

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 unfortunate 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 (\cos^2 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

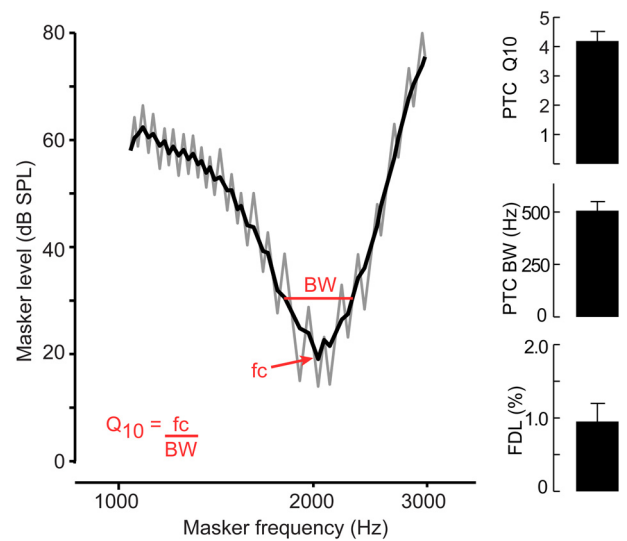


Fig. 1. Psychophysical frequency selectivity and discrimination. (*left*) Exemplar psychophysical tuning curve (PTC). Gray: raw masked thresholds via Bekesy tracking; black: 2-point moving average. (*top and middle right*) Mean frequency selectivity (Q_{10}) and bandwidth (BW) measured from PTCs quantify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

($f_{\text{ref}} = 2$ kHz) and one containing a higher comparison, assigned 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. Participants 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,

behavioral metrics differed less than 4% (PTCs) and 4.5% (FDLs) between runs, respectively.

2.4. Electrophysiological data acquisition and analysis

2.4.1. ABR response recording and preprocessing

Participants reclined comfortably in an electro-acoustically shielded booth to facilitate recording of neurophysiologic responses. They were instructed to relax and refrain from extraneous body movement, ignore the sounds they hear (to divert attention to the stimulus), and were allowed to watch a muted subtitled movie to maintain a calm yet wakeful state. Stimulus presentation was controlled by MATLAB 2013 routed to a TDT RP2 interface. Stimuli were delivered binaurally at an intensity of 91.8 pedB SPL through insert earphones (ER-2A) using fixed, rarefaction polarity. Stimuli were calibrated in a 2-cm³ coupler (IEC 60126). Listeners heard 3000 exemplars of each paired click stimulus presented at a rate of 19.1/s (SOA = 52.4 ms). Conditions were randomized within and across participants.

Neuroelectric activity was recorded differentially between Ag/AgCl disc electrodes placed on the scalp at the high forehead at the hairline (~Fpz) referenced to linked mastoids (A1/A2). Another electrode placed on the mid-forehead served as the common ground. Interelectrode impedance was maintained ≤ 3 k Ω . Continuous EEGs were digitized at 10 kHz (SynAmps RT amplifiers; Neuroscan) using an online passband of DC–4000 Hz. EEGs were then epoched [0–40 ms window] and averaged in the time domain to obtain ABRs for each stimulus condition. Sweeps containing activity exceeding ± 50 μ V were rejected as artifacts prior to averaging. Neural responses were then bandpass filtered between 250 and 1200 Hz to minimize post-auricular muscle artifact from contaminating ABR responses [11].

2.4.2. ABR analysis

ABRs to the first and second clicks of a pair overlapped. For each condition, the second click was isolated via point-by-point subtraction of the response to the single click stimulus (ICI = 0 ms) from the response to the paired click stimulus [8]. ABR recovery was defined as the proportion between the peak amplitude of the response to the second click divided by the peak amplitude of the response to the single click stimulus [8].

A two-parameter sigmoid function was fit to individual subjects' ABR recovery function using standard logistic regression: $R = 1/[1 + e^{-\beta_1(x - \beta_0)}]$, where R is the proportion of recovery for a given ICI, x , the ICI along the stimulus continuum, and β_0 and β_1 the location and slope of the logistic fit estimated using least-squares fitting. Electrophysiological temporal thresholds were then estimated from each subject's fitted profile as the ICI yielding 50% ABR amplitude recovery.

