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RESEARCH ARTICLE

Motion-onset auditory-evoked potentials critically depend on history

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Abstract The aim of the present study was to determine whether motion history affects motion-onset auditory-evoked potentials (motion-onset AEPs). AEPs were recorded from 33 EEG channels in 16 subjects to the motion onset of a sound (white noise) virtually moving in the horizontal plane at a speed of 60 deg/s from straight ahead to the left (−30°). AEPs for baseline and adaptation were compared. A stimulus trial comprised three consecutive phases: 2,000 ms adaptation phase, 1,000 ms stationary phase, and 500 ms test phase. During the adaptation phase of the adaptation condition, a sound source moved twice from +30° to −30° to top up preceding adaptation. In the baseline condition, neither top-up nor pre-adaptation were exerted. For both conditions, a stationary sound was presented centrally in the stationary phase, moving leftwards in the test phase. Typical motion-onset AEPs were obtained for the baseline condition, namely a fronto-central response complex dominated by a negative and a positive component, the so-called change-N1 and change-P2 after around 180 and 250 ms, respectively. For the adaptation condition, this complex was shifted significantly into the positive range, indicating that adaptation abolished a negativity within a time window of approximately 160 to 270 ms. A respective shift into the negative range was evident at occipito-parietal sites. In conclusion, while adaptation has to be taken into account as a potential confound in the design of motion-AEP studies, it might also be of benefit in order to isolate AEP correlates of motion processing.

Keywords Motion · AEP · Adaptation · Human · Cortex

Introduction

Numerous studies indicate the existence of auditory motion detection, i.e., of direction-selective processing of moving sound sources (humans: neuro-imaging: Griffiths et al. 1998; Baumgart et al. 1999; Lewis et al. 2000; Bremmer et al. 2001; Warren et al. 2002; lesion studies: Griffiths et al. 1996; Clarke et al. 2002; Ducommun et al. 2004; psychophysical studies: Grantham 1986, 1997; Getzmann 2008; animal electrophysiology: Spitzer and Semple 1991; Ahissar et al. 1992; Moiseff and Haresign 1992; Toronchuk et al. 1992). The relevant computations appear to reside in cortical areas such as the planum temporale, the premotor cortex, and the parietal lobe. To characterise the neural mechanisms that underlie auditory motion processing in humans, auditory potentials evoked by moving sound sources (motion-onset AEPs) are a novel complement in the neurophysiologist's arsenal. Several recently published AEP studies demonstrated a fronto-central response complex to be associated with auditory motion onset, namely a large negative deflection around 140 ms after motion onset, cN1 ('change'-N1), and a large positive deflection around 230 ms, cP2 ('change'-P2). This motion-onset AEP signature is reproducible across laboratories and paradigms

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(Krumbholz et al. 2007; Getzmann 2009; Getzmann and Lewald 2010). As a consequence, the possibility of a detailed temporally resolved analysis of human auditory motion detection with motion-onset AEPs appears to be opened.

The scope of an event-related potential analysis of the neural underpinnings of motion detection can be appreciated by turning attention to equivalent investigations into the visual system (Heinrich 2007). Here motion-onset visual-evoked potentials (motion-onset VEPs) were used to identify and characterise the neural substrate of motion direction-specific cortical visual processing (Bach and Ullrich 1997; Bach and Hoffmann 2000; Hoffmann et al. 2001; Maurer and Bach 2003). This way the existence of at least two speed channels (Heinrich et al. 2004; Lorteije et al. 2008) and the impact of ego-motion (Hoffmann and Bach 2002) and of implicit motion on visual motion processing (Lorteije et al. 2007) were substantiated. One key in this analysis of the motion system was the use of motion adaptation paradigms. Prolonged motion exposure adapts the visual motion system within seconds (e.g., Bex et al. 1999; Hoffmann et al. 1999), inducing the percept of illusionary motion of a stationary stimulus into the direction opposite to the previous adaptor, which is known as the motion aftereffect (Mather et al. 1998). It was demonstrated that this motion adaptation has a profound and rapid impact on the shape of the motion-onset VEP (Bach and Ullrich 1994; Hoffmann et al. 1999). On the one hand, it had to be learned that paradigm designs had to take the potential of the motion-onset test stimulus to adapt the motion system as a potential confound into account (Bach and Ullrich 1994; Hoffmann et al. 1999). In fact, initially, groups using stimuli with a great adaptation potential obtained VEPs dominated by a positive ‘motion component’, while those using stimuli with little adaptation potential demonstrated that it is actually a negativity which reflects the primary motion detector response (reviewed in Heinrich 2007). On the other hand, the susceptibility of motion-onset VEPs to adaptation was utilised to characterise human motion vision with motion-onset VEPs in several variations of cross-adaptation studies (Bach and Hoffmann 2000; Hoffmann et al. 2001; Heinrich et al. 2004; Lorteije et al. 2007, 2008).

Given the increasing interest in motion-onset AEPs, it is topical to clarify whether motion adaptation has an effect on the shape of the motion-onset AEP similar to that observed for motion-onset VEP. For perception, there are indeed similarities of the adaptation characteristics of auditory and visual motion adaptation in humans. For both sensory systems, motion aftereffects were reported in a number of previous studies (auditory: Grantham 1998; Dong et al. 2000; Neelon and Jenison 2003, 2004; visual reviewed in: Mather et al. 1998). Furthermore, in both sensory systems motion adaptation appears to build up within seconds (auditory: Neelon and Jenison 2004; visual: e.g., Bex et al. 1999; Hoffmann et al. 1999). Consequently, not only for the visual, but also for the auditory system, adaptation has an impact on motion perception. The aim of the present study was to determine whether motion history affects the signature of the motion-onset AEP. Motion-onset AEPs were compared for a condition with little and a condition with strong motion history. For the latter, pre-adaptation was achieved by repetitive virtual motion of a sound source from right to left for 1 min, which was topped up by another two repetitions prior to each actual motion-onset stimulus. Pronounced effects on the motion-onset AEPs were observed.

