

cochlear nucleus to the medial superior olive and then to the motor nuclei of the facial and trigeminal nerves. The inferior colliculus has also been implicated in many auditory reflexes. It seems important for the startle response to loud sounds, and for the development of audiogenic seizures, a motor response resulting from a central hypersensitivity of the auditory system following early deprivation of auditory input. Auditory influences on spinal reflexes also seem to require an intact inferior colliculus. The inferior colliculus further affects the animal's attention to auditory stimuli. Learning has been shown to produce modification of neuronal responses in the inferior colliculus and medial geniculate body, but we do not know if the modification resulted from neuronal plasticity at those levels, or was due to descending influences from, say, the cortex.

I. Further Reading

The anatomy of the cochlear nucleus has been reviewed by Cant and Mores (1984) and J. K. Moore (1986b). The physiology has been reviewed by Young (1984) and Brugge and Geisler (1978). Neurotransmitters of the nerve and nucleus have been reviewed by Wenthold and Martin (1984), Caspary (1986), and in chapters in *Auditory Biochemistry* edited by D.G. Drescher (Charles C. Thomas, Springfield, 1985). The superior olivary complex has been reviewed by Brugge and Geisler (1978). The inferior colliculus has been reviewed by Aitkin (1986), who also gives a general review of the brainstem. The brainstem in relation to sound localization has been reviewed by Masterton and Imig (1984). An excellent general review of the brainstem is given by Irvine (1986).

7. The Auditory Cortex

The anatomical definition of auditory cortex has been simplified by the introduction of axonal transport techniques, which allow a definition of cortical areas on the basis of thalamic connections, and by detailed electrophysiological mapping, which allows a definition on the basis of tonotopic organization. The anatomical and physiological organization of the auditory cortex will be described, together with what is known of the neuronal responses. The auditory cortex has been a favourite target for behavioural scientists: unfortunately the behaviour-ablation method has in recent years proved to be less powerful for analysing the function of the auditory cortex than it seemed to be 20 years ago. The general functions of the auditory cortex are still not certain, and some hypotheses are listed.

A. Organization

1. Anatomy and Projections

The auditory cortex has been most commonly studied in the cat, where it is displayed on the surface of the brain. Until recently, much less work has been done in primates, where the auditory cortex lies on the superior temporal plane hidden in the lateral or Sylvian fissure.

A framework for analysing the areas of the cat auditory cortex can be built on Rose's (1949) delimitation of the cytoarchitectural areas of the temporal cortex (Fig. 7.1). By defining areas with constant cellular characteristics as seen with the Nissl stain, he described primary auditory cortex (AI), secondary cortex (AII), and a further auditory area on the posterior ectosylvian gyrus (Ep). Primary auditory cortex was described as being cytoarchitecturally similar to other primary sensory cortex, with six layers and a high density of pyramidal and granule cells in layers II, III and IV, but with sparse staining in layer V. The high density of granule cells leads to the term koniocortex, or "dust cortex". Additional auditory areas were

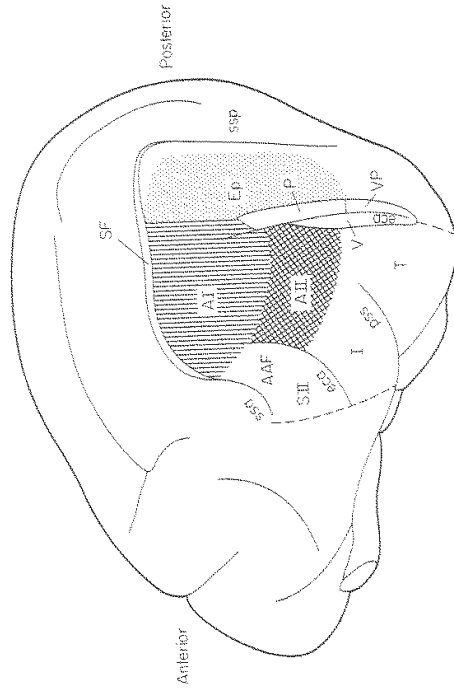


Fig. 7.1 The divisions of the cat's auditory cortex described by Rose (1949) are indicated by shaded areas, together with the other auditory cortical areas now recognized. Cortical areas: AI, primary auditory cortex, AII, secondary auditory cortex; AAF, anterior auditory field; Ep, posterior ectosylvian sulcus; P, posterior field; V, ventral field; VP, ventral posterior field; SII, secondary somatosensory area; I, insular area; T, temporal area; SF, suprasylvian fringe area, buried on the upper surface of the suprasylvian sulcus; Sulci, ssa and ssp, anterior and posterior suprasylvian sulci; eca and ecp, anterior and posterior ectosylvian sulci; pss, pseudosylvian sulcus. Adapted from Rose (1949, Fig. 1), with additions from Brugge and Reale (1985).

defined by other methods. Rose and Woolsey (1958) showed that the secondary somatosensory area (SII) and the insulo-temporal area (I-T) were also auditory areas on the basis of their thalamic connections. Reale and Imig (1980) have more recently used microelectrode mapping to subdivide the previous auditory areas to give in addition the anterior auditory field (AAF), and the ventral (V), posterior (P), and ventral posterior (VP) fields (Fig. 7.1).

The projection from the thalamus to the auditory cortex was worked out with the horseradish peroxidase technique by Winer *et al.* (1977) and Niimi and Matsuoka (1979). The conclusions of these studies are shown in Fig. 7.2, although some of the minor projections have been omitted. The major part of the ventral division of the medial geniculate, the specific auditory relay, projects mainly to AI, with smaller projections to the other areas. The medial division projects to almost all the areas of the auditory cortex, and the dorsal division, as defined in Chapter 6, projects to AII, the insulo-temporal area and Ep. Thus we can define a "core" system, running from

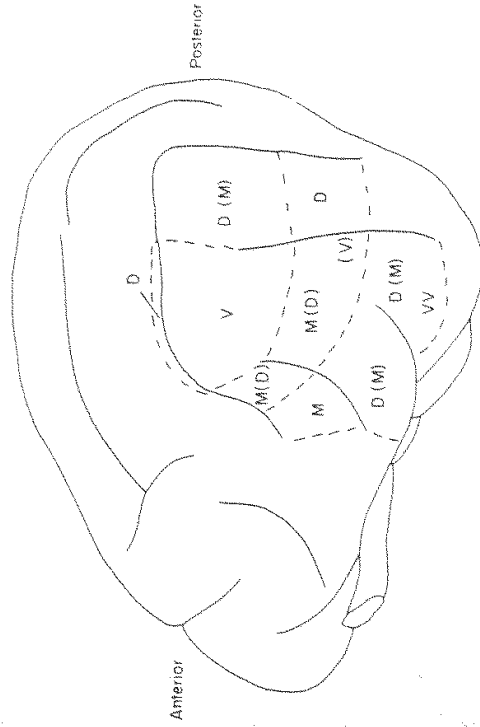


Fig. 7.2 Divisions of the medial geniculate body projecting to the auditory cortex are indicated on a map of the cat auditory cortex. The smaller projections are indicated in brackets. V, from ventral division; M, from medial division; D, from dorsal division; VV, from extreme ventral (non-laminar) division. Many still smaller contributions are not shown. Primary auditory cortex (AI) receives projections only from the ventral division. The surrounding areas receive their projections from the dorsal and medial divisions. Adapted from Ravizza and Belmore (1978, Fig. 3), to incorporate the results of Niimi and Matsuoka (1979).

the specific thalamic auditory relay, namely the ventral division of the medial geniculate body, to the primary auditory cortex. One or more "belt" or "diffuse" systems, surrounding AI, receive projections from the other divisions of the medial geniculate. The belt also receives projections from other thalamic groups, and in particular the posterior group of thalamic nuclei. There are intense reciprocal connections between the cortical areas, and back from the cortex to the brainstem (Diamond *et al.*, 1969; Andersen *et al.*, 1980).

The afferent fibres from the ventral division of the medial geniculate end mainly in layer IV but also in the other layers (Mitani *et al.*, 1985). The constituent cells of AI, especially in layer IV, appear to be organized in vertical columns. In the cat, the cells appear to be situated around the periphery of small vertical cylinders, of 50–60 μm diameter, oriented with their axes at right angles to the cortical surface (Sousa-Pinto, 1973). Vertical columns have also been described in layer IV of human beings and monkeys (Seldon, 1981a; Smith and Moskowitz, 1979). Many of the cells show direct soma-to-soma contacts with other cells in the column. Smith and Moskowitz suggest these may represent gap junctions between the cells in one column.

