Oscillatory cortical activities in the gamma band in the human EEG induced by visual stimuli - representation of the stimulus?

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Abstract. The present work presents three experiments investigating cortical activities in the gamma band in humans. On the basis of theoretical models and animal experiments, synchronized oscillatory neuronal activity is discussed as the key mechanism by which the brain binds information processesed in different cortical areas to form a percept. Using an identical stimulation design - the same as used in animal studies - it was shown that induced gamma band responses in the EEG resemble the same features as those found in the intracortical recordings of animals. In addition, the present work demonstrates that these cortical activities are not higher harmonics of the alpha band and that they are senstive to the features of the stimulus. These results support the notion that gamma band activity is not just a by-product of neuronal activity and that alpha- and gamma band activies most certainly represent different cortical funtional states.

INTRODUCTION

Oscillatory cortical activities in the human brain do not form a homogeneous class of responses. Rather, they are diverse in many ways with respect to their significance and their underlying mechanisms. Historically, the frequency components of the EEG are divided into the following bands: (1) Delta: 0.5-3.5 Hz, (2) Theta: 4-7.5 Hz, (3) Alpha: 8-12 Hz, (4) Beta: 13-25 Hz, and, (5) Gamma: above 25 Hz (Berger 1929, Walter 1959). In recent years, research in the EEG frequency domain focused more and more on cortical activities in the gamma band range. In 1992, Galambos introduced the following classification with respect to gamma band responses (GBRs, Galambos 1992):

1. Spontaneous gamma rhythms. Occur in the EEG and are not related to any stimulus.

2. Evoked gamma band responses. Elicited and precisely time-locked to a stimulus. In expansion to the classification by Galambos, one should further divide this category into (a) transient evoked gamma band responses and (b) driven responses like the 40 Hz auditory steady--state response.

3. Emitted gamma band oscillations. Gamma band activity time-locked to a stimulus that has been omitted.

4. Induced gamma band rhythms. Are initiated by but not time- and phase-locked to a stimulus.

On the basis of theoretical considerations and results of experiments performed on animals, presented below, it was suggested that induced gamma band responses may be related to the computational operation of the cerebral cortex to link consistent relations among incoming signals (Molner 1974, Malsburg and Schneider 1986, Singer 1995, Singer and Gray 1995). Singer (1995) discussed two mechanisms of how the brain copes with the tremendous amount of feature constellations. "First, hard-wired neurons detect and represent relations that are particularly frequent and important. Second, dynamic grouping mechanisms, which allow for a flexible recombination of responses from hard-wired neurones, enable higher order relations to be analyzed and represent successively within the same hardware" (page 758). A dynamical grouping mechanism has several advantages over a hard-wired mechanism (see also Engel et al. 1991a):

(1) Assemblies are constituted of synchronized oscillating neurones, i.e. the phase-information permits the distinction of assemblies and the selective binding of distributed features of an object.

(2) Even in the case of spatial interleave, the temporal coding mechanism permits the discrimination of two assemblies.

(3) Object representations are created in a flexible manner, which allows a given cell to "switch" rapidly from one assembly to another.

In 1988, Eckhorn and colleagues (Eckhorn et al. 1988) reported synchronized oscillatory neuronal activity in the gamma band range in the visual cortex of the cat, which seemed to fit with Milner's and von der Malsburg's model perfectly. One year later, Gray and co-workers also recorded such activity in cat visual cortex (Gray and Singer 1989, Gray et al. 1989) by means of intra-cranial recordings. This activity was neither time nor phase locked to the stimulus (a long bar moving over the respective receptive fields) but was synchronized intercolumnar in Area 17 (Gray et al. 1989) or between different cortical areas, such as A 17 and 18 (Eckhorn et al. 1988, Engel et al. 1991c)[1]. Both groups interpreted the functional relevance of this synchronized cortical activity as being the mechanism by which the brain binds different features of an object or separate receptive field properties together.

In the following years, a series of experiments demonstrated synchronization in different brain areas (see Singer and Gray 1995 for an overview) and even interhemisspheric synchronization of induced gamma band activity in the visual cortex of anaesthetized cats (Engel et al. 1991b). However, the model also predicts that response synchronization should occur in a stimulus-dependent manner. This was shown in experiments conducted on anaesthetized cats. In the "conflicting stimulus paradigm" (Engel et al. 1991a), the simultaneous presentation of stimuli with optimal and orthogonal orientation reduced the oscillatory modulation of the response (Engel et al. 1990, Gray et al. 1990, Engel et al. 1991a). It has also been shown that long-range synchronization in area 17 of the anaesthetized cat reflects global stimulus properties (Gray and Singer 1989). In this experiment, multiunit activity was recorded from two sites which preferred vertical orientations and were

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[1] It should be mentioned, however, as early as 1975, Freeman described oscillatory field potentials recorded from the olfactory bulb of rabbits in a frequency range of 35-90 Hz which were linked to a previously learned odor.

separated by 7 mm. The corresponding receptive fields were non-overlapping and colinearly arranged. This arrangement allowed three different stimulus conditions: (1) a long continuous light bar moving across both fields, (2) two independent light bars moving in the same direction, and (3) the same two bars moving in opposite directions. The results showed that the induced gamma band responses of the two receptive fields were synchronized, when the long bar was presented. In the case of the two independent bars, moving in the same direction, the synchronization across the two receptive fields became weaker and totally disappeared if the motion of the stimuli was incoherent. However, the neuronal activity in the respective receptive field was strongly synchronized. These results gave raise to the notion that induced gamma band activity is related to the features of the stimuli.

Moving bars have frequently been used as stimuli to elicit gamma band oscillations in animal research. Using moving bars, the presence of induced gamma band responses has been demonstrated in the visual cortex of anaesthetized cats (Eckhorn et al. 1988, Gray et al. 1989, Eckhorn et al. 1990, Gray et al. 1990, Engel et al. 1991a,b,c, Eckhorn 1992, Gray 1992, awake behaving monkeys (Kreiter 1992, Kreiter and Singer 1992), in the optic tectum of pigeons (Neuenschwander and Varela 1993, Neuenschwander et al. 1996), and in the dorsal cortex and the dorsal ventricular ridge of pond turtles (Prechtl 1994). On the other hand, experiments on monkies measuring single-unit activity have also failed to find oscillations using moving light bars (Young et al. 1992), dynamic random dot displays with a fraction of dots moving coherently (Bair et al. 1994) and static stimuli (Tovee and Rolls 1992). These findings raised doubts as to whether gamma band oscillations are relevant for feature binding and higher cognitive processes in general, leading to the consideration that they simply represent an epiphenomenom without functional relevance (Kirschfeld 1992). However, it may well be the case, that recordings at the cellular level, which have the disadvantage of a spatial sampling bias, may not see the synchronization of large populations of neurones. As a result, rhythmic activity is prominent at the level of field potentials, but is weak or not apparent at the level of single-unit activity (Young et al. 1992, Singer and Gray 1995).

