A cross-laboratory study of event-related gamma activity in a standard object recognition paradigm

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This study proposes a standard paradigm for the investigation of visual information processing by means of gamma activity and presents a novel set of stimuli with a broad range of complex, coloured familiar real world and unfamiliar nonsense objects which are well matched with respect to physical stimulus properties. In order to demonstrate that the paradigm and stimulus set yield reliable results both were employed in two electrophysiological investigations in two independent laboratories. Participants were required to discriminate familiar from unfamiliar stimuli. The pattern of results was very consistent across laboratories. Early event-related potentials were not influenced by the stimulus type suggesting that physical stimulus properties did not confound object familiarity. Induced gamma band activity was stronger for familiar than for unfamiliar objects, supporting the notion of gamma activity as a signature of cortical networks underlying object representations.
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Introduction

A great deal of research in cognitive neuroscience has relied on established experimental paradigms which have been tailored for investigations of a certain cognitive or perceptual phenomenon. For instance, spatial attention has been studied intensively with spatial cueing paradigms in which the P1 and N1 event-related potentials (ERPs) are larger for stimuli presented at cued locations than for stimuli presented at uncued locations. Researchers who have employed this paradigm could reveal that visuo-spatial attention acts as a sensory gain-control at early stages of visual processing (cf. Herrmann and Knight, 2001; Luck et al., 2000; Müller and Hillyard, 2000). This example shall illustrate that the

success of an experimental paradigm relies on its capability to elicit reliable responses and on the extend to which one can interpret these responses as a correlate of the cognitive or perceptual process in question. The present article offers a similarly feasible experimental paradigm for the investigation of visual object processing by means of high-frequency EEG oscillations in the gamma band range (frequencies above 20 Hz).

Although the precise functional role of gamma band activity in human EEG is still a matter of debate it seems very likely that high-frequency oscillations are closely linked to memory-related processes and visual object processing (Tallon-Baudry et al., 1998; Gruber et al., 2004b; Herrmann et al., 2004c; Müller and Keil, 2004). Induced gamma band responses signify activated contents of long-term memory, which have to be integrated in order to establish a cortical object representation of a stimulus and which consist of perceptual, semantic, and task-related features (Gruber and Müller, 2005, 2006). Cell assemblies underlying such representations can be distributed across different functional brain areas (Singer and Gray, 1995; Gruber et al., 2006; Tallon-Baudry and Bertrand, 1999). The fact that the semantic content is emphasised in this definition argues for the use of experimental designs which employ stimuli with substantial semantic content. Furthermore, it appears that such high-frequency activity can provide information which is not readily obtained from ERPs. For instance, Herrmann et al. (2004b) found that early phase-locked (evoked) gamma activity elicited by line drawings of familiar objects is stronger than gamma responses evoked by nonsense figures. In this study effects in the gamma band considerably preceded those of the broadband ERP. Gruber and Müller (2005) demonstrated that later non-phase-locked (induced) gamma activity dissociates between associative stimulus content during repetition priming, whereas ERPs did not. Moreover, in a recognition memory experiment induced gamma activity was found to be larger for subsequently recognised items during encoding and larger for old as compared to new stimuli at test (Gruber et al., 2004b). These gamma band effects preceded those of ERPs.

According to the match-and-utilisation model (MUM, cf. Herrmann et al., 2004c) a match between a stimulus and perceptual memory traces enhances the early evoked gamma activity by

means of enhanced synaptic connections and stronger feedback from higher into lower visual areas. Gruber and colleagues proposed a similar matching mechanism for the later induced GBR. In particular, they pointed out that induced GBRs do not only reflect the activation and integration of perceptual stimulus properties but also of the semantic features of an object (Gruber and Müller, 2005). Furthermore, it was demonstrated that the activation of an object representation is not merely an automatic consequence of incoming sensory information, but is influenced by implicit and explicit mnemonic requirements (Gruber and Müller, 2006). This interpretation is in line with some aspects of MUM, in which it is claimed that induced gamma oscillations signify the "utilisation" of a cortical network based on memory processes.

Future studies on the role of gamma activity in visual object processing and visual memory would benefit from a common experimental paradigm, similar to the established paradigms mentioned above. This seems all the more important as research on gamma activity in human EEG is frequently contested. Part of the criticism is based on failures to find gamma activity at all (Juergens et al., 1999) or claims that gamma band activity cannot be detected in scalp recorded EEG (Menon et al., 1996). Furthermore, it has been argued that part of the gamma band response is a purely sensory phenomenon (Karakaş and Başar, 1998). In a series of studies we were able to demonstrate that the magnitude of gamma oscillations as such is related to many non-specific factors like subjects' age (Böttger et al., 2002), task difficulty (Senkowski and Herrmann, 2002) or stimulus properties (Busch et al., 2004; Fründ et al., under review b). Furthermore, the extent of top-down modulations of gamma activity is also contingent upon parameters of the experimental paradigm (Busch et al., 2006). It hence appears indispensable to carefully design an experimental procedure for the investigation of visual object processing such that it promotes the occurrence of gamma activity in general, maximises the effect of the experimental manipulation of interest and does not confound such effects with other factors (for instance stimulus properties).