The cell types of the primary auditory cortex appear to be similar to those of other cortical areas, including for instance pyramidal cells (with axons extending into the white matter) and fusiform cells (with two tufts of dendrites) (e.g. Winer, 1985b; Mitani *et al.*, 1985). It appears that dendrites and axons ramify horizontally more than is typical of sensory cortex (Souza-Pinto, 1973), especially along the iso-frequency lines running across the cortex (Glaser *et al.*, 1979). There is also a particularly rich ramification vertically within each column of cells. Callosal afferents, from the contralateral cortex, ramify vertically within "callosal columns", i.e. within columns of cells having a particularly rich callosal innervation (Code and Winer, 1986).

2. Tonotopic Organization

The tonotopic organization of the afferent projections was worked out with gross evoked potentials by Woolsey (1960). His plan for the cat (Fig. 7.3A) shows that auditory evoked potentials were recordable in many auditory areas. Tonotopic organization was shown for some of these areas and is indicated by the representation of the base of the cochlea (B) or the apex (A). Tunturi (1952), in the dog, showed that between these two extremes there was a complete representation of stimulus frequency, with areas having the same frequency lying in strips at right angles to the line of frequency progression (Fig. 7.3B).

Merzenich *et al.* (1975) and Reale and Imig (1980) showed that the tonotopic organization of the cortex was preserved at the single cell level (Fig. 7.4). In AI, cells were sufficiently sharply tuned for best frequencies to be clearly definable, and tonotopic organization and iso-frequency strips as described above were found. In AII, by contrast, the degree of tonotopicity appeared to be poor, with cells in the same region having a wide range of characteristic frequencies (Reale and Imig, 1980; Schreiner and Cynader, 1984). The increased detail from single unit studies has also permitted closer parcellation of the different fields. For instance, Knight (1977) and Reale and Imig (1980) suggested that the region anterior to AI, which Woolsey (1960) thought was the low-frequency continuation of the suprasylvian fringe, was in fact a separate area of its own with a tonotopic frequency map in its own right (the anterior auditory field; Fig. 7.1). This technique also enabled them to define the posterior and ventral posterior fields on the anterior edge of the Ep field, buried in the posterior ectosylvian sulcus, and the ventral field on the posterior edge of Woolsey's AII field (see Fig. 7.1).

The map of frequency therefore seems to undergo a series of transformations up the auditory pathway. A sound of one frequency is represented by a single point in the cochlea, by a two-dimensional sheet of cells in each of

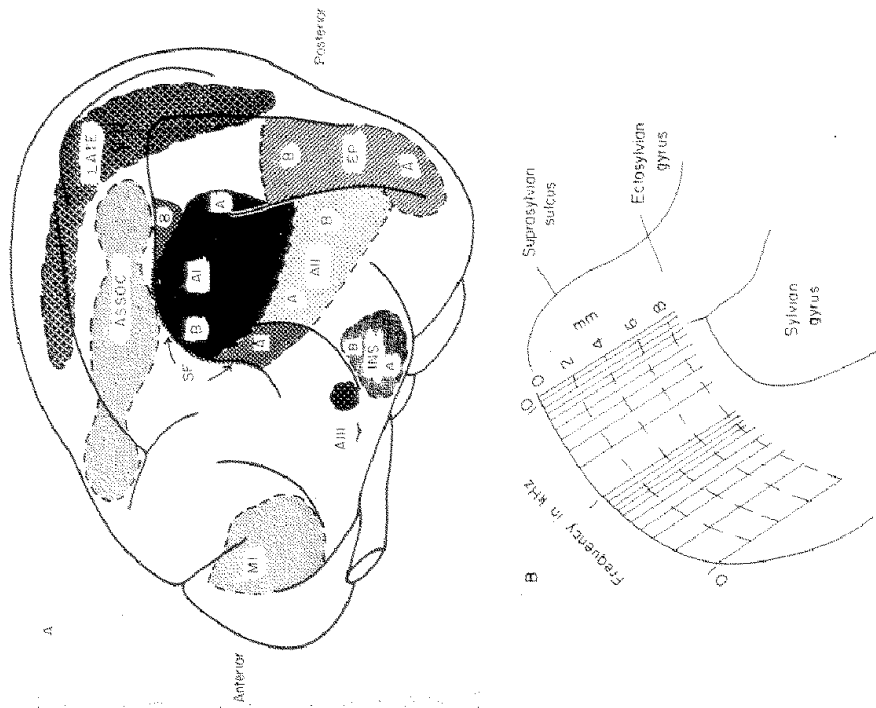


Fig. 7.3 (A) Auditory areas and their tonotopic organization were shown with gross evoked potentials by Woolsey (1960) in the cat. Where the areas are organized tonotopically, the representation of the high-frequency base of the cochlea (B), and of the low-frequency apex (A) are indicated. MI, precentral motor area. AIII is now called SH. Other abbreviations as in Fig. 7.1. The part of "SF" labelled "A" is now called the anterior auditory field, with a tonotopic organization in its own right, AII now contains the ventral field, and Ep now contains the posterior and ventral posterior fields (see Fig. 7.1). From Woolsey (1960), *Neural Mechanisms of the Auditory and Vestibular Systems* (eds G. L. Rasmussen and W. F. Windle). Courtesy of Charles C. Thomas, Springfield, Illinois. (B) Iso-frequency strips in the dog auditory cortex. From Tunturi (1952, Fig. 2).

the intervening auditory nuclei, and by a one-dimensional strip of cells in each of the tonotopically-organized fields of the cortex, with multiple representations in the different fields.

Tonotopicity is less obvious in unanaesthetized cats (Evans *et al.*, 1965). The cortical areas have been investigated less extensively in primates. The primary area is situated on the superior temporal plane within the Sylvian fissure (Fig. 7.5A). Again, there is a tonotopic organization of AI, with low frequencies represented rostrally and high frequencies caudally (Merzenich and Brugge, 1973; Imig *et al.*, 1977). As in the cat, AI is surrounded on all sides by other auditory areas (Fig. 7.5B), some of which are tonotopically organized, although the terminology differs between investigators, and the apparent details of the fields differ between the different species of primate. In man, in which the limits of the auditory cortex have to be defined on cytoarchitectonic rather than electrophysiological grounds, the auditory cortex appears to be in a similar position (Economo and Horn, 1930). Its detailed anatomy has been described more recently by Seldon (1981a,b, 1985). Positron emission tomography in alert human subjects has shown auditory responses to be tonotopically organized

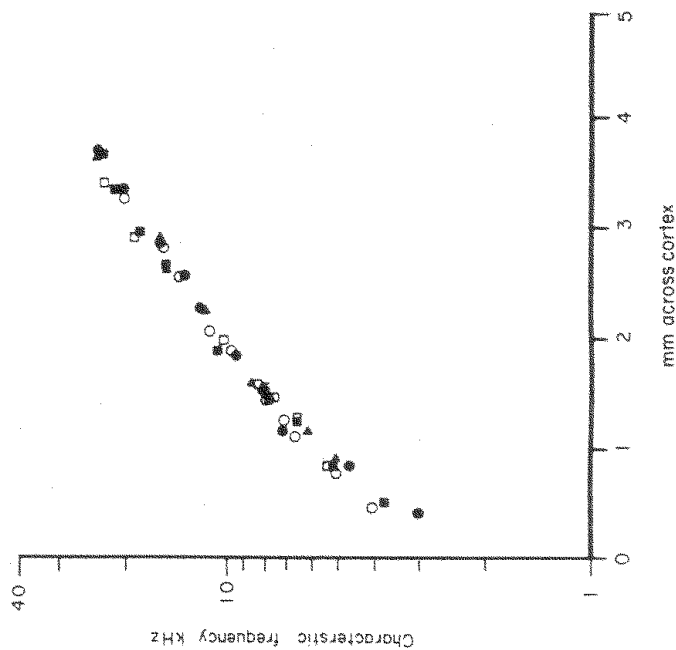


Fig. 7.4 Best frequencies of neurones in a single cat's auditory cortex are plotted as a function of distance across the cortex. The neurones were located on five parallel lines across the cortex, and different symbols are used for each line. From Merzenich *et al.* (1975, Fig. 6).

