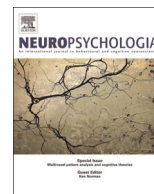




ELSEVIER

Contents lists available at ScienceDirect

Neuropsychologia

journal homepage: www.elsevier.com/locate/neuropsychologia

Involvement of the human midbrain and thalamus in auditory deviance detection



Raffaele Cacciaglia^{a,b}, Carles Escera^{a,b,*}, Lavinia Slabu^{a,b}, Sabine Grimm^{a,b}, Ana Sanjuán^{c,d}, Noelia Ventura-Campos^c, César Ávila^c

^a Institute for Brain, Cognition and Behavior (IR3C), University of Barcelona, Passeig de la vall d'Hebron 171, 08035 Barcelona, Catalonia, Spain

^b Cognitive Neuroscience Research Group, Department of Psychiatry and Clinical Psychobiology, University of Barcelona, Passeig de la vall d'Hebron 171, 08035 Barcelona, Catalonia, Spain

^c Department of Psychology, University Jaume I, Avenguda de Vicent Sos Baynat, 12 071 Castellón de la Plana, Spain

^d Language Group Wellcome Trust Centre for Neuroimaging University College of London, 12 Queen Square, WC1N 3BG London, United Kingdom

ARTICLE INFO

Article history:

Received 6 August 2014

Received in revised form

29 December 2014

Accepted 1 January 2015

Available online 1 January 2015

Keywords:

Auditory deviance detection

Stimulus-specific adaptation

fMRI

Inferior colliculus

Medial geniculate body

ABSTRACT

Prompt detection of unexpected changes in the sensory environment is critical for survival. In the auditory domain, the occurrence of a rare stimulus triggers a cascade of neurophysiological events spanning over multiple time-scales. Besides the role of the mismatch negativity (MMN), whose cortical generators are located in supratemporal areas, cumulative evidence suggests that violations of auditory regularities can be detected earlier and lower in the auditory hierarchy. Recent human scalp recordings have shown signatures of auditory mismatch responses at shorter latencies than those of the MMN. Moreover, animal single-unit recordings have demonstrated that rare stimulus changes cause a release from stimulus-specific adaptation in neurons of the primary auditory cortex, the medial geniculate body (MGB), and the inferior colliculus (IC). Although these data suggest that change detection is a pervasive property of the auditory system which may reside upstream cortical sites, direct evidence for the involvement of subcortical stages in the human auditory novelty system is lacking. Using event-related functional magnetic resonance imaging during a frequency oddball paradigm, we here report that auditory deviance detection occurs in the MGB and the IC of healthy human participants. By implementing a random condition controlling for neural refractoriness effects, we show that auditory change detection in these subcortical stations involves the encoding of statistical regularities from the acoustic input. These results provide the first direct evidence of the existence of multiple mismatch detectors nested at different levels along the human ascending auditory pathway.

© 2015 Elsevier Ltd. All rights reserved.

1. Introduction

In order to detect relevant information, our sensory systems continuously monitor the external environment. This is particularly true for the auditory system, which receives time-varying signals that are transient in nature and thus require to be tracked over time. To achieve this, the auditory system automatically extracts statistical regularities from the ongoing acoustic input and generates predictions enabling to detect unexpected deviant sounds (Bendixen et al., 2012; Winkler et al., 2009). Such automatic change detection promotes the formation of meaningful auditory objects (Bizley and Cohen, 2013; Griffiths and Warren, 2004) and drives a rapid attention shift towards potentially

relevant stimuli (Escera et al., 1998; Escera and Corral, 2007). Auditory deviance detection has traditionally been associated to a particular brain event occurring at 150–250 ms from change onset, the Mismatch Negativity (MMN) of the event-related potentials (ERPs) (Näätänen et al., 1978, 2007), generated in supratemporal (Recasens et al., 2014; Maess et al., 2007) and prefrontal areas (Deouell, 2007; Rinne et al., 2000).