In humans, induced gamma band responses have been reported in the visual cortex (Lutzenberger et al. 1995, Tallon et al. 1995, Müller et al. 1996, Tallon-Baudry et al. 1996, Muller et al. 1997, Tallon-Baudry et al. 1997),

in the auditory cortex (Jokeit and Makeig 1994), in the sensorimotor cortex (Kristeva-Feige 1993) and during procession of words and pseudo words (Lutzenberger et al. 1994, Pulvermüller et al. 1995, 1996a, Eulitz et al. 1996) by means of non-invasive EEG or MEG measurements. As in the animal literature some authors have also questioned theses findings. One question was, whether the activity one can see in the gamma band does only reflect higher harmonics of the alpha band (Jürgens et al. 1995). A second, more fundamental question was, whether one is able to detect this activity with surface electrodes since electrocorticogram recordings in two humans have shown that spatially correlated activity was restricted to a very small area in the somatosensory cortex (Menon et al. 1996). However, a closer inspection of the findings of Menon et al. (1996) gives rise to some questions about the interpretation of the results as provided by the authors and of the appropriateness of paradigm used in this investigation (Lutzenberger et al. 1997).

Nonetheless, the mechanism which generates synchronous gamma band activity is not fully understood. It might be the case, that thalamocortical as well as cortico-cortical mechanisms play a role. It was shown that some cells of the intralaminar nuclei of the thalamus fire rhythmic bursts of extremely rapid spikes (up to 1,000 Hz), with an interburst interval in the gamma range (Steriade et al. 1993). In a subsequent study, extra- and intracellular recordings from the thalamus and the cortex has demonstrated that thalamic oscillations in the gamma band range become synchronized with the oscillations in the cortex (Steriade et al. 1996). A thalamocortical mechanism was not only hypothesized by Steriade and co-workers (Steriade 1996, Steriade et al. 1990, 1993, 1994, 1996) but also by Llinas and Ribary (Ribary et al. 1991, Llinas 1992, Llinas and Ribary 1992, 1993). With respect to the cortico-cortical mechanisms, recently Gray and McCormick (1996) found cells in the superficial layers of visual cortex of the cat firing with an extremely high intraburst firing rate (up to 600 Hz) 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 neurones. However, taking the evidence for thalamocortical and cortico-cortical mechanisms together, it seems possible that gamma oscillations may be generated in both the thalamus and cortex and it was suggested that the oscillations in the intralaminar

nuclei are required to co-ordinate the oscillations between different cortical regions, rather than driving the cortical oscillations (Steriade 1996).

Taken together, despite some uncertainties, a series of hypothesis exists to explain why cell assemblies oscillate.

1. Synchronized oscillatory activity is the mechanism how various brain regions form one percept and therefore are the key mechanism for feature binding (Gray et al. 1989, Singer and Gray 1995). The underlying physiological mechanism of how these oscillations are paced is not fully understood, but it may be the case that so-called "chattering cells" are the pacemakers for the widespread gamma oscillations (Gray et al. 1996)

2. According to Freeman (Freeman and Prisco 1986, Dijk 1987, Freeman and Dijk 1987, Freeman 1992, 1996) the stimulus itself might be coded in oscillations, or, more precisely as a nonlinear dynamic pattern which appears to the observer as oscillation. On the basis of intracortical recordings from the olfactory bulb of the rabbit Freeman and Di Prisco (1986) concluded that after the presentation of a learned odor, the system switches from a spatially and temporally unpatterned chaotic state to global odor-specific state which is characterized by a single near-limit attractor. In other words, the attractor governing the dynamic pattern is related to stimulus encoding, everything that is not coherent to this signal is dismissed as noise.

3. With respect to oscillations in the alpha range, it was hypothesized that these oscillations reflect idling in neural mass systems (Pfurtscheller and Aranibar 1979, Pfurtscheller 1992, Pfurtscheller and Klimesch 1992, Pfurtscheller et al. 1993, Hari and Salmelin 1997). These 10 Hz oscillations can be seen over the posterior parts of the brain (alpha), over the rolandic regions (mu) and was recorded from the supra-temporal auditory cortex (tau). This idling state would allow the system to start more rapidly than by a "cold start" (Hari and Salmelin 1997). In the somato-motor system such oscillations can be measured not only in the alpha range but also in a frequency range around 20 Hz (Kristeva-Feige et al. 1993, Hari and Salmelin 1997, Pfurtscheller et al. 1997). Both, the rolandic mu rhythm and the 20 Hz oscillations is dampened by limb movements and tactile stimulation.

4. Oscillations have no functional meaning but are simply a by-product of neuronal activity (Kirschfeld 1992).

In the present chapter, a total of three experiments were conducted on induced gamma band responses. The main purpose was to investigate, whether these cortical activities are related to the features of a stimulus (see hypothesis 1 and 2), whether they represent a different functional state as compared to the oscillations in the alpha range (hypothesis 3) and, finally, that they are not simply a by-product of neuronal activity (hypothesis 4).

In the first two experiments, we investigated whether visually induced gamma band responses can be extracted from the human EEG. As in the animal studies described above, the "long bar" paradigm from Gray et al. (1989) was used to test the feature dependence of induced GBRs from the stimulus. Induced GBRs were extracted by means of the Discrete Gabor Transform (DGT), an algorithm developed in co-operation with the Cuban Center of Neuroscience in Havana. Prior to the application to human EEG data, this algorithm was tested with data from intracortical recordings from monkey primary visual cortex to test whether this method is able to detect the short bursts of gamma band activity. In addition it was examined whether the results obtained in the gamma band can be explained in terms of higher harmonics of the alpha band. Differences in the temporal and spatial features between the two bands would strongly suggest, that the two bands represent two different functional cortical states e.g., idling *versus* working brain.

Contrary to results related to a simple stimulus like a moving bar, Vijn and co-workers (Vijn et al. 1991, 1992, Vijn 1992, van Dijk et al. 1994) reported a GBR power reduction (in the 20 to 40 Hz range) when complex stimuli are presented in motion as compared to a standing complex stimulus. This was consistently found in cats (van Dijk et al. 1994), in local field potentials and surface recordings of the awake monkey (Vijn 1992, Vijn et al. 1992) and in the human EEG (Vijn et al. 1991, 1992) . The authors hypothesized two functionally different states in the visual cortex to explain for the suppression effect: the "scanning state" and the "detection state". During the "scanning state", the cortex is scanning the environment for relevant information. Since there is no information on which information is of relevance e.g. motion, color, luminance, this state requires a global analysis in which many spatially distributed neurons are involved. After a cue appeared, the visual cortex switches to the "detection state". A certain assembly loosens its connections with the broad environment, resulting in a drop in gamma band activity, and strengthens the connections with the neurones within the assembly. According to Vijn (1992), the "detection state" has been measured in the above mentioned animal studies. The third experiment presented in this chapter was conducted

to compare the induced gamma band activity of a complex moving stimulus with a complex standing stimulus to see if Vijn's findings can be replicated, which would give strong support to the hypothesis that induced GBRs are related to the features of a stimulus and thus have a functional meaning.

