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Contextual modulation of sound processing in the auditory cortex

C Angeloni and MN Geffen

In everyday acoustic environments, we navigate through a maze of sounds that possess a complex spectrotemporal structure, spanning many frequencies and exhibiting temporal modulations that differ within frequency bands. Our auditory system needs to efficiently encode the same sounds in a variety of different contexts, while preserving the ability to separate complex sounds within an acoustic scene. Recent work in auditory neuroscience has made substantial progress in studying how sounds are represented in the auditory system under different contexts, demonstrating that auditory processing of seemingly simple acoustic features, such as frequency and time, is highly dependent on co-occurring acoustic and behavioral stimuli. Through a combination of electrophysiological recordings, computational analysis and behavioral techniques, recent research identified the interactions between external spectral and temporal context of stimuli, as well as the internal behavioral state.

Address
Department of Otorhinolaryngology: HNS, Department of Neuroscience, Psychology Graduate Group, Computational Neuroscience Initiative, University of Pennsylvania, Philadelphia, PA, United States

Corresponding author: Geffen, MN (mgeffen@med.upenn.edu)

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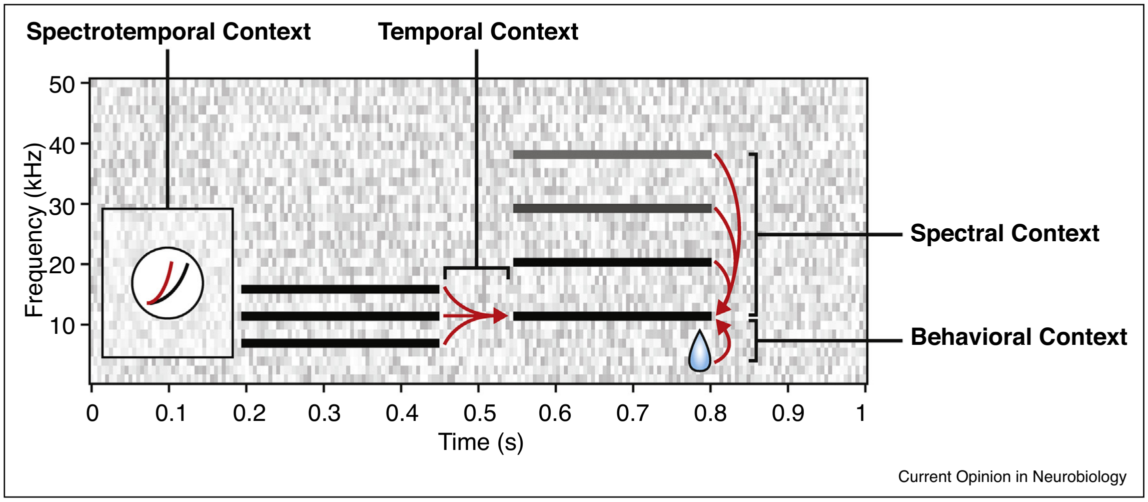
At the first stage in the auditory processing cascade, the cochlea decomposes the incoming sound waveform into electrical signals for distinct frequency bands, creating a frequency-delimited organization that persists throughout the central auditory processing centers. The inferior colliculus, the auditory thalamus and the auditory cortex all exhibit tonotopic organization through a systematic neuronal best frequency gradient across space. Therefore, tonotopy has been considered a fundamental feature of auditory processing and, historically, auditory neuroscientists used pure frequency tones to systematically characterize the response properties of the auditory system. However, while pure tones are useful for determining the tuning properties of individual cells and the tonotopic arrangement of different brain regions, they ultimately do not capture the complex spectral profile of many natural sounds. Natural acoustic stimuli like speech, conspecific vocalizations, and environmental sounds, are comprised of signals with power across multiple frequency bands. Encoding complicated spectral profiles is behaviorally important, as these types of sounds provide cues for identifying different speakers and call types and for sound localization. However, how a complex sound is encoded is not immediately evident by looking at the responses to individual frequency components: rather, responses to distinct spectral components of sounds interact with each other in frequency and time. From moment to moment, a neuron's response does not necessarily reflect only the frequency band it is best tuned to, but also depends on nonlinear integration of stimulus power across the spectral and temporal domains. Furthermore, behavioral state or task engagement can modify this representation. Here, we review recent investigations on how spectral, temporal and behavioral contexts affect sound representation in the auditory cortex (Figure 1).

