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Early gamma-band responses reflect anticipatory top-down modulation in the auditory cortex

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ABSTRACT

For efficient and fast encoding of our complex acoustic environment, not only aspects of bottom-up processing are significant, but rather top-down influences such as attention, memory, and anticipation promote specific behavior and perception. Neural oscillatory activity in the gamma-range (30–80 Hz) is discussed as a conceivable candidate to represent very rapid modulations of top-down factors.

We investigated effects of anticipation on early gamma-band responses (GBRs) of the EEG and event-related potentials (ERPs) in response to tone sequences. These sequences were composed of six sinusoidal tones, which could be either regularly ascending or descending in frequency. Thus, the sequences reflected a good continuation of pitch, which also resulted in the buildup of strong expectancies for the upcoming stimulus within the sequence. However, some of the tone sequences contained a violation of the good continuation of pitch at the third or fifth tone position.

The early phase-locked portion of the gamma-band activity was significantly increased when tones were in line with the good continuation of sequences compared to deviant tones. Further, a pronounced early negative ERP response, starting at 150 ms, was elicited by deviant tones at the third and fifth position.

Our results support the notion that gamma-band oscillations reflect perceptual grouping processes of concurrent sounds and anticipatory top-down modulation, which involves some of the first stages of auditory information processing.

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Introduction

We live in an extremely complex acoustic environment and are surrounded by simultaneously occurring sounds such as music, speech, and noises from multiple sources. Therefore, it requires a perceptual organization of this extensive mixture of sounds. The auditory system has to segregate and integrate different sounds into meaningful auditory units or objects, which is also known as auditory scene analysis (Bregman, 1994). Bregman (1994) distinguished the perceptual organization along a horizontal (time) and a vertical axis (frequency). The horizontal axis comprises the sequential grouping of sounds over time (e.g. melody), whereas the processing along the vertical axis involves the integration of simultaneous sounds (e.g. forming chords). These grouping processes are governed by both primitive automatic (bottom-up) and learned (top-down) constraints.

Recently, it was suggested that oscillatory activity in the gamma-range (20–80 Hz) is related to bottom-up and top-down factors as well as to the integration of both (Herrmann et al., 2004c). Thus, gamma-band responses (GBRs) might provide additional insights regarding the basic sensory analysis of auditory information as well as

the influence of this analysis by top-down processes. Generally, GBRs are divided in an early evoked and a late induced portion. While evoked activity is defined to be time- and phase-locked to an event, induced GBR is time-locked, but shows a high phase variability across trials (Galambos, 1992; Pantev, 1995). Phase-locked oscillatory activity has been reported to be modulated by physical stimulus properties during a very early time interval in the visual (Tzelepi et al., 2000; Bodis-Wollner et al., 2001; Busch et al., 2004; Fründ et al., 2007; Schadow et al., 2007b) and auditory modality (Schadow et al., 2007a; Lenz et al., 2008). The later non-phase-locked GBR between 200 and 400 ms after stimulus onset is mainly associated with a more elaborated processing and is therefore linked to cognitive mechanisms such as attention (Gruber et al., 1999; Tallon-Baudry et al., 2004) and memory (Lutzenberger et al., 2002; Lenz et al., 2007; Busch et al., 2008). However, it has been shown that such top-down modulations can already occur much earlier and can be represented in the evoked gamma-band activity, too. Several visual and auditory experiments have shown an increase in the early evoked activity for target stimuli that capture a higher amount of attention than non-target stimuli (Tiitinen et al., 1993; Herrmann et al., 1999; Debener et al., 2003; Busch et al., 2006). Similarly, the match of a presented stimulus with a memorized template resulted in an enhanced evoked gamma-band response compared to new stimuli (Herrmann et al., 2004d; Busch et

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al., 2008), which demonstrates a top-down modulation at the earliest stages of information processing. In addition to attention and memory resulting in a faster and more efficient analysis of the upcoming stimulus, most events in everyday life occur predictably for us. Thus, we often anticipate events and are therefore able to prepare a faster and more accurate behavior. Widmann et al. (2007) reported that visual symbolic information affect early auditory sensory processing at 42 ms after tone onset. The authors observed an increase of phase-locked evoked GBR in response to sounds that matched with a corresponding visual symbol and discussed the finding in relation with matching of incoming information against an expectation.

The present study aimed to investigate auditory perception and whether anticipatory processes also result in such early modulation of the auditory evoked GBR. Therefore, we presented regularly ascending and descending tone sequences with six sinusoidal tones. These sequences reflected a good continuation of pitch, which also resulted in the buildup of an expectation for the upcoming stimulus by the listener during the presentation. However, some of the tone sequences contained a violation of the good continuation at the third or fifth tone position. Thus, the sequences violated the listener's expectation at different levels of expectation buildup. Gamma-band activity in response to regularly presented and deviant tones at the third and fifth position of each sequence was compared. If GBRs reflect matching with expectation, responses to regular tones within ascending/descending sequences should be larger than to deviating tones. We assume that regularly occurring tones might be processed by a pretuned population of neurons which is not the case for deviant tones.