GENERAL METHODS OF DATA ANALYSIS

Frequency analysis

The frequency analysis was obtained by means of the Discrete Gabor Transform (Qian and Chen 1993). The Discrete Gabor Transform (DGT) is capable of decomposing finite sequences of data into complex values with a family of Gabor functions. The analysis windows (256 ms in the present case) are down weighted towards the extremes by means of a Gaussian function. To determine time changes in the intensity of oscillatory activity, the evolutionary spectrum was used (Priestley 1988). This was obtained by shifting the analysis window by steps of 64 ms over the data epoch. Since the focus was on oscillatory activity, which is not deterministically time or phase locked to the stimuli, the mean overall artifact free epochs was subtracted from each epoch prior to transformation in the frequency domain. The resulting time-frequency matrixes (with a frequency resolution of 3.9 Hz) of the single trials were then averaged to obtain the mean evolutionory spectrum for each subject and electrode (see also Müller et al. 1996). The power was obtained by calculating the sum of the squares of the real and imaginary components.

Data reduction for statistical analysis

Unless not otherwise stated, data reduction and statistical analysis in the frequency domain was performed in experiments 1 to 3 in the following manner:

Two bands were chosen for statistical analysis: (1) a broad gamma band, which represents the averaged spectral power from 39-94 Hz, and (2), the alpha band from 8-12 Hz. Since Eckhorn (1993) reported of high frequency gamma oscillations (60-90 Hz) in the awake monkey, we decided to extend our gamma band range to 94 Hz. The standing stimuli period served as a baseline (see Method sections in experiment 1 to 3). We divided the first 1,472 ms while stimuli were in motion into seven time windows (192 ms each). These windows were obtained by averaging across 3 successive time points (64 ms each) in the frequency domain of the respective spectral power of each band. Thus, each 192 ms window contains 448 ms in the time domain. For every window, the natural logarithm was calculated to approximate a Gaussian distribution and the natural logarithm of the respective mean baseline power (i.e., the power while the stimulus was motionless) was subtracted. Thus, the normalized time windows represented the spectral power relative to baseline. These normalized time windows were subject to statistical analysis.

EXPERIMENT 1: INDUCED GAMMA BAND ACTIVITY

First, the ability of the DGT to extract short bursts of induced gamma band activity by analysing local field potentials measured from area 17 of an awake fixating macaque monkey (macaca fascicularis) was tested. It was then investigated whether induced gamma band activity can be extracted from the human EEG with the "long bar" stimulus design. On the basis of the animal experiment (Gray et al. 1989) it was hypothesized that the long bar induces gamma band responses in the human EEG.

Methods - monkey field potential recordings

The stimulus was a 1 deg by 1 deg light bar moving with a velocity of 1 deg/s over the receptive field. For intracortical extracellular field recordings, glass insulated elgiloy electrodes (1 MΩ at 100 Hz) were used. Data was recorded with a sampling frequency of 1,000 Hz, and the raw signal was filtered from 10 to 100 Hz. The training of the animal, the implantation of the recording chamber and the description of the recording session was extensively reported in Kreiter (1992) and Kreiter and Singer (1992). All surgical and behavioural procedures were performed in accordance with the German guidelines for the welfare of experimental animals. Animal carc was in accordance with the guidelines issued by the Federal Government of Germany.

Results - monkey data

Figure 1 depicts three examples of an evolutionary spectrum of a single sweep and the grand mean of evolutionary spectra over 10 single sweeps from the monkey local field recordings.

A

μV^2

B

C

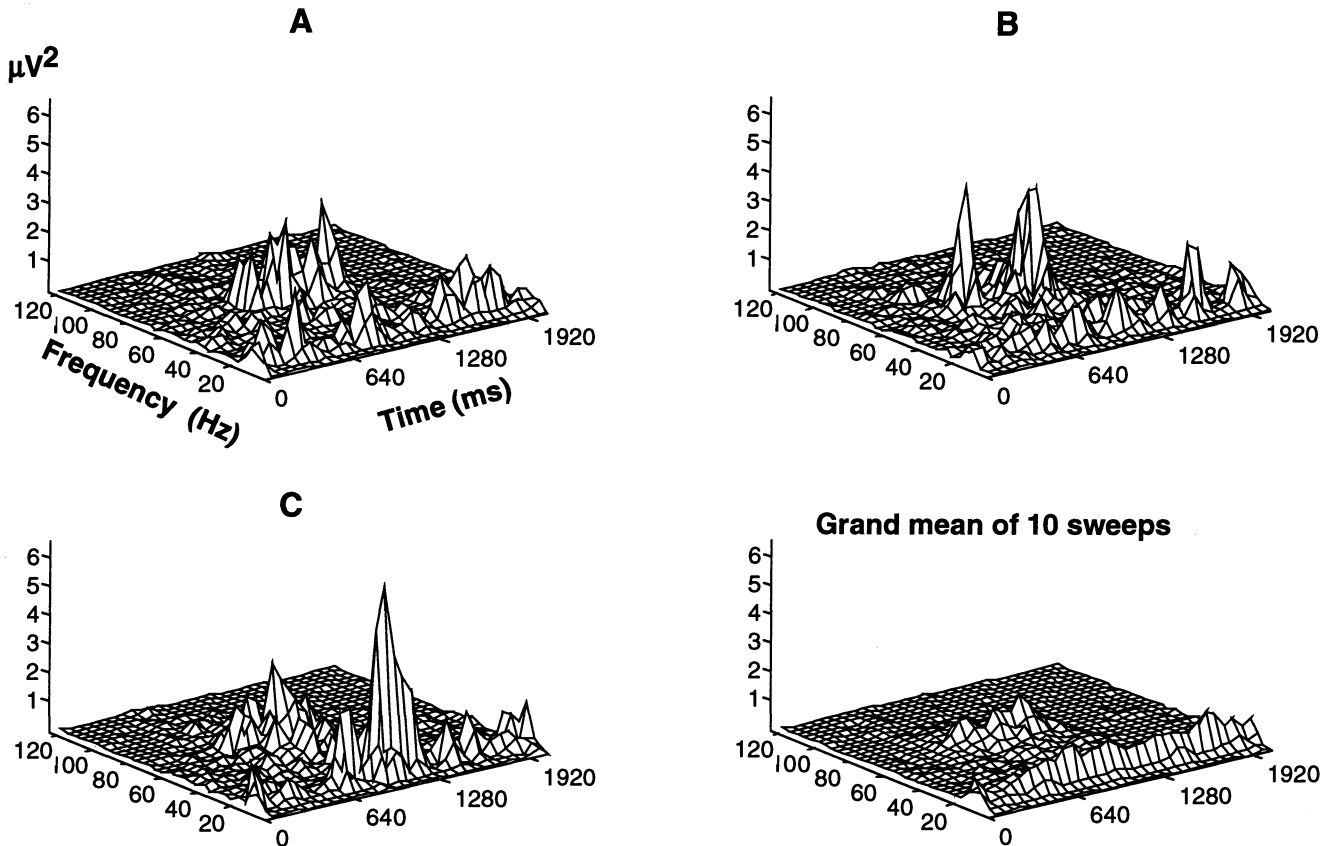## Grand mean of 10 sweeps

Fig. 1. Evolutionary spectra of three single sweeps (panels A-C) and grand mean evolutionary spectra of ten single sweeps (panel D) of local field potentials from Area 17 of the awake behaving monkey while attending to a moving stimulus (adapted from Müller et al. 1996).