The present study intends to introduce an effective experimental paradigm for the investigation of gamma band activity and visual object processing that can be easily adopted by other researchers. In previous studies, object recognition has been probed in simple discrimination paradigms, in which gamma band responses were shown to be augmented for Kanizsa figures (Tallon-Baudry et al., 1996; Herrmann et al., 1999; Csibra et al., 2000), faces (Keil et al., 1999; Rodriguez et al., 1999), words (Fiebach et al., 2005), and identifiable objects (Gruber et al., 2002; Herrmann et al., 2004b) as opposed to control stimuli (i.e., incoherent figures, inverted faces, pseudo-words, and unidentifiable fragments, respectively). Although these studies are largely consistent with respect to effects of experimental manipulations, some of these studies also differ considerably with respect to latency, topography, frequency, or magnitude of gamma activity. It could be argued that gamma activity is not a reliable signal. However, it is also conceivable that these inconsistencies were caused by subtle differences in experimental paradigms, stimulation, participants, or technical equipment. The present study was conducted to demonstrate that highly reproducible results can be obtained even across different laboratories using the same experimental procedure, but different technical equipment and analysis tools. We elaborate on earlier suggestions, which have proposed to use line drawings of objects to reliably elicit GBRs (Gruber et al., 2006; Herrmann et al., 2004b). In particular, we present a dedicated set of stimuli which, in contrast to some of the previous studies mentioned above,

comprises a wide range of depicted objects and which is well controlled with respect to physical stimulus parameters.

Methods

The experiment was conducted in two different laboratories at the Institute of Psychology I at the University of Leipzig (Leipzig Laboratory) and at the Department of Biological Psychology at the University of Magdeburg (Magdeburg Laboratory). Both assays employed the identical experimental paradigm, stimulus set, and the same data analysis protocol, but used different recordings systems and different software for analysis (see below).

Subjects

The study protocol conformed with local ethics guidelines and the Declaration of Helsinki. 10 subjects participated in each laboratory (Leipzig Laboratory: mean age: 22; 7 female; Magdeburg Laboratory: mean age 25; 3 female; all right handed), all were paid for participation. Subjects gave informed consent prior to the start of the experiment. All subjects had normal or corrected to normal vision and had no recorded history of neurological or psychiatric disorders.

Stimuli and procedure

Familiar (meaningful) stimuli were 200 pictures of concrete objects taken from a standard picture library (Hemera Technologies, 1997). Unfamiliar, meaningless pictures were created by randomly distorting the original images until they were not recognisable as concrete objects (see Fig. 1 for examples of the stimulus material). Given the susceptibility of the early evoked GBR to perceptual stimulus properties (Busch et al., 2004), it was intended to match the spatial frequencies of an unfamiliar object to its corresponding familiar image. In order to achieve this, the amplitude spectrum of a familiar picture was combined with the phase spectrum of its distorted counterpart. In a first step, two-dimensional Fourier transforms of familiar pictures and their unfamiliar counterparts were calculated. Next, a modified unfamiliar picture was computed via the inverse Fourier transform using the amplitude spectrum of the familiar picture and the phase spectrum of the distorted picture. This method was applied separately to each colour plane and resulted in equalised spatial frequencies of a familiar picture and its modified unfamiliar counterpart. Furthermore, this procedure leads to a slightly blurry background of the adjusted unfamiliar pictures (see Fig. 1). In order to give the familiar pictures a similar look, a similar procedure was applied both to familiar pictures and adjusted unfamiliar pictures. The averaged amplitude spectra across all 400 pictures (200 familiar and 200 unfamiliar) were combined with the phase spectrum of each individual image (see Sadr and Sinha, 2004, for a discussion of methods for image processing).[1]

Two experimental lists were created from the stimulus pool: for each subject 100 stimuli were randomly chosen from the "familiar" and "unfamiliar" lists of images, respectively. Importantly, a different picture was presented in every experimental trial to avoid previously reported repetition suppression effects of the GBR (Gruber and Müller, 2002; Gruber et al., 2004a). Stimuli were presented foveally in