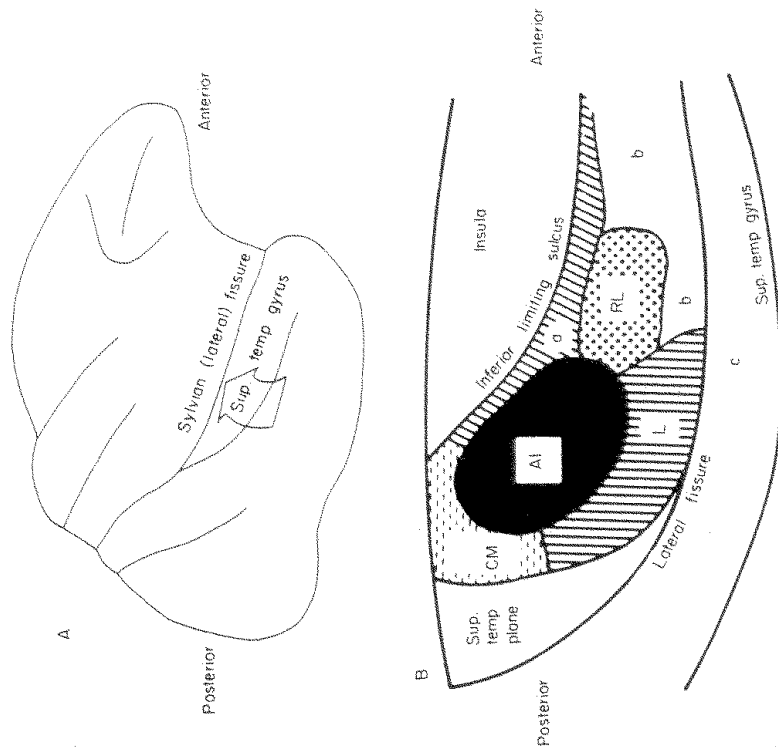


Fig. 7.5 (A) The auditory cortex in the monkey lies buried in the Sylvian or lateral fissure (arrow). If the cortex above the fissure is removed, the areas of cortex on the lower surface of the fissure, the superior temporal plane on the upper surface of the superior temporal gyrus, become visible. (B) The superior temporal plane seen from above, after removal of the overlying cortex. AI, primary auditory area; RL, rostral lateral field; L, lateral field; CM, caudomedian field; a, b, c, additional auditory areas. From Merzenich and Brugge (1973, Fig. 14).

(Lauter *et al.*, 1985). In this technique, positron emission from radioactive ^{15}O -rich H_2O is detected, as modulated by changes in regional blood flow resulting from altered neuronal activity.

3. Columns in the Auditory Cortex

Within AI, many attempts have been made to identify functional columns of cells similar to those described in somatosensory and visual cortices (e.g. Mountcastle, 1957; Hubel and Wiesel, 1963). It had been found in such

studies that cells in a single radial column of the cortex had similarities in their optimal stimulus characteristics. Neighbouring columns may have different stimulus characteristics, and there would be a sharp jump in the characteristics measured as a sampling electrode left one column and entered another. In the auditory cortex, the possibility of frequency-specific columns within the overall tonotopic organization was first investigated. Thus Merzenich *et al.* (1975) reported that cells in a single radial electrode penetration of the cortex had the same frequency, and that stepwise changes in frequency were often observed in oblique penetrations. In a systematic analysis, Abeles and Goldstein (1970) showed that units close together had similar best frequencies. However, there was no sign of discrete transitions between adjacent columns. Either there are smooth transitions in frequency across the iso-frequency contours, or the frequency columns are too small (100 μm or less) to be detectable by the technique. Sousa-Pinto's (1973) anatomical cylinders of cells were 50 μm across. He did not think they could be associated with discretely different frequencies, because the separation of the columns was less than the lateral spread of the incoming axonal arborization.

With an analysis of binaural sensitivity, however, there appears to have been more success in identifying functional columns. In AI, Imig and Adrian (1977) showed that cells excited by stimuli in one ear but inhibited by stimuli in the other ear (EI cells) were located in discrete radial columns. They were separate from cells excited by stimuli in both ears (EE cells). The different categories of cells were located in discrete radial columns. In a surface view, the two types of cell formed patches wandering over the surface of the cortex. Middlebrooks *et al.* (1980) suggested that these patches were organized in strips running roughly at right angles to the iso-frequency contours (Fig. 7.6). There was a close relation between the electrophysiological responses and the innervation as shown anatomically, since those areas showing electrophysiological evidence of a strong input from the contralateral half of the brain had a particularly rich innervation from the contralateral auditory cortex via the corpus callosum (Imig and Brugge, 1978; Code and Winer, 1986). Thus the two-dimensional sheet of the auditory cortex seems to be organized in both directions. In one direction, it is organized in frequency, although probably with smooth rather than stepwise transitions in frequency between the iso-frequency strips. At approximately right angles to this, the cortex is organized in terms of binaural dominance; the strips in this direction seem to have discrete borders.

B. The Responses of Single Neurones

1. Response Types

In the early stages of the auditory pathway there seemed to be some hope that an objective classification into discrete response types might be possible,

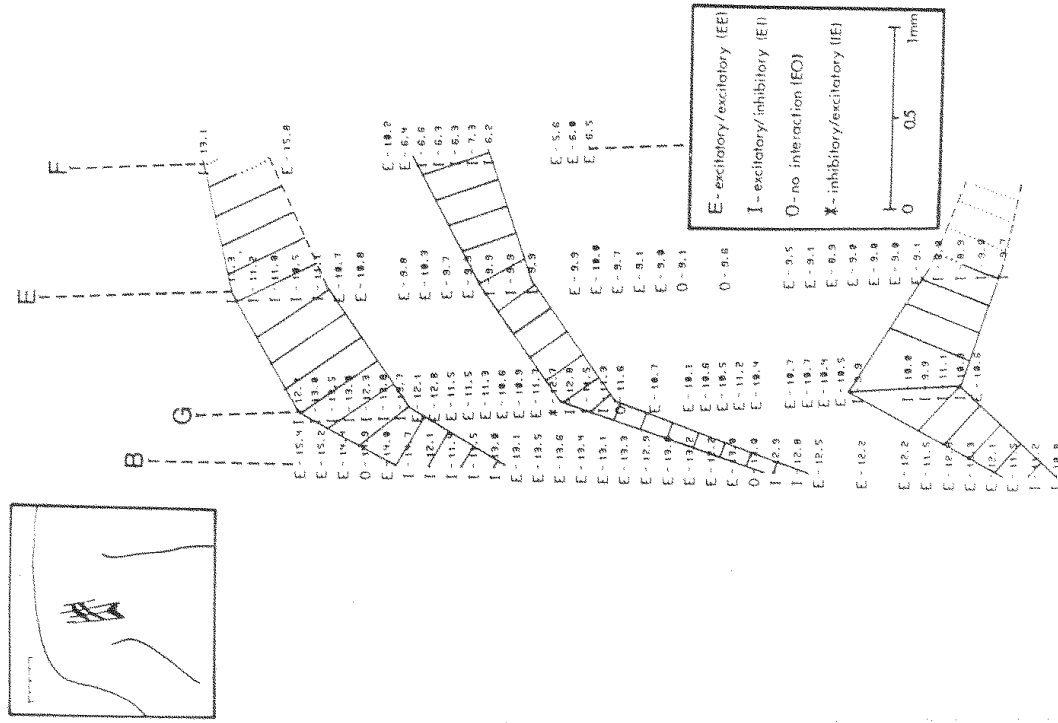


Fig. 7.6 Columns of cells that are excited by one ear and inhibited by the other (EI cells, shown in cross-hatched areas) are segregated from columns of cells that are excited by both ears (EE cells). The cell CFs are indicated by numbers along the electrode tracks. Inset shows the cortical area sampled. From Middlebrooks *et al.* (1980, Fig. 4).

and that the classes might correspond to anatomically-separable classes of cells. However, in the auditory cortex, there seems such a diversity of response types, and such a degree of dependence on the behavioural state of the animal, that this does not at the moment seem possible. In addition, even in the unanaesthetized, paralysed animal, a certain proportion of the units (20% according to Goldstein and Abeles, 1975) do not seem to respond in a determinate way.

Only a certain proportion of neurones seem responsive to sound at all. In the anaesthetized cat, Erulkar *et al.* (1956) found that only 66% of neurones in AI were responsive to sound. In the unanaesthetized and freely moving, or unanaesthetized and paralysed, cat this proportion seems higher, being 77% according to Evans and Whitfield (1964), and 95% according to Goldstein *et al.* (1968).