On average, spectral power was centered around 60 Hz. Figure 1A-C clearly depicts the variance of frequency and time of onset of the induced gamma band activity in the single sweeps. These features correspond to the ones typically described in animal studies as well as parallel the findings of Kreiter (1992). Averaging of evolutionary spectra of 10 single sweeps resulted in a depression of the spectral power in the grand mean (Fig. 1D). Thus, it can be concluded that the DGT is able to extract synchronized oscillatory spindles in the gamma band range as they were observed in animal studies.

Methods - human EEG recordings

SUBJECTS

EEG was recorded from seven human subjects (mean age 26.1 years, 4 males, 3 females) with normal or cor-rected-to-normal vision. Subjects received monetary compensation for participating in the experiment (25 DM). All subjects were naive with respect to the scientific goals of the experiment.

STIMULI AND DESIGN

The stimulus configuration corresponded to that used in animal studies (Gray et al. 1989). There were two stimulus configurations. The first consisted of a single moving bar, which was expected to activate one single synchronously firing neuronal assembly. The second contained two identical bars moving in opposite directions. The dimensions of the light bars were 9.8 deg x 0.46 deg for the coherent and 4 deg x 0.46 deg for the incoherent stimulus condition, and their velocity was 1.9 deg/s. The two bars stimulus was expected to evoke activity in at least two separate neuronal assemblies

which are not synchronized, resulting in a reduction or even elimination of macroscopically visible gamma band responses. Bars were presented in the left visual hemifield in order to avoid cancellation of superimposed electrical vectors of cortical activity due to folding within the visual cortex.
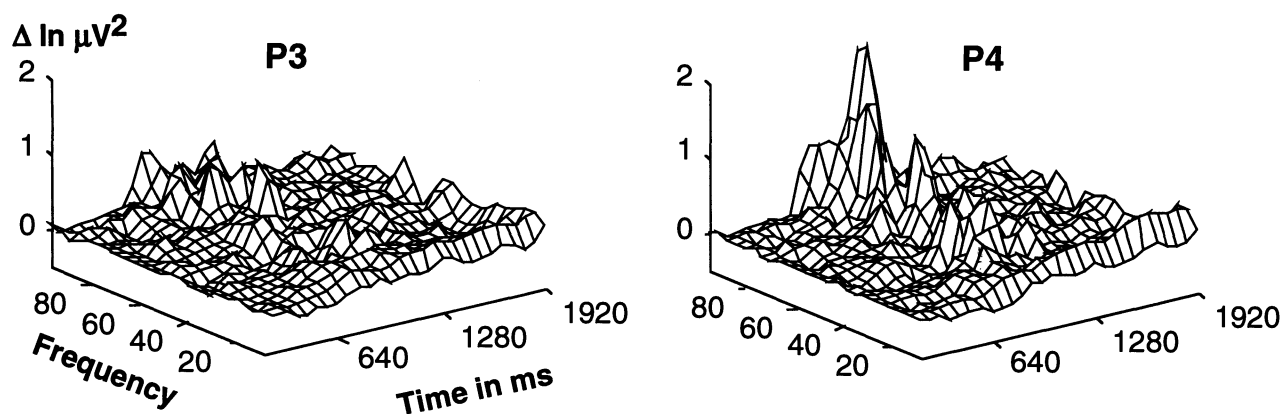
Luminance of bars and background was 1.0 and 0.05 cd/sqm, respectively. Each condition comprised of 100 stimuli. The long bar and the two bars were presented in a random order with an interstimulus interval of 1,750 ms. Prior to motion-onset, the bars were presented as standing stimuli for 260 ms. Motion-onset occurred directly thereafter, beginning 9.64 deg lateral to the fixation point and ending 3,700 ms later (2.58 deg lateral to

fixation point) with the disappearance of the bars. Stimuli and fixation point were presented on a 20 inch monitor with a frame rate of 60 Hz (non interlaced) one meter in front of the subject's eyes. Subjects were instructed to fixate on a cross at the center of a screen while attending to the presented stimuli.

ELECTROPHYSIOLOGICAL RECORDINGS AND STATISTICAL ANALYSIS

EEG was recorded, using Ag-AgCl electrodes from Pz, Oz, P3, P4, T5, T6, O1, O2, VEOG (international 10-20 system) with a sampling rate of 1,000 Hz (pass band: 0.3 to 300 Hz), referenced to linked earlobes. Electrode
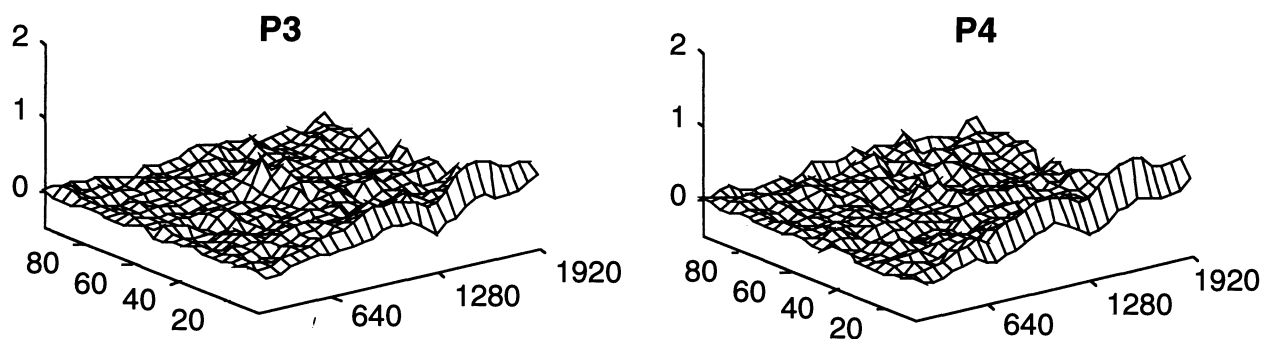

Fig. 2. Grand mean normalized evolutionary spectra over all subjects for the coherent (top panel) and incoherent (lower panel) motion for electrodes P3 and P4.

impedance for all electrodes was below 5 kΩ. Trials with EOG artifacts were rejected when the absolute value of the amplitude exceeded 75 μV. One subject, whose data contained more than 60% artifacts, was removed from further analysis. The evolutionary spectrum was calculated by means of the DGT across an epoch, defined as 256 ms pre-motion to 1,792 ms after motion-onset of the bars.

