tion reaction was used to transform *Escherichia coli* [C. L. Hseih *et al.*, *Mol. Cell. Biol.* **11**, 3972 (1991)] by electroporation; the bacteria were grown overnight on agar plates containing ampicillin (100 μg/ml; Sigma). Colonies were expanded for plasmid DNA isolation and double-stranded DNA sequencing with the use of PRISM Ready Reaction Dyedeoxy Terminator Cycle sequencing reactions as recommended by the supplier (Applied Biosystems, Foster City, CA) with a $V_\beta 3$ primer (CTCTGCTGAGTGTCCTTCAA) ($V_\beta 3.2$); we then performed gel electrophoresis with detection and analysis of the fluorescent product using the Applied Biosystems model 373A DNA sequencing system. No repeat sequences were found in either the naive resting group or the unactivated populations; one of 24 sequences was repeated in the 8 weeks post-primary group [and this bore the typical NNA motif (where N is Asn and A is Ala) of PCC reactivity]. Many repeats were found in both activated groups. In the primary-activated group, 11 unique sequences were found among the 30 clones; of these sequences, four were repeated 12, 6, 3, and 2 times. In the memory-activated group, there were eight unique sequences of the 26 clones from the population analysis; of these, four were repeated 12, 5, 3, and 2 times. Of the 15 single cells, there were 10 unique sequences, two of which were repeated 5 and 2 times.

30. Abbreviations for the amino acid residues are A, Ala; C, Cys; D, Asp; E, Glu; F, Phe; G, Gly; H, His; I, Ile; K, Lys; L, Leu; M, Met; N, Asn; P, Pro; Q, Gln; R, Arg; S, Ser; T, Thr; V, Val; W, Trp; and Y, Tyr.

31. Immunization, staining for flow cytometry, cell sorting, cDNA synthesis, PCR, "nested" PCR, and DNA sequencing were undertaken as described (*29*) with variations as follows. Individual cells were sorted into tubes containing 5 μl of cDNA reaction mix with the use of oligo(dT) for priming (Becton Dickinson Labware, Bedford, MA). All 5 μl of the cDNA reaction was used for the first 35 cycles of PCR with β chain–specific primers $C_\beta.2$ and $V_\beta 3.L.2$ (*29*) together with a C_α-specific primer (GTTTTGTCAGTGATGAACGT) ($C_\alpha.1$) and $V_\alpha 11$ leader–specific primer (ATGCAGAGGAACCTGGGAGC) ($V_\alpha 11.L1$). For the second 35 cycles of PCR, "nested" primers for each chain were used in separate reactions: C_β-specific (AATCTGCAGCACGAGGGTAGCCTTTTG) ($C_\beta.3$) and $V_\beta 3$-specific (AATCTGCAGAATTCAAAAGTCATTCAG) ($V_\beta 3.1$) for the TCRβ chain and C_α-specific (AATCTGCAGCGGCACATTGATTTGGGA)($C_\alpha.2$) and $V_\alpha 11$ leader–specific (AATCTGCAGTGGGTGCAGATTTGCTGG) ($V_\alpha 1.12$) for the TCRα chain. The primer $V_\beta 3.2$ (*29*) and one specific for C_α (GGCGTCGTCGACGAACAGGCAGAGGGTGCTGTCCTGAG) ($C_\alpha.3$) were used for direct sequencing of the PCR product after column separation of PCR product from primers.