3. Results

3.1. Behavioral FDLs and PTCs

An exemplar behavioral PTC, group mean frequency selectivity (Q_{10} , BW), and discrimination acuity (FDLs) measured at 2 kHz are shown in Fig. 1. PTCs showed a typical "V-shape" with a low-frequency tail, highly selective tip frequency, and steep high-frequency skirt characteristic of auditory filters measured with a variety of techniques [14,15]. On average, listeners obtained Q_{10} s on the order of ~ 4 corresponding to a filter bandwidth of ~ 500 Hz at 2 kHz. Listeners' FDLs were on the order of ~ 1 –2%, consistent with thresholds reported in previous psychoacoustic studies for stimuli of similar frequency (2 kHz) and duration (200 ms) [3,4].

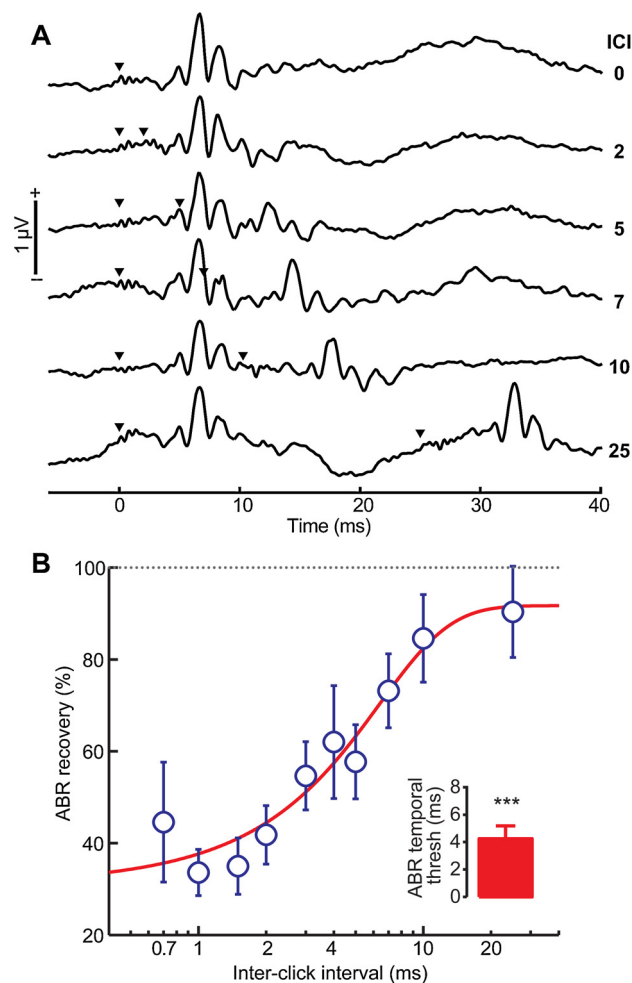


Fig. 2. ABR responses to paired click stimuli. (A) Grand-averaged time-waveforms for select ICIs. Arrows = click onsets. (B) ABR amplitude recovery across ICIs. Sigmoidal data fits = solid curve. Recovery is defined as the amplitude of the response to the second click expressed as a percentage of the amplitude evoked by the single click (ICI = 0 ms). Note the larger response suppression at shorter (1 ms) ICIs and near full recovery at longer ICIs (20 ms). Electrophysiological temporal thresholds were defined as the ICI yielding 50% ABR recovery. (inset) Estimated auditory temporal resolution from ABRs is ~ 4 ms. Error bars = \pm SEM. *** $p < 0.001$.

