Attentional Modulation of Cortical Neuromagnetic Gamma Response to Biological Movement

Processing of biological motion represented solely by a set of lights on the joints of a human body is traditionally viewed as largely independent of attention. Here, by manipulating attention-related task demands, we assess changes in the neuromagnetic cortical response to a point-light walker. Irrespective of task demands, biological motion evokes an increase in oscillatory gamma activity over the left parieto-occipital region at 80 ms post-stimulus. Only an attended walker, however, yielded further peaks over the right parietal (120 ms) and temporal (155 ms) cortices. By contrast, the magnetoencephalographic (MEG) response to an ignored walker is restricted to the left parieto-occipital region. In addition, peaks in oscillatory activity occur in response to both attended (canonical and scrambled) configurations at 180–200 ms from stimulus onset over the right fronto-temporal regions, most likely reflecting maintenance of the target configuration in working memory. For the first time, we demonstrate that the time course and topographic dynamics of oscillatory gamma activity in response to biological movement undergoes top-down influences and can be profoundly modulated by the withdrawal of attention.

Keywords: biological movement, magnetoencephalography, oscillatory gamma brain activity, point-light walker, task-driven attention, time course, topography

Introduction

The visual system is exquisitely tuned to biological motion represented solely by a set of dots attached to the main joints of an otherwise invisible human body. In both healthy perceivers and patients, point-light stimuli have proven to be a valuable tool for exploration of the brain capacity to integrate the local motion of dots into a cohesive percept (Johansson, 1973; Pavlova and Sokolov, 2000; Tadin et al., 2002; Fine et al., 2003; Grossman et al., 2004; Thornton and Vuong, 2004; Vaina and Gross, 2004; Watson et al., 2004). Early studies proposed that point-light biological motion attracts attention automatically, independent of intention or of the current task, but recent psychophysical work has led to a revision of this idea (Cavanagh et al., 2001; Thornton et al., 2002; Battelli et al., 2003). Functional brain imaging indicates the engagement of parietal cortical regions, the amygdala and the lateral cerebellum in processing point-light displays (Bonda et al., 1996; Grèzes et al., 2001; Vaina et al., 2001). These regions are also recruited in deployment of visual attention (Kastner and Ungerleider, 2000). Here we ask whether and, if so, how the pattern of cortical activity in response to point-light biological motion is affected by the withdrawal of attention. To this end, we analyzed the time course and topography of the oscillatory neuromagnetic brain response recorded during performance of attention-demanding tasks with biological motion displays.

Binding of widely spread cell assemblies by synchronizing their high-frequency oscillatory activity (20–80 Hz) is thought to underlie cohesive stimulus representation in the human brain. In accord with this assumption, changes in gamma electroencephalographic (EEG) and magnetoencephalographic (MEG) activity have been considered as indicators of processing Gestalt-like patterns (e.g. Keil et al., 1999; Rodriguez et al., 1999; Bertrand and Tallon-Baudry, 2000; Herrmann and Mecklinger, 2000). In recent years, however, evidence has accumulated to suggest that both evoked (phase-locked to stimulus onset) and induced (non-phase locked) gamma response may be profoundly affected by task-driven attention (e.g. Tiitinen et al., 1993; Gruber et al., 1999; Sokolov et al., 1999; Haenschel et al., 2000; Engel et al., 2001; Yordanova et al., 2002; Debener et al., 2003; Müller and Keil, 2004; Sokolov et al., 2004; Tallon-Baudry et al., 2005). Active visual search for a camouflaged target, for example, leads to an increase in the gamma response (Tallon-Baudry et al., 1997). Previously, we showed that when a task requires attention to both a point-light biological motion and a similar moving noise, only a point-light walker elicits a specific pattern of enhancements in the evoked gamma MEG response (Pavlova et al., 2004). For a better understanding of the relationship between feature integration and task-driven influences in modulation of oscillatory gamma activity, in the present work we manipulated both stimulus coherence and attention-related task demands. Healthy volunteers were presented with a canonical point-light walker and a scrambled configuration for which spatial positions of dots were randomly rearranged on the screen so that the display lacked the implicit spatial structure of a canonical figure. In two separate runs, we had participants respond to the third identical, either canonical or scrambled, point-light configuration in a randomized set of both types of stimuli while ignoring the stimuli of the other type (for details, see Experimental Design).