32. Animals were immunized and populations sorted by phenotype as described (*29*). "Sequence" in Table 1 shows a summary from data presented in Fig. 2. "Dot blot" shows the results from screening PCR products containing $V_\beta 3$-amplified DNA from the sorted populations as described (*29*). These products were titrated onto Hybond N (Amersham, Arlington Heights, IL) nylon filters and probed with ^{32}P kinase-labeled oligonucleotide specific for the N(N/S)A sequence and three nucleotides in each of $V_\beta 3$ and $J_\beta 1.2$ (CTGAACAATGCAAAC) and subsequently with an oligonucleotide specific for all $V_\beta 3$ sequences (primer: $V_\beta 3.2$) (*29*) under conditions where only 2 base pairs of mismatch was tolerated, with hybridization at 54°C and washing at 58°C in 3 M tetramethylammonium chloride solution as described [R. P. Dong *et al.*, *Tissue Antigens* **39**, 106 (1992)]. Filters were exposed to a phosphor screen and quantified on a Molecular Dynamics PhosphoImager with ImageQuant software (Molecular Dynamics, Sunnyvale, CA). "Colonies" in Table 1 shows the results after subcloning PCR products from the sorted populations (*29*). The colonies were then transferred onto Hybond N and probed with the same labeled oligonucleotide in 30% formamide containing 3× SSPE hybridization solution at 42°C for 5 hours, and washed finally in 0.2% SSPE at 30°C. Overall, this mode of analysis greatly increased the size of sample screened from each population (500 to 4000 $V_\beta 3^+$ colonies screened) and gave similar results from two independent screens of clones derived from separate ligation reactions. We estimated the total cell counts by extrapolating the frequency obtained by the colony lift assay to the total cell counts estimated by flow cytometric analysis (as described in Fig. 1) for cells with the appropriate phenotype.

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Processing of Complex Sounds in the Macaque Nonprimary Auditory Cortex

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Neurons in the superior temporal gyrus of anesthetized rhesus monkeys were exposed to complex acoustic stimuli. Bandpassed noise bursts with defined center frequencies evoked responses that were greatly enhanced over those evoked by pure tones. This finding led to the discovery of at least one new cochleotopic area in the lateral belt of the nonprimary auditory cortex. The best center frequencies of neurons varied along a rostrocaudal axis, and the best bandwidths of the noise bursts varied along a mediolateral axis. When digitized monkey calls were used as stimuli, many neurons showed a preference for some calls over others. Manipulation of the calls' frequency structure and playback of separate components revealed different types of spectral integration. The lateral areas of the monkey auditory cortex appear to be part of a hierarchical sequence in which neurons prefer increasingly complex stimuli and may form an important stage in the preprocessing of communication sounds.

In 1973, Merzenich and Brugge described several auditory areas on the supratemporal plane (STP) of the macaque brain, surrounding primary auditory cortex AI (*1*). One of these areas, which they termed L, extends laterally alongside AI and onto the exposed lateral surface of the superior temporal gyrus (STG). Anatomically, several areas have been identified in this region on the basis of cyto-, myelo-, and chemoarchitecture (*2–4*). In particular, the term "belt" has been introduced to characterize the cortical region that adjoins the koniocortical primary area laterally (*2*). Little is known about the functional properties of neurons in any nonprimary auditory cortical areas of the monkey, because these neurons tend to respond poorly and inconsistently to conventional pure-tone (PT) stimuli (*5*).

Neurons in the nonprimary visual cortex similarly do not respond well to small stationary spots of light. Extrastriate neurons have larger receptive fields and prefer more complex stimuli than do neurons in the striate cortex (*6*) because they integrate visual information spatially over a larger range. By the same token, auditory neurons that are higher up in the processing pathway might be expected to integrate information over a larger range of frequencies. We therefore used one set of auditory stimuli that consisted of bandpassed noise (BPN) bursts with variable bandwidth around a given center frequency. This type of stimulus is directly analogous to a bar or spot of light with variable size at a given receptive field position in the visual system. Thus, our experiments were designed to test for the existence of neurons that prefer a certain bandwidth of BPN bursts, just as neurons in the extrastriate cortex prefer a certain size of visual stimulus (*7*).

We selected a second type of auditory stimulus on the basis of the following considerations. In humans, the lateral surface of the STG includes areas 42 and 22 of Brodmann, which correspond to areas TB and TA, respectively, of von Economo (*8*). Lesions in these areas, especially in their posterior parts, cause deficits in speech perception but have relatively little effect on general auditory discrimination (*9*). Hence, from an evolutionary and comparative neuroanatomical perspective, it was of interest to include species-specific communication calls as another type of wide-band signal. Previous nonhuman primate studies of this type have been performed only with squirrel monkeys (*10*).

Electrode penetrations were made along both sides of the lateral fissure into the

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STG and STP of the left hemisphere in seven adult rhesus monkeys (*Macaca mulatta*) (*11*). In six of the monkeys, recordings were obtained from the lateral belt region. For comparison, recordings were obtained from the primary-like areas AI and R [the rostral area (*4*), previously termed RL or rostrolateral area (*1*)] in three of the monkeys. An average of 15 electrode tracks per monkey were distributed across the STG and STP; their orientation was approximately orthogonal to the cortical surface. At least three recordings per penetration were obtained, yielding a total of 400 recording sites.

