Cortical processing of complex sounds

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Work on the functional organization of auditory cortex in nonhuman primates has recently gained increasing attention. Neurophysiological studies using complex stimuli, combined with anatomical tract tracing, reveal a hierarchy of cortical processing comparable to other sensory systems. On the basis of these findings from animal studies, together with the advent of modern neuroimaging methods used in human cortex, the field of auditory neuroscience could soon arrive at a detailed understanding of the cortical representation of complex sounds, including speech.

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Abbreviations

A1	primary auditory cortex
AL	anterolateral area
CL	caudolateral area
CM	caudomedial area
FM	frequency modulation, frequency-modulated
fMRI	functional magnetic resonance imaging
ML	middle lateral area
PET	positron emission tomography
R	rostral area
STG	superior temporal gyrus

Introduction

Complex natural sounds arrive at the ear as a mixture of multiple frequencies. As has been known for some time, the cochlea of the inner ear efficiently breaks down these complex, time-varying frequency spectra into narrow bands [1,2]. Neural processing in the ascending auditory pathways, amplified by positive feedback from corticofugal projections, achieves increasingly finer tuning of single neurons for a best frequency [3•,4•]. Preservation of neighborhood relationships between best frequencies leads to the well-known tonotopic representation in primary auditory cortex, analogous to the topographic maps found in other sensory systems, such as retinotopy in the visual cortex and somatotopy in the somatosensory cortex.

Work on the more peripheral stations of the auditory system using pure-tone stimuli, however elegant, does not explain how information about the tonal composition of complex sounds is re-assembled, how this information gives rise to perceptual and cognitive performance, and how memory traces for music or voices that can be recognized among thousands of others are formed. The obvious place in the brain in which these higher functions are performed is the cerebral cortex. If the ultimate goal is to understand the neural basis of human auditory cognition, including spoken language, then it may be advantageous to study animal models with brains most similar (i.e. closest in evolution) to those of humans.

Studies of nonhuman primates have led to a remarkable amount of knowledge about the cortical functional organization underlying visual perception. In addition to a detailed understanding of the primary visual cortex (V1) [5], these studies have revealed the existence of multiple representations, seemingly specialized for the processing of particular aspects of the visual world [6,7]. One influential suggestion [8] has been that the cortical visual pathways are organized into two processing streams: a ventral stream, which leads into the inferior temporal cortex, for visual pattern recognition or object identification; and a dorsal stream, which leads into the parietal lobe, for visual motion and spatial analysis.

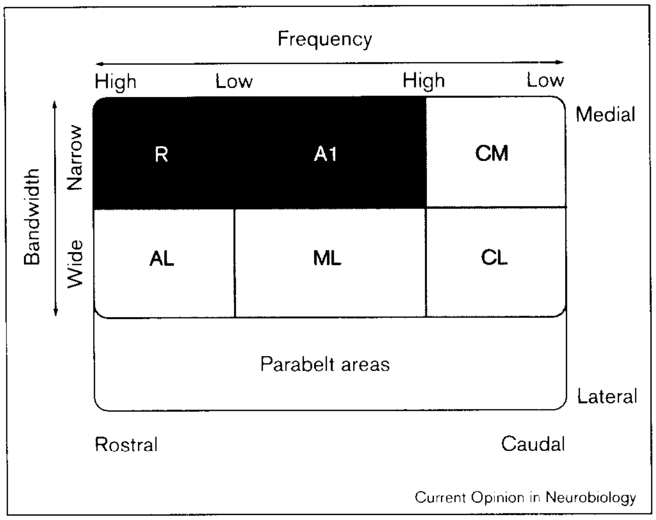
In this review, I will discuss recent results of single-unit recordings from primary and nonprimary auditory cortex in nonhuman primates, as well as anatomical tracer studies in the same animals. The responses of neurons to various types of complex sounds, including species-specific vocalizations, will receive particular attention, and the neural mechanisms of how selectivity for such sounds is attained will be discussed in relation to other species. Finally, I will present recent results of functional imaging studies from auditory cortex in humans and compare them with the findings from nonhuman primates. All these results taken together provide initial evidence for the existence of a dorsal stream for the processing of auditory spatial information and a ventral stream for the processing of auditory patterns, including communication sounds and speech.

