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Cortical Connections of Electrophysiologically and Architectonically Defined Subdivisions of Auditory Cortex in Squirrels

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ABSTRACT

Multiunit recordings with microelectrodes were used to identify and delimit subdivisions of auditory cortex in squirrels. In the same animals, cortical connections of subdivisions of auditory cortex were determined by placing injections of the tracer wheat germ agglutinin conjugated with horseradish peroxidase (WGA-HRP) into electrophysiologically defined locations. The electrophysiological results and patterns of connections were later related to myeloarchitectonic distinctions in brain sections cut parallel to the surface of the artificially flattened cortex. As previously described (Merzenich et al.: *J. Comp. Neurol. 166:*387–402, '76), a primary auditory field, A-I, was characterized by (1) neurons narrowly tuned to tone frequency; (2) a tonotopic map with high frequencies, which represented caudal to low frequencies; and (3) dense myelination. A-I was reciprocally connected with a rostral field, R, a parietal ventral somatosensory representation, PV, cortex ventral to A-I, and other nearby regions of cortex of the same hemisphere. Callosal connections of A-I were with A-I, R, and two or more other regions of temporal cortex. The less densely myelinated rostral field, R, also had neurons that were frequency tuned, but the neurons were often less securely driven. R appeared to have a tonotopic organization that roughly mirrored that of A-I. Ipsilateral connections of R included A-I, PV, and cortex ventral and caudal to R. Callosal connections were with R, A-I, PV, and other locations in temporal cortex. Cortex in caudal PV, ventral to A-I, and ventral to R was responsive to auditory stimuli, but responses to pure tones were weak and inconsistent, and habituation to a repeated stimulus was rapid. The cortex responsive to auditory stimuli included some but not all of the cortex connected with A-I and R. The results lead to the conclusion that auditory cortex of squirrels contains at least two tonotopically organized fields, possibly as many as five or more auditory fields, and at least two auditory-somatosensory fields.

Key words: rodents, myeloarchitecture, corpus callosum, tonotopic maps, primary auditory cortex

The present study is part of an effort to determine the basic organization of auditory cortex in mammals and how that organization has been modified and extended in various lines of descent. Currently, little is known about how auditory cortex is organized in different mammals. Auditory cortex is best understood in cats (see Brugge and Reale, '85, for review), where a number of studies suggest that auditory cortex includes a primary field, A-I, a second field, A-II (which is much different from the original concept of A-II), a bordering anterior auditory field, AAF, a posterior field, P, and a ventroposterior field, VP. Much of the cortex surrounding these fields is also responsive to auditory stimuli, but the organization of this cortex is less certain. Interconnections exist between A-I, AAF, P, and VP, and these fields have additional connections with surrounding cortex. Auditory cortex has been less extensively studied in primates, but both New World owl monkeys and Old World

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macaque monkeys appear to have similar subdivisions (see Merzenich and Brugge, '73; Imig et al., '77). A primary field, A-I, is recognized and assumed to be homologous with A-I in cats. Tonotopically organized fields surround A-I, and these fields have been named by position the rostral, R, anterolateral, AL, posterolateral, PL, rostromedial, RM, and caudomedial, CM, areas. Connection patterns are not completely known, but A-I projects to R, AL, PL, RM, and CM, and R projects to A-I, AL, PL, and RM in the same hemisphere (FitzPatrick and Imig, '80). Except for A-I, the different terminologies reflect major uncertainties about possible homologies between fields in cats and monkeys (however, see Woolsey and Walzl, '82). Thus, both carnivores and primates seem to have a number of tonotopically organized auditory fields, but only one field, A-I, is recognized as the same in both lines.

A better understanding of the similarities and differences in auditory cortex of monkeys and cats could come from a broader survey of auditory cortex in mammals, but we are hindered by the sparseness of available data. The auditory cortex of echolocating bats has been shown to contain several functionally distinct fields (e.g., Suga, '82), but the extreme specialization of these mammals has complicated comparisons with other mammals. Rabbits appear to have both an A-I and additional auditory fields of uncertain organization (Kraus and Disterhoft, '82); tree shrews have a presumed A-I, with a tonotopic organization from low to high frequencies in a caudoventral to rostrodorsal direction, and surrounding auditory cortex of uncertain organization (Oliver et al., '76); a marsupial possum has been shown to have at least a presumed A-I with a frequency representation from low to high in a ventrodorsal direction (Gates and Aitkin, '82).

Among rodents, auditory cortex has been most extensively studied in squirrels. Kaas et al. ('72) originally described a large temporal anterior region, TA, which had denser myelination and a broader, more cell-dense layer IV than surrounding cortex. At least part of TA appeared to be auditory in that lesions in dorsal TA produced retrograde cell loss in the medial geniculate complex. Subsequently, Merzenich et al. ('76) related the results from microelectrode mapping to cyto- and myeloarchitecture in squirrels and defined a primary field, A-I, in dorsal TA. This primary field had low frequencies represented rostral to high frequencies, dense myelination, and a layer IV that was densely packed with small, darkly staining neurons. Neurons in cortex adjacent to A-I were responsive to auditory stimuli and best frequencies could be defined for some of these neurons, but further subdivisions of auditory cortex were not determined. More recently, Krubitzer et al. ('86) have explored somatosensory cortex in squirrels with microelectrodes and described a somatosensory representation in the parietal ventral area, or PV, that was ventral to the secondary somatosensory field, S-II, caudal to the primary somatosensory field, S-I, and at least partly responsive to auditory stimuli. Unlike neurons in A-I, neurons in PV were poorly driven by pure tones, and they habituated rapidly to repeated auditory stimuli. Connections of electrophysiologically defined auditory fields in rodents are only known from injections confined to the somatosensory-auditory field, PV, of squirrels (Krubitzer et al., '86; Krubitzer and Kaas, '87), where connections with both somatosensory and auditory fields were revealed. Auditory cortex has also been mapped with microelectrodes in another rodent, the guinea pig, where an A-I, with an organization much like A-I of squirrels, and a caudally adjoining field with a mirror-reversal tonotopic organization were found (Hellweg et al., '77; Redies and Creutzfeldt, '87). Azizi et al. ('85) found neurons responsive to clicks and tone bursts in area 41 (Krieg, '46) and surrounding regions of cortex in the rat. Other studies of rodent auditory cortex have used cytoarchitectonic methods to subdivide cortex (e.g., Brodmann, '09; Krieg, '46; Rose, '49; Caviness, '75; Zilles et al., '80), and degeneration methods have been used to study connections of proposed subdivisions (Caviness and Frost, '80; Cipolloni and Peters, '83; Vaughan, '83; Faye-Lund, '85).

In the present study, we had three goals. The first was to electrophysiologically differentiate auditory cortical fields on the bases of tonotopic patterns and neural response characteristics. Our data confirmed the tonotopic organization of A-I; evidence was obtained for a second tonotopically organized field, R, in cortex rostral to A-I; and the responsivity of surrounding cortex to auditory stimuli was specified. In addition, observations were made on response properties of neurons in different fields. A second goal was to relate electrophysiological findings to cortical architecture. The present data revealed that electrophysiologically distinct fields are also myeloarchitectonically distinct. A final goal was to study ipsilateral and callosal connections of auditory cortex by placing injections of tracers into known locations in electrophysiologically defined fields. We were able to do this for two fields, A-I and the newly defined rostral field, R. Thus, we provide the first description of the connections of electrophysiologically identified locations in auditory cortex of a mammal other than cats and primates. Some of the results of the present report have been briefly described elsewhere (Luethke et al., '85) and subcortical connections will be presented in a subsequent paper.

MATERIALS AND METHODS

Multiunit microelectrode recording methods were used to identify and delimit subdivisions of auditory cortex in 11 adult grey squirrels (*Sciurus carolinensis*). In the same animals, cortical connections were revealed by injecting anatomical tracers within the borders of two different electrophysiologically defined auditory cortical fields. The physiological and connectional results were related to cortical architecture in sections cut parallel to the surface of the artificially flattened cortical hemispheres. Recording and anatomical procedures closely follow those used previously in our laboratory (e.g., Sur et al., '81; Sesma et al., '84; Krubitzer et al., '86).

Each squirrel was initially anesthetized with ketamine hydrochloride (130 mg/kg) supplemented with acepromazine (4.3 mg/kg). Subcutaneous injections of 0.1 cc of 2% xylocaine hydrochloride, a local anesthetic, were placed where the scalp was to be cut. Additional doses of ketamine were given as needed to maintain a surgical level of anesthesia (see White et al., '82). During anesthesia, the skull overlying auditory cortex was removed and the dura was retracted. An acrylic dam was built around the skull opening and filled with protective silicone fluid. The head was tilted to allow for electrode penetrations perpendicular to the cortical surface. The exposed cortex was then photographed so that the blood vessel pattern could be used to mark the locations of electrode penetrations during the experiment.

Recordings were made with low-impedance tungsten microelectrodes (0.9–1.2 MΩ at 1,000 Hz) with tip exposures

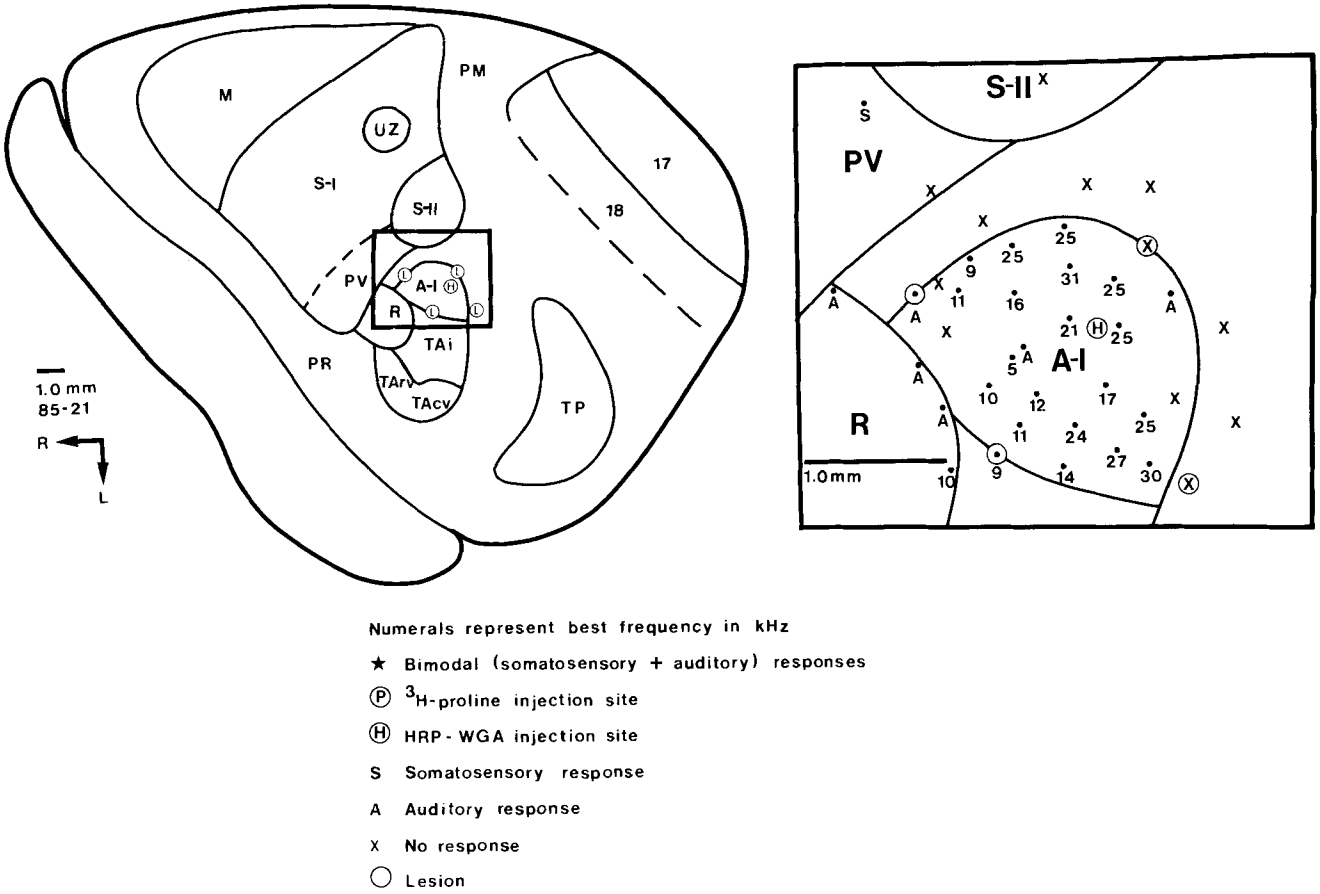

Fig. 1. The distribution of best frequencies of neural clusters in A-I for squirrel 85-21. Note the progression of high to low frequencies represented in a caudal to rostral direction and the similarity of best frequencies in rows of penetrations oriented in a dorsal to ventral direction. Left: Solid lines mark clear architectonic borders, while dashed lines indicate estimated borders. M, motor cortex; S-I, primary somatosensory area; UZ, unresponsive zone; PM, parietal medial area; S-II, secondary somatosensory area; PV, parietal ventral area; PR, parietal rhinal region; A-I, primary auditory area; R, rostral auditory area; TAi, TAcv, and TArv, temporal anterior intermediate, caudoventral, and rostroventral regions, respectively; TP, temporal posterior region; TI, temporal intermediate region; 17 (or V-I), primary visual area; 18 (or V-II), secondary visual area. The boxed region is magnified at right. Right: In this magnified view, dots mark penetrations where responses to auditory or somatosensory stimuli were elicited. Numerals denote best frequencies in kHz, while A indicates neural response to auditory stimuli (tones or clicks) when best frequency was not determined. An S indicates responsiveness to somatosensory stimuli; X indicates a lack of responsiveness to auditory or somatosensory stimuli. Encircled Xs or dots mark lesion sites; the encircled H indicates the HRP-WGA injection site. R, L = rostral, lateral.

designed to record from small clusters of neurons. The electrodes were advanced with a stepping microdrive and the recording depths were noted. Recording depths were typically 900–1,200 μm from the pial surface for recordings of auditory responses. Recordings of somatosensory responses from neural clusters in PV were typically obtained at shallower depths (see Results).

Pure tone stimuli were generated and the sound pressure level of the stimuli was regulated by a Krohn-Hite oscillator and shaped by an electronic switch with a rise-fall time of 6 msec and a duration of 100 msec. Stimuli were delivered to the animal at a rate of approximately one per second via hollow ear tubes coupled to audiometric drivers. The outputs of the audiometric drivers were calibrated prior to each experiment by using a one-half-inch condenser microphone coupled to a one-third octave-band filter and sound level meter.

