We examined gamma-band magnetoencephalographic (MEG) activity in humans manipulating attention to visual stimuli by auditory distractors. After exposure to both visual and auditory noise (a baseline), subjects attended to the first of two stimuli (either regular motion of bars or a tone sequence) presented asynchronously, and responded to its offset. A spectral power analysis revealed an increased, relative to baseline, 40 Hz MEG response to attended coherent motion. The enhancement occurred within the initial 50–250 ms from motion onset over modality-specific (occipital) cortices. The increase was not observed when attention was captured by auditory distractors. Our findings suggest that 40 Hz activity in the human visual cortex is related to integration of featural information that is supported by attention.

Key words: Attention; Feature binding; Gamma-band; Human cortex; Magnetoencephalography; Vision

Introduction

Current research views the high-frequency cortical oscillations as subserving feature-binding mechanisms for processing of coherent stimuli [1–5]. In the visual modality, for example, a stronger enhancement of gamma-band EEG activity was found to a real and an illusory Kanizsa triangle than to a similar non-coherent configuration [6–8]. The task used (silent counting of a curved Kanizsa triangle), however, favored a subject’s attention to coherent stimuli over the apprehension of a non-coherent figure. Therefore, the increase in the γ range might relate to stimulus coherency that is supported by attention.

Cortical γ-band activity was also suggested to reflect attentional mechanisms [9–11]. For instance, an enhancement of the auditory 40 Hz EEG response occurred in humans who attended to single tones presented in one ear while discarding concurrent tones in the other [12]. However, attention was not varied between coherent stimuli.

In the present study, we examined γ-band MEG activity manipulating attention to visual coherent motion of bars by auditory distractors. Passive observation of such regularly moving bars was reported to alter the 40 Hz EEG power [13]. In this experiment, following exposure to both visual and auditory noise, we had subjects attend to the first of two stimuli (either visual motion or a tone sequence) presented asynchronously. The patterns of motion were identical in the attended and unattended conditions. We hypothesized that if γ-band activity underlies attention-related processing of a coherent stimulus, then the 40 Hz MEG response to identical regular motion will be stronger in the attended than in the unattended conditions.

Materials and Methods

A visual stimulus was represented as an array of horizontal bars (8.5 × 0.5° each or 13.5 × 0.7 cm viewed from 90 cm; luminance 60 cd/m²) moving coherently downwards at a velocity of 3 deg/s either in the upper or lower half of the screen (50 × 42°). Visual dynamic noise (irregular displacement of the bars) was simultaneously presented in the other half of the screen. For baseline recording, visual noise was presented over the whole screen. With both visual noise and coherent motion, the bars appeared at random locations at a rate of 25 Hz (a bar was
shown for 40 ms and then abruptly changed its position). Their average density was 10 bars per 4.5° area. An auditory stimulus (distractor) was represented as a sequence of two alternating tones (with frequencies 300 and 1000 Hz). It was applied binaurally through earphones with intensity 60 dB SPL (single tone duration 60 ms, ISI = 0 ms). For baseline recording, auditory white noise of the same intensity was used.

Twelve (seven male and five female) healthy right-handed paid subjects (aged 22–36 years) with normal vision and hearing participated. An informed written consent was obtained from each of them.

Each subject sat in a dark shielded chamber with her or his head placed inside a helmet-shaped MEG dewar; they fixated their eyes on a cross in the middle of the screen. On each trial (Fig. 1) subjects were simultaneously presented with both visual dynamic noise and auditory white noise. Following a 800–1200 ms interval, in half the trials the visual noise was replaced (for 700–1100 ms) by regular motion of bars. After 500 ms from visual motion onset, a tone sequence appeared. In the other half of the trials, the auditory stimulus occurred first. Trials with the visual stimulus or auditory distractor presented first were randomized. The overall trial duration varied between 1.9 and 2.7 s. Each run lasted 8–10 min: 200 trials and 24 breaks (of 3 s each) for eye movements.

On each trial, subjects had to accurately determine whether the visual or auditory stimulus appeared first. They attended to the first stimulus, monitored it as fast as possible to its offset. Subjects triggered a light barrier signal by lifting either a forefinger (to the visual stimulus) or a middle finger (to the visual one). Response upon stimulus offset eliminated an influence of movement on cortical activity. All subjects responded with their right hand.

MEG responses were collected using a whole-head 151-channel MEG system (CTF Systems, Inc.) with a sampling rate of 312.5 Hz in the frequency range 0–100 Hz. A baseline was recorded within 200 ms prior to onset of a stimulus that was presented first in a trial. The whole epoch length was 2.350 s. Vertical eye movements were monitored by EEG/EOG-recording from the left eye (impedance <5 kΩ). Artifact-free trials with correct behavioral responses (eye movements less than ±100 μV, without a response within the stimulation interval) were entered for data processing.

The slow MEG activity was quantified with dipole fits. Spectral amplitude analysis of MEG responses was performed using Welch windows of 200 ms duration. In the attended conditions, this window was applied from 50 ms after onset of a first stimulus, and in the unattended conditions, from 550 ms from its onset (because of the 500 ms stimulus asynchrony; Fig. 1). Differences in the amplitude spectra were assessed by statistical mapping based on paired t-tests for the group of subjects. The t-values were converted into Z-values. A data point was considered significant if the mean of two consecutive Z-values met the significance criterion. The MEG channels with significant effects in the maps were further evaluated by amplitude demodulation in the γ-band. A non-causal Gabor (Gaussian curve shaped) filter in the frequency domain with a center frequency of 40 Hz and a width of ±5 Hz was used. To calculate amplitude demodulation, we applied a Hilbert transformation. The differences in the strength of dipole sources and in the averaged magnitudes of MEG γ-band activity were assessed by two-way ANOVAs with factors visual field (upper, lower) and condition (attended, unattended).