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[1] The stimulus set is available upon request. We encourage readers to contact the authors in case of interest in the stimuli or cooperation.
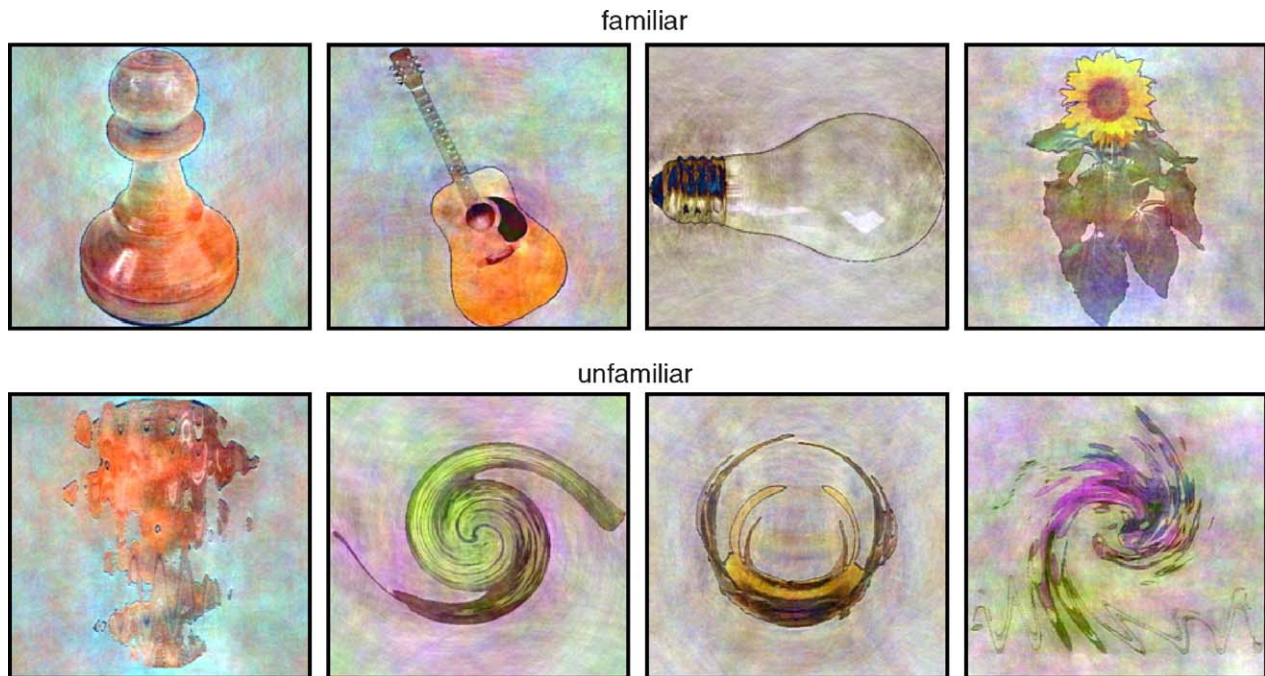
familiar

unfamiliar

Fig. 1. Excerpt of a sequence of familiar and unfamiliar stimuli. Note that the leftmost unfamiliar picture was derived from the pawn in the first row.

randomised order. The images covering a visual angle of approximately $6 \times 6°$ were shown on a light-grey background. Picture onset was synchronised to the vertical retrace of the monitor. Each trial consisted of a randomised 500- to 700-ms baseline period during which a fixation cross $(0.3 \times 0.3°)$ was presented, followed by a picture presented for 700 ms. The stimulus was then replaced by the fixation cross which remained on screen for another 800 ms. In order to minimise the influence of motor-related activity onto the EEG signal, responses had to be delivered only after the end of each epoch, after which a query was presented requiring the subject to indicate whether the presented image was a familiar or an unfamiliar entity by means of a button-press. Subjects were asked to avoid eye movements and blinking during the display of the fixation cross or a stimulus. In order to allow for a resting interval, the 200 experimental trials were divided into two blocks of 100 trials each.

Data acquisition and data processing

Leipzig Laboratory

EEG was recorded continuously from 128 Ag/AgCl electrodes with a BioSemi Active-Two amplifier system (see Fig. 2 for a schematic representation of the recording array) in an electrically shielded and sound attenuated room. A CRT monitor used for stimulation was placed outside this cabin behind an electrically shielded window. To monitor for eye movements and blinks the horizontal and vertical electrooculogram (EOG) were recorded. EEG and EOG were sampled at 512 Hz. Two additional electrodes near channel CPz (CMS—Common Mode Sense and DRL— Driven Right Leg, see Fig. 2 for exact locations) were used as reference and ground. For further offline analysis the Average Reference was used. EEG was segmented to obtain epochs starting 500 ms prior and 1500 ms following picture onset. Artifact correction was performed by means of "statistical correction of artifacts in dense array studies" (SCADS; Junghöfer et al., 2000).

This procedure is widely accepted in the field and was applied and described in several publications (e.g., Gruber et al., 1999).

Magdeburg Laboratory

The experiment was conducted in an electrically shielded and sound attenuated room. A TFT monitor used for stimulation was placed outside this cabin behind an electrically shielded window. All devices inside the cabin were battery operated to avoid interference of the line frequency. EEG was recorded with a BrainAmp amplifier (Brain Products, Munich) using 64 sintered Ag/AgCl electrodes mounted in an elastic cap (Easycap, Falk Minow Services, Munich, see Fig. 2) and placed according to the 10–10 system, with a nose tip reference and ground electrode between Fz and Cz. Electrode impedances were below 10 kΩ. Data were sampled at 500 Hz and analog filtered between 0.01 and 200 Hz during recording. An automatic artifact rejection excluded trials from averaging if the standard deviation within a moving 200-ms time interval exceeded 40 μV. All trials were also visually inspected for artifacts and rejected in case of eye movements (abrupt voltage transitions at EOG electrodes or channels Fp1 or Fp2) or slow voltage drifts at single electrodes which can result from changes in skin or electrode impedances (see Luck, 2005, for details).