Neuronal responses were conventionally amplified, filtered, and displayed. Best frequencies for neurons in given penetrations were determined by varying stimulus frequency and intensity until a threshold (just notable) response was obtained. Stimuli were typically presented to the contralateral ear alone since stimulating both ears or the ipsilateral ear alone did not seem to affect estimates of best frequency (also see Merzenich and Brugge, '73). Patterns of tonotopic organization within regions of cortex were determined by obtaining the best frequencies for a number of closely spaced recording sites. In some penetrations, neural clusters were responsive to auditory clicks (produced by tapping two metal rods together) but not to pure tones (see Results). Somatosensory receptive fields were obtained by lightly touching the skin and moving hairs on the body surface with fine probes (see Krubitzer et al., '86). Borders of auditory fields were defined by a change in tonotopic organization noted across rows of recording sites or by a marked change in responsiveness to tonal or other auditory stimuli.

After the response characteristics and physiological borders were defined for a given auditory field, the borders were marked with small electrolytic lesions for later correlation of physiologically defined borders with architectonic borders. Next, an anatomical tracer (0.05–0.1 μl of 0.1%

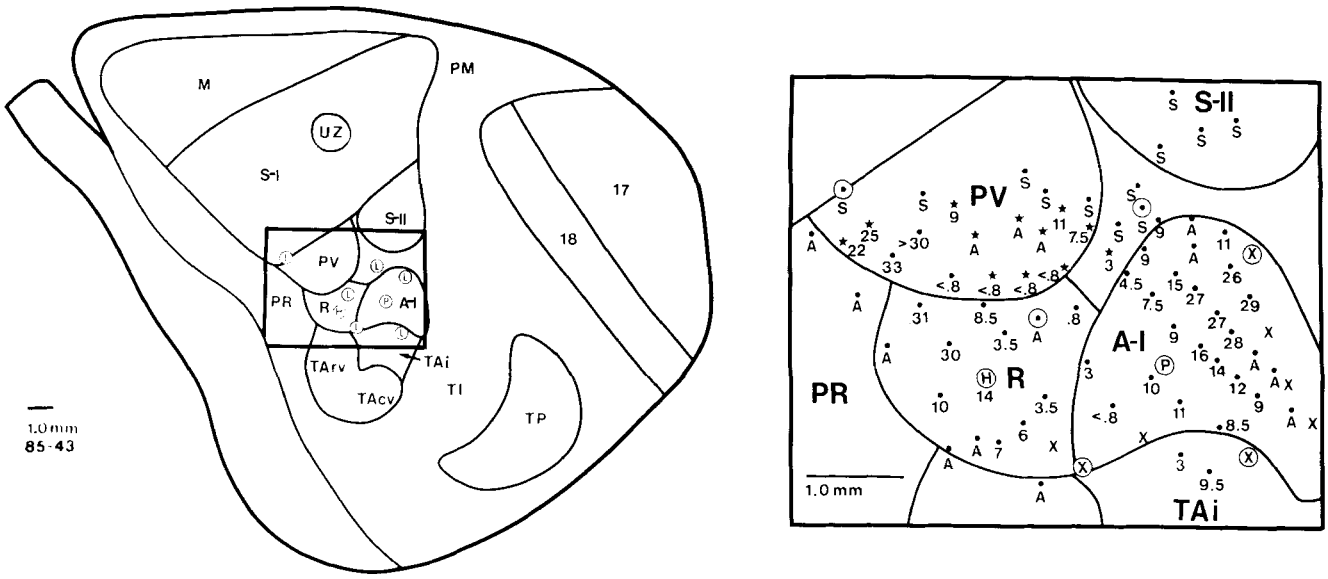

Fig. 2. The distribution of best frequencies of neural clusters in A-I and R for squirrel 85-43. Note the reversal of best frequencies across the A-I/R border, with a caudal to rostral progression of low to high frequencies in R. Bimodal (both auditory and somatosensory) responses in PV are indicated by stars. The encircled P marks the site of an injection of tritiated proline. Other lines, abbreviations, and symbols as in Figure 1.

horseradish peroxidase conjugated to wheat germ agglutinin [HRP-WGA] and/or 0.1 μl of 33 μCi/μl of tritiated proline) was injected via calibrated glass micropipettes (tip diameters 10–50 μm) into one or more electrophysiologically defined fields. Following the injection, the skull opening was covered with an acrylic cap and the skin was sutured. After 48 hours, the animal was given a lethal dose of sodium pentobarbital and perfused through the heart with 0.9% saline followed by 1.5% glutaraldehyde and 1% paraformaldehyde in phosphate buffer (pH 7.4). The brain was removed from the skull and the cortex was dissected from the brainstem, flattened between glass plates, and soaked in 30% sucrose phosphate buffer for 24 hours (see Gould and Kaas, '81). The flattened cortical hemispheres were frozen and 40-μm-thick sections were cut parallel to the cortical surface. In cases with only HRP-WGA injections, every other section was processed with tetramethyl benzidine to reveal transported HRP, and the remaining sections were stained for myelin by using the Gallyas ('79) silver procedure. In cases in which both HRP-WGA and ^{3}H-proline were injected, a set of one in four of the sections was processed for myelin, a set of one in four of the sections was processed for HRP, and a set of two in four was processed for autoradiography and counterstained with cresyl violet.

Detailed enlarged projection drawings were made of histological sections to show injection sites, anterogradely labeled axon terminals, retrogradely labeled cells, and electrolytic lesions. Other sections were drawn to show architectonic boundaries. Drawings of individual sections of cortex were then aligned by using blood vessels, tissue artifacts, and electrolytic lesions to form one comprehensive reconstruction. These reconstructions summarized the extent of the injection site, the distribution of transported tracer, architectonic boundaries, and physiological results of the cortex for each case.

RESULTS

Multiunit microelectrode recordings were used to determine neuron response characteristics to auditory stimuli and patterns of tonotopic organization of temporal cortex in squirrels. The electrophysiological results guided the placement of injections of anatomical tracers in the same animals to disclose patterns of cortical connections. Both the electrophysiological results and the patterns of connections were subsequently related to cortical myeloarchitecture.

Subdivisions of auditory cortex

While the results indicated that a broad expanse of temporal cortex is related to the auditory system, this auditory region is not homogeneous in myeloarchitecture, responsiveness to auditory stimuli, or connections (see Fig. 1). Much of the auditory region corresponds with the temporal anterior region (TA) of Kaas et al. ('72). The most dorsal third of TA contains the primary auditory field of Merzenich et al. ('76) and a tonotopically organized field, R, which is rostral to A-I. Patterns of connections and architectonic features (described in detail, below) demonstrate that the remaining portion of TA has functional subdivisions, but the number and boundaries of such subdivisions remain uncertain. However, for purposes of describing and discussing present results, we distinguish three sectors within the portion of TA which is ventral to A-I and R. We refer to the middle portion of TA, just ventral to A-I, as the intermediate segment, TAi, while ventral TA is divided into rostroventral, TArv, and caudoventral, TAcv, segments. The parietal ventral area, PV, just rostral to dorsal TA, was described by Krubitzer et al. ('86), and the parietal rhinal region, PR, just rostral to ventral TA, corresponds to the region denoted as PR by Krubitzer et al. ('86). We refer to

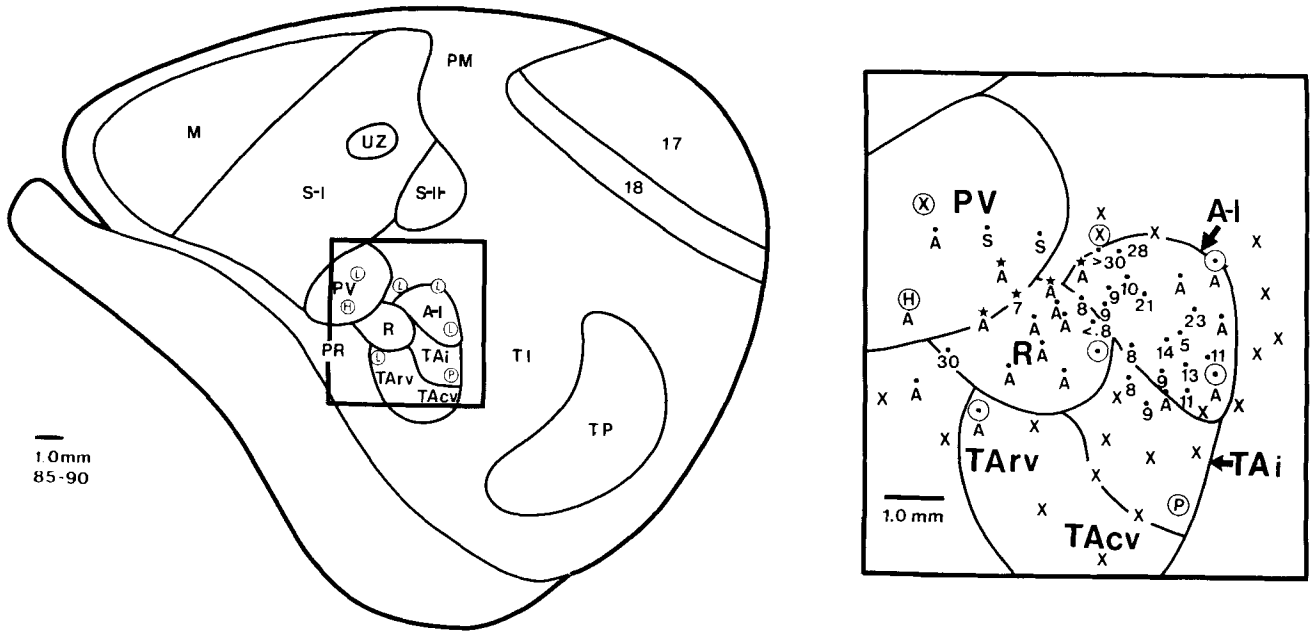

Fig. 3. The distribution of best frequencies in A-I and auditory and somatosensory responsiveness in surrounding cortex for squirrel 85-90. While R was highly responsive to tones and clicks in this animal, best frequencies were difficult to determine. Note the dorsocaudal to rostroventral direction of high- to low-frequency representation in A-I, and the general lack of responsiveness to tones or clicks in cortex caudal to A-I and the intermediate and ventral lateral regions of TA. Conventions as in Figure 1.

the narrow fringe of cortex along the dorsocaudal border of A-I with connections with A-I as the auditory fringe.

The primary auditory area, A-I. By location, tonotopic organization, and architectonic features, one representation corresponded with the field previously defined as A-I by Merzenich et al. ('76). Recordings were obtained from neurons in A-I in 11 squirrels. Major observations were as follows. Neurons in A-I were highly responsive to auditory stimuli, including broad-band clicks and pure tones. Repeating stimuli at rates up to several times per second did not result in a notable reduction in response magnitude. Whereas neurons at given recording sites were activated by a range of tone frequencies at moderate tone intensities, this range substantially decreased with reductions in sound intensities. Near threshold intensities, neurons responded to only a narrow range of frequencies, and best frequencies (the effective frequency at threshold) were easily determined. Neurons throughout single penetrations perpendicular to the cortical surface had similar best frequencies; however, most recordings were obtained from middle cortical layers where neurons were most responsive to tonal stimuli. Neurons in A-I differed in best frequency according to the location of the electrode penetration, but neurons in several electrode penetrations could have quite similar best frequencies. By relating best frequencies of neurons to the locations of electrode penetrations, both patterns of systematic change in frequency representation and isofrequency contours were revealed. Best frequencies ranged from less than 800 Hz to 33 kHz.

Results from individual cases revealed the tonotopic organization of A-I. The best frequencies for neurons in different electrode penetrations are shown for three of the more extensively explored cases in Figures 1–3. Neurons for most penetrations within the A-I region were highly responsive to tones, but in occasional penetrations, neurons failed to respond to auditory stimuli or responded so poorly that a best frequency was not determined. These penetrations with reduced responsiveness possibly resulted from inadvertent local damage or temporary cortical depression, since no consistent pattern was seen in the locations of the few recording sites with attenuated responsiveness.

Each case demonstrated a tonotopic pattern in A-I, but the pattern varied somewhat from case to case. Results from case 85-21 are shown in Figure 1. A group of penetrations characterized by neurons with high best frequencies (21–31 kHz) was obtained in a diagonal zone that extended rostrodorsally to caudoventrally across caudal A-I. In a more rostral band of cortex of similar orientation, penetrations with a middle range of best frequencies (9–17 kHz) were found. The rostroventral sector of the A-I region was not well explored in this case; one penetration in this sector encountered no responsive neurons, and another was poorly responsive and judged to be on the border. However, a third clearly responded to lower frequencies (a best frequency of 5 kHz). The results from this case support the conclusion that frequencies are represented from low to high in a largely rostrocaudal sequence, while neurons responding to similar frequencies are grouped into bands coursing dorsoventrally with a slight caudalward inclination (the "isofrequency" lines; see Merzenich et al., '76).

Borders of A-I were estimated by changes in responsiveness. Neurons in cortex caudal and dorsal to A-I were not driven by auditory stimuli. Rostral to A-I, neurons responded in a manner that was roughly similar to those in A-I, but the neurons were typically somewhat less responsive to auditory stimuli and often they were more broadly tuned to pure tones. In addition, the tonotopic pattern of best frequencies differed from the pattern in A-I (see below).