We directly compared single-unit responses to PT and BPN stimuli at the same intensity levels in 158 neurons of the lateral belt region (*12*). Although PT bursts often had little effect, BPN bursts elicited a clear response in more than 90% of the neurons. In 129 of the 158 neurons, the response to BPN exceeded the response to PT. In one such example (Fig. 1, A and B), PT bursts elicited only a small response, while BPN bursts evoked a markedly enhanced response at every center frequency. Both center frequency and bandwidth were varied over a wide range for 81 cells (Fig. 1C; see also Fig. 3). Responses to PT and BPN were then compared quantitatively at the best frequency and bandwidth (that is, those that elicited a maximal response) by calculating the ratio (BPN − PT)/PT × 100% for each neuron. In 50 of the 81 neurons (61.7%), enhancement of the response to BPN over the response to PT was greater than 50%, and increases above even 150% were seen in 18 neurons (22.2%). The opposite effect (that is, a suppression of the response by more than 50%) occurred in only two neurons (2.5%).

On the basis of these responses, we determined best center frequencies (BF_c's) for most neurons. In electrode tracks perpendicular to the cortical surface, BF_c's remained largely unchanged, so that a BF_c value could be assigned to each penetration from the average of all neurons recorded in it. Maps of BF_c's were plotted on the STG and STP; these maps revealed continuous rostrocaudal progressions, with two reversals (Fig. 2). From the central portion of the mapped region, BF_c increases caudally, then reverses and decreases until a nonresponsive area is reached close to the junction of the lateral sulcus and the superior temporal sulcus. Proceeding rostrally from the central portion, BF_c decreases, reverses, and then increases again. Similar BF_c's were found in adjacent portions of the STP in all monkeys. Thus, at least three coarsely cochleotopic areas can be defined within the lateral belt of the macaque auditory cortex. We term these the anterolateral (AL), middle lateral (ML), and caudolateral (CL) areas, respectively (*14*). Area CL has not been described physiologically before, but its location relative to AI and the caudomedial area (CM) (*1*) on the STP suggests that it might correspond, at least in part, to (cytoarchitectonically defined) area Tpt (*2*).

In the 81 neurons discussed above (19 in AL, 55 in ML, and 7 in CL), we quantitatively analyzed integration along the frequency domain with six or more bandwidths ranging from PT to white noise (WN). BPN bursts were centered around the BF_c. A best bandwidth could be determined for 69 of the neurons. In the most common response profile, seen in 49 neurons (60.5%), a neuron responded poorly to PT or WN but responded strongly to BPN bursts with a certain bandwidth of ⅓ to 2 octaves (Fig. 3A). Occasionally, two peaks were found in the bandwidth tuning curve, one of which could include PT or WN. In five neurons (6.2%), responses increased monotonically with increasing bandwidth; in seven neurons (8.6%), responses decreased monotonically with increasing bandwidth (the most typical response profile for AI neurons). The best bandwidth for a given neuron was largely unaffected by increases of sound level over a wide range. Although the degree of enhancement sometimes varied at different sound levels, the peak of the bandwidth tuning curve usually remained the same (Fig. 3A). This level tolerance of best bandwidth included neurons that were nonmonotonic for sound