Methods

Subjects

A total of 16 healthy subjects (median age 28 years, range, 19–35 years, 9 female, 15 right-handed) with normal hearing took part in the study. They gave their written informed consent and were paid for their participation. The procedures followed the tenets of the Declaration of Helsinki (World Medical Association 2000), and the protocol was approved by the ethics committee of the University of Magdeburg, Germany.

Stimuli

The generation of the auditory stimuli that virtually move in the horizontal plane followed a previously applied procedure (Baumann and Greenlee 2007): The moving sound was Gaussian white noise of 16.66-ms duration per position which was convolved with a generic head-related transfer function (HRTF) for each of the positions along the motion trajectory in discrete steps of 1°. Subsequently, it was smoothed using a Hanning window to create the percept of a smoothly moving sound source. The motion trajectory comprised positions from 0 to −30° azimuth angle (negative: left) for the test stimulus, and from +30° to −30° for the adaptation stimulus. The sound sources moved at a speed of 60 deg/s. For the stationary sound, the same Gaussian white noise was convolved with the HRTF for the position of 0° azimuth. To reduce responses due to sound onset and offset, another Hanning window was applied to the obtained sounds, with a window width of 500 ms for the onset of the stationary sound and for both adaptation stimulus onset and offset. Furthermore, a Hanning window of a width of 100 ms was applied to create a gradual offset of the test stimulus, i.e., affecting the last 100 ms of the test stimulus. The generation of the sounds was implemented in Matlab V7 (The MathWorks, Inc.) and the complete sound sequences were created with Adobe Audition 3.0 (Adobe Systems Inc.).

The time courses of the different sound stimulus types are schematically depicted in Fig. 1. They comprised three consecutive phases, (a) an ‘adaptation phase’ (duration: 2,000 ms), (b) a ‘stationary phase’ (duration: 1,000 ms), and (c) a ‘test phase’ (duration 500 ms), which were presented in a cyclic design. Three different stimulus types were tested, (1) baseline, (2) adaptation, (3) no onset. (1) The baseline condition served the purpose to determine auditory motion-onset potentials with little motion history (duty cycle of motion: 14%) according to a previously used approach (Getzmann 2009). Here, stimulation was absent in the adaptation phase, a stationary stimulus was presented in the stationary phase, and a motion-onset stimulus in the test phase. (2) The adaptation condition served the purpose to determine auditory motion-onset potentials with strong motion history (duty cycle of motion: 71%). A 1,000-ms stimulus moving from +30° to −30° was presented twice in the adaptation phase. This adaptation stimulus was modulated with an envelope leaving the strongest stimulus at 0°, i.e., the location of the motion onset during the test phase (see Fig. 1). Thus, position onset and offset adaptation at +30° to −30° was minimised and a component of motion in depth added. A stationary stimulus was presented in the stationary phase, and a motion-onset stimulus in the test phase. (3) The no-onset condition served as a control to test whether responses in the test phase arise only, if there is an onset or stimulus change in this phase. For this condition, no stimulus was present in the adaptation phase, and a stationary stimulus was presented both during the stationary and the test phase. Thus, no stimulus onset was present in the test phase.

To maintain a constant level of vigilance during the experimental session, subjects had to perform a simple visual detection task. Numbers and letters (1.1° of visual angle) were presented in random order at the centre of a CRT monitor (frame rate: 60 Hz; viewing distance: 120 cm). The subjects had to respond to the presentation of numbers via button press. The interstimulus intervals for this task were 10–15 s. A collision with the auditory motion onsets was avoided by sparing the test stimulus phase from the presentation of visual targets. Thus, also potential confounds of a distracting task on the motion-onset responses were reduced (Beer and Röder 2004; Xiang et al. 2004).

Procedure

Motion-AEPs were recorded in six blocks presented in a counter-balanced blocked design (no onset, baseline, adaptation, adaptation, baseline, and no onset). Adaptation blocks were preceded by 1-min motion adaptation [30 repetitions of the motion adaptation stimulus (two repetitions of motion from +30° to −30°) used in the adaptation condition in the adaptation phase for top-up adaptation, see Fig. 1], and followed by a 5-min recovery break during which the subjects were allowed to look around freely. In each block, 100 trials were presented. After artefact rejection, at least 130 trials were obtained per condition for each subject. The sounds were presented via insert earphones (ER-2, Etymotic Research Co., Elk Grove Village, IL, USA) at a maximal intensity level of approximately 60 dB(A) SPL (Brüel & Kjær Precision Sound Level Meter Type 2235 and Artificial Ear Type 4135). The commercial software Presentation (Neurobehavioral Systems, Albany, CA) was used for both visual and auditory stimulation (24-bit soundcard SoundBlaster X-Fi 5.1, Creative Labs (IRL) Ltd).

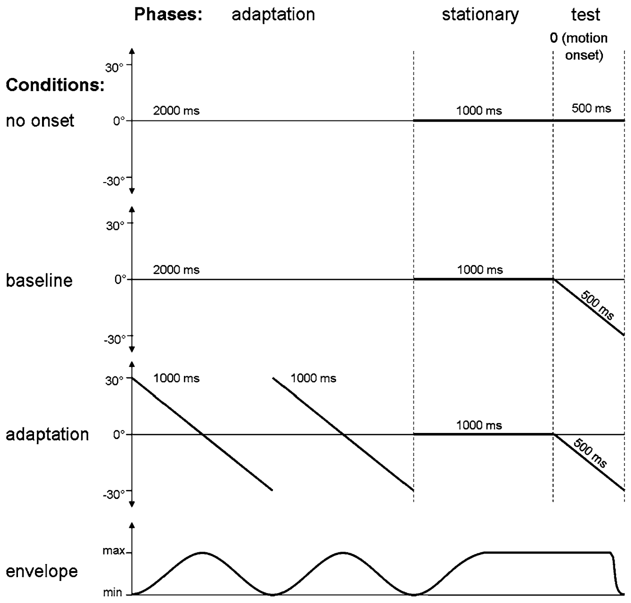

Fig. 1 Schematic of the sound stimuli used. The time courses for the three different conditions (no onset, baseline, adaptation) are depicted in the top three rows as virtual position vs. time. The different stimulation phases (2,000 ms adaptation, 1,000 ms stationary, and 500 ms test) are separated by *dotted lines*. The sequence is repeated in a cyclic design within separate blocks for each stimulus condition. In the bottom row, the envelope is depicted, by which the sound levels are modulated to eliminate confounding effects

