

available at [www.sciencedirect.com](http://www.sciencedirect.com)[www.elsevier.com/locate/brainres](http://www.elsevier.com/locate/brainres)**BRAIN  
RESEARCH****Research Report****Human EEG very high frequency oscillations reflect the number of matches with a template in auditory short-term memory**

Daniel Lenz<sup>a</sup>, Marcus Jeschke<sup>b</sup>, Jeanette Schadow<sup>a</sup>, Nicole Naue<sup>a</sup>,  
Frank W. Ohl<sup>b,c</sup>, Christoph S. Herrmann<sup>a,\*</sup>

<sup>a</sup>Otto-von-Guericke-University Magdeburg, Department of Biological Psychology, PO Box 4120, 39016 Magdeburg, Germany

<sup>b</sup>Leibniz Institute for Neurobiology, Brennekestrasse 6, 39118 Magdeburg, Germany

<sup>c</sup>Otto-von-Guericke University Magdeburg, Institute for Biology, PO Box 4120, 39016 Magdeburg, Germany

**ARTICLE INFO****Article history:**

Accepted 16 October 2007

Available online 28 October 2007

**Keywords:**

40 Hz

Auditory

EEG

Frequency-modulated sound

Gamma activity

**ABSTRACT**

Auditory perception comprises bottom-up as well as top-down processes. While research in the past has revealed many neural correlates of bottom-up processes, less is known about top-down modulation. Memory processes have recently been associated with oscillations in the gamma-band of human EEG (30 Hz and above) which are enhanced when incoming information matches a stored memory template. Therefore, we investigated event-related potentials (ERPs) and gamma-band activity in 17 healthy participants in a Go/NoGo-task. They listened to four frequency-modulated (FM) sounds which varied regarding the frequency range traversed and the direction of frequency modulation. One sound was defined as target and required a button press. The results of ERPs (N1, P2, N2, and P3) were consistent with previous studies. Analysis of evoked gamma-band responses yielded no significant task-dependent modulation, but we observed a stimulus dependency, which was also present in a control experiment: The amplitude of evoked gamma responses showed an inverted U-shape as a function of stimulus frequency. Investigation of total gamma activity revealed functionally relevant responses at high frequencies (90 Hz to 250 Hz), which showed significant modulations by matches with STM: Complete matches led to the strongest enhancements (starting around 100 ms after stimulus onset) and partial matches resulted in intermediate ones. The results support the conclusion that very high frequency oscillations (VHFOs) are markers of active stimulus discrimination in STM matching processes and are attributable to higher cognitive functions.

© 2007 Elsevier B.V. All rights reserved.

**1. Introduction**

In order to perceive an object, the information entering our brain is matched with existing representations in long-term

memory (LTM). If the result of the match is positive, this leads to the perception of a known object. Otherwise we perceive a new, unknown object. Similar matches are required in order to compare incoming information with the content of short-term

\* Corresponding author. Fax: +49 391 67 12222.

E-mail address: [christoph.herrmann@nat.uni-magdeburg.de](mailto:christoph.herrmann@nat.uni-magdeburg.de) (C.S. Herrmann).

memory (STM). Here, we would like to investigate which physiological processes reflect the matching of incoming information with STM.

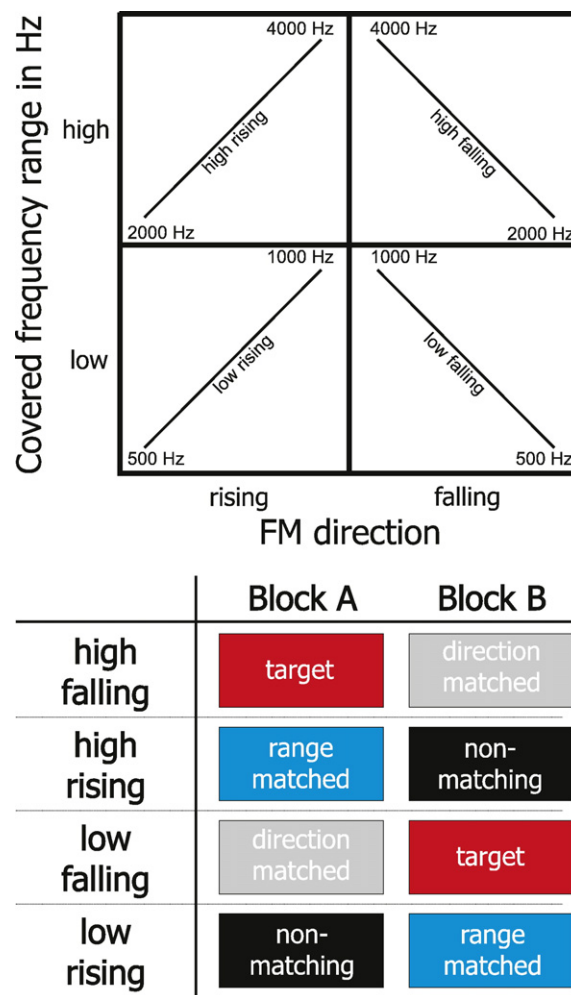
One electrophysiological correlate of memory processes can be found in oscillatory brain activity in the gamma-range (30 Hz and above), first reported in the early 1940s in hedgehogs (Adrian, 1942). Initially studied in animals, the association between synchronous neuronal firing in the gamma-band (gamma-band responses, GBR) and feature binding could be demonstrated (Gray et al., 1989; Singer and Gray, 1995). Subsequently, it has also been thoroughly investigated in humans for the visual (Lutzenberger et al., 1995; Tallon-Baudry et al., 1996; Keil et al., 1999; Herrmann and Mecklinger, 2001) as well as the auditory system (Pantev et al., 1991; Knief et al., 2000; Crone et al., 2001; Kaiser et al., 2007). While many authors were able to reveal gamma oscillations as correlates of cognitive functions, others failed to find this type of activity in humans at all (Juergens et al., 1999). This is most likely due to the fact that gamma oscillations depend strongly on physical stimulus parameters (Busch et al., 2004).

Dealing with GBRs requires the differentiation between an early phase-locked and a late non-phase-locked component (Galambos, 1992). The first is referred to as evoked activity, which appears within the first 100 ms after stimulus onset and is strictly phase-locked to it. Evoked activity can therefore be analyzed by transforming the averaged single-trials, i.e. the event-related potential (ERP), into the frequency domain. The second component, the so-called induced activity, occurs after about 150 ms, shows a higher phase jitter and is revealed by transforming single-trials and averaging them subsequently.

The functional role of GBRs has become a topic of a lively debate within the last few years (Başar-Eroglu et al., 1996; Başar et al., 1999). For induced gamma oscillations, multiple authors were able to reveal cognitive correlates (for reviews see Tallon-Baudry and Bertrand, 1999; Engel and Singer, 2001). For evoked oscillations, however, the case was less obvious. Some authors argued that the latter are merely correlates of sensory processing without cognitive function (Karakaş and Başar, 1998). However, other authors were able to identify cognitive correlates of evoked GBRs, such as attention (Tiitinen et al., 1993; Yordanova et al., 1997; Debener et al., 2003). This discrepancy probably results from the large bottom-up influence on evoked gamma oscillations, driven by stimulus parameters such as size (Busch et al., 2004), spatial frequency (Frund et al., 2007), stimulus contrast (Schadow et al., 2007b), or loudness (Schadow et al., 2007a). Meanwhile it has been demonstrated that evoked GBRs reflect the interaction of bottom-up and top-down processes (Busch et al., 2006b).

With respect to memory processes, GBRs have been repeatedly correlated with different aspects of STM and LTM. In the visual domain, induced GBRs were associated with STM (Tallon-Baudry et al., 1998; Gruber et al., 2002, 2004) as well as LTM (Busch et al., 2006a). In addition, evoked GBRs were found to correlate with STM (Herrmann and Mecklinger, 2001) and LTM (Herrmann et al., 2004b; Freunberger et al., 2007). In the auditory domain, mainly induced GBRs have been shown to reflect processes of LTM (Lenz et al., 2007) and STM (Lutzenberger et al., 2002; Kaiser et al., 2003). Herrmann et al. (2004c) summarized these findings in the ‘match-and-utilization model’ (MUM), which states that a match with an existing

memory representation leads to enhanced GBRs due to stronger feedback from higher cortical areas. These matching processes can take place at very early stages (about 100 ms after stimulus onset) of visual processing (Herrmann et al., 2004b). Debener et al. (2003) also reported increased early evoked GBRs for auditory targets in a novelty oddball task, where two sine tones served as standard and target stimuli, respectively. To identify the target, a comparison of the stimulus with a template stored in STM is necessary and results in higher evoked GBRs when stimuli match with the target template. However, Lenz et al. (2007) only found differences in the later induced gamma-band comparing real-world environmental sounds, which matched with LTM representations, and physically comparable sounds without any LTM representation. Since this identification is based on a complex sound analysis, which requires processing of changes in frequency and amplitude over time, it seems plausible to expect these matching processes in a later time-window.

