

Research report

Bisensory stimulation increases gamma-responses over multiple cortical regions

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Abstract

In the framework of the discussion about gamma (approx. 40 Hz) oscillations as information carriers in the brain, we investigated the relationship between gamma responses in the EEG and intersensory association. Auditory evoked potentials (AEPs) and visual evoked potentials (VEPs) were compared with bisensory evoked potentials (BEPs; simultaneous auditory and visual stimulation) in 15 subjects. Gamma responses in AEPs, VEPs and BEPs were assessed by means of wavelet decomposition. Overall maximum gamma-components post-stimulus were highest in BEPs ($P < 0.01$). Bisensory evoked gamma-responses also showed significant central, parietal and occipital amplitude-increases ($P < 0.001$, $P < 0.01$, $P < 0.05$, respectively; prestimulus interval as baseline). These were of greater magnitude when compared with the unisensory responses. As a correlate of the marked gamma responses to bimodal stimulation we suggest a process of ‘intersensory association’, i.e. one of the steps between sensory transmission and perception. Our data may be interpreted as a further example of function-related gamma responses in the EEG. © 2001 Elsevier Science B.V. All rights reserved.

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1. Introduction

Due to their excellent temporal resolution event-related potentials (ERPs¹) are widely used to analyze perceptual and cognitive processes. As correlates for these, ERP components in the gamma-band (frequency range of 30–80 Hz) have been proposed [37,29,38,85,8].

The present study is an attempt to find ERP correlates associated with processes of multisensory convergence, i.e. the initial steps of joining the information from more than one sensory modality.

1.1. Bisensory convergence

The majority of our *real* world experiences and our *virtual* inner representations consists of complex signals. Elementary inputs from different modalities are used to create in a highly complex manner what we call *perception*.

Wundt [91] furthermore distinguished pure sensory perception from ‘apperception’ (attentive perception, the recognition and association of that perception). Later on Flechsig [31] proposed apperception to be one of the leading functions of the frontal lobes.

It has been suggested that one step to the better understanding of conscious (*cognitive*) processes would be to focus on how the streams of sensory information are organized throughout the brain and how a stream is joined to be part of a robust multisensory perception (association) and on the other hand can be maintained as an elementary

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¹The term ‘ERP’ will be used as a general term to subsume auditory evoked potentials, visual evoked potentials and bisensory evoked potentials.

impression to be extracted from the whole (discrimination) [43].

Functional specialization of the mammalian brain, according to most modular concepts, develops with the occurrence of internal and external experiences. Various electrophysiological studies support the assumption of intersensory relationships between functionally and locally different cortical areas:

- In congenitally deaf persons the lack of early auditory experiences influences the organization of the human brain for visual processing. Visually evoked potentials (VEPs) from congenitally deaf adults are altered to be significantly larger over both auditory and visual cortical areas when compared to normal hearing adults [59].
- Plasticity of primary-sensory cortices (somatosensory and visual) has been demonstrated in blind Braille-readers [24,79]. ‘Blindsight’, i.e. the ability of cortically blind to react to stimuli in the ‘blind’ visual field at well-above chance levels [89], interferes with the view of strict localization once more.
- Variants of perception like *synaesthesia* (e.g. impression of color when listening to words which are neutral in this respect) illustrate that the analysis of intermodal integration is promising for comparing localized modular versus dynamic network properties of the brain [61,72].

1.2. Gamma-band phenomena

High frequency oscillations in the gamma-range (≈ 40 Hz) have become a widely discussed phenomenon in the neurosciences. Computer simulations of several parts of the brain suggest that gamma rhythms can be generated by pools of excitatory neurones, networks of inhibitory neurones, or networks of both excitatory and inhibitory neurones [44]. Extending both beyond species [20,36] and localization [76,8], a large body of experimental findings stresses the rather complex nature of this group of brain rhythmicities.

First interest in these phenomena was triggered by the pioneering studies of Adrian [2], who reported the occurrence of fast (35–45 Hz) rhythmical discharges in the olfactory bulb of the hedgehog upon application of odorous stimuli. According to Lavin et al. [49] and Hernandez-Peon et al. [42] 40 Hz activity was not restricted to olfactory stimuli but could rather be elicited by a wide range of other conditions. Başar and Özesmi [10] introduced the term ‘gamma-response’ to describe hippocampal gamma-range activity to external stimuli in cats. Enhanced gamma-activity was especially seen in structures which were able to fire in this mode spontaneously (‘gamma-resonance’). 40 Hz oscillatory responses were also ob-

served in humans [37]. Further studies found gamma-range activities associated with visual [29,38] and olfactory [33,34] sensation. For a comprehensive review cf. [14,6,7].

Galambos [36] suggested to classify the various findings of gamma-band activities measured in different species in a categorical system:

1. The *spontaneous* gamma-activity, i.e. a fraction of the total EEG energy at any given moment without intentional stimulation [10,75].
2. The *induced* gamma-activity, i.e. activity initiated by, but not tightly coupled to a stimulus [2,33,35].
3. The *evoked* gamma-activity, which is both elicited by and strictly time-locked to a stimulus. Numerous examples have been studied in different brain regions of man and cat [5,12].
4. The *emitted* gamma-activity, i.e. activity which is not bound to a stimulus but rather to an internal process, which has been demonstrated for instance by use of the ‘omitted stimulus’ paradigm in non-mammalian vertebrates like fish [21] or mammals like cat [12].

Recent studies suggest that the 40 Hz oscillatory activity is not restricted to sensory processing, but can rather be modulated or triggered by cognitive processes as well [85,63,83]. Başar et al. [8] have argued that gamma-responses occur throughout the brain, i.e. in a distributed way, as correlates of brain functions, which can be sensory and cognitive in origin as well.

Since gamma-responses appear as correlates of various brain functions the question is raised whether gamma-activity is related to the linkage of different functions, e.g. the intersensory processes between audition and vision. If so, then the simultaneous presentation of pure stimuli in both modalities should lead to a change in amplitude, latency and/or distribution of the gamma-response when compared to unisensory conditions.

1.3. Wavelet decomposition of ERP

In order to quantify the amount of induced and evoked gamma-activity following bisensory stimulation, we used time–frequency analysis of single-trial ERPs.

Up to the moment, the most used quantitative method in the evaluation of EEG data is the Fourier transform (FT), which quantifies the amount of activity in frequency bands [28,50]. However, FT requires stationarity of the signal. EEGs (and ERPs by definition) are highly non-stationary [58,50,18,1]. Thus FT neglects the time evolution of the frequency patterns.

