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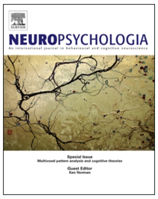

Differences in evoked potentials during the active processing of sound location and motion

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ABSTRACT

Difference in the processing of motion and static sounds in the human cortex was studied by electroencephalography with subjects performing an active discrimination task. Sound bursts were presented in the acoustic free-field between 47° to the left and 47° to the right under three different stimulus conditions: (i) static, (ii) leftward motion, and (iii) rightward motion. In an active oddball design, subject was asked to detect target stimuli which were randomly embedded within a stream of frequently occurring non-target events (i.e. 'standards') and rare non-target stimuli (i.e. 'deviants'). The respective acoustic stimuli were presented in blocks with each stimulus type presented in either of three stimulus conditions: as target, as non-target, or as standard. The analysis focussed on the event related potentials evoked by the different stimulus types under the respective standard condition. Same as in previous studies, all three different acoustic stimuli elicited the obligatory P1/N1/P2 complex in the range of 50-200 ms. However, comparisons of ERPs elicited by static stimuli and both kinds of motion stimuli yielded differences as early as ~100 ms after stimulus-onset, i.e. at the level of the exogenous N1 and P2 components. Differences in signal amplitudes were also found in a time window 300-400 ms ('*d*300-400 ms' component in '*motion*-minus-*static*' difference wave). For motion stimuli, the N1 amplitudes were larger over the hemisphere contralateral to the origin of motion, while for static stimuli N1 amplitudes over both hemispheres were in the same range. Contrary to the N1 component, the ERP in the '*d*300-400 ms' time period showed stronger responses over the hemisphere contralateral to motion termination, with the static stimuli again yielding equal bilateral amplitudes. For the P2 component a motion-specific effect with larger signal amplitudes over the left hemisphere was found compared to static stimuli.

The presently documented N1 components comply with the results of previous studies on auditory space processing and suggest a contralateral dominance during the process of cortical integration of spatial acoustic information. Additionally, the cortical activity in the 'd300-400 ms' time period indicates, that in addition to the motion origin (as reflected by the N1) also the direction of motion (leftward/rightward motion) or rather motion termination is cortically encoded. These electrophysiological results are in accordance with the 'snap shot' hypothesis, assuming that auditory motion processing is not based on a genuine motion-sensitive system, but rather on a comparison process of spatial positions of motion origin (onset) and motion termination (offset). Still, specificities of the present P2 component provides evidence for additional motion-specific processes possibly associated with the evaluation of motion-specific attributes, i.e. motion direction and/or velocity which is preponderant in the left hemisphere.

1. Introduction

In neuropsychological and functional imaging studies as well as in studies in animal models it is debated whether moving and stationary sounds are processed in at least partly distinct neuronal systems which would ask for the existence of specialized neuronal motion processing circuitries (e.g. Hall, Hart, & Johnsrude, 2003). The alternative hypothesis postulated that auditory motion processing is achieved by location tuned neurons (snapshot theory; Grantham, 1986). Accordingly, auditory motion processing would not be based on a genuine motion-sensitive system, but rather on a comparison process of spatial positions of motion origin (onset) and motion termination (offset) (e.g. Middlebrooks & Green, 1991; Salminen, Tiitinen, & May, 2012). Still, neurophysiological in vivo studies in different animal models documented neurons sensitive to moving sounds at different levels of the

