Attentional Modulation of the Inner Ear: A Combined Otoacoustic Emission and EEG Study

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Attending to a single stimulus in a complex multisensory environment requires the ability to select relevant information while ignoring distracting input. The underlying mechanism and involved neuronal levels of this attentional gain control are still a matter of debate. Here, we investigated the influence of intermodal attention on different levels of auditory processing in humans. It is known that the activity of the cochlear amplifier can be modulated by efferent neurons of the medial olivocochlear complex. We used distortion product otoacoustic emission (DPOAE) measurements to monitor cochlear activity during an intermodal cueing paradigm. Simultaneously, central auditory processing was assessed by electroencephalography (EEG) with a steady-state paradigm targeting early cortical responses and analysis of alpha oscillations reflecting higher cognitive control of attentional modulation. We found effects of selective attention at all measured levels of the auditory processing: DPOAE levels differed significantly between periods of visual and auditory attention, showing a reduction during visual attention, but no change during auditory attention. Primary auditory cortex activity, as measured by the auditory steady-state response (ASSR), differed between conditions, with higher ASSRs during auditory than visual attention. Furthermore, the analysis of cortical oscillatory activity revealed increased alpha power over occipitoparietal and frontal regions during auditory compared with visual attention, putatively reflecting suppression of visual processing. In conclusion, this study showed both enhanced processing of attended acoustic stimuli in early sensory cortex and reduced processing of distracting input, both at higher cortical levels and at the most peripheral level of the hearing system, the cochlea.

Key words: alpha oscillation; auditory steady-state responses; cochlea; DPOAE; selective attention

Introduction

Everyday life in complex multisensory environments requires the ability to selectively attend to a specific subset of incoming pieces of sensory information while ignoring others. This can be achieved by selectively directing attentional resources to single modalities or to distinct features of a stimulus. The attentional gain control leads to an enhanced processing of the selected stimulus reflected by faster reaction times and higher response accuracies (Ward, 1997; Carrasco et al., 2004).

The mechanism underlying attentional gain control might consist of a neuronal enhancement of relevant information or a suppression of distractors (Fritz et al., 2007; Couperus and Mangun, 2010). It is still a matter of debate regarding at which level of the processing hierarchy in the CNS selective attention exerts its influence. Electrophysiological studies in humans have concluded that attention affects the initial stages of cortical processing (Karns and Knight, 2009; Saupe et al., 2009), but not

subcortical stages (Picton et al., 1971; Connolly et al., 1989). In contrast, previous researchers highlighted that the most peripheral stage of the hearing system, the cochlea, could be modulated by attention (Meric and Collet, 1994; Giard et al., 2000; de Boer and Thornton, 2007). Several human and animal studies have shown that sound processing in the peripheral auditory system, investigated by otoacoustic emissions (Puel et al., 1988; Maison et al., 2001; Smith et al., 2012), cochlear microphonics (Delano et al., 2007), or auditory brainstem potentials (Lukas, 1980), is modulated during tasks requiring focused attention on either auditory or visual stimuli. However, the described effects were small and sometimes contradictory (Avan and Bonfils, 1992; but see negative results by Michie et al., 1996).

Physiologically, the peripheral effects of attention are supposed to be mediated by the medial olivocochlear (MOC) efferent system, consisting of neurons that originate in the brainstem, project to the cochlea, and innervate the outer hair cells (Guinan, 1996; Russell and Lukashkin, 2007). Outer hair cells are the core element of the cochlear amplifier because they amplify the basilar membrane vibrations of low-level sounds by actively changing their cell length and thereby reinforcing the vibration (Robles and Ruggero, 2001; Ashmore, 2008). Therefore, the olivocochlear efferent system can modulate the sound amplification characteristics of the cochlea.

