

Cortical processing of auditory motion cue information

Stephan Getzmann^{1,2} & Jörg Lewald^{1,2}

¹ Leibniz Research Centre for Working Environment and Human Factors, D-44139 Dortmund, Germany

² Ruhr University Bochum, D-44780 Bochum, Germany. Email: getzmann@ifado.de, joerg.lewald@rub.de

Introduction

In humans, the localization of a sound source in the horizontal plane is mainly based on interaural time and intensity differences (ITDs and IIDs, respectively). For sound elevation, spectral cues arising from filtering effects of pinna, head, and body are the primary spatial cues (see [1] for review). Usually, these localization cues interact in a complex manner: While spatially impoverished cues (i.e., ITDs or IIDs presented via headphones) result in the impression of a sound source originating at a lateral position inside the listener's head, realistic sound sources containing ITDs, IIDs, and spectral cues are perceived as located at a spatial position outside the head.

In natural environments, the perception of sound motion is an essential function of the auditory system. Although the mechanism of auditory motion processing is still unclear, there is some evidence of the existence of cortical areas specifically activated by moving sound [2]. This hypothesis is supported by studies using EEG, indicating a prominent cortical response specific to moving sound: In particular, the onset of motion in an otherwise continuous sound elicited a motion onset response (MOR) that differed in morphology and topography from the response to sound energy onset, suggesting motion-specific processing in the human auditory system [3]. However, as the majority of previous studies on auditory motion perception used spatially impoverished cues, it is yet unclear whether or not gradual shifts in IID or ITD are comparable with realistic sound motion in space.

The aim of the present study was to investigate effects of motion cues on neural correlates of auditory motion processing by employing high-density EEG. Listeners were presented with different motion cues while auditory-evoked potentials were measured. The sound motion started after a stationary period of the stimulus at a central location. Motion was simulated in the form of gradual shifts in (a) ITD or (b) IID, or (c) by virtual 3D sound generated using generic head-related transfer function (HRTF) filters, or (d) real motion was presented by successive activation of 45 loudspeakers along the horizontal plane. The effect of motion cues on behavioral performance was tested with a reaction-time task in which the listeners indicated as fast as possible the direction of motion in a subset of trials.

Method

A total of 20 subjects (mean age 26.6 years) with normal hearing participated in the study. Listeners were presented with a sound stimulus consisting of two successive phases, a stationary phase with 700 ms duration and a motion phase with 500 ms duration. The stimulus was otherwise continuous and consisted of band-pass-filtered 100-Hz sine-wave-

form modulated white noise. Four different motion cue conditions were presented blockwise: (1) Real free-field motion was generated by successively activating one loudspeaker after the other along an horizontal loudspeaker arrangement, with the sound moving at 180 deg/s toward left (0° to -90°) or right (0° to 90°) positions (Fig. 1A). (2) Virtual 3D motion was simulated by presenting sounds that was passed through HRTF filters delivered by Tucker Davis Technologies with otherwise identical stimulus parameters as used for real motion. (3) ITDs of the sound stimulus were changed linearly from zero to +/-600 μ s. (4) IIDs were changed linearly from zero to +/-20 dB. In conditions 2-4, stimuli were presented by insert earphones.