Electrophysiological recordings

Participants were seated in a comfortable chair under sound-shielded conditions. Multi-channel-recordings [33 EEG channels referenced to nose and 2 pairs of EOG channels (one bitemporal horizontal EOG and one vertical EOG of the left eye)] were performed using an EEG cap (Head Cap, GVB Gelimed, Bad Segeberg, Germany) with equidistantly arranged Ag-/AgCl-sintered ring electrodes based on the international 10–20 system (American Encephalographic Society 2006), amplified with a physiological amplifier (NuAmps amplifier, NeuroScan Labs, Sterling, VA, USA), band-pass filtered (low- and high-frequency cut-offs 1 and 100 Hz), and digitised at 1,000 Hz. A ground electrode was centred on the forehead, between FPz and Fz. Impedances were kept below 5 kΩ.

Data analysis

Trials were analysed offline with BrainVision Analyzer 2.0 (Brain Products, Gilching, Germany) and Igor Pro V6.1 (WaveMetrics, Inc., Lake Oswego, OR, USA) for an interval from −100 to 700 ms relative to motion onset. The data were filtered offline between 0.1 and 40 Hz (slope: 48 db/oct). It should be noted that offline low-pass filter settings can be found throughout the motion-AEP literature ranging from 25–50 Hz cut-off (Beer and Röder 2004, 2005; Getzmann 2009; Getzmann and Lewald 2010, in press). Here, a moderate filter setting was chosen to reduce high-frequency artefacts while still including comparatively fast components in the analysis. Finally, the data were re-referenced to the average of the 33 EEG channels. The average reference, although debatable (Desmedt and Tomberg 1990; Desmedt et al. 1993), was used for better comparability with recent motion-onset AEP studies (Krumbholz et al. 2007; Getzmann 2009; Getzmann and Lewald 2010, in press). Trials with blinks, detected with a threshold criterion of ±100 µV and upon individual inspection, were discarded. The remaining epochs were baseline corrected to the 100-ms interval preceding motion onset and averaged separately for each subject and each condition. cP2 peaks were defined as the positive maximum in a time window of 150–300 ms after motion onset and were detected automatically. It should be noted that, in order to avoid a bias in the data, the entire cohort of 16 subjects entered the analysis, as none were rejected on the basis of their EEG signals. Thus, also subjects with alpha-waves in the EEG waveform were included, which accounts for some residual alpha-waves, particularly at Pz.

Statistical analysis

To determine the electrodes with AEP deflections significantly different from 0, "running *t*-tests" were performed on the respective AEP traces of each electrode. To reduce the rate of false positives due to multiple testing, significances were thresholded at a p-value <0.001 for five consecutive time points. This is supported by the fact that no significant responses were obtained for the "no-onset" condition (data not shown) for this criterion. The presence of a significant deflection is indicated in the respective figures by "*".

For additional analyses, peak amplitudes and latencies were determined in each individual for a subset of electrodes (FC1, Cz, and FC2) and tested for significance using a two-way ANOVA (factor one—electrode, factor two—condition). For subsequent post-hoc tests, Student's *t*-test was used and corrected for multiple testing using the sequential Bonferroni correction (Holm 1979).

Results

For the baseline condition, typical motion-onset AEPs were obtained as demonstrated by the grand mean traces depicted in Fig. 2. The vertex response was dominated by a negative deflection around 180 ms and a positive deflection around 250 ms, cN1 and cP2, respectively. Significant deflections of both cN1 and cP2 were evident at FC1, Cz, and FC2. Other significant response patterns were evident at C3, C4, T8, and, in inverted polarity, at P8 and A1.

For the adaptation condition, significant responses were evident at the sites FC1, Cz, FC2, C3, C4, P8, and A1, as for the baseline condition, and additionally at the frontal sites F3, Fz, F4, FC5, and the occipito-parietal sites TP8, Pz, P4, P7, PO3, PO4, O1, Oz, and A2 (see Fig. 3). Similar to the baseline condition, fronto-central traces appeared to be inverted in polarity compared to occipito-parietal traces. The trace shapes for the adaptation condition were clearly different from that obtained for the baseline conditions, which can be appreciated particularly from the difference traces depicted in Fig. 4. The difference, baseline condition minus adaptation condition, leaves a negative deflection at fronto-central sites. At occipito-parietal sites, the difference is positive, reflecting a similar inversion of polarity for fronto-central vs. occipito-parietal traces as for the raw traces depicted in Figs. 2 and 3.

For the recording sites with particularly pronounced baseline responses, i.e., FC1, Cz, and FC2, the effect of motion history on the responses is highlighted in Fig. 5. Here, the relevant traces are juxtaposed and the difference traces included. Thus, a trend is evident for more negative responses for baseline than for adaptation in a time window from around approximately 160–270 ms, which reaches significance at FC1 (significance peaks at 216 and 276 ms) and FC2 (significance peak at 231 ms). The results of a corresponding single-peak analysis are given in Fig. 6. In Fig. 6a, the latencies and the amplitudes of the individuals' cP2, determined as described in Methods, are depicted for the baseline and adaptation condition. Two-way repeated-measures ANOVAs [factor one: condition (baseline and adaptation); factor two: electrode (FC1, Cz, and FC2)] revealed a significant effect of the factor condition on response amplitudes, but not on response latencies. The significance of the differences between baseline and adaptation amplitudes was tested post hoc with paired *t*-tests [sequentially Bonferroni-corrected (Holm 1979)], which revealed significant effects at each recording site (FC1: $p = 0.0015$, Cz: $p = 0.002$, FC2:

