

# What's that sound? Matches with auditory long-term memory induce gamma activity in human EEG

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## Abstract

In recent years the cognitive functions of human gamma-band activity (30–100 Hz) advanced continuously into scientific focus. Not only bottom-up driven influences on 40 Hz activity have been observed, but also top-down processes seem to modulate responses in this frequency band. Among the various functions that have been related to gamma activity a pivotal role has been assigned to memory processes. Visual experiments suggested that gamma activity is involved in matching visual input to memory representations. Based on these findings we hypothesized that such memory related modulations of gamma activity exist in the auditory modality, as well. Thus, we chose environmental sounds for which subjects already had a long-term memory (LTM) representation and compared them to unknown, but physically similar sounds. 21 subjects had to classify sounds as ‘recognized’ or ‘unrecognized’, while EEG was recorded. Our data show significantly stronger activity in the induced gamma-band for recognized sounds in the time window between 300 and 500 ms after stimulus onset with a central topography. The results suggest that induced gamma-band activity reflects the matches between sounds and their representations in auditory LTM.

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## 1. Introduction

Humans explore the world not only by using their eyes. Information from different modalities has to be integrated as a coherent perception. This is achieved by comparing perceived stimuli to experience-based memory. The results of such comparisons then serve to select an appropriate behavioral response. These mechanisms are important in daily life: if one hears a wild dog barking which is approaching, the most likely action will be to ‘clear off and seek shelter’. This happens because an internal representation is activated by hearing the sound which is recognized as ‘barking’ and associated with biting, danger, and flight. The aim of this study was to investigate the neural correlates of such matching processes.

Our investigation was focused on gamma-band activity because it has been recently proposed that matching processes

between sensory input and memory representations involve gamma oscillations (Herrmann et al., 2004c). In recent years there has been growing interest to complement EEG analysis with analysis of oscillatory EEG activity by means of frequency and time–frequency analysis (Başar et al., 1999, 2001). Especially oscillatory activity in the gamma-band (30–100 Hz) has attracted a lot of interest (Başar-Eroglu et al., 1996). Regarding oscillatory activity it has been common to distinguish between two different types of oscillations (Galambos, 1992). Evoked gamma activity, which is often seen merely as a result of sensory processing (Karakaş and Başar, 1998), appears mostly within the first 100 ms after stimulus onset, is strongly phase-locked to stimulation, and shows a focal topography which is specific for the sensory modality. Induced gamma activity, on the other hand, is not strictly phase-locked to stimulation, occurs at variable latencies around and after 200 ms relative to stimulus onset with a more widespread topography and seems to be connected to cognitive processes like memory (Gruber et al., 2004b). Gamma oscillations have been initially proposed as a correlate of feature binding and integrated object representations. Gray et al. (1989) demonstrated neural synchronization in the

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gamma-band in cat visual cortex in response to visual stimulation with two bars, moving into the same direction, which could be perceived as parts of one coherent object. Furthermore, in a series of studies Tallon-Baudry et al. demonstrated enhanced gamma activity in human EEG for stimuli which could be perceived as coherent objects (cf. Tallon-Baudry and Bertrand, 1999). In a subsequent study Herrmann et al. (1999) adapted an experiment from Tallon-Baudry et al. (1996) and revealed that target stimuli evoke a stronger gamma-band response (GBR) than all other stimuli irrespective of their object features. They concluded that object selective attention has a larger impact on the 40 Hz response than binding processes (Herrmann and Mecklinger, 2001). In a recent study Debener et al. (2003) compared target sine tones to novel environmental sounds which were irrelevant for the task and observed that the target role of a tone is even more important than its novelty. It is noteworthy to mention that there is a close connection between selective attention and memory: shifting the attention to a target requires comparison with a template stored in memory, which could either refer to simple object features like color, form, or size or to the spatial position of the object. Moreover, matches with memory guide the attentional focus to the corresponding object and lead to faster behavioral responses. Thus, it might be concluded that matching of memory representations and sensory input is a crucial factor for modulations of the GBR. This could be demonstrated by several studies which investigated different aspects of visual memory: Tallon-Baudry et al. (1998) found that the recall of object representations as well as their maintenance in short-term memory (STM) induces higher GBRs. In addition, both perceptual learning tasks (Gruber et al., 2002) and the recall of previously learned stimuli (Gruber et al., 2001) were accompanied by enhanced gamma oscillations. Jung-Beeman et al. (2004) also showed that tasks involving verbal problem solving with aspects of recall of relevant information from long-term memory (LTM) induce gamma activity around 300 ms prior to the actual reaction. Furthermore, Herrmann et al. (2004b) were the first group, who demonstrated, that matches of perceived images with LTM representations evoke early GBRs. In their study, line drawings of objects of daily life for which subjects possessed LTM representations evoked stronger activity over occipital areas than physically similar stimuli without such representations, even though stimulus familiarity was not task relevant. Herrmann et al. (2004c) summarized these results in the ‘Match-and-utilization model’ (MUM). The authors assume that memory contents are stored as strengthened synaptic connections. If the input of thalamic neurons reaches primary cortices, matching with existing memory representations could lead to enhanced activity due to stronger feedback from higher visual areas. As Herrmann et al. (2004b) demonstrated, such matching processes take place at a very early stage of visual processing. According to the MUM, evoked activity correlates with matching processes, while the later induced activity is responsible for the utilization of the obtained matching information for further cortical processing (Herrmann et al., 2004c). If this model was valid, it should also apply to auditory memory, since the human cortex demonstrates a relatively homogeneous architecture which resulted in the synonymous term ‘isocortex’.