Oonishi and Katsuki (1965) described a wide variety of tuning curve shapes in AI of the barbiturate-anaesthetized cat. Some cells were sharply tuned, with the V-shaped tuning curves of units in the lower stages of the auditory system. Others had more than one dip, and were termed multipeaked units. Some had broad tuning curves (Fig. 7.7). The thresholds at the tip of the tuning curve have been reported by some to be as low as in earlier stages of the auditory system (e.g. Goldstein *et al.*, 1968), although others have found best thresholds of 50–60 dB SPL (Evans and Whitfield, 1964).

Different temporal patterns of response can be seen for different cells. For the cells which respond in a determinate way, Abeles and Goldstein (1972) in the unanaesthetized paralysed cat described "through" (i.e. sustained), "on", "on-off" and "off" responses (Fig. 7.8). The same unit may show different temporal patterns for different frequencies of stimulation. A similar variety of response patterns has been described earlier in the auditory system, and it is by no means certain that such an analysis indicates any significant increase in response complexity.

Many cells show wide bands of lateral inhibition in unanaesthetized preparations (Shamma and Symmes, 1985). In multipeaked units, responses to excitatory stimuli in one range can be inhibited only by stimuli in the same frequency range, and in broadly tuned units the inhibitory range of frequencies varies with the frequency of the exciting tone (Abeles and Goldstein, 1972). Some of the latter properties can be explained by the convergence, on to single units, of the projections of cells with different best frequencies, where each of the projecting cells has inhibitory sidebands.

Many neurones show very sharp non-monotonicity in their rate-intensity functions, with the firing rate falling by perhaps 50% for deviations of stimulus intensity by 10 dB or so from the optimum (Fig. 7.9; Brugge and Merzenich, 1973; Benson and Teas, 1976).

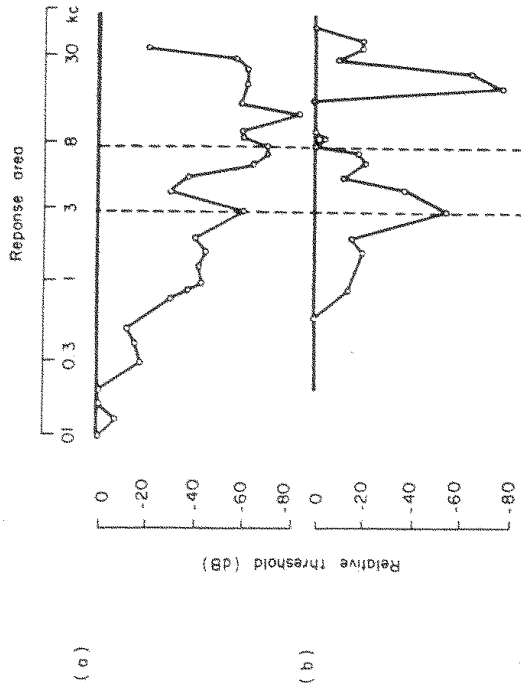


Fig. 7.7 Broad (a) and multipeaked (b) tuning curves are seen in the auditory cortex. Single peaked tuning curves are also present. From Oonishi and Katsuki (1965, Fig. 1).

In the posterior field (Fig. 7.1), most neurones have sharp V-shaped tuning curves. Nearly 90% of rate-intensity functions are reported to be strongly non-monotonic in the cat, as against less than 40% for AI (Phillips and Orman, 1984). The neurones respond with very long latencies, with minimum values of 20–50 ms, compared with 20 ms or less for AI. In AII, tuning curves are broad, and often have complex dips on the low-frequency side. There may well be a continuum in breadth of tuning across both AI and AII, such that the sharpest tuning curves are found in the dorsal part of AI, with a gradual transition to broader tuning across AII (Schreiner and Cynader, 1984).

2. Sound Localization

Many neurones in AI show binaural interactions, being sensitive to interaural phase or intensity differences (e.g. Brugge and Merzenich, 1973; Reale and Kettner, 1986). Many are also selective for the direction of sound sources (Middlebrooks and Pettigrew, 1981). For unilateral stimuli, stimulation of the contralateral ear is generally the more potent, and this has a correlate in the binaural case where the interaural intensity and phase responses are

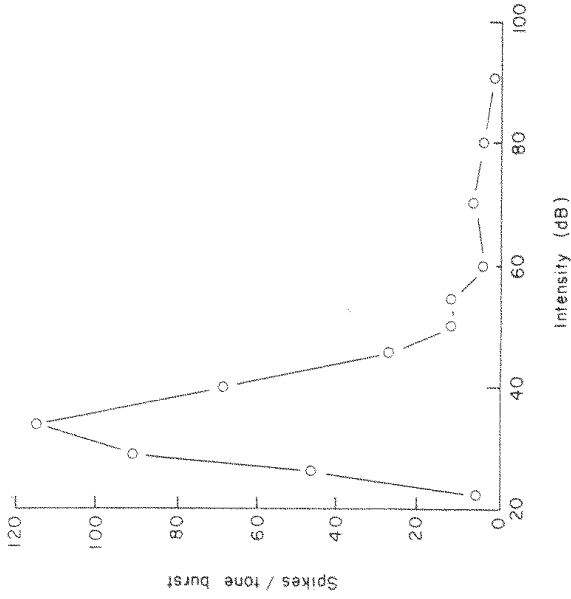
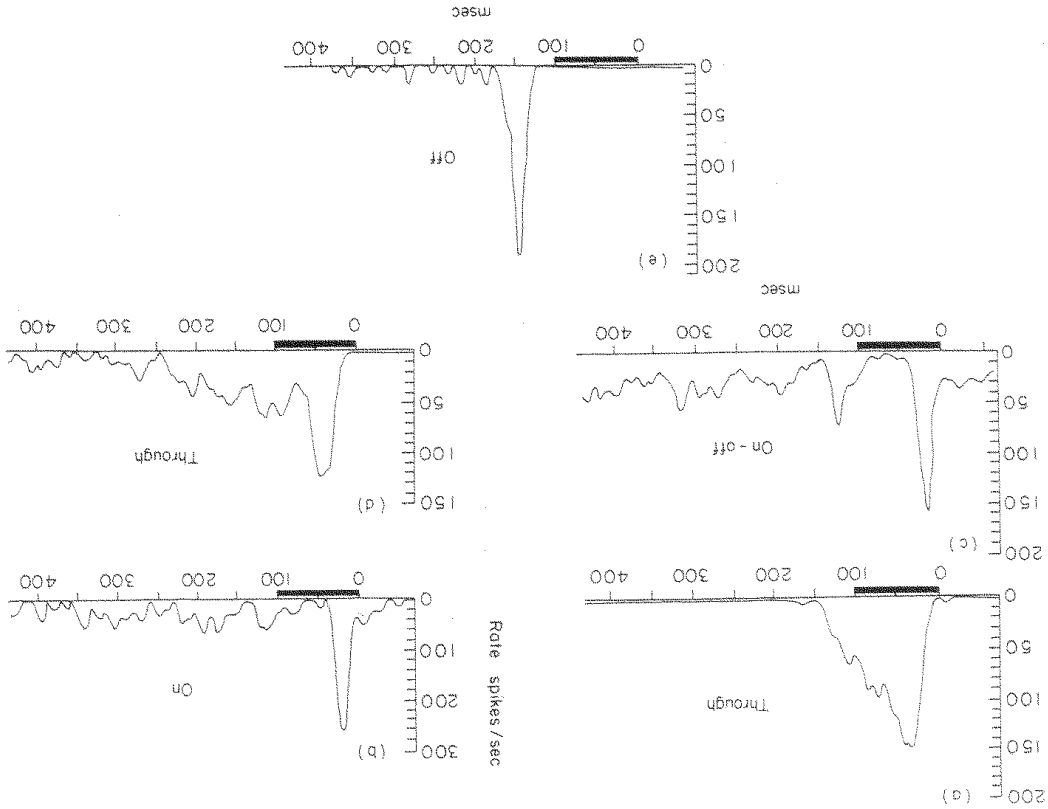


Fig. 7.9 Neurons in the auditory cortex can have very sharply nonmonotonic rate-intensity functions. From Brugge and Merzenich (1973, Fig. 8A).

such that each cortex predominantly responds to stimuli on the contralateral side. It seems that the cells share the directional selectivity of cells in the brainstem, modified by the callosal interactions seen in the cortex. It further seems that different cells in a single cortical binaural interaction column share the same directional selectivity, although they may be optimally responsive to different types of sound (Brugge and Merzenich, 1973).