In case 85-21 (Fig. 1), four penetrations were judged to be on or near the A-I border because of a lack of or reduced

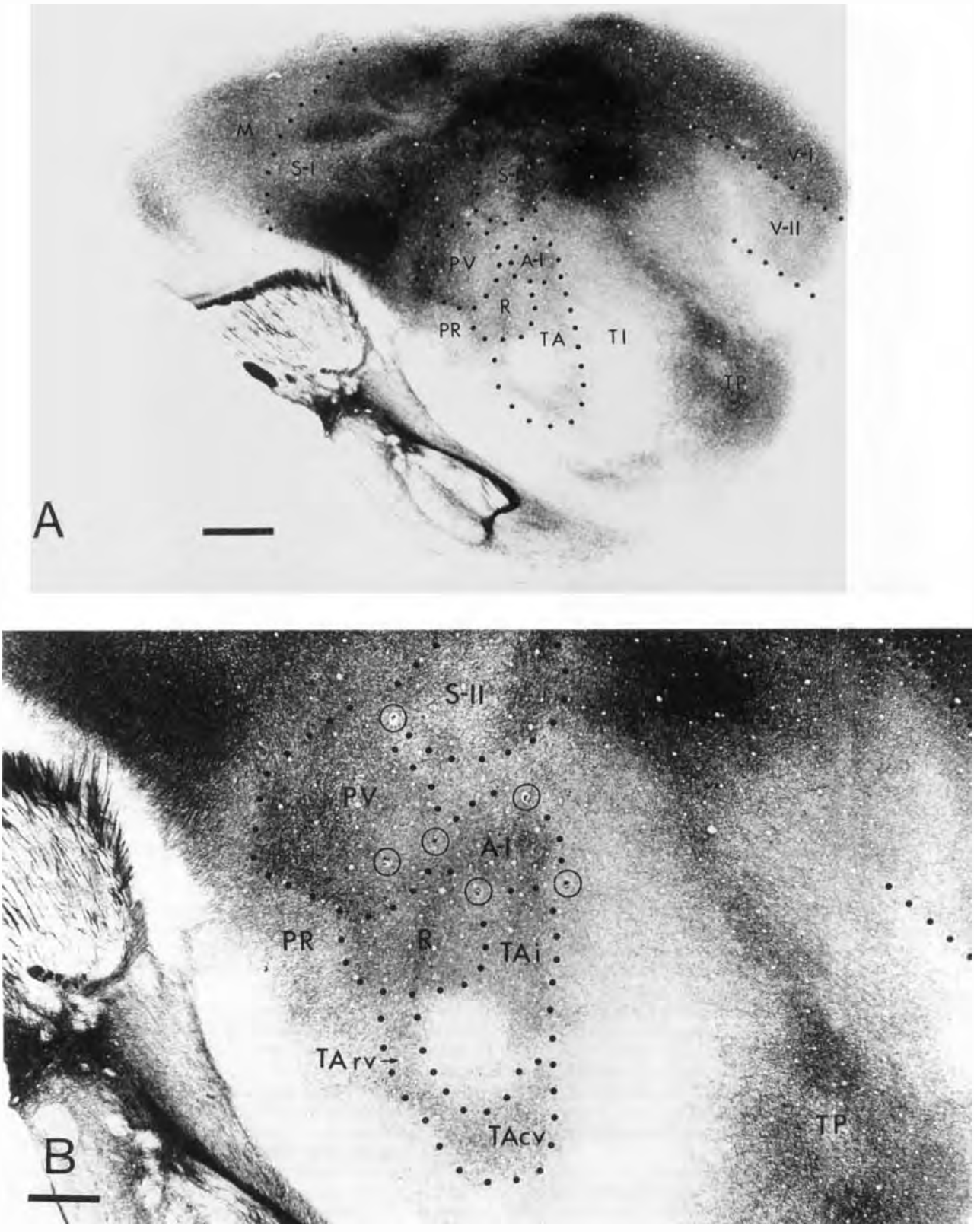

Figure 4

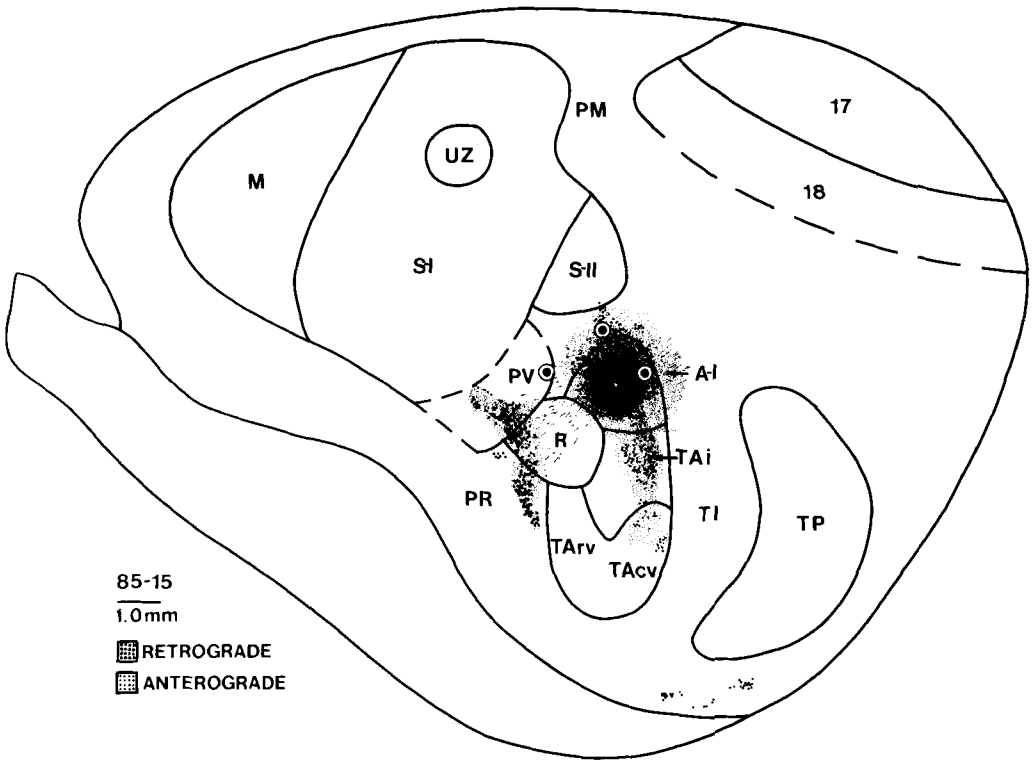

Fig. 5. Cortical connections of A-I in squirrel 85-15. An injection of WGA-HRP (large black circle) was confined to and centered in the architectonically and physiologically defined A-I. Label was drawn from several brain sections and superimposed to form a composite illustration. The larger dots indicate the location of retrogradely labeled cell bodies, while smaller dots represent presumptive anterograde label. Reciprocal connections are seen with R, PV, TAi, TAcv, PR, and the auditory fringe region (see Results). Abbreviations as in Figure 1.

responsiveness to auditory stimuli, and these penetrations were marked with electrolytic lesions. These lesions corresponded closely to the myeloarchitectonic borders of A-I.

Results from another case (85-43) are shown in Figure 2. Again, a dorsoventral band of caudal cortex responded to high frequencies (best frequencies of 26–29 kHz), a middle dorsoventral band was activated by middle frequencies (8–16 kHz), and a rostral band related to low frequencies (.8–5 kHz). In a third case (85-90, Fig. 3) the isofrequency bands appeared to course more in a rostrodorsal to caudoventral fashion, so that high-frequency neurons were dorsocaudal and low-frequency neurons were rostroventral. Again, borders were indicated by changes in responsiveness, and these borders closely corresponded to architectonic borders. Results from these and eight other cases show that there is a consistency across cases in the basic pattern of tonotopic organization. In addition, differences in the details of the patterns and the shapes of the myeloarchitectonic field suggest that minor individual differences exist.

The rostral auditory area, R. A rostral area was defined as a systematic representation of the frequency range from less than 1 to over 30 kHz in cortex immediately rostral to A-I. Although neurons in the middle cortical layers of R often responded vigorously to auditory stimuli and typically failed to habituate to rapidly repeated stimuli, the tonotopic organization of R was more difficult to determine than A-I. Neurons in R were often less responsive to pure tones, and sometimes the neurons appeared more broadly tuned than neurons in A-I. In these penetrations broadband clicks were more effective stimuli than tones. Yet, a tonotopic pattern was revealed across and within cases, and this pattern was roughly a reversal from that found in A-I.

Because the reduced responsiveness of neurons in R to pure tones made mapping more difficult, best frequencies were usually determined only for two to five penetrations in individual cases. Results from the most extensively mapped case are shown in Figure 2. Neurons in penetrations in a dorsocaudal sector of R were responsive to low frequencies as in the adjoining sector of A-I. In a middle dorsoventral strip of cortex middle frequencies were represented, whereas neurons activated by high frequencies were encountered in a rostral sector of R. Similar tonotopic pat-

Fig. 4. **A:** Lightfield photomicrograph of the myeloarchitecture of the neocortex in the grey squirrel. Several architectonic borders are apparent in this section cut parallel to the surface of the artificially flattened cerebral hemisphere. The caudal border of area 17 or V-I is easily identified because it is more densely myelinated than the adjacent secondary visual area, area 18 or V-II. Because of the plane of section, area 18 is unevenly myelinated. The temporal posterior region (TP) is a densely myelinated region surrounded by lightly myelinated cortex, and all of its borders are distinct throughout the layers of cortex. The rostral border of S-I is easily identified since S-I is more heavily myelinated than the adjacent motor cortex. Other borders were determined from more superficial or deeper layers. Scale bar = 2 mm. **B:** Enlarged view of portions of the temporal and somatosensory regions of cortex. A-I is an oval-shaped region of cortex which, in successively deeper layers of cortex, is first lightly myelinated and then more densely myelinated. A-I is surrounded by more lightly stained cortex except at its rostrolateral border where it adjoins R. R also is progressively more densely myelinated in deeper sections. The rostral extent of R is bordered medially and laterally by more lightly myelinated cortex and rostrally by the more densely myelinated somatosensory parietal ventral region, PV. The caudal portion of R is bounded medially by the darker A-I, caudally by TAi, and laterally by a moderately myelinated TArv. The circles enclose lesions placed at the electrophysiologically defined borders of A-I, R, and PV. Scale bar = 1 mm. Other conventions as in Figure 1.

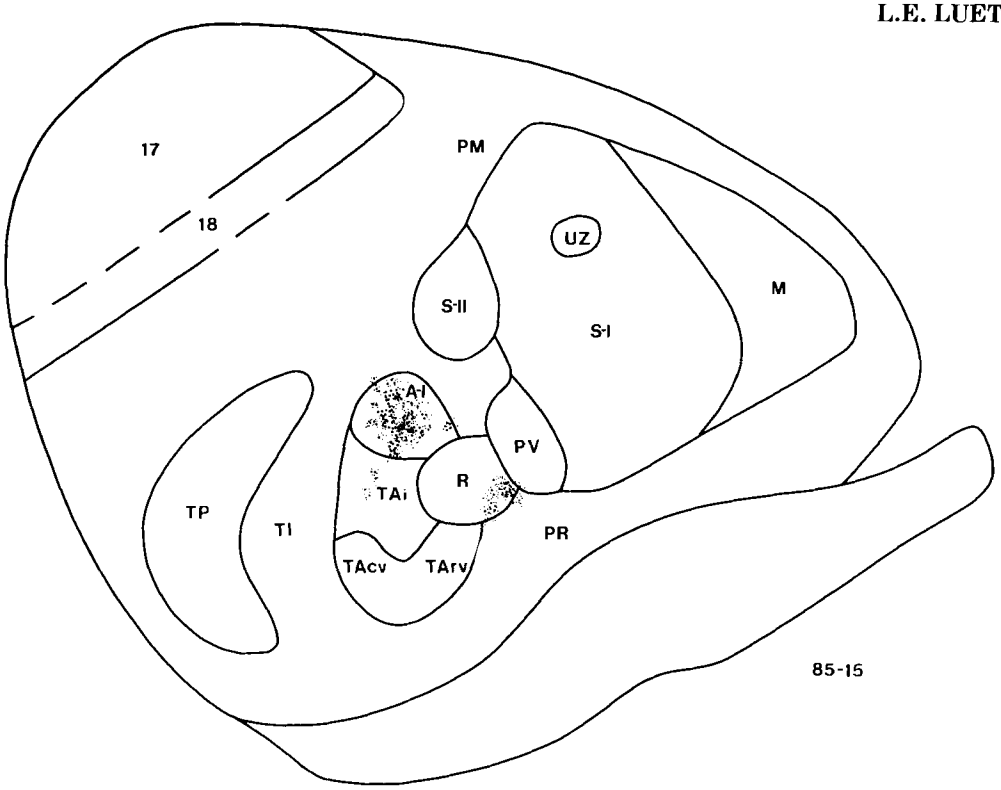

Fig. 6. Contralateral cortical connections of A-I in squirrel 85-15 (see Fig. 5). Note the dense reciprocal connections with the center portion of A-I. Connections with rostral R and TAi are also shown. Abbreviations as in Figure 1.

terns were also revealed in other cases. Best frequencies were determined from two to eight penetrations in R in a total of five other cases. Overall, these results were consistent with those illustrated in Figure 2, with some of the variability undoubtedly related to difficulties in determining best frequencies.

Because neurons in both rostral A-I and caudal R responded best to low tone frequencies, the physiological border of A-I with R was usually determined by the reduced responsiveness of neurons in R to pure tones. The junction between R and PV was best revealed by the responsiveness to somatosensory stimuli in PV. Other borders of R were indicated by a marked reduction or lack of responsiveness to auditory stimuli (see below).

Cortex surrounding A-I and R. In the anesthetized squirrel, much of the cortex surrounding A-I and R was unresponsive to auditory stimuli, even though some of this cortex can be considered auditory on the basis of connections with A-I and R (see below). In particular, cortex caudal and dorsal to A-I was not activated by tones or clicks (Figs. 1–3). In addition, cortex over much of the TA region and over much of the parietal rhinal area, PR, was unresponsive to auditory stimuli under our recording conditions. However, some cortex outside A-I, R, and PV was responsive to auditory stimuli. Most notably, recording sites judged by architectonic criteria to be just ventral to A-I, in the temporal anterior intermediate area (TAi; see below), were sometimes responsive to auditory stimuli (Figs. 1, 2). Often best frequencies could be obtained for neurons in this region, and they typically matched those for nearby neurons in A-I. One interpretation of these observations is that we have misjudged the ventral border of A-I and that these penetrations are within A-I. However, this interpretation would extend the ventral border of A-I by 200–500 μm in some cases into cortex less densely myelinated than the rest of A-I. Another possibility, given the parallel tonotopic arrangements of A-I and A-II in cats (see Schreiner and Cynader, '84), is that another narrow, tonotopically organized field exists along the ventral border of A-I.

Neurons responsive to auditory stimuli were occasionally noted in cortex just ventral to R (e.g., Figs. 2, 3). However, these responses were recorded only within 500 μm of the estimated R border. Other auditory as well as somatosensory responses were recorded in penetrations between A-I and PV (e.g., Fig. 2). Such responses could reflect error in border estimations, or fringe areas of responsive cortex. Such fringe regions of responsive cortex around A-I were also noted by Merzenich et al. ('76).

Auditory responses in the parietal ventral area, PV. A complete representation of the contralateral body surface was recently described as PV by Krubitzer et al. ('86). Neurons in PV were found to respond to light cutaneous stimuli. In addition, in some electrode penetrations in PV, neurons responded to auditory stimuli.