MUM seems to be in line with investigations of auditory STM. In a delayed matching-to-sample task Lutzenberger et al. (2002) showed parietal and frontal GBR increases related to remembering auditory spatial information, while auditory pattern recognition enhanced oscillatory activity in the left inferior-frontal and anterior-temporal regions and the prefrontal cortex (Kaiser et al., 2003). So far, there have been no studies examining the relevance of gamma activity for auditory LTM. However, event-related potential (ERP) studies reported electrophysiological correlates of auditory LTM: Cycowicz and Friedman (1998) reported a larger P3 component for unidentifiable sounds which can be explained by attentional demands or the development of a memory representation. Furthermore, Opitz et al. (1999) showed that recognized sounds evoke a larger N400. Generally, multiple cortical areas are involved in processing features of such complex sounds (Griffiths et al., 2004) like their temporal structure, contained frequencies, volume, timbre or rhythm. Therefore, one has to assume that sound representations exist already in the primary auditory cortex (Weinberger, 2004). Imaging studies using PET or fMRI were able to show aspects of sound recognition and temporal pattern analysis already in the lateral temporal regions (Maeder et al., 2001). Lewis et al. (2004) compared environmental sounds to the same sounds played backwards and obtained stronger activation, e.g. in the primary auditory cortex for the former than the latter.

Our investigation aimed to reveal, whether the results from visual LTM and its role for human GBRs (Herrmann et al., 2004b) are transferable to the auditory modality. We used everyday environmental sounds for which people had acquired memory representations and compared them to unrecognizable, but physically similar sounds.

We examined the following hypotheses:

- (1) Given that both stimulus types (recognizable and unrecognizable) should be comparable in their physical features, there should be no difference in early ERP components like P50 or N100 (Neukirch et al., 2002).
- (2) Findings concerning later ERP components should be replicated, resulting in a larger N400 component for identifiable sounds (Opitz et al., 1999). We expected no P3 difference (Cycowicz and Friedman, 1998), since our paradigm is not suited to evoke a typical target P3.
- (3) If gamma oscillations are indeed modulated by LTM processes (Herrmann et al., 2004b), this should be also true for auditory LTM, leading to higher gamma-band activation for recognizable sounds with memory representations.

## 2. Methods

### 2.1. Subjects

Twenty-one paid subjects (13 female) with a mean age of  $26.2 \pm 5$  years participated in the study. They reported no obvious hearing problems or any kind of neurological or psychiatric disorders. All subjects gave written and informed consent

for their participation and received detailed task instructions. Two subjects had to be excluded from further analysis due to excessive eye blinks.

## 2.2. Procedure and material

Subjects listened to environmental and novel sounds and had to decide whether or not they recognized the presented stimulus. 241 real-world non-verbal and easily recognizable sounds were either recorded or collected from an Internet-sound-database ([www.audiosparx.com](http://www.audiosparx.com), 2004). For these sounds it could be assumed that the subjects already had a representation in LTM (e.g. a train whistle, characteristic sounds of tools, machines, or animals). These sounds served as the basis for a set of another 241 sounds, which were not recognizable anymore. Given that not only visual stimulus properties (Busch et al., 2004), but also the characteristics of auditory stimuli (Schadow et al., 2005) influence the gamma-band response, both types of sounds (recognizable and unrecognizable) had to be comparable regarding their physical features in order to prevent possible confounds due to feature dissimilarity. Therefore, the original stimuli were processed using Matlab V6.3 (MathWorks GmbH, 2004). At first we applied a Fast-Fourier-Transform to obtain the sound-specific frequency distribution. Subsequently, amplitudes within this frequency range were shuffled randomly, while the phases were not changed. This new sound was then transformed back into the time domain. The spectral envelope was comparable to the original sound. Thus, the physical features remained roughly unchanged, but both stimulus types differed regarding their LTM representation. All sounds had a sampling-rate of 44,100 Hz with a length of 1 s. They were saved as uncompressed and unfiltered wav-stereo-files, where the left and right channel contained the same signal. The sound-volume was normalized for all sounds.

