

# Functional and Topographic Organization of the Auditory Cortex

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## 1. Organization of Auditory Cortical Fields

a) Redefinition of field boundaries: Four cochleotopically organized fields have now been defined in the cat auditory cortex, on the basis of extensive microelectrode mapping studies within these fields (Figure 1). A1 borders an anterior auditory field (AAF) rostrally<sup>12,16</sup> and a posterior auditory field (PAF) caudally.<sup>16,21</sup> There is a highly ordered representation of the cochlear sensory epithelium within A1, with the cochlear apex (lowest frequencies) represented rostrally. There is a reversal in the representational sequence across both the rostral and caudal borders of A1, i.e., highest frequencies are represented along the AAF-A1 border; lowest frequencies are represented along the PAF-A1 border; and the frequency sequences within AAF and PAF are in a reverse order to (mirrors) those in A1. Ventrally, the posterior field borders a fourth topographically organized field, the ventro-posterior field (VPAF). There is a reversal in representational sequence across the VPAF-PAF border, with highest frequencies represented along this border, and with the representational sequence in VPAF the reverse of that described for PAF.

As has been described earlier,<sup>16,17,12</sup> the boundaries of these

identified fields are somewhat different from those of the earlier defined fields of Woolsey<sup>26,27</sup> (see Figure 1). This is at least principally because Woolsey always assigned large evoked response foci generated by apical or basal cochlear

## AUDITORY CORTICAL FIELDS

## EARLIER VIEW (after Woolsey)

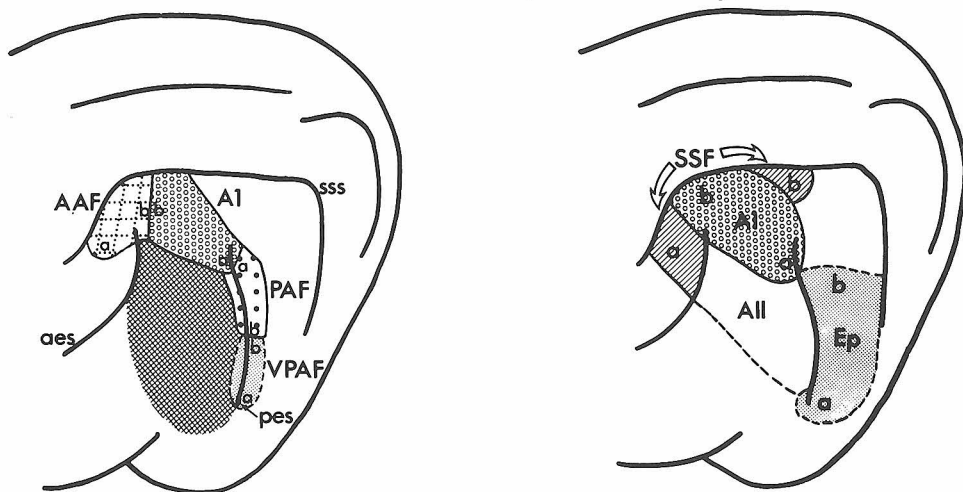


Fig. 1. LEFT: Schematic representation of the basic organization of auditory cortical fields in the cat. AI= primary auditory field; AAF=anterior auditory field; PAF=posterior auditory field; VPAF=ventroposterior auditory field. PAF and VPAF are largely buried within the posterior ectosylvian sulcus (pes). AAF is usually largely buried within the anterior ectosylvian sulcus (aes) and suprasylvian sulcus (sss); AI almost always lies partly within the sss, pes, and less frequently, the aes. The region of representation of the cochlear apex (a) and cochlear base (b) is indicated for all four of these cochleotopically organized fields. AI, AAF, PAF and VPAF comprise four principle cortical divisions of the so-called "cochleotopic auditory system" (see text). All and the so called temporal fields (collectively the area crosshatched in the figure) comprise the cortical fields of a parallel "diffuse auditory system". The number of these "non-topographic" cortical fields and their boundaries are not known; the cortical area that they occupy is very large. Note that the actual boundaries of these fields are very different in different cats. Therefore, this schematic drawing can not be taken as representing cortical field locations or boundaries in any given cat. RIGHT: Earlier view of cat auditory cortical fields, after Woolsey<sup>26,27</sup>. Ep=posterior ectosylvian field, SSF=suprasylvian fringe; other abbreviations as above.