Data analysis

Spectral changes in oscillatory activity were analysed by means of Morlet wavelets with a "width" of 12 cycles per wavelet. The method is described in detail elsewhere (cf. Bertrand and Pantev, 1990; Tallon-Baudry and Bertrand, 1999; Herrmann et al., 2004a). In brief, Morlet wavelets can be thought of as "band-pass filters", with a Gaussian shape both in the time domain and in the frequency domain around their central frequency. The method thus provides a time-varying magnitude of the signal in each frequency band,
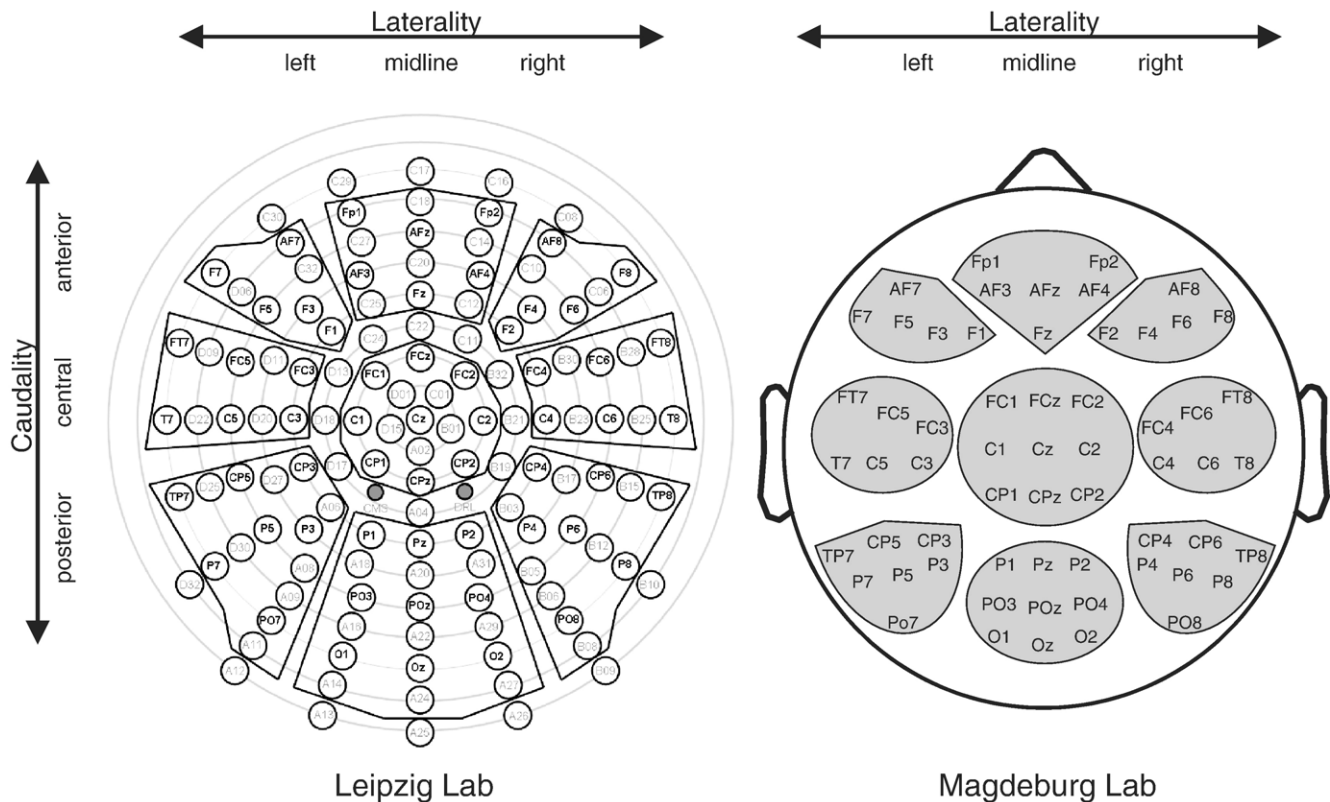
Fig. 2. Electrode montages and regions of interest used for statistical analyses. Locations of channel labels are slightly displaced for graphical display.

leading to a time by frequency representation of the data. Usually, the characteristics of a wavelet are denoted as $2\sigma_t$ and $2\sigma_f$. The standard deviation σ_t of the Gaussian temporal envelope is reciprocally related to the frequency ($\sigma_t \approx \frac{1}{f}$). The standard deviation in the frequency domain is given by $\sigma_f = \frac{2\pi}{\sigma_t}$. The time resolution of this method thus increases at higher frequencies, while the frequency resolution decreases at higher frequencies. Here we applied wavelets with a constant ratio $\frac{f_0}{\sigma_f} = 2\pi$, which corresponds to a temporal wavelet duration $\left(2\sigma_t = \frac{2}{f_0} \right)$ of two cycles at the wavelet's center frequency f_0, and a frequency bandwidth of $2\sigma_f = \frac{f_0}{\pi}$. Accordingly, a wavelet with a center frequency of 40 Hz employed in this study had a wavelet duration of $2\sigma_t = 50$ ms and a spectral bandwidth of $2\sigma_f = 12.71$ Hz. Importantly, due to the fact that non-phase-locked (induced) gamma band responses occur with a jitter in latency from one trial to another (Eckhorn et al., 1990), they tend to cancel out in the averaged evoked potential. Thus, induced activity was analysed by performing the wavelet transform for each single trial, and averaging the absolute values of the resulting transforms. In the Leipzig Laboratory the evoked response (i.e., the unfiltered ERP averaged across conditions) was subtracted from each trial before frequency decomposition, similar to previous publications (cf. Fiebach et al., 2005; Gruber and Müller, 2005; Gruber et al., 2006). To reveal the evoked fraction of gamma activity, the wavelet transform was performed on the averaged and unfiltered evoked potential.