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ascending auditory pathway (e.g. Ahissar, Ahissar, Bergman, & Vaadia, 1992; McAlpine, Jiang, Shackleton, & Palmer, 2000; Stumpf, Toronchuk, & Cynader, 1992; Wagner & Takahashi, 1992; Wilson & O'Neill, 1998). However, to date studies are rare which demonstrated that neurons selectively responded to auditory motion but not to stationary sounds (Sovijärvi & Hyvärinen, 1974). Also studies in humans do not reveal a unified picture: when compared with a silent baseline, moving sounds produce bilateral activation in primary and non-primary regions of the auditory cortex, as stationary sounds do (e.g.; Bremmer et al., 2001; Lewis, Beauchamp, & DeYoe, 2000). Correlation of activation to stationary and moving sounds for the most part did not yield significant differences (Bremmer et al., 2001; Lewis et al., 2000, review Hall et al., 2003). However, human neuroimaging studies do provide evidence for a specialized motion processing system by showing selective activation to moving sounds in circumscribed cortical regions (Baumgart, Gaschler-Markefski, Woldorff, Heinze, & Scheich, 1999; Griffiths, Bench, & Frackowiak, 1994; Griffiths et al., 1998; Warren, Zielinski, Green, Rauschecker, & Griffiths, 2002). Furthermore, the perception of sound motion was found to be selectively impaired (i) in the hemifield contralateral to the side which underwent hemispherectomy (Poirier, Lassonde, Villemure, Geoffroy, & Lepore, 1994), (ii) in patients suffering from right hemisphere stroke (Griffiths et al., 1996), (iii) in patients suffering from left hemispheric lesions (Clarke, Bellmann, Meuli, Assal, & Steck, 2000) as well as (iv) in one patient suffering from a resection of the right anterior temporal lobe and the right posterior superior temporal gyrus (Ducommun et al., 2004).

Also EEG and MEG techniques were used to acquire cortical responses to both static and motion stimuli (Altman & Vaitulevich, 1990; Ducommun et al., 2002; Getzmann, 2009, 2011; Getzmann & Lewald, 2009, 2011; Kreitewolf, Lewald, & Getzmann, 2011; Krumbholz, Hewson-Stoate, & Schönwiesner, 2007; Xiang et al., 2002; Xiang, Holowka, Ishii, Wilson, & Chuang, 2004; Xiang et al., 2005). Here, the focus was on the acoustic feature-sensitive N1 and P2 components, which were tested for their sensitivity to the mode of stimulation (*motion* or *static*) and/or the location of stimuli (Altman & Vaitulevich, 1990; Palomäki, Tiitinen, Makinen, May, & Alku, 2005; Tiitinen et al., 2006). Evidence for distinct motion processing derived from greater amplitudes of N1 and P2 components to motion (simulated by dynamic ITD variations in headphone stimulation) versus static auditory stimuli (Altman & Vaitulevich, 1990).

Ducommun et al. (2002) directly compared cortical responses to auditory location and motion perception (also simulated by variable ITDs in headphone stimulation), and focussing on late cortical responses (250–900 ms after stimulus onset), they revealed different activation topographies between motion discrimination and spatial localization. However, the processing of isolated acoustic cues, i.e. ITDs, cannot be put on a level with the processing of externalized auditory spatial information and thus a differentiation between both modes of signal processing – lateralization versus localization – still waits to be explored. This objection even more so holds for the processing of motion sounds.

Accordingly, the present EEG study was performed in the acoustic free field and the emphasis was laid on (i) potential divergent cortical processes for static and motion stimuli and on (ii) functional hemispheric asymmetry. The analysis focussed on the exogenous components P1–N1–P2 and also on later ERP components. In contrast to previous studies, static and moving free field stimuli were employed to ensure a natural spatial-acoustic setting with congruent changes of ITD, IID and spectral modulations resulting in externalized precepts of acoustic sounds. The experimental design took into account that auditory motion stimuli have at least two features which may be processed in parallel. On the one hand, the (basic) acoustic signal characteristics, i.e. sound frequency and intensity and on the other hand dynamically changing signal attributes, i.e. sound velocity and sound direction arising by dynamic change of interaural stimulus differences (ITD, IID) (Xiang et al., 2002). The cortical processing of static sounds was contrasted with that of moving sounds with defined velocity, while taking specific care that the basic stimulation parameters were kept constant. The analysis focussed on the N1 and P2 components and also on later ERP components (around 300 ms after stimulus onset). Deviating N1 and P2 amplitudes for motion relative to static stimuli would provide evidence for a particular processing of acoustic motion information (cf. Altman & Vaitulevich, 1990). Additionally, different cortical responses for the respective stimulus conditions were also anticipated in later time windows around 300 ms after stimulus onset indicating the involvement of distinct cortical networks in the processing of moving and static sounds (cf. Ducommun et al., 2002).