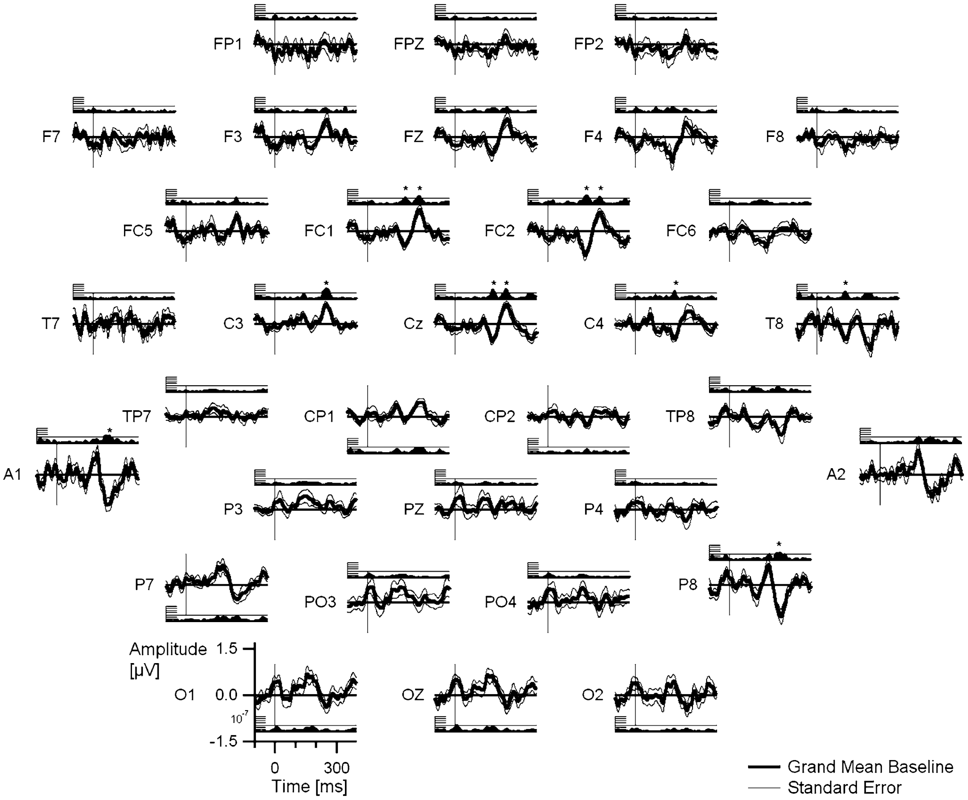

Fig. 2 Topography of grand mean motion AEPs for the baseline condition (mean ± SEM; $n = 16$). Motion onset, i.e., beginning of the test phase, is indicated by the vertical line. Each panel consists of two plots, voltage vs. time and logarithmised p-value vs. time. The latter is logarithmically scaled from 10^0 to 10^{-7} (scale on the left of each trace), $p < 0.001$ is indicated by a *horizontal line*. Deflections that differed significantly from 0 as defined in "Methods" ($p < 0.001$ for at least five consecutive samples) are indicated by "*". The typical response complex comprising cN1 and cP2 is evident at fronto-central sites

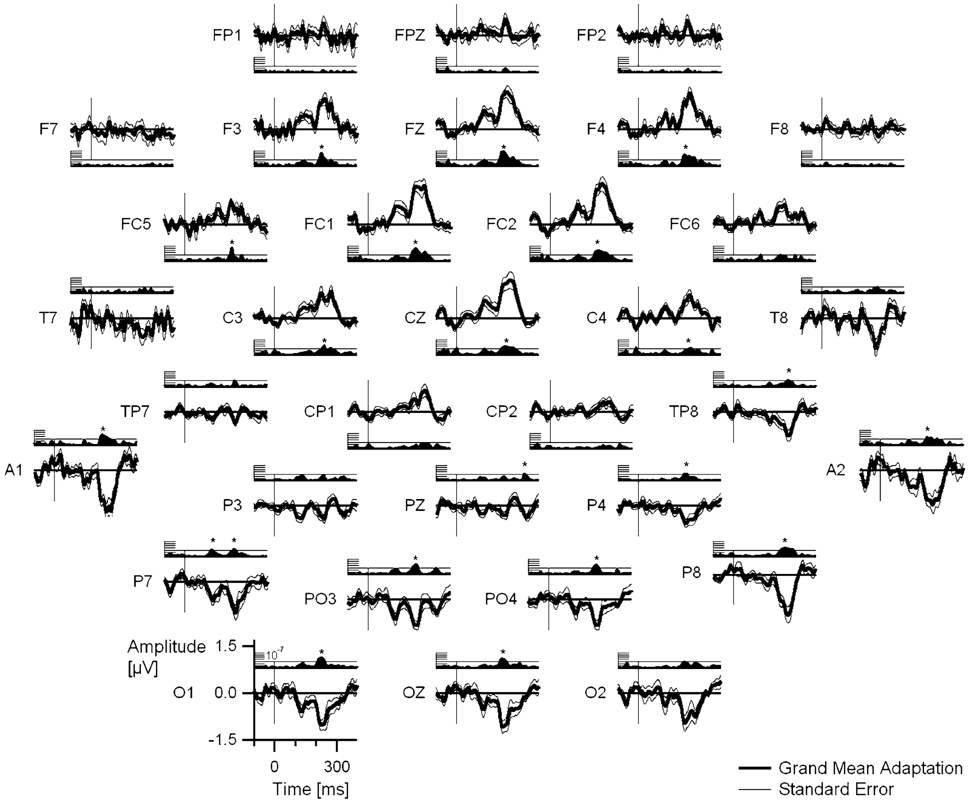

Fig. 3 Topography of grand mean motion AEPs for the adaptation condition (mean ± SEM; $n = 16$). Conventions as in Fig. 2. The fronto-central cN1 and cP2 complex evident for the baseline condition is shifted into the positive range