The statistical analysis of ERPs and gamma band activity was performed on regional means. By averaging across selected electrodes channels were pooled into nine regions of interest (ROIs, see Fig. 2) which were located along a rostro-caudal and a

left–right axis. Note that the number of electrodes included in the ROIs was larger in the Leipzig than in the Magdeburg laboratory. Due to different ERP latencies different definitions of ERP components were used for statistical analysis in the two laboratories. ERP components were defined as mean amplitudes in the time intervals from 105 ms to 135 ms (P1), 155 ms to 185 ms (N1), and in a later interval between 260 ms to 400 ms (first late component, L1) in the Leipzig Laboratory and as mean amplitudes in the time windows from 90 ms to 120 ms (P1), 140 ms to 170 ms (N1), and 250 ms to 450 ms (L1) in the Magdeburg Laboratory, respectively. The exact frequency of gamma band responses varies considerably between subjects and usually also differs between evoked and induced gamma. Therefore, the frequency of gamma activity used for statistical analysis was determined individually for every subject. The choice of individual evoked gamma frequencies was conducted as follows:

(1) The time–frequency transform was computed on the average of all trials (see above), irrespective of experimental condition, for every channel.
(2) After subtraction of the baseline (300 to 100 ms prior to stimulus onset) time–frequency scalograms were further averaged across all electrodes of the three posterior ROIs (see Fig. 2).