In the present experiments, further observations were made on the responses of neurons in PV to auditory stimuli. Some neurons in PV were activated by tones and best frequencies could be estimated, while neurons in other penetrations responded adequately to clicks but not to tones. For most auditory neurons in PV, responses habituated rapidly. Thus, clicks and tone bursts that were repeated at rates of several times per second were most effective on the first presentation and were largely ineffective by the third or fourth presentation. Not all penetrations in PV encoun-

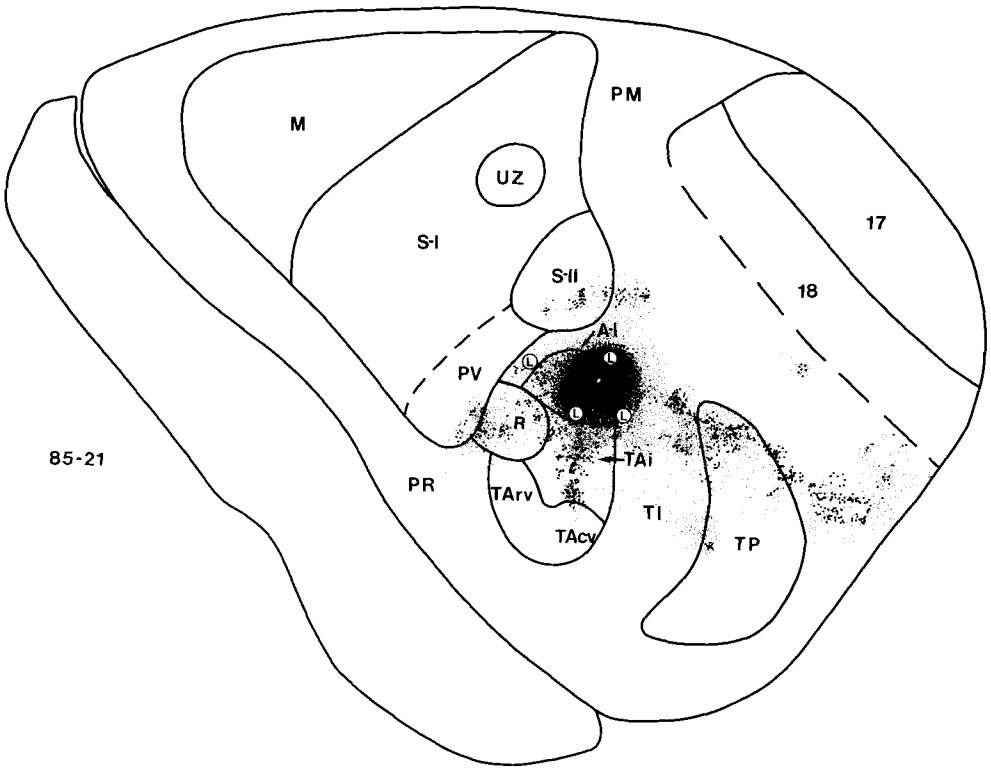

Fig. 7. Cortical connections of A-I in squirrel 85-21. An injection of WGA-HRP was largely confined to A-I but extended slightly into cortex caudal to A-I. The additional connections with TI, TP, cortex caudal to TP, and S-II (compare to Fig. 5) are presumably connections of the cortex caudal to A-I involved in the injection core. Abbreviations as in Figure 1.

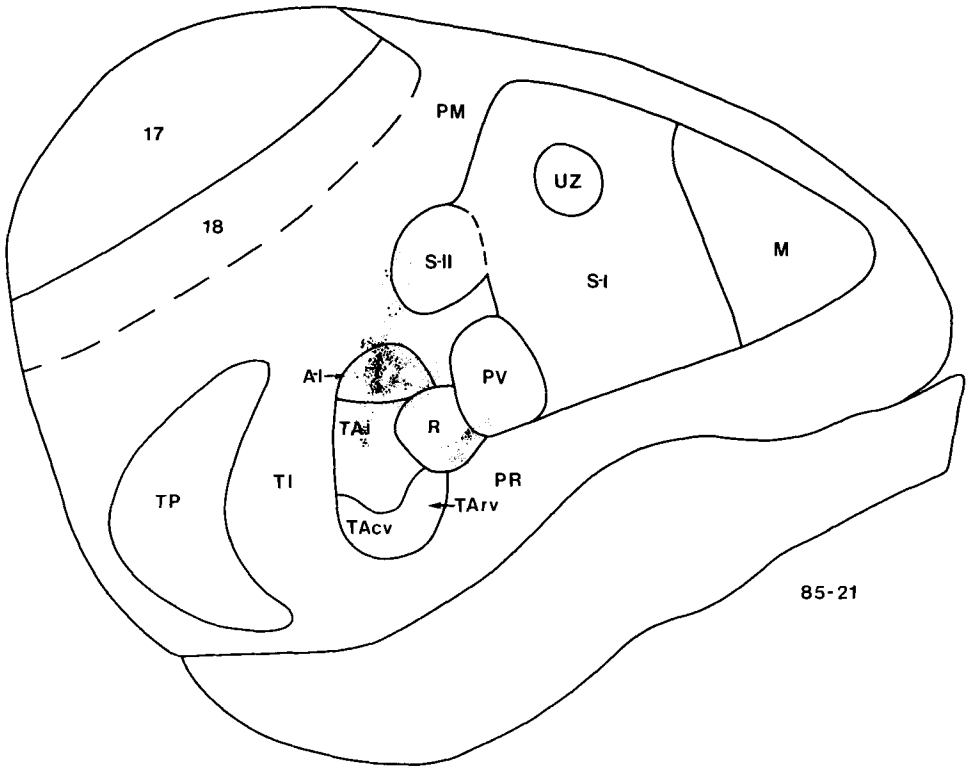

Fig. 8. Contralateral cortical connections of A-I in squirrel 85-21 (see Fig. 7). The densest connections are very similar to those seen in Figure 6 and are concentrated in A-I, with less dense reciprocal connections with rostral R and TAi.

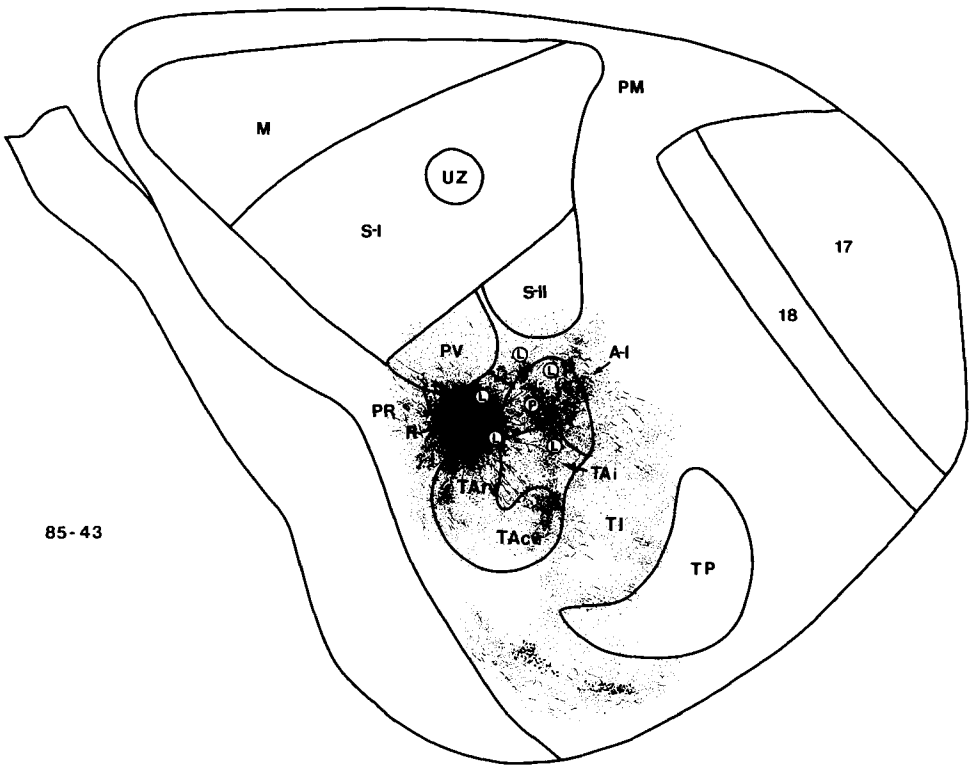

Fig. 9. Cortical connections of R in squirrel 85-43. WGA-HRP was injected and confined within the architectonically defined borders of R. Note the widespread reciprocal connections with A-I, TArv, TAcv, and TAi. Reciprocal connections are also seen with PR, the region ventral to TP, and sparsely with ventral PV. Abbreviations as in Figure 1.

tered neurons responsive to auditory stimuli, and the proportion of such penetrations varied from case to case (also see Krubitzer et al., '86). However, in one case (85-63, not illustrated), 16 electrode penetrations placed in PV recorded responses evoked by both auditory and somatosensory stimuli, and in another case (85-43, Fig. 2) neurons in 11 penetrations in PV were activated by auditory stimuli. Furthermore, best frequencies were determined for neurons in some of these penetrations, with the suggestion that high frequencies are represented rostrally and low frequencies caudally. The best auditory responses were frequently obtained deeper in the penetrations (900–1,200 μm) than somatosensory responses (500–900 μm) although responses to both types of stimuli were sometimes obtained at the same recording depths, though not necessarily from the same neurons.

Myeloarchitectonic features of auditory cortex

The experimental brains were artificially flattened and cut parallel to the surface, and a series of sections was stained to reveal myeloarchitecture. Because some curvature of temporal cortex remained after the flattening procedure, single sections usually did not adequately reveal the total extent of auditory fields. Yet, by examining and superimposing sections from several depths, borders could be reliably and consistently determined with good agreement across observers.

For orientation, Figure 4A shows a single section including most of the cortex of one hemisphere. Different densities of myelin in a single section reflect both areal variations and laminar differences as different cortical depths appear in various parts of the section. One of the most obvious fields in this section is area 17 (or V-I) in the caudomedial portion of the section. An adjoining field, area 18 or V-II, is also apparent, but the myelination of area 18 is much less dense caudally than rostrally because of the more superficial plane of the caudal part of the section. More rostrally, primary somatosensory cortex, S-I, is identified as a densely myelinated zone. Within S-I, narrow, lightly myelinated zones separate the representations of major body parts (see Krubitzer et al., '86, for more details). Rostral to S-I, motor cortex is associated with less dense and fairly uniform myelination.

Temporal cortex has a number of architectonic fields. Three major regions of temporal cortex have been previously described by Kaas et al. ('72). The temporal posterior region, TP, of unknown but probably visual function (Johanson et al., '86), is densely myelinated. More rostrally, a lightly myelinated temporal intermediate zone, TI, is found. The temporal anterior region, TA, occupies the most rostral portion of temporal cortex. The dorsal third of TA, which contains A-I and R, is densely myelinated, while the middle region just ventral to A-I and caudal to R, TAi (temporal anterior intermediate), is more moderately myelinated. A very lightly myelinated oval of cortex is centered in the ventral half of TA and is surrounded by a "U-shaped" strip of moderately myelinated cortex. We have termed the rostral and caudal portions of this ventral strip of cortex TArv (rostroventral) and TAcv (caudoventral), respectively (see Fig. 17). The architectonic features of these fields are more apparent in the higher magnification shown in Figure 4B.

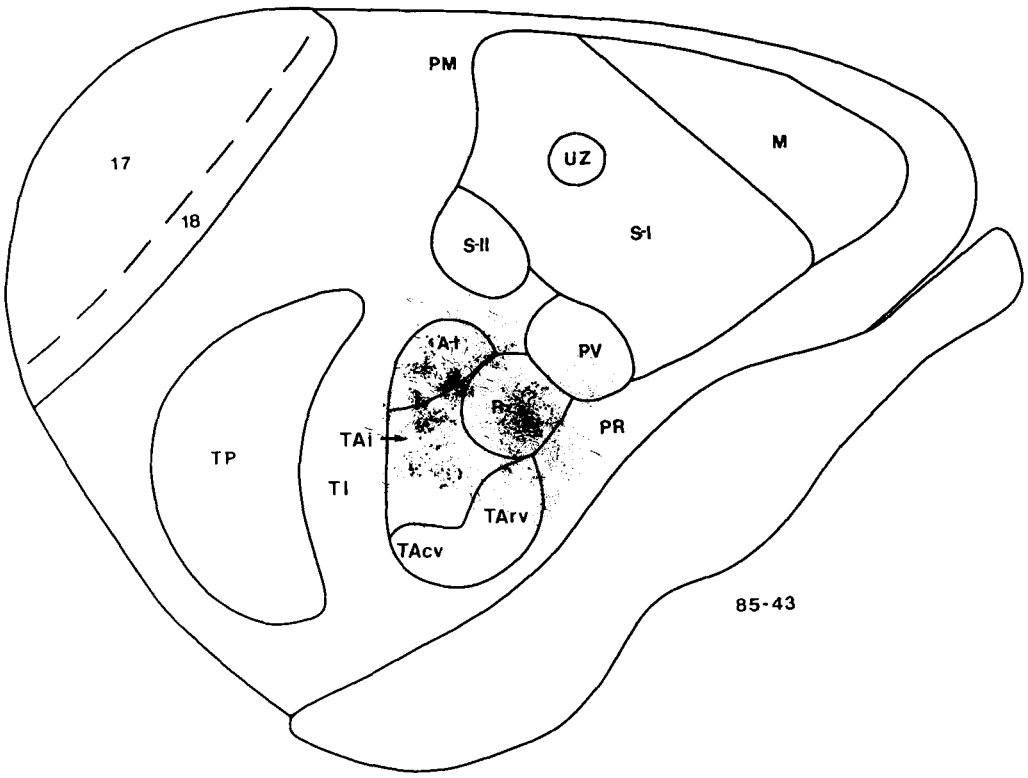

Fig. 10. Contralateral cortical connections of R in squirrel 85-43. Note the dense reciprocal connections with the same region of R that was injected in the opposite hemisphere (Fig. 9) and the foci of label located in A-I and other regions of TA. Conventions as in Figure 1.

Primary auditory cortex, A-I. In brain sections cut parallel to the brain surface and stained for myelin, A-I appears as a darkly stained oval (2 × 1.5 mm) that is bounded rostrally, dorsally, and caudally by lightly to moderately myelinated cortex and rostroventrally and ventrally by moderately to densely myelinated cortex. Figure 4B shows A-I in a case where a number of microlesions were placed at recording sites near the borders of A-I as well as in other locations. These and related results from other cases clearly demonstrate that A-I is within a densely myelinated oval of cortex occupying the dorsal part of TA.

The rostral area, R. The rostral area is apparent as a densely myelinated oval on the rostroventral border of A-I. In Figure 4B, the field is outlined by four marker lesions placed at the physiologically defined borders of R. In favorable sections, R is almost as densely myelinated as A-I and is more densely myelinated than more ventral parts of TA and the PR region.

Cortical connections

Injections in A-I. Under electrophysiological guidance, injections of HRP-WGA were placed in A-I of four squirrels, and ^{3}H-proline was injected into A-I of one additional squirrel. The dense injection core was judged to be completely confined to A-I in three cases, while the injection core minimally included cortex caudal to A-I in two other cases. Both ipsilateral and contralateral hemispheres were examined for labeled connections.

