



## Research paper

## The effect of spatial adaptation on auditory motion processing

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## ABSTRACT

The effect of acoustic pre-stimulation on cortical processing of subsequent sound motion was investigated in free-field space, using electroencephalography and a psychophysical motion-discrimination task. Subjects heard sound stimuli that moved from a central position ( $0^\circ$ ) to the left or right. The onset of motion was preceded by either stationary sound at  $0^\circ$  or spatially scattered sound on the left ( $0$  to  $-32^\circ$ ), right ( $0$ – $32^\circ$ ), or both ( $-32$  to  $32^\circ$ ) sides. Following stationary sound, the start of auditory motion elicited a motion-specific onset response as described in previous studies. Following scattered sound, the amplitude of the motion-onset response was lower and reaction times in motion discrimination were longer than with the stationary pre-stimulus. Both these effects were most pronounced when the pre-stimulation by scattered sound was on the same side as the motion, whereas effects were only weak when pre-stimuli and motion were on different sides. These results are compatible with the view that spatial adaptation plays a role in auditory motion perception, and that motion processing could be triggered by release of adaptation of populations of location-specific neurons.

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## 1. Introduction

In natural environments, the ability to perceive sound motion is a key feature of hearing. Several studies have focused on the cortical mechanisms of auditory motion perception. Employing electro- and magneto-encephalography (EEG/MEG) it was revealed that the brain's response to moving sound consists of a series of deflections specific to processing of motion (Altman and Vaitulevich, 1990; Mäkelä and McEvoy, 1996; Ducommun et al., 2002; Jerger and Estes, 2002; Xiang et al., 2002). In particular, the analysis of auditory evoked potentials (AEPs) to static and moving sounds suggested a modular organization of motion processing, consisting of an initial analysis of sound features and a subsequent processing of sound motion (Ducommun et al., 2002).

In these previous EEG/MEG studies, AEPs to motion onset were related to AEPs to the onset of stationary sound. Thus, cortical processing of sound onset may have interfered with genuine

motion processing. In order to exclude this possible confound a modified paradigm has been introduced, in which the onset of motion is delayed relative to the sound-energy onset (Krumbholz et al., 2007). This delayed-motion paradigm revealed that the onset of motion in an otherwise continuous sound elicits a prominent AEP that differs in morphology and topography from the AEP to sound-energy onset: The so-called motion-onset response (MOR) starts later than the energy-onset response (EOR) and is lateralized to the hemisphere contralateral to the presentation of motion (Krumbholz et al., 2007; Getzmann and Lewald, 2010a). Moreover, there is a close relationship between the MOR and behavioral performance in motion detection. In particular, higher motion velocity was associated with both larger (and earlier) MORs and shorter reaction times. The MOR has therefore been interpreted to be a neurophysiological indicator of motion sensitivity (Getzmann, 2009).

While the delayed-motion paradigm appears as an elegant way to distinguish between EOR and MOR, the question arises whether the delay of motion onset in the otherwise continuous sound might affect motion processing as such. Specifically, it is possible that the stationary spatial information immediately preceding the motion onset could modulate the MOR. In a previous psychophysical study, the introduction of a motion-onset delay reduced reaction times (RTs) in a motion detection task, suggesting that a stationary sound presented during motion-onset delay accelerated motion perception (Getzmann, 2008). This is compatible with the assumption of

*Abbreviations:* AEP, auditory evoked potential; ANOVA, analysis of variance; EEG, electroencephalography; EOG, electro-oculography; EOR, energy-onset response; LED, light-emitting diode; MEG, magnetoencephalography; MOR, motion-onset response; RMS, root mean square; RT, response time.

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an early integration of acoustic stimulus features (e.g., pitch or space) within a temporal window of approximately 200 ms width (e.g., Yabe et al., 1998, 2001; Ducommun et al., 2002).

The hypothesis that auditory motion processing is, unlike visual motion processing, based on the analysis of successive instantaneous location estimates has long been set forth (Grantham, 1986). Currently, this idea is receiving increasing support by physiological findings. In the mammalian auditory midbrain, motion sensitivity has been related to a process of adaptation-of-excitation in location-tuned neurons, in which motion perception is triggered by the release of adaptation in a map of ("stationary") auditory space (McAlpine et al., 2000; McAlpine and Palmer, 2002; Ingham et al., 2001). Whether comparable processes exist also in cortex is, on the one hand, debatable since a place code for auditory space, composed of location-tuned neurons, has so far not been found in cortical structures. On the other hand, in the human cortex, evidence of location-specific adaptation effects was provided by a recent MEG study revealing that the N1m response to a probe sound is substantially attenuated by a preceding adaptor sound presented in the same hemispace as the probe (Salminen et al., 2010). Using MEG, location-specific adaptation was also found in a task in which listeners attended to sound location; these feature-specific attention effects may arise from enhanced tuning of receptive fields of task-relevant neuronal populations (Ahveninen et al., 2006).