3.2. Electrophysiological data

3.2.1. ABR temporal recovery

ABR responses are shown as a function of ICI in Fig. 2A. Time-waveforms reveal a monotonic increase in neuroelectric response amplitude with increasing ICI, ranging from substantial suppression ($< 30\%$, 1-ms click spacing) to near full recovery ($> 90\%$, 25-ms spacing) (Fig. 2B)¹. A mixed-model ANOVA (ICI as fixed, subjects as random factor) revealed a significant effect of ICI on ABR amplitude recovery [$F_{9,81} = 6.63$, $p < 0.0001$]. As expected, *a priori* contrasts revealed significant differences between ABR recovery in the three shortest (0.7, 1, 1.5 ms) and longest (7, 10, 25 ms) ICIs [$t_{81} = 7.11$, $p < 0.0001$]. Recovery was also much lower for short ICIs (1 ms) and much higher for longer ICIs (25 ms) relative to the medium ICI condition (3 ms) [3 vs. 1 ms: $t_{81} = 2.59$, $p = 0.034$; 25 vs. 3 ms: $t_{81} = 2.59$, $p = 0.034$]. Electrophysiological temporal thresholds, computed as the ICI yielding 50% ABR recovery from fitted neurometric

¹ At the shortest ICIs (0.7 ms), the subtraction procedure can lead to a residual response amplitude from the first click and thus an imperfect derivation of the second click ABR. In such cases, the ABR recovery is likely overestimated.

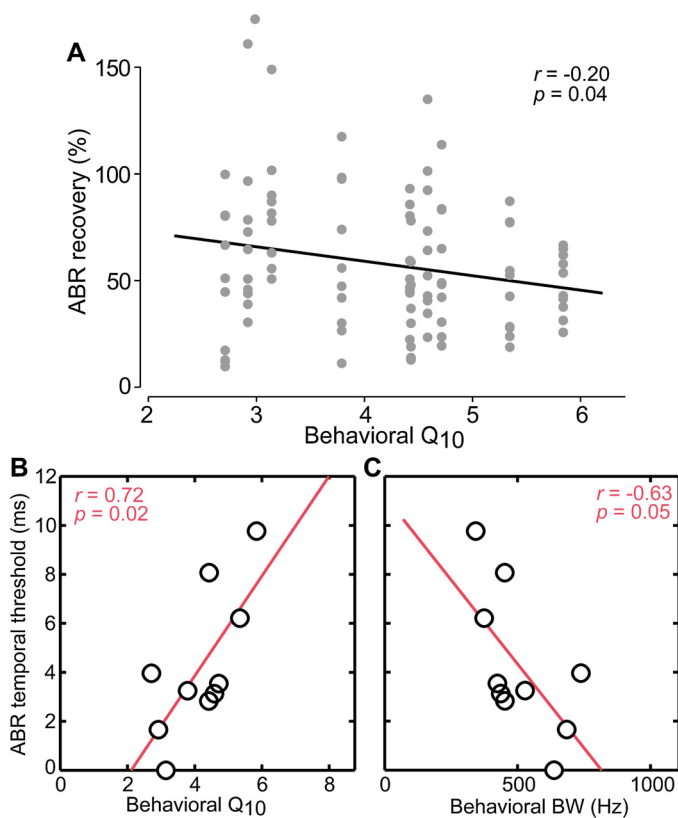


Fig. 3. Neural correlates of spectrotemporal tradeoff in the human auditory system. (A) Correspondence between behavioral and neural measures of auditory frequency and temporal resolution. Each subject's behavioral auditory filter Q_{10} is plotted against their ABR recovery across all stimuli (gray points). PTC Q_{10} (i.e., filter "sharpness") negatively correlates with the degree of ABR recovery. (B and C) Frequency selectivity (Q_{10} and BW) is correlated with ABR temporal thresholds; sharper frequency tuning is associated with poorer (i.e., larger) neurophysiological temporal thresholds.

functions, revealed reliable thresholds of ~ 4 -ms (t -test against a null of 0 ms threshold; $t_9 = 4.54$, $p = 0.0014$). These estimates based on brainstem responses are consistent with behavioral estimates of temporal resolution reported in the psychoacoustic literature (e.g. [6,10]).