This disadvantage is partially resolved by using a Short-Time FT. With this approach, FT is applied to time-evolving windows of a few seconds of data smoothed with an appropriate function [71,19,64]. Then, the evolution of

the frequencies can be followed and the stationarity requirement is at least partially satisfied by considering the signals to be quasi-stationary in the order of a few seconds. However, one critical limitation to windowing data is an analogue of the Uncertainty Principle [22,23,80]. If the window is too narrow, the frequency resolution will be poor, and if the window is too wide, time localization will probably not be sufficient (and also, as for EEG signals, the stationarity requirement will not be satisfied). This limitation becomes important when the signal has transient components localized in time as is particularly the case in ERPs.

Grossmann and Morlet [40] introduced the Wavelet Transform (WT) in order to overcome some of these problems. Wavelets have a varying window size which leads to an optimal time–frequency resolution for all frequency ranges. That means a better localization in time can be achieved, and on the other hand, for a given time a better resolution in frequency can be obtained [52,22,80]. Furthermore, wavelet decomposition lacks the requirement of stationarity. These advantages are particularly important when analyzing event related potentials, where the latency jitter in the response of a certain frequency band can make the interpretation difficult.

In the last years WT has been introduced to the analysis of transient brain signals [4,1]. Preliminary results showed some advantage over the standard Fourier based methods [71,17,9,25,65].

1.4. Aim of this study

Frequency-selective enhancements of EEG-activity following audio–visual stimulation have been described earlier [7,70]. They appear as late theta-range components (4–7 Hz, \approx 150–200 ms latency), mostly fronto-centrally organized components of the bisensory evoked potentials. The following study will now concentrate on the early appearance of fast activities.

In this study we aimed to investigate evoked gamma-range (31–62 Hz) EEG-oscillations related with the processes originating from audio–visual stimulation, i.e. the evaluation of the time–frequency responses contained in unisensory (auditory, visual) versus bisensory (audio–visual) evoked potentials. In order to retain both time and frequency domain information of evoked responses multi-resolution decomposition based on the wavelet transform was performed. Wavelet coefficients obtained were analyzed in regard to temporal, spatial and modality-dependent characteristics.

We will introduce an easily reproducible experimental setup with use of simultaneously presented stimuli (auditory and visual). According to the aforementioned we predicted the surplus of information inherent in the simultaneous audio–visual stimulus presentation to be an active modifier of the gamma-response system as well.

2. Methods

2.1. Subjects

EEG and event-related potentials were measured from 15 right-handed subjects (8 male, 7 female, age: 26 (\pm 3) years) who had neither any known neurological deficit nor reported intake of drugs known to affect the EEG. Subjects rested comfortably in a sound-proof investigation chamber dimly illuminated and well climatized. Preceding our measurements basic personal data (handedness, age, name, past medical history, medical family history covering neurological and psychiatric aspects) was acquired during a standardized interview. Informed consent was obtained from all participants.

2.2. Data recording

Raw data was recorded with a set of Ag–AgCl disc electrodes placed on frontal, vertex, central, temporal, parietal and occipital recording sites (F3, F4, Cz, C3, C4, T3, T4, P3, P4, O1, O2) according to the international 10–20 system and referenced to linked earlobe-electrodes. Signals were amplified by means of a Schwarzer EEG machine. To prevent aliasing-effects a pass-band filter (0.1–70 Hz, -24 dB/octave) was applied. Additionally a 50 Hz notch filter (-36 dB/octave) was used to avoid main interferences. EEG–EP epochs (1 s pre- and 1 s post-stimulus) were digitized at a rate of 500 Hz. During all sessions paper recordings and video monitoring were used to reveal gross artifacts. Bipolar EOG (vertical–horizontal) and surface EMG of the frontalis muscle were recorded for off-line artifact rejection.

2.3. Experimental paradigms

A recording session consisted of 4 parts:

1. Registration of 2 min of spontaneous EEG within 60 sweeps with eyes open. This was used as a technical control and to ascertain that subjects were comfortable in the experimental surroundings (i.e. for visual inspection only).
2. AEP: Registration of 120 sweeps covering 2 s time-windows with 1 s application of unimodal stimulation presenting a 2 kHz sinusoidal tone binaurally at 80 dB (SPL).
3. VEP: Registration of 120 sweeps covering 2 s time-windows with 1 s application of unimodal stimulation using a rectangular light-stimulus centered in the visual field at a distance of 1.5 m. This resulted in intensities exceeding surrounding illumination by approximately 5 Lx.
4. BEP: Registration of 120 sweeps covering 2 s time-

windows with application of multimodal stimulation, i.e. stimuli of (2) and (3) were applied simultaneously.

All interstimulus intervals were pseudo-randomized ranging from 1.0 to 3.0 s on all conditions. Each subject was instructed to view and listen passively while maintaining focus on a marker placed in the middle of the visual stimulation field.

2.4. Data analysis

After visual inspection of the data, the last 30 sweeps free of artifacts were selected for each modality for future analysis. This was done in order to include only those trials where subjects were least affected by the novelty of the situation and thus were presumably viewing (listening) passively (i.e. ignored the stimuli). The multiresolution decomposition based on the wavelet transform was applied to each single sweep using a quadratic B-Spline function as mother wavelet (software by courtesy of Professor T. Demiralp and Doctor A. Ademoğlu, Istanbul, Turkey [1]). Quadratic B-Splines are semiorthogonal functions with compact support and nearly optimal time–frequency resolution [22,80].

After a five octave wavelet decomposition, the coefficients for the following frequency bands were obtained: 63–125 Hz, 31–62 Hz (gamma), 16–30 Hz (beta), 8–15 Hz (alpha) and 4–7 Hz (theta); the residues were in the 0.5–4 Hz band (delta). In this study, only the coefficients corresponding to the gamma band were analyzed.

For each subject the gamma coefficients of the 30 single sweeps were averaged. To obtain ‘grand averages’ results were averaged across subjects. We used a bicubic spline interpolation procedure [62] in order to map the absolute of the ‘grand average’ wavelet coefficients topographically for illustrative purposes.

2.5. Statistical analysis

For statistical analysis, the maximum absolute wavelet coefficient within a given frequency band was computed for each subject in a time window of 250 ms post

stimulation. These were subjected to a multiple factor ANOVA (MANOVA) for repeated measurements. Factors were modality with levels AEP, VEP and BEP, and electrode-site with levels according to montage. Greenhouse–Geisser correction procedure was applied to the analyses. The corrected degrees of freedom (*df*) and the probability values from reduced *df* are reported here (cf. [27] for a detailed description of statistical procedures).

Furthermore, maximum wavelet coefficients and their absolute differences in a time window of 250 ms pre- and post-stimulus were compared by means of paired *t*-tests in order to check for statistical significance of amplitude enhancements for each electrode and modality.

