Introduction

Recent advances in functional neuroimaging have made it possible to visualize the cortical regions that are activated during sensory perception. Apparently unitary perceptual experience actually involves the parallel activation of many different sensory representations on the cortical surface. For example, visually responsive regions cover more than 30% of the cortical surface and are divided into more than 30 distinct visual cortical fields that analyze different attributes of visual stimuli [1] including complex biologically significant signals such as faces [2].

Primate auditory cortex is also thought to contain more than a dozen auditory cortical fields (ACFs) as shown in Fig. 1a [3]. Central regions of auditory cortex are divided into core fields that receive direct projections from the ventral nucleus of the medial geniculate body and have the cellular characteristics of primary sensory cortex and surrounding belt fields that receive projections from the dorsal medial geniculate body and have cytoarchitectonic characteristics of association cortex [3,4].

Some progress has been made in understanding the role that different ACFs play in the analysis of auditory signals. However, auditory cortex is small (occupying less than 8% of the total cortical surface) and includes a number of fields that are largely inaccessible to neurophysiological recordings because of their locations within the Sylvian fissure. Roughly half of the ACFs so far studied show some evidence of tonotopic organization [5]. Functional magnetic resonance imaging (fMRI) studies of humans have revealed an organizational plan that is similar to that found in other primate species as summarized in the current review.

Locating human auditory cortex

Recent advances in neuroimaging technology [6] have made it possible to create average anatomical maps from populations of human participants that preserve the
detailed patterns of cortical folding and curvature to permit the accurate visualization of gyral structures, including Heschl’s gyrus, at the center of auditory cortex (Fig. 1b). fMRI activations can be coregistered with these anatomical maps to permit the cortical activations elicited by unattended sounds to be precisely localized on the cortical surface. These studies reveal that auditory cortex occupies 50–80 cm² of the cortical surface surrounding Heschl’s gyrus (Fig. 1c). Human auditory cortex (HAC) extends anterior–posteriorly from the planum polare to the planum temporale and mediolaterally from insular regions slightly medial to the tip of Heschl’s gyrus to the lateral surface of the superior temporal gyrus (STG).

Primary auditory cortex is characterized by its granular cytoarchitecture that has been mapped in the human brain using combined postmortem imaging and histological studies [7–10]. When the three-dimensional stereotaxic coordinates of A1 described in these histological studies are projected onto an average cortical curvature map using cortical-surface meta-analysis tools (http://www.ebire.org/hcnlab), A1 has a relatively consistent anatomical location in relation to surrounding gyral structures: A1 is typically centered slightly posteriorly to the tip of anterior Heschl’s gyrus and extending posterior-medially in Heschl’s sulcus and onto the superior temporal plane (Fig. 1d).

**Figure 1 A representation of primate auditory cortex**

(a) Twelve auditory cortical fields (ACFs) in the macaque with tonotopic fields colored to show frequency organization (red indicates high, blue indicates low). Core regions (A1, R, and RT) show mirror-symmetric tonotopic organization. See [3] for further details. (b) Average cortical curvature pattern of 60 participants. Green indicates gyri, red indicates sulci. The entire hemisphere is displayed using a Mollweide equal-area projection with auditory cortex at the center. (c) Population-averaged activations produced by broadband acoustic stimuli (speech sounds and speech-spectrum noise bursts) during visual attention when sounds were unattended. Activations are restricted to auditory cortex surrounding HG and the STG. The rectangular region shows the area enlarged in subpart (d) and in Fig. 2 below. (d) Meta-analysis of cortical-surface locations of Te1.1 (equivalent to A1) identified in postmortem cytoarchitectonic studies. Yellow indicates cortical-surface locations seen in more than 50% of participants. The rectangle shows region highlighted in subpart c. See text for further details. HG, Heschl’s gyrus; STG, superior temporal gyrus.

**Tonotopic organization**

Anatomical and functional studies of primates have suggested that auditory cortex contains a number of ACFs that are divided into central core fields and surrounding belt and parabelt fields as shown in Fig. 1a [11]. Many ACFs are organized tonotopically, that is, with a frequency representation mapped onto the cortical surface. In particular, the core fields at the center of auditory cortex have a mirror-symmetric tonotopic organization. Primary auditory cortex (A1) has a high-to-low frequency representation that abuts with a mirror-imaged representation (i.e., low-to-high) in the rostral core field (R). In addition, many of the belt fields also show tonotopic organization that often parallels that of the adjacent core field [12]. The mirror-symmetric tonotopic organization has been verified in fMRI studies of macaques [13].

A number of studies have examined the tonotopic organization of human auditory cortex [14–22] with results that vary somewhat based on stimulus and scanning parameters. However, when the distributions reported in these studies are subjected to meta-analysis and the results projected onto average cortical-surface anatomy, a relatively consistent tonotopic organization emerges (Fig. 2a). High-frequency sounds activate a small lateral region anterior to the intersection of Heschl’s gyrus and the STG and a more extensive medial region posterior to the tip of Heschl’s gyrus. In contrast, low-frequency sounds activate lateral regions centered on mid-Heschl’s gyrus and extending posteriorly along the STG.

