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Research Paper

Neural representation of interaural correlation in human auditory brainstem: Comparisons between temporal-fine structure and envelope

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ABSTRACT

Central processing of interaural correlation (IAC), which depends on the precise representation of acoustic signals from the two ears, is essential for both localization and recognition of auditory objects. A complex soundwave is initially filtered by the peripheral auditory system into multiple narrowband waves, which are further decomposed into two functionally distinctive components: the quickly-varying temporal-fine structure (TFS) and the slowly-varying envelope. In rats, a narrowband noise can evoke auditory-midbrain frequency-following responses (FFRs) that contain both the TFS component (FFR_{TFS}) and the envelope component (FFR_{Env}), which represent the TFS and envelope of the narrowband noise, respectively. These two components are different in sensitivity to the interaural time disparity. In human listeners, the present study investigated whether the FFR_{TFS} and FFR_{Env} components of brainstem FFRs to a narrowband noise are different in sensitivity to IAC and whether there are potential brainstem mechanisms underlying the integration of the two components. The results showed that although both the amplitude of FFR_{TFS} and that of FFR_{Env} were significantly affected by shifts of IAC between 1 and 0, the stimulus-to-response correlation for FFR_{TFS}, but not that for FFR_{Env}, was sensitive to the IAC shifts. Moreover, in addition to the correlation between the binaurally evoked FFR_{TFS} and FFR_{Env}, the correlation between the IAC-shift-induced change of FFR_{TFS} and that of FFR_{Env} was significant. Thus, the TFS information is more precisely represented in the human auditory brainstem than the envelope information, and the correlation between FFR_{TFS} and FFR_{Env} for the same narrowband noise suggest a brainstem binding mechanism underlying the perceptual integration of the TFS and envelope signals.

1. Introduction

It is astonishing to know how the brain is able to selectively track target-sound steams when multiple sounds are heard (the "cocktail party problem", Cherry, 1953). To achieve a successful sound selection, localization and recognition, a critical central process is to compute the similarity of acoustic signals at the two ears (i.e., the interaural correlation (IAC), Jeffress and Robinson, 1962). The processing of IAC also plays a role in both sound localization (Coffey et al., 2006; Franken et al., 2014; Soeta and Nakagawa, 2006) and target-object detection/recognition in noisy environments (Durlach et al., 1986; Palmer et al., 1999).

To achieve the processing of IAC, the auditory system must precisely represent dynamic sound signals. For example, depending on the bandwidth, fluctuations of both interaural phase and interaural level of narrowband noises are the important cues for processing IAC (including the detection of interaural incoherence, Goupell and Hartmann, 2006, 2007a,b). In the peripheral auditory system, a complex sound is initially filtered into multiple narrowband waves, and then each narrowband wave is decomposed into both quickly-varying temporal fine structures (TFSs) and slowly-varying envelopes (Moore, 2008; Rosen, 1992). Therefore, steady-state narrowband noises are naturally useful for examining the

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central representations of TFS and envelope signals. Whether the TFS and envelope components are functionally different remains debated (Apoux et al., 2013; Hopkins et al., 2008; Hopkins and Moore, 2009, 2010; Lorenzi et al., 2006; Shamma and Lorenzi, 2013; Smith et al., 2002; Swaminathan et al., 2016; Zeng et al., 2004). Also, some studies have emphasized the mutual facilitation between TFS and envelope (Moon et al., 2014; Swaminathan and Heinz, 2012). If binaural processing is critical for sound localization/recognition and the TFS is functionally different from the envelope, it is of interest to know whether the neural representation of TFS signals and that of envelope signals are different in the sensitivity to IAC.

Theoretically, a steady-state Gaussian narrowband noise with a center frequency of c Hz and a bandwidth of b Hz has not only the TFS energy around c Hz, but also the envelope energy within the frequency range between 0 and b Hz (Longtin et al., 2008). Thus, steady-state narrowband noises are very useful for extracting the TFS and envelope components when the IAC value is modulated artificially.

Scalp-recorded frequency-following responses (FFRs) are sustained neuro-electrical potentials representing the periodicity of acoustic stimuli (Worden and Marsh, 1968) with the origin site in the auditory midbrain, including the inferior colliculus (IC, Bidelman, 2015; Chandrasekaran and Kraus, 2010; Du et al., 2009; Luo et al., 2017; Marsh et al., 1974; Ping et al., 2008; Smith et al., 1975; Sohmer et al., 1977; Wang and Li, 2015, 2017, 2018; Weinberger et al., 1970). FFRs can encode both the sound TFS (e.g., Chandrasekaran and Kraus, 2010; Du et al., 2011; Galbraith, 1994; Krishnan, 2002; Krishnan and Gandour, 2009; Luo et al., 2017; Russo et al., 2004; Wang and Li, 2015, 2017, 2018) and envelope components (also called envelope-following response) (e.g., Aiken and Picton, 2006, 2008; Dolphin and Mountain, 1992, 1993; Hall, 1979; Luo et al., 2017; Shinn-Cunningham et al., 2013; Supin and Popov, 1995; Wang and Li, 2015, 2017; 2018; Zhu et al., 2013).