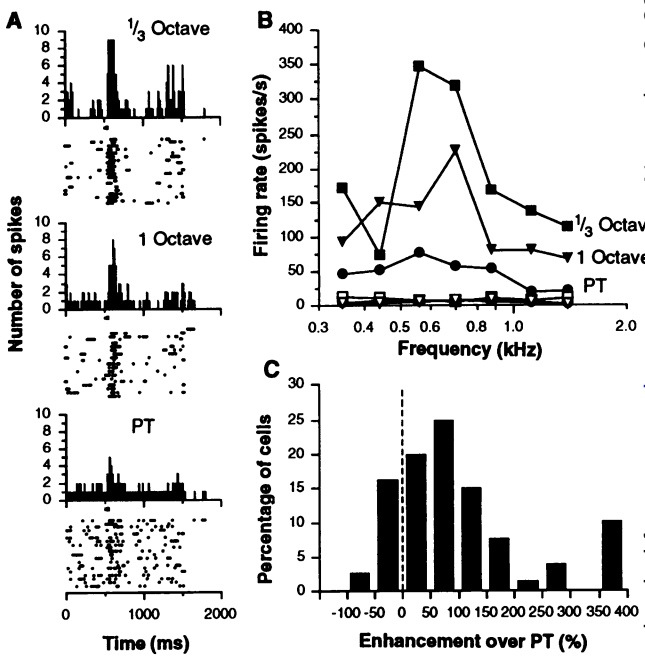

Fig. 1. Enhancement of auditory single-unit responses in the superior temporal gyrus (lateral belt) of rhesus monkeys by varying the bandwidth of a sound burst. (**A** and **B**) Responses of a neuron in area AL (*14*) to sound bursts (50 ms, 75-dB SPL, 5-ms rise and fall times) of different bandwidths. In (A) PSTHs and raster displays are shown in response to a PT of 600 Hz and BPN bursts centered at the same frequency with two different bandwidths (1 octave and ⅓ octave). Dark bars under the PSTH indicate duration of the stimulus. In (B) rate-frequency curves for the same neuron and the same types of stimuli are shown: PT (●), BPN bursts of 1-octave bandwidth (▼), and BPN bursts of ⅓-octave bandwidth (■). Open symbols refer to the corresponding baseline activity in the 500-ms interval before stimulus onset. All stimuli were energy-matched on the basis of root-mean-square values (*12*). (**C**) Proportions of neurons (n = 81) with different degrees of enhancement of response to BPN bursts over response to PT. Positive values indicate enhancement; negative values indicate suppression.

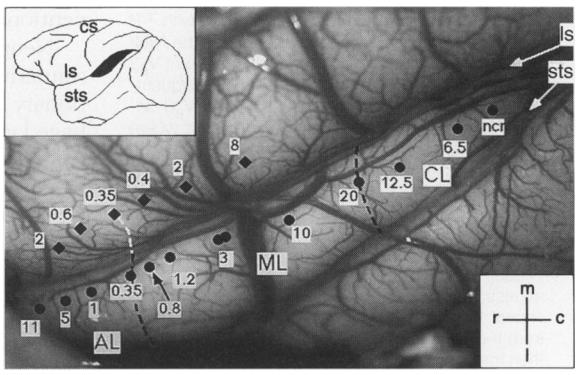

Fig. 2. Map of BF_c's (in kHz) along the lateral sulcus (ls) in one monkey; ncr, no clear response. Similar maps were found in all other monkeys. The posterior part of the STG is seen in the center; electrode tracks that entered directly into its lateral surface (●) and tracks that entered the STP after traveling through the overlying parietal cortex (◆) are shown. All electrode tracks were verified by histology. Values of BF_c were determined for each penetration from averages of at least three recordings at different depths. AL, anterolateral area; ML, middle lateral area; CL, caudolateral area; sts, superior temporal sulcus; cs, and central sulcus. Upper inset: Lateral view of the left hemisphere of a rhesus monkey brain, with the explored area emphasized by stippling. Lower inset: m, medial; l, lateral; r, rostral; and c, caudal.

level (Fig. 3A, upper right panel). When responses were compared at different mediolateral positions, best bandwidth increased along that axis—that is, roughly orthogonally to the BF_c axis (Fig. 3B; $P < 0.003$, Spearman rank correlation). By analogy to the visual system, and to areas DL and V4 (7) in particular, it is reasonable to assume that a neuron's preference for certain bandwidths is the result of integration over different frequency bands and of complex excitatory or inhibitory interactions. However, the exact nature of these interactions has yet to be explored.