Previous research has already revealed electrophysiological correlates of such mechanisms, e.g. the mismatch negativity (MMN), a component of the event-related potential (ERP) after about 150–250 ms (Näätänen, 1992; Näätänen et al., 2007), which is linked to processing of tone sequences and reflects a violation from the preceding stimulus or regularities in complex auditory information (Yabe et al., 2001; Kanoh et al., 2004; van Zuijlen et al., 2004; Sussman and Gumenyuk, 2005; Kujala et al., 2007). The MMN operates basically at the sensory memory level and is an automatic process, irrespective of cognitive factors (Schröger, 1997; Näätänen and Winkler, 1999; Schröger et al., 2007). Hence, no behavioral task is needed to elicit a MMN. However, when stimuli are attended for example by a task, then the MMN is partially overlapped by the N2b. The N2b is linked to the expectation of regularly appearing stimuli and indexes deviance detection only if a deviant stimulus is attentively recognized (Näätänen et al., 1982; Novak et al., 1992; Eimer et al., 1996; Rüsseler and Rösler, 2000; Carrión and Bly, 2007). Therefore, we also expected a larger negative ERP response to deviant tones compared to regularly occurring tones within the sequence.

Materials and methods

Participants

Seventeen healthy volunteers (9 females, 8 males, mean age 25 ± 3.8 years) participated in the current study. They had no history of hearing impairments and showed no signs of psychiatric or neurological disorders. All participants received a written task instruction and gave informed written consent to participate. They received money or course credits for their participation. The experiment was conducted in accordance with the Declaration of Helsinki.

Stimuli and task

Ten different sinusoidal tones with a duration of 500 ms (10 ms rise and fall times) and a frequency, ranging from 700 to 1177 Hz in semitone steps on the musical scale, were generated using Adobe Audition V1.0 (Adobe Systems Inc., 2004). Five ascending and five descending stimulus sequences, each comprising six tones, were

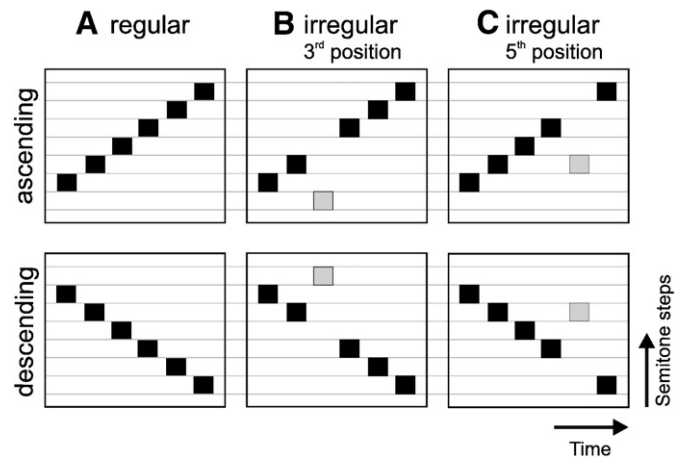


Fig. 1. Schematic illustration of the paradigm. Black squares indicate tones that regularly fit in the ascending or descending sequence. In contrast, gray squares illustrate a violation either at the 3rd or 5th position of the sequence.

composed. Some of these ascending or descending tone sequences were further modified either at the third or fifth position in their frequency to trigger a violation of the good continuation of the sequence. This sine wave tone deviated from the regularly presented tone about three semitone steps, either below for ascending or above for descending sequences (see Fig. 1).

Consequently, we obtained three different categories of tone sequences:

- A. tone sequences with a good continuation (= regular)
- B. tone sequences with a violation at the 3rd position (= irregular)
- C. tone sequences with a violation at the 5th position (= irregular).

All stimulus sequences were pseudo-randomly presented with a constant intertone interval of 1200 ms. The randomized interval between two adjacent tone sequences was set between 1600 and 2000 ms. Sequences were repeated such that each of the three categories comprised the same number of trials (100 trials).

Auditory stimuli were applied to both ears by insert earphones (EARTone 3A). Before the experiment started, the individual hearing thresholds for the left and right ear were determined by a staircase procedure in intensity steps of 2 dB for each participant and each sine tone. Based on the individual sensation level (SL), an intensity of 75 dB above the threshold was set for each tone. A calibrated attenuator was used to control the sound levels (Tucker-Davis Technologies, model PA5).