The details of tonotopic organization can be more precisely visualized when activations are analyzed directly to the cortical surface of individual participants [19,20]. For example, Formisano et al. [23] found clear evidence of mirror-symmetric tonotopy when activations to tones of different frequency were mapped to the cortex of individual participants. Details of single-participant cortical-surface maps may be influenced by idiosyncrasies in the venous anatomy of individual participants [24], but population-averaged cortical-surface analysis reveals a similar pattern, as shown in Fig. 2b [25]. High-frequency tones (red) produce two foci of activation: a prominent band of activation posterior to Heschl’s gyrus (H1) and a smaller patch of activation anterior to Heschl’s gyrus near its border with the STG (H2). Low-frequency tones (blue) produce a consistent activation in mid-Heschl’s gyrus (L1) and inconsistent activations in more lateral fields (L-Lat). Finally, intermediate-frequency tones activate intervening regions (M1 and M2) along the H1–L1–H2 axis. In contrast, lateral
parabelt regions of auditory cortex show a general preference for low and middle frequencies but no consistent tonotopic organization that is evident in population-averaged analyses.

**Processing other acoustic features**

Activations in central regions of auditory cortex surrounding Heschl’s gyrus are strongly influenced by the acoustic parameters of sounds. For example, increasing the intensity of sounds results in systematic increases in the amplitude of activations in central regions of auditory cortex [21,25,26–29]. Moreover, the spatial distribution of activations changes with changes in sound intensity, consistent with an ampliotopic organization [25,30]. Activations in auditory cortex are also influenced by sound location: activations in each hemisphere are substantially larger to sounds delivered to the contralateral than to the ipsilateral ear [22,31], whereas binaural sounds elicit activations that are similar to those produced by contralateral monaural sounds [25,32].

In addition, changes in sound features elicit activations that can reveal the tuning properties of different regions of auditory cortex. Primate studies show that neurons in posterior ACFs appear to be more sharply tuned to the sound location than more anterior ACFs [5] whereas neurons in anterior ACFs are more sharply tuned to spectral features [33]. Figure 2c shows the results of the meta-analysis of 26 studies comparing the activation foci associated with the detection of infrequent pitch changes (red crosses) with the activation foci associated with infrequent changes in the sound location (blue crosses). The average location of activations to pitch changes was significantly anterior to the activation foci to location changes, consistent with suggestions of...
distinct auditory ‘what’ and ‘where’ auditory pathways in HAC [34–36].

Complex stimuli: vocalizations
Neurophysiological studies suggest that anterior belt fields in macaques are preferentially engaged in the analysis of primate vocalizations [33], and Petkov et al. [37] recently used fMRI to identify a vocalization-specific area in the anterior parabelt fields. Its location was similar to that of vocalization-specific regions previously identified in human fMRI studies [38,39]. Figure 2d shows speech-specific activations in the human parabelt vocalization area (PVA) isolated in conditions in which participants were performing a difficult visual task. Speech-specific enhancements in activations were restricted to the PVA, whereas activations in tonotopically organized central ACFs were slightly larger to the speech spectrum noise bursts. These results suggest that in humans, as in macaques, there is an anterior PVA that is specialized to process conspecific vocalizations.

The critical role of auditory attention
Although auditory attention is difficult to investigate in nonhuman primates, human studies demonstrate that attention has a powerful influence on auditory processing in many regions of HAC [40–47]. Intermodal selective attention studies [22,25,44,48,49] reveal that the largest attentional modulations are seen in lateral regions of auditory cortex. Interestingly, attention does not simply amplify sensory activations in a manner similar to increasing sound intensity. Rather, attention enhances activations in nontonotopic lateral regions of auditory cortex, whereas increasing sound intensity enhances activations in central ACFs as shown in Fig. 2c.

Conclusion
Brain imaging studies have revealed that HAC shares a pattern of functional organization with nonhuman primate species. These similarities are reflected in a schematic model of HAC shown in Fig. 2f. Central regions of HAC show a tonotopic organization similar to that seen in other primate species. Frequency-specific fMRI activations likely reflect activations at the boundaries of ACFs where several adjacent fields share similar frequency tuning.

Activations in central core and belt areas are largely determined by basic acoustic features, including intensity, spectral content and sound location. Anterior regions preferentially analyze spectro-temporal content whereas posterior regions preferentially analyze sound location. Although activations in core regions of auditory cortex can be modulated by attention, attention effects increase in surrounding belt and parabelt regions. These lateral regions lack tonotopic organization, are tuned to more complex and behaviorally relevant sounds such as speech and are strongly modulated by attention.

References and recommended reading
Papers of particular interest, published within the annual period of review, have been highlighted as:
• of special interest
• • of outstanding interest
Additional references related to this topic can also be found in the Current World Literature section in this issue (p. 416).