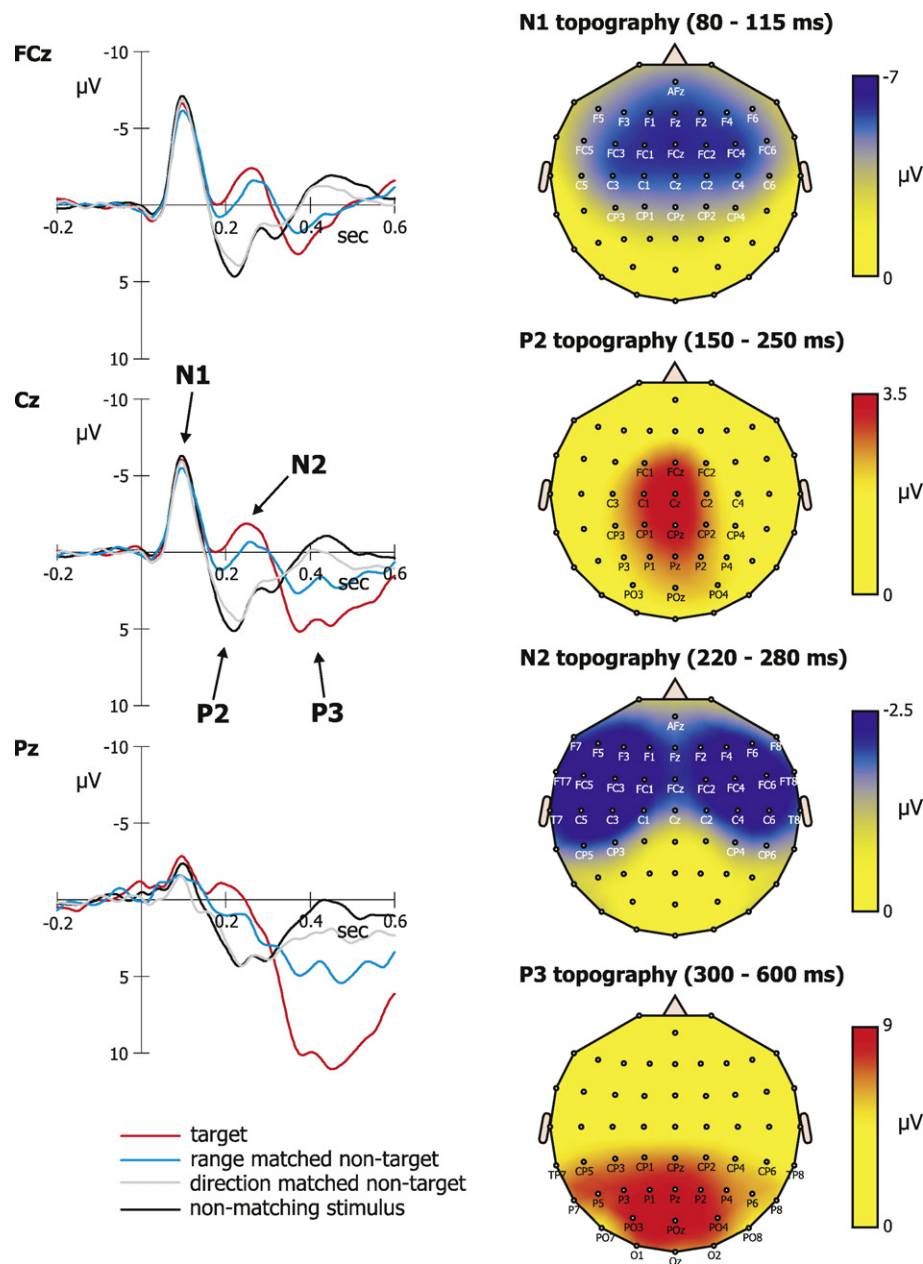


**Fig. 1 – (Top)** The subjects were asked to listen to four different FM sounds which varied regarding their two features ‘frequency range’ and ‘FM direction’. **(Bottom)** The same four stimuli were used in two experimental blocks (A and B). However, the task differed across blocks, i.e. which stimulus was considered as target and required a button-press.

Recently, we were able to implement a spiking neural network model which also revealed enhanced gamma oscillations when processing stimuli which were ‘stored’ in its synaptic connections (Fründ and Herrmann, 2007). From the model, we could derive an important prediction for human EEG experiments for the model to be valid: Partial matches with memory contents should lead to intermediate levels of GBRs.

In a study adapted from Tallon-Baudry et al. (1996), Herrmann and Mecklinger (2001) used four Kanizsa figures, where one stimulus was defined as the target. The detection process required the comparison of two stimulus features (form and collinearity) with the stored memory template. Thus, the standard stimuli varied either in a single or in both features. The

authors observed maximal GBR enhancements when both features matched with stored information, followed by stimuli, which resembled the target in one feature, whereas the non-matching stimulus evoked the lowest activity. For the auditory domain, however, such a paradigm investigating partial matches has not yet been carried out. Therefore, we aimed to design a similar target detection experiment to study such feature processing in the auditory modality. We decided to use linearly frequency-modulated sounds (FM), as this entailed some advantages. Frequency-modulated sounds can be determined by the two features ‘frequency range traversed by the modulation’ and ‘direction of frequency modulation’. Thus, to detect a target, frequency range and FM direction have to be



**Fig. 2 – Grand-average ERPs as time-courses at central electrodes (left column) and scalp distributions of the analyzed components (right column). The topographies show the condition which exhibited the strongest activation in the relevant time-window (N1: target, P2: non-matching stimulus, N2: target, P3: target). Electrode labels are given for those channels which were included in the ROI for statistical analysis of the according ERP component.**

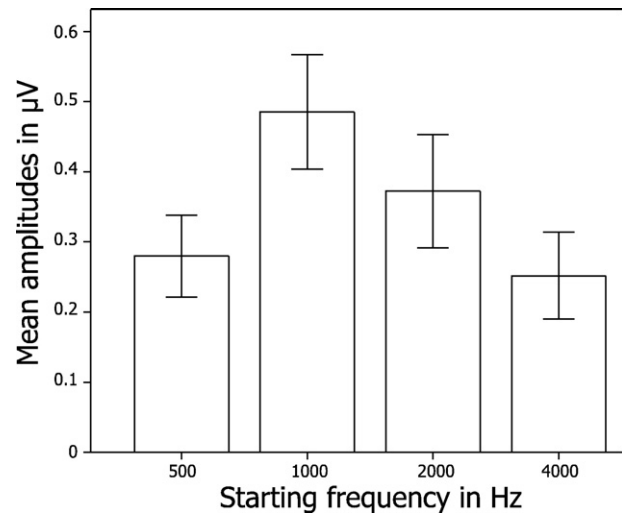
analyzed. As we intended to use two different frequency ranges and rising vs. falling FM directions, this yielded four different sounds: one target sound, one stimulus with the same frequency range but different FM direction (range matched non-target), one sound with different frequency range but same FM direction (direction matched non-target), and one non-target, matching neither in frequency range nor in FM direction (non-matching stimulus; see Fig. 1 and Experimental procedures for details). The second argument that favored FM sounds was to conduct the same experimental design with Mongolian gerbils (see Jeschke et al., 2008) that have been successfully trained and investigated using FM sounds (Ohl et al., 1999, 2000, 2001). This offered the opportunity to complement non-invasive results from human EEG with intracranial recordings of rodents to get more detailed information about the involved mechanisms.

Thus, we tested the hypothesis that sounds matching in both stimulus features (targets) should yield maximum GBR increases, followed by stimuli containing one target feature (range or direction matched non-targets). Stimuli composed of no target feature should result in lowest GBRs (non-matching stimuli).

## 2. Results

### 2.1. Behavioral data

Participants performed the task with high accuracy (97% hits, 1.5% false alarms) and a mean reaction time of 495.8 ms (SD=73.2 ms). However, there was a trend for slightly more false alarms following stimuli with the same frequency range

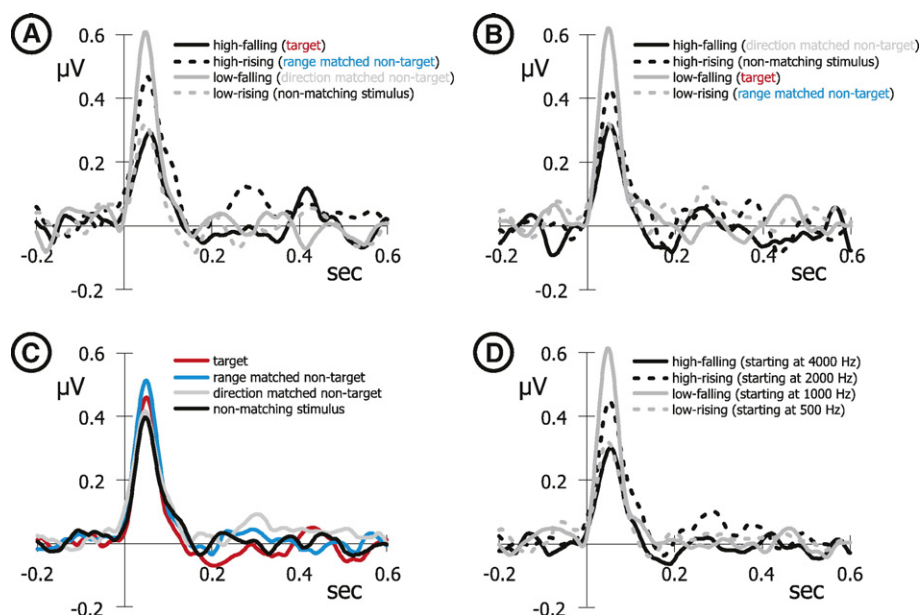


**Fig. 4 – Grand-average amplitudes and standard errors of evoked gamma activity in the defined fronto-central ROI depicted for each stimulus type. Signals showed the largest amplitudes for stimuli starting at 1000 Hz (low-falling) and the smallest for stimuli starting at 500 Hz (low-rising) and 4000 Hz (high-falling), respectively.**

as the target, although this did not reach statistical significance ( $F_{2,32}=3.35$ ;  $p=0.074$ ).