$p = 0.0015$). Significant effects were obtained for the above ANOVA neither for the factor electrode nor for the interaction of condition and electrode. These results were corroborated by an analysis of the individual difference trace peaks depicted in Fig. 6b. The difference trace amplitudes (peaking at 217, 219, and 219 ms for FC1, Cz, and FC2, respectively)

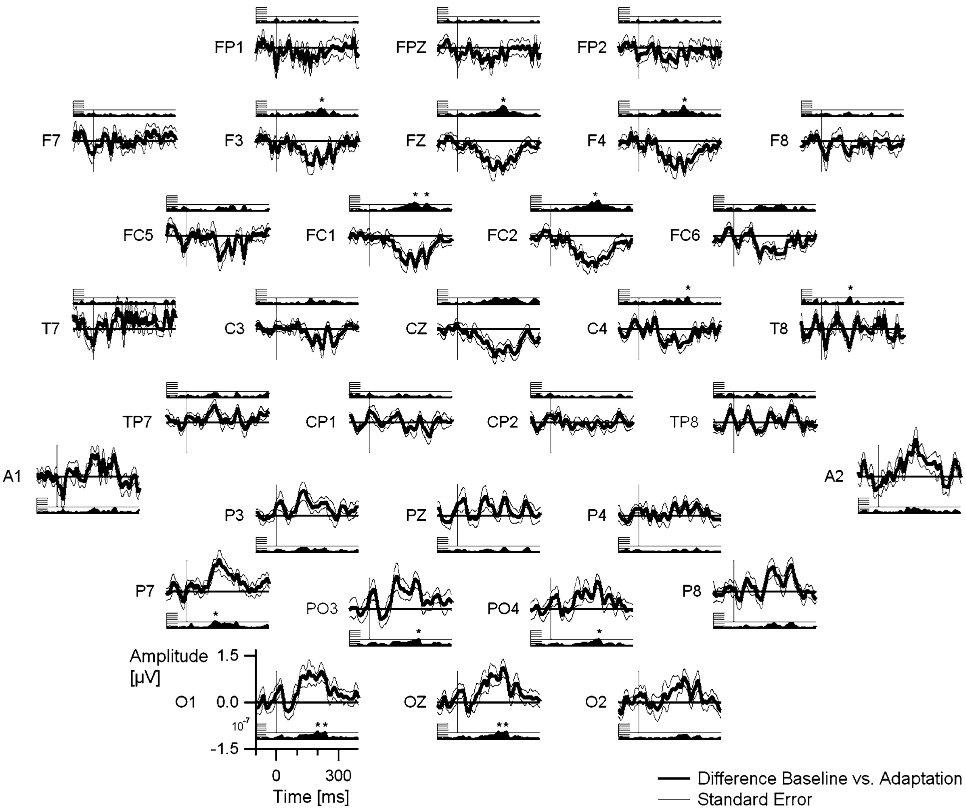

Fig. 4 Topography of the grand mean of the difference traces baseline minus adaptation condition motion-onset AEPs (mean ± SEM; $n = 16$). Conventions as in Fig. 2. The component eliminated in the adaptation condition is a negativity from around 160 to 270 ms at fronto-central sites. As in Figs. 2 and 3, deflections that differed significantly from 0 as defined in "Methods" ($p < 0.001$ for at least five consecutive samples) are indicated by "*"

differed significantly from 0 at each of the three electrodes [FC1: $p = 9.7 \times 10^{-6}$, Cz: $p = 1.3 \times 10^{-6}$, FC2: $p = 5.9 \times 10^{-6}$; one-sample *t*-test sequentially Bonferroni-corrected for multiple testing (Holm 1979)].

Discussion

In accordance with previous studies (Krumbholz et al. 2007; Getzmann 2009; Getzmann and Lewald 2010), auditory motion-onset potentials without an immediate history of a virtually moving sound source evoked a fronto-central response complex dominated by a cN1 and cP2. Strikingly, motion adaptation appeared to eliminate a negative component from these responses within a time window of around 160–270 ms. It is thus demonstrated that motion-onset AEPs critically depend on the history preceding the motion onset. On the one hand, this highlights that caution must be exerted when comparing motion-onset AEPs across studies, as varying histories might result in differing shapes of the motion-onset AEPs. On the other hand, this finding indicates that adaptation might be a powerful tool to dissect the different components of the motion-onset AEP and to identify and investigate veridical neuronal correlates of human auditory motion perception.

Response topography

The neural generators underlying the motion-onset AEP evoke responses at various recording sites. Interestingly, the responses from fronto-central sites appear to be inverted in polarity compared to responses from occipito-parietal sites, as demonstrated in the present and previous studies (e.g., Getzmann and Lewald in press). On the one hand, this distributed pattern coined by polarity inversion might be related to the spatial characteristics of the underlying network. On the other hand, it might also be related to the usage of an average reference, which can result in an apparent dispersion of focal activity and in polarity changes (Desmedt and Tomberg 1990; Desmedt et al. 1993). Remarkably, the polarity inversion is also characteristic of the traces obtained for the adaptation condition and for the baseline-adaptation difference. While this indicates similarities in the underlying neural networks for the different conditions, activity for the adaptation condition and particularly the baseline-adaptation difference appears to be more widespread than during the baseline condition. These topographical changes might be suggestive of a change in the actual set of generators contributing to the motion-onset AEP after motion history. This clearly deserves attention in further studies.

