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Review

Evidence against attentional state modulating scalp-recorded auditory brainstem steady-state responses

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ARTICLE INFO

Article history:
Accepted 24 June 2015
Available online 14 July 2015

Keywords:
Frequency-following response
FFR
Envelope-following response
Attention
Auditory processing

ABSTRACT

Auditory brainstem responses (ABRs) and their steady-state counterpart (subcortical steady-state responses, SSSRs) are generally thought to be insensitive to cognitive demands. However, a handful of studies report that SSSRs are modulated depending on the subject's focus of attention, either towards or away from an auditory stimulus. Here, we explored whether attentional focus affects the envelope-following response (EFR), which is a particular kind of SSSR, and if so, whether the effects are specific to which sound elements in a sound mixture a subject is attending (selective auditory attentional modulation), specific to attended sensory input (inter-modal attentional modulation), or insensitive to attentional focus. We compared the strength of EFR-stimulus phase locking in human listeners under various tasks: listening to a monaural stimulus, selectively attending to a particular ear during dichotic stimulus presentation, and attending to visual stimuli while ignoring dichotic auditory inputs. We observed no systematic changes in the EFR across experimental manipulations, even though cortical EEG revealed attention-related modulations of alpha activity during the task. We conclude that attentional effects, if any, on human subcortical representation of sounds cannot be observed robustly using EFRs.

This article is part of a Special Issue entitled SI: Prediction and Attention.

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http://dx.doi.org/10.1016/j.brainres.2015.06.038
0006-8993/

1. Introduction

The ability to selectively attend to a particular talker in "cocktail party" situations depends on the fidelity of sensory encoding throughout the auditory pathway (Shinn-Cunningham and Best, 2008). In human listeners, numerous electroencephalography (EEG), magnetoencephalography (MEG), and electrocorticography (ECoG) studies over the past four decades have shown that selective attention (i.e., "selecting" and focusing on a particular sound source from among multiple sound sources; Shinn-Cunningham, 2008) modulates how sound is encoded in primary auditory cortex. The P1-N1-P2 complex in the auditory-evoked potential (AEP), which is a stereotyped response occurring approximately 100 ms after sound onset that localizes to auditory cortex (Scherg et al., 1989), is enhanced when a listener actively pays attention to the evoking sound (e.g., Hillyard et al., 1973). Conversely, this response is suppressed when sounds are ignored in dichotic listening tasks (Sussman et al., 2005; Bidet-Caulet et al., 2007; Choi et al., 2013). The auditory steady-state response (ASSR), also originating in auditory cortex, has been reported to behave similarly during selective listening (Bharadwaj et al., 2014). "Inter-modal" selective attention (e.g., paying attention to visual stimuli while ignoring simultaneously presented auditory stimuli) has also been shown to modulate the strength of cortical auditory responses. Specifically, the magnitude of the AEP (Hackley et al., 1990; Choi et al., 2013) and ASSR (ASSR; Wittekindt et al., 2014) both have been observed to increase when subjects are actively listening for an auditory stimulus compared to when they perform a visual task and are ignoring the same auditory inputs.

In contrast to the well-described effects of attention on auditory-related neuroelectrical responses originating in the cortex, it is less clear whether selective listening or inter-modal attentional shifts modulates responses originating in subcortical auditory structures. At least one previous study has suggested that attentional modulation of phase-locked neural activity may not occur at processing stages below auditory cortex (Gutschalk et al., 2008). However, there exist corticofugal projections from auditory cortex to subcortical structures that have the potential to modulate the function of lower nuclei (see Winer, 2006 for a concise review). What remains unclear is whether the actions and specific anatomical targets of these projections are specific enough to support selective attention, or even whether these projections to lower nuclei *actively* sculpt neural processing based on task demands at all.

In animals, efferent projections from auditory cortex play a role in the long-term plasticity of the neural firing properties of a number of different subcortical structures, including outer hair cells (Xiao and Suga, 2002), neurons in inferior colliculus (Yan and Suga, 1996, 1999; Bajo et al., 2010), and possibly at later subcortical processing stages as well. Similar long-term changes have also been reported in humans, seen in modifications of subcortical steady-state responses (SSSRs) obtained from the brainstem (e.g., Skoe and Kraus, 2010b). Here, we focus not on long-term plasticity, but rather on the question of whether cortical feedback shapes sub-cortical processing to aid performance "online" flexibly and in an immediate, task-dependent manner. Some awake behaving animal studies suggest that this occurs. Attention to visual stimuli was found to reduce the amplitude of transient evoked responses elicited by broadband auditory stimuli in the cochlear nucleus (Hernandez-Peon et al., 1956; Oatman, 1971, 1976) and the auditory nerve (Oatman, 1971, 1976), as well as of transient (Oatman and Anderson, 1977) and steady-state (Oatman and Anderson, 1980) responses to pure tones at a variety of frequencies in the cochlear nucleus in awake felines. Cochlear sensitivity, as measured by compound action potentials obtained from a round-window electrode