### 2.2. Event-related potentials

The ERPs and scalp topographies are presented in Fig. 2. All conditions were characterized by a strong fronto-central



**Fig. 3 – Time-courses of evoked gamma activity depicted as grand-average at electrode Cz. (A and B) Blocks A and B showed nearly identical activations if stimuli are sorted according to physical properties. (C) Averaging stimuli depending on the subjects' task (factor CONDITION) revealed no task-dependent modulation. (D) Averaging the physically identical stimuli irrespective of their task relevance yielded a significant effect of STIMULUS TYPE with larger amplitudes evoked by stimuli starting at 1000 Hz (low-falling sounds).**

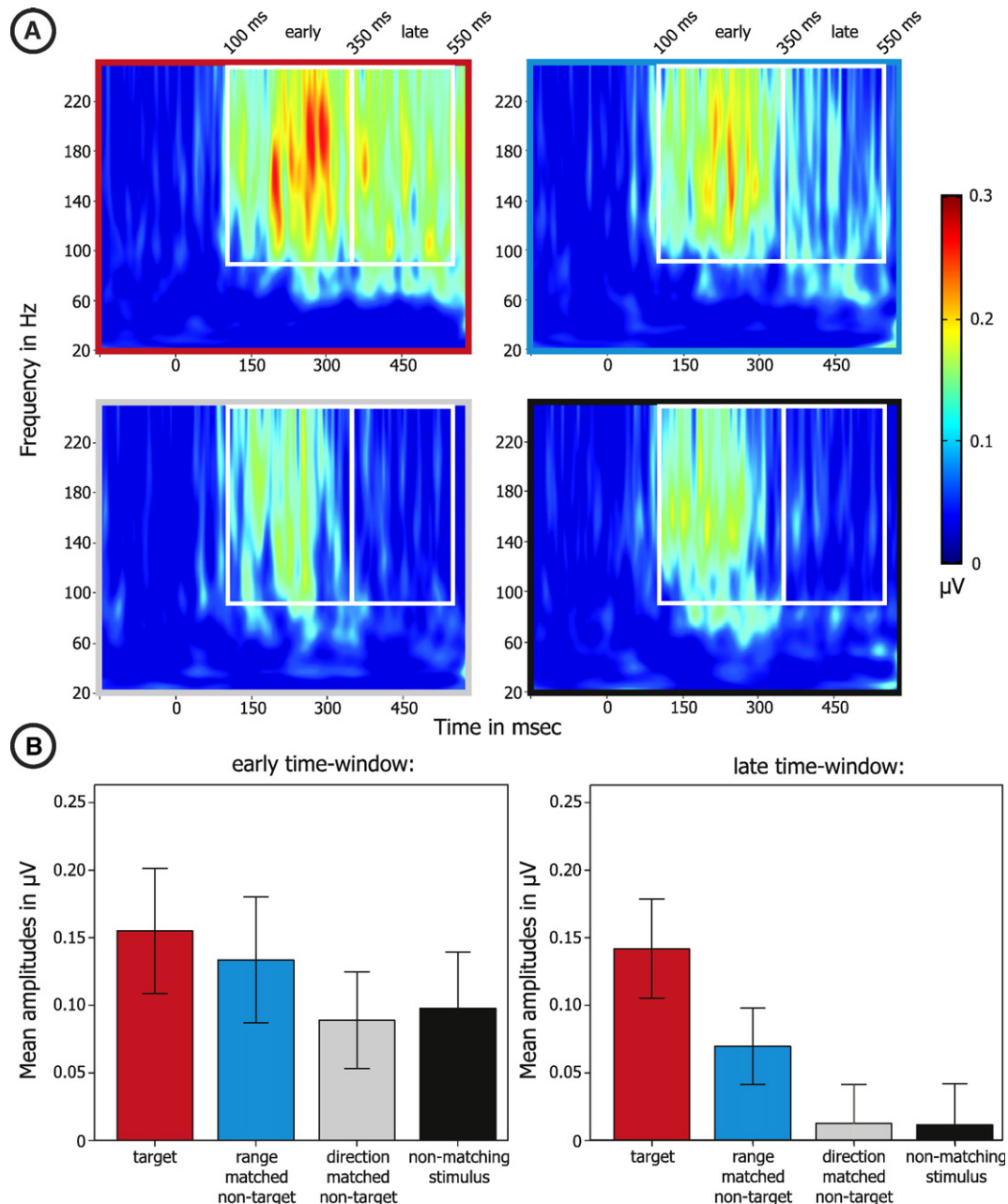


negativity after approximately 100 ms (N1), followed by a central positivity around 200 ms (P2) and a frontal negativity around 250 ms (N2). However, not all conditions reached a negative maximum for this component. Starting at 300 ms, posterior electrodes exhibited a strong positivity with higher amplitudes for target stimuli.

Repeated measures ANOVAs tested for effects of BLOCK (A vs. B) and CONDITION (four levels: target, range matched non-target, direction matched non-target, non-matching stimulus).

There were no significant CONDITION  $\times$  BLOCK interactions. Therefore, ERPs were averaged across blocks.

While N1 amplitudes ( $F_{3,48}=3.28$ ;  $p=0.061$ ) and latencies ( $F_{3,48}=0.81$ ;  $p=0.487$ ) in the fronto-central ROI did not differ significantly, the ANOVA for the P2 component in the central ROI resulted in a significant effect both for amplitude ( $F_{3,48}=17.98$ ;  $p<0.001$ ) and latency ( $F_{3,48}=11.06$ ;  $p<0.001$ ), indicating larger amplitudes and longer latencies for non-matching stimuli. The ANOVA for the N2 time-window at frontal



**Fig. 5 – Grand-average of total gamma activity as mean of the defined ROI. (A)** Time-frequency planes for all four conditions (red: target, blue: range matched non-target, grey: direction matched non-target, black: non-matching stimulus) revealed differences in both time-windows in the frequency band between 90 Hz and 249 Hz, but not in the lower frequency band between 30 Hz and 90 Hz. **(B)** Mean amplitudes and standard errors of the defined ROI in the early time-window reveal a significant condition effect. The effect was even stronger in the late time-window. Targets induced stronger GBRs, stimuli with the same frequency range induced intermediate GBRs and stimuli with the same FM direction as well as non-matching stimuli induced the lowest GBRs.

electrodes also yielded a significant effect for amplitude ( $F_{3,48}=19.12$ ;  $p<0.001$ ) and a tendency for latency ( $F_{3,48}=4.36$ ;  $p=0.012$ ), with larger amplitudes and shorter latencies for target stimuli, followed by range matched non-targets and direction matched non-targets. Non-matching stimuli led to the smallest amplitudes and the longest latencies. The posterior ROI showed a strong condition effect in the P3 time-window ( $F_{3,48}=49.32$ ;  $p<0.001$ ), with the largest amplitudes for targets, followed by range matched non-targets and direction matched non-targets. Non-matching stimuli revealed the lowest activation.

### 2.3. Evoked gamma activity

The analysis of wavelet transformed data yielded no significant effect of the factor CONDITION for evoked gamma-band activity ( $F_{3,39}=0.97$ ;  $p=0.403$ ) (see Fig. 3C). However, we found a trend for a CONDITION  $\times$  BLOCK interaction ( $F_{3,39}=5.20$ ;  $p=0.013$ ), illustrated in Figs. 3A and B. As depicted in Figs. 3D and 4, after averaging the physically identical stimuli across both blocks irrespective of the subjects' task (factor STIMULUS TYPE: high-falling, high-rising, low-falling, low-rising), there were significant higher activations evoked by stimuli starting at 1000 Hz ( $F_{3,39}=4.09$ ;  $p=0.017$ ).