In one type of experiment, stimuli are presented separately to the two ears, and the relative timing or intensity of the stimuli is varied. When interaural phase is varied, the firing of many units shows a cyclic function similar to those obtained at the lower stages of the auditory pathway (Fig. 7.10). In some cases the time disparity for maximum response is independent of stimulus frequency (Fig. 7.10A), indicating that it is appropriate to think in terms of a characteristic delay. In others, this is not the case (Fig. 7.10B). For such a unit, it is appropriate to think in terms of sound localization at all, we would expect the optimal location of the sound source to vary with stimulus frequency. In these studies continuous tones were presented to the two ears, and the interaural phase delay varied. However, it is also possible to vary the interaural phase delay in the onset or temporal envelope of a stimulus. In one group of neurones studied by Kitzes *et al.* (1980), a very sharp peak of sensitivity was found for zero or near-zero disparities in

Fig. 7.8 Temporal response patterns in primary auditory cortex, according to Abeles and Goldstein (1972, Fig. 2).



onset time, indicating that the cells could code sound sources directly, or nearly directly, ahead. Time disparities for click stimuli have been studied as well (Benson and Teas, 1976; Brugge and Merzenich, 1973). In some cells the functions for time disparities measured with clicks matched the functions for interaural phase delays measured with tones. In other cells, however, they clearly did not. For these cells, a simple explanation in terms of sound localizing ability does not seem appropriate.

A sound source in space can give rise to differences in intensity at the two ears, as well as to differences in phase. In a corresponding way, some neurones give their optimal response for specific intensity differences between the two ears (Brugge and Merzenich, 1973; Phillips and Irvine, 1983). There is a tendency for cells with the more strongly contralaterally-dominated responses to be situated more ventrally along each iso-frequency line (Reale and Kettner, 1986).

In the experiments described so far, directionality of the sound source was simulated by varying the interaural phase and intensity differences. However, some units (50%) are able to code the real direction of sound sources, measured by moving a speaker around a cat's head (Middlebrooks and Pettigrew, 1981). As in lower auditory nuclei, some of the cells have small, circumscribed receptive fields centred on the acoustic axis of the pinna nearest to the sound source. These cells tend to have high characteristic frequencies (> 12 kHz), and tend to be sensitive to interaural intensity differences. Middlebrooks and Pettigrew presented evidence that the cells obtained their directional selectivity from the strong directionally-selective amplification produced by the pinna in this frequency range, maintained and enhanced by the cells' sensitivity to interaural intensity differences (Middlebrooks and Pettigrew, 1987). Other cells responded to sound sources over the whole of the contralateral hemifield. They tended to have characteristic frequencies below 12 kHz, and it was suggested that they obtained their selectivity from the lesser directional selectivity of the pinna in this frequency range, again maintained and enhanced by the cells' sensitivity to interaural intensity differences.

Sovijärvi and Hyvärinen (1974) have described units specifically responsive to the direction of movement of a sound source. In response to stationary stimuli such cells gave a complex on-off response, indicating that this particular sensitivity arose from multiple excitatory and inhibitory inputs to the cell.

3. The Detection of Other Features

Whitfield and Evans (1965) in the unanaesthetized, unrestrained cat described cells apparently specifically responsive to frequency-modulated

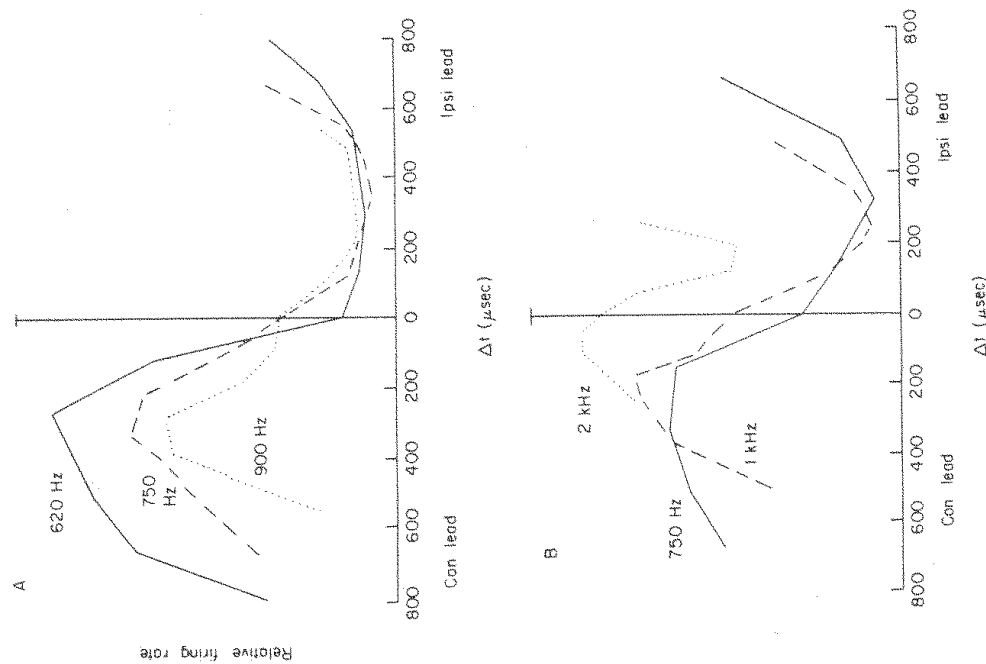


Fig. 7.10 The cyclic dependence of firing rate on interaural time delay indicates in A a neurone with an optimal time disparity which is independent of stimulus frequency, and in B one with disparity which is dependent on stimulus frequency. From Benson and Teas (1976, Fig. 4).

(FM) tones. Many seem to be specifically sensitive to one particular direction of frequency modulation, and some are tuned to a certain rate of frequency modulation (Mendelson and Cynader, 1985). Other cells are strongly driven by amplitude-modulated stimuli, again being tuned to a specific frequency of modulation (Schreiner and Urbas, 1986). In some of these units, and particularly those with complex temporal patterns of discharge, the response to modulated tones cannot be predicted from the response to steady tones (see also Funkenstein and Winter, 1973). As was described above, some such units have been described as early as the dorsal cochlear nucleus (Britt and Starr, 1976b). However, the FM-sensitivity of cells in the cortex shows a significant advance over that in the cochlear nucleus. Cells in the cortex tend to show a greater specificity in their sensitivity to sweep direction. Moreover, the effective range of frequency modulation found by Whitfield and Evans, sometimes $\pm 2.5\%$ or less, is much smaller than that necessary in the dorsal cochlear nucleus. In some cases they found responses to small modulations when the modulated frequency range lay entirely within the steady tone response area. In other cases they found responses to frequency-modulated stimuli with stimuli entirely outside the steady tone response area. This was in accordance with the observation that frequency-modulated stimuli were in general the more effective stimuli for cortical cells, as was the observation that some units could be driven by frequency-modulated stimuli but not steady tones at all.

Such studies show that a degree of response specificity for feature extraction exists in the cortex. But the extent to which we are able to divide such cells into separate classes of specific feature detectors, analogous to, say, simple or complex cells in the visual system, is doubtful. Thus, while Goldstein and Abeles (1975) report that FM stimuli were very effective stimuli for cortical cells, the FM-sensitive cells were situated on a continuum of cells responding to a range of complex features.

If we wanted to pursue the idea of a hierarchy of specific feature detectors, we might expect neurones at the highest levels of the nervous system to respond only to stimuli of particular significance for the animal concerned. Attempts have therefore been made to measure the responses of cortical cells to the vocalizations of the species, or to other sounds of presumed biological significance. However, by comparing the responses to normal and time-reversed species-specific vocalizations in unanaesthetized squirrel monkeys, Glass and Wollberg (1983) concluded that there was no particular evidence that cells were generally more responsive to the normal (non-reversed) vocalizations. Instead, the cells seem to be responsive to their discrete stimulus components in the vocalizations, and in particular to their transients. Similarly, in response to human speech sounds, the cells appear to be particularly affected by transients in the stimuli (Steinschneider *et al.*,

1982). Although these experiments suggest that the cortex is indeed involved in the handling of complex sounds, these results cannot be used to suggest that animal calls, or indeed other stimuli of presumed biological significance when not incorporated in a behavioural task, form special classes which are specifically represented in the cortex.