Yet, a convergent body of evidence suggests that regularity violations can be detected earlier and in lower stations of the auditory hierarchy (Escera and Malmierca, 2014). Indeed, mismatch responses for simple deviant features have been observed at latencies much shorter than those of MMN, in different components of the middle latency response (MLR) of the human ERPs, peaking at 18–50 ms from stimulus onset (Escera et al., 2014; Grimm et al., 2011, 2012; Slabu et al., 2010a; Sonnadara et al., 2006), and in the complex auditory brainstem response (Slabu et al., 2012), suggesting the involvement of the human inferior colliculus (IC) in deviance detection. Animal single- and multi-unit

* Corresponding author at: Cognitive Neuroscience Research Group, Department of Psychiatry and Clinical Psychobiology, University of Barcelona. Passeig de la Vall d'Hebron 171, 08035 Barcelona, Catalonia, Spain. Fax: +34 934 021 584.

E-mail address: cescera@ub.edu (C. Escera).

recordings have shown that neurons in the primary auditory cortex of the cat (Ulanovsky et al., 2003), and in the medial geniculate body (MGB) and IC of the rat (Antunes and Malmierca, 2011; Malmierca et al., 2009; Pérez-González et al., 2005), display stimulus-specific adaptation (SSA), a reduction in neuronal firing rates for repetitive sounds, that is restored for rare stimuli. Moreover, a recent study employing functional magnetic resonance imaging (fMRI) showed that the IC significantly responded to rarely occurring auditory stimuli in rats (Gao et al., 2014). These animal and human data favor the idea of deviance detection being a ubiquitous and hierarchically organized property of the auditory pathway (Grimm and Escera, 2012). Yet the involvement of the human subcortical auditory system in deviance detection remains to be proven. Using event-related fMRI during a frequency oddball paradigm, we here report that auditory deviance detection occurs in the human auditory cortex, the MGB and the IC.

The underlying neural mechanisms of the MMN and more generally of auditory change detection are not yet fully understood. Two major theoretical accounts have been proposed within the past years: a former model that puts forward the formation of an auditory sensory memory based on the encoding of statistical regularities from the acoustic input (Näätänen et al., 2005), and a complementary view that ascribes deviance detection to a mechanism of release from neural adaptation (May and Tiitinen, 2010). Here, by implementing a random condition controlling for stimulus probability and the related neural refractoriness effects (cf., Schröger and Wolff, 1996), we show that change detection in the MGB and IC is likely based on a mechanism of regularity encoding and therefore cannot be explained by mere adaptation phenomena.

2. Materials and methods

2.1. Subjects

Twelve volunteer participants (7 female, mean age=27.5 years, standard deviation [SD]=3.4, 4 left-handed) took part in our experiment. None of them was under current or chronic medication. All participants had normal hearing, with a mean hearing threshold below 25 dB sound pressure level (dB-SPL), as assessed with binaural audiometric test using pure tones at five frequencies (250, 500, 1000, 3000, and 8000 Hz). The experimental protocol was approved by the Ethical Committee of the University of Barcelona and was in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki). Written informed consent was obtained before the experiment.

2.2. Stimuli

Stimuli consisted of 70 ms bursts of broadband noises with no rise and fall time, which were generated with the STIM software (Neurosoft, El Paso, TX, USA). They were band-pass filtered in steps of 500 Hz, from 500 to 1000 Hz (referred as S1), from 1000 to 1500 Hz (referred as S2), from 1500 to 2000 Hz (referred as S3), from 2000 to 2500 Hz (referred as S4) and from 2500 to 3000 Hz (referred as S5) (Fig. 1). These stimuli were chosen on the base of a previous study in which they elicited reliable auditory brainstem responses (Slabu et al., 2010a). All stimuli were binaurally delivered at a constant stimulus onset asynchrony (SOA) of 150 ms through a MR-compatible headphone set which attenuates scanner noise by ~15 dB (VisuaStim digital, Resonance Technology Inc., Northridge, CA, USA). Intensity was individually calibrated as being 20% above the discrimination level with respect to the scanner noise.