Modulation of auditory processing by spectral context

Indeed, in the central auditory pathway, neural response properties to spectrally complicated stimuli are not well predicted by their tuning to pure tones. In the periphery, auditory nerve fibers typically transmit a linear, narrowband representation of pure tone stimuli that is determined by their frequency tuning [1]. However, when presented with pairs of pure tones, auditory nerve fiber responses at best frequency are often suppressed by the presence of a second tone, a well-studied phenomenon called two-tone suppression (Figures 1 and 2; for review, see [2]), which arises from nonlinearities in the mechanics of the basilar membrane of the cochlea [3–5]. Many cortical neurons also nonlinearly integrate spectral components, showing multi-peaked tuning [6–9], two-tone suppression and facilitation (Figure 2a) [10–12], or combination sensitivity [13,14] when presented with sounds composed of multiple frequencies. This selectivity for complex spectral stimuli is thought to arise from a combination of excitation and lateral inhibition, as belied by the suppressive effects of multiband stimuli on single-peaked neuronal responses [10,15]. Thus, rather than combining responses to inputs at different frequencies in an additive fashion, the auditory system facilitates nonlinear interactions across spectral bands.

Figure 1



Schematic of auditory context effects. *Spectral context*. The effects of spectral energy in near and distant frequency bands on characteristic frequency responses, as demonstrated with two-tone suppression and harmonic facilitation. *Temporal context.* The effects of preceding tones on a probe stimulus, as demonstrated by forward suppression and related to SSA. *Spectrotemporal context.* The joint effects of energy distributed across frequency and time, often resulting in adaptation of nonlinear response properties to suit persistent environmental statistics. *Behavioral context.* The effects of reward contingency on auditory responses.

Sensitivity to spectral context is useful for encoding sounds composed of several distinct frequencies, a feature common to many mammalian vocalizations [12,13]. Many communication sounds contain harmonic components, a broadband acoustic feature that is highly perceptible by many mammalian species [16–18]. Indeed, harmonic features are perceptually useful, and can be used to discriminate between different sound sources or speakers [19] or to hear vocalizations in noisy environments [20], indicating that harmonicity is a prominent acoustic feature for auditory processing. In auditory cortex, single-peaked and multi-peaked neurons are often suppressed or facilitated by harmonically spaced tone pairs (Figure 2a) [12] and can be selective for higher order harmonic sounds [21–23] demonstrating that auditory cortex is highly sensitive to the harmonic content of natural stimuli, possibly through a harmonic arrangement of alternating excitatory and inhibitory inputs [23]. These studies demonstrate that spectral processing in the auditory system combines a linear, tonotopic representation of frequency with a nonlinear representation, which creates sensitivity to features of the spectral context outside of a neuron's best frequency.

Modulation of auditory processing by temporal context

Just as the spectral context outside of the best frequency is integrated in cortical neurons, the temporal history of an acoustic waveform also impacts neural responses to proceeding stimuli. Sensitivity to temporal context is important for identifying auditory objects, allowing sequences of auditory stimuli to be perceptually grouped or separated based on their temporal properties [24,25] or for detecting novel or rare sounds by decreasing responsivity to redundant sounds [26,27].

In the auditory cortex, responses to a probe tone are suppressed by a preceding masking tone, a phenomenon known as forward suppression (Figure 2b) [11,28–31]. The magnitude of forward suppression depends on the frequency and intensity of the masker, creating a suppressive area that matches the frequency response area (FRA) of the neuron, and decays at large delays between the probe and masker, approximately 250 ms after masker onset [11,28,29]. The suppressive effect of the masker is released with increasing probe intensities, suggesting a competitive interaction between excitatory responses to the probe, and delayed inhibitory responses to the masker (Figure 2b) [30]. Whole-cell recordings show that inhibitory conductances elicited from the masker last only 50–100 ms, indicating the involvement GABA-mediated synaptic inhibition at short timescales, but also that long-term synaptic depression may underlie suppression observed at longer delays [32]. Notably, there is considerable diversity in forward masking in awake mice, with mixtures of suppression and facilitation by the masker, and nonlinear relationships between responses to the masker and the probe, further implicating synaptic inhibition mediated by cortical interneurons as a potential mechanism for temporal context sensitivity [31].

Prolonged stimulus history also affects neural sensitivity. Stimulus specific adaptation (SSA) is one such phenomenon, in which neurons reduce their response to a tone