3. Results

Gamma wavelet coefficients of a typical subject are shown in Fig. 1. Wavelet coefficients according to each stimulus condition (AEP, VEP, BEP) and electrode position (9 positions, indicated at the bottom of each particular curve) are displayed for their pre-stimulus (–1 s) and post-stimulus (1 s) course. In comparison with unisensory EPs, bisensory evoked gamma amplitude enhancements (pre- versus post-stimulus) are more pronounced in central electrodes. In this case, pre-stimulus peak-to-peak amplitude is less than 5 (in arbitrary units) and post-stimulus amplitudes reach up to 12 in Cz. Further increases are seen in right frontal and right occipital electrodes, in the latter case appearing with some delay. Similar curves were observed in 12 of our 15 subjects.

Fig. 2, instead, corresponds to another subject with no evoked gamma response, this behavior being also present in two other subjects (out of 15). A possible explanation for the lack of enhancement is the presence of muscle artifacts in nearly all the recordings, generating a poor signal to noise ratio that hides any possible evoked response. Arousal level, high pre-stimulus activity and low phase locking between single sweeps can also have a determinant effect.

The grand average of all 15 subjects is shown in Fig. 3. With auditory stimulation enhancements are visible in

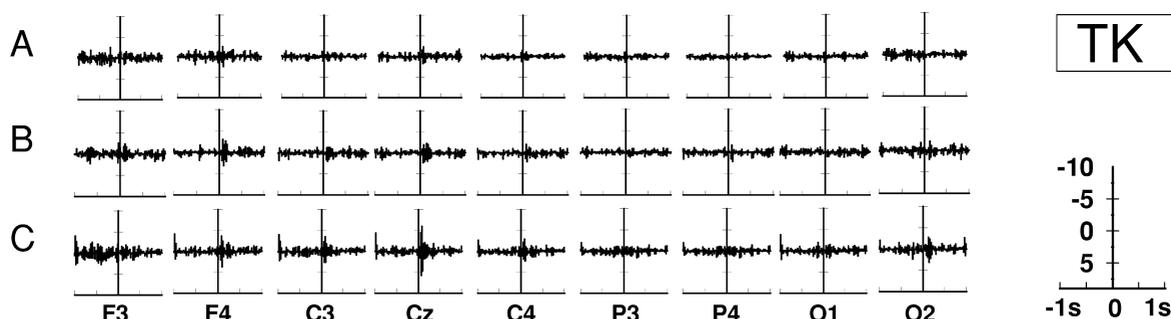


Fig. 1. Gamma band wavelet coefficients for a typical subject (TK). Along the x-axis one second pre- and post-stimulus are plotted with y-values in arbitrary units. (A) Auditory evoked potentials, (B) visually evoked potentials and (C) bisensory evoked potentials.

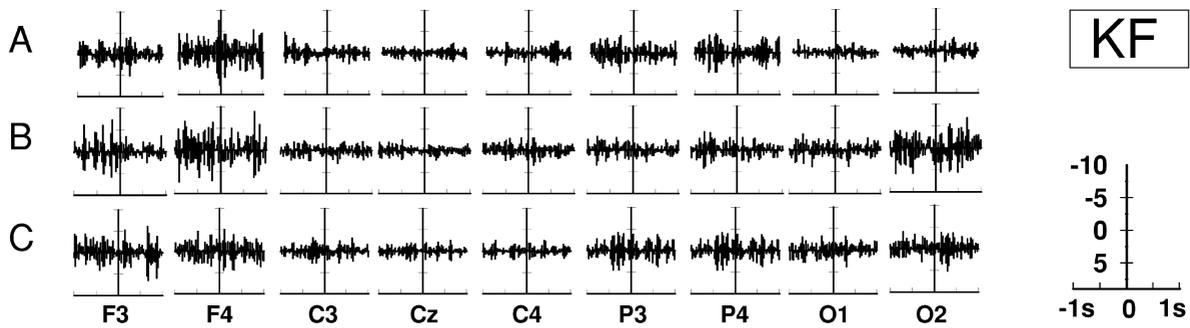


Fig. 2. Gamma band wavelet coefficients for a subject (KF) with no evoked gamma response. Along the x-axis one second pre- and post-stimuli are plotted with y-values in arbitrary units. (A) Auditory evoked potentials, (B) visually evoked potentials and (C) bisensory evoked potentials.

central locations and more poorly defined in the occipital ones. Visual stimulation shows enhancements only in C4 and Cz. On the other hand, bimodal stimulation evokes significantly higher enhancements than the other two modalities (also see Fig. 8). These enhancements are distributed diffusely in the surface EEG, being most pronounced in the central locations. On this stimulus condition the pre-stimulus EEG yield a peak-to-peak amplitude lower than 3 and post-stimulus responses reach values up to 9. Although distributed diffusely, bimodal responses are most overt in central electrodes and especially in the frontal ones, where enhancements occur upon bimodal stimulation exclusively.

Topographical maps of the rectified gamma-coefficients following auditory, visual and bimodal stimulations are shown in Figs. 4–6. Note that only the post-stimulus courses and these normalized to the prestimulus mean are illustrated. Here a very low gamma-signal can be seen at the start of AEP activity (about 64 ms) in central sites. AEP activity remains nearly restricted to these areas, thus finishing around 112 ms after stimulus presentation. VEP gamma-activity starts later, at about 80 ms, in central and posterior sites, then spreading diffusely, thus ending around 180 ms after stimulus presentation. BEP activity starts markedly in central sites at about 64 ms, then spreading to the whole head, thus ending around 160 ms after stimulus, with occipital activity lasting up to 220 ms.

Multivariate statistics (Table 1) disclosed the significant

effect of factors ‘modality’ and ‘lead’ on the amplitude of maximum gamma-coefficients following stimulation (both $P < 0.01$). There were no differences in spatial patterns of gamma-responses across stimulation paradigms that were unexplained by random variance (‘modality*lead’ interaction, n.s.).

In Fig. 7, the comparisons between the maximum coefficient before and after stimulation are shown for each electrode and modality. Enhancements are highest upon bimodal stimulation in right frontal, parietal and central electrodes, where they reach high significance ($P < 0.001$).

Fig. 8 shows the grand average of differences in gamma-band wavelet coefficients before and after stimulation. In BEP increases are significantly higher when compared to AEP and VEP ($P < 0.01$, respectively). Furthermore the increases in BEP are significantly greater than the linear sum of AEP and VEP (AEP+VEP).