Subjects were seated in a sound-attenuated and electrically shielded cabin, where no AC-devices were operated. Auditory stimulation was conducted using EARtone 3A insert-phones, which were connected to a calibrated attenuator (Programmable Attenuator PA5, Tucker Davis Technologies, Alachua). This allowed us to identify the individual left and right ear hearing thresholds of every subject in steps of 1 dB before auditory stimulation. Stimulus presentation was accomplished using Presentation (Neurobehavioral Systems, Albany) running on an IBM compatible PC. The 482 sounds were presented at 75 dB HL in a pseudo-randomized order in 4 blocks of equal length. The inter-stimulus interval varied randomly between 1500 and 2200 ms. Since a pilot study revealed large inter-individual differences in recognition performance, we decided to explicitly use this judgement (recognized vs. unrecognized) as task during the main experiment. This gave us the opportunity to contrast the responses to sounds with and without memory representation. The subjects had to press a button with their left index-finger if they did not recognize the sound. They had to press another button with their right index-finger in case of recognized sounds. Furthermore, they were instructed to keep their eyes

open and to fixate a cross at the center of a screen at 100 cm distance.

## 2.3. EEG recording

EEG was recorded using 32 Ag/AgCl electrodes placed in an elastic cap (Easy-cap, Falk Minow Services, Herrsching-Breitbrunn) according to the international 10–20-system and connected to a BrainAmp amplifier (BrainProducts, Munich). The signal was referenced to the nose tip, while the ground electrode was placed at the centerline between Fz and Cz. Eye movements were registered by an electrode below the right eye. Data were sampled at 500 Hz and analog filtered between 0.02 and 200 Hz. Electrode impedances were kept below 5 k $\Omega$ . Data were digitally saved for later offline analysis.

## 2.4. Data analysis

Reaction times and response types (recognized vs. unrecognized) were recorded and analyzed. Reaction times which exceeded two standard deviations of the mean were excluded from further analysis. Subjects with less than 25% trials judged ‘unrecognized’ were excluded from the EEG analysis to avoid large differences in trial numbers between both conditions. This resulted in 13 remaining subjects (9 female, mean age  $25.8 \pm 5$  years) for further analysis. Analysis of the EEG data was conducted using EEProbe (ANT Software, Enschede). An automatic artifact rejection excluded trials in which amplitudes exceeded the standard deviation in a moving 200 ms long time window by more than 25  $\mu$ V. Additionally, all trials were visually inspected for artifacts and removed if necessary. Averages of ERPs and GBRs were calculated between  $-200$  ms and 800 ms relative to stimulus onset. Baseline correction was applied using the  $-200$  ms to  $-100$  ms time window. To avoid loss of statistical power electrodes were pooled into regions of interest (ROIs), with one anterior (Fz, Fp1, Fp2, F3, F4, F7, F8, Ft9, Ft10), central (Fc1, Fc2, Fc5, Fc6, Cz, C3, C4, Cp1, Cp2, Cp5, Cp6), and posterior (Tp9, Tp10, Pz, P3, P4, P7, P8, O1, O2) ROI for the analysis of ERPs. For the analysis of gamma-band activity a Morlet based wavelet transform with a width of 12 cycles was employed in order to provide a continuous measure of the amplitude of a frequency component (for details refer to [Herrmann et al., 2004a](#)). Morlet wavelets can be thought of as ‘bandpass filters’ having a Gaussian shape both in the temporal and in the frequency domain around their central frequency. To reveal the evoked fraction of gamma activity, the wavelet transform was performed on the averaged evoked potential. In order to also analyze activity which is not strictly phase-locked to the stimulus, the wavelet transform was performed for each single trial, and the absolute values of the resulting transforms were averaged. This measure reflects the total activity for a certain frequency range, irrespective of whether it is phase-locked to the stimulus or not. Mean baseline values were computed for the interval from  $-200$  to  $-100$  ms and subtracted before averaging. Seven electrodes (Cz, Fc1, Fc2, C3, C4, Cp1, Cp2) were pooled in one central region of interest (ROI) representing the highest gamma activity after auditory stimulation.