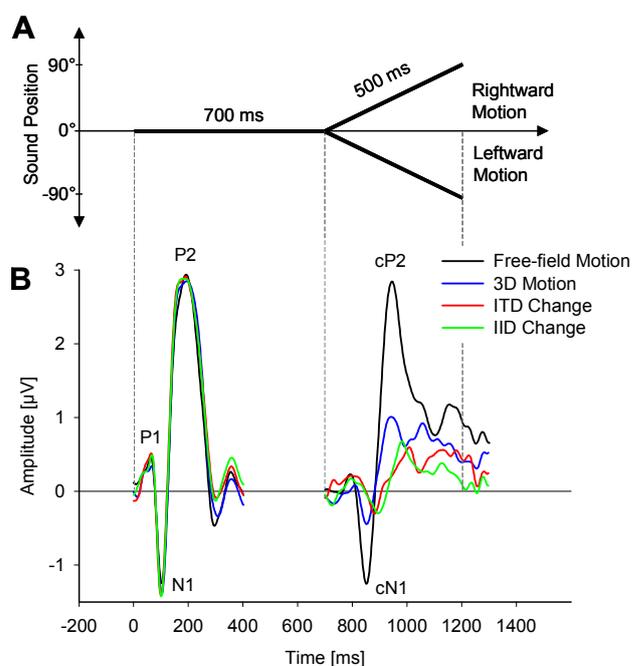


Figure 1: A) Schematic illustration of the sound sequences presented: Each sequence consisted of a 700-ms stationary sound, and a simulated 500-ms leftward or rightward sound motion. (B) Grand-average responses at a vertex electrode (Cz) plotted as a function of time relative to the sound onset and the motion onset, shown separately for free-field motion, virtual 3D motion, ITD or IID changes. The horizontal bars indicate the time period of motion.

The continuous EEG was sampled at 500 Hz using 57 Ag/AgCl electrodes (referenced to a vertex electrode at FCz) and two cascaded NuAmps amplifiers (NeuroScan Labs, Sterling, VA). Electrode positions were based on the International 10-10 system. The raw data were band-pass filtered

off-line between 0.5 and 25 Hz, and re-referenced to the average of 58 channels (56 EEG and 2 mastoid electrodes). Data were corrected for ocular artifacts using the Gratton and Coles procedure, and the automatic artifact rejection implemented in the BrainVision Analyzer software (Brain Products, Gilching, Germany). A statistical analyses of the MOR were carried out for the vertex electrode (Cz).

Results

The listeners responded faster to the free-field motion and the virtual motion than to changes in ITD and IID: reaction times (RTs) to free-field motion (784.3 ms) and 3D motion (797.0 ms) did not differ significantly, whereas RTs to ITD changes (889.3 ms) and IID changes (909.2 ms) were significantly larger than those to free-field motion and virtual motion (all $p < 0.001$; Bonferroni-corrected t -tests). RTs to ITD and IID changes did not differ significantly. There were only few errors in motion discrimination (free field: 2.9%; virtual: 1.7%; IID: 2.3%; ITD: 1.6%) that did not differ significantly between motion cues.

The onset of acoustic stimulation produced a vertex response (Cz) that mainly consisted of a negative deflection (N1) and a large positive deflection (P2), and that did not differ between motion cue conditions (Fig. 1B). However, the MOR, consisting of a negative (the so-called change N1, cN1) and a positive (cP2) deflection, clearly depended on motion cues. On the one hand, latencies of cN1 and cP2 did neither differ between free-field motion and virtual 3D motion, nor be-

tween ITD and IID changes (all $p > 0.05$). On the other hand, latencies with free-field or virtual motion were significantly shorter than with ITD or IID changes (all $p < 0.01$) (Fig 2A, B). The amplitudes of the MOR to free-field motion were much larger than those to virtual motion, ITD changes, or IID changes (all $p < 0.01$), whereas no differences occurred between amplitudes to virtual motion, ITD changes, and IID changes (all $p > 0.05$) (Fig. 2C, D). Interestingly, real free-field motion thus even produced a substantially stronger cortical activation than virtual 3D motion. In order to determine the cortical sources of this extra activation, source localization was carried out using standardized low-resolution brain electromagnetic tomography (sLORETA) and the sLORETA-built-in voxelwise randomization test (5000 permutations) based on statistical non parametric mapping (SnPM) [4]. SLORETA indicated a highly significant difference in activation between free-field motion and virtual 3D motion (cN1: $p < 0.0038$; cP2: $p < 0.0004$), and revealed that the stronger cN1 and cP2 to free-field motion mainly resulted from activation in inferior frontal gyrus and middle frontal gyrus (Brodmann Areas 9, 45, 46), and in Insula (Brodmann Area 13) (Fig. 3).

Figure 2: Relation between latencies (A, B) and amplitudes (C, D) of the cN1 and cP2 in no-response trials, and mean reaction times on response trials for free-field motion, virtual 3D motion, and ITD or IID changes. Error bars indicate standard errors (SE) across participants (N = 20).