The present experiment was constructed as a discrimination task. Participants were asked to decide, whether the presented tone sequence is predominantly ascending or descending irrespective of a violation. Since it has been demonstrated that stimulus-related motor activation modulates the gamma-band response (De Pascalis and Ray, 1998; Yordanova et al., 2001; Yordanova et al., 2002), all trials required a motor response to avoid confounding effects. Participants were instructed to press a button with the right index finger in response to descending sequences and another button with the left index finger in response to ascending sequences. Participants were asked to respond at the end of each sequence, which was signaled by a color change of the fixation cross from white to red. During the entire experimental session, participants were instructed to fixate the cross in the center of the screen to reduce eye-movement artifacts.

Data acquisition

EEG was recorded with a BrainAmp amplifier (Brain Products, Munich; Germany), using 31 sintered Ag/AgCl electrodes mounted in an elastic cap (EasyCap, Falk Minow Services, Munich, Germany). The

electrodes were placed according to the 10–10 system, with a nose-tip reference and ground electrode between Fz and Cz. Eye-movement activity was monitored with an electrode placed suborbitally to the right eye. Electrode impedances were kept below 10 k Ω . Data were acquired with a band-pass filter of 0.016–250 Hz and a sampling rate of 1000 Hz. Stimulus markers and EEG were stored on hard disk for further analysis. The EEG was recorded while participants sat in an electrically shielded, sound-attenuated cabin (IAC, Niederkrüchten, Germany). The monitor was placed outside behind an electrically shielded window. All devices inside the cabin were operated on batteries to avoid interference from the line frequency (50 Hz in Germany). Digitized EEG data were transferred to a computer outside the cabin using a fiber-optic cable. Averaging epochs lasted from 200 ms before to 800 ms after tone onset for event-related potentials and gamma-band responses. Baselines were calculated in the interval from -200 ms to -100 ms and subtracted before averaging. An automatic artifact rejection was computed which excluded trials from averaging if the standard deviation within a moving 200 ms time interval exceeded 40 μ V. All epochs were also visually inspected for artifacts and rejected in case of eye-movements, electrode drifts, or electromyographic activity. While data analysis was performed on unfiltered data, event-related potentials are displayed low-pass filtered at 20 Hz.

Data analysis

Behavioral data

Only trials with responses given between 150 and 2000 ms after the presentation of the red fixation cross were included in the analysis. False trials were excluded from the analysis of reaction times, as well as trials in which the reaction time (RT) exceeded two standard deviations from the mean. On average a number of 30 trials were excluded.

Event-related potentials

In order to test differences in the neural responses to regular and irregular occurring tones, we analyzed amplitudes of the early negativity in the time interval from 150 ms to 350 ms. The statistical analysis of this early negativity was performed after channels that exhibited the strongest activity in the critical time window were pooled into a posterior region of interest (ROI): CP1, CP2, P3, Pz, P4, O1, O2. The statistical analysis was conducted on the peak amplitude in this time interval and ERPs at the third and fifth position in response to regular and irregular tone sequences were compared. Amplitudes were analyzed using a repeated measures ANOVA with the factors REGULARITY (regular vs. irregular) and TONE POSITION (3rd vs. 5th). The Greenhouse–Geisser correction, an adjustment used in univariate repeated measures when the sphericity assumption is violated, was applied where appropriate.

Evoked and total gamma-band responses

For the analysis of gamma-band activity, a wavelet transform was computed by convolving the raw EEG signal with a complex modulated Gaussian (Herrmann et al., 2004a). At 40 Hz, the wavelet had a time resolution of $2\sigma_t = 50$ ms and a frequency resolution of $2\sigma_f = 13$ Hz. The exact time-frequency resolution of the wavelet depended on the analyzed frequency. Different methods of evaluation are required to assess evoked and induced GBRs. To analyze the evoked GBR, the wavelet transform was applied to the averaged event-related potentials. However, for the non-phase-locked portion of the GBR, each trial was first transformed to the frequency domain and then the resulting wavelet transforms were averaged. This measure represents the total activity comprising the phase-locked and non-phase-locked fractions of the GBR. Additionally, the amount of phase-

locking across trials was computed. The values yield a number between 0 and 1 determining the degree of phase-locking, where 1 indicates perfect phase alignment across trials and values close to 0 reflect a high phase variability.

Previous studies have shown that the frequency of oscillatory brain activity varies notably between subjects (Busch et al., 2004; Klimesch, 1999). Therefore, wavelet analysis was performed for each frequency bin in the gamma-frequency range. The resulting time-frequency representations were averaged across electrodes in the fronto-central ROI (Cz, FC1, FC2, Fz) and across the four interesting conditions (regular and irregular at the 3rd and 5th position). Afterwards, the individual gamma frequency was defined as the frequency showing the highest amplitude in the time interval between 20 and 90 ms after stimulus onset. The peak frequencies of the individually identified evoked GBRs ranged from 20 Hz to 64 Hz (mean 42.4 Hz, SD = 13.8 Hz). The peak amplitude for this individual frequency was used for further statistical analyses of the evoked GBR, phase-locking, and total gamma activity in the respective early time interval. Channels were pooled into a ROI comprising the following four fronto-central electrodes which exhibited the strongest GBRs: Cz, FC1, FC2, Fz (see Fig. 4). We performed a repeated measures ANOVA using the factors REGULARITY (regular vs. irregular) and TONE POSITION (3rd vs. 5th).