4. Discussion

In order to summarize the results of our investigations briefly it can be stated that gamma band enhancements were significantly higher upon bimodal stimulation, especially in central electrodes. This phenomenon was observed in the grand average as well as in the single subject plots. Furthermore, our data imply that bimodal responses are not a pure superposition of the auditory and visual

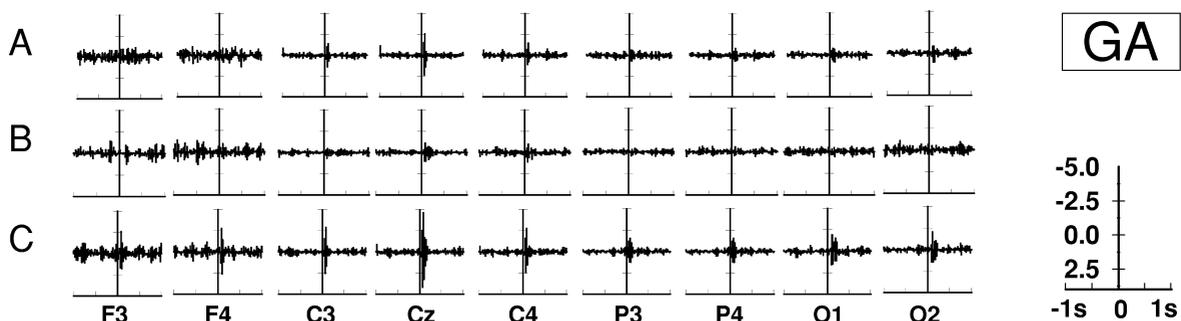


Fig. 3. Grand average (GA, $n = 15$) of the gamma band wavelet components. Along the x-axis one second pre- and post-stimuli are plotted with y-values in arbitrary units. (A) Auditory evoked potentials, (B) visually evoked potentials and (C) bisensory evoked potentials.

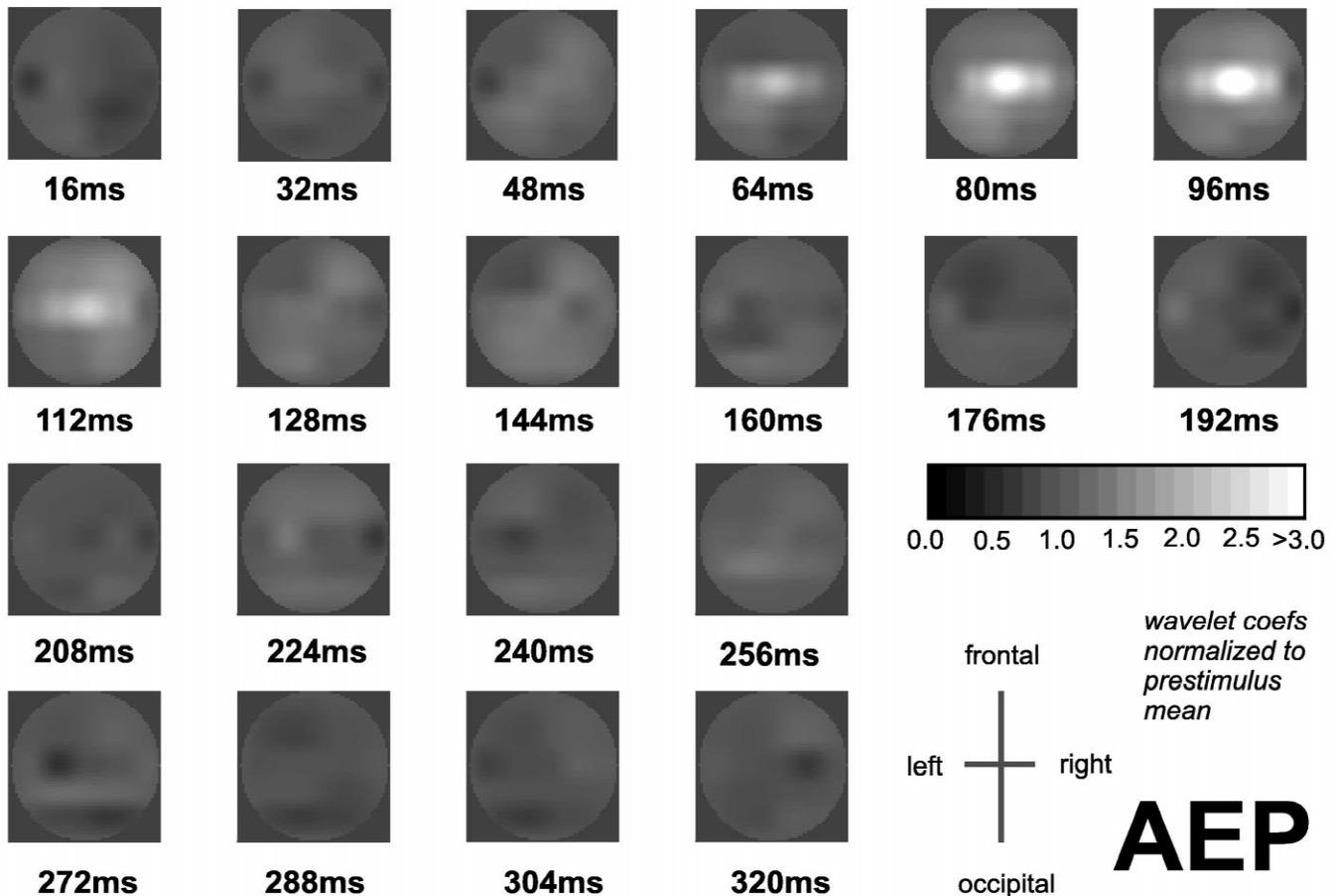


Fig. 4. Topographical representation of the rectified amplitude response for the gamma band (mean values, $n = 15$). Auditory evoked potentials.

ones. Then, a sensory process solely related with the appearance of both stimuli together (and not with the mechanisms triggered by each stimulus separately) should be considered.

One hypothetical explanation of this bimodal response could be a fast synchronized activity, transmitting the information that two different sensations are manifestations of the same process.

In the following we will discuss these issues both in view of our methodological approach and the basis of previous studies. In conclusion, a comprehensive model on the function of human gamma-range brain activities will be suggested.

4.1. Methodological issues — new parameters and techniques

One of the main advantages of WT over conventional digital filtering is the lack of the stationarity requirement. This assumption is crucial in the analysis of brain signals, already known to be highly non-stationary. Moreover, owing to the varying window size of the WT, an optimal time–frequency resolution for all frequency ranges can be

achieved allowing a more precise determination of the responses to the stimulus. Indeed, with WT we obtained a time resolution of 8 ms and a frequency resolution of 31 Hz (comprising the gamma band, between 31 and 62 Hz), both being crucial for the present study. We should remark that no time resolution is obtained by using the FT and that in the case of the Short-Time FT, parameters such as the window size and the tapering function should be carefully set in order to obtain a reasonable resolution. General advantages of WT in brain signals were discussed in previous works [4,84,71,3,15,17,25,9,65]. The particular details of the algorithms used in this study were comprehensively discussed by Ademoğlu et al. [1] and Başar et al. [9].