Multiple areas in monkey auditory cortex

Perceptually, the auditory system has to deal with the same basic problems as the visual system: that is, identify patterns or objects and determine the spatial location of a stimulus. Both functions are achieved by integrating auditory information across its two major dimensions, frequency and time. By comparison with the visual system, much less is known about the functional organization of higher auditory pathways, even though a considerable amount of anatomical and gross electrophysiological information was collected early on [9,10]. The studies by Pandya and colleagues (see e.g. [10]) divided the auditory cortex (like other sensory cortices) into core and belt areas on the basis of cytoarchitectonics and connectivity. The first microelectrode mapping study of rhesus monkey auditory cortex was published a quarter of a century ago by Merzenich and Brugge [11]. They described several tonotopic areas on the supratemporal plane. Some of these areas were later characterized with modern histochemical techniques [12–14]. The existence of 2–3 core areas and several belt and parabelt areas has now also been confirmed on the basis of cortico-cortical connectivity [15••].

My colleagues and I [16••] have recently investigated the connections from the thalamus to the tonotopic areas on the supratemporal plane using a combination of lesion and anatomical tracing techniques. We found that the main relay nucleus in the auditory thalamus, the ventral part of the medial geniculate, projects independently to both the primary auditory cortex (A1) and the rostral area (R), whereas other areas, such as the caudomedial area (CM), receive input only from the dorsal and medial parts of the medial geniculate nucleus. Correspondingly, lesions of A1 abolished responses in CM, but not R. Thus, the cortical pathways in monkey auditory cortex are organized both in series and in parallel.

Figure 1



Schematic illustration of the relative sites of auditory cortical areas on the STG of the macaque monkey, as characterized by both single-unit mapping [16••,17] and anatomical (histochemical and tracing) techniques [15••]. Core areas are shown in dark shading, belt areas in light shading. Parabelt areas, which have yet to be characterized in detail by physiological mapping, are shown in white. Additional areas can be found rostrally and medially [15••].

Responses of superior temporal neurons to complex sounds

Thorough microelectrode mapping of nonprimary auditory cortex in macaque monkeys had not been performed until recently, because auditory neurons in these areas are hard to drive using conventional pure-tone stimuli. A few years ago, my colleagues and I [17] found that we were able to elicit reliable responses from most neurons in the lateral belt region by simply broadening the bandwidth of frequency-centered sound bursts. Somewhat surprisingly though, the majority of the neurons did not simply increase their response monotonically with increasing bandwidth, but preferred specific bandwidths (of such band-pass stimuli) over others. This finding of bandwidth selectivity is reminiscent of size selectivity in visual area V4 of the monkey [18]. Importantly, the neurons' bandwidth preferences are independent of sound intensity, which makes these cells highly suitable for auditory pattern recognition. In addition, bandwidth tuning seems to vary systematically along an axis that is orthogonal to the cochleotopic organization of best-center frequencies. Related findings have been reported for other species [19,20•]. The concomitant reversal of best-center frequencies permits a distinction of the lateral belt into at least three areas — anterolateral (AL), middle lateral (ML), and caudolateral (CL) — that are situated on the open surface of the superior temporal gyrus in parallel to areas R, A1, and CM, respectively (see Figure 1).

Another prominent feature of lateral belt neurons is their tuning for direction and rate of frequency modulation (FM) [21], as has been found in nonprimary areas of the cat's auditory cortex [22,23•]. Although FM selectivity is commonly found throughout the auditory pathways, it seems to be more pronounced in the lateral belt. The appropriate analogy to the visual system is tuning for movement direction and speed, which is also common in visual cortical areas. Tuning for FM rate varies between different cortical areas, both in cats and monkeys, and may provide hints as to the functional specificity of these areas in the processing of certain types of complex sounds.