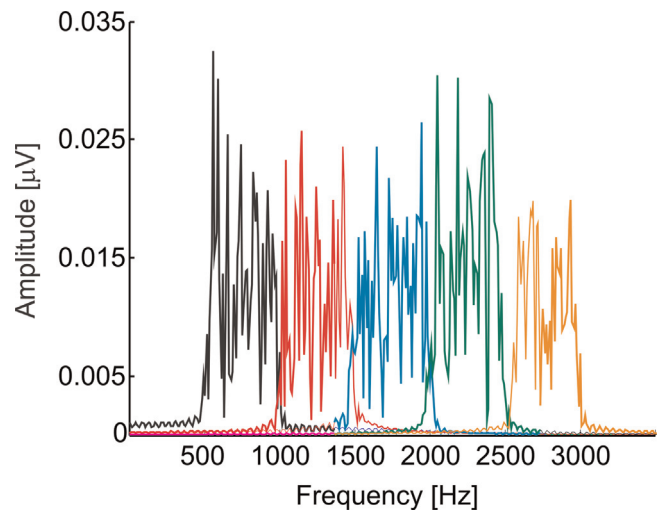


Fig. 1. Experimental stimuli. Amplitude spectrum of the five stimuli used in the experiment. Frequency bands are color-coded as follows: S1 (black), S2 (red), S3 (cyan), S4 (green), S5 (orange). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

2.3. Experimental design

The experiment consisted of a passive frequency oddball paradigm, which was followed by a random condition controlling for neural refractoriness effects. In the oddball paradigm, two stimuli were used, one of which (S1) acted as standard, while the other (S2) as deviant. Deviant sounds had a probability of 20% and were embedded in trains of 20 stimuli, occurring at pseudorandom positions in the second half of the train, that is, between the tenth and the twentieth sound. Specifically, deviant sounds were placed at positions 12, 14, 17, 20, or 10, 12, 15, 19, or 11, 13, 16, 18, in separate trains (Fig. 2a). These grouping arrangements produced three different deviant conditions which will be referred as DEV₁, DEV₂, and DEV₃, according to the positions occupied by S2. The inter-train interval was the same of the SOA (150 ms). One-hundred-twenty-five trains each containing 4 deviant and 16 standard stimuli (40 DEV₁, 40 DEV₂ and 45 DEV₃) were randomly interleaved with 125 trains containing 20 standards stimuli only (STD condition). In this way, a single functional volume could be acquired for each train (see *Image Acquisition* section). Thereafter, a control condition (CON), consisting of 125 consecutively presented trains of 20 stimuli was administered. In each train, five different stimuli (S1, S2, S3, S4 and S5) were randomly arranged equiprobably, with the only constrain that the stimulus (S2) acting as deviant during the oddball paradigm, preserved the same physical position also in the control condition, following the same grouping arrangements as in the DEV condition (see above) (Fig. 2b). Thus, also the CON condition could be further subdivided in CON₁, CON₂, and CON₃, each of these matching the respective DEV₁, DEV₂ and DEV₃ for the physical position of S2. Such a random condition was firstly introduced by Schröger and Wolff (1996) in order to control for refractoriness effects, as neural populations responsive to the CON stimuli presumably reveal the same degree of refractoriness as neurons responsive to the DEV stimuli. A similar control condition was already successfully implemented in event-related fMRI studies (e.g., Opitz et al., 2005; Szycik et al., 2013), in human ERPs (e.g., Jacobsen and Schröger, 2003) and animal multi-unit recordings (e.g., Taaseh et al., 2011).

Participants lay inside the scanner throughout the experiment. They were instructed to ignore the sounds and to watch a silent subtitled movie, which was projected using VisuaStim XGA goggles (VisuaStim digital, Resonance Technology Inc., Northridge, CA, USA).

Download English Version:

<https://daneshyari.com/en/article/7320377>

Download Persian Version:

<https://daneshyari.com/article/7320377>

[Daneshyari.com](https://daneshyari.com)