### 2.4. Total gamma activity

There were no significant CONDITION  $\times$  BLOCK interactions. Therefore, conditions were averaged across blocks.

The analysis of total gamma activity revealed no significant effects of CONDITION in the lower frequency band (between 30 Hz and 90 Hz), neither in the early ( $F_{3,39}=0.89$ ;  $p=0.401$ ) nor in the late time-window ( $F_{3,39}=0.81$ ;  $p=0.491$ ). However, examining the higher frequency band between 90 Hz and 249 Hz revealed strong CONDITION effects in the early ( $F_{3,39}=8.57$ ;  $p=0.002$ ) as well as the late time-window ( $F_{3,39}=14.38$ ;  $p<0.001$ ), with higher activations for targets, followed by range matched non-targets. Smallest amplitudes were induced for direction matched non-targets and for non-matching stimuli (see Fig. 5 for details). This difference was even stronger in the late time-window (post hoc comparisons are depicted in Table 1).

The ANOVAs investigating hemispheric differences after responses to target stimuli resulted in no significant effects of the factor LATERALITY (left vs. right) in the early ( $F_{1,13}=0.02$ ;  $p=0.880$ ) as well as the late time-window ( $F_{1,13}=0.03$ ;  $p=0.870$ ).

**Table 1 – Post hoc comparisons for total gamma activity revealed a target effect in the early and late time-window with stronger differences starting at 350 ms**

Comparison	Early time-window	Late time-window
Target vs. range matched non-target	$t[13]=1.722$ , $p=0.327^{n.s.}$	$t[13]=3.00$ , $p=0.03$
Range matched non-target vs. direction matched non-target	$t[13]=3.117$ , $p=0.024$	$t[13]=4.10$ , $p=0.003$
Direction matched non-target vs. non-matching stimulus	$t[13]=0.893$ , $p=1.000^{n.s.}$	$t[13]=-0.09$ , $p=1.000^{n.s.}$

## 3. Discussion

The purpose of the present study was to further assess the role of electrophysiological activity above 30 Hz for memory matching. Therefore, we adapted a visual target detection experiment by Herrmann and Mecklinger (2001): Participants listened to four different FM sounds and had to detect a target stimulus by evaluating the two sound features 'frequency range' and 'FM direction'. Thus, one sound matched in both features (the target), two sounds matched in one feature with the target template and one sound was characterized by sharing no target feature.

### 3.1. Behavioral data

Analysis of behavioral data indicated that the subjects performed the task quickly and with high accuracy. However, there were slightly more errors after presentation of stimuli composed of the same frequency range, followed by stimuli with the same FM direction. This implies that the dimension 'frequency range' is more salient for auditory target detection than the dimension 'FM direction', leading to more false alarms during the target classification process. A similar pattern was found in our companion study investigating a nearly identical experiment in Mongolian gerbils (see Jeschke et al., 2008).

### 3.2. Event-related potentials

We did not observe a task effect in the N1 time-window at fronto-central electrodes. This seems plausible as this component is mostly modulated by exogenous stimulus parameters such as its intensity (Näätänen and Picton, 1987) which was adapted for in our experiment by using individually hearing levels.

At central electrodes, P2 amplitudes and latencies were enhanced for non-matching stimuli and range matched non-targets, whereas stimuli comprising the same frequency range resulted in lower amplitudes and latencies. Target stimuli hardly reached a positivity in this time-window at all. The results correspond to findings by García-Larrea et al. (1992), who stated that this component may index the stimulus-classification process in oddball tasks.

Similar results were found for N2 and P3 amplitudes which are both involved in target detection (Näätänen and Picton, 1986; Polich, 1986). It has been shown that attended target stimuli elicit a distinct negativity around 200 ms after stimulus onset (Ritter et al., 1992; Nager et al., 2001) which is larger for those sounds that differ more strongly from frequent standard stimuli (Näätänen et al., 1980; Näätänen and Picton, 1986). Our results support this conclusion, because N2 amplitudes were largest for target stimuli and lowest for non-matching stimuli.

The analysis of the P3 component, which is associated with an active stimulus identification process (Hillyard et al., 1973; Polich, 1986) and is typically revealed in oddball paradigms (García-Larrea et al., 1992; Başar-Eroglu et al., 2001), also yielded a clear target effect with largest amplitudes for stimuli matching in both target features, followed by range matched

and direction matched non-targets. Lowest P3 signals were found for stimuli matching in none of the sound features with the target template.

Hence, examination of event-related potentials is in line with previous findings. The result that non-matching stimuli and direction matched non-targets yielded comparable amplitudes as well as range matched non-targets and target stimuli supports our assumption for the frequency range being the more salient feature in the target classification process than the FM direction of a stimulus.

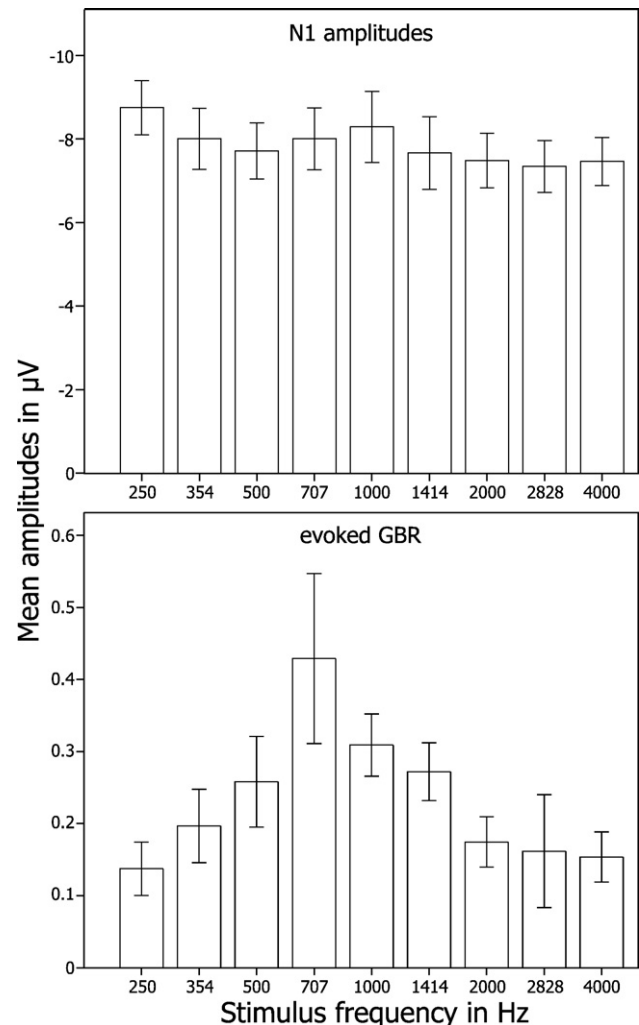
### 3.3. Evoked gamma activity

Top-down modulations of human auditory GBRs have previously been reported for the early evoked GBRs (Tiitinen et al., 1993; Yordanova et al., 1997; Debener et al., 2003). However, we did not observe a top-down modulation of evoked gamma activity in our data. This is in line with our recent study showing no auditory LTM effects in this early phase-locked response (Lenz et al., 2007). We argued that this lack of an effect is due to the fact that perception of complex sounds requires the evaluation of its spectro-temporal pattern over time, which makes memory matches around 50 ms, where evoked GBRs usually occur, very unlikely. The fact that the stimuli used in the present study were more complex than simple sine tones could explain the difference to Tiitinen et al. (1993), Yordanova et al. (1997) and Debener et al. (2003).

Nevertheless, we found another interesting result: Analysis of evoked GBRs demonstrated no significant difference of CONDITION across the two experimental blocks. Thus, as the stimuli evoked nearly identical amplitudes, there seemed to be no top-down modulation at all. Analysis of the factor STIMULUSTYPE across both blocks yielded a strong stimulus effect with maximum amplitudes for low-falling sounds. This finding suggests that evoked GBRs depend on the starting frequency of our stimuli. To verify the hypothesis that early GBRs depend upon stimulus frequency, we conducted a control experiment, where nine sine tones (250 Hz to 4000 Hz in steps of half an octave) served as standard stimuli and a noise stimulus was defined as target stimulus in a forced-choice discrimination task (see Fig. 6 and caption for details). This study revealed similar results: The amplitude of evoked GBRs increased from 250 Hz to frequencies around 707 Hz or 1000 Hz and decreased at higher frequencies.

A potential explanation for this frequency dependence might lie in the frequency tuning of the auditory system starting with the hair cells of the inner ear. While these hair cells all have tuning curves with one best frequency, the width of the tuning curves differs across frequencies (Pickles, 1988). Fig. 7 displays how wider tuning curves around 1000 Hz might lead to the observed frequency dependence of evoked GBRs.

