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THE present study was based on earlier findings that the observation of a coherently moving long bar induced gamma-band activity in humans. The power in the EEG-gamma-band was reduced during the presentation of two incoherently moving short bars. The present study demonstrates the replicability of this cortical activity pattern and illustrates intersubjective variability in its topography. In addition, cortical alpha-activity was examined to test whether gamma-band activity might reflect changes in harmonics of alpha waves. Results indicate that induced gamma-band activity cannot be secondary to changes in the amplitude of alpha waves, since the latter would require both a similar time course of both frequency bands while stimuli are in motion and an identical topographical pattern. The present results suggest that oscillations in the gamma- and the alpha-bands are two different brain activities, with different functional implications.

Key words: Alpha; EEG; Induced gamma; Motion processing; Visual cortex

Visually induced gamma-band responses to coherent and incoherent motion: a replication study

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Introduction

It is widely agreed that the analysis of a stimulus is not only achieved through hierarchical processing stages but also through parallel processing. This is particularly obvious for a visual stimulus whose features, such as shape and color, are processed in different regions of the visual cortex. Hence, neurons in distributed processing areas must be connected in some way to form the physiological substrate of the percept. It has been proposed that synchronization of neural activity might be essential in linking the anatomically distant cell assemblies that represent the various features of the stimulus.[1,2] A coherently moving stimulus assembly, such as a long bar, should produce such synchronized activity, in contrast to separately moving stimulus configurations or objects. When confronted with such a stimulus, oscillations above 15–20 Hz (often > 30 Hz, i.e. in the EEG gamma-band) were observed in the visual cortex of anesthetized cats[3] and awake behaving monkeys.[4] By comparing animal and human data, we could demonstrate that similar gamma-band responses can also be extracted from the scalp-recorded EEG while human subjects are attending to a moving long bar.[5] However, since other investigators, failed to detect gamma-band oscillations while moving stimuli were presented[6,7] the present study aimed at testing the robustness of the phenomenon by replication, i.e. whether or not gamma-band activity is greater while subjects are attending to a moving long bar than when the stimulus is two incoherently moving short bars.

From our earlier findings, we concluded that the increased gamma-band activity upon attending to the coherently moving bar indicated the synchronized activity of neurons in the primary and higher-order visual areas when encoding the coherently moving stimulus (long bar).[5] However, in order to prove this exclusive functional significance of the gamma-band response or the specific relationship between induced gamma-band and synchronous firing of neuronal assemblies, the relationship of gamma- and alpha activity has to be clarified. For instance, Rosler and colleagues have argued that gamma-band activity in the human EEG are simply harmonics of the alpha activity.[8] As of yet, studies investigating gamma-band responses in the human EEG have given little or no attention to alpha activity. If induced gamma-band activity is indeed a harmonic of alpha waves, the same time course of spectral power should occur for alpha and for gamma-band activity at the same electrode and the intrasubjective topography of alpha and gamma-band should be significantly correlated.

Materials and Methods

The EEG was recorded from four healthy women (ages 20–32) with normal or corrected-to-normal vision. Subjects were instructed to fixate on a cross at the center of a 20 inch monitor while attending to a single moving bar (coherent motion), or two identical bars, moving in opposite directions (incoherent motion). Dimensions of the light bars were 9.8 × 0.46° for the coherent and 4 × 0.46° for the incoherent

