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Mapping Pitch Representation in Neural Ensembles with fMRI

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The auditory cortex of macaque and human is located in the superior temporal plane (Fig. 1). In the macaque, three core areas, including primary cortex (A1), run posterior to anterior. Using functional magnetic resonance imaging (fMRI), each can be seen to demonstrate distinct tonotopic (frequency) mapping (Petkov et al., 2006). Adjacent belt areas also show some degree of tonotopicity. In humans, organization of the auditory areas based on tonotopic mapping is currently debated (for recent human fMRI reports see Formisano et al., 2003; Talavage et al., 2004; Woods et al., 2009; Humphries et al., 2010; Da Costa et al., 2011; Langers and van Dijk, 2011). There is consensus that primary cortex is located in the medial part of the first transverse temporal gyrus (Heschl’s gyrus, HG) in the superior temporal plane, while the status of lateral HG as a core or belt homolog is debated. Studies of human pitch representation have sought an area that is specialized for pitch coding within HG and adjacent auditory areas including the planum temporale (PT), posterior to HG.

Introduction

The auditory cortex of macaque and human is located in the superior temporal plane (Fig. 1). In the macaque, three core areas, including primary cortex (A1), run posterior to anterior. Using functional magnetic resonance imaging (fMRI), each can be seen to demonstrate distinct tonotopic (frequency) mapping (Petkov et al., 2006). Adjacent belt areas also show some degree of tonotopicity. In humans, organization of the auditory areas based on tonotopic mapping is currently debated (for recent human fMRI reports see Formisano et al., 2003; Talavage et al., 2004; Woods et al., 2009; Humphries et al., 2010; Da Costa et al., 2011; Langers and van Dijk, 2011). There is consensus that primary cortex is located in the medial part of the first transverse temporal gyrus (Heschl’s gyrus, HG) in the superior temporal plane, while the status of lateral HG as a core or belt homolog is debated. Studies of human pitch representation have sought an area that is specialized for pitch coding within HG and adjacent auditory areas including the planum temporale (PT), posterior to HG.

fMRI approaches to pitch

fMRI pitch studies have used subtraction methodology in which responses to a stimulus associated with pitch are compared with a control stimulus with no pitch. These experiments have sought to control for aspects of the different stimulus structure of the pitch and control sound to which fMRI might be sensitive, including the frequency composition (spectrum) of the sound (Oxenham, 2012). The first fMRI studies of cortical pitch responses used regular-interval noise (RIN), which is a type of noise to which the stimulus property of temporal regularity and the percept of pitch can be applied by a synthetic delay-and-add algorithm (Patterson et al., 2002; Hall et al., 2006). The use of low-pitch values, and a high-pass filter, minimizes the spectral ripple that occurs in the stimulus so that the stimulus can be compared with a control noise with the same passband to demonstrate responses that cannot be explained by changes in the time-averaged spectrum. The studies demonstrated maximal responses to RIN in lateral HG (although more medial responses in primary cortex are also observed; see Griffiths et al., 2010), which have been interpreted as pitch mappings. Similar activation in lateral HG has been demonstrated in an experiment in which a comparison was made between resolved harmonics (with high pitch salience) and unresolved harmonics (low pitch salience) in the same pass band (Penagos et al., 2004). Other studies have used forms of binaural pitch (Hall and Plack, 2007, 2009; Puschmann et al., 2010), in which the imposition of a phase shift between the ears in a particular passband can be associated with a pitch. The experiments with binaural pitch have demonstrated responses in lateral HG and the adjacent part of PT.

These human studies suggest a regional specialization for pitch in the lateral superior temporal plane. The precise interpretation of the studies is critically dependent on differences between pitch and control stimuli other than the presence of pitch. For example, the modeled representation of RIN stimuli in the auditory pathway (Hall and Plack, 2009) demonstrates slow fluctuations in the spectrum over time and, perceptually, the creation of RIN from noise produces timbral as well as pitch change. Experiments using a more refined type of control noise containing similar fluctuations did not show differences in RIN-related activation in lateral HG that are significant (Barker et al., 2012). Experiments using resolved and unresolved harmonics produce differences in the auditory spectrum as well as differences in the pitch percept. The experimental manipulations to produce binaural pitch also cause a difference in the perceived spatial location.
of a sound, although it is possible to control for this to some extent (Puschmann et al., 2010).