The time-frequency planes did not reveal any late gamma-band activity in the typical time interval between 200 and 600 ms that exceeded the noise level. Therefore, further analyses and the description of the results are focused on the early gamma-band activity.

Dipole modeling of the evoked GBR

Source modeling of evoked GBRs was conducted using ASA 4 (ANT Software, Enschede, The Netherlands). A band-pass filter covering 10 Hz above and below the mean of GBR peak frequencies of all participants was applied to the grand-average ERP (mean peak frequency: 42 Hz, filter-band: 32–52 Hz). There were no differences in the scalp topographies of evoked GBRs following regular tones at 3rd and 5th position. Therefore, further calculations were done on the average of both conditions. As we obtained no individual MRI data from our participants, source modeling was performed using the standard MRI and head model data included in ASA. In order to verify the hypothesis that the sources of the evoked GBR lie in the primary auditory cortex, the scalp signal was modeled using two symmetrical dipoles placed within the left and right primary auditory cortex and fixed in position (AC–PC coordinates: $x = -50$, $y = -7$, $z = 7$ (left dipole); $x = 50$, $y = -7$, $z = 7$ (right dipole)). Afterwards, the “goodness-of-fit” (GOF) as a measure of the model accuracy was calculated for the time window between 50 and 60 ms.

Results

Behavioral data

Participants performed the task with high accuracy (ascending sequences: 94% correct, standard deviation (SD) = 6% and descending sequences: 95% correct, SD = 5%). The reaction times to the ascending (441 ms, SD = 87 ms) and descending sequences (447 ms, SD = 97 ms) were nearly identical. Neither the accuracy [$t(16) = -0.77$, $p = 0.455$] nor reaction times [$t(16) = -1.14$, $p = 0.271$] were significantly influenced by the task.

Event-related potentials

Time courses and scalp topographies of the event-related potentials to regular and irregular tones at the 3rd and 5th position within the sequences are depicted in Fig. 2. A distinct early negativity between 150 and 350 ms at posterior electrodes was elicited when an irregular tone was presented at both possible positions. Amplitudes in