stimulation and arising from regions of representational reversals to a single cortical "field". Recent microelectrode maps have revealed, again, that these response foci invariably arose from the bordering regions of two fields. Considered in this light, the experimental data of Woolsey and colleagues is wholly consistent with the results of contemporary microelectrode mapping studies. But: 1) A1 is much smaller than as defined by Woolsey (see Figure 1); 2) there is a complete representation (AAF) just rostral to A1, i.e., this rostral representation does not extend caudally over the top of A1 as a "suprasylvian fringe"; and 3) there are two complete fields in the classical "Ep" region.

It should also be emphasized that these fields have an inconstant location, when referenced to brain surface landmarks<sup>27</sup> 16,17,12 which are themselves inconstant<sup>23,11,16</sup>. As a consequence of these factors, for example, in some cats most of A1 is within or caudal to the posterior ectosylvian sulcus; while in other cats, most of A1 is rostral to the posterior ectosylvian sulcus, and may lie partially within the anterior ectosylvian sulcus. Therefore the schematic drawing in Figure 1 represents the organization of fields in a hypothetical cat, not to be presumed to apply for any other.

The inconstancy of field location and redefinition of field boundaries in cats (and in monkeys<sup>14,15</sup>) raise serious problems for auditory cortical research. First, all earlier cortical ablation-behavioral, recording and anatomical studies have been conducted with reference to the earlier maps, and must be interpreted accordingly. But as cortical field locations are

inconstant, those interpretations are invariably further clouded.

Thus, these factors necessitate definition of cortical field boundaries as a part of any experiment within specific auditory cortical fields. In actual practice neurophysiological controls (limited maps) are required, as the cytoarchitectonic boundaries of auditory cortical fields are difficult to define (especially in the cat, where the rostral and caudal borders of A1 commonly fall within sulci).

b) Internal organization of the topographically organized cortical fields. "Cochleotopic" representation and binaural bands: One unique feature of the auditory nervous system is the representation of the sensory epithelium across one axis of the cochleotopically organized auditory fields. The auditory sensory epithelium is a line of cells, of insignificant width. In its representation in the cortex, any point along this line is itself represented along an a line (an "iso-frequency contour") in A1. It was Woolsey and Walzl<sup>28</sup> who first appreciated a mediolateral extension of response in A1, consequent from stimulation of a point along the sensory epithelium. Tunturi<sup>25</sup> and Merzenich and colleagues<sup>16</sup> later emphasized this unique feature of organization of auditory cortical fields, and revealed in strychnine spike and unit mapping studies that any given sector of the auditory sensory epithelium occupied a band of cortex of constant width, that extended across A1 from edge to edge. This basic organization is illustrated for A1 and AAF in Figure 2A. All other defined cochleotopically organized fields appear to have this same



basic organization (see Knight<sup>12</sup> and Imig, et al.<sup>9</sup>).

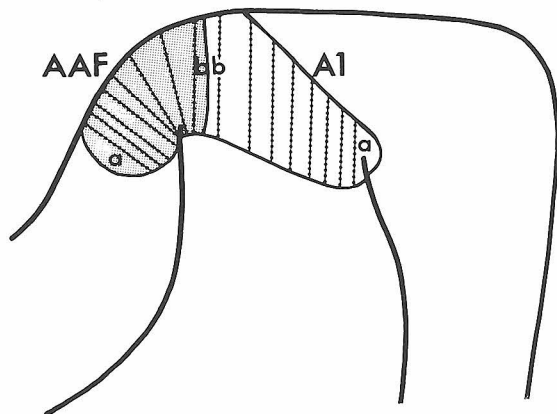
Recently, studies in A1 have revealed a segregation of neurons with different binaural response properties into bands roughly orthogonal to isofrequency contours<sup>18,19,6,7</sup> (see Figure 2).