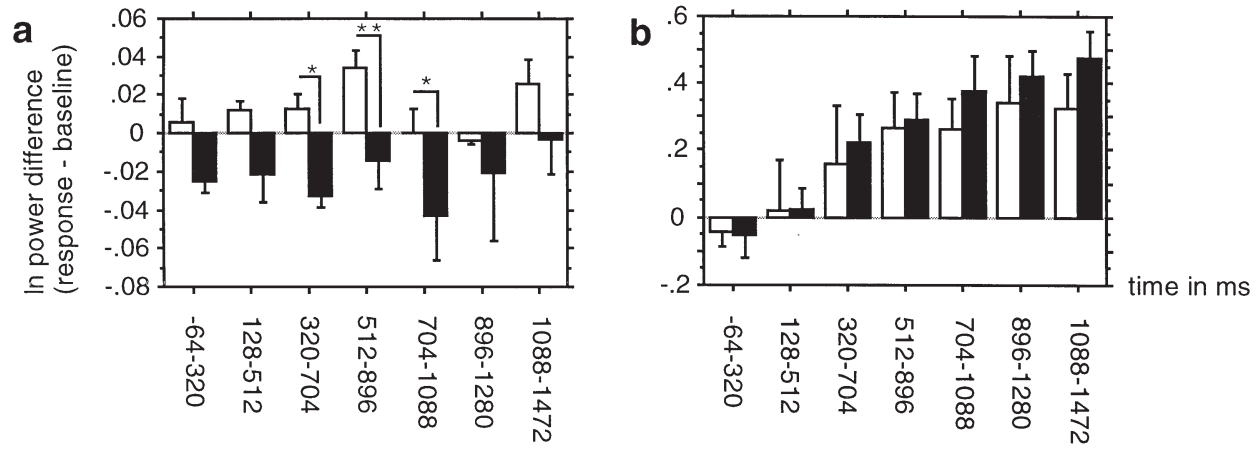

FIG. 1. Baseline normalized means and SEs (natural log) across electrodes T5, T6, O1, Oz and O2 of the seven time windows for coherent (white bars) and incoherent (black bars) motion. (**a**) Gamma-band (40–96 Hz), (**b**) alpha-band (8–12 Hz). $*p < 0.05$, $**p < 0.01$. Time ranges refer to epochs in time domain.

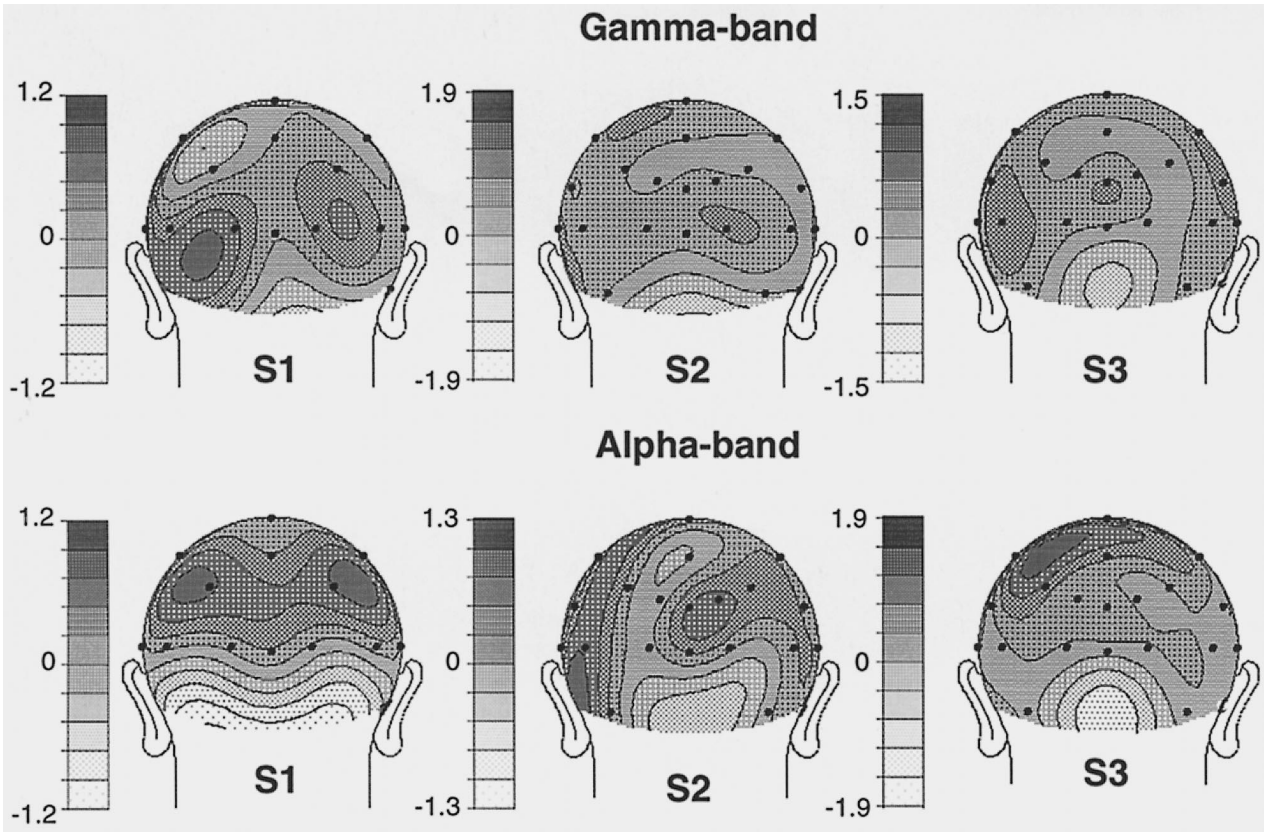

FIG. 2. Spline interpolated isocontour maps of baseline corrected and by McCarthy and Wood[13] normalized gamma- and alpha-band spectral power for all subjects for coherent motion in time period of most pronounced gamma-band activity (512–896 ms, see Fig. 1). *x*-values are given in $(\mu A/m^3)^2$.

stimulus condition. Velocity was 1.9°/s. Luminance of bars and background was 1.0 and 0.05 cd/m^2, respectively. For each condition (coherent and incoherent movement) 100 trials were presented in the left visual field in a random order. Stimulus motion started 260 ms after the appearance of the bars and ended 3000 ms later with their disappearance. The standing stimulus served as a baseline period.

