-Vento, 1998) effects of attention were seen in the event-related potentials (ERPs) to the attended versus unattended stimuli, which were presented after the cue, with a bilateral enhancement of the stimulus-evoked N1 component to attended stimuli compared with unattended.

Topographic analysis reveals that the increase in α -band oscillatory activity related to preparatory attention has a focal distribution that is maximal over posterior occipital sites ipsilateral to the cued direction of attention, suggesting that its source corresponds to brain areas processing the unattended location. Figure 3*A–D* shows the topographic distribution of α -band activity averaged over the 250 msec before the onset of the impending stimulus. To illustrate the evolution of this effect over time, Figure 3*E* shows a series of topographic maps at different time points during the trial for one condition. A significant interaction between cue direction and hemisphere is seen over occipital electrodes ($F_{(1,9)} = 9.28$; $p < 0.05$). Importantly, there is also a

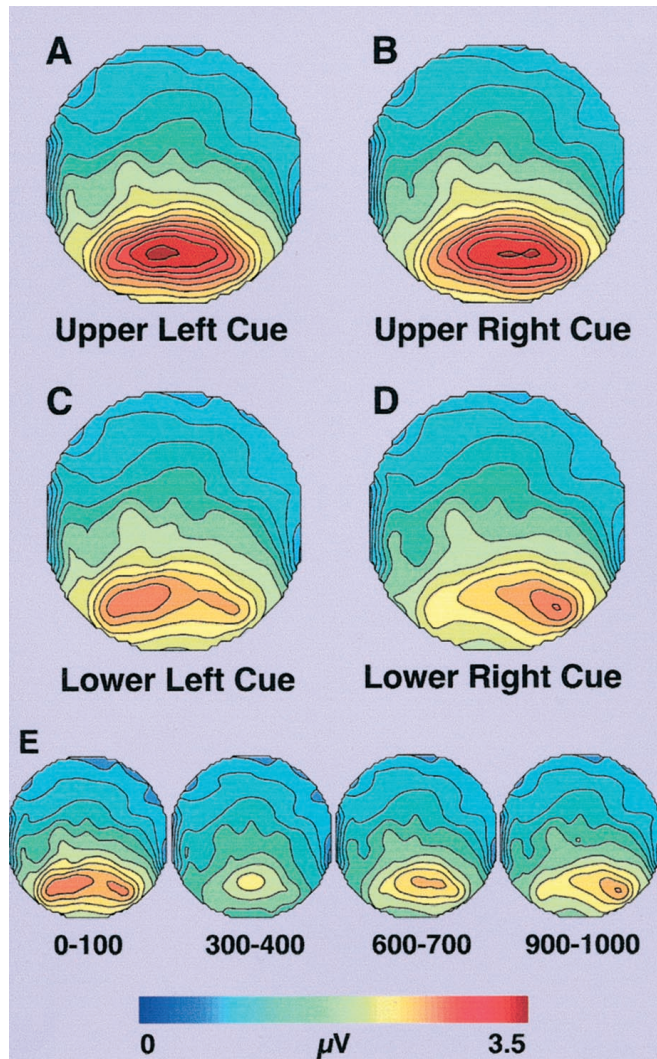


Figure 3. Cubic spline interpolated topographic maps for average TSE amplitude over a 250 msec window before onset of the stimulus (750–1000 msec after cue). *A, B*, Data for the upper left and upper right cues, collapsed over motion and orientation blocks. *C, D*, Data for lower left and lower right cues. Focal regions of increased α -band activity are seen ipsilateral to the cued side of attention. Foci are more ventral and lateral when attention is cued to the lower visual field relative to the upper visual field. *E*, Average TSE amplitude topographies for attend lower right trials for four 100 msec periods after cue.

significant shift in the topographic distribution of the α foci depending on whether attention was allocated in the upper or lower quadrants. The local increase in α -band activity moved more medially and dorsally when attention was allocated to upper visual field locations in contrast to lower visual field locations. A significant interaction was seen between visual field location (upper and lower) and electrode eccentricity ($F_{(2,8)} = 5.76$; $p < 0.05$), and a strong trend was seen for an interaction between visual field location and electrode elevation ($F_{(2,8)} = 3.46$; $p = 0.08$). A trend was also seen between electrode eccentricity and elevation ($F_{(4,6)} = 3.85$; $p = 0.07$), indicating that as the α foci moved to scalp positions farther from the midline, they also tended to move more dorsally. Neither the first-order interaction between task (motion or orientation) and electrode eccentricity nor that between task and electrode elevation was statistically significant. However, a significant three-way interaction was seen

among task, eccentricity, and elevation ($F_{(4,6)} = 4.95$; $p < 0.05$), which indicates that there may be differential involvement in feature-specific cortical areas depending on the expected features of an impending stimulus.

An amplitude difference was seen between upper and lower visual field presentations with larger values for the upper field stimulus locations ($F_{(1,9)} = 14.68$; $p < 0.005$). A large literature exists regarding perceptual asymmetries between upper and lower fields (see Previc, 1990), and these amplitude differences may reflect a difference in task difficulty, although evidence for this was not seen in the behavioral data. Behavioral accuracy was calculated as (number of hits – number of false alarms)/(number of hits + number of misses). A slight accuracy advantage was seen for left visual field presentation (two-tailed paired $t_{(9)} = 2.38$; $p < 0.05$). However, no accuracy differences were seen for upper versus lower field presentation ($t_{(9)} = 0.95$; NS) or for motion versus orientation blocks ($t_{(9)} = 1.48$; NS). In general, subjects reported finding the tasks difficult, and overall accuracy was ~80%.