In alternating bands in at least anesthetized cats (see Irvine and Phillips<sup>20</sup>), neurons are predominantly "excitatory-inhibitory" (driven by contralateral stimulation with driven responses inhibited by ipsilateral stimulation); or, in the second set of bands, "excitatory-excitatory" (driven by both contralateral and ipsilateral stimulation; or driven by one or the other ear, with the response strongly facilitated by stimulation of the other). There are probably three excitatory-inhibitory (EI) bands, and two or three excitatory-excitatory (EE) bands in A1 (see Figure 2B for a schematic description of this organization).

There is anatomical evidence suggesting that the three other topographically organized fields in the cat also have alternating EE and EI binaural bands (see Andersen<sup>1</sup> and Imig and Reale<sup>8</sup>). Corresponding alternating EI and EE response sequences have recently been recorded in AAF<sup>9</sup>.

It should be noted that there is also anatomical evidence for a banded organization of at least A1 in primates, inherent in the classical cytoarchitectonic descriptions of the koniocortex in man especially by von Economo. He described auditory koniocortex as banded, with the koniocortical bands separated by less granular cortical strips. However, there is as yet no direct physiological demonstration of an alternating EE and EI banding in auditory cortical fields in primates.

**CAT A1 & AAF**  
**Isorepresentation Contours (2mm steps)**



**CAT A1**  
**Binaural Bands**

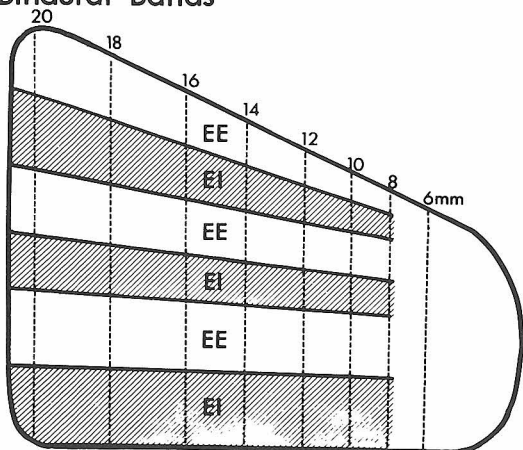


Fig. 2. Internal organization of cochleotopically auditory fields in the cat. TOP: Representation of the cochlea within two auditory fields, the "primary" field (A1) and the anterior field (AAF). Dotted lines are isorepresentational contours, indicating the lines over the cortical map over which points on the cochlear sensory epithelium about 2 mm apart are represented. The most apical isorepresentational contour represents a point on the cochlear 6 mm from the extreme apex. Note that any given sector of the cochlea (any given band of frequency) is represented across a band of cortex in A1 of approximately constant width, that extends across the field from edge to edge. This "rerepresentation" of the sensory epithelium across one axis of these fields is a unique feature of auditory cortical representations. Also note the disproportionately greater areal representation of the basal cochlea. Modified

c) "Non-topographic" auditory cortical fields: The auditory system is unique, in that there are cortical fields bordering the above defined topographically organized fields in which no clearly ordered representation of the cochlear sensory epithelium can be defined. By contrast to the topographically organized fields, tuning curves of neurons studied in these "non-topographic" cortical fields are characteristically very broad; and when best frequencies can be defined for these poorly tuned neurons, it is difficult to demonstrate an orderly representational sequence within these fields. The response characteristics of neurons within these "non-topographically" organized fields have been little studied. There are several such fields in cats, and at least one such field (the "caudo-medial field") in primates<sup>15</sup>.

d) The "cochleotopic" and "non-topographic" fields appear to constitute cortical processing regions for two largely segregated auditory projection systems: Recent neurophysiological and especially neuroanatomical studies<sup>1-4</sup> have led to the hypothesis that there are two large and largely segregated auditory projection systems in the cat. A "cochleotopic" system projects from the central nucleus of the inferior colliculus in the mid-