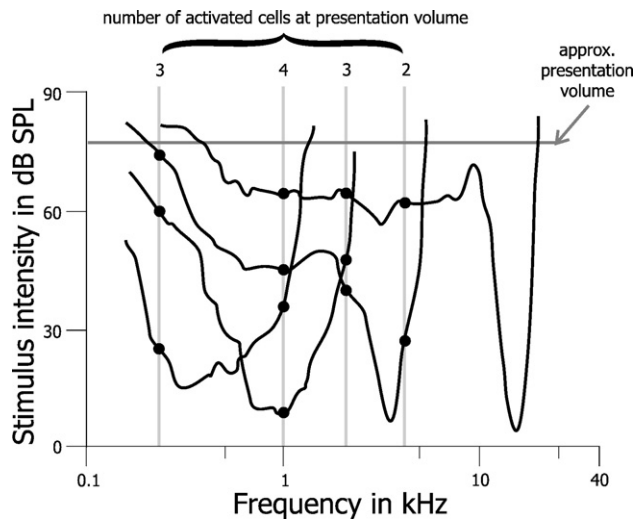
However, a corresponding explanation is offered by the cortical organization of tonotopic maps. Intracranial recordings from animals (Budinger et al., 2000) as well as fMRI data from humans (Yetkin et al., 2004; Langers et al., 2007) suggest that the representation of frequencies around 1000 Hz occupies more cortical space than other frequencies. This could also explain the enhanced evoked GBRs around 1000 Hz.



**Fig. 6 – Control experiment: (Top)** We found no effect of sound frequency on N1 amplitude ( $F_{8,96}=1.31$ ;  $p=0.277$ ; grand-average mean amplitudes and standard errors in the N1 ROI). This indicates that we have successfully adjusted the intensity of our sounds to the individual hearing thresholds. **(Bottom)** The evoked GBRs peaked around 50 ms and showed a trend for maximum values for 707 Hz sine tones ( $F_{8,96}=2.84$ ;  $p=0.048$ ; grand-average mean amplitudes and standard errors in the fronto-central GBR-ROI). Thirteen participants (mean age  $25 \pm 3$  years, 8 female) had to discriminate sine tones (250 Hz up to 4000 Hz in steps of half an octave) from a broadband noise sound by pressing one of two buttons with their left or right index finger. Each stimulus had a length of 500 ms with 10 ms rising and falling time. Before the experiment, we determined the individual hearing threshold separately for the left and right ear in steps of 2 dB for each stimulus. During the experimental session, the sounds were presented in pseudo-randomized order at 75 dB HL and each stimulus was repeated 100 times. The other methods were identical to the first study and are described in Experimental procedures.

Thus, in addition to intensity of auditory stimuli (Schadow et al., 2007a), the sound frequency seems to modulate auditory evoked GBRs.





**Fig. 7 – Schematic illustration of tuning curves of hair cells in the inner ear. Cochlear hair cells are sensitive to specific frequency ranges, exemplary shown here for four cells (black curves). These cells respond to their ‘best frequency’ even at low stimulus intensities. However, increasing the stimulus intensity results in more unspecific responses and the cells are activated by a wider frequency range. Thus, setting the intensity to about 80 dB SPL leads to activation of many cells even if the stimulation frequency is far away from their best frequency. The vertical grey bars indicate stimulation at 250 Hz, 1000 Hz, 2000 Hz and 4000 Hz, respectively. The pattern of overlap results in a maximum of activated cells around 1000 Hz. Thus, at this stimulus intensity, a 1000 Hz stimulus activates a larger number of neuronal cells leading to stronger cortical responses. This is a potential explanation for the higher amplitude of evoked GBRs around this frequency (adapted from Pickles (1988) as redrawn in Kandel et al. (2000), p. 599).**

### 3.4. Total gamma activity

Induced activity in the gamma-range is linked to auditory STM (Lutzenberger et al., 2002; Kaiser et al., 2003; Kaiser and Lutzenberger, 2004) as well as LTM processes (Lenz et al., 2007). However, in the present study, time-frequency analysis of total GBRs (containing phase-locked and non-phase-locked activity) yielded no significant task effect in the frequency range between 30 Hz and 90 Hz, but in the higher frequency band starting at 90 Hz.

Neural networks demonstrate several oscillatory bands covering frequencies up to 500 Hz or higher (Buzsáki and Draguhn, 2004; Canolty et al., 2006). Such very high frequency oscillations have been found in intracranial recordings of animals (Logothetis et al., 2001; Brosch et al., 2002; Siegel and König, 2003) as well as in human invasive recordings (Edwards et al., 2005; Lachaux et al., 2005; Trautner et al., 2006) and magnetoencephalographic studies (Siegel et al., 2007) and seem to be modulated by sensory and cognitive events (Crone et al., 1998, 2001). Although these oscillations were demonstrated to be involved in pathological states such as epilepsy (Fisher et al., 1992; Bragin et al., 1999), they were also observed up to 200 Hz in

electroencephalographic studies investigating healthy subjects (Hall et al., 1967, 1968). Moreover, Gonzalez et al. (2006) described very high frequency oscillations (VHFOs) in EEG and linked them to motor-related processes. They stated that these VHFOs may play a functional role in the human brain and are not only of pathological origin. This notion is supported by our results. Starting around 100 ms after stimulus onset, we found considerable activations up to 250 Hz, which were significantly modulated by task variables, leading to the largest activations for target stimuli and the lowest amplitudes for non-matching stimuli. Especially the later time-window starting at 350 ms highlighted particular differences between the task conditions. Stimuli that matched in both target features resulted in the largest activations followed by sounds that shared the same frequency range. The lowest VHFOs were found for stimuli containing the same FM direction and non-matching stimuli. This is clear evidence that these VHFOs reflect top-down modulations for proper target detection, which is based on the evaluation of two stimulus features in comparison to a memory stored template. In consistence with the proposed ‘match-and-utilization-model’ (Herrmann et al., 2004c), VHFOs were enhanced when the comparison of both stimulus features yielded a positive result. Matches of the sound’s frequency range also led to an increase, which was somewhat lower. Non-target stimuli matching in none of the target features showed therefore lowest activity. Positive comparison of the feature ‘FM direction’ led to similar amplitudes as non-matching stimuli. This activation pattern represents further evidence for the feature ‘frequency range’ being the more salient property in target classification and is in accordance with our behavioral results and ERP data.

However, this is in contrast to Herrmann and Mecklinger (2001), who reported a similar effect for visual processing, but for early evoked activity. As pointed out, our effect seems to be a consequence of complex sound processing, which is based on analyzing spectro-temporal features over time. Hence, early memory matches are very unlikely, since it is necessary to listen to more complex sounds for some time in order to recognize them (Lenz et al., 2007).

The spatial resolution of our EEG recordings does not suffice to infer the location of the neural generator of the GBRs. However, it seems plausible to assume the sources in the primary auditory cortex (A1). First of all, nearly the same experiment has been carried out in Mongolian gerbils with intracranial recordings from A1 (see Jeschke et al., 2008). The total GBRs from gerbils’ area A1 resemble our pattern of total GBR, suggesting similar sources. Moreover, intracranial recordings from monkey A1 also revealed evoked as well as induced GBRs (Brosch et al., 2002) and intracranial recordings in patients revealed induced GBRs in the superior temporal gyrus (Crone et al., 2001). Thus, our data seem to suggest that induced (total) GBRs from the primary auditory cortex reflect matches with STM. This notion is in line with animal recordings that show learning induced plasticity in A1 (Ohl and Scheich, 2005) responsible for LTM (Weinberger, 2004) as well as associative memory (Weinberger, 2007). However, the frequency of the oscillations in the Mongolian gerbil (approx. 40 Hz) did not match those of the VHFOs in humans (>100 Hz). This could either be due to differences across species or might



indicate that the underlying neural generators are different. Further experiments are needed to address this issue.

The VHFOs in human EEG have hardly been studied. One could ask, why are there only few studies reporting activity above the traditional gamma-band (30 Hz–90 Hz). In our opinion, this could be related to the fact that most studies employ low-pass filters around 100 Hz and therefore ignore higher oscillations. Furthermore, analysis of VHFOs requires very accurate measurement and analysis methods. Our data assessment was based on very low impedances to get a good signal to noise ratio and we even removed minimal myogenic activity after exact visual inspection of the raw data. In addition, if our activation pattern would merely result from random artifacts, there should be no significant differences between conditions. The presence of VHFOs was not restricted to regions associated with motor activity and showed no hemispheric difference. Instead of that, they were spread in a fronto-central region and were found in all conditions, which implies that they are not purely caused by motor responses to target stimuli. Instead, we interpret them as one marker of active stimulus discrimination in STM matching processes and attribute them to higher cognitive functions. Experiments investigating electrophysiological correlates of STM and LTM frequently also find oscillations in the theta frequency range to be associated with memory phenomena (O'Keefe, 1993; Klimesch, 1999). Recently, it has been demonstrated that the amplitude of gamma oscillations is modulated by the phase of theta oscillations (Canolty et al., 2006; Demiralp et al., 2007). However, these studies investigated the two types of oscillations in perceptual and motor tasks rather than during memory experiments. Thus, future studies should test the hypothesis that this interaction is relevant for memory processes.

