Auditory processing in primate cerebral cortex

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Auditory information is relayed from the ventral nucleus of the medial geniculate complex to a core of three primary or primary-like areas of auditory cortex that are cochleotopically organized and highly responsive to pure tones. Auditory information is then distributed from the core areas to a surrounding belt of about seven areas that are less precisely cochleotopic and generally more responsive to complex stimuli than tones. Recent studies indicate that the belt areas relay to the rostral and caudal divisions of a parabelt region at a third level of processing in the cortex lateral to the belt. The parabelt and belt regions have additional inputs from dorsal and magnocellular divisions of the medial geniculate complex and other parts of the thalamus. The belt and parabelt regions appear to be concerned with integrative and associative functions involved in pattern perception and object recognition. The parabelt fields connect with regions of temporal, parietal, and frontal cortex that mediate additional auditory functions, including space perception and auditory memory.

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Abbreviations

AI	primary auditory cortex
AL	anterolateral field
CL	caudolateral field
CM	caudomedial field
EP	evoked potential
MG	medial geniculate complex
MGd	dorsal division of MG
MGm	medial division of MG
MGv	ventral division of MG
ML	middle lateral field
R	rostral core field
RT	rostrotemporal field
STG	superior temporal gyrus
TG	transverse gyrus of Heschl

Introduction

Recent years have witnessed a growing interest in the basic neural mechanisms underlying auditory cortical processing in primates. This interest has been kindled, in part, by the development of noninvasive techniques for physiological investigations of auditory perception in humans. Because microelectrode recordings in human auditory cortex are possible only under the rarest of circumstances, and *in vivo* tracer studies not at all, advances in knowledge about single-unit physiology, connectivity, and physiological–microanatomical correlates are fueled by research in nonhuman primates and other mammals [1,2]. For anatomical [3,4], functional [5,6], and phylogenetic reasons, research in macaque auditory cortex may be especially relevant to humans.

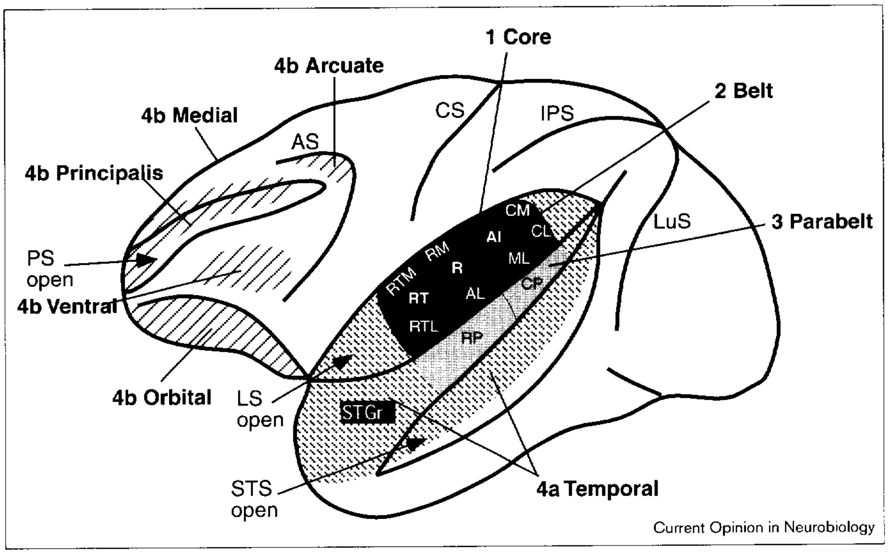
Physiological and functional data are best interpreted within an anatomical framework for auditory processing in superior temporal cortex. We subdivide primate auditory cortex into three areas — the core, belt, and parabelt — on the basis of their cochleotopic organization, connectional relationships, and architectonic features (Figure 1). Each region includes several subdivisions with parallel connections, and each region constitutes one stage in a series of connections. Connections of the parabelt with heteromodal and supramodal regions of temporal, frontal, and parietal cortex form a distributed network for auditory cognition (Figure 2). This review describes current views of auditory cortical processing in primates based on recent anatomical and physiological studies.