Means comparisons across the 7 windows across all electrodes were calculated to test the difference between coherent and incoherent motion over time for the alpha- and the gamma band, respectively. P-values were adjusted by Huynh-Feldt correction. In addition, paired t-tests (coherent/incoherent) of mean values across electrodes were conducted for each time window.

Results - human data

Grand mean normalized evolutionary spectra over all subjects for electrode positions P3 and P4 for the coherent (long bar) and incoherent motion (two bars) are shown in Fig. 2.

Relative to the standing stimuli, the grand averages of the evolutionary spectra for the different electrode positions (not all shown here but see Müller et al. 1996) revealed several important features:
1. The single bar condition was associated with enhanced gamma band (39-94 Hz) activity with two peaks, one in the 60 Hz range, and the other in the range of 80 Hz, which is not present in the incoherent condition when two bars moved in opposite direction.

2. This activity was most pronounced over the contralateral parietal scalp sites (P4, T6 and O2) in a time window between approximately 300 and 1,000 ms post motion-onset and far exceeds the standing stimulus level, particularly in P4.
3. In the presence of two incoherently moving bars, no comparable enhancement of activity in the gamma range was observed at any electrode site.
4. Alpha activity was less pronounced in coherent as compared to incoherent motion.
5. After a short period of little difference in alpha activity between standing and moving stimuli, alpha showed an ongoing recovery during the time course of motion.
6. Topography and time course of alpha for both experimental conditions were not found in any other frequency (see Fig. 3).

Figure 3 depicts the baseline normalized gamma and alpha band activity of the 7 time windows.

The statistical analysis of the normalized time windows showed significantly larger spectral power in the gamma band in all time windows for coherent motion as compared to incoherent motion ($F_{1,65} = 9.34$, $P<0.05$). Differences were most pronounced in the time window between 320-704 ms ($t(6) = 2.0$, $P=0.05$) and 512-896 ms post motion-onset ($t(6) = 2.5$, $P=0.01$, Fig. 3). In contrast, the relative changes in power over all time windows in the alpha band (8-12 Hz) was significantly lower in coherent as compared to incoherent motion ($F_{1,65} = 10.21$, $P<0.01$, Fig. 3).
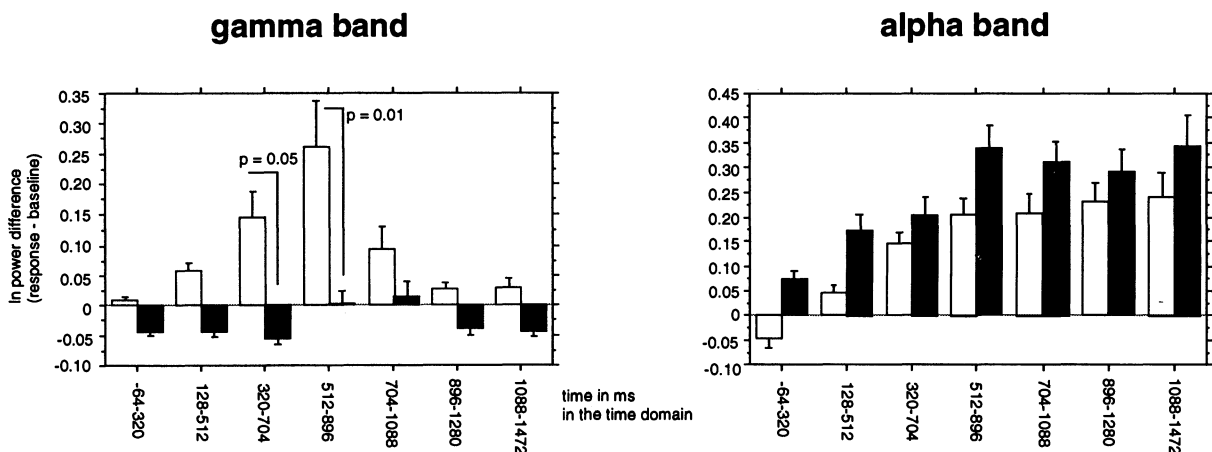

Fig. 3. Means and standard errors across all subjects and electrodes for the normalized gamma (left) and alpha band (right) spectral power for the 7 time windows. White bars, coherent motion; black bars, incoherent motion. Note: time borders refer to the epoch in the time domain.

Conclusion

These results prove that the DGT is able to extract short bursts of non time- and phase-locked gamma band activity. The results with respect to the human EEG data show that gamma band responses in the human EEG were induced by a coherently moving bar stimulus, but disappear in the presence of two independently moving bars. The observation of stimulus induced gamma band activity in extracranial human EEG recordings suggests that many neurons have synchronized their activity in response to the single moving bar stimulus. The lack of macroscopically visible gamma band activity in the presence of two bars, moving simultaneously in opposite directions (incoherent stimulation), can be explained if each bar is producing an oscillatory activity in separate neuronal assemblies but the activity of these assemblies is not synchronized. In the macroscopically measurable activity, this results in a reduction or even cancellation of gamma band signals.

EXPERIMENT 2 - RELIABILITY AND INDEPENDENCE OF ALFA AND GAMMA ACTIVITY IN HUMAN EEG

Experiment 2 was designed to test the replicability of the findings of experiment 1. In order to map the topographical distribution, multi-electrode recordings were used. Cortical alpha activity was also examined to test whether gamma band activity might reflect changes in harmonics of alpha waves. If so, the same temporal features of spectral power should occur for alpha- and for gamma band activity at the same electrode site and the intrasubjective topography of alpha- and gamma band should be significantly correlated.

Methods

SUBJECTS

EEG was recorded from four healthy women (ages 20 to 32) with normal or corrected-to-normal vision. Subjects received monetary compensation for participating in the experiment (25 DM). All subjects were naive with respect to the scientific goals of the experiment.

STIMULI AND DESIGN

Stimuli and stimulus presentation was identical to experiment 1. 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). Stimulus motion-onset began 260 ms after the appearance of the bars and ended 3,000 ms later with their disappearance. The standing stimulus served as a baseline period. For each condition, 100 trials were presented in the left visual field in a random order.

ELECTROPHYSIOLOGICAL RECORDINGS AND DATA ANALYSIS

The EEG of one of the subjects was recorded from 20 Ag-AgCl electrodes (montage according to the international 10-20 system) integrated into an elastic cap (Electrocap). For the three other subjects a 27 channels montage referenced to Fpz was used to increase the spatial sampling rate for the topographical maps. Standard 10-20 sites were Fz, F3, F4, Cz, C3, C4, Pz, P3, P4, 01, 02, T3, T4, T5, T6, and left mastoid. Non-standard sites were IPz, INz, IN3, IN4, P01, PO2, TO1, TO2, CP1, CP2, CT5 and CT6 (see Müller et al. 1997 for exact electrode positions, see also Fig. 5). Additional electrodes were fixed to monitor horizontal and vertical eye-movements (EOG). The sampling rate was 1,000 Hz (DC - 300 Hz). Electrode impedance was kept below 5 kΩ. Trials with horizontal EOG exceeding 1 deg of lateral eye movements, blinks and EMG artifacts were rejected. Following this procedure, the data of one subject had to be rejected from further analysis. For the three other subjects an average of 78.5% of artifact free trials remained for further analysis.