3.2.2. Brain–behavior relationships reflecting spectrotemporal tradeoffs

Correlations between psychophysical frequency resolution (behavioral FDLs and Q_{10}) and ABR response properties explored potential spectrotemporal tradeoffs in auditory processing. Behavioral FDLs quantify frequency discrimination and are widely thought to reflect a listener's spectral acuity [3]. Yet, no correlations were observed between FDLs and ABR temporal measures ($ps \gg 0.5$). In contrast, behavioral Q_{10} extracted from PTCs showed a negative correspondence with ABR response recovery [$r = -0.20$, $p = 0.04$], such that higher Q_{10} values (i.e., sharper filters) were associated with poorer ABR recovery (Fig. 3A). Similarly, behavioral auditory filter Q_{10} [$r = 0.72$, $p = 0.02$] and their corresponding bandwidths [$r = -0.63$, $p = 0.05$] were positively and negatively correlated with neurophysiological ABR temporal thresholds, respectively (Fig. 3B and C). The inverse relationship between behavioral measures is expected given the reciprocal relationship between Q_{10} and filter bandwidth (i.e., $Q_{10} = f_c/BW$). Nevertheless, the robust relationship between both behavioral measures and ABR temporal thresholds indicate that sharper, more selective frequency tuning (i.e., higher Q_{10} , smaller BW) predicts poorer auditory temporal resolution, i.e., larger ABR temporal thresholds and

less recovery. No reliable correlation was found between behavioral FDL and Q_{10} measures [$r = -0.39$, $p = 0.26$] suggesting an independent (or at least unobservable) relationship between listeners' perceptual frequency selectivity and frequency discrimination [3] (see also SI Discussion).

4. Discussion

Our results demonstrate two primary findings: (i) temporal resolution of auditory brainstem responses corresponds well with psychophysical estimates of temporal acuity (~ 3 – 4 ms); (ii) temporal resolution of subcortical neural processing inversely predicts listeners' behavioral spectral acuity. These data support the notion of a spectrotemporal tradeoff in the resolving power of the human auditory system (e.g. [5]) whereby temporal processing is limited by the frequency decomposition performed by cochlear filtering; superior temporal resolution is achievable at the expense of reduced spectral resolvability.

4.1. Brainstem correlates of auditory temporal resolution

ABR response recovery functions revealed temporal thresholds (i.e., 50% recovery point) on the order of 3–4 ms. In this regard, our results align closely with previous studies reporting a similar temporal resolution of the scalp-recorded ABR in humans [13,17,18] and animal models [8]. They also converge with behavioral estimates of temporal resolution measured psychophysically in humans via gap-detection paradigms [6,7,10] and late cortical evoked potentials [1]. The close correspondence we observe between electrophysiological and behavioral measures indicates that the ABR could be used as an objective assay of temporal processing. While a variety of AEPs may offer a proxy of temporal acuity, we infer that brainstem potentials are likely preferable to other evoked brain responses (e.g., cortical AEPs) given that they (i) are recordable in the absence of an overt behavioral task and (ii) are unaffected by attention and other extraneous subject factors [4].

4.2. Neurobiological basis of brainstem temporal resolution

It is conceivable that differences in temporal acuity across listeners may reflect differences in peripheral auditory filter bandwidth. This is suggested by the observation that in hearing impaired listeners – who have broader and more variable auditory filters – bandwidth is similarly negatively correlated with cochlear response time (i.e., traveling wave delay); wider filters generate faster temporal responses [17]. While all participants in the current study had normal hearing, some variation in filter width might be expected given normal variability inherent to any psychophysiological measure. Indeed, as suggested by our previous computational modeling studies of auditory nerve (AN) responses, temporal resolution measured via paired-click recovery functions depends heavily on cochlear filter bandwidth [8]. AN ensemble responses demonstrate that even minimal broadening of tuning can improve paired-click recovery functions and heighten temporal resolution [8]. Some psychophysical studies have also observed better temporal modulation sensitivity in individuals with hearing loss [2]. These human data converge with recent recordings in animal models, which demonstrate that broader filters produce decreased response latency in AN fibers [9]. This converging evidence reveals that while broadened filters reduce peripheral frequency selectivity, they cause less temporal ringing along the cochlear partition, improving the overall temporal resolving power of the system. While listeners in the current study all had normal hearing, it is possible that some variation in cochlear tuning may account for the distribution and correlations with ABR temporal thresholds observed in our cohort.