The aim of the present study was to investigate intermodal selective attention in humans at different levels of the auditory system simultaneously. To access peripheral effects, we used dis-

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Figure 1. Schematic illustration of the task and the EEG layout. **A**, Paradigm: Simultaneous acoustic (40 Hz amplitude modulated two-tone stimulus) and visual (Gabor patch) stimulation. After 3 s, a visual cue indicated the to-be-attended modality (visual or auditory). The target (stimulus deviation) occurred in the time range of 3–5 s after the cue and had to be responded to by an immediate button press. **B**, EEG electrode layout with 41 electrodes. **C**, Exemplary frequency spectrum of the DPOAE measurement including the primary tones (f1: 1390 Hz; f2: 1682 Hz) and the 2f1–f2 DPOAE. The noise level is marked by the gray line.

tortion product otoacoustic emissions (DPOAE) to reveal the cochlear activation state (Kemp, 2007). Simultaneously, we measured neuronal activity by electroencephalography (EEG) and analyzed the auditory steady-state response (ASSR) as a marker of processing in the primary auditory cortex (Gutschalk et al., 1999; Engelien et al., 2000). Furthermore, we investigated oscillatory neuronal activity (alpha-band activity), which might reflect the impact of attentional processes at higher cortical levels (Foxe and Snyder, 2011; Klimesch, 2012). To our knowledge, our study is the first that simultaneously tested changes of DPOAEs and cortical activity in the context of selective attention.

Materials and Methods

Participants. Twenty-three healthy volunteers (13 females, age range: 20–39 years) participated in this study. All participants were right-handed and did not report any known hearing deficit. Subjects received a remuneration of 10 Euros per hour. All subjects were informed about the experimental procedure and the aims of the study and gave written informed consent. The study was approved by the Ethics Committee of the University of Frankfurt Medical Faculty.

Experimental paradigm. We investigated intermodal selective attention and measured cochlear and neuronal responses simultaneously by recording DPOAE and EEG, respectively. To ensure highly controlled attentional conditions, we did not use a block design as in previous otoacoustic emission studies in humans (Puel et al., 1988; Froehlich et al., 1993; Smith et al., 2012), but rather chose a paradigm in which a cue predicted the modality (auditory or visual) to attend in each trial, a common approach for behavioral investigations of attention (Ward, 1997; Green and McKeown, 2001; Carrasco et al., 2004).

Measurements were performed in a sound-attenuated, electrically shielded chamber (Industrial Acoustic Company) in which subjects sat

quietly on a comfortable chair. The visual stimulus was a continuously displayed Gabor patch (diameter: 3.3 degrees of visual angle; 2.1 cycles per degrees) of low contrast presented on a computer screen placed outside of the chamber behind an electrically shielded window (distance: 1.4 m). The acoustic stimulus was a continuous stimulus consisting of 2 simultaneously presented tones (duration 6–8 s, half cosine ramp: 25 ms, for details, see Acoustic Measurement and Analysis section below) presented binaurally via ear inserts.

The paradigm was designed in the style of classical cueing paradigms (Posner, 1980) with two experimental conditions, Attend Auditory and Attend Visual, in a pseudorandomized order. Figure 1A illustrates the experimental paradigm schematically. Each trial started with a period of nondirected attention. After 3 s, a cue was shown (0.5 s duration) on the computer screen, indicating the to-be-attended modality. An eye-symbol indicated the Attend Visual condition and a musical note indicated the Attend Auditory condition. During the following time period, the participants had to attend selectively to the indicated modality. The task was to detect a target in the selected modality appearing 3–5 s after the cue. The cue was 100% informative (valid) to avoid divided attention and to achieve a maximal focusing of attention. The target in the visual modality was a slight turn (angle change) of the Gabor patch; the target in the auditory modality was a short (200 ms) level decrease of the amplitude-modulated stimulus at the DPOAE recording ear. The participant was requested to react immediately by pressing a button with the right index finger when detecting the target. The time window to respond lasted for 0.85 s after target appearance. Slower responses were counted as misses. Consecutive trials were separated by a fixed intertrial time interval of 1.7 s with no auditory or visual stimulation.

Five blocks of 50 trials were performed. In each of the blocks, the difficulty of the task was adjusted individually by a staircase method to ensure high challenge and comparable demands between conditions and between subjects. The target deviation ranged between a level change of

1–12 dB for the auditory task and an angle change of 0.5–12° for the visual task.