2.5. Statistical analysis

Averages and standard deviations were calculated for reaction times and response types. To compare reaction times for recognized and unrecognized sounds a two-tailed paired *t*-test was performed.

Mean ERP amplitudes were analyzed in the time windows 42–58 ms (P50), 85–110 ms (N100), 140–230 ms (P200) and 270–470 ms (N400). While statistical analyses were performed on unfiltered data, ERPs were low-pass filtered at 20 Hz for display. Statistical analyses of GBRs were performed on mean amplitudes in the time window 30–70 ms for evoked activity and 300–500 ms for total activity. Because of considerable inter-individual variability in subjects’ peak gamma-frequency, we decided to use each subject’s individual frequency for the wavelet transform by examining time–frequency plots for electrode Cz in the ‘recognized’ condition (as done before e.g. by Senkowski and Herrmann, 2002; Herrmann et al., 2004b).

Analysis of the ERP components P50, N100, P200 and N400 was conducted using a repeated measures ANOVA with the two

factors ROI (three levels: anterior, central, posterior) and CONDITION (two levels: recognized, unrecognized). Post hoc two-tailed *t*-tests were also applied for each ROI to evaluate significant main and interaction effects. Two-tailed *t*-tests were performed to compare evoked and total gamma responses to recognized and unrecognized stimuli in the specific ROI. All reported *F*-values are Greenhouse–Geisser corrected, degrees of freedom are uncorrected. The alpha level for all statistic tests was a priori determined as 0.05.

3. Results

3.1. Behavioral data

Reaction times were faster (929 ms vs. 1152 ms; standard errors 206 ms vs. 243 ms) for recognized than for unrecognized sounds ( $t(18) = -9.826; p < 0.001$ ).

For the analysis of EEG data subjects were excluded which categorized less than 25% of all presented stimuli as unrecognized. The remaining 13 subjects judged an average of 296