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Cont. Fig. 2.  
from Merzenich, et al.<sup>17</sup> and Knight<sup>12</sup>. BOTTOM: Schematic representation of the binaural bands of primary auditory cortex (A1) in the cat. Within this large cortical field, neurons within alternate bands orthogonal to the isorepresentational (or isofrequency) contours (dashed lines) have predominantly excitatory-excitatory or excitatory-inhibitory (shaded) response. Contours representing points along the cochlear sensory epithelium 2 mm apart (6 to 20 mm) are illustrated schematically. There is actually very significant variability in the widths and exact position of these bands in different individual cats. Based on studies of Middlebrooks, et al.<sup>19</sup>

brain to the ventral division and deep part of the dorsal division in the auditory thalamus to the cochleotopically organized AI, AAF, PAF and VPAF; and a "diffuse" system, projects from the pericentral nucleus of the inferior colliculus via the caudal part of the dorsal nucleus and the ventrolateral nucleus in the thalamus to the non-cochleotopically organized auditory cortical fields (see Figure 1). Ascending and descending projections interconnecting the central nucleus of the inferior colliculus, component thalamic nuclei and the cochleotopically organized fields in the cochleotopic system are complex, but are all highly ordered. No clear order to the almost equally complex projections interconnecting the pericentral inferior colliculus with component thalamic nuclei and non-topographically organized cortical fields of the "diffuse" system can be discerned. Within the cochleotopic system, as reviewed before, neurons commonly have sharply defined best frequencies (sharply peaked tuning curves), and all component nuclei of the system can be demonstrated to be strictly cochleotopically organized. Within the diffuse system, tuning curves are characteristically very broad, and with the exception of the pericentral nucleus of the inferior colliculus, no topographic order has been demonstrated in any of its component nuclei or cortical fields.

2. There are Complex Convergent Projection Arrays from the Auditory Thalamus to Auditory Cortical Fields

Note that within the component nuclei of the cochleotopic projection system, there is a further dimension of the representation of the cochlea, i.e., within these nuclei, any point along the cochlear sensory epithelium is represented across a

sheet of neurons that extends across these nuclei from edge to edge<sup>17</sup>. Retrograde injection (HRP) tracing studies have revealed that a restricted cortical locus less than 1 mm in diameter (i.e., extending across only a fraction of the length of an A1 isofrequency contour) receives input from the topographically appropriate sheet of neurons, about 1 1/2 to 4 mm in length and 1-2 mm high in the ventral nucleus; as well as from a column of neurons several mm long, continuous from the medial division through the deep part of the dorsal division, and through the lateral part of the posterior group<sup>5</sup>. This basic neuronal array is seen to project to restricted cortical sites all along A1 isofrequency contours, for injections that spread only 1/4-1/5 of the distance across the field. If multiple injections are made along isofrequency contours, this array does not change, i.e., the array projecting to 1/4 of the isofrequency contour is the same as that projecting to all of it. This suggests that there are spatially equivalent projections to repeating cortical subunits, e.g., to each of a set of adjacent EE and EI bands.

With still smaller injections, projection arrays in the ventral division are commonly seen to be discontinuous, i.e., there are columns of label within the framework of the overall projecting lateral neuronal sheet. From one to five columns of label have been seen in different projection cases, separated by columns or bands in which labelling is far lighter (or in which no labelling is recorded). We do not yet understand how this discontinuous labelling relates to the banded organization of the cochleotopically organized fields.