In comparison with adaptive digital filtering methods based on FT [5] the newer WT widely confirms the frequency-characteristics of the EEG under stimulation [69,9,65] with the surplus of a simultaneous time–frequency resolution.

A method such as WT with good resolution in both time and frequency domains is advantageous for comparing psychophysiological correlates of responses in different frequency ranges. In particular it is possible to differentiate

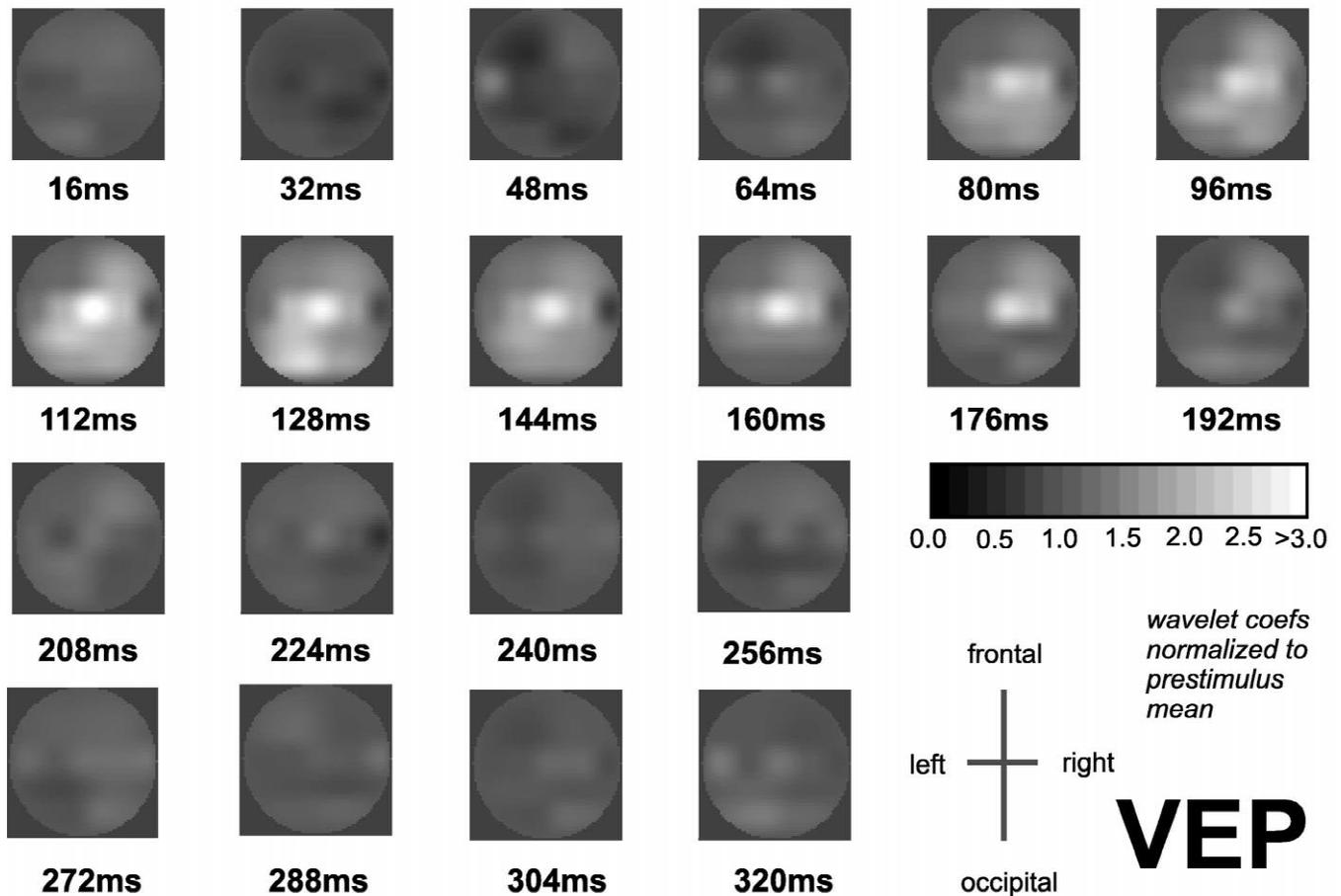


Fig. 5. Topographical representation of the rectified amplitude response for the gamma band (mean values, $n=15$). Visually evoked potentials.

between early gamma responses and later theta responses (4.0–7.0 Hz, approx. 150–200 ms), the latter with a latency rather not related with primary sensory responses.

4.2. Experimental studies of bisensory integration and its role in perception

Studying processes of bisensory integration sheds light on both localized modular and dynamic network properties of the brain. Two exemplary variants of perception illustrate this idea:

- It is well known that in a small percentage of a population (synaesthetists) visual and auditory perception is not strictly divided so that experiences from one modality could reproducibly trigger sensations in the other. Both electrophysiological methods [72] and brain imaging by PET [61] suggest a crucial role of anterior brain areas.
- McGurk and MacDonald [53] demonstrated the phenomenon that speech perception is not simply an

auditory but an intermodal one ('McGurk effect'). The effect of this mismatch between auditory signal and the visual signal was to create a third phoneme different from both the original auditory and visual speech signals. An example is dubbing the phoneme /ba/ to the visual speech movements /ga/. This mismatch results in 'hearing' the phoneme /da/. It can be demonstrated in children but is stronger in adults. Mismatches between haptic (touch) speech input and auditory speech input also creates the McGurk effect [32,81].

Mainly on the animal level phenomena of intersensory facilitation have been studied extensively. It was reported that not only subcortical structures (e.g. superior colliculus) [54,55,41] but also higher areas of both archi- and neocortical origin [87,88,78] are involved in processes of multimodal convergence. Yet no time–frequency analyses have been reported in this scope.

Some data is available on the role of 40 Hz oscillatory processes in audio–visual integration. At least two studies explored intermodal effects on driven gamma-rhythms.