Hierarchical and parallel processing in the core, belt, and parabelt

Over the past several years, microelectrode recordings, tracer studies, and histochemical analyses [7,8,9••,10, 11••–13••] have provided a detailed account of the hierarchical and parallel organization of macaque auditory cortex. The core area has histological features of primary sensory cortex: koniocellular architecture, dense myelination, and dense reactivity for cytochrome oxidase, acetylcholinesterase, and parvalbumin. Initially, much or all of the core area was considered to be the classical primary auditory field, AI. However, recent studies have revealed that the core contains three cochleotopically organized fields, all of which receive dense inputs from the ventral division of the medial geniculate complex (MGv). In AI, the largest, most caudal field, the histological features listed above are most pronounced, and low-to-high frequencies are mapped anterolaterally to posteromedially. In the rostrotemporal field (RT), the smallest, most rostral field, the above histological features are least pronounced and low-to-high frequencies are mapped. The rostral core field, R, which is intermediate to AI and RT in position, size and histological features, has a posterior-to-anterior representation of low-to-high frequencies. This anatomical organization, together with physiological evidence that ablation of AI does not abolish neuronal pure tone sensitivity in R [11••], suggests that auditory information is processed in series from the MGv to the core and in parallel within the three core fields.

In the human literature, there exists some variability across studies concerning the prevalence and precise orientation of cochleotopy within the transverse gyrus of Heschl (TG),

Figure 1



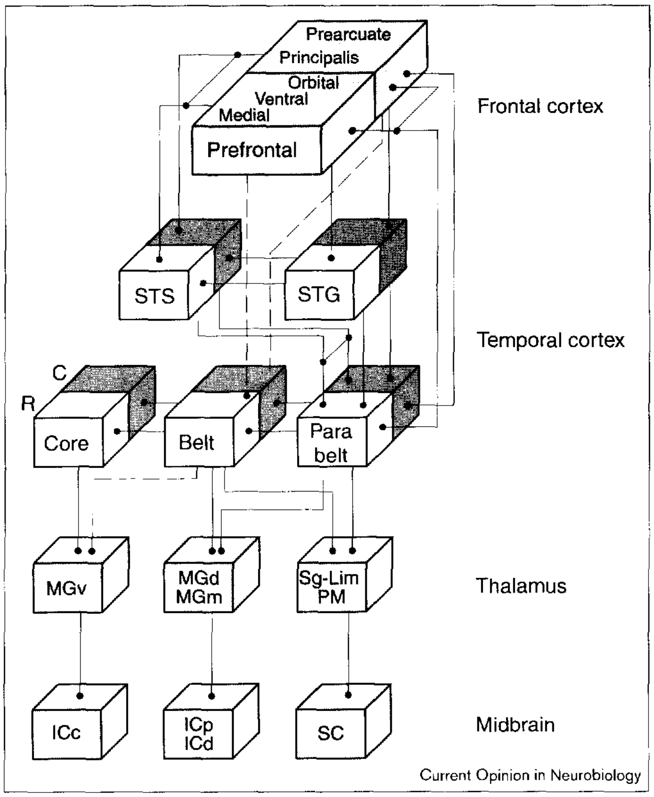
Levels and regions of auditory cortical processing. The lateral sulcus (LS) has been opened to show auditory areas of the lower bank (upper bank not shown), and the superior temporal sulcus (STS) has been opened to show the extension of auditory-related cortex into this sulcus. Level 1 represents the core (darkest shading); level 2 represents the belt (moderate shading); level 3 represents the parabelt (light shading); level 4a represents the temporal region (dense hatching); and level 4b represents the frontal region (sparse hatching).
AL, anterolateral; AS, arcuate sulcus; CL, caudolateral; CS, central sulcus; IPS, intraparietal sulcus; LuS, lunate sulcus; ML, middle lateral; PS, principal sulcus; RM, rostromedial; RTL, lateral rostrotemporal; RTM, medial rostrotemporal; STGr, rostral superior temporal gyrus. Based on data from [12••,13••,37•,38•].

wherein koniocortex resides [4]. The current consensus among magnetic and electrical evoked potential (EP) studies [14–16], functional imaging studies (for a review, see [17]), and a microelectrode study in an epilepsy patient [18] is that low-to-high frequencies are mapped anterolaterally to posteromedially in TG — similar to the orientation found in macaque AI. Some EP results [19] and preliminary functional imaging data [17] raise the possibility of two cochlear representations in TG that could constitute the human homologs of macaque AI and R. In macaques and humans, the functional consequences of bilateral lesions involving the core area or its inputs typically include a profound deficit in sound detection that at least partially resolves over months and leaves the listener with trouble perceiving what is heard and where it is coming from [5,20–22].