## 4. Conclusion

In summary, we demonstrated that evoked GBRs are more sensitive to sound frequency than N1. This has to be taken into account for future studies. Furthermore, we demonstrated that there is functionally relevant activity above the traditional gamma-band which is largely unexplored in human EEG of healthy subjects. This should be the topic of subsequent research. Most importantly, the amplitude of these VHFOs reflected the complete and partial matches with STM.

## 5. Experimental procedures

### 5.1. Participants

Seventeen paid subjects (7 female) with a mean age of  $24 \pm 3$  years participated in this study and gave their written and informed consent. They reported no hearing deficits and had no history of any kind of neurological or psychiatric disorders. All participants received a written task instruction. The study was approved by the ethics committee of the Otto-von-Guericke-University Magdeburg and was conducted in accordance with the Declaration of Helsinki.

### 5.2. Stimuli and task

Subjects listened to four types of linearly frequency-modulated (FM) sounds. The digitally synthesized FMs (44.1 kHz sampling rate) lasted 250 ms with 5 ms ramps at the beginning and end. The FMs covered one octave and differed in their frequency range traversed by the modulation (center frequency: 750 Hz vs. 3000 Hz) and direction of frequency modulation (rising vs. falling). Thus, the sounds were determined by two features: FM direction and frequency range. The overview of all stimuli used is depicted in Fig. 1. The sounds were delivered binaurally using insert earphones (EARTone 3A). To avoid confound resulting from different stimulus intensities (as shown by Schadow et al., 2007a), sound volume was adapted to each subjects' individual hearing level (HL). Therefore, the hearing thresholds for each subjects' left and right ear were determined for both falling FMs in intensity steps of 1 dB using a calibrated attenuator (Tucker-Davis Technologies, Alachua, USA; model PA5). During the experiment, we used the same sound level (75 dB HL) for the rising FMs as for the falling FMs with same frequency range. As we aimed to study Mongolian gerbils using the same experimental procedure with intracranial recordings (see Jeschke et al., 2008), the task had to be as similar as possible in both studies. Therefore, the experiment was conducted as a Go/NoGo-Task where one stimulus was defined as the target-sound. The participants were instructed to listen carefully to the sounds and press a button with their right index finger as soon as they identified the target-stimulus. To avoid possible effects resulting from different stimulus properties, we performed the experiment in two blocks: In one block, the high-falling sound was defined as the target and in the other block the low-falling sound was specified as the target sound. Hence, during each block, two remaining sounds matched with only one target-feature (either same frequency range or same FM direction) and one sound matched neither in frequency range nor in FM direction. This is depicted in Fig. 1.

Each block consisted of 400 stimuli with 100 repetitions of each stimulus. The sounds were presented in pseudo-randomized order with interstimulus intervals between 1300 ms and 2000 ms. The sequence of the blocks was counterbalanced across subjects. To avoid eye-movement artifacts, the subjects were instructed to keep their eyes open and to fixate a cross at the center of a screen throughout the entire experimental session.

### 5.3. Data acquisition

Subjects were seated in a sound-attenuated and electrically shielded cabin. To avoid interferences by line frequency (50 Hz in Germany), no AC-devices were operated inside the cabin. The electroencephalogram was recorded using 64 sintered Ag/AgCl-electrodes mounted in an elastic cap (Easycap GmbH, Herrsching-Breitbrunn). These were placed according to the 10–10 system and connected to a BrainAmp amplifier (Brain Products, Munich). Signals were referenced to a nose-tip electrode, the ground electrode was placed between Fz and Cz. Eye-movement activity was recorded using two electrodes placed suborbitally to the left eye and at the outer canthus of the right eye. All signals were sampled at 500 Hz and analog

filtered between 0.016 and 250 Hz with an amplitude resolution of 16 bit. Electrode impedances were kept below 5 k $\Omega$ . Data were digitally saved on a computer outside the cabin for later offline analysis.

#### 5.4. Data analysis

##### 5.4.1. Behavioral data

Reaction times and responses were recorded and analyzed. Reaction times which exceeded two standard deviations from the mean were removed from further behavioral analysis.

##### 5.4.2. Electrophysiological data

The EEG analysis was conducted using EEProbe (ANT Software, Enschede). Averaging epochs lasted from 200 ms before until 600 ms after stimulus onset. An automatic artifact rejection excluded epochs from further analysis if the standard deviation within a moving 200 ms time interval exceeded 25  $\mu$ V. Additionally, all trials were visually inspected and rejected in case of electrode drifts, eye-movements or electromyographic activity. Baselines were calculated between 200 ms and 100 ms before stimulus onset and subtracted from each epoch. Both blocks of the study were averaged regarding the four conditions target, range matched non-target, direction matched non-target and non-matching stimulus. Peak amplitudes were analyzed for N1 (80 ms–115 ms), P2 (150 ms–250 ms) and N2 (220 ms–280 ms) components. Mean amplitudes were computed in the P3 time-window (300 ms–600 ms). To avoid loss of statistical power, electrodes which showed the highest activity according to the analyzed component, were pooled into regions of interest (ROIs). This resulted in a fronto-central ROI for N1 analysis, a central ROI for P2 analysis, a frontal ROI for N2 analysis and a posterior ROI for P3 analysis. Fig. 2 illustrates which channels are included in each ROI. Time-frequency analyses were performed on a fronto-central ROI, which exhibited strongest activations after auditory stimulation and comprised the electrodes AFZ, F3, F1, Fz, F2, F4, FC3, FC1, FCz, FC2, FC4, C3, C1, Cz, C2, C4, CP1, CPz and CP2. A morlet based wavelet transform (WT) with a width of 12 cycles was applied, which offers a continuous measure of amplitudes of a frequency component (for details, see Herrmann et al., 2004a). Wavelet transform on the averaged potentials reveals the evoked fraction of gamma activity, performing the WT on single trials and averaging the absolute values also allows analysis of not strictly phase-locked activity (total GBRs). Thus, total GBRs contain evoked as well as induced responses. Statistical analyses of evoked GBRs were performed on peak amplitudes in the time-window between 30 ms and 70 ms after averaging conditions of both blocks as well as averaging physically identical stimuli. Because of considerable inter-individual variability in subjects' peak gamma-frequencies, we used each subject's individual frequency for the wavelet transform, defined as the highest peak in the time-frequency plots averaged across all conditions and ROI electrodes in the prementioned time interval and the frequency band between 30 Hz and 90 Hz (Senkowski and Herrmann, 2002; Herrmann et al., 2004b; Lenz et al., 2007). Analysis of the broader (in respect to the covered frequencies) total GBRs was conducted by employing WT on single trials for each frequency bin in the range between 1 Hz and 249 Hz (in steps of 1 Hz) and averaging

each amplitude value within four time-frequency domains resulting from two frequency bands (low gamma-band: 30 Hz–90 Hz, high gamma-band: 90 Hz–249 Hz) and two time-windows (early: 100 ms–350 ms, late: 350 ms–550 ms). This was done after averaging the conditions across both blocks.

Three subjects were excluded from the whole time-frequency analysis as they did not show any gamma activity at all.

##### 5.4.3. Statistical analysis

Averages and standard deviations were computed for reaction times and false alarms. False alarms were investigated using a repeated measures ANOVA with three factor steps for each wrong response (button presses after stimuli with the same frequency range or same FM direction, and after non-matching stimuli).

Statistical ERP analyses were run on unfiltered data. Data of both experimental blocks were averaged, if the ANOVA yielded no significant CONDITION (four factor steps: target, range matched non-target, direction matched non-target, non-matching stimulus)  $\times$  BLOCK (two levels: A and B) interactions. Amplitudes and latencies of each ERP component were examined using a repeated measures ANOVA with the factor CONDITION.

To detect differences in the evoked GBRs, two repeated measures ANOVAs were computed with the factors CONDITION and STIMULUS TYPE (four levels: low-rising, low-falling, high-rising, high-falling). Total GBRs in the lower as well as the higher gamma-band were investigated by repeated measures ANOVAs with the factor CONDITION, covering both the early and the late time-window. Post hoc t-tests for specific examination of significant ANOVA effects were additionally calculated (target vs. range matched non-target, range matched non-target vs. direction matched non-target, direction matched non-target vs. non-matching stimulus).

For investigation of possible motor-related origins of the activity in the higher frequency band, additional ANOVAs were computed with the factor LATERALITY (left vs. right) for the target condition after pooling the ROI electrodes (except electrodes at the central midline) into two smaller ROIs according to their hemispheric position.

All ANOVA models were Greenhouse–Geisser corrected, and degrees of freedom were uncorrected. P-values of post hoc t-tests were Bonferroni corrected. The alpha level for ANOVAs was a priori determined as 0.01; for post hoc t-tests as 0.05.

## Acknowledgments

This study was supported by the German Research Foundation (DFG, Grant HE3353/2-2 and SFB/TR31-A09, A03). The authors would like to thank Stefanie Thaerig and Franziska Bauch for their help during data acquisition and analysis.

