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Electrophysiological correlates of auditory change detection and change deafness in complex auditory scenes

Sebastian Puschmann ^{a,*}, Pascale Sandmann ^b, Janina Ahrens ^a, Jeremy Thorne ^b, Riklef Weerda ^a, Georg Klump ^{c,d}, Stefan Debener ^{b,d}, Christiane M. Thiel ^{a,d}

- ^a Biological Psychology, Department of Psychology, Carl-von-Ossietzky Universität Oldenburg, Oldenburg, Germany
- ^b Neuropsychology, Department of Psychology, Carl-von-Ossietzky Universität Oldenburg, Oldenburg, Germany
- c Animal Physiology and Behaviour, Department of Biology and Environmental Sciences, Carl-von-Ossietzky Universität Oldenburg, Oldenburg, Germany
- ^d Research Center Neurosensory Science, Carl-von-Ossietzky Universität Oldenburg, Oldenburg, Germany

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ABSTRACT

Change deafness describes the failure to perceive even intense changes within complex auditory input, if the listener does not attend to the changing sound. Remarkably, previous psychophysical data provide evidence that this effect occurs independently of successful stimulus encoding, indicating that undetected changes are processed to some extent in auditory cortex. Here we investigated cortical representations of detected and undetected auditory changes using electroencephalographic (EEG) recordings and a change deafness paradigm. We applied a one-shot change detection task, in which participants listened successively to three complex auditory scenes, each of them consisting of six simultaneously presented auditory streams. Listeners had to decide whether all scenes were identical or whether the pitch of one stream was changed between the last two presentations. Our data show significantly increased middle-latency Nb responses for both detected and undetected changes as compared to no-change trials. In contrast, only successfully detected changes were associated with a later mismatch response in auditory cortex, followed by increased N2, P3a and P3b responses, originating from hierarchically higher non-sensory brain regions. These results strengthen the view that undetected changes are successfully encoded at sensory level in auditory cortex, but fail to trigger later change-related cortical responses that lead to conscious perception of change.

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Introduction

Human listeners are experienced in handling complex auditory stimulation. Despite this, intense changes in auditory input, wellabove the sensory detection threshold, can sometimes remain undetected (Backer and Alain, 2012; Cervantes Constantino et al., 2012; Dalton and Fraenkel, 2012; Eramudugolla et al., 2005, 2008; Fenn et al., 2011; Gregg and Samuel, 2008, 2009; Gregg and Snyder, 2012; McAnally et al., 2010; Pavani and Turatto, 2008; Vitevitch, 2003; Vitevitch and Donoso, 2011). This change deafness is assumed to originate from restricted attention capacities, as the effect increases with enlarging scene size and can be prevented when the listener's attention is directed to the changing stream (Eramudugolla et al., 2005). Change deafness represents the auditory counterpart of change blindness, which describes an error to detect a salient change in a complex visual setting (Beck et al., 2001, 2006; Busch et al., 2010a,b; Huettel et al., 2001; Pessoa and Ungerleider, 2004; Pourtois et al., 2006; Rensink, 2002; Simons and Rensink, 2005). Similarities

E-mail address: sebastian.puschmann@uni-oldenburg.de (S. Puschmann).

and differences between effects in both sensory modalities are discussed in recent articles by Gregg and Snyder (Gregg and Snyder, 2012; Snyder and Gregg, 2011).

Remarkably, several studies on change deafness reported that this effect occurs despite successful encoding of the presented scene, so that participants could subsequently retrieve information about the presented auditory scene even if they did not detect a change (Fenn et al., 2011; Gregg and Samuel, 2008). However, other work could not find any evidence for an intact memory representation of undetected changes (McAnally et al., 2010). Corresponding with the view that even undetected sounds are represented to some extent in the auditory system, electrophysiological studies on auditory target detection under informational masking have shown similar middlelatency responses to both detected and undetected targets up to the P1m component (Gutschalk et al., 2008; Königs and Gutschalk, 2012), indicative of common early sensory processing of detected and undetected target sounds. In addition, recent electroencephalography (EEG) experiments also reported change-related amplitude differences between an established standard sound and an acoustic deviant in auditory middle-latency responses (Grimm et al., 2011; Slabu et al., 2010). This effect was suggested to reflect feature-specific differences in sensory processing between the standard and the

 $^{^{\}ast}$ Corresponding author at: Carl-von-Ossietzky Universität Oldenburg, 26111 Oldenburg, Germany. Fax: +49 441 798 3848.

deviant, since it was shown to depend critically on the changing sound feature (Alho et al., 2012; Grimm et al., 2011; Leung et al., 2012). However, these studies did not investigate responses to undetected changes.

Acoustic deviance is usually associated with a significant negative signal deflection at about 100-200 ms after stimulus onset (Näätänen et al., 2011). It is argued that this mismatch response arises either from: i) a release from N1 adaptation caused by differences in sensory processing between the deviant and an established standard sound, or ii) an error signal indicating a mismatch between actual auditory input and a predictive model of future auditory input stored in sensory memory (Bendixen et al., 2012; Garrido et al., 2009; May and Tiitinen, 2010). Irrespective of its origin, this mismatch signal is assumed to trigger further attentive processing of change, in particular within the insula and the anterior cingulate cortex, as indexed by central N2b and P3a components (Menon and Uddin, 2010). Later conscious processing of changes or target stimuli additionally involves memory processes that are typically reflected in the P3b response (Polich, 2007). Several previous studies have reported auditory cortex mismatch signals in response to unperceived deviations in the auditory input (Allen et al., 2000; Van Zuijen et al., 2006), indicating that unperceived changes are still represented at this level of processing. In contrast, recent EEG data on change deafness have shown a negative signal deflection at this latency range for detected changes, but not under change deafness (Gregg and Snyder, 2012).