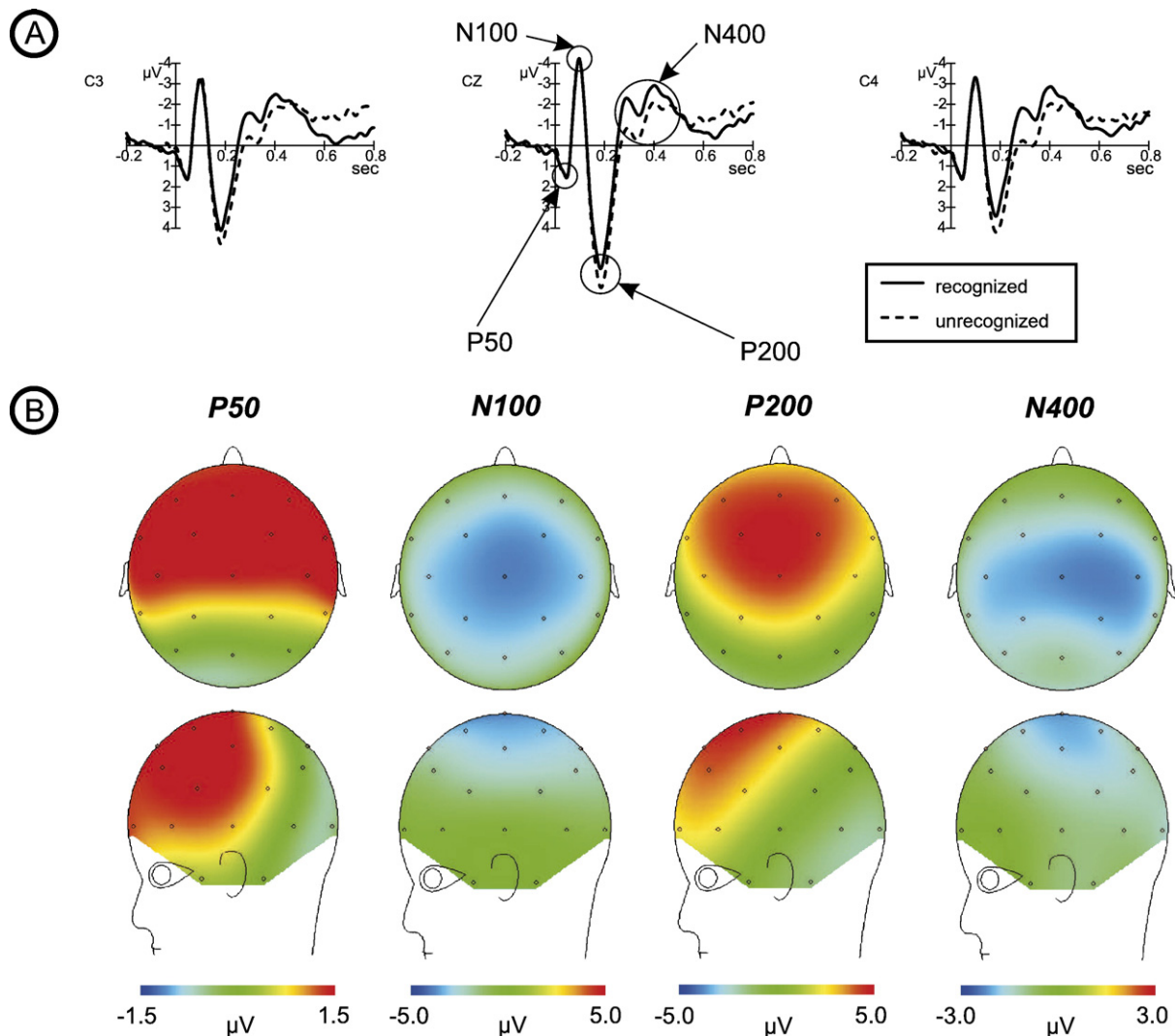


Fig. 1. A: Grand-average ERPs ( $N=13$ ) at three representative electrodes. Note the significant condition effects with larger amplitudes for unrecognized (P200) and recognized sounds (N400), respectively. B: Scalp topographies of the analyzed ERP components, depicted for the ‘known’-condition.

(SD=36) sounds as recognized and 181 (SD=36) sounds as unrecognized, representing 61% and 39% of all stimuli.

### 3.2. Event-related potentials

The averaged ERPs and scalp topographies are depicted in Fig. 1. Approximately 50 ms after stimulus onset the first component is visible as a short positive wave (P50). A strong negativity was observed around 100 ms (N100) and a similarly pronounced positivity around 200 ms (P200). The last component reached a maximum negativity after about

400 ms (N400). All components exhibited a fronto-central distribution.

For the P50 time window between 42 and 58 ms the ANOVA solely resulted in a significant effect for ROI ( $F_{(2,24)}=31.118$ ;  $p<0.001$ ). We abstained from further post-hoc tests of the ROI effect, because we were only interested in condition differences.

The analysis of the N100 yielded a significant effect of ROI ( $F_{(2,24)}=18.380$ ;  $p<0.001$ ) and an interaction effect of ROI  $\times$  CONDITION ( $F_{(2,24)}=3.818$ ;  $p=0.044$ ). However, post-hoc  $t$ -tests revealed no significant effect in any of the three regions.