Material and Methods

Participants

Fourteen (seven females) paid right-handed volunteers, aged between 20 and 32 years, with normal or corrected-to-normal vision participated in the study. None had a history of neurological or psychiatric disorders. Informed written consent was obtained in accordance with the requirements of the Ethical Committee of the Faculty of Medicine at the University of Tübingen.

Stimuli

Two types of computer-generated point-light configurations were used. A canonical point-light walker consisted of 11 dots attached to the head and main joints (ankles, shoulder, etc.) of an otherwise invisible human body moving as if on a treadmill (with no net translation), in a sagittal view, facing right (Fig. 1b). A gait cycle was completed in 40 frames with...
frame duration of 31 ms that produced a walking speed of ~48 complete cycles per minute. The scrambled configuration contained the same number of dots moving as if attached to the joints of the canonical figure. The spatial locations of dots on the screen were randomized in such a way that the resulting display lacked the implicit coherent structure of a canonical figure (Fig. 1c). The motion of each point of the scrambled configuration matched the motion of one of the points defining the canonical figure. The size, luminance, velocity and phase relations of the moving dots also remained unchanged. The figures were created by Cutting's algorithm (Cutting, 1978). Both configurations subtended a visual angle of 9° in height and 6° in width.

**Experimental Design**

In two separate sessions, participants were presented with a randomized set of 200 stimuli with an equal number of stimuli of both types (100 canonical and 100 scrambled). They were asked to lift their right forefinger after the offset of the third identical either canonical (in one run) or scrambled (in the other run) configuration while ignoring stimuli of the other type. This movement triggered a light barrier signal in a response box. For example, in a string of stimuli W (walker) and S (scrambled) (WWSWWSWWSWWSWWSWWSW), asterisks designate the requested points of the responses to the canonical walker. Participants had no explicit identification task. Instead, they were asked about their visual impressions only after the recording session was completed. The order of runs was counterbalanced across subjects. Participants visually fixated a gray cross in the middle of the screen that was seen during the entire run. The stimulus appeared for 650 ms on a blank screen with an inter-stimulus interval that varied randomly between 2.5 and 3 s. For each participant we calculated the miss rate as the ratio of the number of failures to respond to the third stimulus to the total number of required responses (~33 per participant and per run). Similarly, for the false alarm rate, the number of false alarms was divided by the total number of trials in which this type of error might occur.

**MEG Recording and Data Analysis**

A participant was seated in an electromagnetically shielded chamber (Vakuum-Schmelze, Hanau, Germany). The cortical responses were recorded with the whole head MEG system (CTF Systems, Inc.; Vancouver) consisting of 151 hardware first-order magnetic gradiometers distributed with an average distance of 3 cm between the sensors. The signals were sampled at a rate of 312.5 Hz in the frequency range of 0–100 Hz. A baseline was recorded during a pre-stimulus duration of 300 ms. Participants were instructed to blink only during inter-trial intervals. Vertical eye movements were monitored by EOG/electro-olfactogram recording from the left eye (impedance was kept below 5 kΩ). Both at the beginning and at the end of each recording session, the participant’s head position was determined with three localization coils fixed at the nasion and the preauricular sites. Sessions with head movements exceeding 0.5 cm were discarded. Each MEG recording session lasted 10–12 min. The entire experimental session including the preparatory period, instructions, familiarization, and recording took ~1.5 h per participant.