The EEG of one of the subjects was recorded from 20 Ag–AgCl electrodes (montage according to the international 10-20 system) integrated into a elastic cap (Electrocap). For the three other subjects a 27

channel montage was used to increase the spatial sampling rate for the topographical maps. Additional channels were CB1/2, POz, TO1/2, and CT5/6 (see Fig. 2). Additional electrodes were fixed above and below the left eye and as near as possible to the outer canthi to monitor horizontal and vertical eye-movements (EOG). All electrodes were referenced to Fpz. A sampling rate of 1000 Hz (pass band: DC to 300 Hz) was used. Electrode impedance was kept < 5 kΩ. Trials with horizontal EOG exceeding 1° of lateral eye movements, blinks and EMG artifacts were rejected. Following this procedure, the data of one subject was excluded from further analysis, while an average of 78.5% of artifact-free trials remained for further analysis for the three other subjects. Current source densities (CSDs) were calculated for each time point of each trial and electrode in order to obtain a reference-free estimation of cortical activity.[9] The evoked response averaged across trials was subtracted from every single trial prior to transformation into the frequency domain. The evolutionary spectrum[5,10] was then computed for every single trial by means of the discrete Gabor transform.[5,11] This was achieved by sliding a time window of 256 ms in length in 64 ms steps across an epoch of 256 ms pre-motion to 1792 ms during motion of the bars. The resulting frequency resolution was 3.9 Hz (0.48–125 Hz, with downsampling for analysis to 250 Hz). Since a main purpose of the present study was to replicate our previous findings, we defined the alpha- and gamma-band in the same frequency ranges as before, i.e. the alpha-band was defined as the spectral power between 8 and 12 Hz; the gamma-band was scored as average power from 40 to 96 Hz. The first 1400 ms of motion were subdivided into seven windows. These windows were obtained by averaging across three successive time points (64 ms each) in the frequency domain of the respective spectral power of each band. Thus, the 192 ms of each window comprised 448 ms of time domain data, respectively. For each window, the natural logarithm was calculated to approximate a Gaussian distribution and the natural logarithm of the respective baseline power (i.e. the power while the stimulus was still motionless) was subtracted. Since electrodes T5, T6, O1, Oz and O2 showed the maximum of power in the gamma-band at occipito-temporal electrodes, they were used for statistical analysis. Means comparisons between the summed windows averaged over all electrodes for the respective condition for the alpha- and the gamma-band were calculated to test the difference between coherent and incoherent motion across time. The time course of the baseline corrected mean values across trials in both bands was tested by a three factor (electrode × time window × coherent/incoherent motion) repeated measurement ANOVA. p values were adjusted by Huynh-Feldt correction. In addition, paired t-tests (coherent/incoherent) of mean values across the five electrodes were conducted for each time window.

Spherical spline[12] isocontour maps of the baseline corrected spectral power for the gamma-band were calculated and the spectral power of both bands were normalized by means of a procedure suggested by McCarthy and Wood,[13] resulting in a value range between 0 and 1. Data were normalized separately for the two conditions in the time bin where gamma-band activity was most pronounced. Similarity of intrasubjective scalp distributions of the two bands was examined by means of calculating the correlation across electrodes. Correlation coefficients were z-transformed for statistical evaluation.

Results

The mean time course of the gamma-band across the five electrodes is illustrated in Fig. 1a, while the corresponding variations for the alpha-band response are depicted in Fig. 1b. Gamma band activity was significantly more pronounced during coherent motion than during incoherent motion ($F(1,26) = 22.66$, $p < 0.01$). The first time bin with a significant difference between conditions was the 320–704 ms time window ($t = 4.63$, $p < 0.05$; the time range relates to first to last data point in the time domain), while the most pronounced difference occurred in the following time bin of 512–896 ms ($t = 9.1$, $p = 0.01$). A significant difference between conditions in the time window 704–1088 ms ($t = 4.39$, $p < 0.05$) was due to a marked gamma suppression during the incoherent motion as compared to the coherent motion, but this effect did not reach significance ($F(1,26) = 4.20$, $p = 0.08$). As in our first study, alpha suppression due to stimulus presentation maintained at motion onset (–64–320 ms time bin), but dissipated during the time course of motion, as confirmed by the main effect of time window ($F(6,12) = 27.90$, $p = 0.01$). No significant effect of the gamma-band on time course was found.