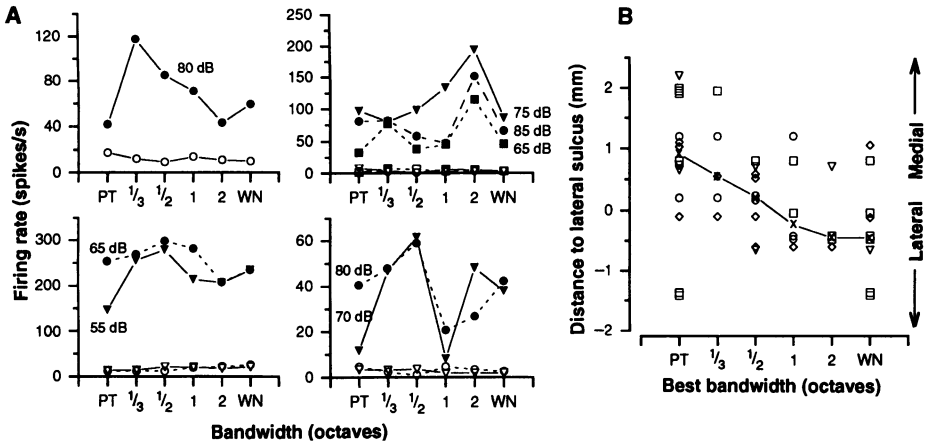

Fig. 3. Preference of single neurons in the lateral auditory areas for the bandwidth of a BPN burst at the BF_c. (**A**) Examples of bandwidth tuning curves from three different monkeys. The sound level of the energy-matched stimuli was varied as indicated. Open symbols represent baseline activity. WN, white noise. (**B**) Position of neurons with different best bandwidths relative to the lateral sulcus in one monkey. Medians (×) in each group are connected with a solid line. BF_c ranges: ○, 1 kHz; ▽, 2.5 kHz; □, 4 kHz; ◇, 15 kHz.

To further investigate spectral integration in neurons of the lateral auditory areas, we used rhesus monkey vocalizations as stimuli. From a battery of calls digitally recorded under natural conditions (*15*), we selected a standard set of seven representative examples that were energy-matched on the basis of root-mean-square values (*12*). Ninety-seven neurons in areas AL, ML, and CL of the lateral belt were tested with these stimuli. Of this group, 87 neurons (89.7%) responded better to certain calls than to others (Fig. 4A) (*16*); 56 neurons (58%) showed only a weak stimulus preference, but 31 neurons (32%) showed a strong preference for certain calls. An additional seven neurons (7.2%) clearly favored one call