Apart from cochlear filtering, the pattern of observed neural recovery may reflect differences in other factors, in addition to filter bandwidth, known to influence auditory temporal processing. The refractory period of individual neurons can affect responsiveness to sounds separated by intervals up to 20–30 ms, and adaptation mechanisms within the cochlear synapse can operate over even longer timeframes under some stimulus conditions [20]. Moreover, the magnitude of neural adaptation is generally stronger in higher, relative to lower-level auditory structures [20]. Increased adaptation along the ascending auditory pathway may account for the larger electrophysiological temporal thresholds derived from near- and far-field cortical evoked responses (5–10 ms) [1] as compared to those observed in brainstem potentials (3–4 ms) (current study; [8,18]), or auditory nerve fiber/ensemble responses (1.5–3 ms) [12]. Discrepancies between threshold estimates across evoked potential studies may result from differences in adaptation in the neural generators underlying the various scalp-recorded AEPs (see also, SI Discussion). Yet, to invoke adaptation as the sole explanation for our data (Fig. 3) would require the interpretation that listeners with better behavioral frequency selectivity also have less neural adaptation, a proposition that seems unlikely.

4.3. Tradeoff between temporal and spectral processing

Our data link the resolution and psychophysical limits of temporal processing to early, pre-attentive responses from the brainstem. The strong reciprocal relation between neural (temporal) and behavioral (spectral) measures observed in our listeners supports the notion of a tradeoff between auditory frequency and temporal resolvability (Fig. 3). ABR recovery was negatively correlated with behavioral PTC Q_{10} tuning such that superior temporal processing (i.e., larger ABR recovery) was associated with poorer frequency resolution (smaller Q_{10}). Similarly, ABR temporal thresholds showed strong positive (Q_{10}) and negative (BW) correspondence with tuning metrics extracted from psychophysical tuning curves. That is, poorer neural processing in time (larger ABR temporal thresholds) was associated with better selectivity in frequency (larger Q_{10}) and vice versa. These findings reveal a fundamental link between brain and behavioral mechanisms supporting auditory time–frequency analysis and are remarkably consistent with the principles of linear systems theory: filters with narrower bandwidths have impulse responses with longer temporal “ringing.” Taken together, the observed brain-behavior connections support the notion that (i) temporal and spectral auditory processing are intimately linked via an inverse relation and (ii) temporal resolution is, at least in part, limited by peripheral auditory filtering performed by the cochlea.

The reported spectrotemporal tradeoffs between peripheral cochlear filtering and brainstem responses are reminiscent of other time–frequency compromises found throughout the auditory pathway and other physical systems. The acoustic uncertainty principle states that precise simultaneous measurements of an auditory event in both the time and frequency domain cannot be realized. Stated formally, $\Delta f \times \Delta t = 1$, where Δf is the bandwidth of signal’s power spectrum and Δt is its duration [19; p. 41]. This formulation implies a tradeoff between the precision of temporal and spectral information whereby increased temporal resolution can only be achieved at the expense of spectral resolution and vice versa. These physical properties of acoustics bear direct resemblance to the time–frequency tradeoff between spectral acuity and temporal processing we find biologically. In relation to audition, spectrotemporal tradeoffs have been observed in the biases of various auditory brain mechanisms. Most notably, in the well-known right vs. left hemispheric brain asymmetry for fine spectral vs. temporal

analysis [19]. Electrophysiological responses from the human auditory cortex [19] to the cochlea [16] similarly reveal evidence for lateralized neural activity dependent on the temporal and spectral characteristics of stimulus acoustics. It is possible that the tradeoffs we observe between spectral acuity and early, pre-attentive brainstem processing reflect similar neurobiological time–frequency compromises. Collectively, the auditory brain seems well equipped to manage the spectrotemporal tradeoffs inherent to physical and biological systems at multiple levels of brain processing.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.neulet.2014.04.037>.

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