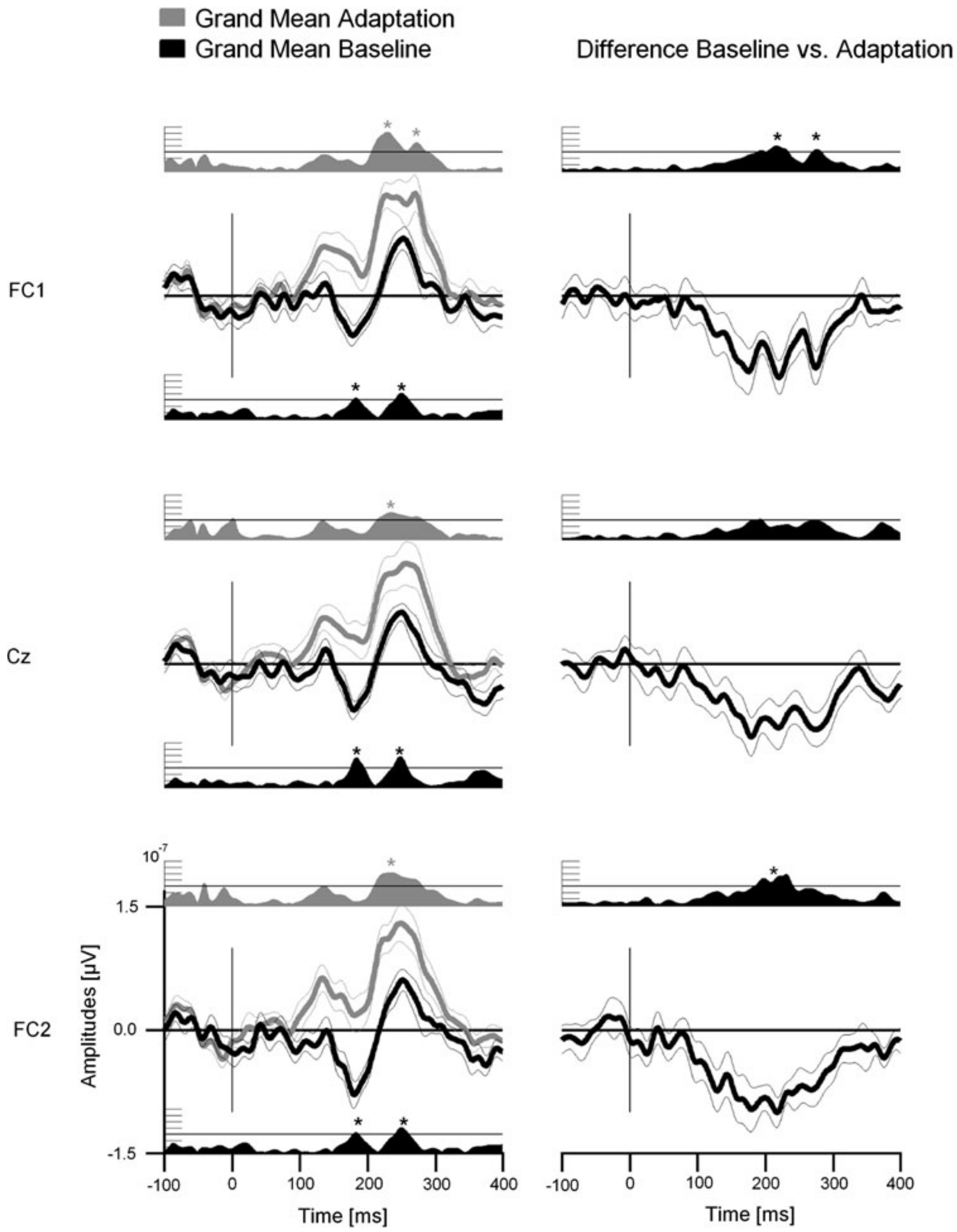

Fig. 5 Detailed depiction of the grand mean traces (mean ± SEM; $n = 16$) for the sites at FC1, Cz, FC2. Conventions as in Figs. 2, 3, 4. Significance levels for the differences from 0 are given in the respective panels for baseline in *black*, adaptation in *gray* (left column), and for the difference trace in *black* (right column)

Mechanisms generating motion-onset AEPs

In a number of previous studies as well as in the present study, care was taken to dissociate noise-onset and motion-onset responses in the AEP. This was achieved by a temporal offset between the noise onset and the motion onset (Krumbholz et al. 2007; Getzmann 2009; Getzmann and Lewald 2010, in press). As a consequence, the resulting AEP is expected to be driven primarily by the virtual motion of an auditory sound source. However, this way it is not at all guaranteed that only motion-processing mechanisms are activated by such a stimulus. In fact, several processes are triggered and might, as a consequence, give rise to the evoked neural responses, only one of these processes being veridical auditory motion detection, i.e., direction-selective processing (Wagner et al. 1997). Other processes might be activated by stimulus-induced loudness changes per se, or by position changes per se, i.e., processes that are independent of the direction, or by the change of interaural stimulus differences. Thus, a variety of different potential generators are likely contributors to the motion-onset AEP. Consequently, before the neural substrate of human auditory motion can be characterised with motion-onset AEPs, ways to investigate its motion-specific components in isolation must be found. As demonstrated in the present study, this might be assisted by the fact that auditory motion perception is susceptible to adaptation processes acting in the temporal range of seconds (Neelon and Jenison 2004).

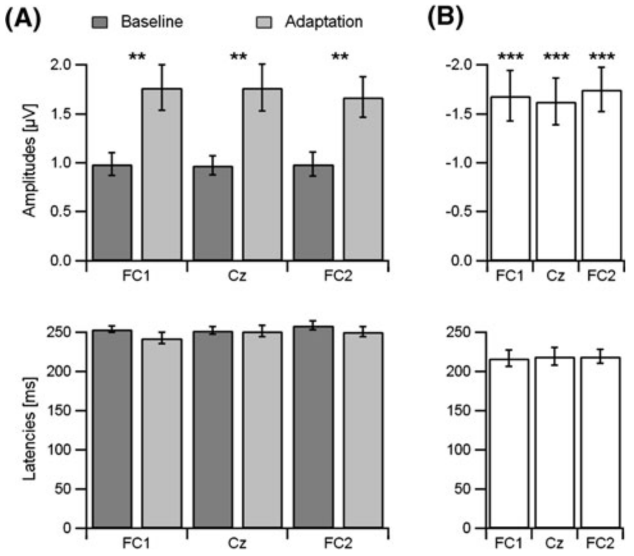

Fig. 6 cP2 amplitudes and latencies (mean ± SEM; $n = 16$) for the baseline and the adaptation condition (**a**) and for the difference traces (**b**) as determined with a single-peak analysis in each individual for the sites FC1, CZ, and FC2. Significance levels are indicated as "**" for $p < 0.01$, and "***" for $p < 0.001$ (statistics are detailed in "Results")