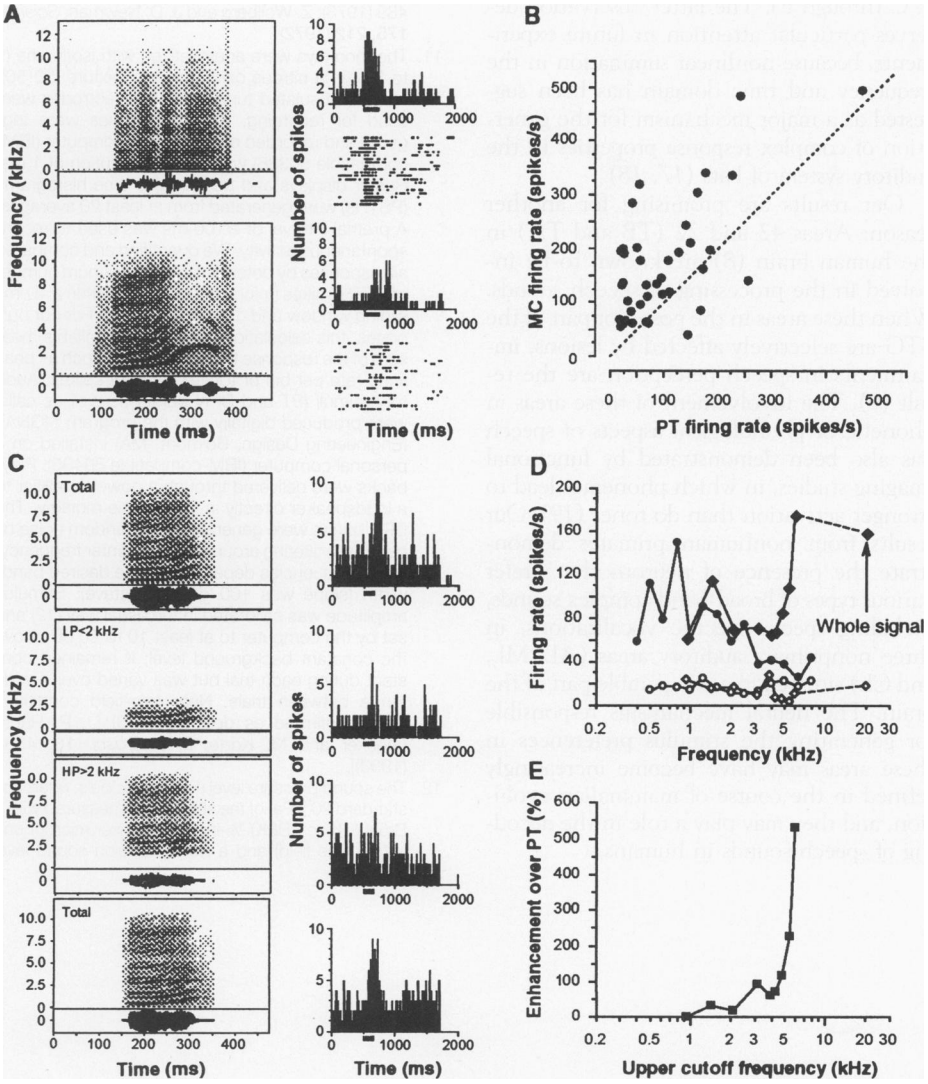

Fig. 4. Responses of neurons in the lateral areas to communication calls. (**A**) Preference for a noisy call (upper panel, 80-dB SPL) over a harmonic call (lower panel, 82-dB SPL) with a similar overall bandwidth. Spectrograms and time signals are displayed to the left of the single-unit response PSTHs and raster displays. (**B**) Scattergram comparing response to monkey calls (MC) and response to PT in the same neurons ($n = 41$). The dashed line bisects the quadrant; points above the line correspond to neurons responding better to MC than to PT, and vice versa. (**C** through **E**) Nonlinear summation of different frequency components in the processing of calls by a neuron in area ML. The call (a "coo," 80-dB SPL) consists of a number of harmonic components (C, left panel) and elicits a good response (C, top right). If the call is sent through a low-pass (LP) filter with a cutoff frequency of 2 kHz, a much smaller response is obtained (C, second row) than with the unfiltered version of the call. The same is true for the high-pass (HP)–filtered version (C, third row). Stimulation with the whole signal is repeated to demonstrate stability of the phenomenon (bottom row). PSTHs in (C) are summed from 20 presentations of the stimulus. In (D) the same neuron, when tested with tone bursts (●), prefers frequencies from 0.4 to 2 kHz, with a best frequency around 0.8 kHz. Nevertheless, when the "coo" signal is LP-filtered in steps that eliminate one harmonic component at a time (◆), higher harmonics enhance the response significantly. After the eighth harmonic (upper cutoff frequency around 6 kHz) is added, the same response is reached as for the whole signal. At this point, the sound of the filtered "coo" also becomes indistinguishable from the original "coo" to human observers. Open symbols represent baseline activity. In (E) the response enhancement over PT is plotted as a function of the upper cutoff frequency.

over the others. Increasing the sound level of the calls by 20 to 30 dB did not change the overall preference score: A comparison of preference indices (4.19 ± 1.60 and 4.15 ± 1.73) measured at the highest and lowest sound levels, respectively, did not reveal a significant difference ($P > 0.05$, t test). Neurons in all three areas obviously preferred monkey calls over energy-matched PT stimuli (Fig. 4B) ($P < 0.0001$, binomial test). Comparison of responses to monkey calls and BPN stimuli in 46 neurons also revealed a preference for the calls ($P < 0.01$, binomial test). This preference was found for both noisy and harmonic calls (*15*), but not for tonal calls.

To identify components of the calls that are responsible for these stimulus preferences, we segmented some of the preferred calls in the frequency or time domain and used the components as separate stimuli. When different frequency segments were tested, the response was often predictable from the suprathreshold frequency tuning curve (that is, the BF_c obtained during BPN stimulation). In other neurons, however, clear indications of nonlinear summation were obtained (Fig. 4, C through E). The latter observation deserves particular attention in future experiments, because nonlinear summation in the frequency and time domain has been suggested as a major mechanism for the generation of complex response properties in the auditory system of bats (*17*, *18*).