### 3. Response Characteristics of Cortical Neurons in A1;

#### Specific Sources of Input to the Auditory Cortical Fields

The sources of input to the binaural bands of A1 have not been defined. A large number of auditory nuclei project to the central nucleus of the inferior colliculus, the source nucleus for the "cochleotopic" projection system. (Indeed, if response-specific neuronal populations of the cochlear nucleus complex are considered as separated sources, 13 major neuronal populations project to the central nucleus.) It has recently been demonstrated that these different inputs are processed at least largely in parallel in at least largely segregated regions of the ICC (see Roth et al.<sup>22</sup> and Jones<sup>10</sup>). Anatomical studies suggest that every source nucleus of the ICC of the cat has a different target region within it<sup>22</sup>, sometimes clearly overlapping with the target regions of other sources. Despite these apparently non-coincident target regions of different source nuclei, some sources of input to the ICC appear to be convergent on others. Thus, neurons in the ICC never respond as if they were deriving their input from at least two major anatomically-defined sources<sup>22</sup>. Finally, it is clear that input from these various sources all projects onto the same basic neural processing machinery, the cell laminae of the ICC. This complex and largely segregated multisource projection to the midbrain is without parallel in other sensory systems. What neuronal processing could be performed in common by the ICC on its various binaural and monaural inputs? How is this multisource information processed separately or convergently in the complex divergent-convergent projections from ICC to cor-

tical fields? And just what input in what form is actually delivered to the binaural bands of auditory cortical fields? These are now central questions for auditory anatomists and neurophysiologists. Embedded within these questions is a more elementary one, relevant to cortical field organization: Are the binaural bands of auditory cortical fields individual cortical processing units - e.g., terminal processing units of source-specific parts of the cochleotopic projection system? Or is A1 the processing machine?

In the recent important studies of auditory cortex in the mustache bat, Suga and colleagues have demonstrated that sectors of a large cochleotopically organized cortical field spatially represent different aspects of this bat's behaviorally important echolocation signals, i.e., they have described a series of functional maps beyond the cochleotopic map in a large auditory cortical field (see reference 24, for an introduction to this important work). Are the binaural bands of A1 in the cat singly or together (EE and EI pairs) equivalent subdivisions of the field, individually accounting for some aspect of auditory perception or behavior? Consistent with that possibility is the observation that the response properties of neurons in different binaural bands of like class are not identical. Against that conclusion is abundant anatomical evidence that different bands of the same class (i.e., all EE or all EI bands) receive input from the same thalamic neuronal arrays; and all appear to receive input from any single band of the same class in other cortical fields. As with the studies of Suga and colleagues, the practical question devolves to what is

represented along isofrequency contours within the binaural bands of A1. That question is now being intensely investigated.

It should be noted that the several almost equal-sized cochleotopically organized fields in the cat are complexely, reciprocally interconnected<sup>1,9</sup>. The anatomical relationships, heavy direct thalamic inputs and physiological response properties strongly suggest that they should be regarded as parallel information processing areas, simultaneously activated and in operation for any auditory stimulus, i.e., A1 has no obvious primacy over the other cochleotopic cortical fields.

The sources of input to the very large "diffuse" projection system are, astoundingly, not known, i.e., the sources of input to the pericentral nucleus of the inferior colliculus have still not been unequivocally determined. Note that the "non-topographic" fields of this system are only defined as such on the basis of their apparent lack of cochleotopic organization, i.e., there may be another basis for their topographic order. Thus, for example, Knudsen and Konishi<sup>13</sup> have recently described a systematic representation of sound space in an apparently non-cochleotopic region in the midbrain in the barn owl. Interestingly, this nucleus has a similar relationship to the apparent cochleotopically organized homologue of the mammalian central nucleus, as does the pericentral nucleus to the central nucleus of the cat.

From this brief summary of recent and ongoing work in the auditory forebrain, it should be evident that we are now be-



ginning to understand the basic framework of the cortical processing machinery in the auditory system. The organization of projections to the system are more complex than in other sensory systems. We have seen interesting evidence for potentially very sophisticated spatial processing of information. We are uncertain as to how information from the many different brain stem sources are distributed to different cortical fields, or to the binaural bands within the cochleotopically organized fields. But we have made the essential step of defining large cortical processing subunits, so that a productive, directed search for how auditory perception and behavior are a product of the auditory forebrain can begin in earnest.

**Acknowledgments:** This work was supported by NIH Grant NS-10414, by the John C. and Edward Coleman Memorial Fund, and by Hearing Research, Inc. Described work from the Coleman Laboratory included the research contributions of many investigators as well as the authors, especially Drs. Linn Roth, Lindsay Aitkin, Robert Dykes, Steven Colwell, Paul Knight and Russell Snyder.

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