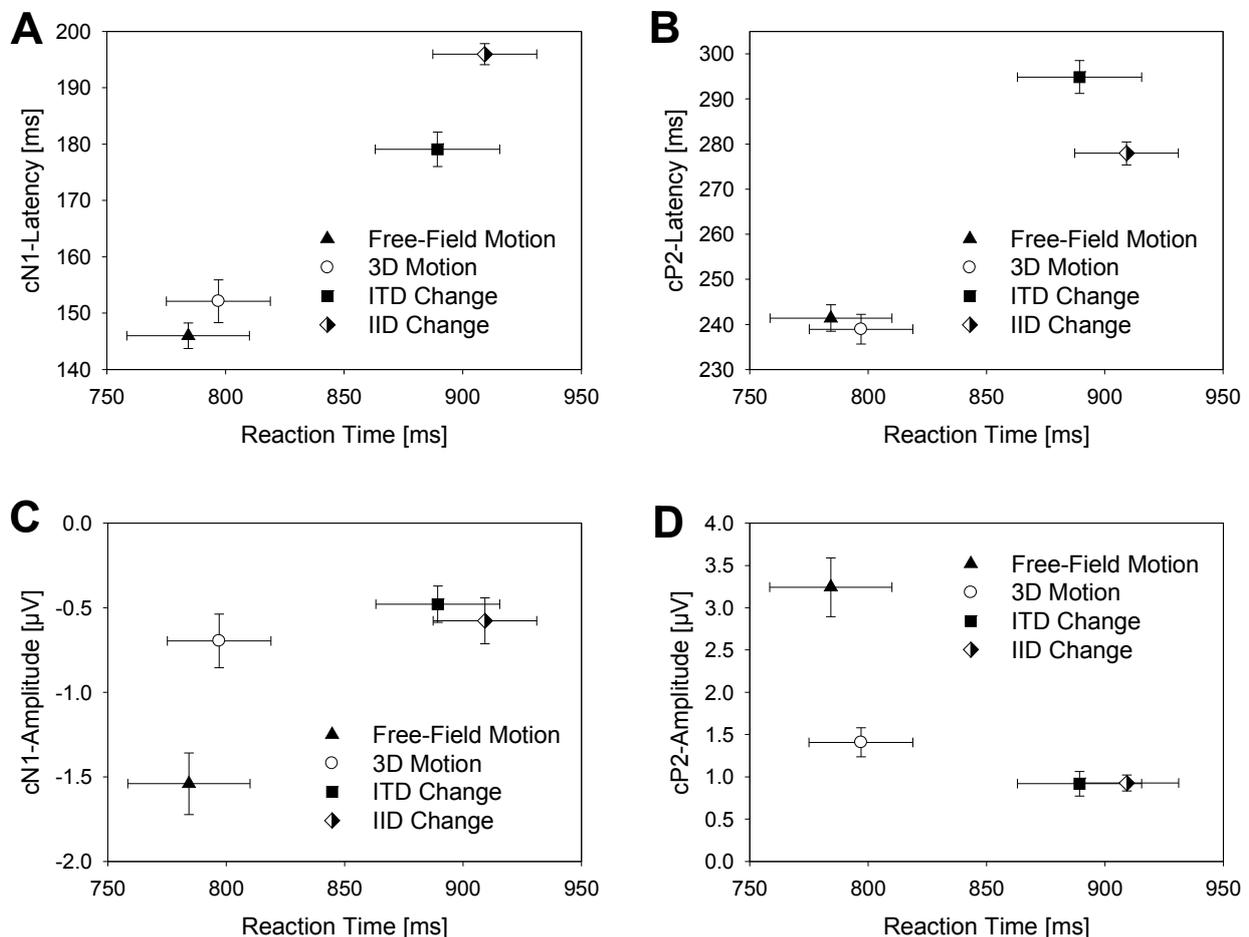
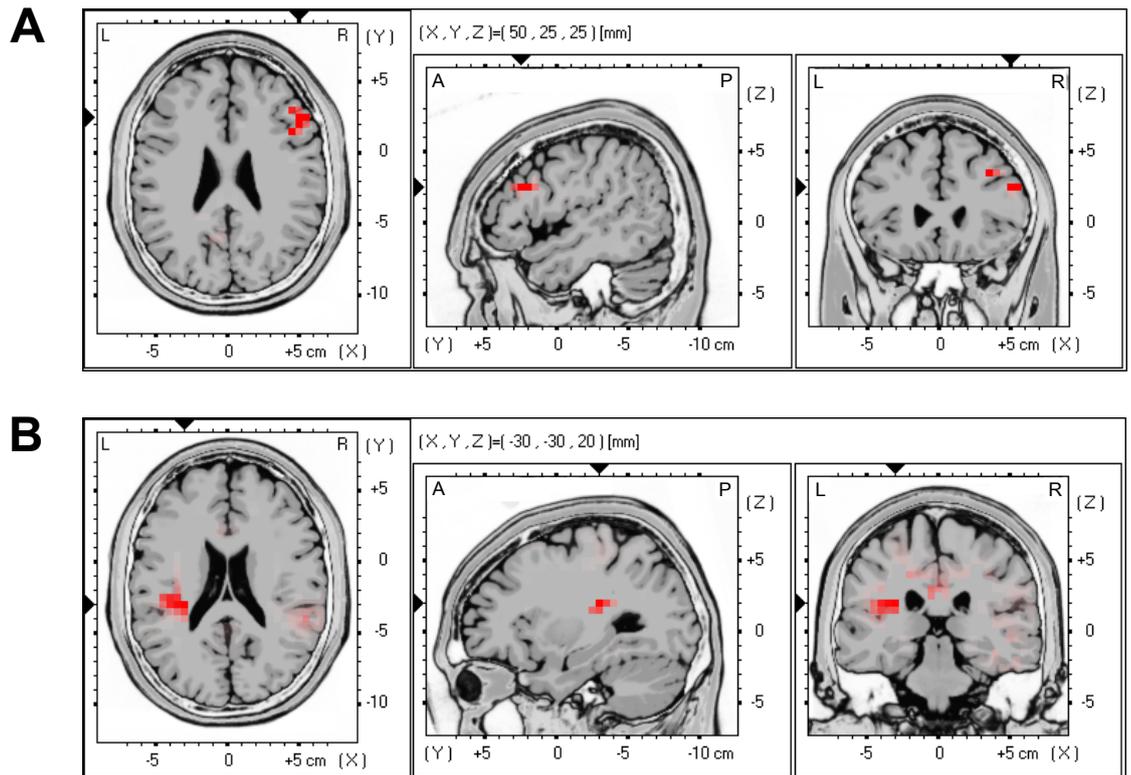