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 (Law et al. 1993). Frequency analysis, frequency bands and data reduction for statistical analysis were identical to experiment 1. 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. In addition to the statistical tests described in experiment 1, the time course of the baseline corrected mean values across trials for both bands was tested by a three factor (electrode x time x coherent/incoherent motion) repeated measurement ANOVA. P-values were adjusted by Huynh-Feldt correction.

Spherical spline (Perrin et al. 1989) 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 (1985), 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 underwent a z-transformation for statistical evaluation.

Results

The mean time course of the gamma and alpha band across the 5 electrodes is illustrated in Fig. 4.

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 ($t(2)$ = 4.63, $P<0.05$; time range refers to the time domain), while the most pronounced difference occurred in the following time bin of 512-896 ms ($t(2)$ = 9.1, $P=0.01$). A significant difference between conditions in the time window 704-1,088 ms ($t(2)$ = 4.39, $P<0.05$) was due to a marked gamma suppression during the incoherent motion relative to baseline. In contrast, activity in the

alpha band was somewhat higher for the incoherent motion as compared to the coherent motion, but this effect did not reach the significance level ($F_{1,26}$ = 4.20, $P=0.08$). As in experiment 1, alpha suppression due to stimulus presentation was maintained at motion-onset (-64-320 ms time bin), but dissipated during the time course of motion, as confirmed by the main effect TIME ($F_{6,12}$ = 27.90, $P=0.01$). No significant effect of the gamma band on time course was found.

The topographical maps of baseline corrected values in time bin 512-896 ms were normalized according to McCarthy and Wood (1985). The maps are displayed in Fig. 5 for two of the three subjects.

As obvious from Fig. 5, the scalp distribution of gamma- and alpha activity varied considerably between subjects. The intrasubjective correlation-coefficients did not reach the significance level and were 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.
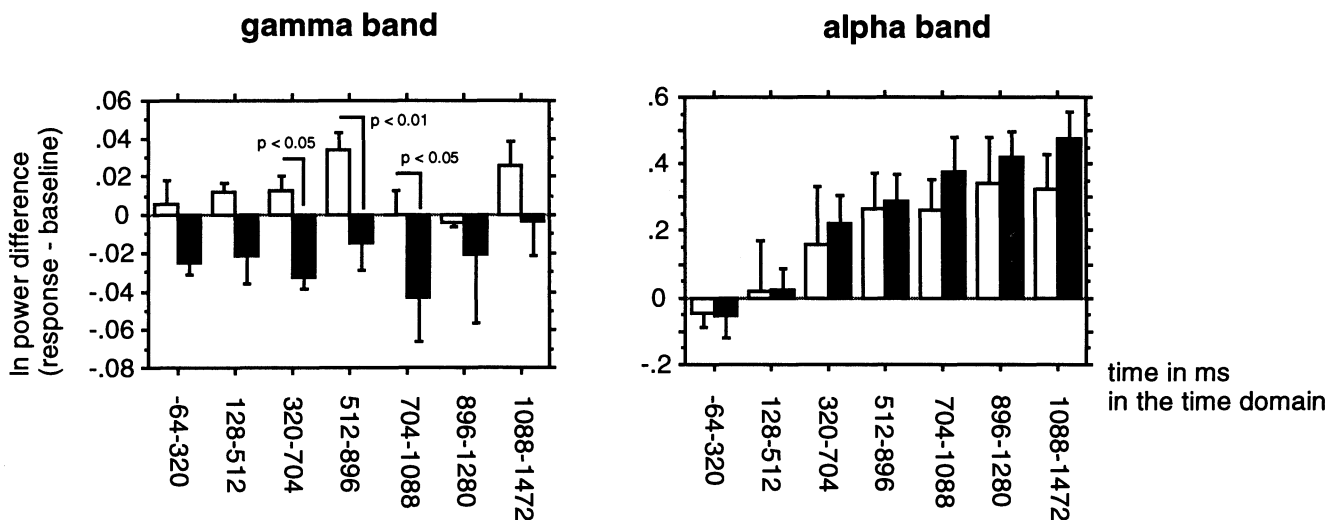

Fig. 4. Means and standard errors across all subjects and electrodes T5, T6, O1, Oz and O2 for the normalized gamma (right) and alpha band (left) spectral power for the 7 time windows. White bars, coherent motion; black bars, incoherent motion. Note: time borders refer to the epoch in the time domain (adapted from Müller et al. 1997).
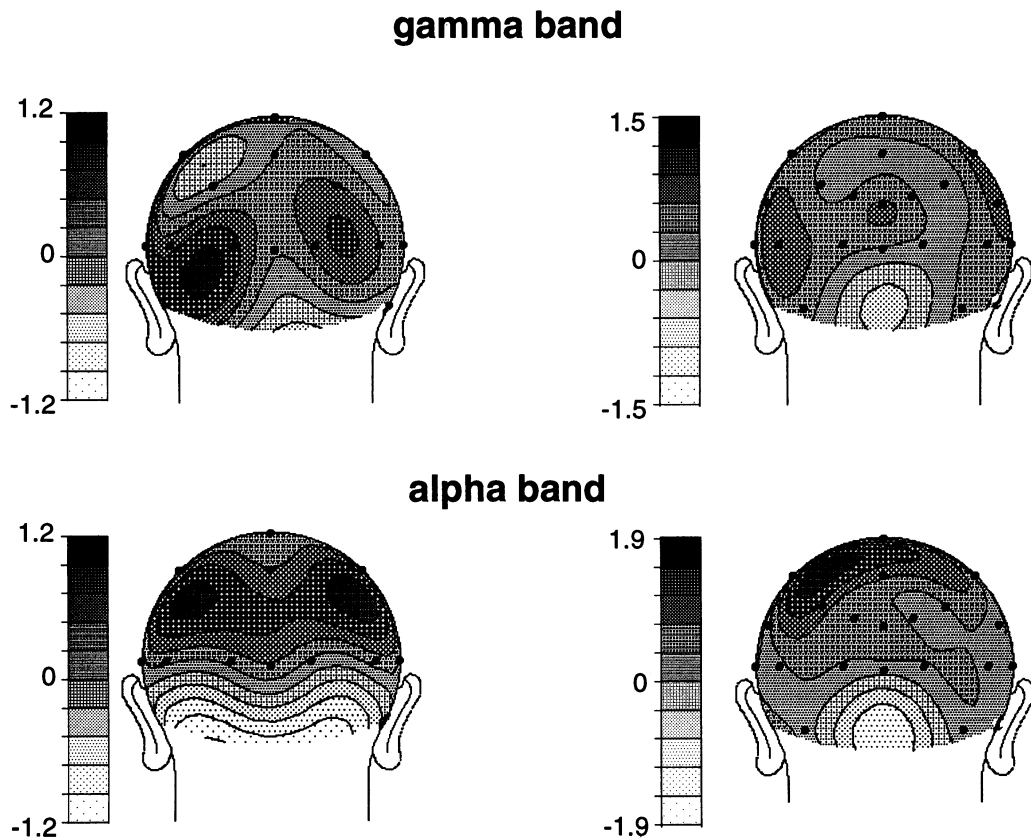
gamma band

alpha band

Fig. 5. Spline interpolated isocontour maps of baseline corrected normalized gamma- and alpha band spectral power two subjects for coherent motion in the time period of most pronounced gamma band activity (512-896 ms). Note: x-values are given in $(\mu A/m^3)^2$.