The baseline corrected and normalized McCarthy and Wood[13] topographical maps at time bin 512–896 ms for gamma- and alpha-band spectral power for the coherent motion are displayed in Fig. 2 for all three subjects. As obvious from the figure, the scalp distribution of gamma- and alpha activity varied considerably between subjects. The intrasubjective correlation coefficients did not reach the significance level, ranging from 0.28 to –0.30, indicating that gamma-band activity was not dominated by harmonics of the alpha waves. In contrast, intrasubjective consistency was high for the alpha-band,

as demonstrated by significant intrasubjective correlations between coherent and incoherent motion in all three subjects (S1: r = 0.65, $p = 0.003$; S2: r = 0.64, $p = 0.0004$; S3: r = 0.88, $p < 0.0001$). For the gamma-band, no significant correlation was found between coherent and incoherent motion.

Discussion

The functional significance of induced gamma-band responses is still under debate. Gray and his colleagues found that cells responding to a bar, even those separated by the anatomically large distance of 7 mm, oscillated in nearly perfect synchronization. When the center of a long bar was removed so that both ends, i.e. two bars were moved separately, the cells fired still, but the synchronization disappeared.[3] Further studies in animals and humans suggested that this so-called 'binding problem' might be experimentally tracked.[14–19] Other authors failed to observe synchronized oscillating activity in the visual cortex,[6,7] raising doubts that gamma-band oscillations were relevant for feature binding and higher cognitive processes in general. They were rather considered to represent just an epiphenomenom without functional relevance.[20] Gray and McCormick[21] found cells firing with an extremely high intraburst firing rate and an interburst interval in the gamma frequency range. This 'chattering', Gray and McCormick argued, might be the pacemaker for the widespread gamma oscillations because rapid bursts of action potentials are very effective to depolarize other neurons. This rhythmic depolarization should be observable in the EEG as gamma-band activity.
The present study demonstrates replicability of induced gamma-band activity while subjects were attending to a coherently moving long bar, and the significant enhancement 320 ms after motion onset parallels results of Tallon-Baudry and co-workers,[22] who found induced gamma-band activity in a visual search task with a latency of about 280 ms.

Gamma- and alpha-band activity exhibited a different time course while bars were in motion and the topography was not correlated with the one of alpha. Taken together, these results strongly suggest that gamma cannot be considered just a harmonic of alpha-waves. Furthermore, we did not obtain significant intraindividual correlations between the gamma-band topography during the coherent and during incoherent motion in any of the subjects. This indicates that generator structures are different for the two different conditions. It also provides further evidence that the induced gamma-band activity is unlikely to result from muscle activity, since the topographical pattern of activity would be correlated assuming that similar muscle groups would be activated during the two conditions. Unlike gamma, the topographical distribution of alpha for the coherent and incoherent condition was highly correlated within all subjects. This indicates that alpha generators do not differentiate conditions and thus cannot be related to the specific type of processing.

The present results are comparable to those of Pulvermüller *et al.*,[16] who demonstrated that alpha-band in contrast to gamma-band activity does not differ when words or pseudowords were presented. Pfurtscheller and Neuper[23] described simultaneous occurrence of alpha desynchronization and enhanced evoked 40 Hz (gamma-band) activity during finger movement and concluded that alpha-band activity is characteristic for cortical areas at rest, while gamma-band activity represents the 'working brain', e.g. the activity of cell assemblies which are required to encode sensory information or to perform a motor task. Thus, the two frequencies are related to different functional meanings of cortical activity.

Overall, the difference in magnitude between the coherent and incoherent condition might be explained by an oversimplified model. When subjects attend to the coherently moving long bar, extended neuronal activity might by synchronized in one cell assembly to encode form and motion of this single object. In the incoherent condition, however, at least two neuronal assemblies are needed to encode the two incoherently moving objects. These neuronal assemblies fire independently out of phase. In a macroscopical recording of the EEG, this should result in a lowered amplitude and in a different topographical distribution. This was observed in our study.

Conclusion

We replicated previous find of enhanced gamma-band activity while subjects watched a long bar moving coherently across a computer screen as opposed to two fractions of this bar, moving incoherently. The study also demonstrated that alpha- and gamma-band activity exhibit a different time course while stimuli were in motion and the topography is not correlated in a time window of most pronounced gamma-band activity. The findings support the notion that alpha and gamma represent different functional mechanisms in the brain. The possibility to measure gamma-band activity noninvasively opens a field for future research on brain functioning and its deviations.

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