To ascertain that effects seen in the TSE waveforms did not reflect broad-band activity nonspecific to α , a corresponding analysis was performed on the theta (3–7 Hz) band, and no effects of cue direction were seen. Examination of the late phase of the evoked responses to the cues (Fig. 2*B,C*) also shows no evidence of large evoked transients, which might contribute power in the α , as well as other, frequency bands.

DISCUSSION

The fact that the topography of the α -band increase is focal and that its scalp location shifts depending on whether attention is directed to upper or lower visual field locations as well as left or right indicates that at least some of the areas contributing to these effects are retinotopically mapped at the level of visual quadrants. This suggests an active process rather than a passive idling state of all visual regions other than those representing the attended location. In this paradigm there was a high (50%) likelihood of distractor stimuli occurring at noncued locations, and both cued and noncued locations were continuously marked on the screen. Therefore, it was to subjects' advantage to actively inhibit stimulus processing at noncued locations. Increased α levels over the hemisphere ipsilateral to the cued direction of attention suggest that cortical regions corresponding to the noncued spatial locations were involved in generating these effects.

α -Band activity has been associated with event-related decreases in cortical processing, including attention-related decoupling of parietal–occipital visual processing (Pfurtscheller et al., 1996; Vanni et al., 1997; Foxe et al., 1998). Based on the physiology of similar oscillations in animals, it has been suggested that α may be a functional gating mechanism (Lopes da Silva, 1991). A network of brain areas has been shown to be important for the generation of such rhythms, which includes parietal and occipital cortices and visual thalamic nuclei (Lopes da Silva, 1991; Lindgren et al., 1999). These same structures are central to many theories of visual attention (Posner and Petersen, 1990; Van der Heijden, 1991; LaBerge, 1997). One influential view of attention is the “biased competition” model (Desimone and Duncan, 1995). Under this view, multiple stimuli activate competing populations of neurons, and competition between populations may be biased in favor of behaviorally relevant stimuli by top-down attentional processes. Evidence for such biasing has been seen in the form of increased baseline neural firing rates (Luck et al., 1997) and increased hemodynamic responses (Kastner et al., 1999). In ad-

dition to enhancement of neural activity related to attended stimuli, such a bias could be implemented by suppression of competing stimuli. Our findings suggest that the focal α increases described here may be a signature of an inhibitory biasing process in the spatial domain in preparation for attentive processing of an expected stimulus at another location. In support of this proposition, a number of recent behavioral experiments have presented evidence that spatial locations containing attentionally irrelevant objects are actively inhibited (Watson and Humphreys, 1997; Cepeda et al., 1998).

In this study, the noncued location was always in a mirror-symmetric position across the vertical meridian from the cued location. It is possible that the effects described reflect collosally mediated competitive interaction between hemispheres, which has some retinotopic specificity. In this case, the increased α over one hemisphere would be a byproduct of the deployment of attention in the opposite hemisphere. The results of Foxe et al. (1998) argue against this interpretation, because relative α increases were seen over parietal-occipital cortex when subjects prepared to attend to the auditory modality. Presumably in that case, there would be no visuotopically specific attentional increases that would result in focal α increases elsewhere.

Examination of TSE time courses (Fig. 2) indicates the presence of relatively high "baseline" α in the precue period. It is possible that the differential effects that we report represent a general suppression of α after cue presentation followed by return to baseline α levels in cortex corresponding to nonattended locations and a continued suppression of α activity in cortex corresponding to attended locations. Although we contend that the focal, ipsilateral nature of the regions of increased α activity, combined with the topographically distinct distributions corresponding to different retinotopic stimulus configurations, argue against this interpretation, we cannot explicitly rule this out. It is important to note, however, that the theoretical role of α as an index of suppressive attentional gating specifically predicts high levels of α activity in the baseline period for this paradigm. Our attention-directing cues were very briefly presented (35 msec), were isoluminant against their immediate background, and occurred unpredictably in time. Subjects, therefore, had to be in a state of high focal attention at fixation to detect the direction of the arrow cues. Therefore, it is likely that the high levels of α activity in the baseline period correspond to attentive suppression of extrafoveal regions of visual space as a consequence of directed foveal attention. Supporting this, a metabolic tracing study in monkeys showed suppressive effects peripherally to a centrally presented stimulus (Vanduffel et al., 2000). The sequence of topographic maps in Figure 3E showing the distribution of α at different points during the trial also appears to support this position: a bilateral distribution early in the trial, followed by a general suppression, then a developing α focus over cortex corresponding to the to-be-ignored stimulus.

Differences in the α -band effects that were related to the type of stimulus to which the subjects were preparing to attend were weak and difficult to interpret in the context of a three-way interaction among stimulus type, electrode eccentricity, and electrode elevation. In the context of the much more robust effects seen related to the direction of attention and the vertical hemifield in which the stimuli were presented, this suggests that the biasing process reflected in the focal α increases is generated primarily in relatively early sensory regions, before the segregation of perceptual information into the dorsal and ventral streams that have been associated with the processing of spatial informa-

tion and object recognition, respectively (Ungerleider and Mishkin, 1982). It has been previously predicted on the basis of modeling that attentional suppression may be expected to operate predominantly at earlier stages of visual processing (Posner and Dehaene, 1994).

It has been shown that sustained allocation of attention in one sensory modality can result in deactivation of regions associated with another sensory modality (Haxby et al., 1994; Fiez et al., 1995; Kawashima et al., 1995; Foxe et al., 1998). Within the visual modality, directing attention to a word-parsing task results in decreased processing of unrelated motion stimuli (Rees et al., 1997), and suppressive effects have been shown in foveal extrastriate regions during sustained visuospatial attention (Tootell et al., 1998). Our results indicate that targeted inhibitory processes, indexed by increased α -band oscillatory activity, can be directed to specific regions of space and that these processes may be deployed before the onset of distractor stimuli at these locations.

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