Although some cells respond to auditory stimuli in a repeatable, if complex, way, there are others which do not. For instance, Manley and Müller-Preuss (1978) found that 50% of cells in AI, and 62% of cells in AII, spontaneously varied their response to a constant vocalization. Evans and Whitfield (1964) noted that the responses of many units habituated rapidly. In these units, the apparent novelty of the stimulus was an important factor in governing their response. Some cells responded only when the attention of the animal was drawn to the source of the sound, perhaps by visual means, and in some cases the response to sound disappeared when the animal was induced to shut its eyes (Evans, 1968). These may be the "attention" units described in auditory cortex by Hubel *et al.* (1959). Such units responded only to novel stimuli, and once the response to one stimulus had habituated, a new stimulus would again evoke a response. It is apparent that the animal's behavioural relation with the stimulus is an important factor in governing the response of such neurones. Some studies have attempted to control this by recording responses under different conditions of arousal, or by using the auditory stimulus in a behavioural task.

Thus a greater number of action potentials are found to auditory stimuli in the awake than in the drowsy or sleeping animal (Brugge and Merzenich, 1973; Pfingst *et al.*, 1977). Responses may be enhanced by using the stimulus in a conditioning task; some cells even change the tuning of their response areas in such cases (Weinberger and Diamond, 1987). These studies suggest that the function of neurones in the auditory cortex might be more satisfactorily assessed by using the stimuli as cues in a behavioural task. It further implies that the most useful data might be obtained if the task is one for which the cortex has been shown to be necessary. In studying the function of a high-level structure such as the auditory cortex, behavioural studies therefore become paramount.

C. Behavioural Studies of the Auditory Cortex

1. Introduction

Considerable effort has been put into analysing the function of the auditory cortex, by testing performance on various auditory tasks before and after cortical lesions. In spite of a great deal of progress, and some intriguing

leads, we are still uncertain about the cortical function, or functions, underlying many of the discovered deficits. For instance, it is still controversial as to whether experimental ablation of the auditory cortex leads to raised absolute thresholds. Although the commonly quoted position is that there are no, or only small, changes in absolute threshold (Kryter and Ades, 1943; Neff *et al.* 1975), some experimenters have found substantial losses (e.g. Hefner and Hefner, 1986a). Tests have generally been aimed at higher-level functions for the auditory cortex. In spite of many attempts to suggest a unifying function for the auditory cortex, it is most likely that there will be several different functions underlying the deficits seen in the different tasks. And it is unfortunately likely too, that apparently small differences in the training and testing procedures, perhaps so small that they were unreported in the original papers, will turn out to have had a decisive influence on the results. Thus, in frequency discrimination, for instance, we are still not sure of the role of the auditory cortex even after more than 40 years of work.

2. Frequency Discrimination

The earliest experiment was performed by Allen (1945), who trained dogs to lift a foreleg to a sound of one frequency, produced by tapping a bell, but not to a sound of another frequency, produced by tapping a tin cup. He showed that the discrimination was lost after large lesions of the auditory cortex. Later, Meyer and Woolsey (1952) trained cats in a rotating cage to remain still to a short series of 1.0-kHz tone pips but to rotate the cage when the series was terminated by a pip at 1.1 kHz. The discrimination could be relearned if any portion of the auditory field (i.e. AI, AII, Ep, SII of Fig. 7.3A) remained intact, but not if all areas were ablated bilaterally. Thus at this time it seemed that the auditory cortex was necessary for frequency discrimination, and that any sector of the auditory cortex remaining could mediate the discrimination. There followed an interesting series of experiments which showed that under some circumstances cats were indeed able to make frequency discriminations after cortical lesions. Two concepts emerged from these experiments: (i) after cortical lesions, cats were only able to detect stimuli, and not identify them on an absolute basis, and (ii) after cortical lesions, cats had difficulty withholding responses to irrelevant stimuli (e.g. Thompson, 1960; Elliot and Trahiotis, 1970; Neff *et al.*, 1975). While these hypotheses undoubtedly summarize many aspects of the animals' behaviour, they unfortunately are not true in an absolute way: Cranford *et al.* (1976a) showed that with appropriate methods of training cats are able to perform satisfactorily on both counts after cortical lesions.

Task difficulty is a confounding factor here. It seems that when the method of training was chosen such that the task was easy for the animal, performance survived the lesion, but with methods of training that made the task more difficult, it did not. This suggests that lesions may interfere with complex strategies; alternatively they may just produce a generalized interference with behaviour, which is revealed only with difficult tasks.

3. Sound Localization

A very different task, with important implications for the function of the auditory cortex, is that of sound localization. Many experiments have found changes in the ability to localize sounds after cortical ablation. For instance, Neff (1968) trained cats to approach the source of a sound, as in Fig. 7.11. He showed that after bilateral lesions of AI, AII, Ep, I-T, SII and the

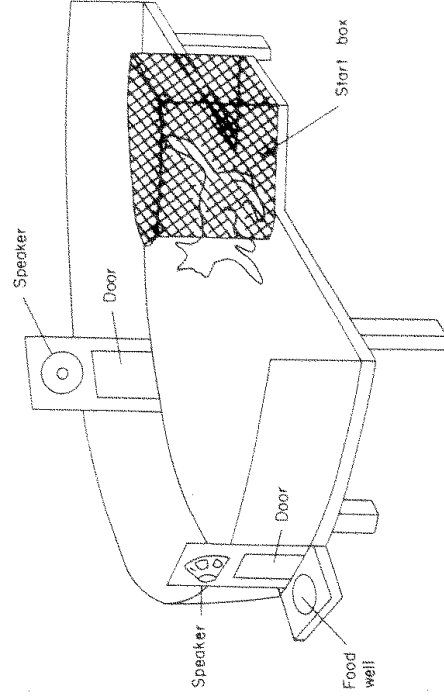


Fig. 7.11 In an apparatus for testing sound localization, one speaker sounds, the cat is released, and has to push open the door under the correct speaker.

suprasylvian gyrus (defined as in Fig. 7.3A), cats were unable to approach the correct box. If the suprasylvian gyrus was spared, performance was still poor post-operatively, although better than chance (Neff, 1968; Strominger, 1969). Wegener (1973) found analogous effects in the monkey, and some effects have also been reported in man (e.g. Jerger *et al.*, 1969).

More recent data shows that the position is not entirely clear-cut, because with different methods of testing normal performance can be found after these lesions (Cranford, 1979a).

The results of sound localization experiments become clarified if two conditions are observed: (i) the sound signals are brief (i.e. <40 ms), so that the subject cannot orient or explore within the sound field while the stimulus is sounding, and (ii) there must be several speakers, rather than two as in Fig. 7.11, so that the subject has to make a genuine choice of direction, rather than a simple left-right decision (Jenkins and Masterton, 1982).

Using these techniques, Jenkins and Merzenich (1984) showed that cats had profound deficits in sound localization after unilateral lesions confined to AI. The deficits were confined to the hemifield contralateral to the lesion, with performance in the ipsilateral hemifield being unaffected. If lesions were confined to a single iso-frequency strip in AI, deficits in localization were found for tone pips of only the corresponding frequency. If the complementary experiment was performed, and a narrow iso-frequency strip was left in AI while the rest of AI was removed, sound localization was possible only for the frequencies represented by the strip. The results of Jenkins and Merzenich's experiment strongly indicate that AI is required for sound localization, and that sound locus is coded in a frequency-specific way. The results are in entire agreement with the electrophysiological evidence. Electrophysiological experiments show that cortical cells respond preferentially to sound sources on the contralateral side of the head. Moreover, they suggest that information about sound location is coded according to stimulus frequency, since cells responding to binaural information have best frequencies for stimulation and are tonotopically organized (see Chapter 6 and sections A.3 and B.2 in this Chapter).

For the result to hold, the two above conditions had to apply: Firstly, if longer (200 ms) stimuli were used, no effect was found. Jenkins and Merzenich suggested that with long stimuli the animal would be able to scan by means of head movements, and perform the task on the basis of monaural cues. However, an additional effect is possible, since there is evidence that animals have general difficulty with short stimuli after cortical lesions (see below). Secondly, if a simple left-right decision is needed, sound localization is possible even with brief stimuli (Jenkins and Masterton, 1982). Jenkins and Merzenich suggested that it would not be possible to measure unilateral deficits in this case, because sound sources on the unaffected side could still be localized, and the subject would be able to achieve good detection of sound direction by categorizing all sounds as localizable (i.e. from the unaffected side), or as unlocalizable (i.e. from the affected side). However, while this may account for the effects of unilateral lesions, it does not account for the lack of effects of bilateral lesions on certain simple left-right lateralization tasks.

