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Spectrotemporal resolution tradeoff in auditory processing as revealed by human auditory brainstem responses and psychophysical indices

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HIGHLIGHTS

- Spectrotemporal tradeoffs assessed via auditory brainstem and behavioral responses.
- Neural temporal resolution (~4 ms) was inversely related to spectral acuity.
- Temporal processing is limited by cochlear filtering and auditory frequency tuning.

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ABSTRACT

Auditory filter theory dictates a physiological compromise between frequency and temporal resolution of cochlear signal processing. We examined neurophysiological correlates of these spectrotemporal tradeoffs in the human auditory system using auditory evoked brain potentials and psychophysical responses. Temporal resolution was assessed using scalp-recorded auditory brainstem responses (ABRs) elicited by paired clicks. The inter-click interval (ICI) between successive pulses was parameterized from 0.7 to 25 ms to map ABR amplitude recovery as a function of stimulus spacing. Behavioral frequency difference limens (FDLs) and auditory filter selectivity (Q_{10} of psychophysical tuning curves) were obtained to assess relations between behavioral spectral acuity and electrophysiological estimates of temporal resolvability. Neural responses increased monotonically in amplitude with increasing ICI, ranging from total suppression (0.7 ms) to full recovery (25 ms) with a temporal resolution of ~3–4 ms. ABR temporal thresholds were correlated with behavioral Q_{10} (frequency selectivity) but not FDLs (frequency discrimination); no correspondence was observed between Q_{10} and FDLs. Results suggest that finer frequency selectivity, but not discrimination, is associated with poorer temporal resolution. The inverse relation between ABR recovery and perceptual frequency tuning demonstrates a time–frequency tradeoff between the temporal and spectral resolving power of the human auditory system.

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1. Introduction

In the auditory system, the sensory end-organ is typically conceived as bank of overlapping bandpass filters that performs a spectral decomposition on the incoming sound. Bandwidths of the cochlear filters thus determine the frequency resolution of the system (i.e., minimum detectable spectral difference). One

consequence of auditory filter theory is an inherent compromise between the physiological frequency and temporal resolution of cochlear signal processing. A filter's bandwidth and its time constant (i.e., impulse response duration) are inversely related [5]. Given this reciprocal relation, narrower auditory filter bandwidths improve frequency resolution but worsen temporal resolvability; superior temporal processing is achievable but only at the expense of reduced spectral resolvability and vice versa. This spectrotemporal tradeoff hypothesis is well supported by theoretical models of cochlear biomechanics [5] and recordings from basilar membrane and single units in animal models [9,14]. However, there is an unfortunately paucity of electrophysiological evidence for similar spectrotemporal tradeoffs in human listeners.

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Scalp-recorded auditory evoked potentials (AEPs) provide an objective assay of auditory function and thus, may offer important insight into the brain mechanisms supporting spectrotemporal processing tradeoffs not available behaviorally. AEPs have been used to evaluate temporal processing in both humans [12,13] and animal models [8]. In most prior experiments, gap-detection stimuli are used to probe the recovery of the AEP following a brief interruption in the ongoing stimulus. With this approach, temporal resolution has been estimated neurophysiologically using whole-nerve compound action potentials [12], auditory brainstem responses (ABRs) [13,18], and cortical evoked responses [1]. Collectively, studies have revealed neuroelectric correlates of temporal resolution across multiple timescales of auditory processing; specific thresholds vary with the specific stimuli and AEP paradigm, but generally converge to suggest temporal resolvability on the order of 3–10 ms, in agreement with psychophysical reports [6,7,10]. Unfortunately, tradeoffs between temporal biomarkers and frequency acuity, as predicted by cochlear filter theory, have been largely unexplored.

Here, we assessed spectrotemporal tradeoffs in auditory processing by evaluating the degree to which the neurophysiological encoding of rapid temporal events could predict behavioral spectral acuity. Temporal resolution was measured in normal hearing listeners via ABRs elicited by paired-click stimuli. We parametrically varied the inter-click interval (ICI) between successive clicks to map the recovery of ABR and estimate temporal resolution thresholds. Spectral acuity was also assessed in the same ears by measuring behavioral frequency discrimination and auditory filter selectivity. Based on the clear predictions of linear systems and cochlear filter theory, we expected to find a time–frequency tradeoff in the human auditory system whereby superior temporal resolution would be associated with poorer spectral resolution and vice versa.

2. Methods

2.1. Participants

Ten, normal-hearing adults (four female; age: 28.1 ± 4.3 yrs) participated in the experiment. All participants exhibited normal hearing sensitivity between 250 and 8000 Hz and reported no previous history of neuropsychiatric illness. All were right-handed ($75 \pm 0.56\%$ laterality). Participants were paid and gave written-informed consent in compliance with a protocol approved by the IRB of The University of Memphis.