2. Methods

2.1. Subjects

Fourteen right-handed healthy subjects (eight females) with a mean age of 24.1 years (standard deviation = 3.02 years) with normal hearing and no history of hearing disorders or neurological diseases participated in the experiments. All subjects gave informed written consent and were compensated for their participation. This study conformed to the Code of Ethics of the World Medical Association and was approved by the local Ethics Committee of the University of Leipzig.

2.2. Setup and stimuli

The experiment employed an 'active' oddball design with 83.3% standard, 8.3% deviant, and 8.3% target probabilities. The analysis presented in this report is restricted to cortical responses evoked by standard stimuli; deviant and target related effects will be the subject of separate evaluations. Stimuli were low-frequency (0.3–1.3 kHz) Gaussian band-passed noise bursts of 250 ms duration (including 10 ms ramps) presented with an inter-stimulus interval of 1000 ms. Stimuli were presented in an echo- and sound attenuated room free field setup (45 m^2, Industrial Acoustic). Twenty-three active loudspeakers (FRS8 4 Ohm, Visaton) were arranged in a circular section (radius 2.35 m, with the head of the subject in the center position) spanning the front of the subject from 47° left to 47° right (–47° and +47°, respectively). Each loudspeaker was driven by a separate power amplifier (KEMO-M032) and was equilibrated individually. For this, the transmission spectrum was measured using Bruel & Kjaer measuring amplifier (B&K 2610), microphone (B&K 2669, pre-amplifier B&K 4190) and a real-time signal processor (RP 2.1, Tucker Davis Technology, TDT). For each speaker a calibration file war generated and later used to generate acoustic stimuli with flat spectra across the stimulus frequency range. Stimulus generation and test procedures were programmed in Matlab 6.1. (The MathWorks Inc, Natick, USA).

During testing, all stimuli were presented at 50 dB SL (sensation level); the individual thresholds for the respective stimuli (static and motion stimuli [see below]) were determined at the beginning of each experimental session. The actual intensities were on average 61.5–62 dB SPL for both static and moving sounds as measured by using the Brüel & Kjær measuring amplifier (B&K 2610), a microphone (B&K 2669, pre-amplifier B&K 4190) and a real-time signal processor (RP 2.1, System3, Tucker Davis Technologies, TDT). Additionally a stimulus level roving was introduced (increase between 0 and 5 dB) to prevent any effects which could be attributed to loudness cues due to minute differences in the position of the loudspeakers.

Three stimulus types were used: (i) static stimulus (*Stat*), (ii) leftward motion stimulus (*LeMo*), and (iii) rightward motion stimulus (*RiMo*) (Fig. 1).

Static stimuli were generated by jointly activating 23 frontal loudspeakers spanning from –47° to +47°. Simulation of motion stimuli was generated by successive stimulus presentation through 23 neighboring loudspeakers equally spaced at 4.3° from +47° to –47° for "leftward motion" and in opposite direction for "rightward motion". Steadily moving sound percepts were achieved by adjusting the ratio of sound intensity between the respective two neighboring loudspeakers (by linear cross-fading of the output voltages) in the sequence of successively activated loudspeakers. The overlap time from two adjacent loudspeakers was ~22.7 ms (except for the first and the last speaker, where the overlap was ~11.4 ms, see Fig. 1). Before each experiment, a pre-test block was run, in which the three stimulus types were presented with equal frequency of occurrence, respectively (total of 30 stimuli). After the pre-test block subjects were interviewed and asked, what kind of percepts they could differentiate. All subjects reported that they perceived either static or uniformly leftward or rightward motion sounds, and that the different stimulus types had been equally loud.