All epochs of MEG activity were first automatically and then manually inspected for artifacts. Epochs containing blinks or eye movements (> ±100 μV) were rejected. The only trials analyzed were those for which a motor response was not required by the task. This procedure eliminates the influence of motor activity on recorded MEG traces (Kristeva-Feige et al., 1993). If a participant failed to respond to the third identical attended stimulus, all trials from the last correct response were discarded. We also discarded trials between the second and third attended stimuli. The reasons for this were twofold. First, it avoids a possible influence of readiness in responding that could potentially affect gamma-range activity in unattended trials. It has been shown that holding an object representation in visual working memory can facilitate posterior and frontal gamma activity (Tallon-Baudry et al., 1997, 1998, 1999; Bertrand and Tallon-Baudry, 2000; Howard et al., 2003). Second, this procedure ensures that an equal number of trials enter the averages for all types of displays. On average, therefore, a total of 61.8 ± 1.0 artifact-free trials were analyzed for each type of stimulus and each participant. For instance, for attended stimuli and for each participant, 100 trials (in each run) minus 33 trials (with motor responses) minus incorrect responses (misses and false alarms) and discarded artifacts (trials confounded with eye movements) gives the above number of artifact-free trials. The evoked oscillatory response was analyzed primarily because it makes the findings comparable with those from our earlier MEG study with biological motion (Pavlova et al., 2004).

For determining the frequency bands that exhibit significant changes in stimulus-related neuromagnetic activity relative to baseline, we first conducted a broad-band spectral power analysis of the averaged artifact-free MEG traces for each type of stimulus in the attended and unattended conditions. This analysis was done using 200 ms epochs ranging from 300 to 100 ms (pre-stimulus) at baseline and from 0 to 200 ms post-stimulus onset. After the frequency bands with significant changes in MEG activity were detected, a narrow-band analysis was conducted for these specific frequency bands. Because the broad-band analysis revealed the mostly significant increase in spectral amplitude at frequencies of ~25 Hz, an acausal Gaussian shaped Gabor filter with a center frequency of 25 ± 5 Hz was applied separately over the entire epochs of 300 ms pre- and 650 ms post-stimulus onset. To assess the time course of the narrow-band MEG activity, we performed amplitude demodulation of the filtered MEG records using a Hilbert transformation. For elimination of baseline distortions caused by these procedures, the baseline epoch was restricted to 200 ms (from ~200 to 0 ms) pre-stimulus onset. The significance of the observed spectral power values for each frequency bin and MEG sensor was tested using a statistical probability mapping approach based on permutation tests that include corrections both for multiple comparisons and for possible correlations between data either from neighboring frequency bins (for spectral analysis) or time points (for time course analysis). This procedure is described in detail elsewhere (Lutzenberger et al., 2002). For assessment of the cortical topography of significant changes in spectral amplitude, we used a common coil system. For each participant, the sensor positions were assigned to common spatial sensor coordinates of one representative subject, and the spatial locations of changes in spectral amplitude were determined on the 2-D brain model derived from this participant’s structural magnetic resonance imaging (MRI) scan. The reliability of the common coil system for the purposes of the present study, in which the exact source localization was beyond the focus of interest, has been established earlier (for detailed description, see Kaiser et al., 2002; Lutzenberger et al., 2002). The localization errors introduced by employing the common coil system, as opposed to the individual sensor locations, were within the range of spatial resolution determined by the spacing of sensors in the MEG system.

**Results**

**Performance and Stimulus Recognition**

Participants performed the task with great accuracy; they responded to the third stimulus of each type (either canonical
Inspections of the statistical probability maps (Fig. 2) showed that both attended and ignored canonical walkers evoke a significantly increased lower gamma-band (25-30 Hz) MEG activity over the left parieto-occipito-temporal junction ($t > t_{\text{crit}} = 4.74$). For both attended and ignored canonical walkers, these peaks in oscillatory response were observed as early as 80 ms after stimulus onset. The ignored and attended scrambled configurations did not evoke any early increases in oscillatory gamma activity over the modality-specific brain regions.

