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Tone processing in the brain: a linguistic journey from cortex to brainstem

Tonal languages provide a window for tracing the hierarchical transformation of the pitch of a sound from early sensory to later cognitive stages of processing in the human brain. Hemispheric processing preferences for pitch are driven by multiple acoustic-phonetic cues and higher-level category information that interact in real time at cortical and subcortical levels of the cerebrum as well as the midbrain. A fuller understanding of tonal processing must necessarily take into account contributions from both hemispheres. Major issues about tone and the brain include its biological substrates (anatomic structures, brain networks), biotemporal dynamics (hemispheric preferences, stages of processing), separability (tones vs. segments and other suprasegmentals; tonal features), and domain specificity (linguistic vs. musical pitch). To address these issues, we examine findings obtained primarily from positron emission tomography (PET), functional magnetic resonance imaging (fMRI), and auditory electrophysiology (EEG, MEG) at the level of the cerebral cortex (mismatch negativity response, MMN) as well as the auditory brainstem (FFR/frequency following response). In general, left hemisphere engagement depends upon the linguistic status of pitch; otherwise, pitch is lateralized to the right hemisphere. At earlier stages of cortical processing, hemispheric preferences vary depending upon whether the unit is segmental or suprasegmental. Tones, relative to consonants and rimes, yield increased activation in the right hemisphere. Tones, relative to intonation, share processing areas in both hemispheres. As indexed by MMN, tonal processing is shaped by the relative saliency of perceptual features – contour vs. height. Such features are evident at early preattentive stages of processing in the cerebral cortex. Discriminant analysis indicates that pitch contour, not height, effectively separates native speakers of tone languages from non-tone languages. We infer that abstract tonal representations at later stages of processing are grounded in pitch-relevant features that emerge along the auditory pathway. Similarly, language-dependent modulation of pitch-relevant features is observed in the brainstem. Pitch encoding of tone-language speakers is enhanced especially during rapid-glide portions of tonal contours. Language-dependent, functional ear asymmetries in the brainstem override the fixed, structural asymmetries in the auditory pathway. These functional ear asymmetries may foreshadow preferential processing of auditory stimuli in the contralateral hemisphere, or both, depending on their linguistic status. This early shaping of the auditory signal at a preattentive, sensory stage of processing is compatible with the idea that nascent representations of acoustic-phonetic features emerge early along the auditory pathway. Though native speakers of tone languages are able to transfer their abilities in brainstem pitch encoding to the music domain, such effects do not transfer to cognitive stages of processing during music perception. This finding points to a dissociation between subcortical neurophysiological processing and behavioral measures of pitch perception. Perceptual benefits at the cognitive level occur only when that pitch information is behaviorally relevant to the listener. To increase our understanding of the nature of the interplay between levels of pitch processing along the hierarchy, a novel experimental approach enables us to record neural representation of pitch-relevant information at brainstem and cortical levels (CPR/cortical pitch response) simultaneously, and then further compare these neural indices to perceptual measures of pitch. This combined approach gives us a unique window to investigate the coordination between different levels of pitch processing in real time. The close correspondence between neural and behavioral data suggest that neural correlates of pitch salience that emerge in the brainstem may drive and maintain with high fidelity the early, preattentive cortical representations of pitch. Such coordination may otherwise be obscured by inferences drawn from separate evaluation of neural responses evoked by different stimulation/acquisition paradigms or from comparisons across studies.