Some studies have suggested that these two components are different in response patterns (Luo et al., 2017; Shinn-Cunningham et al., 2017; Wang and Li, 2015, 2017, 2018). Particularly, in rats, narrowband-noise-evoked IC FFRs contain both the TFS component (FFR_{TFS}) and the envelope component (FFR_{Env}), representing the TFS and envelope of the narrowband noise, respectively (Luo et al., 2017; Wang and Li, 2015, 2017, 2018). FFR_{TFS} and FFR_{Env} are different in the sensitivity to the interaural time disparity (Luo et al., 2017). To date, however, it is not clear in humans whether the brainstem FFR_{TFS} and FFR_{Env} are different in the sensitivity to IAC. It is important to investigate whether the brainstem FFR_{TFS} and FFR_{Env} are different in the sensitivity to IAC, because this line of research can improve our understanding of how the spatial and non-spatial features of an auditory object are represented in the auditory brainstem, especially under noisy listening conditions.

More importantly, according to the "Binding Theory" (Treisman and Gelade, 1980), the formation of a unified perceptual object depends on certain linking mechanisms for integrating various physiologically decomposed features. Thus, there must be certain central mechanisms underlying the binding of central representation of TFSs and that of envelopes to form a unified sound percept. However, this "binding problem" has not been solved: How are FFR_{TFS} and FFR_{Env} bound to induce perceptual integration of TFS and envelope features?

In this study, binaurally evoked FFRs to narrowband noises were recorded from normal-hearing human participants under either the diotic (IAC = 1) or the dichotic (IAC = 0) condition. The two main issues of this study include: (1) whether FFR_{TFS} and FFR_{Env} are different in the sensitivity to IAC; (2) whether FFR_{TFS} and FFR_{Env} are correlated with a source specificity.

2. Materials and methods

2.1. Participants

Twenty-five university students (12 females and 13 males; mean age = 20.7 years, SD = 2.4 years) participated in the study. The all had symmetrical hearing (no more than 15-dB difference between the two ears) and normal pure-tone hearing thresholds (no more than 25 dB HL at each ear) between 0.125 and 8 kHz (ANSI-S3.6, 2004). All the participants provided informed consent and received stipends for their participation. The experimental procedures were approved by the Committee for Protecting Human and Animal Subjects in the School of Psychological and Cognitive Sciences, Peking University.

2.2. Acoustic stimuli

Two uncorrelated (independent) Gaussian white noises with the duration of 200 ms (including the 5-ms rise/fall periods) were generated with MATLAB (Math Works Inc., Natick, Massachusetts, USA) at the sampling rate of 20 kHz with 16-bit amplitude quantization. The noises were then filtered with a 512-point band-pass FIR filters to obtain two uncorrelated narrowband noises (sound A and sound B) with the center frequency of 500 Hz and the bandwidth of 1/3 octaves (Fig. 1B). After the filtering, the actual correlation coefficient between the two uncorrelated narrowband noises was −0.041, and both the correlation coefficient for the TFS component and that for the envelope component were less than 0.1. In this study, only the single polarity was used. The TFS and envelope signals were separated by band-pass filters during data analyses.

The noise signals were transferred using a Creative Sound Blaster (Creative SB X-Fi Surround 5.1 Pro, Creative Technology Ltd,

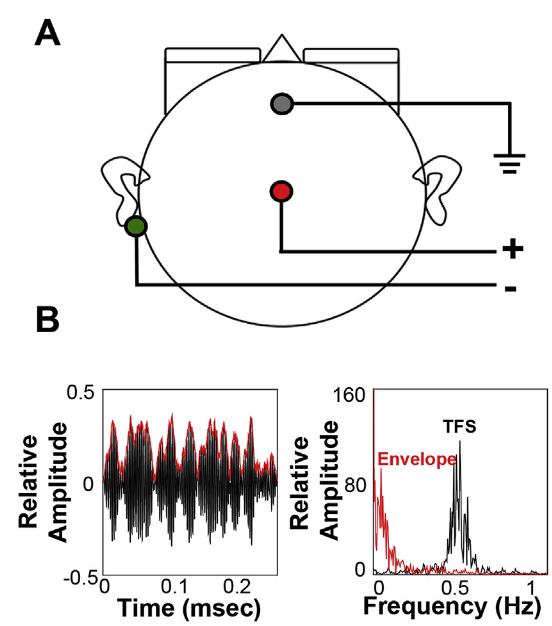

Fig. 1. ***Panel A***: The illustration of the electrode positions for recording human frequency-following responses (FFRs). The active electrode (*red dot*) was placed at the vertex, the reference electrode was at the left mastoid (*green dot*), and the ground electrode (*gray dot*) was on the forehead. ***Panel B***: Two temporal components of a narrowband noise stimulus (sound A, 500-Hz center frequency, 1/3-octave bandwidth). Both the waveforms (*left subpanel*) and the spectra (*right subpanel*) of the acoustic temporal fine structure (TFS, *black curves*) and the acoustic envelope (*red curves*) are presented.

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