Attended and ignored canonical walking figures yield different topographic and temporal dynamics of gamma-range activity (Fig. 2a,b). For the attended walker only, two further consecutive increases in gamma activity occurred over the parietal (at 120 ms) and right temporal (at 155 ms from stimulus onset) cortical areas ($t > t_{\text{crit}} = 4.77$). For the ignored walker an enhancement in evoked oscillatory response was topographically restricted to the left tempo-occipito-parietal junction ($t > t_{\text{crit}} = 4.74$), and attenuated by 180 ms. Figure 3 shows the evoked magnetic fields in response to attended and unattended scrambled configurations. The topography and magnitude of the neuromagnetic response did not substantially differ between these displays. Most important, in the range from 80 to 180 ms we did not find any increases in the gamma oscillatory activity in response to the scrambled displays.

For both attended scrambled and canonical configurations, the peaks in gamma activity occurred in the latency range from 190 to 200 ms over the right fronto-temporal region (Fig. 4a,b). The peak in the oscillatory response to the attended walker occurred at 40 Hz, whereas the response to the scrambled configuration peaked in the lower gamma range at 25 Hz. These peaks of activation were absent in response to both ignored configurations. Analysis of the low frequency (<20 Hz) oscillatory activity and the slow neuromagnetic responses indicated that the effects pertain to the gamma frequency range.

**Oscillatory Gamma-range Activity**

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**Discussion**

By manipulating attention-related task demands, we assessed changes in the evoked oscillatory MEG activity in response to a point-light walker and a similar scrambled configuration that lacked an explicit coherent structure of a canonical figure. The data indicate that both attended and ignored point-light walkers evoke early enhancements in the oscillatory cortical response in the lower gamma-band range (25 Hz) peaking at 80 ms post-stimulus onset. Irrespective of task demands, therefore, a canonical point-light figure yields an early increase in gamma activity. Both attended and ignored scrambled configurations do not elicit any changes in early oscillatory gamma activity over the occipito-parietal regions. These findings correspond to previous data (Pavlova et al., 2004) inasmuch as the early evoked gamma response (80-100 ms) exhibits sensitivity to spatial coherence revealed through biological motion. In this earlier work, the peaks in gamma activity were found in
response to both upright and inverted 180° in the image plane point-light walkers, but not to the scrambled configurations. Notably, in that study both upright and inverted point-light figures were attended. The present data show that even when the task requires the participant to ignore the canonical walker, an early posterior peak in oscillatory cortical response accompanies processing of point-light biological motion. This finding suggests that, although both theoretically and experimentally it appears obvious that attentional resources are required in order to join features or elements into a cohesive percept (Corbetta et al., 1995; Treisman and Kanwisher, 1998; Robertson, 2003), integration of elements may occur despite the task demands to ignore a moving point-light configuration.

Only an attended walker, however, evokes two further consecutive peaks in the gamma response (25 Hz) over the right parietal (120 ms) and temporal (155 ms) cortices. The remarkable similarity in the time course and topography of the pattern of evoked gamma activity in response to the attended point-light walker with our earlier data (Pavlova et al., 2004) obtained with a different (one-back repetition) task and an independent group of participants confirm the robustness of the present findings. These findings agree with, and further illuminate, single cell data indicating that neurons in the macaque superior temporal polysensory area (STPa) rapidly (within 100 ms from stimulus onset) respond to biological motion (for reviews, see Puce and Perrett, 2003; Jellema et al., 2004).

By contrast, the response to the ignored walker is topographically restricted to the left parieto-occipital area. Thus, attended and ignored canonical walkers elicit topographically and temporally distinct patterns of evoked oscillatory gamma MEG activity. One of the important outcomes of the present work, therefore, is that it provides the first direct evidence for the role of visual attention in cortical processing of point-light biological movement.

Although perception of point-light stimuli is traditionally thought to be a kind of ‘pop-out’ phenomenon which is considered the hallmark of pre-attentive processing, recent psychophysical data suggest that the integration of moving dots