Conclusion

Experiment 2 demonstrates the replicability of induced gamma band activity while subjects were attending to a coherently moving long bar. The significant enhancement 320 ms post motion-onset parallels the results of Tallon-Baudry and co-workers (1996), who found induced gamma band activity in a visual search task within a latency of approximately 280 ms.

Gamma- and alpha band activity exhibited a different time course while bars were in motion and their topography was not correlated. Taken together, these results strongly suggest that gamma cannot be considered to be simply a harmonic of alpha waves. Furthermore, no significant intraindividual correlation between the gamma band topography during coherent and incoherent motion was obtained for any of the subjects. This indicates that generator structures are different for the two different conditions. It also provides further evidence that the in-

duced gamma band activity is unlikely to result from muscle activity, since the topographical pattern of activity during the two conditions would be correlated, if one assumes that similar muscle groups are active. 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 between conditions and, thus, cannot be related to the specific type of processing.

EXPERIMENT 3 - COMPLEX MOVING STIMULUS AND HUMAN EEG GAMMA BAND

In contrast to the previous two experiments, which employed simple stimuli, this experiment used complex stimuli. The question was, whether a complex moving stimulus is also linked to enhanced induced gamma band

activity as compared to a standing complex stimulus as was the case for simple stimuli (the long bar), or whether the complex moving stimulus is related to a decrease in gamma band power as predicted by the model of Vijn (1992, see Introduction).

Methods

SUBJECTS

Twelve subjects (three females) with normal or corrected-to-normal vision were recorded. Subjects received monetary compensation (DM 25) for participation and were naive with respect to the scientific goals of the study.

STIMULI AND DESIGN

Coloured squares and rectangles were presented on a 20 inch monitor on a green background. The screen subtended 20.5 x 26.9 degrees of the left visual field. Following a 1,000 ms presentation as a standing stimulus, either (a) the entire stimulus rotated for a period of 2,000 ms in an upward motion or (b) the stimulus remained motionless for an additional 2,000 ms, followed by a

dark screen for 1,000 ms, respectively. Each condition was comprised of 100 trials, which were presented in a random order. Subjects were instructed to fixate on a fixation point affixed to the left border of the screen, and to avoid head/eye movements and blinks during stimulus presentation.

ELECTROPHYSIOLOGICAL RECORDINGS AND DATA ANALYSIS

The same 27 electrodes montage as described in experiment 3 including vertical and horizontal EOG recordings was used. Trials with horizontal EOG exceeding 1 deg of lateral eye movements, blinks and EMG artifacts were rejected. Three subjects were excluded from further analysis due to too many artifacts. For the remaining 9 subjects, an average of 81.2% of artifact free trials were analyzed. Prior to transformation into the frequency domain, CSDs were calculated for every artifact free trial. Frequency analysis and bands, data reduction and statistical analysis were conducted in a manner identical to experiments 1 and 2 with the exception that eight instead of seven 192 ms windows were analysed. Electrodes CT5/6, P3/4, T5/6 and TO1/2 were included for statistical analysis.
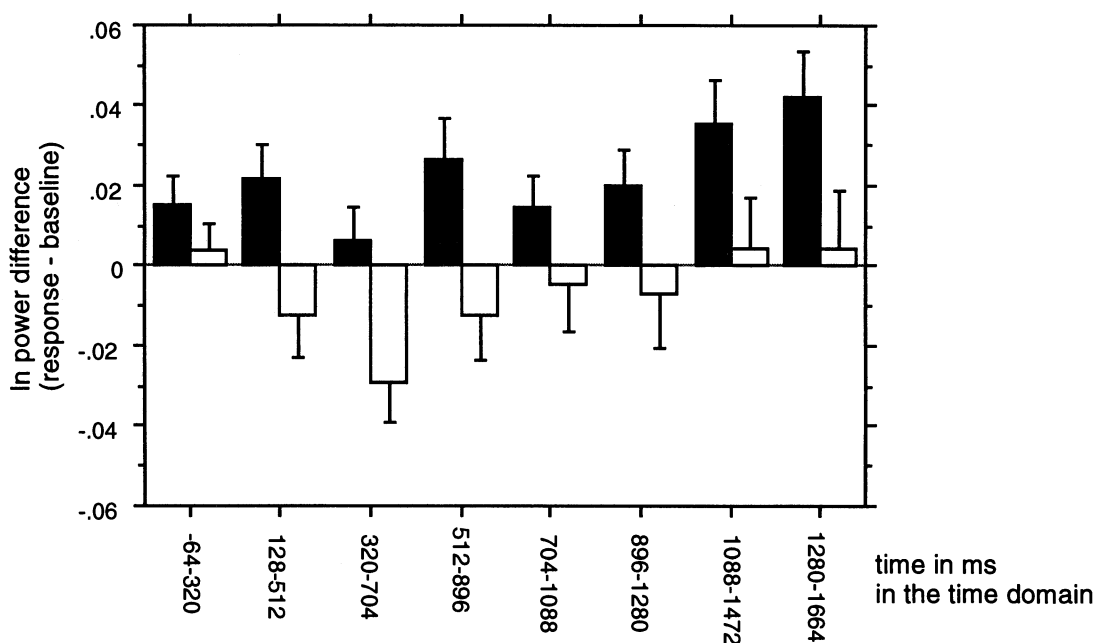

Fig. 6. Means and standard errors across all subjects for the GBR relative to baseline for the moving (white bars) and standing (black bars) stimulus.

Results

Figure 6 depicts the time course of the GBR relative to baseline for the standing and moving stimulus.

A significantly higher power across time and electrodes for the standing as compared to the moving stimulus ($F_{1,8} = 6.0$, $P<0.05$), not due to baseline differences, was found. The significant main effect time ($F_{7,56} = 3.0$, $P<0.05$) showed the most pronounced reduction in gamma band power in the time window 320-704 ms post motion-onset. This is exactly the same time window in which the first significant difference between coherent and incoherent motion in experiments 1 and 2 was found. The reduction of gamma power in that time window was mainly due to the reduction in the motion condition, as was tested by an one group t-test ($t(8) = 0.8$, $P=0.5$ for standing, and $t(8) = -3.5$, $P<0.05$ for motion). As can be seen in Fig. 6, there is a continuous increment of gamma power in the following time windows.