Potential applications of adaptation paradigms

In analogy to the analysis of the motion-onset VEP, adaptation studies of the motion-onset AEP might be promising, and there are a number of potential applications. Two of these are outlined in the following. (1) Testing for direction-specific adaptation might allow for the extraction of a veridical auditory motion component. Similar to the motion-onset VEP, it might be expected that only a part of the strong effect of motion history on the motion-onset AEP is direction-specific and that there is a considerable additional component that does not adapt in a direction-specific manner and is, as a consequence, not related to veridical motion processing. In fact, for motion-onset VEPs, the motion component N2 at occipito-lateral sites was reduced after adaptation by 75% in amplitude. With an assessment of the direction specificity of the adaptation, it was demonstrated that 48% of the adaptation were not specific for motion direction, while 27% were specific for motion direction (Hoffmann et al. 2001). Consequently, direction-specific adaptation of the motion-onset AEPs is most intriguing, as it might allow for the identification of the parts of the extensive cortical network activated by motion onset (e.g., Getzmann and Lewald in press) that comprise the actual motion detection system. Respective studies are currently under way. (2) Adaptation studies might help to assess whether different auditory motion cues engage the same or a different cortical network. Such cues are interaural time differences (ITD), interaural level differences (ILD), or position-dependent sound characteristics that are based on the head-related transfer function as used in the present study. Indeed, a dependence of the motion-onset AEPs on the specific motion cue applied has recently been described (Getzmann and Lewald 2010). It is therefore of interest to test for example whether a history of ILD-based motion affects AEPs to the onset of ITD-based motion and vice versa. Finally, it might be of interest to investigate how attention, both intra- and intermodal, influences the effect of motion history on motion-onset AEPs. Though the potential of such studies is promising, it should be noted as a caveat that there are a number of intricacies to be mastered to incontrovertibly isolate specific components of the motion-onset AEP with adaptation paradigms as specified below.

Comparison of motion adaptation paradigms for AEP and VEP studies

Many motion-onset VEP studies use motion of a pattern within a stimulus window to generate motion onset and motion adaptation. As a result, it is not a moving object but only a pattern within stationary object boundaries that is moving ('pattern motion') in these experiments. This approach has the advantage that the stimulus position stays exactly the same during stimulation or adaptation with motion. As a consequence, an adaptation pattern can move through the stimulus window for any time without additional stimulus onsets. This way the test stimulus can actually be used to create an initial motion onset and to adapt the system via prolonged motion duration. In contrast, recent motion-onset AEP studies use the percept of moving sound sources to evoke motion onset—in fact, it is not straightforward to generate auditory 'pattern motion'. This use of auditory sound source motion results in a distinct deviation of AEP and VEP adaptation paradigms. For adaptation in a certain motion direction, the sound source has to be reset to the start position after each motion trial. Consequently, potential confounds, such as the impact of the onset and offset of the adaptation stimulus during the reset, deserve attention. In the present study, this was addressed with a reduction of the adaptation sound onset and offset by applying an appropriate envelope waveform for the sound-pressure level of the stimuli (see Fig. 1). However, given these differences in the paradigms, further studies are needed to validate whether in both modalities congruent mechanisms contribute to the effects of motion history on the event-related potentials. At present, it should be noted that the effects of motion history on both perception and ERPs appear to be acting with time constants of a similar order of magnitude for the VEPs (Hoffmann et al. 1999) and apparently also for the AEPs. This can be taken as indirect and preliminary evidence that in both modalities the electrophysiological effects of motion history might be similarly related to the motion aftereffect. Appropriate studies are needed to test this specifically.

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References

Ahissar M, Ahissar E, Bergman H, Vaadia E (1992) Encoding of sound-source location and movement: activity of single neurons and interactions between adjacent neurons in the monkey auditory cortex. J Neurophysiol 67:203–215

American Encephalographic Society (2006) Guideline 5: guidelines for standard electrode position nomenclature. J Clin Neurophysiol 23:107–110

Bach M, Hoffmann MB (2000) Visual motion detection in man is governed by non-retinal mechanisms. Vis Res 40:2379–2385

Bach M, Ullrich D (1994) Motion adaptation governs the shape of motion-evoked cortical potentials (motion VEP). Vis Res 34:1541–1547

Bach M, Ullrich D (1997) Contrast dependency of motion-onset and pattern-reversal VEPs: interaction of stimulus type, recording site and response component. Vis Res 37:1845–1849

Baumann O, Greenlee MW (2007) Neural correlates of coherent audiovisual motion perception. Cereb Cortex 17:1433–1443

Baumgart F, Gaschler-Markefski B, Woldorff MG, Heinze HJ, Scheich H (1999) A movement-sensitive area in auditory cortex. Nature 400:724–726

Beer AL, Röder B (2004) Attention to motion enhances processing of both visual and auditory stimuli: an event-related potential study. Brain Res Cogn Brain Res 18:205–225

Beer AL, Röder B (2005) Attending to visual or auditory motion affects perception within and across modalities: an event-related potential study. Eur J Neurosci 21:1116–1130

Bex PJ, Metha AB, Makous W (1999) Enhanced motion aftereffect for complex motions. Vis Res 39:2229–2238

Bremmer F, Schlack A, Shah NJ, Zafiris O, Kubischik M, Hoffmann K, Zilles K, Fink GR (2001) Polymodal motion processing in posterior parietal and premotor cortex: a human fMRI study strongly implies equivalencies between humans and monkeys. Neuron 29:287–296