In the context of motion processing, these findings may imply that in a delayed-motion paradigm stationary sound presented during the motion-onset delay induces spatial short-term adaptation of location-tuned populations of neurons (though the neuronal substrate of this hypothetical mechanism is still unknown). The motion would recruit newly still non-adapted populations of neurons, and the release of adaptation would form the neural basis of the MOR. Assuming a functional aspect in motion perception, the contrast between adapted and non-adapted populations could subserve the faster detection of sudden spatial changes in the auditory environment.

In order to test this hypothesis, the present study was focused on the effect of spatial adaptation by a preceding sound stimulus on the cortical processing of subsequent auditory motion. AEPs were recorded while listeners were presented with sounds that started moving from a central position. A delayed-motion paradigm was used, in which a (non-moving) pre-motion sound stimulus was assumed to act as an adaptor for the subsequent motion stimulus. Unlike earlier studies, two different types of pre-motion stimuli were presented: (1) stationary sound located at the starting position of motion (as previously used in the delayed-motion paradigm); and (2) a spatially distributed "sound array" that spanned an arc of horizontal space that was centered to the starting position of the subsequent motion (i.e., straight ahead), or to the left or right of the starting position. We assumed that this "scattered sound" would induce effects of pre-motion adaptation in a distributed population of spatially-sensitive neurons tuned to a broad range in azimuth, while the stationary sound would result in adaptation of a more limited neuronal population tuned to the narrow range around the adaptor position. Assuming furthermore a mechanism of release-from-adaptation, our expectation was that location-specific adaptation by preceding stationary sound presented at the starting position of motion has stronger effects on the processing of the motion onset than broadly-tuned spatial adaptation by scattered sound centered to the starting position. This hypothesis was based on the assumption that the responsiveness of spatially-sensitive neurons should differ between adapted and non-adapted populations: Specifically, the release from sharply-tuned location-specific adaptation (induced by a single stationary sound source) should be more pronounced than the release from broadly-tuned

and thus less effective adaptation (induced by a scattered sound from multiple locations). Given that the MOR reflects the sum of the neuronal activity related to the motion onset, the MOR was expected to be stronger with stationary, than with scattered, pre-motion sound when both these stimuli were centered to the starting point of motion. Moreover, we expected that after a lateral scatter sound (to the left or right of the motion-onset position) the MOR elicited by sound moving within the pre-stimulated hemispace should be lower in amplitude than the MOR elicited by sound moving in the non-pre-stimulated hemispace or the MOR preceded by stationary sound.

The scattered sound stimulus was designed in way that the extremely fast changes in the position of active loudspeakers were not perceived as illusory "random motion" of a sound source (see Section 2.2). The rationale was that our hypothesis described above implied the involvement of location-specific ("stationary") neurons in the emergence of adaptation, but did not necessarily require the assumption of motion-specific neurons, that is, neurons exhibiting a preference for a specific direction of motion while being insensitive to stationary sound. Even though for the human auditory system the existence of specific motion sensitivity remains still a matter of debate (for further discussion, see Smith et al., 2004, 2007), single subcortical and cortical cells showing such response properties have been found in animal studies (e.g. Spitzer and Semple, 1991; Moiseff and Haresign, 1992). Considering this, we aimed to minimize potential effects of motion-specific adaptation that could superpose the hypothesized processes of location-specific adaptation. Thus, if adaptation by scattered sound is observed, it may be related to populations of neurons concerned with stationary spatial analysis, rather than genuine motion processing.

In addition to the electrophysiological recordings, psychophysical performance in motion perception was explored in a reaction-time task, as we assumed a correspondence between MOR and behavioral measures of motion processing (Getzmann, 2009). Listeners discriminated as fast as possible the direction of motion. In analogy to the considerations mentioned above, it was expected that pre-motion scattered sound induces a deterioration in motion perception: the performance should be worse with motion in the (ipsilateral) hemispace of pre-motion scattered sound than with motion following stationary or contralateral scattered sound.

## 2. Materials and methods

### 2.1. Subjects

A total of 34 healthy subjects (mean age 25.6 years; range 19–42 years; 22 female) with normal hearing participated (16 in the psychophysical experiment, and 18 in the electrophysiological experiment). They were paid for their participation. Thirty-three subjects were right-handed and one subject (in the psychophysical experiment) was left-handed. This study conformed to the Code of Ethics of the World Medical Association (Declaration of Helsinki), printed in the *British Medical Journal* (18 July 1964). All subjects gave their informed consent to participate in the study, which was approved by the Ethical Committee of the Medical Faculty of the Ruhr University Bochum.

### 2.2. Apparatus, stimuli and procedure

The listener sat on a vertically adjustable chair in a dimly lighted, anechoic room (4.4 m wide × 5.4 m long × 2.1 m high), which was insulated by 40 cm (height) × 40 cm (depth) × 15 cm (width at base) fiberglass wedges on each of the six sides. A suspended mat of steel wires served as floor. The ambient background noise

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