Conclusion

The results of experiment 3 were in line with the findings of Vijn et al. (Vijn et al. 1991, 1992, van Dijk et al. 1994), who described a reduction in gamma band power when complex stimuli were in motion *versus* when they were motionless. However, the present experiment was not designed to fully test Vijn's model, so no conclusions can be drawn on the validity of that model based on the results of experiment 3. To test the model, complex and simple (e.g. a bar) standing and moving stimuli would need to be presented. Also, amplitude changes would need to be correlated to topographical changes from a broad to a more focused gamma band distribution.

GENERAL SUMMARY AND DISCUSSION

On the basis of intracranial local field recordings from area 17 of an awake behaving monkey, the ability of the DGT-algorithm to extract synchronized oscillating spindles in the gamma band was demonstrated. The thus obtained evolutionary spectra of single sweeps exhibited exactly the same features as those described in the animal literature (Kreiter 1992, Kreiter and Singer 1992). Averaging the obtained spectra across ten single sweeps resulted in a reduced signal power as the time of onset and the frequency of the spindles varied from trial to trial.

Results of experiment 1 and 2 show that a coherently moving bar stimulus induces gamma band responses in the human EEG, which disappear in the presence of two independently moving bars. The observation of stimulus induced gamma band activity in extracranial human EEG recordings indicates that many neurons must have synchronized their activity in response to the single moving bar stimulus. The lack of macroscopically visible gamma band activity in the presence of two bars moving simultaneously in opposite directions (incoherent stimulation) can be explained if each bar is producing an oscillatory activity in separate neuronal assemblies but the activity of these assemblies is not synchronized. In the macroscopically measurable activity, this results in a reduction or even cancellation of gamma band signals. Animal experiments have indeed shown that cell groups in area 17 of the cat with non-overlapping receptive fields showed synchronous oscillation if they were activated by a single continuous stimulus (long bar). If two bars moving in opposite directions were presented, firing was uncorrelated (Gray et al. 1989, Engel et al. 1992). Evidently, cells join one assembly when they are activated by a single coherent stimulus, whereas they couple to two different assemblies when activated by two incoherent stimuli. These two assemblies are spatially disjunct and desynchronized relative to each other. Same effects had been observed if the cell groups had overlapping receptive fields (Gray et al. 1990).

The present study demonstrates a replication of former findings in human subjects with respect to induced gamma band activity. Gamma- and alpha band activity exhibited a different time course while bars were in motion and the topography was not correlated. All results strongly suggest that gamma is not simply a harmonic of alpha waves, as has been indicated by Jürgens et al. (1995). In addition, no significant intrasubjective correlation was found between the gamma band topography of the coherent and incoherent motion (experiment 2). This can be interpreted in two ways. First, a different generator structure is responsible for the topographical distribution, and, second, induced gamma band activity is not due to muscle activity, since muscle activity most certainly would result in correlated topographical features. Unlike gamma, the topographical distribution of alpha for the coherent and incoherent condition was highly correlated in all subjects. This indicates, that identical alpha generators were active in both conditions. The results of experiment 1 and 2 are also in line with Pulvermüller and co-workers (1995) who have shown

that contrary to gamma, alpha does not differ when words or pseudowords were presented. Pfurtscheller and Neuper (1992) demonstrated a simultaneous alpha de-synchronization 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 encode sensory information or to perform a motor task. Thus, the two frequencies are related to different functional meanings of cortical activity.

On the basis of the results of experiment 3 and the model of Vijn (1992), one might speculate that different coding mechanisms underlie simple and complex stimuli. There was less gamma band activity for the moving complex stimulus as compared to the complex standing stimulus. This fits in perfectly with the findings of Vijn and colleagues (Vijn 1992, Vijn et al. 1991, 1992, van Dijk et al. 1994) who also found a reduction in spectral power up to 40 Hz when a complex stimulus started to move. On the basis of their proposed two stage model, the standing stimulus sets the visual cortex in the "scanning state", whereas the moving stimulus causes a change to the "detection state". Further research is required to investigate the underlying cortical mechanisms, when complex stimuli are presented.

In the long bar experiment (experiment 1 and 2), the induced gamma band activity was most pronounced in a time window beginning 320 ms post motion-onset. The observed latencies of the present work parallel those reported by Tallon-Baudry et al. (1997), who found induced gamma band activity in a visual search task with a latency of approximately 280 ms. Pulvermüller (1996) reported an enhanced power in the gamma band for words as compared to pseudo-words in the latency range of 300 to 500 ms. In the visual cortex of the cat, the reported latencies for the first oscillatory spindles, not phase locked to a moving stimuli, occured at approximately 400 ms (Eckhorn et al. 1990, Bauer et al. 1995), which is consistent with the findings in the human EEG, where induced gamma band activity does not appear earlier than 256 ms. However, stimulus evoked activity (i.e. responses phase locked to the stimulus) occur within the first 100 ms after stimulus presentation (Eckhorn et al. 1990, Bauer et al. 1995, Pantev et al. 1995). The late appearance of stimulus induced activity suggests a fundamental difference between evoked and induced oscillations. Eckhorn and co-workers (1990) speculated on the complementary features of the two types of oscil-

lations. They assumed that "evoked responses serve to define crude instantaneous "preattentive percepts", and stimulus-induced oscillatory synchronization mainly support the formation of more complex, "attentive percepts" that require iterative interactions among different processing levels and memory" (page 302).

A similar interpretation was provided by Pulvermüller (1996) with respect to word processing. He assumes that the first fast evoked responses may be related to the activation or ignition of a cell assembly and the later induced responses are related to the sustained activity of the network which might also include further cognitive processes.

For now it seems that induced gamma band activity occurs later than the evoked cortical activity. Differences in latencies across studies may be attributed to different tasks and the respective time resolution of the analysis method used. However, the relation between early evoked components and late induced components remain speculative until further research provides clearer evidence.

The functional relevance of induced gamma band responses is still under debate (e.g. Tovee and Rolls 1992, Young et al. 1992, Bair et al. 1994, Singer and Gray 1995). Evidence that induced gamma band responses may be linked to feature binding was recently put forth by Tallon and co-workers (1995). The presentation of an illusory triangle (Kanizsa triangle) produced 30 Hz-activity most pronounced around the vertex (Cz). A control stimulus without the illusory quality (achieved by rotation of the inducing disks) elicited no such gamma band response. In a subsequent study, Tallon-Baudry et al. (1997) found induced gamma band responses when subjects had to perceive a Dalmation. In addition, it was shown that induced gamma band activity is related to word processing (Lutzenberger et al. 1994, Eulitz et al. 1996, Pulvermüller 1996, Pulvermüller et al. 1996a,b) and to a sensory motor task (Kristeva-Feige et al. 1993). These findings are lending strong support to the hypothesis that macroscopically visible gamma band activity is functionally relevant. Nonetheless, more conclusive evidence is needed to determine whether this response is actually linked to feature binding.

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