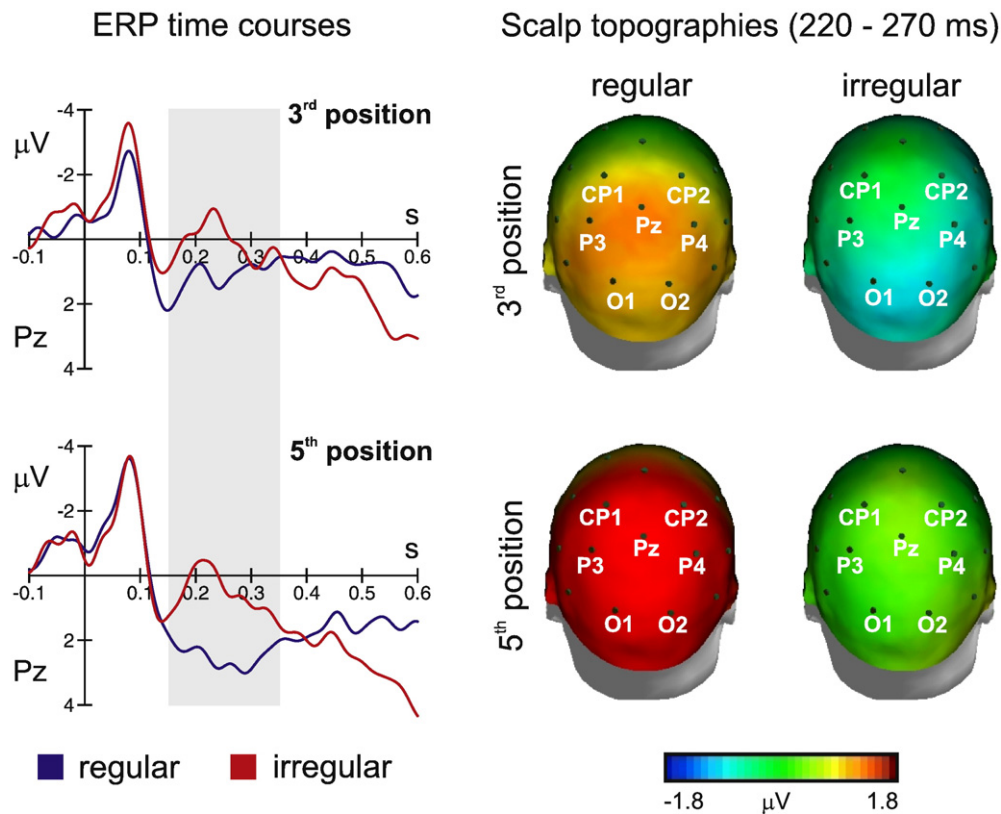


Fig. 2. Time courses (left) and scalp topographies (right) of the event-related potentials for regular and irregular tones at the 3rd and 5th position of sequences are displayed. The gray bar highlights the statistically analyzed time interval (150–350 ms) of the early negativity. Irregular tones elicited a larger negativity than regular tones. The potential maps were calculated over a narrower time window from 220 to 270 ms.

response to irregular tones were significantly larger than in response to regular tones (main effect of REGULARITY: $F(1,16) = 89.85$, $p < 0.001$). Although this difference tended to be larger at the 5th than at the 3rd position, the interaction of REGULARITY and TONE POSITION only shows a statistical trend [$F(1,16) = 3.88$, $p = 0.066$].

Evoked gamma-band responses

The wavelet analysis revealed an increase in the early evoked GBR for regularly presented tones. This is illustrated in Fig. 3 by the baseline-corrected time-frequency representations.

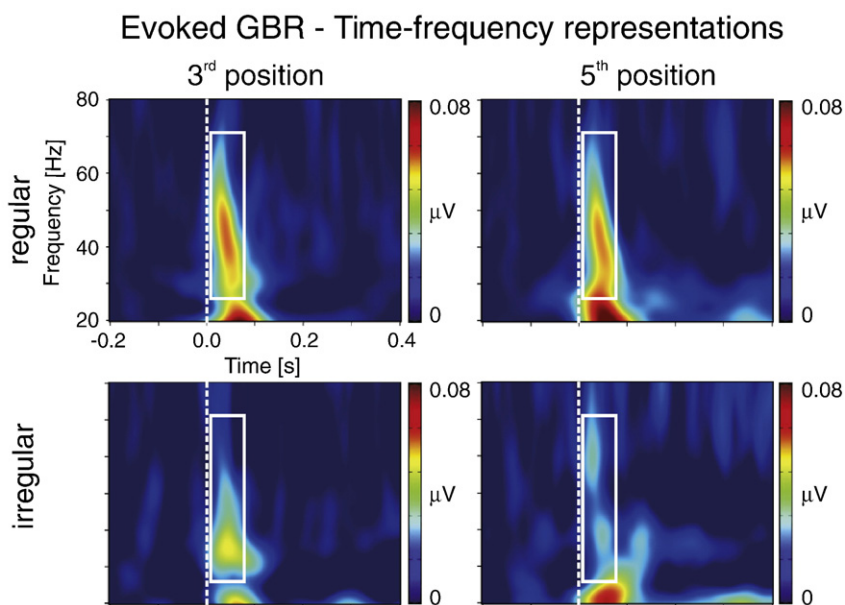


Fig. 3. Time-frequency representations of the evoked GBR for regular and irregular tones at the 3rd and 5th position of sequences are displayed and averaged across the central ROI. The dashed white line highlights the stimulus onset (at 0 ms) and the rectangle indicates the range of the early gamma-band activity. Evoked gamma-band amplitudes were significantly enhanced in response to regular tones at both positions.

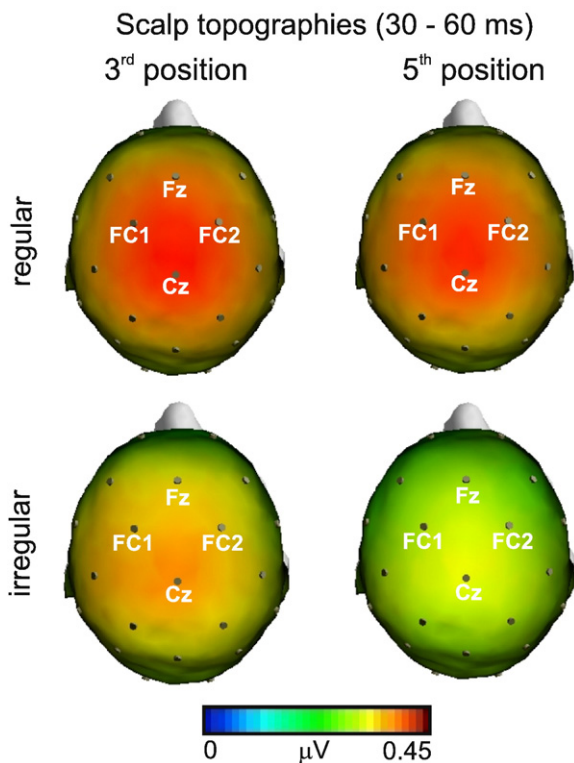


Fig. 4. Scalp topographies (view from top, anterior is upwards) of the evoked GBR for regular and irregular tones at the 3rd and 5th position. Regular tones evoked stronger responses than irregular tones at fronto-central electrodes. The potential maps were calculated averaging signal values between 30 and 60 ms.

