From: MARK TRAMO <[redacted]>
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Subject: Revised last Paragraph for our paper: Perception of the "Missing" F0 following bilateral aud cortex strokes
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Numerous authors have addressed the question of how a stimulus containing multiple tones evokes a unitary pitch percept (for reviews see Moore 2013 Intro book 6th ed; , de Cheveigne 2005 in Plack & Oxenham book). All the proposed theories fall into two main categories: temporal processing and spectral pattern matching. Pattern recognition models carry out two serial operations: frequency analysis and template matching. For example, Goldstein (1973) postulated that the central auditory system contains an "optimum processor" that carries out a low-level analysis of resolvable stimulus frequencies then at a higher level scans stored templates of harmonic series to find the closest match to the pattern of stimulus frequencies, such that the pitch of the stimulus corresponds to the F0 of the template with the best fit. The results of previous lesion effect studies in cats (Whitfield 1980) and humans (Zatorre 1988) employing the method of constant stimuli have been interpreted as evidence that auditory cortex lesions spare frequency analysis and impair pattern matching. However, subsequent studies of neurological patients with auditory cortex lesions using pure-tone stimuli and the adaptive method showed elevations in frequency difference thresholds for pitch direction discrimination (for review see Tramo et al. 2005). However, no direct comparisons between difference thresholds for pure-tones versus missing-F0 complex tones were made, so it remained unclear if the elevations in pure-tone difference thresholds might be sufficient to cause the missing-F0 pitch discrimination deficits previously reported in cats and neurological patients. The comparisons of difference thresholds measured with pure-tones, harmonic-tones, and harmonic-tones without spectral energy at F0 in the present experiments indicate that loss of finely-tuned neurons caused by lesions of primary auditory cortex and neighboring areas is sufficient to cause impaired perception of missing-F0 pitch. At the same time, the results do not rule out the existence of a second, pattern-matching stage of central processing, nor do they rule out the possibility that primary auditory cortex contributes to pattern matching. With respect to pathophysiology, the observed deficits can be attributed to loss of neurons finely tuned to pure-tone frequency (for review see Aitkin 1990), harmonic-tone F0 (Schwarz and Tomlinson 1990), harmonic-tone pitch (Bendor and Wang 2005), or some combination thereof. With respect to temporal processing models of pitch perception, it remains unclear whether there are sufficient numbers of primary auditory cortex neurons capable of generating temporal representations of pitch in their interspike interval distribution [e.g., the cat A1 cell of de Ribaupierre et al. (1972) that showed phase-locking to clicks at 1000 Hz)] or whether translation of time codes into rate codes in the auditory brainstem gives rise to the rate coding reported by Bendor and Wang (2005) for missing-F0 pitch. In either case, bilateral A1 lesions would be sufficient to cause the deficits observed in the present experiments. More generally, the present observations of coarsened frequency resolution caused by auditory cortex lesions add to existing empirical evidence against the differential assignment of "low-level" processing to subcortical and peripheral auditory structures and "high-level" processing to auditory cortex.

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