Clarke S, Bellmann Thiran A, Maeder P, Adriani M, Vernet O, Regli L, Cuisenaire O, Thiran JP (2002) What and where in human audition: selective deficits following focal hemispheric lesions. Exp Brain Res 147:8–15

Desmedt JE, Tomberg C (1990) Topographic analysis in brain mapping can be compromised by the average reference. Brain Topogr 3:35–42

Desmedt JE, Tomberg C, Raspe G, Ducarme D (1993) Inadequacy of the average reference for identifying focal changes in EEG and evoked potential studies [3]. Electroencephalogr Clin Neurophysiol Evoked Potentials 88:534–536

Dong CJ, Swindale NV, Zakarauskas P, Hayward V (2000) The auditory motion aftereffect: its tuning and specificity in the spatial and frequency domains. Percept Psychophys 62:1099–1111

Ducommun CY, Michel CM, Clarke S, Adriani M, Seeck M, Landis T, Blanke O (2004) Cortical motion deafness. Neuron 43:765–777

Getzmann S (2008) Effects of velocity and motion-onset delay on detection and discrimination of sound motion. Hear Res 246:44–51

Getzmann S (2009) Effect of auditory motion velocity on reaction time and cortical processes. Neuropsychologia 47:2625–2633

Getzmann S, Lewald J (2010) Effects of natural versus artificial spatial cues on electrophysiological correlates of auditory motion. Hear Res 259:44–54

Getzmann S, Lewald J (in press) Shared cortical systems for processing of horizontal and vertical sound motion. J Neurophysiol

Grantham DW (1986) Detection and discrimination of simulated motion of auditory targets in the horizontal plane. J Acoust Soc Am 79:1939–1949

Grantham DW (1997) Auditory motion perception: snapshots revisited. In: Gilkey RHAA, Timothy R (eds) Binaural and spatial hearing in real and virtual environments. Lawrence Erlbaum Associates, Mahwah, pp 295–314

Grantham DW (1998) Auditory motion aftereffects in the horizontal plane: the effects of spectral region, spatial sector, and spatial richness. Acustica 84:337–347

Griffiths TD, Rees A, Witton C, Shakir RA, Henning GB, Green GG (1996) Evidence for a sound movement area in the human cerebral cortex. Nature 383:425–427

Griffiths TD, Rees G, Rees A, Green GG, Witton C, Rowe D, Buchel C, Turner R, Frackowiak RS (1998) Right parietal cortex is involved in the perception of sound movement in humans. Nat Neurosci 1:74–79

Heinrich SP (2007) A primer on motion visual evoked potentials. Doc Ophthalmol 114:83–105

Heinrich SP, van der Smagt MJ, Bach M, Hoffmann MB (2004) Electrophysiological evidence for independent speed channels in human motion processing. J Vis 4:469–475

Hoffmann MB, Bach M (2002) The distinction between eye and object motion is reflected by the motion-onset visual evoked potential. Exp Brain Res 144:141–151

Hoffmann M, Dorn TJ, Bach M (1999) Time course of motion adaptation: motion-onset visual evoked potentials and subjective estimates. Vis Res 39:437–444

Hoffmann MB, Unsöld AS, Bach M (2001) Directional tuning of human motion adaptation as reflected by the motion VEP. Vis Res 41:2187–2194

Holm S (1979) A simple sequentially rejective multiple test procedure. Scand J Stat 6:65–70

Krumbholz K, Hewson-Stoate N, Schonwiesner M (2007) Cortical response to auditory motion suggests an asymmetry in the reliance on inter-hemispheric connections between the left and right auditory cortices. J Neurophysiol 97:1649–1655

Lewis JW, Beauchamp MS, DeYoe EA (2000) A comparison of visual and auditory motion processing in human cerebral cortex. Cereb Cortex 10:873–888

Lorteije JA, Kenemans JL, Jellema T, van der Lubbe RH, Lommers MW, van Wezel RJ (2007) Adaptation to real motion reveals direction-selective interactions between real and implied motion processing. J Cogn Neurosci 19:1231–1240

Lorteije JA, van Wezel RJ, van der Smagt MJ (2008) Disentangling neural structures for processing of high- and low-speed visual motion. Eur J Neurosci 27:2341–2353

Mather G, Verstraten FAJ, Anstis SM (1998) The motion aftereffect. A modern perspective. MIT Press, Cambridge

Maurer JP, Bach M (2003) Isolating motion responses in visual evoked potentials by pre-adapting flicker-sensitive mechanisms. Exp Brain Res 151:536–541

Moiseff A, Haresign T (1992) Response of auditory units in the barn owl's inferior colliculus to continuously varying interaural phase differences. J Neurophysiol 67:1428–1436

Neelon MF, Jenison RL (2003) The effect of trajectory on the auditory motion aftereffect. Hear Res 180:57–66

Neelon MF, Jenison RL (2004) The temporal growth and decay of the auditory motion aftereffect. J Acoust Soc Am 115:3112–3123

Spitzer MW, Semple MN (1991) Interaural phase coding in auditory midbrain: influence of dynamic stimulus features. Science 254:721–724

Toronchuk JM, Stumpf E, Cynader MS (1992) Auditory cortex neurons sensitive to correlates of auditory motion: underlying mechanisms. Exp Brain Res 88:169–180

Wagner H, Kautz D, Poganiatz I (1997) Principles of acoustic motion detection in animals and man. Trends Neurosci 20:583–588

Warren JD, Zielinski BA, Green GG, Rauschecker JP, Griffiths TD (2002) Perception of sound-source motion by the human brain. Neuron 34:139–148

World Medical Association (2000) Declaration of helsinki: ethical principles for medical research involving human subjects. JAMA 284:3043–3045

Xiang J, Holowka S, Ishii R, Wilson D, Chuang S (2004) Dynamic neuromagnetic responses to auditory motion: a novel index for evaluation of attention. Neurol Clin Neurophysiol 2004:106