In such left-right lateralization tasks, the animal did not have to locomote to the source of the sound, but had to indicate its direction by making another response. For instance, in the experiments of Ravizza and Masterton (1972), opossums were trained to drink from a water spout when sounds came from the right, but to stop when sounds came from the left. They were still able to localize after nearly complete removal of the neocortex. In the experiments of Cranford (1979a), binaural signals differing in phase and intensity were presented to the two ears through headphones. In these conditions, in man at least, the sound appears to be coming from one side or the other. Cranford (1979a) showed that after bilateral ablations of AI, AII, Ep, SII and I-T, cats could be trained to use a change in binaural intensity or phase disparity as a signal to move across a shuttle box. Moreover, the threshold disparities were little greater than those of normal animals. The negative effects of bilateral lesions with these tasks has an interesting implication. The results suggest that locomotion towards the source of the sound might be essential if a deficit is to appear. That is, the animals might have had difficulty in orienting in auditory space, or in locomotion, or in relating the two.

Experiments by Hefner (1978) addressed these possibilities. He trained dogs to approach one of two goal boxes not on the basis of the position of a sound source, but on the basis of the rate of a brief train of clicks presented through a central speaker. After bilateral removal of primary and secondary auditory cortices the dogs were able to use this cue to approach one goal box or the other. But if the very same stimuli, presented now through one of two speakers over the goal boxes, were used in the localization task, the animals failed. Thus under these conditions, neither making a motor reaction, nor remembering the correct response, nor attending to a brief stimulus, were the critical factors. It appears that the dogs had a specific deficit in connecting the location of a sound source with the necessary movement towards it. As Neff *et al.* (1975) say: "Perhaps, in the absence of auditory cortex, organization of a 'spatial world' based on acoustic information is no longer possible."

The auditory cortex is also necessary for the discrimination of binaural signals simulating moving sound sources, when signals are presented to the two ears with a varying time delay between them (Altman and Kalmykova, 1986). Again, unilateral lesions affect performance only for sound sources contralateral to the lesion.

We should end with a word of caution. Although hypotheses of complex function for the cortex are attractive, we should not be seduced away from simpler, if less interesting, hypotheses. Thus Jerger *et al.* (1969) found that a patient with unilateral damage to the temporal lobe had deficits in sound localization and also abnormal thresholds for short stimuli. Plainly,

abnormal temporal integration of brief stimuli, if unilateral, could lead to a distortion of auditory space, with the result that the subject might not be able to walk to or point to the source of a sound, while still being able to discriminate changes in source position. He would still have the concept of auditory space; it merely no longer matches real space, due to a comparatively simple sensory deficit.

4. Ear Selection

Following the complex interpretations of the previous section, we now turn to experiments where a simpler explanation of one aspect of auditory cortex function is at least possible. It appears that if a cat is trained to respond to auditory signals in one ear, and to ignore competing signals in the other ear, performance is reduced by lesions of the auditory cortex contralateral to the attended ear. Kaas *et al.* (1967) trained cats to respond to changes in the pattern of tone pulses, when the elements of the pattern were presented separately to the two ears through headphones. Figure 7.12 shows the

	Neutral stimulus	Avoidance stimulus
Attending ear	L - L - L - L - L - L	L - H - L - H - L - H -
Ignoring ear	- L - H - L - H - L -	- L - H - L - H - L - H
Binaural pattern	L L L H L L H L L L	L L H H L L H H L L H H

Fig. 7.12 In a test of ear selection used by Kaas *et al.* (1967), binaural stimuli were presented through headphones. Cats learned the task by responding to the stimuli in the "attending ear". Attention to one ear was upset by lesions of the contralateral cortex.

paradigm. Although the task can be learned on the basis of the binaural pattern, it is simpler to attend to one ear only, the one in which the pattern changes from L-L-L-L for the neutral stimulus to L-H-L-H for the warning stimulus. Transfer tests showed that this is in fact what the cats did. When the auditory cortex (AI, AII, Ep, SII, I-T) was ablated unilaterally, there were severe initial deficits with lesions contralateral to the attended ear, but not ones ipsilateral to it. It appears, therefore, that each cortex relates specifically to the contralateral ear. It will be recalled that this was also suggested by the electrophysiological evidence; neurones in one auditory cortex are most strongly excited by stimuli in the contralateral ear.

Analogous deficits can be found if the cat has to detect tone pips in one ear in the face of a particular effective masker in the other. Cranford

(1975) used a continuous train of noise bursts as a contralateral masker, synchronized with the tone pips in the signal ear. He showed that unilateral lesions of the cortex, contralateral to the signal ear, increased the amount of contralateral masking. The effect, as we might expect, only appeared with lesions contralateral to the attended ear. It appears, therefore, that unilateral cortical lesions can alter the effective balance of excitation arriving from the two ears. Such an interpretation was supported by the further ablation of the auditory cortex on the other side. Once the cortices on both sides were ablated, the degree of contralateral masking returned to normal.

The above tasks are reminiscent of those that have been used in the analysis of interaural attention in man. A stimulus, such as spoken text, might be presented to one ear, and a competing stimulus to the opposite ear (e.g. Cherry, 1953). The subjects have to respond to one stimulus or the other. Not surprisingly, such tests reveal deficits with unilateral cortical damage (e.g. Berlin and McNeil, 1976).

5. Patterns, Memory and Time

Diamond and Neff (1957) suggested that the auditory cortex might be important for the analysis of auditory patterns, just as the visual cortex is necessary for the analysis of visual patterns. They tested the ability of cats to discriminate changes in an ongoing pattern of 800-Hz and 1-kHz tone pips, when the temporal ordering of the tone pips was changed, but the sequences were otherwise identical. They found that the pattern could be relearned if any part of AI were preserved, but there was complete loss and no relearning if the lesions included AI, AII, Ep and I-T (as defined in Fig. 7.3A). These areas therefore seem necessary for distinguishing the temporal order of auditory stimuli. The I-T area seems to have a particularly important function in this task, since Colatava *et al.* (1974) have shown that such discriminations are lost after lesions of the I-T area alone. It seems probable that the I-T area in the cat has a supramodal role in temporal pattern perception, since Colatava has shown that lesions of I-T upset the perception of visual and somatosensory as well as auditory temporal patterns (Colatava, 1972, 1974). In man, there seems a correlate, since subjects with temporal lobe lesions have difficulty in perceiving the temporal pattern of auditory stimuli (e.g. Karaseva, 1972).

Lesions of the auditory cortex also upset tasks in animals where the subject has to indicate whether two successive sounds are the same or different by having to make a response when they are the same but not when they are different. In cats, dogs and monkeys, lesions of the primary auditory cortex or the belt area prevent the task from being relearned (e.g.

Cornwell, 1967). These animals, therefore, had a difficulty in relating the trace left by one auditory stimulus with the next auditory stimulus, or translating this into response terms, or both.

The same point was investigated by Dewson *et al.* (1970) who trained rhesus monkeys to reproduce a two-element pattern of tone and noise bursts on two panels, one corresponding to each stimulus. The intervals between the two stimuli and the duration of the stimuli were systematically varied by means of a rule that maintained performance around 79% correct. After lesions of the auditory cortex, performance was possible only for a much more limited set of time relations than before, either for shorter stimuli or for shorter silent intervals between them. This suggests that the monkeys had difficulty relating one stimulus to another if the two were separated in time. However, the deficit is not one of short-term memory in general. Forcing the monkeys to wait before making a response did not produce further deficits (Cowey and Weiskrantz, 1976). These subjects, therefore, had a specific difficulty in relating one auditory stimulus to a later one, and could be said to have a deficit in "auditory memory".