Acoustic measurement and analysis. DPOAEs were measured in one of the two ears (right or left ear balanced between the subjects) using a probe assembly, which incorporates a sensitive microphone and two loudspeakers (ER-10C microphone/preamplifier system; Etymotic Research) placed into the subject's meatus with a foam ear tip. The microphone signal was preamplified (+40 dB) and fed into an A/D-recording interface (Edirol FA-66; Roland). The input and output channels of the sound card were sampled at a rate of 48 kHz. To present the defined stimulus levels, the two loudspeakers of the probe assembly were separately calibrated in the test ear immediately before the measurements started by measuring the frequency response of a white noise stimulus. Acoustic stimuli on the non-DPOAE ear were presented via an air-conducting tube with an ear-inserted foam tip (E-A-RTONE 3A; 3M). To ensure equal sound pressure levels (SPLs), all loudspeakers were calibrated using a sound level meter (120–0014; REED Instruments). Digital stimulus generation and data acquisition were controlled by custom-written MATLAB scripts (version 7.10; The MathWorks).

DPOAEs are generated when stimulating the ear with two pure tones of different frequencies (f_1 and f_2 , $f_1 < f_2$) and appropriate f_2/f_1 frequency ratios delivered through two separate loudspeakers. The f_2 frequency was set between 1000 and 2000 Hz and was adjusted in each participant to the frequency evoking the highest DPOAE level. The frequency ratio f_2/f_1 was 1.21 and the levels of the two primary tones were 65 dB SPL (f_1) and 55 dB SPL (f_2). To evoke auditory steady-state responses, the f_1 tone was additionally amplitude-modulated with a modulation frequency of 40 Hz and 100% modulation depth.

DPOAE levels were determined for each trial separately by calculating the frequency spectrum using a fast Fourier transform (FFT, Hanning window) and taking the amplitude at the $2f_1$ – f_2 DPOAE frequency. To obtain the time course of DPOAEs across trials, we used a moving window method (window size: 1000 ms, shifted from 0–6 s in steps of 250 ms). The background noise level in the test ear was calculated as the mean sound level at frequencies around the DPOAE frequency (10 data points below and above $2f_1$ – f_2). Only clearly measurable DPOAEs, defined as $2f_1$ – f_2 levels above mean noise level plus two SDs, were taken into account for further analysis. Single time points with atypical high background noise, for example, those caused by swallowing, were excluded from the analysis (mean rate of rejected data points: 15.26%, median: 10.08%).

For each participant, the time course of DPOAEs was averaged across trials for both conditions (Attend Visual and Attend Auditory). However, because it is known that DPOAEs show variations over time (Wagner et al., 2008) and the focus of our study was on small DPOAE level changes following the informative cue within each trial, the time period before cue (2–3 s) was taken as a baseline and DPOAE levels were expressed relative to the mean baseline level before averaging across trials.

To analyze the difference between the two selective attention conditions statistically, the DPOAE level was additionally calculated for two longer time windows: before selective attention (defined as the period from 1–3 s after stimulus onset) and during selective attention (defined as the period from 3.5–5.5 s after stimulus onset). The effect of intermodal attention on the otoacoustic emissions, defined as the difference between the DPOAE level during selective attention minus the DPOAE level before selective attention was compared statistically between the two conditions using standard t tests. When calculating this difference between the time periods during and before selective attention, only trials that did not show atypical high background noise in the period before or during selective attention (mean rate of rejected trials per subject: 18.83%, median: 16%) were used.

Electrophysiological recording and analysis. EEG was recorded continuously with a 128-channel QuickAmp amplifier (Brain Products) and 124 Ag–AgCl electrodes mounted in an elastic cap (Falk Minow Services). In the present study, 41 electrodes [including two electrooculography (EOG) channels] were used (Fig. 1B), covering approximately the whole head in concentric shapes with additional electrodes in the frontocentral region, where auditory steady-state responses are expected (Griskova et al., 2009; Saupe et al., 2009b). Two electrodes were mounted infraorbitally

and supraorbitally to the right eye to monitor eye blinks and eye movements. The electrode array was digitized for each participant after the recording using an electrode-localization system (Zebris/ElGuide). All channels were recorded with an average reference, a forehead ground, and impedances of $< \sim 10$ k Ω . The EEG was digitized with a sampling rate of 1000 Hz and an anti-aliasing filter of 135 Hz.