Regularly presented tones elicited significantly larger GBR amplitudes than irregular tones (main effect of REGULARITY: $F(1,12) = 14.604$, $p < 0.01$). This effect is mainly manifested in fronto-central electrodes, which is depicted in Fig. 4. Source modeling of the evoked GBR based on bilateral dipoles in the primary auditory cortex yielded a GOF of 94.77% (see Fig. 5).

Since the ANOVA of mean baseline amplitudes between 200 and 100 ms before stimulus onset showed no significant effects of REGULARITY [$F(1,12) = 0.02$, $p = 0.904$] and TONE POSITION [$F(1,12) = 0.46$, $p = 0.510$], the main effect of early GBR was not elicited by differences in the baseline. The analysis of the GBR latency revealed no significant effects at all.

Fig. 6 displays the time courses of the evoked GBR, phase-locking, and total GBR in comparison. For the evoked GBR, the amount of phase-locking was significantly larger for regularly presented tones at both positions (main effect of REGULARITY: $F(1,12) = 16.910$, $p < 0.01$), whereas the analysis of the total GBR, an index of signal power, revealed no amplitude differences [$F(1,12) = 1.229$, $p = 0.289$]. Thus, the increase in the evoked GBR is most likely based on stronger phase-locking.

Discussion

Event-related potentials

The present study showed that irregular sounds within descending or ascending sequences elicited a larger negative deflection in the ERP than regular sounds. The main amplitude difference occurred in a time interval between 150 and 350 ms with an amplitude maximum at posterior scalp electrodes (relative to a nose reference electrode). This early negativity to irregular tones might reflect the ability of the auditory system to extract and apply sequential regularities. Previous research associated the detection of deviance with the mismatch negativity of the ERP without attentional modulation regarding

simple (for a review, see Näätänen et al., 2007) as well as complex auditory stimuli (Brattico et al., 2006). The MMN usually peaks at 150–250 ms from stimulus onset with a fronto-central scalp distribution that reverses its polarity at mastoids. This, however, does not correspond to our findings. It has been reported that if participants attentively detect deviant stimuli, the MMN is partially overlapped by a further negative component, namely the N2b (Näätänen et al., 1982). We assume, that the early negativity in the current experiment might rather resemble an N2b response than a mismatch negativity. This is further supported by the finding that the N2b peaks later at ~250 ms with a scalp distribution more posterior than that of the MMN (Alho et al., 1986). In contrast to other studies that reported a central scalp distribution for this negativity, we observed a scalp topography with a maximum at posterior electrodes. One possible explanation for this phenomenon might be the attended processing of the presented stimulus sequences in an active task. In this case, the early negativity seems to be intimately linked with a subsequent positivity waveform (Snyder and Hillyard, 1976), which typically increases in magnitude at parietal electrode sites (Johnson, 1993) and is related to attentional processing (Polich, 2007). Furthermore, the P3 is discussed in conjunction with context-updating. If a new stimulus within a sequence is detected, attentional processes govern a change or “updating” of the stimulus representation (Donchin and Coles, 1988; Polich, 2007). Thus, an overlap of N2b and P3 would be conceivable and might explain the posterior scalp distribution.

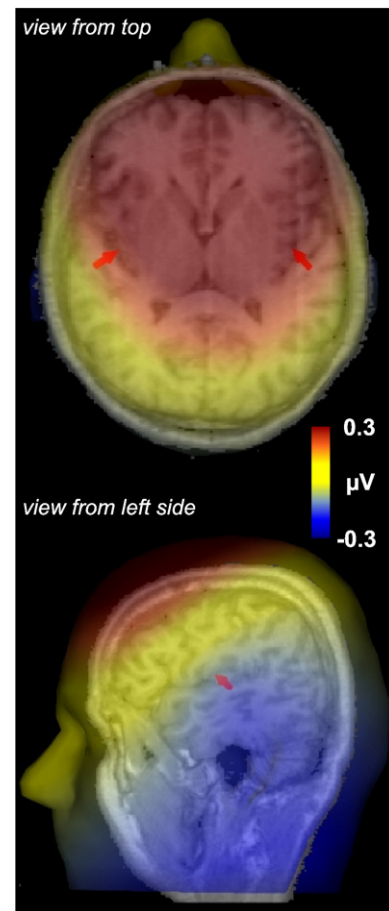


Fig. 5. Source modeling of the evoked GBR for the grand-average of regular tones at the 3rd and 5th position was conducted using two symmetrical dipoles placed bilaterally in the primary auditory cortex. The dipoles are displayed as red arrows and the amplitude of the evoked GBR measured at the scalp is indicated by a color gradient from red to blue. The source estimation yielded a GOF of 94.77%, indicating that the sources are well in line with the measured scalp-data.