The ipsilateral cortical connections of A-I were clearly revealed in the two individual cases with HRP-WGA injections confined to A-I. Results from one of the cases with an injection confined to A-I are shown in Figure 5. As for the other cases, there was a dense core of label around the injection track that presumably corresponds to the effective injection site (see photomicrograph in Fig. 11), a rather uniform halo of label around the dense core that may reflect a mixture of local transport and diffusion, and more distant foci of transported label indicating neurons projecting to the injection site and terminations from neurons in the injection site. The label within A-I suggests that intrinsic connections are limited in horizontal extent and highly uniform in distribution, although some short protrusions of label from the halo were noted. In two cases in which injections sites of HRP-WGA were confined to A-I, reciprocal ipsilateral connections were demonstrated with R, PV, TAi, TAcv, PR, and the fringe of cortex along the dorsocaudal border of A-I (e.g., Fig. 5). While the case with a ^{3}H-proline injection confined to A-I did not result in dense cortical label, projections to R were demonstrated.

The callosally transported label was similarly distributed in both cases in which the HRP-WGA injection was confined to A-I. Contralaterally, the densest label was found within A-I and R (Fig. 6). This label was unevenly distributed in both A-I and R. Small foci of labeled cells and presumptive terminals were also noted in TAi and PR.

Conclusions based on the results from injections confined to A-I are supported by additional findings from two cases in which the HRP-WGA injections were largely within A-I but extended slightly into cortex caudal to A-I. Results from both cases were similar, and one case is illustrated in Fig-

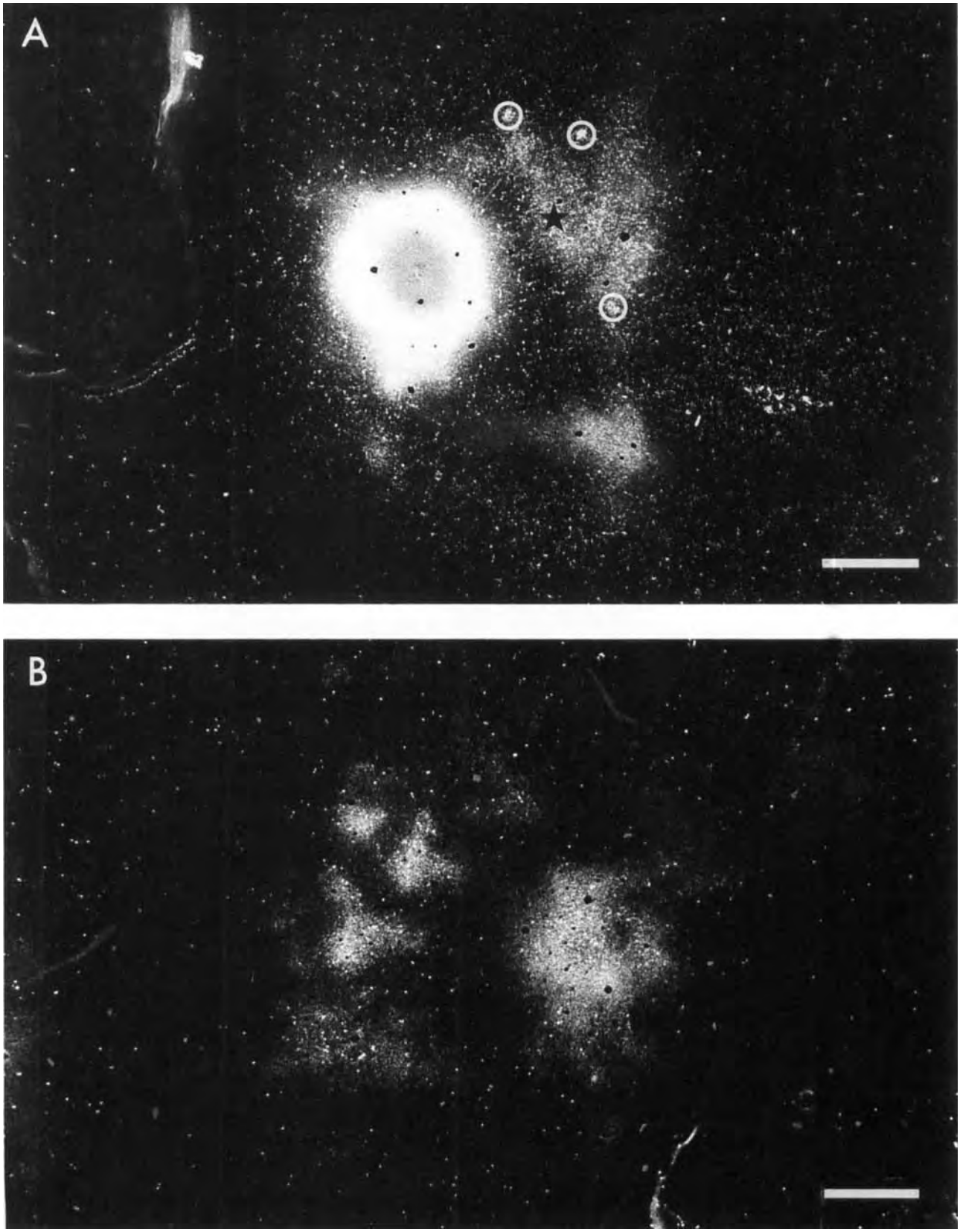

Fig. 11. **A:** Darkfield photomicrograph of a section of flattened cortex processed for HRP, showing an injection site in R and the resulting transported label in case 85-43 (Fig. 9). The injection core is seen as a dense gray circle, while the locally transported label is seen as a white fringe surrounding the core. The V-shaped patch of label caudal to the injection site consists of labeled cell bodies and terminals in A-I, while the patches immediately ventral and caudoventral are labeled cell bodies and terminals in TArv and TAcv, respectively. The small extension of label rostrodorsally is in PV. Three lesions are circled; the ^{3}H-proline injection site is starred. Rostral is to the left; dorsal is to the top. Scale bar = 1 mm. **B:** Contralateral hemisphere of case 85-43 (Fig. 10). Note the dense patch of labeled cell bodies and terminals rostrally in R and the smaller foci of label in A-I and other regions of TA. Rostral is to the right; dorsal to the top. Scale bar = 1 mm.

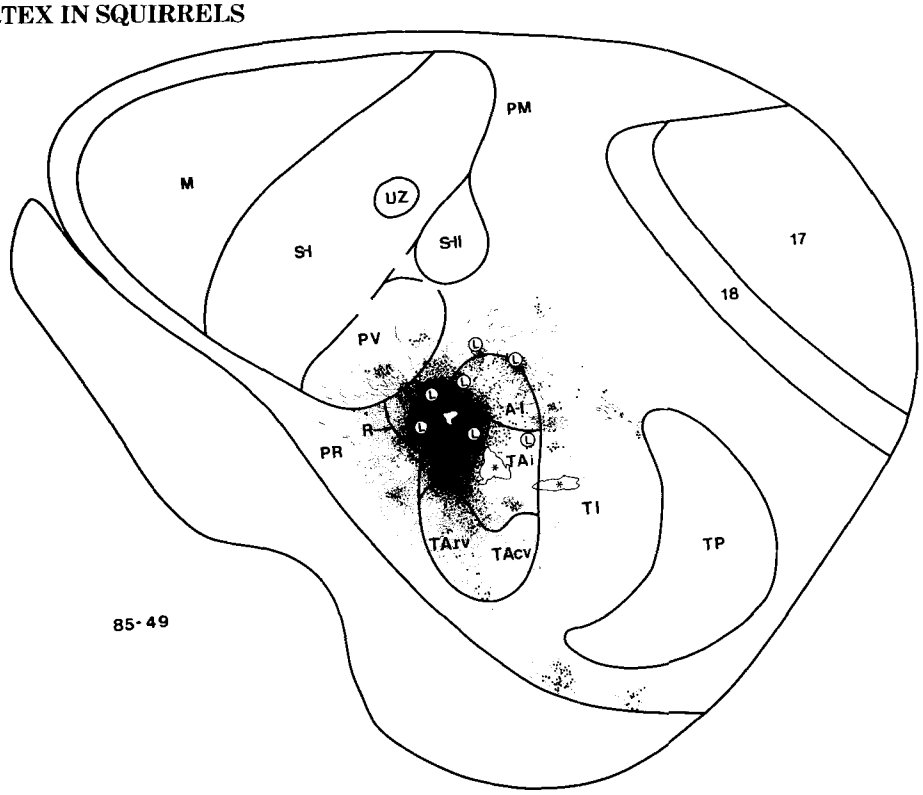

Fig. 12. Cortical connections of R in squirrel 85-49. Again, R is connected with regions of A-I, PV, PR, TAi, TArv, TAcv, and cortex ventral to TP. In addition, label is also found in TI. The asterisks are centered in regions of torn tissue. Other abbreviations as in Figure 1.

ures 7 and 8. Both cases demonstrated ipsilateral interconnections with R, TAi, and TAcv. Transported label was apparent in PV in case 85-21 (Fig. 7) but not in case 85-19 (not shown). Differing from the cases in which the injections were confined to A-I, label was also distributed over more posterior parts of temporal cortex including TI and TP. In case 85-21, but not case 85-19, some label was also noted in S-II and in cortex caudal to S-II. Contralaterally, label was present in A-I, R, and TAi in both cases, as well as in cortex just caudal (case 85-19) or dorsocaudal (case 85-21) to A-I. Case 85-21 had additional contralateral label in cortex just caudal to S-II.

We conclude from the above results that A-I has ipsilateral interconnections with R, PV, PR, TAi, TAcv, and a dorsocaudal fringe of cortex around A-I. Callosal connections are predominantly with A-I and R, but minor connections with TAi and PR also exist. The fringe area just caudal to A-I appears to have broadly distributed connections with several subdivisions of temporal and occipital cortex.

Injections in R. In three squirrels, injections of HRP-WGA were placed in cortex defined by recordings as the rostral auditory field, R. Results from one case are shown in Figures 9–11. In this case, recordings were obtained from both A-I and R; marker lesions were placed at physiologically defined borders; and the dense injection core was judged to be completely within the electrophysiologically and architectonically defined R. The injection core filled much of R but approached A-I only along the rostroventral border of A-I. The label around the injection core in R was fairly uniform, suggesting simple diffusion of label or local and evenly distributed intrinsic connections. More distant foci of labeled cells and fibers were found over a limited extent of ventral PV, concentrated within the middle two-thirds of A-I, in distinctly separate locations in rostral and caudal portions of ventral TA (TArv and TAcv, respectively), in TAi, in portions of PR just ventral to R, in cortex just dorsal to A-I, and in cortex ventral to TP. Label in TI appeared in deeper layers and was judged to be related to fibers of passage.

Label in the contralateral hemisphere in case 85-43 was more restricted (Fig. 10). Labeled cells and fibers were centered in a dense clump in R, distributed in several foci in A-I and TAi, and lightly scattered in TArv (Fig. 11B).

Basically similar results were obtained in a second case with an injection that appeared to be restricted to R (Figs. 12, 13). Ipsilaterally, clumps of labeled cells and fibers were found in AI, PV, TArv, TAi, PR, cortex dorsal and caudal to A-I, and cortex ventral to TP. Labeled cells and fibers were found over much of A-I, but the most dense label was in rostral A-I near the injection in R. Contralaterally, label was most dense in R. Other foci of label were scattered around the borders of A-I, and foci of label were in TA and just caudal and dorsal to A-I.

In a third case (not shown), the injection core was on the estimated caudal border of R. Although cortex caudal to R was apparently involved in the injection core, ipsilateral connections with A-I, several locations in TA, and the PR region, as well as contralateral connections with A-I and the caudal border region joining TA and R were similar to

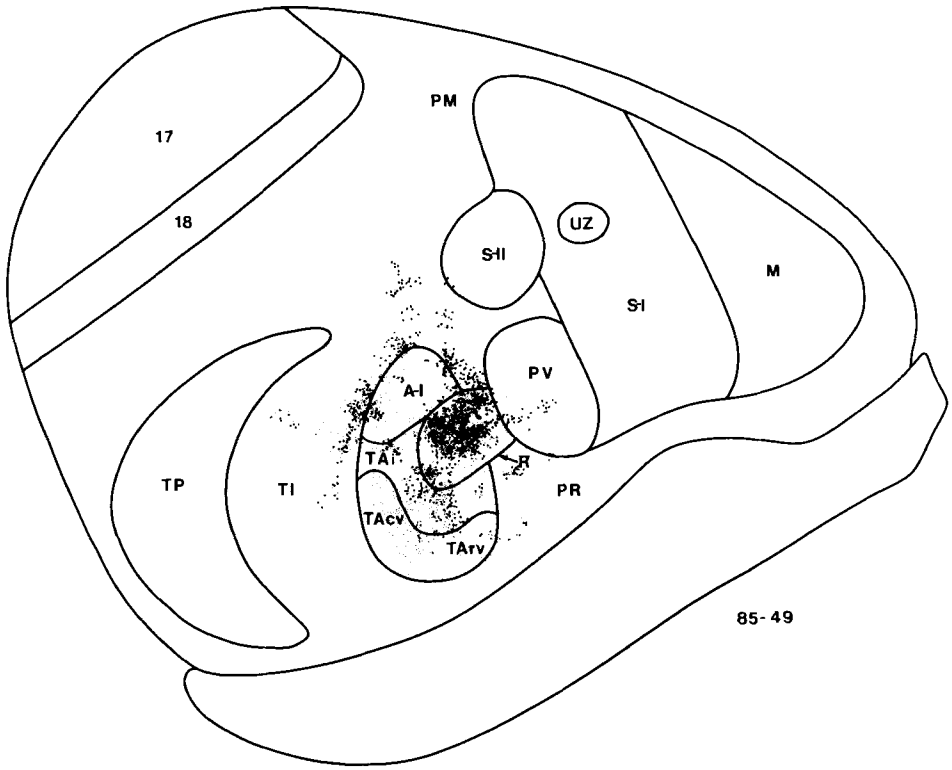

Fig. 13. Contralateral cortical connections of R in squirrel 85-49. Again, the densest connections are in R with other foci throughout and surrounding A-I and TA. Conventions as in Figure 1.

those demonstrated for R. However, a patchlike distribution of labeled cells and fibers in rostral R differed from the more uniform intrinsic pattern seen with injections restricted to R, and these connections could reflect the involvement of TA.

In summary, R appears to have prominent interconnections with A-I and parts of TA ipsilaterally and R, A-I, and portions of TA contralaterally. Regions with minor ipsilateral connections include parietal rhinal cortex ventral to R, PV, and cortex ventral to TP.