The belt region, which surrounds the core, does not exhibit the histological features of primary sensory cortex and does not receive dense projections from MGv. It receives most of its afferent input from the core area and the dorsal (MGd) and medial (MGm) divisions of the medial geniculate complex, with a minor contribution from MGv. The belt region has been subdivided into several different fields on the basis of separate cochlear representations, histochemical features, and trends in connectivity patterns. Acknowledging differences in gerrymandering among different authors and a paucity of systematic microelectrode studies, we interpret existing data as evidence that the belt area contains seven fields, named according to their relative positions along the superior surface of the superior temporal gyrus (STG; Figures 1 and 2). Cochleotopy has been reported in anterolateral (AL), caudolateral (CL), caudomedial (CM), and middle lateral (ML) fields [7,9••,10,11••]. First spike latencies have been found to be longer in the lateral belt than the core in two of three studies in alert macaques [23–25]. Pure tone sensitivity in CM relies on the integrity of AI in anesthetized macaques [11••]. Thus, the belt area represents a second stage in the hierarchical processing of auditory information along the MGv→core→belt pathway. The belt also processes MGd and MGm inputs in parallel with core inputs across its several subdivisions. In humans, the distribution of EP response latencies are consistent with serial processing extending from the core area in TG into surrounding areas along the STG [19,26,27]. Subdural recordings have identified a cochleotopically organized area on STG lying caudal to TG [28], and preliminary functional imaging data suggest two cochleotopic fields on the superior surface of STG [17] that may represent the human homologs of lateral belt fields.

The parabelt area lies adjacent to the lateral belt fields along the lateral surface of the STG. The parabelt has strong connections with the belt area and minimal connections with the core area [12••]. Like the belt, the parabelt receives thalamic input from MGd and MGm; in addition, the parabelt has strong connections with the medial pulvinar, suprageniculate, and limitans nuclei [13••]. The rostral parabelt receives inputs selectively from rostral belt fields, whereas the caudal parabelt receives most inputs from the caudal belt fields. Thus, the parabelt lies within a third stage of cortical processing within the MGv→core→belt→parabelt pathway. The parabelt also processes thalamic inputs in parallel with belt inputs across its subdivisions. In the rostral parabelt, neurons are generally sensitive to white noise but not to pure tones [9••]. In the caudal parabelt, most neurons respond to sounds in contralateral space, many respond to pure tones over a wide range of frequencies, some manifest motion sensitivity and direction selectivity, and few, if any, are heteromodal, visual, or somesthetic [29,30]. In macaques, Cebus monkeys, and humans, bilateral lesions that involve the belt and parabelt but spare at least part of the core typically impair auditory pattern perception

Figure 2



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Connections and levels of processing in the primate auditory cortex. Solid lines denote major connections, and dashed lines denote minor connections. The main stream of processing involves the central nucleus of the inferior colliculus (ICc), the ventral nucleus of the medial geniculate complex (MGv), and the core areas of the auditory cortex. A parallel stream also involves the dorsal (ICd) and pericentral (ICp) divisions of the inferior colliculus, the dorsal (MGd) and medial (MGm) divisions of the medial geniculate complex, and the belt cortex. The superior colliculus (SC) projects to parts of the medial pulvinar (PM), suprageniculate (Sg) and limitans (Lim) nuclei, as a possible third source of auditory input to the parabelt cortex. Additional levels of processing involve cortex of the superior temporal gyrus (STG) adjoining the belt and parabelt regions, superior temporal sulcus (STS), and prefrontal cortex. The preferential connections of rostral (R) and caudal (C) sectors of cortex are indicated.

(e.g. discrimination of tone sequences) with little or no effect on sound detection [31–34]. Some human functional imaging studies demonstrate greater STG activation during passive stimulation with speech or music than with noise [35,36]. Auditory priming in humans can be sustained after complete bilateral lesions of the core area, presumably because spared portions of the belt and parabelt continue to receive auditory input via parallel pathways ascending from nonMGv thalamus [21] and to sustain reciprocal connections with memory-related structures.