## REFERENCES

- Adrian, E.D., 1942. Olfactory reactions in the brain of the hedgehog. *J. Physiol.* 100 (4), 459–473.

- Başar, E., Başar-Eroglu, C., Karakaş, S., Schürmann, M., 1999. Are cognitive processes manifested in event-related gamma, alpha, theta and delta oscillations in the EEG? *Neurosci. Lett.* 259 (3), 165–168.
- Başar-Eroglu, C., Demiralp, T., Schürmann, M., Başar, E., 2001. Topological distribution of oddball 'P300' responses. *Int. J. Psychophysiol.* 39 (2–3), 213–220.
- Başar-Eroglu, C., Struber, D., Schürmann, M., Stadler, M., Başar, E., 1996. Gamma-band responses in the brain: a short review of psychophysiological correlates and functional significance. *Int. J. Psychophysiol.* 24 (1–2), 101–112.
- Bragin, A., Engel, J., Wilson, C.L., Fried, I., Mathern, G.W., 1999. Hippocampal and entorhinal cortex high-frequency oscillations (100–500 Hz) in human epileptic brain and in kainic acid-treated rats with chronic seizures. *Epilepsia* 40 (2), 127–137.
- Brosch, M., Budinger, E., Scheich, H., 2002. Stimulus-related gamma oscillations in primate auditory cortex. *J. Neurophysiol.* 87 (6), 2715–2725.
- Budinger, E., Heil, P., Scheich, H., 2000. Functional organization of auditory cortex in the Mongolian gerbil (*Meriones unguiculatus*): III. Anatomical subdivisions and corticocortical connections. *Eur. J. Neurosci.* 12 (7), 2425–2451.
- Busch, N.A., Debener, S., Kranczioch, C., Engel, A.K., Herrmann, C.S., 2004. Size matters: effects of stimulus size, duration and eccentricity on the visual gamma-band response. *Clin. Neurophysiol.* 115 (8), 1810–1820.
- Busch, N.A., Herrmann, C.S., Müller, M.M., Lenz, D., Gruber, T., 2006a. A cross-laboratory study of event-related gamma activity in a standard object recognition paradigm. *NeuroImage* 33 (4), 1169–1177.
- Busch, N.A., Schadow, J., Fründ, I., Herrmann, C.S., 2006b. Time-frequency analysis of target detection reveals an early interface between bottom-up and top-down processes in the gamma-band. *NeuroImage* 29 (4), 1106–1116.
- Buzsáki, G., Draguhn, A., 2004. Neuronal oscillations in cortical networks. *Science* 304 (5679), 1926–1929.
- Canolty, R.T., Edwards, E., Dalal, S.S., Soltani, M., Nagarajan, S.S., Kirsch, H.E., Berger, M.S., Barbaro, N.M., Knight, R.T., 2006. High gamma power is phase-locked to theta oscillations in human neocortex. *Science* 313 (5793), 1626–1628.
- Crone, N.E., Boatman, D., Gordon, B., Hao, L., 2001. Induced electrocorticographic gamma activity during auditory perception. *Clin. Neurophysiol.* 112 (4), 565–582.
- Crone, N.E., Miglioretti, D.L., Gordon, B., Lesser, R.P., 1998. Functional mapping of human sensorimotor cortex with electrocorticographic spectral analysis: II. Event-related synchronization in the gamma band. *Brain* 121 (Pt 12), 2301–2315.
- Debener, S., Herrmann, C.S., Kranczioch, C., Gembris, D., Engel, A.K., 2003. Top-down attentional processing enhances auditory evoked gamma band activity. *NeuroReport* 14 (5), 683–686.
- Demiralp, T., Bayraktaroglu, Z., Lenz, D., Junge, S., Busch, N.A., Maess, B., Ergen, M., Herrmann, C.S., 2007. Gamma amplitudes are coupled to theta phase in human EEG during visual perception. *Int. J. Psychophysiol.* 64 (1), 24–30.
- Edwards, E., Soltani, M., Deouell, L.Y., Berger, M.S., Knight, R.T., 2005. High gamma activity in response to deviant auditory stimulus recorded directly from human cortex. *J. Neurophysiol.* 94 (6), 4269–4280.
- Engel, A., Singer, W., 2001. Temporal binding and the neural correlates of sensory awareness. *Trends Cogn. Sci.* 5 (1), 16–25.
- Fisher, R.S., Webber, W.R., Lesser, R.P., Arroyo, S., Uematsu, S., 1992. High-frequency EEG activity at the start of seizures. *J. Clin. Neurophysiol.* 9 (3), 441–448.
- Freunberger, R., Klimesch, W., Sauseng, P., Griesmayr, B., Höller, Y., Pecherstorfer, T., Hanslmayr, S., 2007. Gamma oscillatory activity in a visual discrimination task. *Brain Res. Bull.* 71 (6), 593–600.
- Fründ, I., Herrmann, C.S., 2007. Simulating evoked gamma oscillations of human EEG in a network of spiking neurons reveals an early mechanism of memory matching. In: Descalzi, O., Rosso, O.A., Larrondo, H.A. (Eds.), *Nonequilibrium statistical mechanics and nonlinear physics*. Vol. 913 of AIP Conference Proceedings. American Institute of Physics, Melville, pp. 215–221.
- Fründ, I., Busch, N.A., Körner, U., Schadow, J., Herrmann, C.S., 2007. EEG oscillations in the gamma and alpha range respond differently to spatial frequency. *Vis Res.* 47 (15), 2086–2089.
- Galambos, R., 1992. A comparison of certain gamma band (40 Hz) brain rhythms in cat and man. In: Başar, E., Bullock, T. (Eds.), *Induced Rhythms in the Brain*. Birkhäuser, Boston, pp. 201–216.
- García-Larrea, L., Lukaszewicz, A.C., Mauguière, F., 1992. Revisiting the oddball paradigm. Non-target vs. neutral stimuli and the evaluation of ERP attentional effects. *Neuropsychologia* 30 (8), 723–741.
- Gonzalez, S.L., de Peralta, R.G., Thut, G., Millán, J. del R., Morier, P., Landis, T., 2006. Very high frequency oscillations (VHFO) as a predictor of movement intentions. *NeuroImage* 32 (1), 170–179.
- Gray, C.M., König, P., Engel, A.K., Singer, W., 1989. Oscillatory responses in cat visual cortex exhibit inter-columnar synchronization which reflects global stimulus properties. *Nature* 338 (6213), 334–337.
- Gruber, T., Müller, M.M., Keil, A., 2002. Modulation of induced gamma band responses in a perceptual learning task in the human EEG. *J. Cogn. Neurosci.* 14 (5), 732–744.
- Gruber, T., Tsivilis, D., Montaldi, D., Müller, M.M., 2004. Induced gamma band responses: an early marker of memory encoding and retrieval. *NeuroReport* 15 (11), 1837–1841.
- Hall, R.A., Yarbrough, R., Rappaport, M., Yeager, C.V., 1968. High frequency transients in EEG's of psychiatric patients and normal subjects. *Electroencephalogr. Clin. Neurophysiol.* 24 (4), 396.
- Hall, R.A., Yeager, C., Yarbrough, R.B., 1967. Preliminary observations on high frequency EEGs. *Electroencephalogr. Clin. Neurophysiol.* 22 (3), 290.
- Herrmann, C.S., Grigutsch, M., Busch, N.A., 2004a. EEG oscillations and wavelet analysis. In: Handy, T.C. (Ed.), *Event-Related Potentials: A Methods Handbook*. Bradford Book, Cambridge, MA, pp. 229–259.
- Herrmann, C.S., Lenz, D., Junge, S., Busch, N.A., Maess, B., 2004b. Memory matches evoke human gamma-responses. *BMC Neurosci.* 5, 13.
- Herrmann, C.S., Mecklinger, A., 2001. Gamma activity in human EEG is related to high-speed memory comparisons during object selective attention. *Vis. Cogn.* 8 (3–5), 593–608.
- Herrmann, C.S., Munk, M.H.J., Engel, A.K., 2004c. Cognitive functions of gamma-band activity: memory match and utilization. *Trends Cogn. Sci.* 8 (8), 347–355.
- Hillyard, S.A., Hink, R.F., Schwent, V.L., Picton, T.W., 1973. Electrical signs of selective attention in the human brain. *Science* 182 (108), 177–180.
- Jeschke, M., Lenz, D., Budinger, E., Herrmann, C.S., Ohl, F.W., 2008. Gamma oscillations in gerbil auditory cortex during a target-discrimination task reflect matches with short-term memory. *Brain Res.* 1220, 70–80.
- Juergens, E., Guettler, A., Eckhorn, R., 1999. Visual stimulation elicits locked and induced gamma oscillations in monkey intracortical- and EEG potentials, but not in human EEG. *Exp. Brain Res.* 129 (2), 247–259.
- Kaiser, J., Leiberg, S., Rust, H., Lutzenberger, W., 2007. Prefrontal gamma band activity distinguishes between sound durations. *Brain Res.* 1139, 153–162.
- Kaiser, J., Lutzenberger, W., 2004. Frontal gamma-band activity in magnetoencephalogram during auditory oddball processing. *NeuroReport* 15 (14), 2185–2188.