The preprocessing of the EEG data and the statistical analyses were performed with MATLAB (Version 8.0) and the open-source FieldTrip toolbox for EEG/MEG analysis (Oostenveld et al., 2011). The signal was band-pass filtered (0.1–150 Hz) and re-referenced to the average of the two mastoid electrodes. Epochs of 7.5 s, starting 1000 ms before stimulus onset, were extracted. Trials with artifacts were rejected by an automatic approach: trials with muscle artifacts were detected by means of thresholding the z -transformed value of the preprocessed raw data (110–150 Hz band-pass filter, Hilbert analytic amplitude, z -score cutoff = 20) and rejected. Additional artifacts were defined as voltage jumps exceeding 60 μ V. First channels with > 20 artifact-contaminated trials were fully excluded. After that, remaining trials with artifacts were rejected. The mean rate of remaining trials after artifact rejection across all participants was 87.9% (visual trials: 88.3%; auditory trials: 87.6%). To remove eye artifacts, the data underwent an independent component analysis (runica) and components correlating with the EOG channels ($r > 0.3$) were automatically rejected.

For ASSR estimation, epochs were averaged per participant, condition, and electrode site thus emphasizing stimulus-locked activation while suppressing induced brain responses and non-brain-related noise. The resulting event-related field was transformed into a time-frequency response using Hanning tapers with a fixed time window of 1000 ms, shifted from -1 to 6 s poststimulus onset in steps of 50 ms, and power was calculated by FFT. Because the relevant frequency was defined by the modulation frequency of the evoking stimulus, temporal power profiles and topographic distribution were calculated only for the 40 Hz (ASSR) component.

In addition to the evoked auditory steady-state response, stimulus-induced oscillatory activity was estimated by first analyzing the signal by time frequency on a single-trial basis (Hanning taper, time window: 500 ms; moving window from -1 prestimulus to 6 s poststimulus onset in steps of 50 ms) and then averaging across the trials. Alpha activity was defined as the mean power of the frequency band between 8 and 14 Hz. Statistical analysis of alpha and ASSR power was performed by nonparametric cluster-based permutation tests (Maris and Oostenveld, 2007).

Results

Performance was very similar for both conditions. The average hit rates were 82.99% (± 0.04 SD) for the visual task and 82.47% (± 0.05 SD) for the auditory task. They did not differ between conditions (paired t test: $t_{(22)} = 0.71$, $p = 0.48$). False alarm rates (visual: 1.29%, auditory: 1.32%) and missed trials (visual: 15.72%, auditory: 16.21%) were also comparable between conditions and did not show significant differences (paired t tests for false alarms: $t_{(22)} = 0.07$, $p = 0.94$; for missed trials: $t_{(22)} = 0.87$, $p = 0.40$). The reaction times for correct responses were slightly but significantly longer for visual (0.50 s) than for auditory (0.48 s) trials (paired t tests: $t_{(22)} = -2.26$, $p = 0.03$).

Acoustic data: otoacoustic emissions

DPOAE measurements were optimized by individually adjusting the f_2 frequencies. The resulting f_2 frequencies were in the range of 1000–1888 Hz (mean 1568 Hz). Figure 1C gives an example of the spectrum of the acoustic recording in the ear canal, with the amplitude-modulated f_1 tone, the pure f_2 tone, and the resulting distortion product at frequency $2f_1$ – f_2 visible as distinct peaks.

Figure 2A shows the DPOAE time course for the Attend Visual and Attend Auditory conditions averaged across all subjects. Directly after stimulus onset, DPOAE level showed a clear level decrease (onset adaptation). In the Attend Auditory condition,

Figure 2. Impact of intermodal attention on DPOAEs. **A**, Averaged time course of DPOAE level across the task duration ($n = 23$, mean $\pm$ SE). Red solid line, auditory task; blue dotted line, visual task. The DPOAE level is depicted relative to baseline. **B**, Mean DPOAE level change during attention compared with the time window before attention ($n = 23$, $\pm$ SE). The time windows are indicated by gray boxes in **A**. There was a significant difference between the auditory and visual conditions (t test, $p = 0.01$).