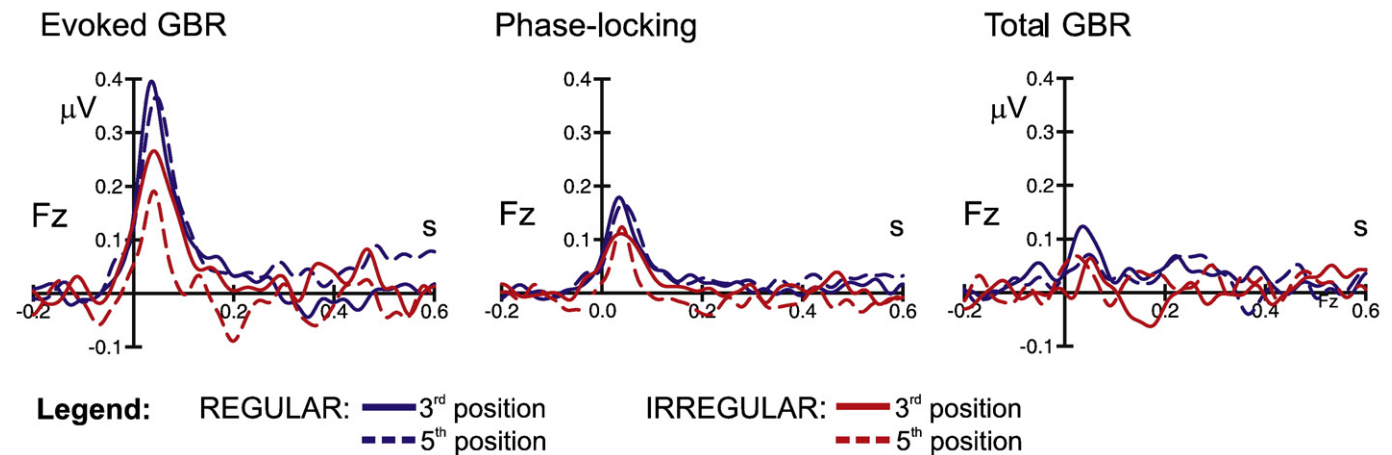


Fig. 6. Averaged time courses of the evoked GBR, phase-locking, and total GBR at electrode Fz. Regular tones at the 3rd (solid line) and 5th (dashed line) position of sequences are displayed in blue, whereas irregular tones at the 3rd (solid line) and 5th (dashed line) position are shown in red. Since total GBRs do not show differences between conditions, the enhanced evoked GBRs for regular tones seem to be due to enhanced phase-locking.

The processing of rules is also well investigated in language and music. Both, language and music are structured by complex syntactic rules and therefore evoke an expectation for upcoming events within a specific musical or linguistic context (Maess et al., 2001). In recent studies, the violation of regularities has shown to be reflected in an early right anterior negativity for musical stimuli (ERAN; Koelsch et al., 2002; Koelsch et al., 2007) and in an early left anterior negativity for linguistic stimuli (ELAN; Friederici, 1997, 2002) with an amplitude maximum around 200 ms. In contrast to the N2b, these EEG components rather reflected initial and automatic neural mechanisms that were contributed to the processing of irregularities.

Gamma-band responses

In the current study, we investigated in which way anticipation modulates early auditory gamma-band activity during listening to different tone sequences. Regularly presented tones matching the good continuation of a sequence elicited a considerably larger evoked GBR compared to irregular (deviant) tones with strongest responses at fronto-central electrodes. This corresponds very well to our source modeling of the evoked GBR. The dipole model with two bilateral dipoles in the primary auditory cortex accounted for 95% of the variance of the measured gamma-band activity. Previous investigations of the early evoked gamma-band activity also described the largest amplitudes in response to auditory stimuli at central electrodes and found the neural generators of this activity in the auditory cortex (Pantev et al., 1993; Mulert et al., 2007).