Auditory processing extends beyond auditory cortex via connections of the parabelt and, to a lesser extent, the belt with specific regions of adjacent temporal cortex, medial temporal cortex, prefrontal cortex, and parietal cortex [8,12••,37•,38•]. In awake macaques, neuronal activity in auditory cortex is influenced by level of arousal, general attention, directed auditory attention, and perceptual task requirements [25,29,39,40], probably through descending projections from these cortical regions as well as ascending projections from the reticular activating system and nonspecific thalamic inputs [41]. Many neurons in these regions are heteromodal and participate in cognitive aspects of auditory processing [30,42–45]. In humans, EPs have been recorded in the frontoparietal operculum using intracortical [46] and subdural [47] electrodes. Increased blood flow in dorsolateral prefrontal cortex has been reported during phoneme and pitch discrimination [35], possibly in relation to its role in working memory [48]. Cognitive aspects of auditory processing have been of great interest in human EP and functional imaging studies [49–51]. Lesions involving the temporoparietal junction or posterior parietal cortex, especially in the right hemisphere, are often associated with impaired spatial localization, extinction, or frank neglect of auditory stimuli presented in contralateral acoustic space [52]. Similarly, ablations of the inferior parietal lobule and temporoparietal junction in macaques produce hemi-inattention to contralateral auditory and other sensory stimuli [53]. Right frontal lobe lesions in humans are also associated with auditory hemi-inattention [54].

Neural coding of spectral, temporal, and spatial information

Individual neurons in the core and belt areas change the rate and timing of their activity as a function of the spectral content of an auditory stimulus, its temporal features, and its spatial location. Recent quantitative analyses of frequency-dependent changes in firing rate at threshold and suprathreshold intensities have demonstrated sharp tuning in alert [55•,56–58] and anesthetized monkeys [9••,11••,59]. Populations of AI neurons sensitive to a particular frequency range synchronize their firing during pure tone stimulation, and coordination of spike timing provides information about the stimulus even when mean firing rates do not change [60]. In anesthetized monkeys, peaks in isointensity and isorate functions for on-excitation are generally sharper in core than in belt areas [9••,11••]. Whereas neurons in the core region tend to discharge at higher rates during stimulation with pure tones than with narrowband noise, the opposite is true of neurons in the lateral belt areas [10]. These results suggest a convergence of inputs from core neurons sensitive to adjacent frequencies onto each lateral belt neuron. In general, lateral belt neurons also fire more vigorously during stimulation with species-specific vocalizations than with pure tones [10].

In the absence of barbiturate anesthesia, many neurons show frequency-dependent patterns of excitation and inhibition that unfold over time in relation to the stimulus — for example, on-excitation at one spectral location, and on-inhibition or off-excitation at another [39,55•,58,61–63]. Receptive field dynamics in auditory cortex may provide a neural mechanism for the integration of spectral information over time necessary to perceive natural sounds, including vocal communication sounds [64]. Recent accounts of developmental and acquired language disorders have emphasized the contribution of temporal processing mechanisms to speech processing in humans [65,66].

Most neurons in unanesthetized squirrel monkey auditory cortex synchronize their firing and/or increase their firing rate as a function of periodic fluctuations in the temporal envelope of complex waveforms [67]. AI neurons generally show better temporal resolution than neurons in surrounding areas. Phase-locking to slow envelope fluctuations in a species-specific vocalization has been observed across subpopulations of AI neurons in barbiturate-anesthetized marmosets [68]. Averaged multi-unit activity in AI of unanesthetized macaques is time-locked to abrupt envelope changes in consonant–vowel syllables and to envelope periodicities embedded in vowel sounds and click trains [69,70,71•]. While there is EP evidence that periodicity pitch is represented by the place of maximal activity in human AI [72], single-unit and averaged multi-unit recordings in macaques show no evidence of place-rate coding [73,74]. Because stimulus fundamental frequencies associated with the upper limits of phase-locking and periodicity-dependent rate changes are well below those associated with pitch percepts for the vast majority of AI neurons, the role of these temporal coding mechanisms in virtual pitch perception has been called into question.

In alert human auditory cortex, the excitatory bandwidths of isointensity functions for most single neurons recorded by Howard *et al.* [18] were roughly compatible with the grain of neuronal frequency selectivity recorded in alert and anesthetized macaques. The coarsening of frequency resolution observed in humans after bilateral lesions of core and belt areas [21,57] may be attributable to loss of frequency-selective neurons. Frequency-specific narrowing of isorate functions, shortening of response latencies, and expansion of areal representation have been observed in anesthetized owl monkey AI following several weeks of training on a frequency discrimination task [59]. These results indicate that neuronal frequency sensitivity and selectivity are dependent on experience into adulthood. In musicians, experience-dependent enlargement of the N100m EP elicited by piano tones relative to pure tones has been reported [75], and the size of the left caudal STG surface correlates with early training and absolute pitch ability [76].