Figure 3. Evoked magnetic fields in response to (a) an unattended, UAN, and (b) an attended, AN, scrambled (noise) configuration at latencies of 100, 120 and 155 ms. In the latency range from 80 to 180 ms there were no significant changes in the oscillatory gamma activity in response to unattended and attended scrambled displays. The x-axis shows the time course of a trial with stimulus onset at 0 s and the y-axis represents the magnitude of the neuromagnetic response in fT.
The brain areas involved in biological motion processing are currently being intensively explored by neuroimaging techniques such as positron emission tomography (Bonda et al., 1996; Ptito et al., 2003) and, especially, functional magnetic resonance imaging (fMRI; Grossman et al., 2000, 2004; Vaina et al., 2001; Grossman and Blake, 2002; Servos et al., 2002; Beauchamp et al., 2003; Pelphrey et al., 2003). The right superior temporal sulcus, the intraparietal cortex, and the lateral occipital complex (primarily the regions corresponding to the kinetic occipital area) are often reported to be activated during viewing of point-light biological movement (for reviews, see Giese and Poggio, 2003; Puce and Perrett, 2003). However, other brain regions, such as the amygdala, the lateral and medial cerebellum, the lingual gyrus at the cuneus border, the occipital and fusiform face areas, and the frontal regions, also exhibit an increased gradient of activation in response to biological motion displays. These studies are restricted to localization of areas that show an increased blood-oxygenation-level-dependent activation, and fail to uncover the fine changes in brain activity unfolding over time. Moreover, it is remarkable that the fMRI findings on point-light biological motion are not congruent, and the areas of activation do not entirely overlap (e.g. Servos et al., 2002).

It appears that the topographic pattern of activation is strongly affected by attention-related task demands. Even in the same subjects, both the magnitude and the topographic pattern of fMRI activation in response to a point-light walker are colored by the attention-related task requirements (Vaina et al., 2001). The present work is the first showing that the withdrawal of attention can profoundly modulate the time course and dynamic topography of oscillatory neuromagnetic cortical activity in response to biological movement.

The other important finding is that, when attended, both canonical and scrambled configurations elicit enhancements in gamma activity over the right fronto-temporal regions in the latency range between 180 and 200 ms post-stimulus onset. The peak in oscillatory response to a meaningful point-light walking figure was found at 40 Hz, whereas the scrambled configuration was accompanied by an enhancement in the oscillatory response in the lower gamma range (25 Hz). These increases in gamma activity were absent in response to both unattended canonical and scrambled configurations, and therefore most likely reflect task-dependent rehearsal of the events in working memory. The present findings dovetail with the data obtained by other research groups. Involvement of prefrontal and frontal regions has been repeatedly reported in short-term memory processes in monkeys and in humans (Goldman-Rakic, 1996; Ungerleider et al., 1998; Munk et al., 2002; Baeg et al., 2003; Compte et al., 2003; Curtis and D’Esposito, 2003). Furthermore, recent EEG and MEG data point to specific frontal increases in gamma-range oscillatory activity that are related to visual (Tallon-Baudry et al., 1997, 1998, 1999; Howard et al., 2003) and auditory (Lutzenberger et al., 2002; Kaiser et al., 2003) working memory load. For example, by using contour figures in a delayed-matching-to-sample task, a boosted gamma activity was found to correspond to the rehearsal of stimulus representation in working memory (Tallon-Baudry et al., 1998). Here, we showed that enhancements in gamma activity in response to both visual events (canonical and scrambled biological motion) occur only when the task requires a response to this particular event with a time delay, and there is therefore a need to maintain for some time the memory trace across trials. Although the task-driven enhancements of oscillatory gamma activity...
over the frontal areas are observed for both a point-light walker and a scrambled configuration, the peak of activity in response to a meaningful scrambled configuration occurs at a lower frequency than for biological motion, and therefore these peaks appear to be stimulus-specific. This assumption agrees well with macaque single-cell results demonstrating that activity of prefrontal neurons reflects processing of the sensory attributes of a remembered stimulus that allows for flexibility in the outcome of a mnemonic process (Constantinidis et al., 2001).

Taken together, the findings suggest that, irrespective of task-driven shifts of attention, early evoked gamma activity reflects stimulus coherence resulting from biological motion. The time course and topography of subsequent gamma responses to point-light biological motion undergo top-down influences, and can be profoundly modulated by task-driven attention. Furthermore, the memory-related peaks of gamma-range activity found over the fronto-temporal regions appear to exhibit stimulus specificity.

Notes

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