We observed this amplitude differences very early at 50 ms after stimulus onset. During anticipatory states, specific neuronal populations may be activated and further enhance subthreshold oscillations in sensory cortical areas (e.g. A1) before the actual stimulation (Engel et al., 2001). Matching of the bottom-up input with an internal prediction about the incoming stimulus therefore results in “resonance phenomena” and, thus, leads to enhanced evoked gamma-band response in a very early time interval. Therefore, events or stimuli that match the expectancy expressed by coherent states of the neuronal network generate more salient and speeded brain responses than non-attended or unexpected stimuli. The top-down process whose modulatory influence we observe 50 ms after stimulus presentation has probably already started much earlier, i.e. when the previous tone was presented and a rule was generated in order to predict the upcoming stimulus. Such an early modulation during auditory stimulus processing has been also reported in an audio-visual integration study (Widmann et al., 2007). In that study, visual symbolic information served as a cue and

preceded the auditory stimulus, while visual and auditory stimuli could be either congruent or incongruent. Only in the case of congruent stimulus presentations, where the prediction about the forthcoming sound matched the sensory input, an enhanced evoked GBR could be observed. The authors discussed their findings with respect to the “match-and-utilization” model (MUM) proposed by Herrmann et al. (2004c) for the visual modality. Hence, our results substantiate the findings of Widmann et al. (2007) and are further in line with the MUM model. Herrmann et al. (2004c) stated that matching between an incoming stimulus and a memory template results in an enhanced evoked gamma-band activity. Thus, the early evoked GBR in the current study appears to reflect this matching mechanism. According to the model, attention represents a determining factor for enabling and facilitating the match. Applied to the present experiment, the regularity of the tone sequence has to be learned and memorized and thus, the participants built up an expectation for the forthcoming tone, which can result in a match or mismatch. During listening to the tone sequences, attended processing was also ensured, since the task required a behavioral response by the participant. Therefore, it is most likely that the larger gamma-band amplitude in response to regularly occurring sounds is due to the higher amount of anticipation or expectation of the listener.

A similar approach is suggested by the “adaptive resonance theory” developed by Grossberg (1999). Grossberg supposes that humans are always anticipating their next behavior and respective consequences. These expectations about the world are permanently matched against actually occurring events. It is assumed, that a match between the current sensory input with existing knowledge causes an amplification of a sensory response, whereas a mismatch leads to an extinction. Further, such top-down expectation can also sensitize or pretune specific cells and therefore prepare them to react quickly to bottom-up inputs that match the top-down prime (Grossberg, 2001). If this is the case, it is conceivable that top-down modulations on GBR already occur at 50 ms. These early influences on oscillatory activity in the gamma-range were previously observed for other cognitive features in humans such as attention- (Tiitinen et al., 1993; Yordanova et al., 1997; Herrmann et al., 1999; Debener et al., 2003; Busch et al., 2006) or memory-related stimulus processing (Herrmann et al., 2004b; Busch et al., 2008).

The status of anticipation or expectation and its influence on the processing of forthcoming stimuli was previously investigated with respect to oscillatory activity in visual and auditory paradigms (Gonzalez Andino et al., 2005; Snyder and Large, 2005; Gómez et al., 2004). Visual gamma-band responses were reported to precede

the perceptual processing of a visual stimulus and correlated significantly with reaction times (Gonzalez Andino et al., 2005). This activity, occurring before stimulus onset, might facilitate the amplification of neural activity in sensory areas in response to the stimulus. This is not restricted to the visual modality: Snyder and Large (2005) studied the relationship between gamma-band responses and the processing of rhythmic tone sequences. Here, induced gamma-band responses appeared to predict tone onsets and persisted even for expected tones that were omitted. In contrast, the evoked GBR occurred in response to tones, but not to tone omissions. The authors concluded that the induced gamma-band oscillations might play a role in developing a mental representation of a temporally structured tone pattern, whereas the evoked activity reflects more stimulus driven aspects. We have previously demonstrated that auditory evoked GBR is modulated by stimulus properties such as sound intensity, too (Schadow et al., 2007a). However, we argue that evoked activity additionally reflects top-down aspects of stimulus processing. This is shown by the current results and earlier studies reporting strong effects of task difficulty (Mulert et al., 2007) and attention (Tiitinen et al., 1993; Debener et al., 2003) on the auditory evoked GBR. Furthermore, we reason that the status of anticipation during our task might affect even more strongly the matching process between the incoming tone and memory template than attentional parameters as was shown by Tiitinen et al. (1993). This seems very plausible to assume since the irregular or deviant tones within a sequence evoked significantly smaller GBR amplitudes than regular tone presentations although deviant stimuli are more powerful in attracting attention as indexed by the enhanced early negative ERP component. Our findings indicate that gamma-band oscillations are functionally more relevant for matching processes than for deviance detection, since regular tones that match the prediction of the listener evoked larger responses than deviant tones.

Conclusion

We conclude that the observed enhancement in early gamma-band activity reflects memory and anticipatory processes supporting the “match-and-utilization” model. Gamma-band oscillations were shown to be more relevant during matching processes than in detecting deviance. Our data suggest that early top-down modulation involves some of the first stages of auditory information processing (~50 ms). The findings correspond to analogous studies in the auditory and visual system considering such early top-down influences.

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