



## Research Paper

# Neural representations of concurrent sounds with overlapping spectra in rat inferior colliculus: Comparisons between temporal-fine structure and envelope

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## ABSTRACT

Perceptual segregation of multiple sounds, which overlap in both time and spectra, into individual auditory streams is critical for hearing in natural environments. Some cues such as interaural time disparities (ITDs) play an important role in the segregation, especially when sounds are separated in space. In this study, we investigated the neural representation of two uncorrelated narrowband noises that shared the identical spectrum in the rat inferior colliculus (IC) using frequency-following-response (FFR) recordings, when the ITD for each noise stimulus was manipulated. The results of this study showed that recorded FFRs exhibited two distinctive components: the fast-varying temporal fine structure (TFS) component (FFR<sub>TFS</sub>) and the slow-varying envelope component (FFR<sub>ENV</sub>). When a single narrowband noise was presented alone, the FFR<sub>TFS</sub>, but not the FFR<sub>ENV</sub>, was sensitive to ITDs. When two narrowband noises were presented simultaneously, the FFR<sub>TFS</sub> took advantage of the ITD disparity that was associated with perceived spatial separation between the two concurrent sounds, and displayed a better linear synchronization to the sound with an ipsilateral-leading ITD. However, no effects of ITDs were found on the FFR<sub>ENV</sub>. These results suggest that the FFR<sub>TFS</sub> and FFR<sub>ENV</sub> represent two distinct types of signal processing in the auditory brainstem and contribute differentially to sound segregation based on spatial cues: the FFR<sub>TFS</sub> is more critical to spatial release from masking.

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## 1. Introduction

In natural environments, both humans and animals often listen to multiple-source sounds with both temporal and spectral overlaps. The ability to perceptually segregate mixed acoustic waves into different auditory streams, a process known as “auditory scene analysis” (Bregman, 1990), is crucial for survival. Several cues are employed by the auditory system to achieve this streaming, including fundamental frequency ( $F_0$ ), onset time, and a few spatial cues such as interaural time difference (ITD) (Moore and Gockel, 2002).

The improvement of signal detection/perception when

(perceived) spatial separation exists between multiple sound sources has been a long-studied psychophysical phenomenon, often referred to as “spatial release from masking” (SRM) (Hirsh, 1950). Previous behavioral studies have provided evidences demonstrating the beneficial effects of (perceived) spatial separation for both humans (Bronkhorst and Plomp, 1988; Freyman et al., 2001; Kidd et al., 1998; Li et al., 2004; Shinn-Cunningham et al., 2001) and animals (e.g., Bee, 2008; Du et al., 2009, 2012; Hine et al., 1994; Schmidt and Römer, 2011). Listeners with impaired hearing usually show reduced effects of SRM (Best et al., 2011; Ching et al., 2011; Peissig and Kollmeier, 1997). Therefore, it is of great interest to understand the underlying neural mechanisms.

To date, most electrophysiological studies in this line of research have focused on some non-spatial segregation cues such as  $F_0$  (Fishman et al., 2014; Keilson et al., 1997), difference frequency (i.e. beats) (Bodnar and Bass, 1999, 2001a, 2001b), sound level

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(Nakamoto et al., 2010; Sinex and Li, 2007), and onset synchrony (Bidet-Caulet et al., 2007). Notably, the acoustic stimuli used in these studies had distinctive spectral features that tagged their sources readily, including pure tones with different frequencies (Bidet-Caulet et al., 2007), different harmonic tones (Fishman et al., 2014; Sinex and Li, 2007), vowels with different periodic components (Keilson et al., 1997; Sayles et al., 2016), and narrowband noises (NBNs) with different frequency ranges (Witten et al., 2010). It remains an open question how mixed sounds with overlapping spectra are resolved by auditory neurons (Day et al., 2012; Keller and Takahashi, 2005), which is often the case in natural environments.

When complex sounds reach the ear, the peripheral auditory system filters the sound waves into narrowband channels through a series of band-pass filters. For each of the narrowband channels, the output signals are further decomposed into the fast fluctuating temporal fine structures (TFSs) and the slowly varying envelopes (Moore, 2008). The contributions of TFS and envelope in auditory processing have long been debated. One notion suggests that while the envelope alone is sufficient for hearing content of speech sounds in quiet, the TFS information plays a crucial role in speech recognition under noisy situations (e.g., Apoux et al., 2013; Lorenzi et al., 2006; Smith et al., 2002; Zeng et al., 2004). However, how the TFS and envelope components contribute to the segregation of concurrent sounds is still poorly understood, especially when interaural integration is involved (Swaminathan et al., 2016).

