Supplementary note

The relationship between tone selectivity and pitch perception

The experiments in this paper involve contrasts between brain activity evoked by harmonic tones (or vocalizations) and spectrally matched noise, as has been commonly used in the neuroimaging literature in pursuit of the neural basis of pitch. There is consensus across several labs that this contrast identifies anatomically stereotyped regions in humans[1–3]. The motivation for the contrast is that tones evoke a pitch percept, whereas noise does not, and thus regions identified as responding more to tones than to noise should be inclusive of any neural substrate for the representation of pitch. But in principle one might expect different results for tones and noise to emerge simply from the standard modulation filter bank models that have long been proposed to explain generic auditory cortical tuning[4,5], in that tones and noise have different spectral modulation properties, and have been found to differentially excite neurons in macaque auditory cortex[6]. Two other observations support the idea that the tone vs. noise contrast identifies something more specifically related to pitch. First, the results of the tone vs. noise contrast in humans are asymmetric – virtually all humans show regions that respond twice as strongly to harmonic tones than noise, but noise-selective regions are generally weak or absent (as we explicitly demonstrate here; see Figure 1d). The direction of the asymmetry suggests privileged processing of tone-like stimuli, as one would expect given the importance of pitch in human hearing. Second, the response of these regions to stimuli varying in their harmonic composition closely tracks the effect of this stimulus manipulation on pitch discrimination thresholds[3]. This similarity provides evidence that the response of these regions is in some way implicated in pitch perception.

At present, the tuning properties of individual neurons in tone-selective regions remains unclear due to the coarse resolution of fMRI. These regions could simply be tuned to fine spectral peaks associated with discrete frequency components, to particular fundamental frequencies (f0s), or to changes over time in individual frequencies or f0. The search for the neural basis of pitch in animal neurophysiology has focused on tuning for f0, often synonymous with "pitch tuning"[7–9], but there is reason to think that the alternative forms of tuning consistent with the fMRI results could also help to subserve pitch perception. For instance, many everyday auditory tasks that require discriminating the f0 of sounds can be performed when stimuli are transformed to be inharmonic, suggesting that humans in some cases track the spectrum rather than the f0[10]. Naïve listeners claim that they are listening to pitch in these instances even though the sounds do not have a well-defined pitch in the classical sense. Outside the lab, these abilities presumably serve to enable discrimination of harmonic sounds differing in F0 (typically considered the domain of pitch perception), but seem likely to depend on neurons sensitive to shifts in the spectrum within or across sounds, rather than neurons tuned to f0. Pitch representations and their underlying cellular basis could thus be diverse. This ambiguity highlights the need for animal models, in which the tuning of individual neurons can be directly assessed. Our results suggest that there are species differences in at least some aspects of the neural tuning underlying pitch perception in humans.

References

1. Patterson, R. D., Uppenkamp, S., Johnsrude, I. S. & Griffiths, T. D. The processing of temporal pitch and melody information in auditory cortex. *Neuron* **36**, 767–776 (2002).
2. Penagos, H., Melcher, J. R. & Oxenham, A. J. A neural representation of pitch salience in nonprimary human auditory cortex revealed with functional magnetic resonance imaging. *J. Neurosci.* **24**, 6810–6815 (2004).

3. Norman-Haignere, S., Kanwisher, N. & McDermott, J. H. Cortical pitch regions in humans respond primarily to resolved harmonics and are located in specific tonotopic regions of anterior auditory cortex. *J. Neurosci.* **33**, 19451–19469 (2013).
4. Chi, T., Ru, P. & Shamma, S. A. Multiresolution spectrotemporal analysis of complex sounds. *J. Acoust. Soc. Am.* **118**, 887–906 (2005).
5. Miller, L. M., Escabí, M. A., Read, H. L. & Schreiner, C. E. Spectrotemporal receptive fields in the lemniscal auditory thalamus and cortex. *J. Neurophysiol.* **87**, 516–527 (2002).
6. Rauschecker, J. P., Tian, B. & Hauser, M. Processing of complex sounds in the macaque nonprimary auditory cortex. *Science* **268**, 111–114 (1995).
7. Schwarz, D. W. & Tomlinson, R. W. Spectral response patterns of auditory cortex neurons to harmonic complex tones in alert monkey (Macaca mulatta). *J. Neurophysiol.* **64**, 282–298 (1990).
8. Bendor, D. & Wang, X. The neuronal representation of pitch in primate auditory cortex. *Nature* **436**, 1161–1165 (2005).
9. Bizley, J. K., Walker, K. M. M., King, A. J. & Schnupp, J. W. H. Neural ensemble codes for stimulus periodicity in auditory cortex. *J. Neurosci.* **30**, 5078–5091 (2010).
10. McPherson, M. J. & McDermott, J. H. Diversity in pitch perception revealed by task dependence. *Nat. Hum. Behav.* **2**, 52 (2018).