Topography of connections between A-I and R. The results produced limited evidence that the connections between A-I and R are tonotopically matched. Although the injection sites were relatively large, injections in the high-frequency caudal region of A-I in two HRP-WGA cases revealed reciprocal connections with the high-frequency rostral region of R. In case 85-21, the injection in A-I was centered between penetrations demonstrating best frequencies of 21 and 25 kHz (Fig. 1). Although R was not mapped in this case, the densest label was found in the rostral portion of R where high frequencies are represented (see Fig. 2 for more complete map of R). In another case (not shown) an injection was placed at a penetration with a best frequency response of 17 kHz. While only the caudomedial half of R representing the low to middle frequencies (3.5–10 kHz) was mapped, the resulting label was concentrated in the rostrolateral half of R in cortex presumed to be responsive to frequencies greater than 10 kHz. In case 85-43, ^{3}H-proline was injected in A-I between penetrations responsive to 9 and 10 kHz (Fig. 2); the resulting label was most dense in the portion of R found to respond to low to middle frequencies (3.5–14 kHz). In the same case, an injection of HRP-WGA was centered at 14 kHz in R (Fig. 2). The resulting label in A-I was densest in regions with best frequencies between 9 and 16 kHz, with some higher- and lower-frequency regions demonstrating less dense connections (compare Figs. 2 and 9).

Results from other cases did not so clearly support the conclusion that interconnections are tonotopically matched. For example, an injection centered in A-I largely labeled a rostral portion of R (Fig. 5). In this case, the physiological borders of A-I were determined by its brisk and nonhabituating responses to auditory clicks and these borders were consistent with the myeloarchitectonic borders. The borders of R in this case were defined solely on the basis of myeloarchitecture. Another case (not illustrated) in which a caudolateral injection (presumably in the middle- to high-frequency region) in A-I resulted in dense labeling in the caudal half of R (presumably low- to middle-frequency region). In this case, A-I was defined by myeloarchitecture and responses to clicks, while R was defined by myeloarchitecture. The remaining inconsistencies in results may simply reflect misjudgments stemming from the incomplete and limited electrophysiological results. While caution is justified and further studies would be valuable, the overall results suggest that regions of the same best frequencies in A-I and R are preferentially interconnected.

Connections revealed by injections outside A-I and R. In two cases, injections were placed in cortex ventral to A-I and caudal to R (TAi). In case 85-94 (Figs. 14, 16), the

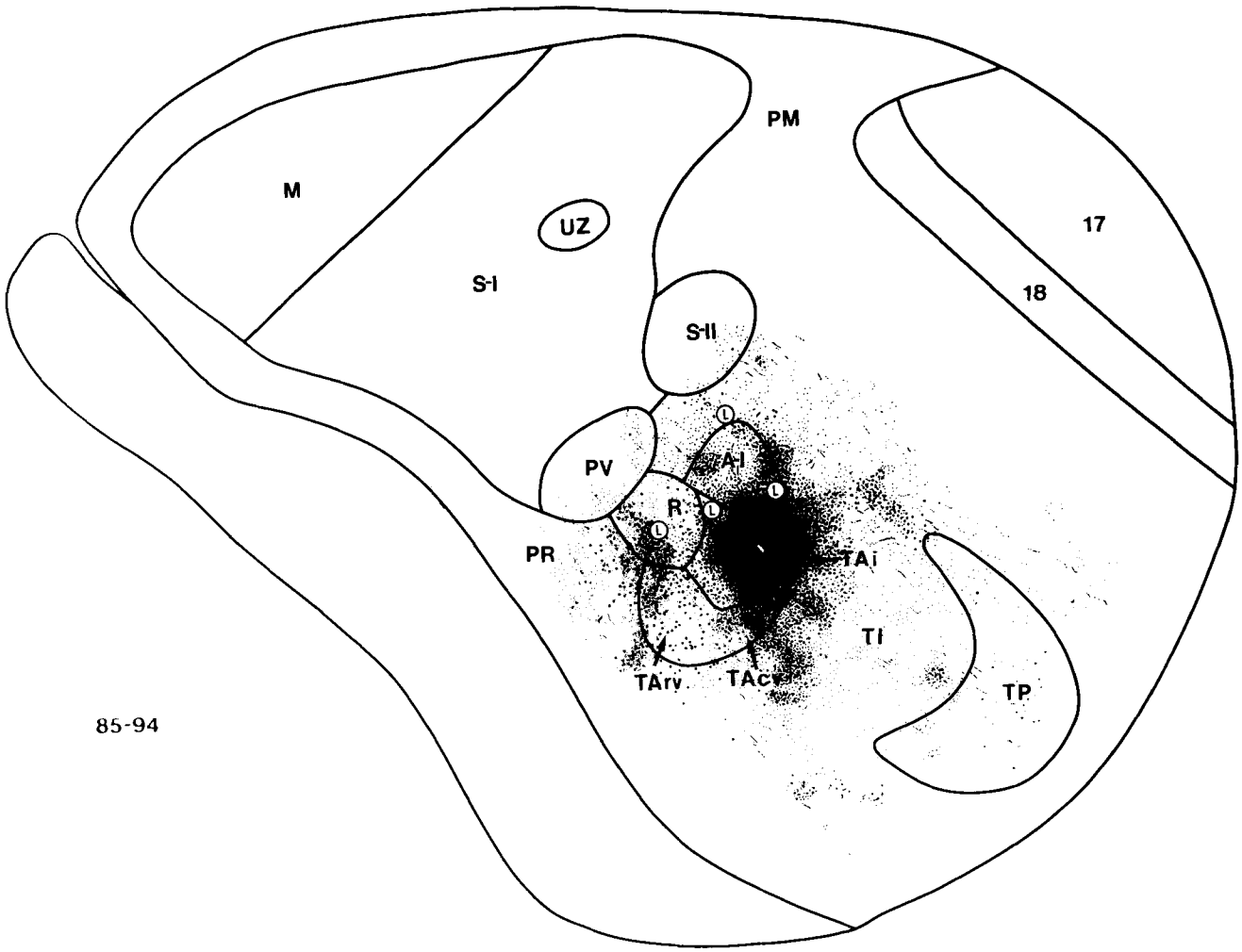

Fig. 14. Cortical connections revealed by an injection in TAi. The injection core also involves A-I slightly. TAi is reciprocally connected with A-I, R, PR, TAcv, and TArv as well as with more caudal cortex (TI and TP). Abbreviations as in Figure 1.

injection was largely in TAi, but a slight involvement of caudal A-I seemed likely. The resulting ipsilateral and contralateral (Fig. 15) connections with A-I and R support the conclusion that TAi is auditory in function. Other cortex with ipsilateral connections with TAi included TArv, TAcv, and regions of TI caudal to TA, suggesting that parts of TI may have a role in processing auditory information as well. In another case (85-90; not shown), an injection in TAi extended into TI. This case also demonstrated ipsilateral connections with A-I, R, TI, and other parts of TA, as well as contralateral connections with TA and adjoining portions of TI. Thus, injections including TAi demonstrate relationships with A-I and R as well as symmetric callosal connections.

DISCUSSION

Anatomical and physiological methods were combined in the same animals to define the subdivisions, response characteristics, and connections of auditory cortex in squirrels. Previous studies of the cortical connections of electrophysiologically defined subdivisions of auditory cortex have been limited to cats and primates. Thus, the present study provides anatomical information related to cortical processing sequences in rodents and allows comparisons of cortical connections in rodents, cats, and primates.

Auditory cortex in squirrels

The present results are interpreted within a framework provided by earlier studies of auditory cortex in squirrels. In early degeneration studies, a large temporal anterior region, TA, was architectonically defined, and lesions producing degeneration in the medial geniculate nucleus identified the dorsal part of TA as auditory in function (Kaas et al., '72). Later, Merzenich et al. ('76), using multiunit mapping techniques, delimited a primary auditory field, A-I, in dorsal TA and revealed responsiveness to auditory stimuli in cortex adjacent to A-I. More recently, Krubitzer et al. ('86) described a systematic representation of the contralateral body surface, the parietal ventral area (PV), that was also partly responsive to auditory stimuli in cortex rostral to A-I.

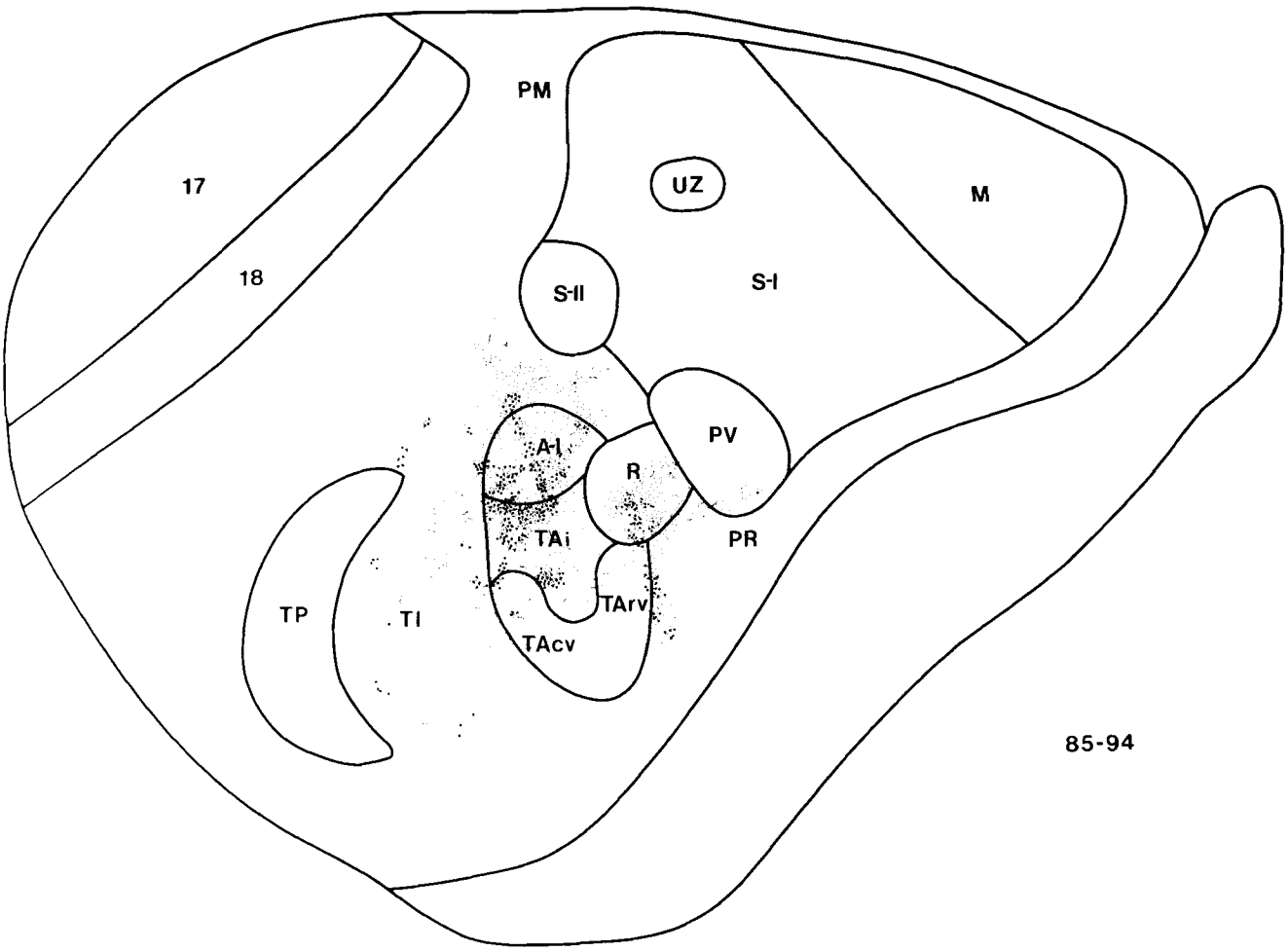

Fig. 15. Callosal connections revealed by an injection in TAi (see Fig. 14 for injection site). Conventions as in previous figures.

Our current concept of how auditory cortex in squirrels is subdivided and organized is presented in Figure 17. First, we support the conclusion that dorsal TA is occupied by a primary auditory field, A-I. A systematic representation of sound frequencies was found in the location of A-I as described by Merzenich et al. ('76). As in the earlier report, high frequencies were found caudally and low frequencies rostrally, with isofrequency lines oriented dorsoventrally with a caudalward slant. Merzenich et al. ('76) illustrated architectonic features of A-I, including dense packing of small neurons in cortical layer IV and dense myelination of the inner and outer bands of Baillarger of A-I. In the present report, we show the outline of the densely myelinated A-I in "surface view" brain sections cut parallel to the brain surface.

Cortex immediately rostral to A-I was also tonotopically organized, although this cortex was more difficult to map in the anesthetized animals. Yet, enough data were gathered across cases to indicate that a systematic representation exists in a region of cortex, about the size of A-I, with low frequencies represented caudally, high frequencies rostrally, and lines of isorepresentation in a dorsoventral orientation with a caudalward slant. We have termed this representation the rostral area, R, and show that it is coextensive with an oval of cortex that is only slightly less myelinated than A-I. While Merzenich et al. ('76) did not define R, they did describe recording sites rostral to A-I with neurons characterized by best frequencies. As in the present study, penetrations adjacent to the A-I border had neurons responsive to low frequencies, while more rostral penetrations had neurons activated by higher frequencies. Thus, the present results are highly consistent with the frequency representation data from the study of Merzenich et al. ('76), and the combined results from the two studies strongly support the concept of a second tonotopically organized field, R, in squirrels.