Processing of communication sounds in monkey auditory cortex

Both types of sounds with intermediate complexity discussed in the previous section (i.e. band-pass noise bursts and FM sweeps) are ubiquitous components of communication sounds in many different species. Previous work on squirrel monkey auditory cortex [24] made it seem interesting to test responses of neurons in the lateral belt of the macaque to complete species-specific vocalizations, which were made available in digitized form from a library of calls collected by Hauser [25]. Perhaps not unexpectedly, considering their preference for broad-band sounds, many of the neurons responded vigorously to the monkey calls or their components. What was surprising, however, was that the lateral belt neurons displayed a fair amount of selectivity for different types of calls, which could not always be explained by mere frequency tuning. In many cases, frequencies outside the pure-tone tuning range of a neuron — which, by definition, do not evoke a response by themselves — led to a clear facilitation of the response when combined with frequencies inside the tuning range [17]. In other cases, two complex sounds evoked a response only when combined in the right temporal order [21]. In the auditory system of bats and songbirds, this property, both in the spectral and temporal domain, has been appropriately termed 'combination sensitivity' [26,27]. Nonlinear summation seems to be the main mechanism creating such selectivity in monkey auditory cortex, although suppression effects are also observed. Spectral summation involves convergence of inputs from more narrowly tuned neurons [28,29••]. Temporal summation occurs over a long time scale of several hundred milliseconds [29••], yielding neurons selective to complex sequences of sounds characterizing the animal's own vocalizations [30•,31•]. Nonlinear summation mechanisms have also been described in the visual system as a basis for selectivity to complex objects [32] and may thus be an important general principle for generating feature specificity in higher-order neurons.

A hierarchy of auditory cortical processing

Responses to species-specific (including human) vocalizations can also be found in A1 [33,34]. At least in the macaque, however, call selectivity is significantly less pronounced in A1 than in the lateral belt (J Fritz, B Tian, JP Rauschecker, unpublished data). Whether even the lateral belt areas are the final stage of communication call processing appears doubtful, but they seem to constitute an important way station in this complicated process. From neuroanatomical studies [13,15••] it looks as though the thrust of feedforward projections is towards anterior and lateral portions of the superior temporal gyrus (STG). If increasing proportions of call-selective neurons were found in these areas (i.e. from A1 to lateral belt to more anterior superior temporal areas), this would be compatible not only with a hierarchical organization of auditory cortical processing, but it would also be comparable to the visual system, in which face-selective neurons are found most commonly in anterior portions of the inferior temporal cortex [32,35]. Such neurophysiological findings from nonhuman primates are also in agreement with data from human studies, old and new, suggesting the processing of phonemes in the superior temporal region [36,37].

Neural representation of speech and music in human auditory cortex

Modern techniques of neuroimaging, in particular functional magnetic resonance imaging (fMRI), permit us to test the existence of hierarchical systems for the processing of complex sounds directly in the human auditory cortex. A first achievement was the demonstration of the tonotopic organization in what is presumably the equivalent of A1 using tonal stimuli [38•]. More complex sounds, similar to those used in nonhuman primates, were used to identify several areas on the STG, conspicuous by the reversal in their frequency organization (CM Wessinger, B Tian, JW VanMeter, RC Platenberg, J Pekar, JP Rauschecker, *Soc Neurosci Abstr* 1997, 23:2073). Comparison of the effects of tones versus band-pass noise revealed that sounds with greater bandwidth cause a more wide-spread activation into lateral regions of the STG. On these bases, it is possible to establish direct correspondences between these areas and those in nonhuman primates (e.g. A1, R, ML, etc.) [29••]. Finally, it has been shown that phonemes lead to even stronger activation in humans than the sounds of intermediate complexity, especially in more lateral regions of the STG, as has also been shown using other techniques [39]. This activation is intensified by selective attention [40•].

Like speech, music is a primarily human capacity. It has often been argued that music is merely a different form of the same ability to organize complex sounds into temporally ordered sequences [41]. Brain imaging and neuropsychological studies have shown that specific aspects of music, such as pitch and timbre, are represented predominantly in the right superior temporal cortex, along with prosody of speech [42,43]. By contrast, rhythm and speech sounds incorporating short-duration spectral changes (such as formant transitions) seem to rely more on left hemisphere mechanisms [44]. The critical period for the development of musical ability appears to be similar to that for the development of speech, ending at around seven years of age [45•].