Figure 3. Correlation between attention effect and individual DPOAE base level. The individual difference of the DPOAE level change in auditory versus visual trials and the subjects' preattentional DPOAE level was negatively correlated ($r = -0.77$; $p < 0.001$).

DPOAE levels remained at baseline level after the presentation of the cue, whereas during visual attention, a distinct DPOAE level decrease was observed in the period of focused attention. Quantifying this effect of focused intermodal attention by calculating the DPOAE change during selective attention compared with precue periods (Fig. 2B) revealed a significant level decrease of ~ 0.2 dB for the visual condition (one-sample t test vs zero, $t_{(22)} = -2.1511$, $p = 0.0427$), but nearly no change for the auditory condition (n.s. vs zero, $t_{(22)} = -0.8149$, $p = 0.4239$). The level change in the period of focused attention compared with the period before focused attention differed significantly between the conditions Attend Auditory and Attend Visual (paired t test: $t_{(22)} = 2.80$, $p = 0.0103$).

Further analysis of the individual data revealed a strong negative correlation between the general DPOAE level, measured as the mean DPOAE level before attention, and the attention effect, defined as the difference between the level change during auditory and during visual attention. As shown in Figure 3, a lower precue DPOAE level was associated with a more pronounced attention effect ($r = -0.77$, $p < 0.001$, Student's t test).

Electrophysiological data: auditory steady-state responses

Maximal 40 Hz ASSR power was observed at frontocentral sensors. To compare the 40 Hz ASSR responses between the conditions of visual and auditory attention, the time period before the informative cue, the time from 1 to 3 s after stimulus onset, served as a baseline. Figure 4 illustrates the results of auditory steady-state responses, averaged across all subjects. The topographic scalp distribution of the ASSR (Fig. 4A) showed a higher ASSR power at frontocentral sensors for the auditory than for the visual attention condition. Statistical comparison of the ASSR power between the visual and auditory conditions in the period of selective attention (0.5–2.5 s after cue) revealed one cluster of electrodes with significant differences between conditions ($p = 0.03$) at 4 time points (4.4–5 s after stimulus onset; Fig. 4B). Investigation of the time course of the ASSR power of this cluster of electrodes during the task revealed an increase of ASSR during auditory attention in the time after the informative cue indicating the to-be-attended modality (Fig. 4C).

Electrophysiological data: alpha activity

The predominant frequency band of the induced oscillatory activity was in the alpha range (8–14 Hz). We compared alpha activity in a time period requiring focused attention to either the visual or the auditory modality (0.5–2.5 s after cue) by cluster-based permutation tests and found two clusters of electrodes where alpha activity was significantly lower ($p < 0.01$) for the visual than for the auditory trials (Fig. 5A). The first cluster was located over the occipitoparietal cortex and the second over the left frontal cortex. The difference in alpha activity between trials requiring auditory and visual attention began shortly after the presentation of the informative cue (Fig. 5B). Task onset and the presentation of the informative cue led to a distinct decrease in alpha power in both conditions. After cue presentation, alpha power remained at a low level for the rest of the task duration in the visual condition, whereas in the auditory condition, the alpha power increased after ~ 1 s to values above the precue level.

Discussion

The present result of different distortion product otoacoustic emission levels during visual attention compared with auditory

Figure 4. Auditory steady-state responses during auditory and visual attention. **A**, Topographical distribution of the 40 Hz ASSR during the period of focused attention averaged across all subjects for auditory (left) and visual (right) trials relative to the baseline period before the cue. **B**, Statistical contrast between conditions (t values). Electrodes of the significant cluster ($p = 0.03$) are marked with crosses. **C**, Time course of the ASSR power at cluster electrodes, mean $\pm$ SE. Red solid line, auditory trials; blue dotted line, visual trials.