Our results are promising for another reason: Areas 42 and 22 (TB and TA) in the human brain (*8*) are known to be involved in the processing of speech sounds. When these areas in the posterior part of the STG are selectively affected by lesions, impairments in speech perception are the result (*9*). The involvement of these areas in phonetic or phonological aspects of speech has also been demonstrated by functional imaging studies, in which phonemes lead to stronger activation than do tones (*19*). Our results from nonhuman primates demonstrate the presence of neurons that prefer various types of broad-band complex sounds, including species-specific vocalizations, in three nonprimary auditory areas (AL, ML, and CL) situated in a comparable part of the brain. The neural mechanisms responsible for generating the stimulus preferences in these areas may have become increasingly refined in the course of mammalian evolution, and they may play a role in the decoding of speech sounds in humans.

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11. The monkeys were anesthetized with isoflurane (1 to 2%) in a nitrous oxide–oxygen mixture (50:50). Lacquer-insulated tungsten microelectrodes were used for recording. Spike responses were triggered and recorded on a personal computer (IBM-compatible 80386) with a time resolution of 1 ms. Raster displays and peristimulus time histograms (PSTHs) were generated from at least 20 averages. A pretrial interval of ≥100 ms was used to record spontaneous activity. We quantified and compared all responses by determining the maximum number of PSTH spikes (minus the baseline) within a 10-ms sliding window and dividing by 10 ms. For our purposes, this calculation yields a more reliable measure of the response than alternatives such as peak firing rate per bin or total number of spikes. Auditory stimuli (PT and BPN bursts as well as calls) were produced digitally with the program SIGNAL (Engineering Design, Belmont, MA) installed on a personal computer (IBM-compatible 80486). Playbacks were delivered through a power amplifier to a loudspeaker directly in front of the monkey. The BPN bursts were generated from random noise by bandpass filtering around a given center frequency; cutoff frequencies depended on the desired bandwidth (slope was 100 dB per octave). Stimulus amplitude was calibrated in the usual way (*12*) and set by the computer to at least 10 to 20 dB above the constant background level; it remained constant during each trial but was varied over a wide range between trials. Near free-field conditions were confirmed as described (*13*) [J. P. Rauschecker and M. Korte, *J. Neurosci.* **13**, 4538 (1993)].
12. The sound pressure level (SPL in decibels, reference standard 20 μPa) of the stimuli was measured with a Brüel & Kjaer (B&K) ½-inch condenser microphone (4133, free-field) and a B&K precision sound level meter (2235; A-weighting scale), which uses a root-mean-square procedure. A B&K 4230 sound level calibrator (1 kHz, 94 dB) was used to calibrate the sound meter. The standard SPL as measured at the monkey's head was 60 to 85 dB, which was well within the linear range of our sound delivery system. The latter system was calibrated with the same B&K equipment. Between 0.4 and 20 kHz, the output varied by ±6 dB with a roll-off above and below this range.
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14. The name CL, rather than PL, was chosen in order to avoid a conflict with previous nomenclatures. Morel *et al.* (*4*) recently subdivided area L (*1*) into two areas on the basis of cytoarchitectonics and cortical connectivity and termed them AL and PL. Area AL of Morel *et al.* most likely is coextensive with our AL, because both are situated alongside area R; their PL seems to correspond to our area ML.
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16. A preference index for responses to monkey calls was defined as follows. The responses to each of the seven monkey calls (MC) were quantified from peak firing rates (10-ms sliding window) in each PSTH. Normalization to the maximum response yielded a "preference score" for each MC between 0 and 1. If the score was ≤0.5, the particular call was considered "nonpreferred." Neurons were then given a preference index based on the number of scores >0.5. Numbers between 1 and 3 indicated "strong preference," numbers between 4 and 6 indicated "weak preference," and a neuron with a preference index of 7 was considered "unselective" for MC.
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18. We have preliminary evidence from recordings in these same areas that nonlinear summation exists in the time domain as well. In addition, neurons specific for the rate and direction of frequency-modulated sounds similar to those in the nonprimary auditory cortex of the cat (*13*) have also been found in the rhesus monkey [J. P. Rauschecker and B. Tian, *ARO Abstr.* **18**, 103 (1995)].
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