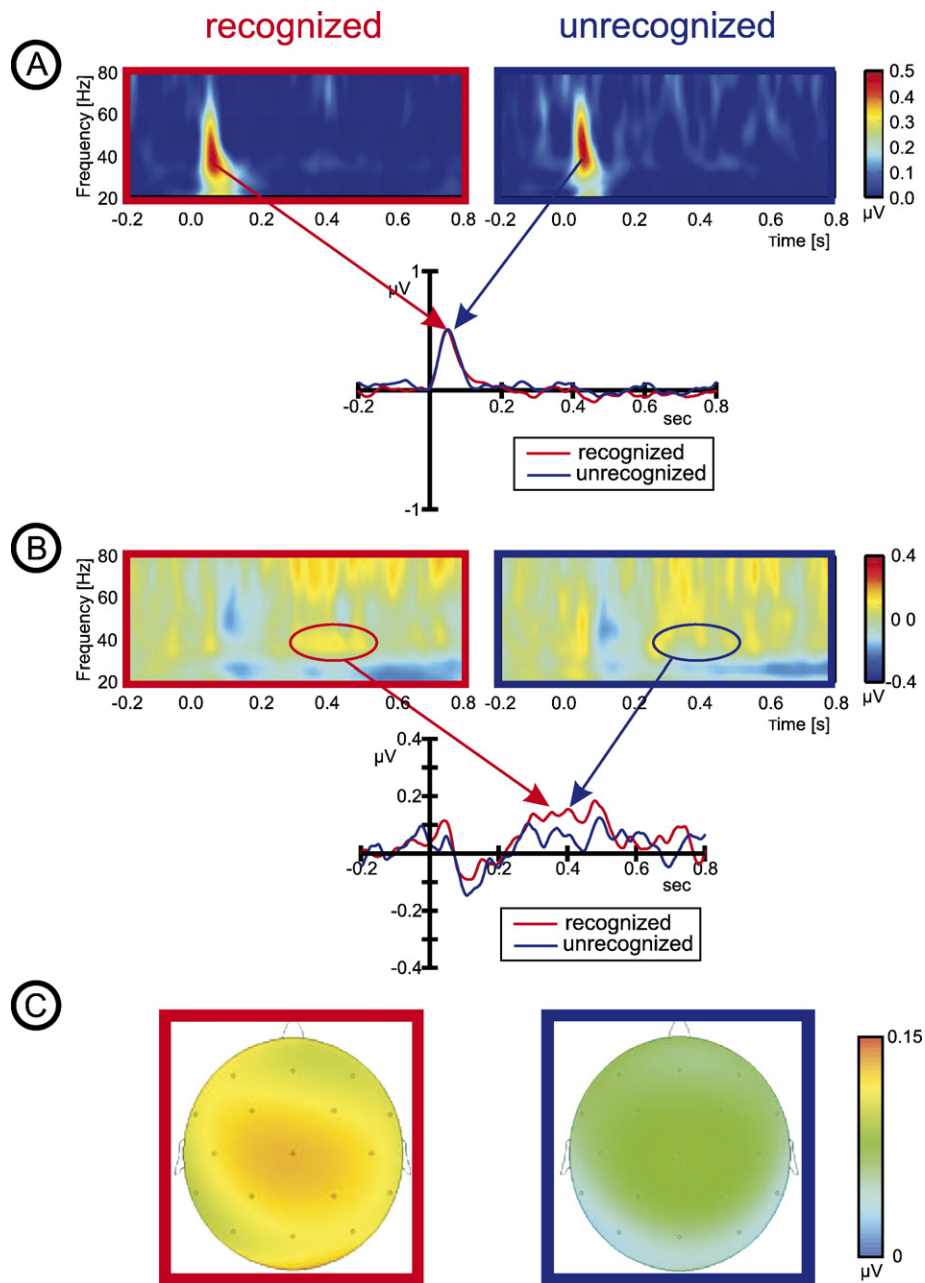


Fig. 2. All pictures display the grand-average at electrode Cz. A: Both time–frequency plots show nearly identical evoked GBRs in the time window 30–70 ms for recognized (left) and unrecognized (right) sounds as well as the individually adapted wavelet transforms (bottom). B: The time–frequency plots of total GBRs exhibit a clear difference in the time window between 300 and 500 ms. This is also clearly visible in the grand-average of wavelet transforms (bottom). C: The topography of the total GBR in the time window between 300 and 500 ms reveals a widespread increase of gamma activity in response to recognized sounds with a maximum at central electrodes.

The ANOVA of P200 resulted in significant effects of CONDITION ( $F_{(1,12)}=8.053$ ;  $p=0.015$ ), ROI ( $F_{(2,24)}=25.710$ ;  $p<0.001$ ), and CONDITION  $\times$  ROI ( $F_{(2,24)}=6.978$ ;  $p<0.007$ ). Subsequent testing yielded significant condition effects for the posterior ( $t(12)=-4.676$ ;  $p<0.001$ ) and central ROI ( $t(12)=-2.635$ ;  $p=0.022$ ), but not anterior ( $t(12)=-0.450$ ;  $p=0.661$ ). In both regions we found larger P200 amplitudes for unrecognized sounds.

For the N400 the ANOVA yielded a significant main effect of ROI ( $F_{(2,24)}=5.039$ ;  $p=0.026$ ) and an interaction of CONDITION  $\times$  ROI ( $F_{(2,24)}=6.465$ ;  $p=0.014$ ). Post-hoc comparisons revealed significant effects for the posterior ( $t(12)=-2.234$ ;  $p=0.045$ ) and central region ( $t(12)=-2.619$ ;  $p=0.022$ ) with mean amplitudes being significantly larger for recognized than for unrecognized sounds.

### 3.3. Time–frequency analysis

A *t*-test comparing the evoked responses within the specific ROI (see above) yielded no significant condition effect in the time interval between 30 and 70 ms ( $F_{(1,12)}=0.002$ ;  $p=0.966$ ). Time–frequency plots and wavelet transforms for recognized and unrecognized stimuli are almost indistinguishable in Fig. 2A.

Total GBRs were significantly larger (0.118  $\mu$ V vs. 0.042  $\mu$ V) for recognized than unrecognized sounds in the time interval between 300 and 500 ms ( $T(12)=2.932$ ;  $p=0.013$ ; see Fig. 2B and C).