2.2. Stimuli

Filtered clicks were generated by applying 0.25 ms ramps (cos² window) to a 0.67 ms sinusoid with a frequency of 2 kHz (Fig. S1). The dominant spectral energy of the click's power spectrum was centered between 1.2 and 3.1 kHz. Paired-click stimuli were created by presenting consecutive clicks at various ICIs: 25, 10, 7, 5, 4, 3, 2, 1.5, 1.0, 0.7, and 0 ms, where 0 ms represents a single click stimulus. While ABRs are typically evoked using broadband transients, filtered clicks allowed us to (i) obtain more frequency-specific ABR responses and (ii) make veridical comparisons between neural responses and behavioral frequency discrimination/tuning at roughly the same cochlear location (2 kHz).

2.3. Behavioral tasks and analysis

Behavioral frequency difference limens (FDLs) were measured for each participant using a three alternative forced choice (3AFC) discrimination task [4]. Participants heard three sequential intervals, two containing an identical reference pure tone ($f_{\text{ref}} = 2$ kHz) and one containing a higher comparison, assigned

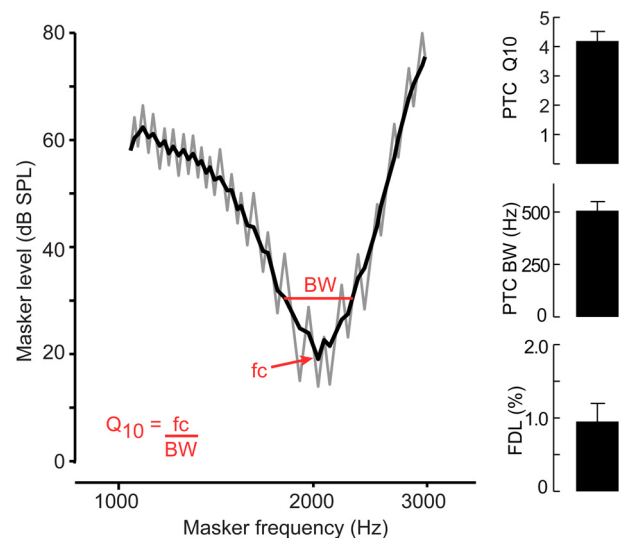


Fig. 1. Psychophysical frequency selectivity and discrimination. (left) Exemplar psychophysical tuning curve (PTC). Gray: raw masked thresholds via Bekesy tracking; black: 2-point moving average. (top and middle right) Mean frequency selectivity (Q_{10}) and bandwidth (BW) measured from PTCs quantify spectral tuning at 2 kHz. (bottom right) Mean frequency difference limens (FDLs) quantifying spectral discrimination acuity at 2 kHz.

randomly. They were required to identify the interval containing the higher sounding tone. Individual tones were 200 ms in duration (ISI = 400 ms). Discrimination thresholds were measured using 2-down, 1-up adaptive tracking (71% performance). Following two correct responses, Δf decreased for the subsequent trial and increased following a single incorrect response (step-size = $\sqrt{2}$). The geometric mean of the last 8/14 reversals was used to compute each listener's frequency difference limen (i.e., $\text{FDL} = 100 \times \Delta f / f_{\text{nom}}$).

Frequency selectivity was assessed in each listener by measuring psychophysical tuning curves (PTCs). PTCs were mapped using the "Fast PTC" method [for details, see [15]]. In this simultaneous masking procedure, listeners monitored a low intensity (18 dB SPL) 2 kHz probe tone concurrent with a masker. A narrowband noise masker (320 Hz bandwidth) was used to reduce the detection of beating between the masker and probe. The probe was a 500 ms pure tone (20 ms ramps), continuously pulsed on/off at a regular rate (ISI: 200 ms) to help subjects maintain attention to the target. Masker center frequency swept upward from 700 to 3000 Hz over 4 min (rate of change was constant on a logarithmic frequency scale). Masker level was continuously varied according to a Békésy track at a rate of 2 dB/s. The run began with initial masker set at 50 dB SPL. Subjects were asked to press and hold a button so long as the probe tone remained audible and release it when it became inaudible. Using this procedure, the masker level needed to just mask the probe frequency was obtained as a function of masker center frequency. Masked threshold plotted against masker center frequency provided an estimate of a listener's PTC at the probe location (2 kHz).

Filter "sharpness" was quantified from PTCs by measuring the quality (Q) factor of the auditory filter. A 2-point moving average was applied to raw PTCs prior to quantification [15] (see Fig. 1). From smoothed PTCs, we measured filter center frequency (f_c), +10 dB bandwidth (BW), and Q_{10} , computed as $Q_{10} = f_c / \text{BW}$. Q_{10} is a normalized measure of filter "sharpness" and quantifies frequency selectivity or tuning for each listener; the smaller the filter BW, the larger the Q_{10} . Response metrics were obtained from two separate PTC measurements and were averaged for each listener to obtain a single estimate of their frequency selectivity. On average,

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