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Review

From sensation to percept: The neural signature of auditory event-related potentials

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ABSTRACT

An external auditory stimulus induces an auditory sensation which may lead to a conscious auditory perception. Although the sensory aspect is well known, it is still a question how an auditory stimulus results in an individual's conscious percept. To unravel the uncertainties concerning the neural correlates of a conscious auditory percept, event-related potentials may serve as a useful tool. In the current review we mainly wanted to shed light on the perceptual aspects of auditory processing and therefore we mainly focused on the auditory late-latency responses. Moreover, there is increasing evidence that perception is an active process in which the brain searches for the information it expects to be present, suggesting that auditory perception requires the presence of both bottom-up, i.e. sensory and top-down, i.e. prediction-driven processing. Therefore, the auditory evoked potentials will be interpreted in the context of the Bayesian brain model, in which the brain predicts which information it expects and when this will happen. The internal representation of the auditory environment will be verified by sensation samples of the environment (P50, N100). When this incoming information violates the expectation, it will induce the emission of a prediction error signal (Mismatch Negativity), activating higher-order neural networks and inducing the update of prior internal representations of the environment (P300).

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1. Introduction

Sounds enter the auditory canal, travel through to the tympanic membrane and cause vibration of the auditory ossicles. The ossicles, comprising the malleus, incus and stapes transmit the sound from the air-filled ear canal to the fluid-filled cochlea. The inner hair cells of the cochlea innervate the afferent nerve fibers of the cochlear nerve, which joins the vestibular nerves to form the vestibulocochlear nerve (i.e. cranial nerve VIII) after which the now re-encoded information travels through the brain, passing intermediate stations from brainstem up to the primary auditory cortex and associated brain areas. The auditory stimuli are processed by the brain, comprising not only the classical pathway, which has a tonotopic distribution and projects to the auditory cortex, but also the non-classical pathway. The non-classical pathway, also known as the extralemniscal system, is phylogenetically the oldest system and has a non-tonotopic distribution. It starts at the brainstem in the cochlear nucleus (Cervera-Paz et al., 2007) and via connections at the inferior colliculus, it projects to the medial and dorsal division of the medial geniculate body of the thalamus to the amygdala, which connects to the secondary auditory cortex and association cortices (Aitkin, 1986; Møller, 2003).

Two different models of perception have been developed (Freeman, 2003). One which assumes that the brain passively absorbs sensory input, processes this information and reacts with a motor and autonomic response to these passively obtained sensory stimuli (Freeman, 2003). However, a second model of perception posits that the brain actively looks for the information it predicts to be present in the environment, based on an intention or goal (Freeman, 2003). This goal or intention can drive action which will influence perception. Perception in this latter model can be seen as the result of top-down indirect information creation, depending on what is expected in the sensory environment and relying on what is stored in memory (Hume, 1739; Merleau-Ponty, 1945). The major difference between passive perception and active perception is that active perception critically depends on predictions of what is likely to occur in the environment, based on intentions or goals arising from experience.

In the following sections we will discuss the auditory processes from sensation to perception by making use of auditory evoked potentials (AEPs), in which we hypothesize that auditory perception is derived by bottom-up and top-down processes jointly. We will interpret this in the light of the Bayesian brain model (Friston, 2010; Knill and Pouget, 2004), in which the brain predicts which information will arrive and when this will happen. Moreover, we will focus on the alterations of latency and amplitude of AEPs in tinnitus, i.e. the perception of a sound in the absence of an external auditory stimulus, as it can further unravel the underlying neurophysiological model and it might give us further insights in the influence of tinnitus on the processing of incoming sounds. But for a good comprehension of these sections, we first give a short overview of the neural correlates of the (late) auditory evoked potentials.