(3) From this averaged time–frequency scalogram we determined individual evoked gamma frequencies as the frequency showing the maximum amplitude in a time window from 60 ms to 120 ms in the frequency range of 30 Hz–100 Hz.
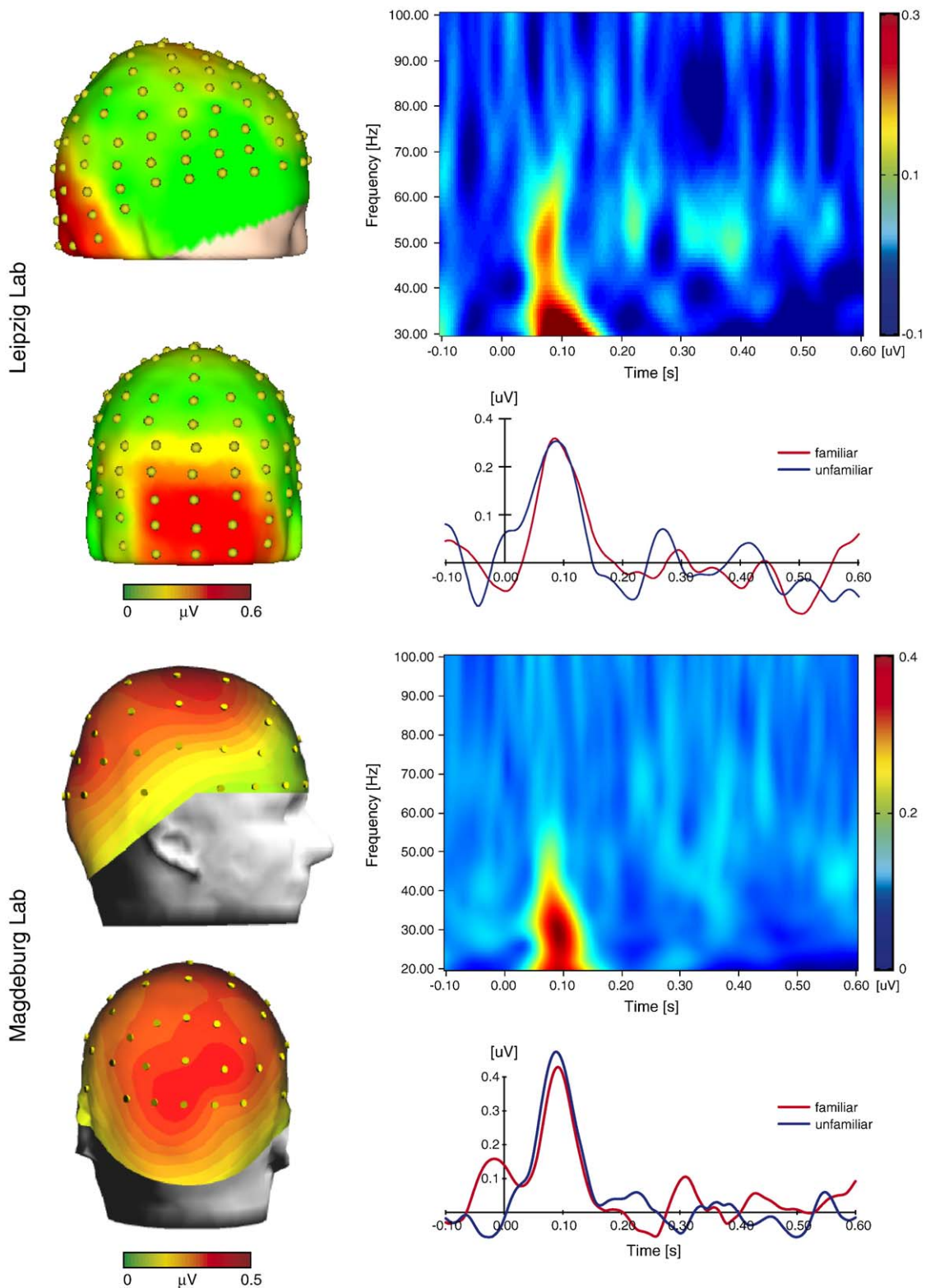
Fig. 3. Summary of results obtained for evoked gamma activity. Topographic maps averaged across experimental conditions in the time interval used for statistical analysis show a posterior distribution of evoked gamma activity. Time–frequency spectra averaged across conditions and posterior electrodes confirm a distinct signal in the frequency range from 20–60 Hz. Note that gamma responses are more circumscribed in frequency in single subject data. Comparison of the time courses (shown here as averaged across the three posterior ROIs, see Fig. 2) did not yield condition effects on evoked gamma activity. The pattern of results was highly consistent between laboratories.
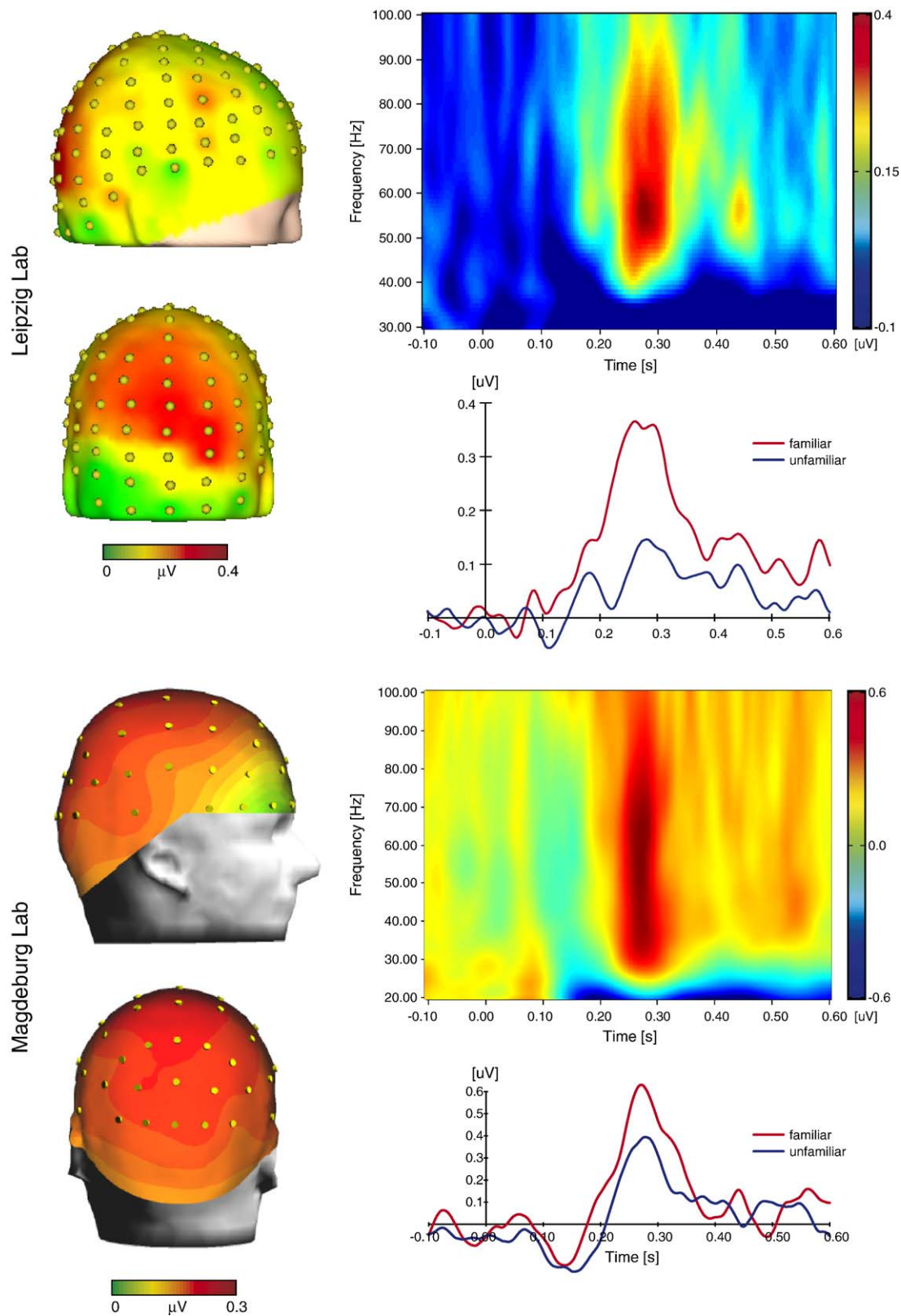
Fig. 4. Summary of results obtained for induced gamma activity. Topographic maps averaged across experimental conditions in the time interval used for statistical analysis show a central-posterior distribution of induced gamma activity. Time–frequency spectra averaged across conditions and posterior electrodes confirm a distinct signal in the frequency range from 30–100 Hz. Time courses (shown here as averaged across the three posterior ROIs, see Fig. 2) reveal stronger induced gamma activity for familiar as compared to unfamiliar objects. The pattern of results was highly consistent between laboratories.