Figure 3: Activations of brain regions as revealed by contrasting the components of the motion onset response (A) cN1 and (B) cP2 to free-field motion and virtual 3D motion (statistical cut-offs cN1: $t \geq 6.99$, cP2: $t \geq 8.76$, $p < 0.01$). Data from all participants are projected onto the relevant axial (left), sagittal (middle), and coronal (right) slices of an averaged normalized brain (MNI-template, sLORETA).



Conclusions

Differences in RTs indicated that the direction of free-field motion and virtual 3D motion is detected faster than shifts in IID or ITD simulating sound motion. Also, faster RTs on free-field motion and virtual 3D motion were associated with shorter latencies of the MOR, suggesting a close relationship between cortical motion processing and behavioral performance. Thus, spatially enriched motion stimuli were processed faster than spatially impoverished, purely binaural changes. This benefit may be based on the simultaneous changes in both ITD and IID cues and on spectral cues that may have contributed to performance facilitation. No RT differences occurred between free-field and virtual 3D motion suggesting that virtual 3D sound generated via generic HRTF filters is well suited for simulating sound motion in the horizontal dimension.

However, free-field motion elicited a much stronger MOR than did virtual 3D motion. Cortical source localization contrasting free-field motion with virtual 3D motion suggested that the extra activation mainly resulted from contribution of those cortical areas that have been found to be associated with attention to motion [5] and sensorimotor action, such as intended cursor movements and immediate pointing operation [6, 7]. Thus, while behavioral performance did not differ between free-field and virtual 3D motion, electrophysiological responses to the onset of auditory motion suggested that virtual 3D sound generated via generic HRTF filters is insufficient to adequately simulate motion in the context of neural processing of auditory dynamic cues.

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