A dorsal stream for auditory space processing

Sound localization is the second task for which the auditory system needs to process spectrally complex information. Compelling perceptions of spatially localized sounds can be created via headphones by programming spectrally specific cues into sounds [46]. Played back during PET imaging, such sounds lead to activation of areas in the parietal cortex previously thought to be involved only in visual spatial processing (RA Weeks, M Hallett, JP Rauschecker *et al.*, *Neurology* 1997, 48:S30.003). The same or nearby areas play a role in the perception of sounds moving in space [47]. Although spatially tuned neurons have been found in cats already at the level of A1 [48], one has to conclude from the human studies that the actual integration of auditory spatial information does not occur until higher levels of processing.

The hypothesis needs to be considered, therefore, that parietal cortex contains several space representations, each specialized for the processing of spatial information from different sensory modalities, including audition. In a next step, these unimodal spatial representations may then be integrated into a supramodal representation of space acting as a sensorimotor interface. A similar proposal has been made previously for cat anterior ectosylvian cortex [49].

Auditory projections to prefrontal cortex

Separate projections from the ventral and dorsal streams of the visual system lead into frontal cortex, where they are initially still kept separate [50,51], but they may eventually converge onto the same target regions [52]. The question arises as to how information from other sensory modalities, such as audition, gets integrated with the known visual pathways to the frontal cortex. Recent studies by Romanski and colleagues (LM Romanski *et al.*, *Soc Neurosci Abstr* 1997, 23:2073) show that tracer injections into physiologically identified locations within the belt areas of the auditory cortex lead to rather distinct patches of labeling in prefrontal cortex. It is conceivable that visual–auditory associations, such as those made during lip-reading [53•], are initially formed in some of these regions, from where top–down influences are exerted via feedback connections into primary sensory areas.