(4) Statistical analyses of evoked gamma activity were performed on the mean amplitude of this individual frequency in all nine regional means in the time window from 60 ms to 120 ms.

Individual induced gamma frequencies were determined as follows:

(1) Time–frequency transforms were computed for single trials and averaged subsequently, irrespective of experimental condition.
(2) After subtraction of the baseline (300 to 100 ms prior to stimulus onset) time–frequency scalograms were further averaged across electrodes of all nine ROIs (see Fig. 2).
(3) From this averaged time–frequency scalogram we determined individual induced gamma frequencies as the frequency showing the maximum amplitude in a time window from 150 ms to 400 ms in the frequency range of 30 Hz–100 Hz.
(4) Statistical analyses of induced gamma activity were performed on the mean amplitude of this individual frequency in all nine regional means in the time window from 150 ms to 400 ms.

It is noteworthy that our approach, namely to average both conditions to define the relevant peaks, seems inevitable to avoid biasing the choice of the time–frequency windows, and thus, the comparisons between conditions in the subsequent ANOVA (see Busch et al., 2006; Fiebach et al., 2005; Gruber and Müller, 2006; Gruber et al., 2006, for a similar approach). Repeated measures ANOVAs of gamma band responses and ERPs were computed for the factors "stimulus type" (familiar vs. unfamiliar), "caudality" (anterior, central, posterior), and "laterality" (left, midline, right). Greenhouse–Geisser corrections were used to adjust for violations of the sphericity assumption for repeated measures factors containing more than two levels (cf. Dien and Santuzzi, 2004). Uncorrected degrees of freedom and corrected *P*-values are reported.

Results

Stimulus presentation elicited early evoked gamma band activity which was maximal at posterior recording sites and later induced gamma activity with a more central and widespread topography. Both gamma band signals were well circumscribed both in time and in frequency (see Figs. 3 and 4). In the time domain visual-evoked potentials (P1 and N1) were observed at posterior sites as well as a later negative deflection (first late ERP, L1) at central and posterior electrodes (Fig. 5). Data were largely consistent (especially in the frequency domain) across laboratories with respect to latency, topography and experimental effects. Slight differences in signal magnitudes were probably due to different reference sites, electrode montages (see Fig. 2), and subjects. We recorded one subject in both laboratories (data not included in this analysis) and observed almost identical amplitudes in both recordings.
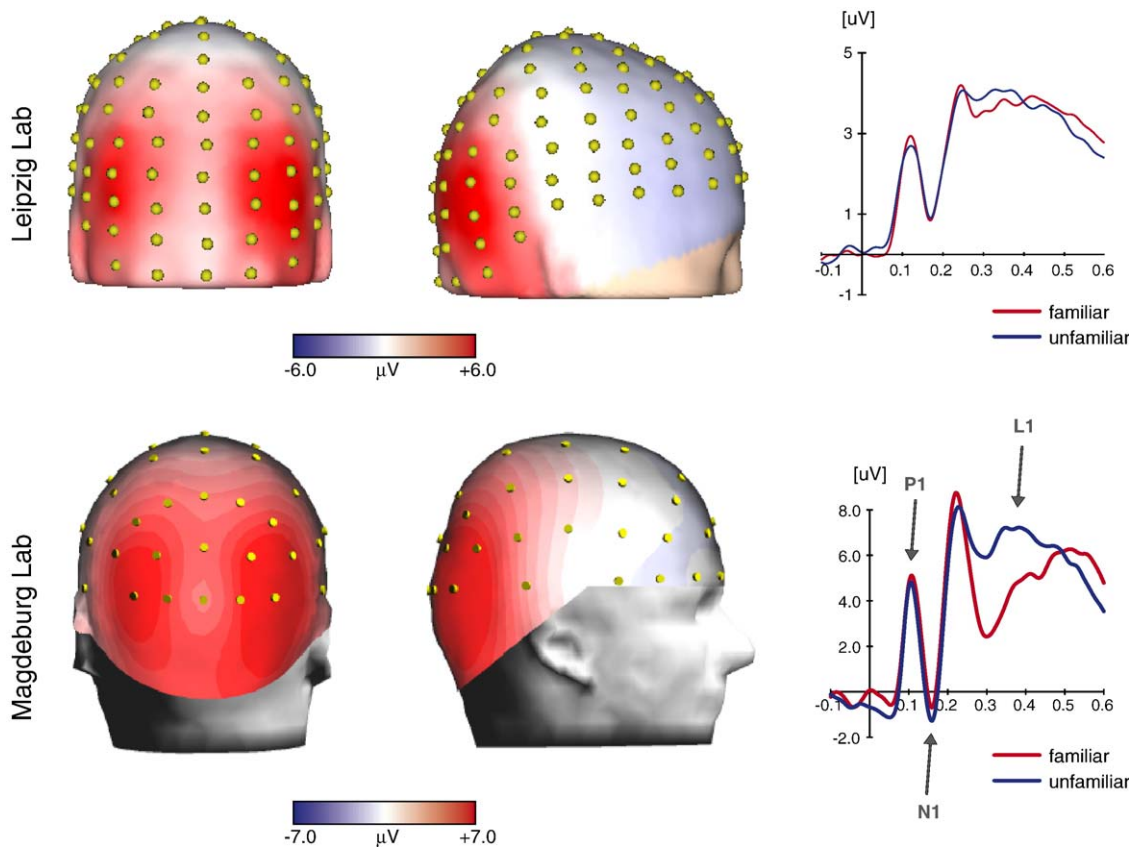