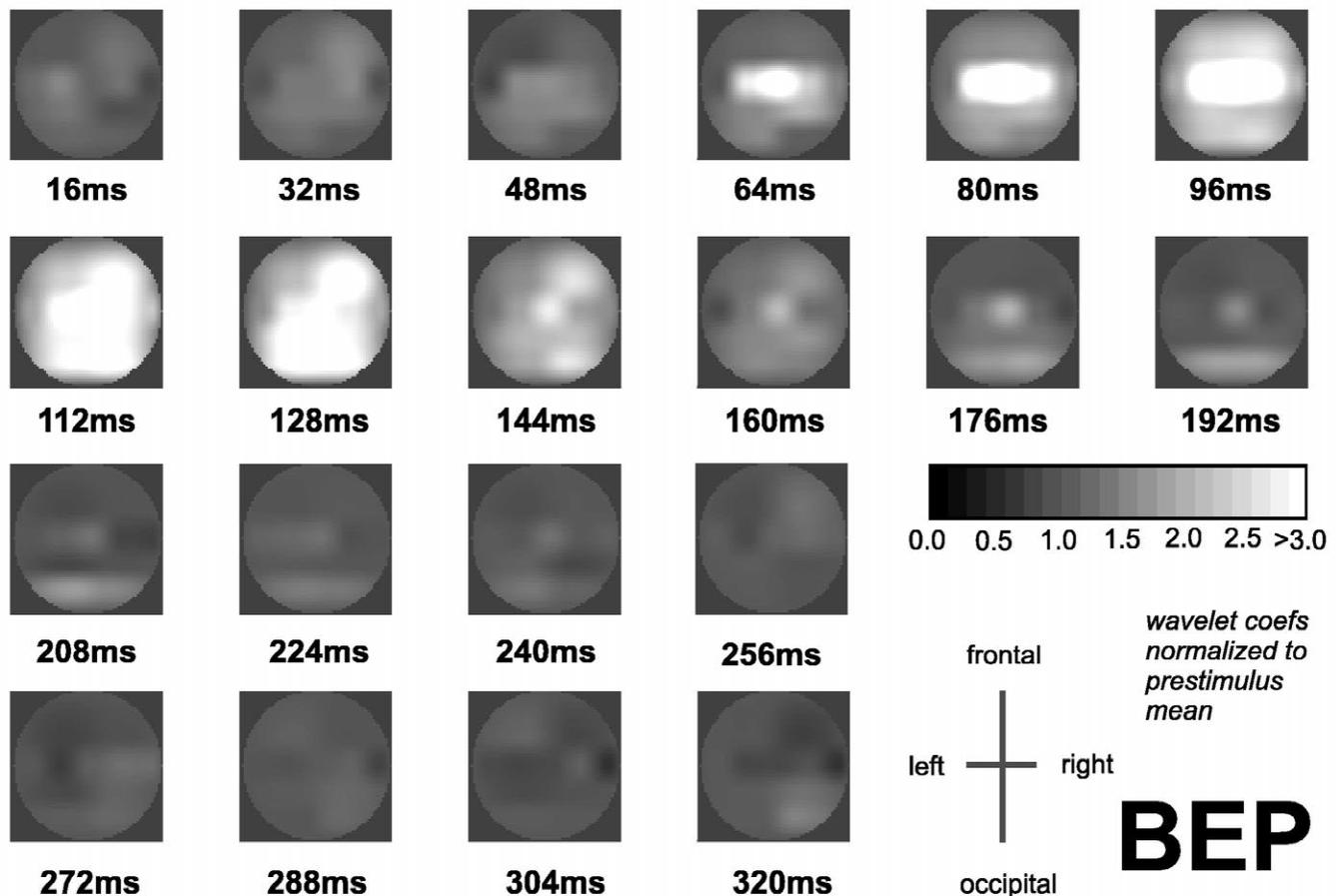


Fig. 6. Topographical representation of the rectified amplitude response for the gamma band (mean values, $n = 15$). Bisensory (audio–visually) evoked potentials.

- Sheer and Schrock [77] conducted their studies on focused attention by looking for modifications in 40 Hz SSRs ('steady-state responses') driven by means of simultaneously applied click-and-flash stimuli, from which one or the other modality had to be ignored. When the stimulus trains were not in phase, they found the 40 Hz SSRs of the non-focused stimulus modality reduced.
- Other modes of intermodal perturbation of the 40 Hz SSRs have been tested by Rohrbaugh et al. [68]. Both salient 'foreground' visual and auditory stimuli induced a latency and amplitude decrease in the 40 Hz auditory steady-state responses. Stimuli of the same modality dominated in effect.

Table 1

Results of Greenhouse–Geisser corrected tests of computed maximum wavelet coefficients on within-subjects factors 'modality', 'lead' and interaction ($n = 15$)^a

	<i>df</i>	<i>F</i>	<i>P</i>
Modality	1.6; 22.9	9.83	**
Lead	3.6; 51.3	5.32	**
m*l	4.1; 56.7	1.61	n.s.

^a Significance indicated: * $P < 0.05$; ** $P < 0.01$.

Thus it is very likely, that intermodal functions are modifiers of the 40 Hz surface EEG.

4.3. Event-related gamma-oscillations

Gamma-range rhythmic potential changes in neural structures have been thoroughly discussed during the last decade. They have been associated with diverse functions, according to their multifold conditions of occurrence. One of the leading questions has been whether they are predominantly associated with 'sensory' or 'cognitive' tasks. According to empirical findings we will stick with this dichotomy and differentiate task- or event-related gamma-activity as either sensory or cognitive gamma responses.

As for event-related gamma oscillations, among the most prominent examples have been oscillatory responses in the frequency range of 40–60 Hz occurring in synchrony within a functional column in the cat visual cortex [39,29]. This has been suggested to be a possible mechanism of feature linking in the visual cortex and was related to the 'binding problem'. This proposal, however, does not fully explain the 'ubiquity of gamma rhythms' [26,73].