Results

Onsets of the visual coherent and acoustic stimuli evoked an increase in MEG activity that was sustained for the whole stimulus duration. The group means of MEG responses were described by two bilateral dipoles found near the auditory areas and one in the visual area. Figure 2 shows the time courses of the dipole strength when coherent motion was delivered to the lower visual field. These three dipoles explain >90% of the variance in MEG activity within 0.2–1.0 s from onset of the first stimulus. The mean strength of visual dipole source did not differ significantly in the attended (0.1–0.5 s) and unattended (0.6–1.0 s) conditions (Fig. 3, right panel); no difference was found between the upper and lower visual fields.

For different types of trials, a spectral amplitude of MEG traces was averaged across subjects. In the
attended conditions, coherent motion evoked a significantly increased, relative to baseline, \(\gamma\)-band (40 Hz) MEG response over the right occipital areas \((p < 0.02\) for the lower and \(p < 0.07\) for the upper visual fields; Fig. 4). The enhancement was topographically distinct, occurring in the modality-specific visual cortical areas. In the frequency range 10–70 Hz, no other significant effects were found. The reliable enhancements of \(\gamma\)-band response were observed within the initial 50–250 ms from visual motion onset.

Averaged individual values of \(\gamma\)-band amplitude of MEG signal filtered in the frequency range 35–45 Hz were submitted to two-way ANOVA with factors visual field (upper, lower) and condition (attended, unattended). The results revealed a highly significant main effect of condition \((F(1,11) = 23.5, p < 0.001;\) Fig. 3, left panel) and a barely significant effect of visual field \((F(1,11) = 5.2, p < 0.04)\). Interaction of visual field \(\times\) condition was not significant \((F(1,11) = 0.1, p = 0.8)\).

For two visual fields together, in the attended conditions we found a significantly enhanced \(\gamma\)-band MEG response \((t(11) = 4.17, p < 0.002)\). In the unattended conditions, however, the \(\gamma\)-band response to regular motion did not differ from baseline \((t(11) = 0.57, p = 0.6)\).

**Discussion**

Attention-related changes of \(\gamma\)-band over the modality-specific cortices: Our findings provide clearcut support for the expectation that visual coherent stimuli supported by task-driven attention lead to an increase in \(\gamma\)-band MEG activity. In the attended conditions we found an enhanced 40 Hz component within 50–250 ms from onset of coherent visual stimuli. It occurred over the modality-specific occipital cortical areas (Fig. 5) and was locked to stimulus onset. When the same coherent stimulus was neglected in favor of a heteromodal distractor, no enhancement of the \(\gamma\)-band MEG response was observed. These findings correspond to the Tallon et al. [6–8] data obtained using EEG. They reported an enhancement in \(\gamma\)-band activity to coherent stimuli, attention to which was directed by the task. In visual search, the attention-demanding conditions also produced a globally increased EEG \(\gamma\)-response to a static camouflaged pattern of the Dalmatian dog [14].

Until now, however, attention has not been varied between identical coherent stimuli. By manipulating attention we found that only an attended pattern of...
visual motion increased γ-band MEG activity. Furthermore, our recent findings indicate that when a task requires attention to both a point-light walker and a similar non-coherent noise, only the coherent pattern evokes an enhancement in γ-band MEG activity [15]. The results, therefore, demonstrate that γ-band activity recorded in MEG is sensitive to coherency of visual stimuli.

For a better understanding of the interrelationship between feature-binding and attentional mechanisms in modulation of γ-band activity, one has to vary both stimulus coherency and allocation of attention. Currently, we are implementing a double dissociation of these factors, comparing MEG traces in the γ range for an attended coherent and an unattended non-coherent stimulus.

Specificity of the enhancement to γ-band: Visual coherent motion elicited low-frequency event-related MEG activity both in the attended and unattended conditions (Fig. 2; Fig. 3, right panel). Significant enhancement of the high-frequency (γ) component that accompanied this slow activity was observed only in the attended conditions (Fig. 3, left panel). This suggests that the effects of attention are specific to γ-band. A transiently enhanced γ power was found rather early, within the initial 50–250 ms of visual motion onset, whereas the visual dipole strength substantially increased at a longer latency of about 200 ms, remaining nearly constant for the whole stimulus duration (Fig. 2, upper panel). Therefore, the low- and high frequency components of MEG response might originate from distinct neural oscillatory sources (see also [14]).

In both the attended and unattended conditions, visual stimulation within a trial was delivered consistently. Instead of stimulus appearance after a blank screen, onset of coherent motion was always preceded by irregular displacement of bars. Changes in recorded overall MEG activity to regularly moving bars, therefore, were not determined simply by appearance of visual stimuli.

In conclusion, manipulating attention to visual regular stimuli by auditory distractors we find an increased 40 Hz MEG activity to coherent motion in the attended conditions. This increase of evoked MEG γ response occurred within 50–250 ms of motion onset over the occipital cortical areas. However, when attention to the same coherent motion was distracted by a heteromodal (auditory) stimulus, no enhancement in the γ range was observed. The effect of attention is specific to the γ-band MEG response, because the lower-frequency activity increased in both conditions while the enhanced high-frequency component was found only in the attended one. Our findings suggest that 40 Hz activity may be generated by neural mechanisms responsible for integration of sensory information that is supported by attention.

References

ACKNOWLEDGEMENTS: The study was supported by Deutsche Forschungsgemeinschaft (SFB 307/B1). We thank John Baird for valuable comments on an earlier version of the manuscript, and Jürgen Dax and Slavica Coric for technical assistance.

Received 22 April 1999; accepted 4 May 1999