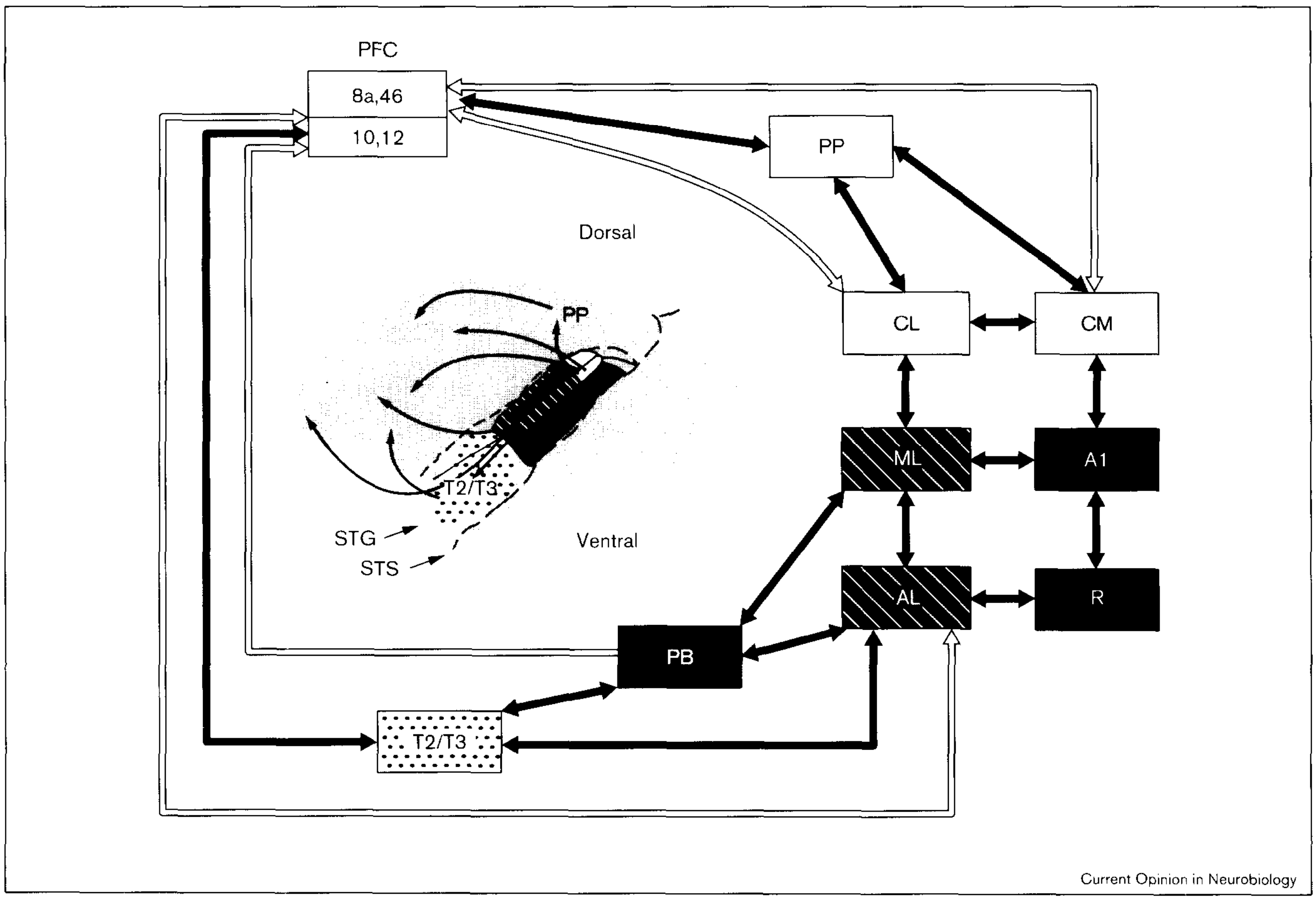
Conclusions

From the existing anatomical and electrophysiological data on the rhesus monkey, supplemented by data from cat electrophysiology and from human brain imaging, it appears that auditory information may be processed in two largely separate cortical streams, comparable to those in the visual system (see Figure 2). Both pathways originate in the core areas of the auditory cortex on the supratemporal plane (areas A1 and R). One pathway, which seems to specialize in the processing of auditory patterns (including sounds used for vocal communication), projects into various areas in the lateral belt (and parabelt) of the superior temporal cortex. The second pathway, specialized for the processing of auditory spatial information, leads into parietal areas. Both pathways eventually converge onto areas of the prefrontal cortex.

In each of these pathways, frequency-specific information is combined in a highly detailed fashion that characterizes auditory patterns and spatially specific sounds by virtue of their spectro-temporal signatures. In this way, the auditory system is no different from the visual system. The existence of multiple representations, organized in a hierarchical way, suggests a similar mode of operation as in other sensory systems, with specialized areas representing specific aspects of the auditory world.

The capacity of humans to use minute differences in frequency, FM rate, bandwidth, and timing as a basis for speech perception suggests that, during evolution, these dimensions might have become more enhanced

Figure 2



Schematic of the flow of information within the cortical auditory system of the macaque monkey. A dorsal and a ventral stream are shown for the processing of auditory spatial and auditory pattern information, respectively. The caudal areas on the STG give rise to the dorsal stream feeding into parietal areas. The anterior portions of the lateral belt give rise to a feedforward loop into the rostral STG. Both streams eventually project to the frontal cortex, which integrates both auditory spatial and object information with visual and other modalities. PB, parabelt areas; PFC, prefrontal cortex (consisting of areas named inside box); PP, posterior parietal cortex (consisting of inferior and superior lobule); STS, superior temporal sulcus; T2/T3, second and third temporal fields [13].

relative to other primate species. Therefore, our unique ability for speech communication may have first resulted from an expansion of a generic auditory communication system. The really new trick about human language, however, seems to be founded in the fact that it ties a high-resolution system for phonological decoding with more efficient memory mechanisms and an ability for abstraction, both residing in a highly developed and expanded frontal cortex.

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