- Kaiser, J., Ripper, B., Birbaumer, N., Lutzenberger, W., 2003. Dynamics of gamma-band activity in human magnetoencephalogram during auditory pattern working memory. *NeuroImage* 20 (2), 816–827.
- Kandel, E.R., Schwartz, J.H., Jessell, T.M., 2000. *Principles of Neural Science*, 4th Edition. McGraw-Hill, New York.
- Karakaş, S., Başar, E., 1998. Early gamma response is sensory in origin: a conclusion based on cross-comparison of results from multiple experimental paradigms. *Int. J. Psychophysiol.* 31 (1), 13–31.
- Keil, A., Müller, M.M., Ray, W.J., Gruber, T., Elbert, T., 1999. Human gamma band activity and perception of a gestalt. *J. Neurosci.* 19 (16), 7152–7161.
- Klimesch, W., 1999. EEG alpha and theta oscillations reflect cognitive and memory performance: a review and analysis. *Brain Res. Brain Res. Rev.* 29 (2–3), 169–195.
- Knief, A., Schulte, M., Bertrand, O., Pantev, C., 2000. The perception of coherent and non-coherent auditory objects: a signature in gamma frequency band. *Hear. Res.* 145 (1–2), 161–168.
- Lachaux, J.-P., George, N., Tallon-Baudry, C., Martinerie, J., Hugueville, L., Minotti, L., Kahane, P., Renault, B., 2005. The many faces of the gamma band response to complex visual stimuli. *NeuroImage* 25 (2), 491–501.
- Langers, D.R.M., Backes, W.H., van Dijk, P., 2007. Representation of lateralization and tonotopy in primary versus secondary human auditory cortex. *NeuroImage* 34 (1), 264–273.
- Lenz, D., Schadow, J., Thaerig, S., Busch, N.A., Herrmann, C.S., 2007. What's that sound? Matches with auditory long-term memory induce gamma activity in human EEG. *Int. J. Psychophysiol.* 64 (1), 31–38.
- Logothetis, N.K., Pauls, J., Augath, M., Trinath, T., Oeltermann, A., 2001. Neurophysiological investigation of the basis of the fMRI signal. *Nature* 412 (6843), 150–157.
- Lutzenberger, W., Pulvermüller, F., Elbert, T., Birbaumer, N., 1995. Visual stimulation alters local 40-Hz responses in humans: an EEG-study. *Neurosci. Lett.* 183 (1–2), 39–42.
- Lutzenberger, W., Ripper, B., Busse, L., Birbaumer, N., Kaiser, J., 2002. Dynamics of gamma-band activity during an audiospatial working memory task in humans. *J. Neurosci.* 22 (13), 5630–5638.
- Näätänen, R., Hukkanen, S., Jarvilehto, T., 1980. Magnitude of stimulus deviance and brain potentials. *Prog. Brain Res.* 54, 337–342.
- Näätänen, R., Picton, T., 1987. The N1 wave of the human electric and magnetic response to sound: a review and an analysis of the component structure. *Psychophysiology* 24 (4), 375–425.
- Näätänen, R., Picton, T.W., 1986. N2 and automatic versus controlled processes. *Electroencephalogr. Clin. Neurophysiol., Suppl.* 38, 169–186.
- Nager, W., Rosenthal, O., Bohrer, I., Teder-Salejari, W.A., Münte, T.F., 2001. Human event-related potentials and distraction during selective listening. *Neurosci. Lett.* 297 (1), 1–4.
- Ohl, F.W., Scheich, H., 2005. Learning-induced plasticity in animal and human auditory cortex. *Curr. Opin. Neurobiol.* 15 (4), 470–477.
- Ohl, F.W., Scheich, H., Freeman, W.J., 2001. Change in pattern of ongoing cortical activity with auditory category learning. *Nature* 412 (6848), 733–736.
- Ohl, F.W., Schulze, H., Scheich, H., Freeman, W.J., 2000. Spatial representation of frequency-modulated tones in gerbil auditory cortex revealed by epidural electrocorticography. *J. Physiol. (Paris)* 94 (5–6), 549–554.
- Ohl, F.W., Wetzel, W., Wagner, T., Rech, A., Scheich, H., 1999. Bilateral ablation of auditory cortex in Mongolian gerbil affects discrimination of frequency modulated tones but not of pure tones. *Learn. Mem.* 6 (4), 347–362.
- O'Keefe, J., 1993. Hippocampus, theta, and spatial memory. *Curr. Opin. Neurobiol.* 3 (6), 917–924.
- Pantev, C., Makeig, S., Hoke, M., Galambos, R., Hampson, S., Gallen, C., 1991. Human auditory evoked gamma-band magnetic fields. *Proc. Natl. Acad. Sci. U. S. A.* 88 (20), 8996–9000.
- Pickles, J.O., 1988. *An Introduction to the Physiology of Hearing*, 2nd Edition. Academic Press, New York.
- Polich, J., 1986. Attention, probability, and task demands as determinants of P300 latency from auditory stimuli. *Electroencephalogr. Clin. Neurophysiol.* 63 (3), 251–259.
- Ritter, W., Paavilainen, P., Lavikainen, J., Reinikainen, K., Alho, K., Sams, M., Näätänen, R., 1992. Event-related potentials to repetition and change of auditory stimuli. *Electroencephalogr. Clin. Neurophysiol.* 83 (5), 306–321.
- Schadow, J., Lenz, D., Thaerig, S., Busch, N.A., Fründ, I., Herrmann, C.S., 2007a. Stimulus intensity affects early sensory processing: sound intensity modulates auditory evoked gamma-band activity in human EEG. *Int. J. Psychophysiol.* 65 (2), 152–161.
- Schadow, J., Lenz, D., Thaerig, S., Busch, N.A., Fründ, I., Herrmann, C.S., 2007b. Stimulus intensity affects early sensory processing: visual contrast modulates evoked gamma-band activity in human EEG. *Int. J. Psychophysiol.* 66 (1), 28–36.
- Senkowski, D., Herrmann, C.S., 2002. Effects of task difficulty on evoked gamma activity and ERPs in a visual discrimination task. *Clin. Neurophysiol.* 113 (11), 1742–1753.
- Siegel, M., Donner, T.H., Oostenveld, R., Fries, P., Engel, A.K., 2007. High frequency activity in human visual cortex is modulated by visual motion strength. *Cereb. Cortex* 17 (3), 732–741.
- Siegel, M., König, P., 2003. A functional gamma-band defined by stimulus dependent synchronization in area 18 of awake behaving cats. *J. Neurosci.* 23 (10), 4251–4260.
- Singer, W., Gray, C.M., 1995. Visual feature integration and the temporal correlation hypothesis. *Annu. Rev. Neurosci.* 18, 555–586.
- Tallon-Baudry, C., Bertrand, O., 1999. Oscillatory gamma activity in humans and its role in object representation. *Trends Cogn. Sci.* 3 (4), 151–162.
- Tallon-Baudry, C., Bertrand, O., Delpuech, C., Pernier, J., 1996. Stimulus specificity of phase-locked and non-phase-locked 40 Hz visual responses in human. *J. Neurosci.* 16 (13), 4240–4249.
- Tallon-Baudry, C., Bertrand, O., Peronnet, F., Pernier, J., 1998. Induced gamma-band activity during the delay of a visual short-term memory task in humans. *J. Neurosci.* 18 (11), 4244–4254.
- Tiitinen, H., Sinkkonen, J., Reinikainen, K., Alho, K., Lavikainen, J., Näätänen, R., 1993. Selective attention enhances the auditory 40-Hz transient response in humans. *Nature* 364 (6432), 59–60.
- Trautner, P., Rosburg, T., Dietl, T., Fell, J., Korzyukov, O.A., Kurthen, M., Schaller, C., Elger, C.E., Boutros, N.N., 2006. Sensory gating of auditory evoked and induced gamma band activity in intracranial recordings. *NeuroImage* 32 (2), 790–798.
- Weinberger, N.M., 2004. Specific long-term memory traces in primary auditory cortex. *Nat. Rev., Neurosci.* 5 (4), 279–290.
- Weinberger, N.M., 2007. Associative representational plasticity in the auditory cortex: a synthesis of two disciplines. *Learn. Mem.* 14 (1), 1–16.
- Yetkin, F.Z., Roland, P.S., Christensen, W.F., Purdy, P.D., 2004. Silent functional magnetic resonance imaging (fMRI) of tonotopicity and stimulus intensity coding in human primary auditory cortex. *Laryngoscope* 114 (3), 512–518.
- Yordanova, J., Kolev, V., Demiralp, T., 1997. The phase-locking of auditory gamma band responses in humans is sensitive to task processing. *NeuroReport* 8 (18), 3999–4004.