## 4. Discussion

In this study we attempted to investigate whether and to which extent the perception of complex environmental sounds for which subjects possess LTM representations modulates human EEG gamma activity. For this purpose we adapted our visual paradigm (Herrmann et al., 2004b) to the auditory modality: Subjects listened to recognizable everyday sounds for which they had an LTM representation and to sounds which they were not able to recognize. Their task was to decide whether they could determine the sound or not.

### 4.1. Behavioral data

Analysis of behavioral data showed that the subjects recognized more sounds than intended. We found large inter-individual differences with some subjects recognizing a lot more than others. Reaction time analysis revealed that subjects needed more time to declare a sound as unrecognized. This might be explained by the task itself: subjects were instructed not only to respond very accurately, but also fast. This could have led them to react immediately upon recognition of a sound, even if the sound presentation was not finished. In contrast, subjects may have searched their ‘mental sound-lexicon’ in case of unrecognizable sounds, and did not react until they were absolutely sure that they did not know that sound. Alternatively, the effect could also be attributed to the fact that every subject had to respond to recognized

stimuli with the dominant right hand. This should be randomized in future studies to exclude it as a potential confound.

### 4.2. Event-related potentials

We found no effects of LTM representation on the early ERP components (P50 and N100). Neukirch et al. (2002) and Schadow et al. (2005) reported that these components are sensitive to stimulus characteristics such as the sound-volume. Thus, we succeeded to generate two physically similar sets of stimuli using real-world sounds as the basis for unrecognizable sounds by just modifying a small part of their frequency spectrum, while nearly maintaining their spectral and temporal envelope. P200 amplitudes were enhanced for unrecognized stimuli over central and posterior regions. The cognitive function of the P2 or P200 has not been completely resolved to date (Crowley and Colrain, 2004) and existing results are inconsistent. However, Novak et al. (1992) suggested that the P200 represents an attention modulating process in oddball paradigms. Similar effects were shown by Garca-Larrea et al. (1992) who proposed that the P200 evaluates stimulus aspects during the classification process and facilitates a first rough stimulus appraisal. Finally, also the extent of required cognitive effort correlates with the P200 (Conley et al., 1999). Thus, P200 reflects attention and discrimination processes as well as task variables. This conclusion is supported by our data. While real-world sounds were recognized fast and easily, longer reaction times for unrecognized sounds could be indicative of higher cognitive demands and increased attention, because these complex sounds show no coherent percept. If the P200 actually is important for discrimination tasks, the observed difference could reflect a first categorization on the basis of stimulus parameters, possibly using rough categories such as harmonic/disharmonic or continuous/discontinuous where real-world sounds would be more likely to stem from the categories harmonic or continuous.

Starting very early around 270 ms the N400 persisted for 200 ms. This component has been associated with semantic aspects of familiarity and typically follows semantic errors. But research concerning the N400 leads to inconsistent results, too, like pseudo-words evoking larger N400 components (Rugg, 1990; Supp et al., 2004) or in contrast larger activation for real words than pseudo-words as found by Hahne and Jescheniak (2001). Furthermore, Opitz et al. (1999) observed an N400 only after presentation of identifiable environmental sounds, which is in line with the results of our present study.

### 4.3. Evoked and induced GBR

If human gamma activity is actually modulated by LTM processes, this should not only apply for visual processing but also for the auditory system. There is evidence that auditory short-term memory modulates late induced gamma-band activity (Lutzenberger et al., 2002; Kaiser et al., 2003). In contrast, visual LTM was found to influence only early evoked GBRs (Herrmann et al., 2004b). The present study failed to

reveal auditory LTM effects for the evoked GBR, but succeeded for the later induced GBR. This is no surprise: The perception of complex sounds develops over time, and the specific spectro-temporal pattern, resulting from changes in frequency and amplitude (Hall et al., 2003), has to be analyzed in order to localize and identify the auditory event. Given that these are changing every millisecond in complex sounds and that the composition of the sound plays a major role when the matching occurs, effects on the evoked GBR around 50 ms are very unlikely. Furthermore, as auditory evoked GBRs are strongly influenced by stimulus properties (Schadow et al., 2005) the absence of an effect of stimulus type provides additional evidence that both stimulus types did not differ in their physical characteristics and that the difference in trial numbers had no critical influence. This made it possible to attribute the effects

on the later induced GBR found between 300 and 500 ms to matching processes with auditory LTM. The fact that the involved neurons are widespread and highly specialized (Jefferys et al., 1996) is in line with our results because induced GBRs also exhibit widespread topographies in contrast to evoked GBRs which have more focal distributions. The topographic distribution of our induced activity (cf. Fig. 2C) with its central activation pattern is in line with previous findings (Haenschel et al., 2000), and can be explained by bilateral sources in primary auditory cortices as found for evoked activity (Pantev et al., 1991). Our results thus suggest that early auditory areas seem to be not only responsible for the analysis of stimulus features, but can also be assumed to serve as the storage location of auditory LTM information as suggested previously by Weinberger (2004). Therefore, matches of auditory input with stored LTM representation result in enhanced auditory gamma oscillations as illustrated in Fig. 3.