A third cortical field, PV, in squirrels has both a systematic representation of the body surface and a distribution of neurons activated by auditory stimuli (Krubitzer et al., '86). As previously reported, neurons in many penetrations in caudoventral PV were found to be responsive to auditory clicks. In addition, many of these auditory neurons in PV were responsive to tones, and best frequencies were obtained for some neurons. There was some evidence that

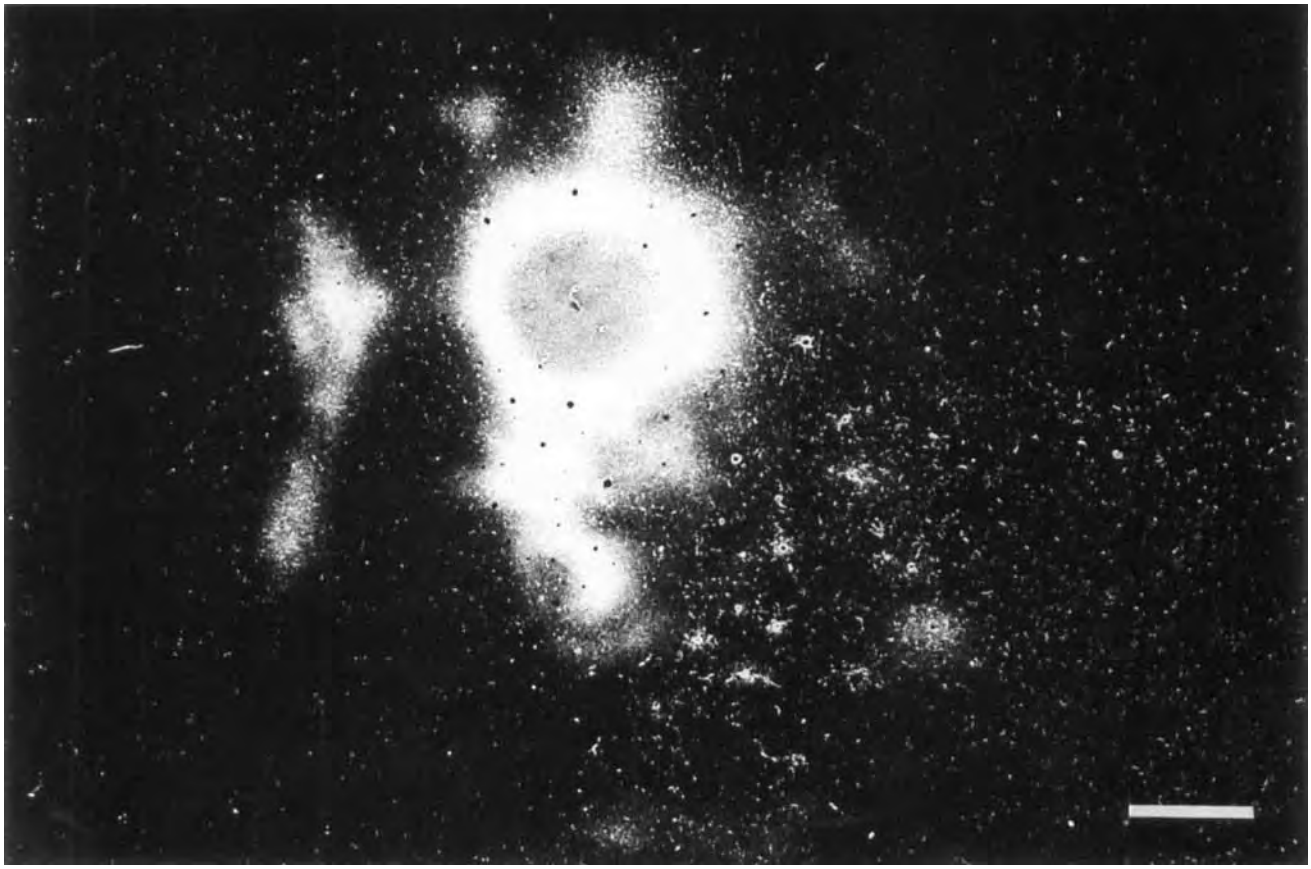

Fig. 16. Darkfield photomicrograph of a section of flattened cortex processed for HRP showing an injection site in TAi in squirrel 85-94 (see Fig. 14). The transported label is evident dorsally in A-I, ventrally in TA, rostrally in R, and caudally in TI. Rostral is to the left; dorsal to the top. Scale bar = 1 mm.

penetrations with neurons best activated by high frequencies were rostroventral in PV in the portion related to the lower face and neck, while lower frequencies activated more caudal cortex related to the limbs and ventral trunk. The significance of the responsiveness to both auditory and somatic stimuli is not clear, but it is intriguing that the portion of PV largely related to the ventral body and limbs is the portion most activated by auditory stimuli. It seems possible that certain stimuli would produce both ground- and air-conducted vibrations that would activate PV.

A fourth auditory field in squirrels is the parietal rhinal region, PR, just ventral to R and PV. PR was previously defined by Krubitzer et al. ('86) as a region of cortex with interconnections with S-I, S-II, and PV. Thus, connections identify PR as a somatosensory field. However, as Krubitzer et al. ('86) also noted, PR is activated by auditory stimuli, while responsiveness to somatic stimuli was less frequently observed in the anesthetized squirrels. The auditory responses in PR habituated rapidly and it was not possible to determine best frequencies. Nevertheless, the responsiveness of PR to auditory stimuli together with inputs from A-I and R (Fig. 18) indicates that PR is an auditory as well as a somatosensory field and may even be predominantly auditory in function, given the greater responsiveness to auditory than to somatic stimuli.

Other recording sites responsive to auditory stimuli were limited to cortex so close to A-I that the sites could have been part of A-I. Thus, there is no unequivocal electrophysiological evidence for auditory fields in addition to A-I, R, PV, and PR, although some recordings near the ventral border of A-I in TAi (Figs. 2, 3) suggested another tonotopic fringelike field. However, several additional auditory fields are suggested by the pattern of connections. First, interconnections between A-I and a narrow band of cortex dorsal and caudal to A-I indicate that this fringe (Fig. 18) may be involved in auditory processing. Injections in S-II (Krubitzer et al., '86) also labeled this region, so it is likely to be involved in somatosensory processing as well. Furthermore, injections involving the auditory fringe labeled more caudal locations, largely in TI, implicating portions of TI in higher-order auditory functions. Connections with the second visual area, V-II, indicate that some of this more caudal cortex in the temporal region is visual in function (Johanson et al., '86). Second, both A-I and R were interconnected with separate intermediate (TAi) and caudoventral (TAcv) locations in TA, suggesting the locations of two more auditory processing stations. Finally, R was interconnected with the rostroventral portion of TA (TArv), revealing the potential location of an additional subdivision of auditory cortex. Thus, the combined architectonic, electrophysiological, and connectional data suggest that auditory cortex in squirrels contains five or more auditory, three or more auditory-somatosensory fields, and possibly one or more auditory-visual fields.

Data gathered in the present experiments also allow us to formulate a preliminary hypothesis for cortical process-

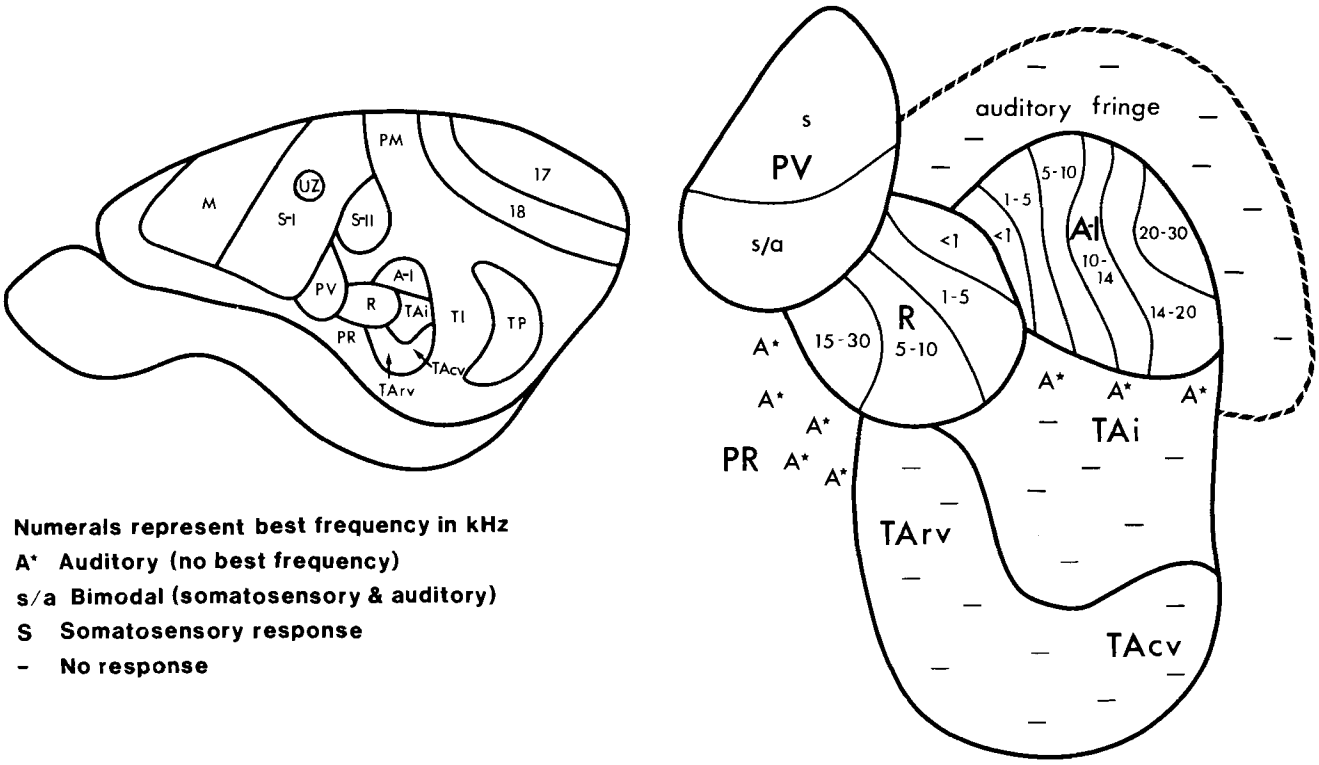

Fig. 17. The auditory cortical fields of squirrels. Left, a lateral view of the brain. Right, an enlarged view of the auditory areas. Numerals in A-I and R indicate best frequency in kHz; lines mark isofrequency contours. M, motor cortex; S-I, primary somatosensory area; UZ, unresponsive zone; PM, parietal medial area; S-II, secondary somatosensory area; PV, parietal ventral area; PR, parietal rhinal region; A-I, primary auditory area; R, rostral auditory area; TAi, TAcv, and TArv, temporal anterior intermediate, caudoventral, and rostroventral regions, respectively; TP, temporal posterior region; TI, temporal intermediate region; 17 (or V-I), primary visual area; 18 (or V-II), secondary visual area.

ing sequences in the auditory system. In some sense, fields A-I and R are at comparable hierarchical levels since both receive major inputs from subdivisions of the medial geniculate complex (Luethke et al., '85). Yet, in other ways, R seems to be a higher-order field than the primary field, A-I. Compared to A-I, neurons in R are more broadly tuned and more difficult to activate; the architectonic features are less pronounced; the callosal connections are more widespread; and the thalamic input is more diverse. In addition, the projections from R to A-I appear to be of the activating or feedforward type (see Weller and Kaas, '81; Maunsell and Van Essen, '83). Area PV appears to be a higher-order bimodal field, with somatic inputs from both S-I and S-II (Krubitzer et al., '86) and auditory inputs from both A-I and R. PR represents a further stage in cortical processing, as evidenced by cortical inputs from PV, as well as S-I and S-II (Krubitzer et al., '86), R and A-I, and by the rapidly habituating responses to auditory stimuli. TAi and TAcv appear to be fields in other parallel streams at levels equivalent to R or PR. TArv may be a higher-order area comparable to PR, while the auditory fringe may correspond to fields at the second or third level of cortical processing. Finally, sectors of TI and TP, apparently with inputs from the auditory fringe, are higher-order regions with auditory and possibly visual functions. While there is no electrophysiological evidence that neurons in TI or TP are influenced by visual stimuli, TP and TI are connected with area 18 (visual area II) of the squirrel (Johanson et al., '86), and much of posterior temporal cortex is visual in some mammals, most notably monkeys (e.g., Weller and Kaas, '87).

Bimodal and multimodal fields

Neurons in most cortical areas studied across sensory systems and across species are activated by only one modality (see Merzenich and Kaas, '80). However, the PV area in squirrels is responsive to both auditory and somatosensory stimuli, and caudalward projections from the auditory fringe suggest that bimodal visual and auditory fields exist. Though apparently uncommon, bimodal and multimodal fields have been reported for other mammals. Microelectrode recordings in mice (Carvell and Simons, '86) revealed convergence of auditory and somatosensory inputs in "S-II." Further, these bimodal responses were confined to the trunk and limb representations, which is similar to our findings and to those of Krubitzer et al. ('86) for PV. Since Carvell and Simons ('86) did not distinguish a PV, recordings attributed to S-II could have been from PV. In monkeys, the superior temporal polysensory area with visual, auditory, and somatosensory activation (Bruce et al., '81) is caudal to the auditory fields in the temporal lobe, and the retroinsular area, Ri, with apparent responsiveness to both auditory and somatosensory stimuli (Robinson and Burton, '80), is in the lateral fissure just medial and rostral to auditory cortex. In cats, the cortex between the anterior auditory area and S-II is known to be responsive to both auditory and somatic stimuli (e.g., Carreras and Anderson, '63; Burton et al., '82) and in the depths of the anterior ectosylvian sulcus, auditory, somatosensory, and visual cells are found intermingled in a region designated as field AES (Clarey and Irvine, '86). Insular cortex in cats, which bor-

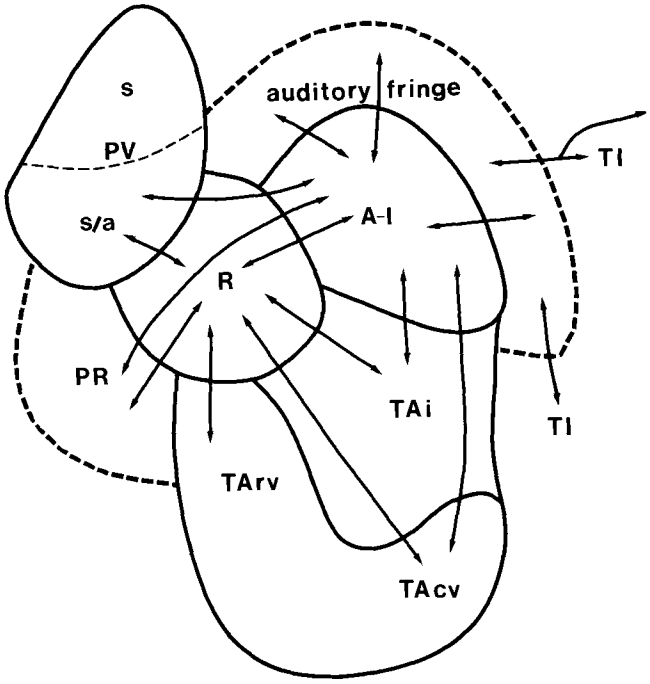

Fig. 18. The ipsilateral cortical connections of auditory cortex in squirrels. A-I, primary auditory area; R, rostral auditory area; TAi, TAcv, and TArv, temporal anterior intermediate, caudoventral, and rostroventral regions, respectively; PR, parietal rhinal region; TI, temporal intermediate region; PV, parietal ventral area. The somatosensory responsive portion of PV is indicated by the s; the bimodal responsive region by the s/a.

ders AES ventrally, has also been shown to contain bimodal neurons which respond to both auditory and visual stimuli (Loe and Benevento '69; Fallon and Benevento, '77). Such bimodal or multimodal fields, of course, would seem necessary for many brain functions.