Figure 5. Attentional modulation of alpha activity (8–14 Hz). **A**, Topographic representation of statistical differences (t values) between alpha activity during auditory and visual attention in the period 0.5–2.5 s after cue presentation. Electrodes of the two significant clusters are marked (first cluster at occipitoparietal sites: $*p < 0.01$, second cluster at left frontal electrodes: $+p < 0.01$). **B**, Time course of alpha power during the task. Averaged values are depicted for the occipitoparietal cluster electrodes for all subjects ($n = 23$, mean $\pm$ SE). Red solid line, auditory trials; blue dotted line, visual trials.

attention demonstrates an influence of intermodal attention on the cochlea as the most peripheral stage of auditory processing. Given the known anatomical structures, the neural substrate of this effect must be the MOC efferent pathway, which is part of the corticofugal system and can modulate the cochlear mechanical state by innervating the outer hair cells directly.

We found a reduction of the otoacoustic emission level during visual attention, which might reflect a reduction of sound amplification in the cochlea. This would be consistent with an inhibition of the irrelevant and distracting acoustic stimulus during visual selective attention. Several previous studies have also found reduced otoacoustic emission amplitudes when human

subjects were engaged in a visual task (Puel et al., 1988; Meric and Collet, 1992; Froehlich et al., 1993). However, in these studies, OAEs were compared between longer periods of visual attention and passive listening, so the observed differences might have been attributable to nonspecific arousal differences. In the present paradigm, we ensured comparable arousal states in both conditions using a trial-wise cueing paradigm. This design also controlled for slow drifts of the DPOAE level over the course of the experiment because we compared the level before and after the informative cue for each trial separately. Moreover, to ensure comparable difficulties between conditions and across subjects, we used an adaptive procedure producing equal hit rates.

Two recent studies using DPOAE found the opposite pattern compared with ours: a reduction of DPOAE level during auditory attention (Smith et al., 2012; Srinivasan et al., 2012). When discussing these contradictory results, it is important to consider the indirect nature of otoacoustic emission measurements. DPOAEs are generated as an acoustic byproduct of the nonlinear amplification in the outer hair cells and show complex and nonlinear characteristics. Small changes in the amplification process mediated by the MOC efferents might elicit level deviations in both directions depending on the choice of DPOAE stimulus frequencies and levels in the different studies. Significant changes of the DPOAE level in both directions during the activation of the olivocochlear efferents due to contralateral acoustic stimulation are described for humans and animals (Müller et al., 2005; Abel et al., 2009; Althen et al., 2012) and could be explained by models assuming shifts of the operating point of the cochlear amplifier (Abel et al., 2009). Delano et al. (2007) investigated the influence of selective attention in behaving chinchillas in a cueing paradigm and found, similarly to our results, a reduction of cochlear sensitivity (reduction of compound action potential amplitude) during visual attention after an informative cue. Also equivalent to our results, this study found no change of the cochlear response during auditory attention. Investigating attention effects in a cueing paradigm allows a very well controlled comparison between periods before and during attention; slow changes of cochlear response level and fluctuations of arousal that might occur during long-lasting block designs can be ruled out. Cueing is widely used in behavioral and neuroimaging studies in human, but our study was the first to apply cueing for the analysis of peripheral effects of selective attention in humans.

Interestingly, we found a negative correlation between the individual DPOAE base level and the magnitude of the attention effect. Subjects with lower DPOAE levels showed the clearest DPOAE modulation during selective attention. Two considerations might explain this observation. First, the olivocochlear efferent modulation of DPOAE has been shown to be more pronounced for low-level stimulation, when the cochlear amplifier is particularly important (Robles and Ruggero, 2001; Ren et al., 2011). Therefore, low DPOAE levels could correspond to the optimal operating range of the cochlear amplifier and thus high sensitivity for efferent modulation. Conversely, the stimulation level was constant for all subjects and a low DPOAE level might rather indicate low hearing sensitivity (Boege and Janssen, 2002). Subjects with higher hearing thresholds and lower DPOAE levels could possibly benefit more from an early attentional impact on cochlear amplification and would therefore use such a modulation more markedly.