2. Auditory evoked potentials

AEPs are the correlates of neural activity elicited by the application of an external sound. In the presence of an intact auditory pathway, the application of an external stimulus will induce an electrical potential at multiple cortical areas, representing the summation of synchronized electrical activity of thousands of neurons in auditory and non-auditory brain regions. The following overview will mainly focus on the neural correlates of the late AEPs obtained with electro-encephalography (EEG) and magnetoencephalography (MEG). In addition, we explicitly mention the brain areas identified with fMRI and intracerebral electrodes to emphasize that the determined areas are almost identical and, hence, not only identified by dipole models. Depending on the latency, AEPs are divided in early, middle or late responses, which are respectively named auditory brainstem responses (ABRs), auditory middle latency responses and auditory late-latency responses (see Fig. 1).

The ABRs, derived from an acoustic stimulus occurring within the first 0–10 ms post-stimulus, are well defined (Moller, 2006b) and comprise five to six consecutive waves reflecting the trajectory of the sound through the brainstem. ABRs are stated not to be influenced by attention (Naatanen and Teder, 1991) and they can be measured in an unconscious state (Moller, 2006b). However, this does not mean that attentional modulation of brainstem activity is not possible. Attention can modulate the brainstem component of the auditory frequency-following responses (FFRs) (Du et al., 2012), which are the sustained evoked potentials generated by continuous presentation of low-frequency tone stimuli based on phase-locked responses of neuron populations, suggesting it is possible to modulate brainstem activity via top-down mechanisms.

The auditory middle latency responses occur within the latency range of 10–50 ms post-stimulus and consist of five peaks (see Fig. 1): P0, Na, Pa, Nb and Pb, of which the P0 is considered to be generated at the higher nuclei of the brainstem and the others right below the auditory cortex. These middle latency responses show a higher variability than the ABRs (Moller, 2006a) and can be modulated by attention (Hansen and Woldorff, 1991) or suppressed by anesthesia (Moller, 2006a).

Although activation of the auditory cortex is a necessary element in the perception of sound, it does not necessarily imply the conscious awareness of the auditory signal. For a stimulus to gain access to the consciousness, a higher-order “awareness” and “salience” neural network has to be co-activated (Langguth et al., 2012; van der Loo et al., 2009). The neural networks underlying the conscious perception of auditory stimuli are more complex and less uniformly identified; therefore, we are mainly interested in the auditory late-latency responses, including the P50, N100, N1–P2 complex, Mismatch Negativity (MMN) and P300.

The P50 is involved in sensory gating and has two main neural generators, the auditory cortex and the dorsal anterior cingulate cortex (dACC) (Grunwald et al., 2003), and possibly the ventrolateral prefrontal cortex (VLPFC) (Korzyukov et al., 2007) (see Fig. 2). This observation suggests that auditory stimuli are processed in parallel, analog to the observations in the somatosensory system (Frot et al., 2008). Moreover, it has been proposed that the extralemniscal system, which projects to the secondary auditory cortex and association cortices, signals that something changes in the auditory environment, the content of which is then processed by the lemniscal tonotopic system ending in the primary auditory cortex. (Jones, 2001; Sherman, 2001). By measuring the P50 amplitude, previous research could not demonstrate significant differences between tinnitus patients and controls, concerning level of arousal or habituation to repetitive sensory stimulation, but they could observe attentional deficits in tinnitus patients compared to controls (Dornhoffer et al., 2006).

The N100 is an event-related potential (ERP) component primarily determined by sensory processing and it has been unambiguously posited that the primary (Huotilainen et al., 1998; Picton et al., 1999; Woods, 1995) and secondary auditory cortices (Lu et al., 1992; Pantev et al., 1995) are the main neural generators. Other involved brain areas are the dACC, as well as the inferior parietal (supramarginal gyrus) and ventrolateral prefrontal cortices (Grau et al., 2007) (see Fig. 2). The N100 is an index of sound detection and is associated with attention-catching properties (Parasuraman and Beatty, 1980; Winkler et al., 1997), rather than subjective contents of perception or discrimination capacities. Furthermore, the