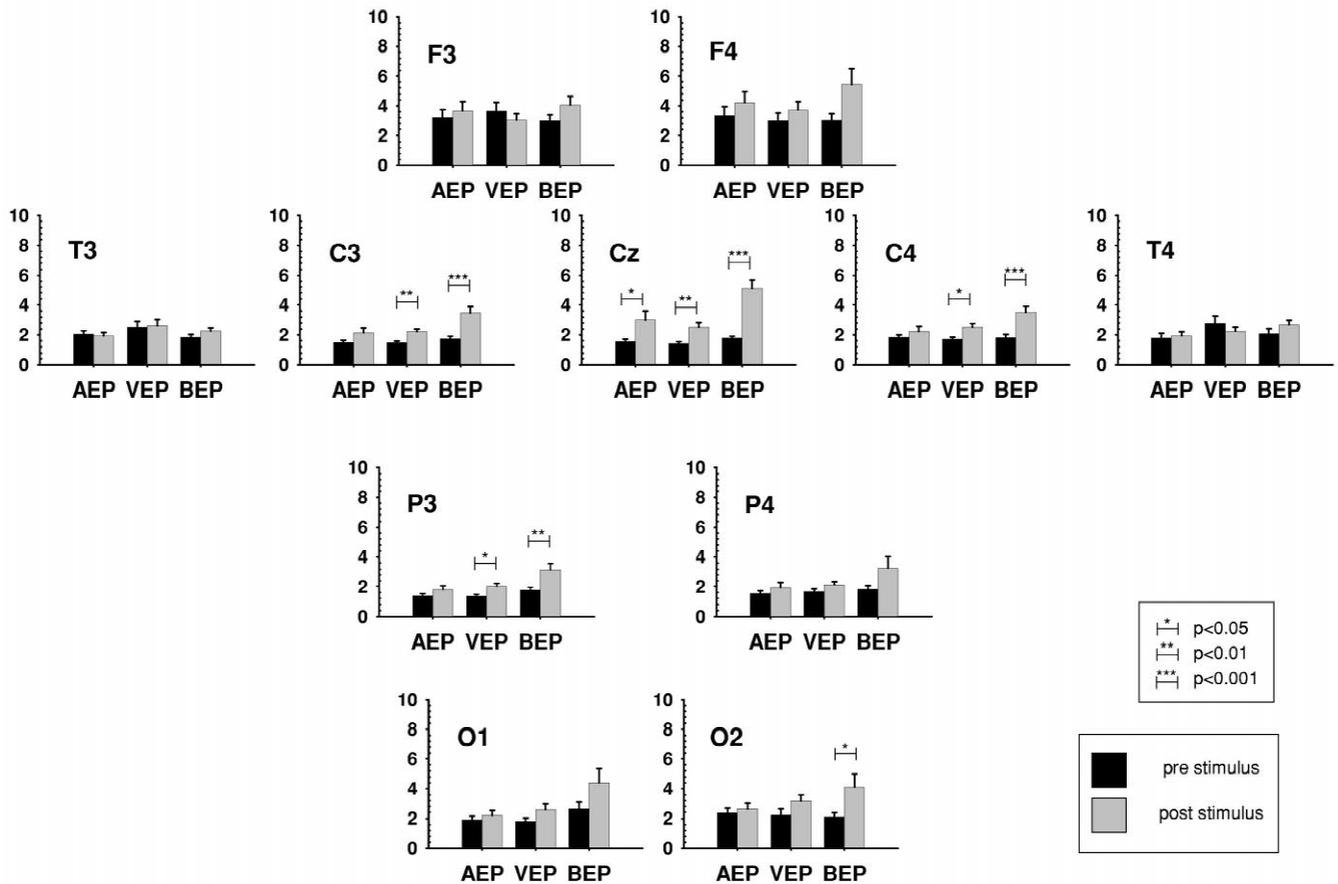


Fig. 7. Comparison of pre- and post-stimuli maximum coefficients for each electrode and modality. Y-values in arbitrary units (mean and standard error). Single graphs represent (from top to bottom) frontal, centro-temporal, parietal and occipital electrode rows.

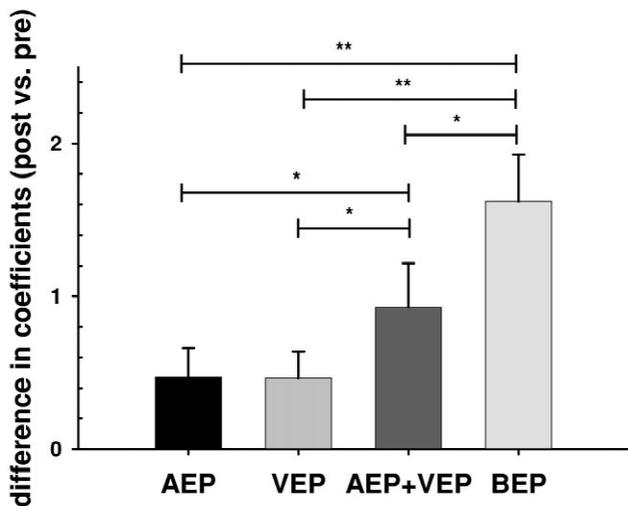


Fig. 8. Difference in gamma band wavelet coefficients before and after stimulus, mean and standard error ($n=15$) for the three modalities: ‘auditory’ AEP, ‘visual’ VEP and ‘bisensory’ BEP. AEP+VEP summed differences of AEP and VEP. Significance indicated for ($P<0.05$: *) and ($P<0.01$: **).

Furthermore, 40 Hz oscillatory activity is not restricted to sensory processing (e.g. encoding of *gestalt*), but can rather be modulated or triggered by cognitive processes as well. Studies suggest that even high-level cognitive functions like selective attention [85] and language processing [51,63] are associated with synchronized gamma-range activity.

4.3.1. Gamma-responses with correlates in sensory processing

Our result of enhanced gamma-responses in bimodal stimulation complements earlier works with respect to synchronized gamma-activity in relation with sensory and cognitive processing. Numerous studies show that gamma-responses are closely related with sensory processing.

- An early phase locked 40 Hz response was recorded in visceral ganglia of *Helix pomatia* using electrical stimulation [74]. In arthropods, light-induced gamma responses have been observed [47].

- In unanaesthetized rats gamma-oscillations have been found in epipial derivations adjacent to somatosensory cortices when afferent information was provided by the vibrissae. It was suggested that synchronized gamma-oscillations may play a role in assembling punctate information into a coherent representation of a somatosensory stimulus [45].
- Auditory and visual gamma responses are selectively distributed in different cortical and subcortical structures. They are phase-locked, stable components of EPs measurable in cortex, hippocampus, brain stem and cerebellum of cats that occur about 100 ms after sensory stimulation and secondly with approximately 300 ms latency [5,73].
- A phase-locked gamma oscillation is also a component of the human auditory and visual response [11]. Converging results with six cognitive paradigms imply that the 40 Hz response in the 100 ms after stimulations has a sensory origin. Here it was suggested that the early gamma-response is independent of cognitive tasks [46].
- The auditory MEG gamma response is similar to human EEG responses with a close relationship to the middle latency auditory evoked response [60].

These examples show that gamma-responses are highly preserved in neural networks extending from snail ganglia up to the highest mammalian brain. They are not likely to be modality-specific and are not restricted to neocortical areas of the brain.

In the current study, maximum wavelet coefficients occurred within 100 ms of sensory stimulation, regardless of stimulus condition. They tended to appear earliest after bisensory stimulation, i.e. starting markedly at 64 ms post-stimulus. These results, however, should not be mistaken for the low amplitude high frequency wavelets that have been observed in the electro-retinogram (ERG) of man. On the basis of simultaneous recordings of surface potentials and ERG wavelets to flash stimuli Whittaker and Siegfried [90] argued that wavelets after 35 ms were more likely generated from subcortical and cortical structures rather than retinal sites.