Frequency following responses (FFRs) are sustained electrical potentials of neuron populations that synchronize to periodicities of low- and middle-frequency sounds (Chandrasekaran and Kraus, 2010; Du et al., 2011; Marsh and Worden, 1969; Moushegian et al., 1973; Weinberger et al., 1970; Worden and Marsh, 1968). Human scalp-recorded FFRs show a response limit up to 1.5 kHz (Glaser et al., 1976), and intracranially recorded FFRs in rats show a response limit up to 4 kHz (Ping et al., 2008). In humans, scalp-recorded FFRs can be evoked by a variety of sounds, from simple tones (Chimento and Schreiner, 1990; Galbraith, 1994) to complex sounds such as speech syllables (Aiken and Picton, 2008; Akhoun et al., 2008; Krishnan, 2002; Russo et al., 2004; Song et al., 2008; Wong et al., 2007) and music (Musacchia et al., 2007). FFRs have been shown to be behaviorally and cognitively relevant, and subject to attentional modulation (Du et al., 2012; Galbraith et al., 1998; Hairston et al., 2013; Hoormann et al., 2004; Lehmann and Schönwiesner, 2014), short-term training (Skoe et al., 2013; Song et al., 2008), and long-term experience (Chandrasekaran and Kraus, 2010; Musacchia et al., 2007; Wong et al., 2007). Release from masking based on binaural spatial cues for FFR has been reported (Du et al., 2009, 2012; Wilson and Krishnan, 2005). Interestingly, both human (Lehmann and Schönwiesner, 2014) and animal studies (Du et al., 2011) have confirmed that FFRs precisely represent concurrent periodical-stimulus sources, with components of different frequency being clearly separated in the FFR spectra. Also, previous reports have shown that FFRs can represent the spectral information conveyed in both the TFS and the envelope components of narrowband noises (Wang and Li, 2015) and speech sounds (Aiken and Picton, 2008; Ananthkrishnan et al., 2016; Skoe and Kraus, 2010). Therefore, FFRs are useful for investigating not only stream segregation that occurs at the brainstem level but also specific representations of the TFS and envelope components (Du et al., 2011).

Intracranial-recorded FFRs have been reported recently in inferior colliculus (IC) of anesthetized rats (Du et al., 2009; Ping et al., 2008; Wang and Li, 2015) and amygdala of awake rats (Du et al., 2012). Particularly, the IC, which is the brainstem hub for auditory processing from lower nuclei converge (Schreiner and Winer, 2005), is generally considered as the major source of

scalp-recorded FFRs (Chandrasekaran and Kraus, 2010; Smith et al., 1975; Sohmer et al., 1977).

To examine the brainstem representation of concurrent sounds with overlapping spectra and the effect of ITD on source segregation of the concurrent sounds, in this study we used pairs of uncorrelated NBNs with the identical center frequency and bandwidth to evoke FFRs in rat IC when the ITD of each NBN was manipulated separately. The TFS and envelope components of FFRs were extracted and investigated separately, focusing on their sensitivities to the ITD.

## 2. Materials and methods

### 2.1. Animal preparation

Sixteen young-adult male Sprague-Dawley rats (270–359 g, purchased from the Vital River Experimental Animal Company, Beijing) were used in this study. They were anesthetized with 10% chloral hydrate (400 mg/kg i.p.). The state of anesthesia was monitored throughout the experiment and maintained by supplemental injection of the same anesthetic. Stainless steel electrodes (10–20 k $\Omega$ ) insulated by silicon tubes (0.3 mm in diameter) except at the 0.25-mm-diameter tip (Du et al., 2009, 2012; Wang and Li, 2015) were inserted in the left or right central nucleus of the IC (left:  $n = 8$ ; right:  $n = 8$ ). Based on the stereotaxic coordinates of Paxinos and Watson (1997), the coordinates of the aimed IC site referenced to Bregma were: AP,  $-8.8$  mm; ML,  $\pm 1.5$  mm; DV,  $-4.5$  to  $-5.0$  mm.

The treatments of animals in this study were in accordance with the Guidelines of the Beijing Laboratory Animal Center. All experimental procedures were approved by the Committee for Protecting Human and Animal Subjects in the School of Psychology and Cognitive Sciences at Peking University.

### 2.2. Apparatus and stimuli

Acoustic stimuli were processed through a Tucker-Davis Technology RZ6 auditory processor and presented by two MF1 loudspeakers. For the close-field sound delivery, two 10-cm PVC tubes were connected to the tips of the loudspeakers, with the other ends being inserted into each of the rat's ear canals. All stimuli were calibrated using a Larson Davis Audiometer Calibration and Electroacoustic Testing System (AUDit and System 824), and the sound pressure level (SPL) was 70 dB for each loudspeaker.

For each rat, a pair of uncorrelated NBNs (24414-Hz sampling rate, 16-bit amplitude quantization) with a center frequency of 1200 Hz and a bandwidth of 400 Hz were drawn from a pool of 500 NBN pairs, which were generated by passing Gaussian white noises through a 512-point filter with MATLAB (MathWorks, Natick, MA) (see Fig. 1A for an example). Since 16 rats were used in this study, a total of 16 different pairs of NBNs were used. These NBN pairs were chosen for their low mutual coherences (mean =  $0.070 \pm 0.016$  SD). To avoid the spectral dominance from one single sound of a NBN pair, the coherence between each individual sounds and the summation of the NBN pair was checked to make sure that the coherence difference within each pair was minimum (mean coherence difference =  $0.067 \pm 0.056$  SD). The stimulus duration was 150 ms with 5-ms Hanning onset/offset ramps. The (offset-onset) inter-stimulus interval was 250 ms.

Under the single-source condition, only one sound from the NBN pair was presented binaurally with the interaural time difference (ITD) of either  $+0.16$  ms (ipsilateral-leading, referenced to the recording site) or  $-0.16$  ms (contralateral-leading, referenced to the recording site). The ITDs of  $\pm 0.16$  ms were chosen because this is not only the natural ITD limit of low-frequency fine structures for

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