For the sake of better visualization of the features which a neuron represents this model is drawn for the visual cortex. However, it should apply to auditory cortex in a similar manner. We suggested a slightly different model for the generation of early evoked gamma activity based on phase modulation previously (Herrmann et al., 2004c). We think that early processes can be assumed to be more strongly influenced by timing issues such as phase ordering than later processes. Early processing stages still operate with much the same latency after stimulus onset if they reside in the same hierarchical level. Later stages, however, accumulate different latencies depending on the number of intermediate synapses leading to greater latency differences (jitter) even within one hierarchical level. Thus, late induced gamma activity is probably not predominantly modulated by the phase of neuronal oscillations but by the number of neurons which oscillate.

## 5. Conclusion

Our results suggest that remembering auditory patterns which are stored as representations in LTM is reflected by increased induced gamma-band oscillations, whereas visual matching processes are observable even in early evoked gamma oscillations. Altogether, gamma oscillations are not only correlates of bottom-up processes, but are related to higher cognitive functions in the visual as well as in the auditory system, with memory access being a crucial factor. It would be interesting for future studies, whether, analogous to the visual system (Gruber et al., 2004a), the auditory GBR increases for unknown complex sounds when a memory representation is built up. Additionally, it is rather unclear to which extent intrapersonal differences between auditory and visual GBR appear and why there are strong inter-personal differences. Combined measurements with EEG and fMRI might offer a closer view on possible anatomic characteristics or generators of gamma activity.

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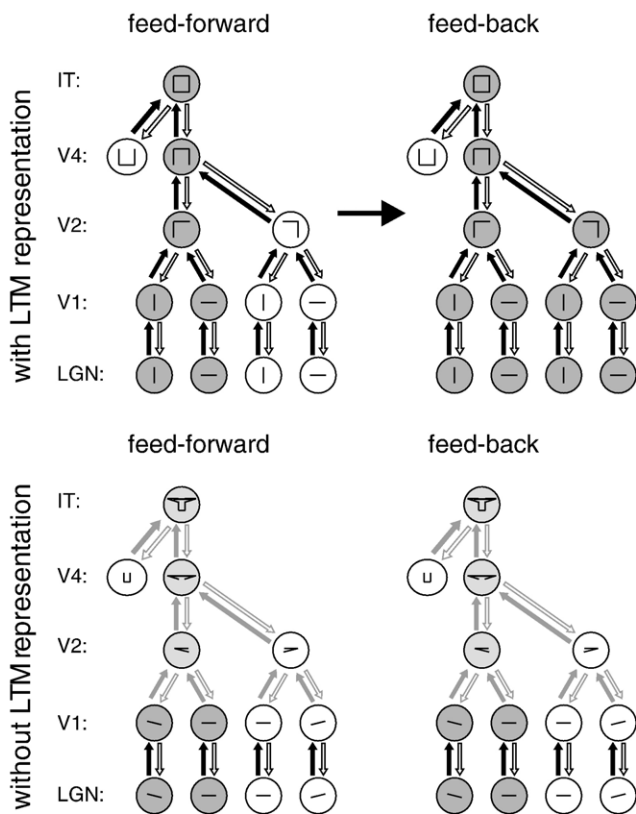


Fig. 3. Schematic model of the generation of gamma oscillations in the visual cortex. Objects are stored within a neural network like the brain by synaptically connecting those neurons which represent features of that object. Top: If horizontal and vertical line detector cells in V1 were involved in perceptions of square outlines for many times they are connected by strong synapses (black arrows) to neurons which represent squares in higher visual areas such as V4 or IT. If these V1 neurons become activated by visual input from the LGN they activate higher visual representations via feed-forward (solid arrows) which in turn also activate other low-level representations via feed-back (outlined arrows) that belong to an object but were not actually perceived. This increased number of activated neurons leads to increased gamma oscillations for recognized objects. Bottom: If, on the other hand, horizontal and slightly tilted lines have not been perceived frequently as parts of some sort of imaginary object then the above mentioned strong connections do not exist (gray arrows). Therefore, activating these V1 neurons leads to less feed-forward activation of higher visual areas and almost no feed-back into other low-level neurons. Therefore, less neurons are active resulting in gamma oscillations of lower amplitude.

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