The studies above were all based on categorical comparison of pitch and control stimuli. Parametric designs, in which pitch strength is manipulated by continuous variation of the stimulus, provide a powerful way of seeking responses from putative pitch areas, which would be predicted to increase as a function of any accompanying change in pitch salience. A recent detailed study...
The experiments above all use external stimuli. A pitch mechanism should be active during the perception of pitch regardless of whether any stimulus is present. Illusory pitch as an aftereffect has been examined using magnetoencephalography (Hoke et al., 1996), but not fMRI. Illusions and contextual effects that change pitch value or salience have not been exploited in fMRI studies to date but will provide a further test of the concept of a perceptual mechanism.
pitch center. A number of studies have addressed musical experience without external stimuli at the level of pitch sequences in studies of musical imagery (Zatorre and Halpern, 2005).

**Pitch sequences and timbre**

Most pitch studies have assessed sequences in which the pitch was fixed, but natural stimuli including vocalizations and music usually contain pitch variation across sequences or in the form of glides. In passive listening experiments, the effect of varying pitch in sequences shows more distributed representation in the superior temporal lobe than that corresponding to a constant pitch. Studies show bilateral activity in the anterior temporal lobes and the posterior part of the superior temporal gyrus (Patterson et al., 2002; Warren and Griffiths, 2003). Pitch-sequence studies in which there is an active listening task also engage the inferior lateral frontal lobe (Overath et al., 2007). Such frontal mechanisms in the right hemisphere have previously been emphasized as a substrate for pitch working memory (Zatorre et al., 1994).

Pitch stimuli are always associated with timbre: a distinct perceptual quality. A detailed discussion of timbre is beyond the scope of this review (see Griffiths et al., 2009), although behavioral evidence suggests an interdependence of pitch and timbre perception (Moore and Glasberg, 1990; Krumhansl and Iverson, 1992; see also Oxenham, 2012). A number of fMRI experiments in which timbral dimensions are modified independently of pitch point to overlapping early substrates in auditory cortex in HG and PT (Warren et al., 2005; Overath et al., 2008, 2010), in addition to the engagement of remote areas such as the superior temporal sulcus. The early overlapping substrates for pitch and timbre in HG and PT might in future be disambiguated using pattern analysis as below.

**Beyond conventional pitch mapping**

Multivariate pattern analysis allows the discrimination of responses to stimuli with different characteristics that cannot be discriminated using conventional fMRI analyses using mass-univariate statistics (Haynes and Rees, 2006). A recent study (Staeren et al., 2009) examined the effect of pitch variation in natural sounds. Distinct patterns of response to different pitch values were demonstrated in the region spanning lateral HG and anterolateral PT. The result is consistent with the earlier studies using conventional fMRI analysis. Another way of examining responses within areas that are not shown by conventional analysis uses the phenomenon of repetition suppression: decrease in BOLD activity as a function of stimulus repetition. The technique allows a search for sensory coding mechanisms in neuronal populations independent of context. Models for the phenomenon (Grill-Spector et al., 2006) include adaptation within a defined population of neurons, a decrease in the pool of neurons from which a response occurs, and alteration in the response time course. The technique allows the search for suppression of responses to repeated pitch in a subpopulation of neurons regardless of the stimulus with which the pitch is associated, another predicted behavior of a pitch mechanism (Baumann et al., 2011).

**Future directions**

The human experiments above implicate regions lateral and posterior to primary auditory cortex in pitch representation, with ongoing debate about precise position. The data suggest a role for this area in pitch analysis based on experiments with different pitch-associated stimuli that might undergo initial sensory analysis in primary cortex. Preliminary data suggest that a similar pitch region lateral to primary cortex exists in the macaque, so that we are now in a position to establish a primate model for pitch perception using paradigms that are comparable to those used in humans. In addition to establishing regional organization, the macaque work will allow identification of key areas within the network for neurophysiology to further establish neural mechanisms for the abstraction and use of pitch.

Human fMRI is particularly suitable for examining the distributed processing circuit supporting pitch cognition, which has not been possible in previous studies based on passive listening. The roles of lateral and posterior portions of the superior temporal plane and their remote connections in active pitch listening, including selective attention, working memory, and object categorization, require further definition.

**References**