Auditory cortex in rodents

Outside of the few studies on squirrels, little is known about auditory cortex in rodents. Primary fields are often denoted by densely packed, small cells in layer IV, and hence the term sensory koniocortex is sometimes used for primary fields (especially in primates, e.g., Sanides, '73). Since auditory cortex is not well differentiated in many rodents, it is not surprising that the early architectonic studies of Brodmann ('09) and Rose ('49) failed to identify an auditory field, although later investigators recognized that Brodmann's area 22 contained much of auditory cortex. Krieg ('46, '47) subsequently identified an oval field, area 41 or area auditoria, as the "auditory receptive cortex" in rats and was able to trace degenerating fibers from the medial geniculate complex to this region by means of the Marchi method. At about the same time, Woolsey ('47) and Le Messurie ('48) recorded evoked slow waves to auditory stimuli in the region of area 41, and a comparably located auditory region was later identified by evoked slow waves in porcupines (Lende and Woolsey, '56), guinea pigs (Ziegler, '64), and mice (T.A. Woolsey, '67). Although Woolsey ('47, '52, '58) divided the responsive area into primary, A-I, and secondary, A-II, fields in rats, evidence for two separate fields was not provided. However, since tonotopic patterns were not revealed by the broad-band clicks and evoked slow waves of these early studies, the auditory responsive cortex could have included several auditory fields.

To our knowledge, multiunit mapping results have been published for only one rodent other than grey squirrels. In a detailed study of auditory cortex in guinea pigs, Hellweg et al. ('77) provided evidence for two auditory fields—a larger anterior region they termed "area I" and a smaller posterior area referred to as "area II." More recently, Redies and Creutzfeldt ('87) have confirmed the existence of these two fields and have referred to the rostral area as field A and the caudal area as field DC. Area I or field A closely resembles A-I of squirrels in that high- to low-frequency tones are represented in a caudorostral sequence, and isofrequency lines are dorsoventrally oriented. Thus, it seems reasonable to conclude that A-I in squirrels and area I in guinea pigs are homologous. Furthermore, given the presence of A-I in these two rodents, as well as in a wide range of other mammals (Fig. 19), A-I is likely to be a field common to most or all rodents.

The more caudal field, area II or field DC, of guinea pigs is organized as a small mirror reversal of A-I, with high frequencies represented rostrally and low frequencies caudally. In squirrels, this cortex would be in the region of the auditory fringe (Fig. 18), where projections from A-I were noted, but where there was no evidence for a tonotopically organized field. Instead, in agreement with the findings of Merzenich et al. ('76), cortex caudal to A-I was unresponsive to auditory stimuli in anesthetized squirrels. The caudal field in guinea pigs could be a specialization not found in all rodents, or the field could have been suppressed by anesthetics or other factors in squirrels. Thus, uncertainties remain about the basic organization of auditory cortex caudal to A-I in rodents.

In addition to mapping studies, 2-deoxyglucose studies have the potential of providing information on the organization of auditory cortex, and one recent abstract (Steffen and Scheich, '86) describes the use of narrow-band auditory stimuli to reveal two mirror-image, tonotopic organizations in gerbils. A caudal field with a low- to high-frequency organization in the caudorostral direction was assumed to be A-I (also see Ryan et al., '82) while a rostral field was termed AF (anterior field). Thus, the tonotopic organization of their A-I is reversed from that of the guinea pig (Hellweg et al., '77; Redies and Creutzfeldt, '87) and squirrel (Merzenich et al., '76; present study). Since no other criteria were used to define A-I, their caudal field may correspond to area II of the guinea pig, and their anterior field may correspond to primary auditory cortex (A-I). HRP injections revealed interconnections between the two fields (Steffen and Scheich, '86).

Studies of connections of auditory cortex in rodents also have been limited. Early studies, such as those of Krieg ('47), demonstrated an input to temporal cortex from the medial geniculate complex. More recently, Caviness and Frost ('80) more thoroughly described thalamocortical projections in mice by using degeneration methods after thalamic lesions. These investigators concluded that the medial geniculate nucleus projects to several previously defined (Caviness, '75) architectonic fields including an oval-shaped area 41, a rostrodorsocaudal fringe (area 22), and a ventral belt (area 36). Using similar procedures in rats and the architectonic fields of Krieg ('46), Vaughan ('83) concluded that the medial geniculate nucleus projects to an oval-shaped area 41 and to adjoining rostral (area 20) and caudal (area 36) fields. By position, these three somewhat different cortical divisions in mice and rats, with apparent medial

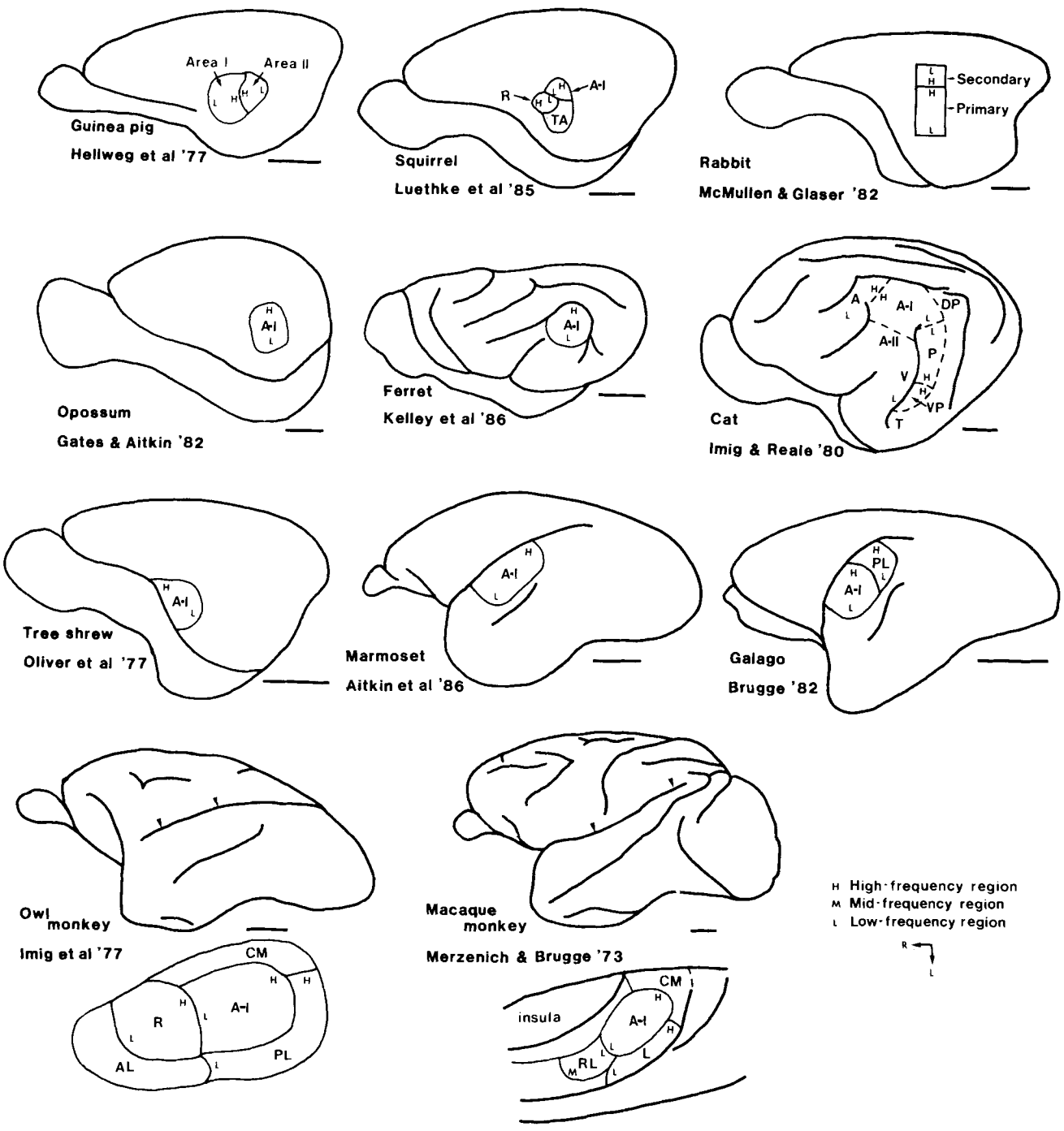

Fig. 19. Auditory areas as defined in a variety of mammals. In owl monkeys and macaque monkeys, auditory cortex is largely buried on the lower bank of the lateral fissure in the regions marked by arrowheads. For these monkeys, enlarged views of auditory cortex are below the lateral views of the brains. See text for further discussion and terminology. R, rostral; L, lateral. Scale bars = 5 mm.

geniculate connections, could include all of the auditory fields of squirrels (Fig. 15), although presently only PV, R, A-I, and TAi have been shown to have connections with the medial geniculate complex (Krubitzer and Kaas, '87). In guinea pigs, Redies and Creutzfeldt ('87) conclude that both field A (A-I) and field DC have connections with the ventral nucleus of the medial geniculate complex.

Except for the present results and the brief report of A-I and AF interconnections in gerbils noted above (Steffen and Scheich, '86), ipsilateral cortical connection patterns of auditory cortex in rodents have not been described. However, some of the reported connections of "insular" cortex in rats (Guldin and Markowitsch, '83) could involve subdivisions of auditory cortex.

The present results on the callosal connections of A-I and R in squirrels indicate that each of these fields is interconnected with several fields of the opposite hemisphere, and the connection pattern with given fields is patchy or discontinuous. Patchy connections suggest the existence of functionally distinct processing modules within auditory areas, such as "columns" of neurons with different binaural interactions as in cats (see Brugge and Imig, '78; Imig and Brugge, '78). In other rodents, total patterns of callosal connections have been related to architectonic subdivisions of temporal cortex (Cipolloni and Peters, '79; Vaughan, '83).

Auditory cortex in other mammals

A primary auditory field, A-I, has been identified in a range of mammalian species (Fig. 19; see Woolsey, '71, for a review of early studies). A-I is characterized by a sequence of representation of high to low tones that generally progresses from caudal to rostral with a ventral slant, although a rotation apparently occurs in cats so that high-frequency tones activate rostral rather than caudal A-I. Yet, the narrow tuning of neurons, the consistent responsiveness to tones and other auditory stimuli, the koniocortical architectonic features, and the dense connections with the principle division of the medial geniculate nucleus are broadly found characteristics that support the conclusion that A-I has been correctly identified (is homologous) in most or all of the reports. Often, A-I is the only field that is highly responsive to auditory stimuli during typical recording conditions in anesthetized preparations. The evidence suggests that A-I is present in most or all mammals.

In addition to A-I, it is likely that all mammals have additional auditory fields, perhaps some in common. However, homologues for other fields are much less certain. The rostral area in squirrels, as a mirror-image tonotopic reversal of A-I along the low-frequency border of A-I, is similar in relative position and tonotopic organization to the rostrolateral area in macaque monkeys (Merzenich and Brugge, '73) and the rostral area in owl monkeys (Imig et al., '77). In cats, allowing for a rotation of the auditory fields, the posterior area, P, is in the relative position of R in squirrels, R in owl monkeys, and RL in macaque monkeys. The posterior area also resembles these other fields by having a tonotopic organization that progresses from low to high frequencies with distance from A-I (Reale and Imig, '80) and by having direct input from A-I (Imig and Reale, '80). Because of the similarities, Woolsey and Walzl ('82) postulated that P in cats and RL in macaque monkeys are homologous. The presence of a similar field in rodents, cats, and monkeys is supportive evidence for the retention of a field from a common ancestor, but we have little understanding of the probability of independently evolving similar tonotopic representations. If R in squirrels, P in cats, and RL in monkeys evolved from a single field in a common ancestor, then a comparable area should exist frequently in members of other branches of mammalian evolution. Presently, evidence for a field similar to R in a wide range of species is lacking, given the limited number of studies on the organization of auditory cortex in addition to those on monkeys and cats. For now, R in rodents, R or RL in monkeys, and P in cats might be regarded merely as possible homologues.

Besides A-I and R, there is evidence that a third field is basic to mammalian auditory cortex and is homologous across a range of species. A tonotopic representation as a mirror reversal of A-I on the high-frequency border of A-I has been described for guinea pigs (Hellweg et al., '77). Although we found no evidence for such a field in squirrels, the projection pattern from A-I implicates cortex in a comparable position in auditory function, and it is possible that further investigation will reveal such a field. A similar representation, allowing for different orientation for auditory cortex, has been reported for rabbits (Fig. 19). While this adjoining field has been termed "area-II" in guinea pigs and the "second auditory field" in rabbits, such terminology should be avoided since it suggests a homology with A-II of cats, which clearly is not supportable. Rather, these fields have the relative position and reversed tonotopic organization of the anterior field, A, of cats. Nothing clearly comparable has been found in primates, although Woolsey and Walzl ('82) suggest that A in cats and PL in macaque monkeys are homologous. Again the sparseness of comparative evidence and the lack of information on the probability of independent evolution of such a field confound an evaluation of the hypothesis that these fields are homologous.

While the problem of identifying homologies remains, it is clear that auditory cortices of squirrels, cats, and monkeys are similar in having a number of complexly interconnected fields. In squirrels, A-I is interconnected with R, PV, the auditory fringe, PR, TAi, and TAcv. In cats, A-I has connections with A, P, A-II, and a dorsal posterior field (Imig and Reale, '80). In owl monkeys A-I projects to R, PL, and other fields termed anterior lateral, AL, rostromedial, RM, and caudomedial, CM (FitzPatrick and Imig, '80). Thus, in all these mammals, A-I projects to five or more ipsilateral fields. A similar pattern emerges if R of squirrels is compared to possible homologues in monkeys and cats. In squirrels, R has connections with A-I, PV, PR, TAi, TAcv, and TArv. P in cats projects to A-I, A-II, and ventroposterior (VP) and temporal (T) fields (Imig and Reale, '80). R in owl monkeys projects to A-I, AL, PL, and RM (Fitzpatrick and Imig, '80).

Callosal connections, though less extensive than ipsilateral connections, also conform to the principle of multiple parallel paths. A-I of squirrels projects to A-I, R, and TAi of the opposite hemisphere. Callosal connections of A-I are with A-I, R, and RM in owl monkeys and A-I, P, A, and possibly other fields in cats. R in squirrels has interhemispheric connections with R, A-I, TAi, and TArv. R in owl monkeys projects callosally to R, A-I, and RM, while P in cats projects callosally to P, A-II, T, and possibly A-I. Thus, in the most studied mammals, auditory cortex appears to be characterized by six or more auditory fields, each subject to the influences of many inputs, and each distributing to many targets. These features, of course, are also found in visual and somatosensory cortex of at least advanced mammals (see Merzenich and Kaas, '80).

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