Neurons in auditory cortex encode spatial location principally through mechanisms of binaural integration that utilize both rate- and time-based codes. Frequency-selective neurons in the core and lateral belt of awake macaques change their firing rate as a function of interaural intensity differences in the range of approximately 5–25 dB SPL (sound pressure level) and, for tones below about 2 kHz, interaural time delays as low as a few hundred milliseconds [77]. Approximately 90% of neurons fire most strongly when a tone or broadband noise is presented at the midline or in the contralateral hemifield [40,78], and there is limited evidence suggesting that neurons lying along a given penetration prefer the same spatial location [40]. Many neurons in the core, lateral belt, caudal belt, and caudal parabelt manifest broad spatial tuning [29,40]. Spatial selectivity for horizontal separations finer than 10 degrees (about three times the psychophysical thresholds in macaques) has not yet been demonstrated in individual neurons [56], but could be supported by rate information carried by populations of neurons [79]. About one-third of neurons in the core area are sensitive to the presence and direction of motion along the horizontal azimuth; in general, azimuthal location determines the temporal pattern of excitation (e.g. transient on-excitation, sustained on-excitation, or off-excitation), and motion determines the magnitude of excitation within the corresponding time epoch [78]. Most prefrontal and posterior parietal neurons respond more strongly or exclusively during processing of contralateral auditory stimuli [44,45].

In both humans and macaques, unilateral lesions of superior temporal cortex and of connected areas in prefrontal and inferior parietal cortex impair the ability to localize sounds within the contralateral hemifield [22,52,80,81]. Inability to detect sound movement using interaural phase and/or amplitude modulation cues has been documented in a patient with a lesion involving the right posterior temporal lobe, inferior parietal lobule, and insula [82].

Conclusions

Recent studies indicate that the auditory cortex of primates has several distinct levels of processing. In the core area, cortical processing is initially carried out in parallel across the three cochleotopically organized fields. The three core fields project to a narrow surrounding belt area comprising approximately seven fields, at least four of which exhibit cochleotopic organization. The belt area also receives medial geniculate inputs through a secondary pathway. The parabelt area, a third level of processing, receives inputs from the belt and thalamus and projects to temporal, frontal, and parietal cortex for higher stages of processing. The degree to which differences in physiological response properties and behavioral functions map onto different anatomical stages of processing is an active area of research. In general, results in monkeys and humans are consistent with the notion that spectral and temporal features of sound are extracted in the core area and integrated in the belt and parabelt areas to form mental representations of auditory objects and their spatial locations. Multimodal integration and cognitive influences on auditory percept formation are realized through connections of the parabelt with heteromodal and supramodal cortices.

Acknowledgements

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Single- and multi-unit recordings in barbiturate-anesthetized macaques disclose greater frequency selectivity and lower intensity thresholds in the core area than in the belt area. The authors relate physiological response properties and tonotopic maps to parvalbumin staining patterns in core, belt, and parabelt fields, and they provide some of the few tuning curves available in the primate auditory cortex literature.

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This study combines microelectrode recordings of fields AI, R, and CM, tracer injections, and selective AI ablation in isoflurane-anesthetized macaques. AI lesions markedly reduced the sensitivity of neurons in field CM to pure tones but often spared their sensitivity to complex stimuli; in contrast, AI lesions had relatively little effect on pure tone sensitivity in field R. Peak firing rates in AI and R were higher for tones than for complex stimuli, whereas peak rates in CM were higher for complex stimuli than for tones. Taken together, the findings support the hypothesis that low-level spectral processing is carried out in parallel across subareas of the core and serially from the core to the belt.

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Injections of anterograde and retrograde tracers were made into numerous areas of the prefrontal cortex of macaque monkeys. The resulting patterns of connections were examined with respect to the auditory belt and parabelt regions. Injections of the rostral and orbital prefrontal areas (areas 10, 46 rostral, and 12) labeled rostral portions of the belt and parabelt most heavily. Injections of the caudal principal sulcus (area 46), periarcuate cortex (area 8a), and ventrolateral prefrontal cortex (area 12vl) primarily labeled the caudal belt and parabelt. The results suggest that rostral and caudal domains of the prefrontal cortex are targeted by divergent projections of the nonprimary auditory cortex that may also be functionally distinct. See also [38•].

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