Fig. 5. Summary of results obtained for event-related potentials. Topographic maps of the late ERP component (L1) averaged across experimental conditions in the time interval used for statistical analysis show a central-posterior distribution. The L1 component (time courses represent the average across the three posterior ROIs, see Fig. 2) was more negative for familiar as compared to unfamiliar stimuli. The pattern of results was highly consistent between laboratories.

Leipzig Laboratory

Gamma band responses

Early evoked gamma band responses were not influenced by the type of stimuli presented. Induced gamma activity was stronger for familiar stimuli (stimulus type: $F(1,9)=8.1$, $P=0.02$).

Event-related potentials

Amplitudes of the P1 and N1 component were not influenced by the type of stimulus. L1 amplitudes were more positive for unfamiliar as compared to familiar stimuli at posterior and central regional means. This effect was found to be reversed at frontal electrodes. The effect was most pronounced at central midline sites (stimulus type × caudality × laterality: $F(4,36)=4.2$, $P=0.03$).

Magdeburg Laboratory

Gamma band responses

Early evoked gamma band responses were not influenced by the type of stimulus presented. Induced gamma activity was stronger for familiar stimuli (stimulus type: $F(1,9)=6.4$, $P=0.032$).

Event-related potentials

Amplitudes of the P1 and N1 components were not influenced by the type of stimulus. L1 amplitudes were more positive for unfamiliar stimuli (stimulus type: $F(1,9)=11.1$, $P=0.009$). This effect was most pronounced at central midline sites (stimulus type × caudality × laterality: $F(4,36)=8.4$, $P=0.001$).

Discussion

The present investigation intended to test the usefulness of a standard paradigm for the investigation of visual information processing by means of gamma activity and a novel set of stimuli comprising familiar and unfamiliar objects. In order to demonstrate the reliability of the outcomes of this paradigm, we conducted the investigation in two different laboratories. We demonstrate that in spite of different recording systems the results were highly consistent across laboratories: stronger induced gamma band oscillations could be observed for familiar as compared to unfamiliar objects, confirming the interpretation of gamma activity as a neural signature of cortical object representations (Gruber et al., 2006; Tallon-Baudry and Bertrand, 1999). The centro-parietal topography, furthermore, suggests that induced gamma activity was not contaminated by neck muscle (EMG) activity which would be expected to be maximal over posterior recording sites. Rather the topographical distribution of the induced gamma band response speaks for the activation of cortically widespread networks, which were previously localised in parietal, temporal and frontal areas (Gruber et al., 2006). In contrast, the evoked gamma band response might originate from cortical structures also generating the conventional P1-N1 complex of the visual-evoked response (Narici et al., 2003; Gruber et al., 2006). It is noteworthy that subtraction of the ERP prior to analysis of induced responses (Leipzig Laboratory) did not yield different results when compared to an analysis without subtraction (Magdeburg Laboratory). Furthermore, the consistency of the results in spite of different reference sites confirms a previous report of the robustness of spectral power measures to different reference schemes (Trujillo et al., 2005). In contrast to induced gamma band activity, earlier ERPs and evoked gamma activity were not influenced by stimulus type in either

laboratory. This result suggests that familiar and unfamiliar stimuli were well matched with respect to physical stimulus properties. In this respect, the present stimulus material differed from previous ones both in the breadth of depicted contents as well as control of physical stimulus parameters, which is an important issue, especially in the field of gamma band research (Busch et al., 2004). Contrary to a previous report (Herrmann et al., 2004b) we could not replicate the finding of increased evoked gamma activity for objects compared to nonsense objects. Top-down effects on evoked gamma activity have been found in studies in which speeded behavioural responses were required (Busch et al., 2006; Herrmann et al., 2004b). In contrast, in the present study subjects were instructed to give a response only after they were prompted to do so. This delayed response might have reduced the need of top-down modifications of early visual processes. In fact, Fründ et al. (under review a) found substantial effects of response speed on early evoked gamma activity, and future studies should investigate the interaction between response speed and top-down effects in gamma band activity. Given the demonstration of the reliability and validity of the results, we suggest that the standard object recognition paradigm and a set of well-matched depictions of familiar and unfamiliar objects as introduced in this report can serve as a versatile tool for research on visual object processing. The procedure proposed here thus complements the paradigm suggested by Hoogenboom et al. (2006) for the investigation of gamma activity in relation to perceptual processes. Future studies might use this tool in order to investigate, for instance, the developmental time course of object recognition or the relative contribution of semantic and perceptual features to the activity of cortical networks underlying induced gamma band activity.

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