4.3.2. Gamma-responses with correlates in cognitive processing

The impact of cognitive tasks on the gamma-band has gained considerable interest in recent years. Long-distance synchronization has been suggested as a mechanism for the linkage of spatially segregated cortical areas [48,86,67].

Our results do support that in contrast to simple light and tone stimuli, processing of simultaneous, bisensory stimuli has to involve preattentive cognitive functions. The synchronization of external stimulus presentations could trigger a counterpart internal synchronization of the systems involved. This in turn could be a key for the internal interpretation of these events as being related to one another.

There are several investigations that imply a relationship of gamma-responses with cognitive processes especially related to (i) perception, (ii) attention and (iii) learning. The following list of exemplary studies emphasizes this conjecture:

- During visual perception of reversible or ambiguous figures a significant increase (almost 50%) in gamma EEG activity can be recorded from frontal scalp positions in humans [13].

Presentation of coherent versus non-coherent visual stimuli triggers an early phase-locked 40 Hz component, maximal at electrodes Cz-C4, which does not vary with stimulation type. A second 40 Hz component appears around 280 ms. This is not phase-locked to stimulus onset and is stronger in response to a coherent stimulus. Tallon-Baudry et al. [82] suggest that this could reflect a mechanism of feature binding on the basis of high-frequency oscillations.

Rodriguez et al. [67] reported that the process of pattern-recognition affects gamma-band activity and (independently) phase-synchrony based on whether coherent ('Mooney' faces) or non-coherent shapes are presented. The authors argue that the process of perception is reflected mainly in phase synchrony.

- The P300 is a positive deflection that typically occurs in human ERPs in response to 'oddball' stimuli or omitted stimuli interspersed as 'targets' into a series of standard stimuli: A P300-40 Hz component has been recorded in the cat hippocampus, reticular formation and cortex (with omitted auditory stimuli as targets). This response occurs approximately 300 ms after stimulation, being superimposed on a slow wave of 4 Hz [12]. Preliminary data indicate similar P300-40 Hz responses to oddball stimuli in humans. However, a suppression of 40 Hz activity after target stimuli has also been reported [30].

Selective attention enhances auditory 40 Hz responses in humans when compared to both 'non-attend' and 'reading' control conditions. This effect is most pronounced over the frontal and central areas [85].

- Tallon-Baudry et al. [83] reported that retrieval of visual experience from short-term memory (mental imagery) is associated with 40 Hz activity. Induced gamma-band activity could be observed during the delay (memorization). When no memorization was required, this activity disappeared.

Gamma-band activity peaked during the rehearsal of the first stimulus representation at both occipito-temporal and frontal electrodes. Gamma-band coherence increases between regions of the brain that received different classes of stimuli (haptic and visual) in an associative learning task [57]. The authors suggest that the increase in coherence could fulfill the criteria required for the formation of hebbian cell assemblies,

thus linking the activities of distant brain areas for associative learning.

These studies indicate that synchronized gamma-activity is associated with cognitive functions. However, time-scale has to be kept in mind critically. In view of previous results [70] enhancements of later ERP-components, shown to be prominent in the theta-band, are rather candidates that have been associated with higher-order cognitive processes. Evoked early gamma-responses are related with sensory processing [46], but, on the other hand, could be also functional correlates of preattentive, intersensory processing. So, in comparison with above cited investigations, bisensory evoked gamma responses within the first 100 ms are not likely to reflect learning processes, whereas these and early phase-locked gamma associated with perceptual activity or attention could be likewise correlates of lower cognitive functions.

4.4. Bisensory gamma responses — generated by a selectively distributed gamma-response system?

According to Raij [66] cortical activation following audio–visually presented stimuli involves multiple cortical regions. The multisensory processing of simultaneously presented phonemes and characters resulted in extensive activity over (pre)rolandic, posterior parietal and superior temporal regions. These were partially overlapping with those areas also involved in visual imagery of the same stimuli.

Our topographical plots of the bisensory gamma-response stress the qualitative differences between bisensory and unisensory stimulus conditions where, upon bisensory stimulation, gamma-responses appear early and spread through the entire surface recording. While our findings imply a significant early frontal, central and occipital activation we emphasize that conclusions about the origin and exact course of evoked activities seem premature, taking into account the number of electrodes we used [16].

Moreover, since fast oscillations have been observed in several brain structures and in association with various functions ranging from pure sensory processing to attention and cognition, it would not be plausible to attribute our findings to one specific system. Possible correlates of frequency-selective enhancements upon audio–visual stimulation could be arousal and/or intersensory association of stimuli. As we observed the maximum rise in gamma-range coefficients to be most expressed in fronto–centro–parietal locations, it could reflect (pre)attentive association processes due to the supramodal workload of the brain.

They could have a conceptual parallel in ‘selectively distributed processing’ of neurocognitive networks [56]. In Mesulam’s neurological model of cognition, the unimodal areas of cortex provide the most veridical building blocks of experience. Transmodal nodes bind information in a way that introduces temporal and contextual coherence.

The formation of specific templates belonging to objects and memories occurs in distributed form but with considerable specialization. This arrangement leads, as Mesulam argues, to a highly flexible and powerful computational system.

Taking into account this hypothesis and the wide spectrum of functionally relevant gamma-responses, the existence of a selectively distributed parallel processing gamma system with multiple functions has been proposed [8,6,7]. According to this hypothesis gamma-oscillations are important building blocks of electrical activity of the brain, related to multiple functions. They may (i) occur in different and distant structures and (ii) show phase locking, time locking or weak time locking [92]. In this framework gamma oscillations have been suggested to represent a universal code of CNS communication [7].

In this context, gamma-band responses that follow bimodal stimulation (as reported in our study) might be electrophysiological correlates of this distributed gamma system. They could be a measurable substrate of those associative (intersensory) activities in the human brain that produce the coupling of subsystems related to different sensory modalities.

5. Conclusion

According to our findings, gamma (40 Hz) responses to bimodal stimuli (occurring less than 100 ms after stimulation and widespread over the scalp) could be a correlate of the process of multisensory convergence.

We tentatively assume that inside the *concerto grosso* of cortical neurons specific subsystems become coactivated in a 40 Hz oscillatory manner. In view of the current findings, this is in congruence with the hypothesis of a selectively distributed gamma-response system as proposed by Başar [6,7]. As with other types of oscillatory activity results from several laboratories imply that it is not possible to assign unique functions to gamma-responses. Especially complex and integrative brain functions appear to be manifested in a superposition of several (delta, theta, alpha and gamma) oscillations.

According to these findings we suggest, that electrophysiological approaches to preattentive (‘close-to-cognitive’) functions of the human brain provide useful keys for the understanding of spatio–temporal information encoding.

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