In our study, like in previous ones, the observed OAE level change during focused attention appeared rather small. However, considering the nonlinear course of DPOAE input–output functions, small alterations might correspond to bigger differ-

ences in the evoking stimulus level, so small changes in the DPOAE level as an indirect indicator of cochlear amplification might resemble bigger, highly relevant changes in auditory processing. Independently of effect direction and the rather small effect size, it is important that the present study, as well as previous ones, demonstrated a significant influence of task demand on the mechanics of the cochlea.

The novel approach of our study was the combination of DPOAE and EEG measurements to assess attentional effects simultaneously on different stages of the auditory system. By measuring auditory steady-state responses, we monitored the effects of attention at early cortical stages. The 40 Hz ASSR showed a frontocentral distribution, similar to the ASSR distribution described by others (Griskova et al., 2007; Saupe et al., 2009; de Jong et al., 2010). Its topography matched the assumed source of ASSRs in the primary auditory cortex located in Heschl's gyrus. As expected, the ASSR varied, with task demands showing significantly higher power during auditory than during visual attention. This is consistent with former studies, such as one by Saupe et al. (2009, 2009b), who found a significant enhancement of ASSR during auditory attention compared with visual attention in an intermodal selective attention task. Similarly, Gander et al. (2010) described changes in ASSR power dependent on the attentional demand (auditory vs visual attention), but only when attention was required for brief (1 s) but not for long (2 min) time intervals. In an earlier study, no effects of attention on the ASSR were seen (Linden et al., 1987). Apparently, an attentional modulation of ASSR at primary auditory cortex is influenced by the specific experimental design and the difficulty and exact time course of the task. It has been suggested that differences in ASSR levels might be obvious only when the target event is defined by a change of the modulation frequency itself (Ross et al., 2004; Skośnik et al., 2007; Saupe et al., 2009b), which was not the case in our paradigm and could explain why the present effect, even though it reached statistical significance, was rather small.

The analysis of induced oscillatory activity in the EEG provided a further control for the attentional demands of the task. We found a suppression of alpha-band activity in the visual trials compared with the auditory trials in the period of selective attention for a cluster of occipital electrodes. Recent studies have suggested an active role of cortical alpha oscillations for cognitive functions, including short-term memory (Kaiser et al., 2007) and attention (Foxe and Snyder, 2011; Händel et al., 2011; Mazaheri et al., 2014). In the context of selective attention, alpha-band activity is suggested to reflect a suppression mechanism. Our results are consistent with this view: during selective attention to visual stimuli, alpha power decreased in occipital regions that most likely correspond to early visual cortex. Thus neural suppression by alpha oscillations is reduced, whereas during auditory attention, alpha power as an attentional suppressor is increased in this area, corresponding to a suppression of the distracting visual input during focusing on auditory stimuli. Changes in alpha-band power have been shown for intermodal attention (Foxe et al., 1998) and for intrasensory spatial and feature-based attention in different sensory domains (Fu et al., 2001; Thut et al., 2006; Klimesch et al., 1998) and seem to reflect a general mechanism for attentional gating when competing sensory input needs to be ignored or selected. The typical alpha effect in the present study further confirmed the effectiveness of our experimental paradigm for the investigation of intermodal attention. The effects at the level of the cochlea are therefore unlikely to reflect arousal differences.

The interindividual variability was rather high in all measures (DPOAE, ASSR, alpha power) and we failed to find correlations between them. This may be attributable to the fact that the different effects we show correspond to different processes associated to selective attention (cochlea: suppression of the distractor in the auditory system; primary auditory cortex: enhancement of the attended stimulus; alpha: suppression of distractor processing in the visual system) and thus do not depend on each other directly. In conclusion, we observed a significant influence of intermodal selective attention at different stages of the auditory processing hierarchy. Attentional modulation of auditory processing was found already at the level of the cochlea. This supports the hypothesis of a cognitive impact on the micromechanical mechanisms in the inner ear, probably mediated by the olivocochlear efferent system. However, further studies will be necessary to integrate the present findings in the general function of the olivocochlear efferent system for human hearing.

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