If stimulus encoding does function correctly under change deafness, we would expect similar early signal deviations for detected and undetected changes, related to the processing of the changed stimulus feature. Here we therefore used EEG to systematically compare middle-latency responses to detected changes, to no-change trials, and under change deafness. We applied a one-shot change detection paradigm, in which participants had to detect pitch changes in complex auditory scenes. The auditory scenes consisted of six simultaneously presented streams, differing in pitch, rhythm, and sound source location. Changes were induced by increasing the frequency of one stream, whereas all other streams remained identical. Since previous EEG data have shown early pitch-change effects in the Nb middle-latency response (Alho et al., 2012; Leung et al., 2012; Marmel et al., 2011), elicited about 30-40 ms after stimulus onset, we also expected significant effects related to sensory processing of the changing pitch information at this latency. As a second aim of our analysis, we examined whether undetected changes, if represented at the level of early sensory encoding in auditory cortex, also evoke a later mismatch response in auditory cortex, but fail to trigger further attentive change detection processes associated with N2b, P3a, and P3b responses.

Material and methods

Subjects

Twenty volunteers (12 female, age range: 20–30 years, average age: 24 ± 2 years) participated in the experiment. All subjects were right-handed, had normal hearing (hearing-loss less than 15 dB HL between 100 Hz and 8 kHz), and no history of neurological disorder. The study was conducted in accordance with the Declaration of Helsinki (World Medical Association, 2008). All experimental procedures were approved by the local ethics committee of the University of Oldenburg, and written informed consent was obtained from the participants. Two subjects were removed from the dataset due to very low numbers of undetected changes during the EEG recordings (less than 10% of all trials containing a physical change in auditory input), resulting in a sample size of 18 participants included in the statistical analyses.

Experimental task

We adapted a one-shot change detection paradigm already used in a previous fMRI experiment on change deafness (Puschmann et al., 2013). As depicted in Fig. 1A, participants listened in each trial to three consecutively presented complex auditory scenes of 666 ms duration, separated by 666 ms of silence. The auditory scenes consisted of six simultaneously presented streams differing in pitch, rhythm, and sound source location, and lacking any kind of semantic information. In each trial, the first two scenes were identical and could be followed either by a third identical scene or by a deviant, in which the pitch of one stream was changed. Listeners were instructed to indicate as fast as possible whether the third auditory scene was identical to the previous scenes or not. Key-presses had to be made with the index finger ("change") or middle finger ("no change") of the right hand. No feedback on the correctness of the answer was provided. The response interval was restricted to 2000 ms after offset of the third scene. Participants were instructed to fixate a cross presented centrally on a screen during the whole task. The inter-trial interval was jittered randomly in steps of 1 ms between 670 ms and 1670 ms, resulting in a total trial duration of 6000-7000 ms. The experimental task was programmed using Presentation (Neurobehavioral Systems, Albany, CA, USA).

Stimuli

As shown in Fig. 1B, the complex auditory scenes consisted of six simultaneously presented streams of 666 ms duration. Each stream consisted of a series of band-pass-filtered noise stimuli of short (1/48 s), intermediate (1/24 s), or long (1/12 s) duration, interrupted by intervals of silence (also 1/12 s, 1/24 s, or 1/48 s in duration). The first sound of each stream was presented at t=0 ms. Sounds were faded in and out using 5 ms Hanning onset- and offset ramps. The noise bands were centred at 200 Hz, 400 Hz, 800 Hz, 1600 Hz, 3200 Hz, and 6400 Hz, with stimulus bandwidths set to 25% of the respective centre-frequency. Sound source locations were separated in space using head-related impulse responses from dummy-head recordings obtained by Kayser et al. (2009) (anechoic room recordings, azimuth: -90° , -60° , -30° , $+30^{\circ}$, $+60^{\circ}$, $+90^{\circ}$, source elevation: 0° , source distance: 300 cm).

To prevent listeners from becoming too familiar with the auditory input, different versions of the standard scene were generated. For each stream, we created an additional "high pitch" version by increasing the centre frequency of the bandpass-filtered noise sounds. Rhythm and sound source location remained identical. Randomly combining these high- and low-pitched versions of the auditory streams resulted in 64 different scenes.

Deviating scenes were then created by switching one stream from the low- to the high pitch version while the rest of the scene remained identical. The frequency differences between low- and high pitch versions were adjusted individually for each listener using a staircase procedure converging at a hit rate (i.e., rate of successfully detected changes) of 70.7% (see next section for more details).

All stimuli were created using MATLAB (The MathWorks, Inc., Natick, MA, USA) and presented to the participants via E-A-RTONE 3A insert earphones (E-A-R Auditory Systems, Indianapolis, IN, USA) at a level of about 75 dB SPL. Within each scene the streams were matched for loudness using loudness level contours (ISO 226:2003).

Procedure

The experiment consisted of four sessions and was conducted on four consecutive days. In the first session, participants underwent training to get used to the complex auditory stimulation and to minimize learning-related changes in performance during the actual experiment. The training consisted of ten blocks of 48 trials. Between blocks, participants were allowed to pause the experiment. Half of the trials contained no change, in the other half the pitch of one stream was increased between the second and third scene presentation. The number of change-trials was identical for each stream. Change

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