Such a deficit may be one aspect of a general deficit in coding or utilizing the temporal dimension of auditory stimuli. One of the most elementary of such deficits was described by Gershuni *et al.* (1967) and Baru and Karaseva (1972), who showed that in man and dogs unilateral lesions of the auditory cortex resulted in a loss of sensitivity to short tones in the opposite ear, but not to long ones, nor to either type of stimulus in the ipsilateral ear (Fig. 7.13). Presumably the cortex plays some role in extending the effect of brief stimuli so that they can influence other neural events. Note, however, that the deficit only appeared for very short stimuli, lasting 10 ms or so. This is an order of magnitude less than the time intervals over which the deficit appeared in the pattern discrimination task of Dewson *et al.* (1970), and so presumably reflects a different mechanism. The subjects appeared to have a general difficulty with short stimuli, because frequency discrimination limens were raised for short but not long stimuli (Gershuni *et al.*, 1967), as has also been found in the cat (Cranford, 1979b).

An example of another temporal task, which used time intervals in the range of the temporal pattern tests described above, was that of duration discrimination. Scharlock *et al.* (1965) trained cats to respond when the duration of tone pips increased from 1 to 4 s. Lesions of AI, AII, Ep and I-T allowed relearning, but if SII was included relearning was not possible.

D. Hypotheses as to the Function of the Auditory Cortex

1. The Analysis of Complex Sounds

Electrophysiological experiments have shown the stimuli to which neurones in the auditory cortex are specially responsive. However, it is very difficult

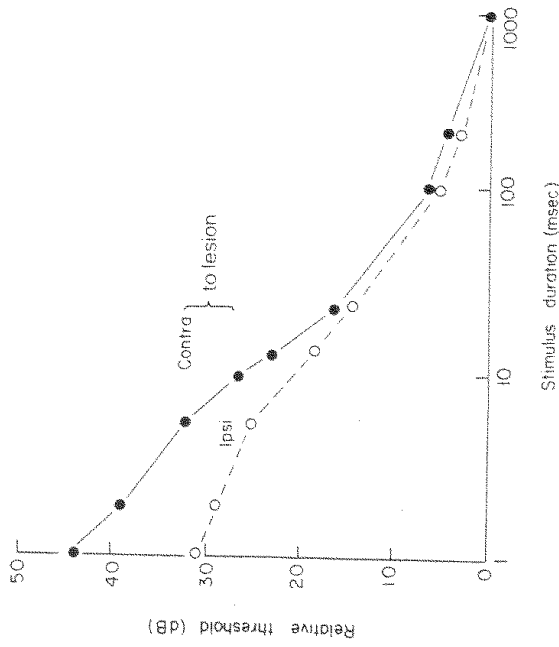


Fig. 7.13 Lesions of the auditory cortex selectively affect the thresholds of short stimuli in the contralateral ear. From Gershuni *et al.* (1967, Fig. 2).

to decide any specific role for the cortex from such experiments. The stimuli to which neurones in the cortex seem specifically responsive, which may include frequency-modulated tones and vocalizations, are in themselves so complex, and on close analysis produce such complex responses, that it is generally very difficult to decide the extent to which the cortex shows any significant advance in processing over the lower stages of the auditory system. Lesion experiments have at least the virtue of indicating whether or not a structure is essential for a particular task; but again pinning down the exact role in complex tasks is also often difficult. Leaving those difficulties aside, there are possible links between the electrophysiological observations of responses to complex sounds (whether or not this represents specific feature detection) and behavioural experiments. The discrimination of complex sounds, such as speech sounds, is upset after cortical lesions. This has been shown in the cat (Dewson, 1964) and the monkey (Dewson *et al.*, 1969), and agrees with the extensive literature in man showing deficits in speech perception after lesions of the temporal cortex.

2. Sound Localization

AI subserves sound localization, representing sounds on the contralateral side. Sound locus is coded in a frequency-specific way in the individual

frequency channels (Jenkins and Merzenich, 1984). It has been suggested that the deficit is in relating the direction of the source to a spatial schema (e.g. Cranford, 1979a). The deficit may be in the formation of "auditory space", and the cortex may be necessary for performing manipulations within such a space.

3. Ear Selection

The cortex may govern interaural attention, the cortex on one side potentiating the effect of stimuli in the opposite ear (Kaas *et al.*, 1967; Cranford, 1975). This may be related to a selective attention to sound sources on the basis of source position.

4. Response Inhibition

A hypothesis which related the auditory cortex to a motor function rather than a sensory function was that of Thompson (1960). He suggested that the auditory cortex was necessary for the inhibition of inappropriate responses. This can no longer be held in its simple form because in some experiments lesioned animals tend to make too few rather than too many responses (e.g. Cranford *et al.*, 1976a,b). The appearance of this particular deficit depends on the method of training, although the hypothesis still seems valid under certain circumstances.

5. Identification Versus Detection

A hypothesis, derived from Neff's (1961) hypothesis of the abilities that survive cortical damage, is that the cortex is necessary for the identification of stimuli on an absolute basis, but not for their detection, nor for the detection of change (Elliot and Trahiotis, 1970). Again, this hypothesis cannot be held in its simple form, because in some experiments lesioned animals could still identify stimuli by their absolute attributes, rather than only by their relative ones (e.g. Cranford *et al.*, 1976a,b; Cranford, 1979a).

6. Discrimination of Temporal Patterns

Deficits have been found in many tasks where animals have to relate one stimulus to another, when the stimuli are separated in time (e.g. Diamond

and Neff, 1957; Dewson *et al.*, 1970). The I-T cortex may play a particularly important role in this, and may govern the utilization of the temporal relations of stimuli in the visual and somatosensory as well as the auditory modalities (Colativa, 1972, 1974). When the time dimension is critical, many auditory tasks have been disrupted, and the cortex may well have a role in prolonging and utilizing the trace left by an auditory stimulus. The deficit may not be in memory generally, but in relating one element of an auditory stimulus to a later one.

7. Concept Formation

Whitfield (1979) suggested that the auditory cortex had a role in forming auditory concepts. More specifically, he suggested that the auditory cortex posits the real objects to which auditory stimuli relate. These posited real objects form the concepts unifying the different auditory stimuli. Transfer tests, in which dichotic click pairs were treated as equivalent to stimuli on one side or the other before and not after cortical lesions, form part of the evidence (Masterton and Diamond, 1964).

8. Task Difficulty

It has been a general finding that difficult tasks tend to be most frequently disrupted by cortical lesions. The difficulty of a task may depend on the details of the training technique used by the experimenter, and will vary with the strategy used by the animal in finding a solution. The function of the auditory cortex should therefore be thought of in terms of strategies rather than the tasks themselves. It has been suggested, for instance, that where the training procedure makes absolute frequency discrimination difficult for cats, cortical lesions produce deficits, but where they are such as to make the task easy, cortical lesions do not (Cranford *et al.*, 1976a). This may occur because cortical lesions produce a generalized interference with behaviour, which is revealed most clearly with difficult tasks. It is also possible that where the task is arranged so as to be difficult, the auditory cortex becomes involved in establishing or maintaining performance. The function of the cortex would therefore be that of helping to store or utilize strategies. The analysis of the strategies actually used by the individual animals in behavioural experiments would therefore be an essential, though forbidding, requirement.

It is obvious that present electrophysiological techniques would have

great difficulty in uncovering the single neurone correlates of the more complex of these hypotheses.

E. Summary

1. The auditory cortex consists of a "core" area, surrounded by a "belt". The core, which is the primary auditory cortex or AI, receives its input from the main specific auditory relay of the thalamus, the ventral division of the medial geniculate body. The belt receives its input mainly from the other divisions of the medial geniculate.
2. The primary auditory cortex, and some of the divisions of the belt area, are tonotopically organized. Iso-frequency strips lie at right angles to the line of frequency progression.
3. A discrete columnar organization of frequency is not obvious in the auditory cortex; although cells in the same radial direction have similar characteristic frequencies, there do not appear to be sudden jumps in frequency as an electrode is moved tangentially in the cortex. Binaural dominance, on the other hand, does seem to be related to the existence of discrete columns. Cells of the same binaural dominance (e.g. one ear excitatory, the other ear inhibitory) lie in the same radial direction in the cortex, and are segregated into discrete strips, running along the cortical surface at roughly right angles to the iso-frequency strips.
4. Not all neurones in the primary auditory cortex show responses to sound. In those that do, a variety of shapes of tuning curve, including broad and multi-peaked ones, can be found. Many neurones show complex temporal patterns of response. Many neurones show binaural interactions suggesting that they code sound direction. Each cortex predominantly represents sound sources on the contralateral side.
5. Many neurones show particular sensitivity to the features of complex sounds. Some cells seem specifically responsive to frequency-modulated stimuli. Others respond only to complex sounds such as animal calls. However, there is no evidence that such cells can be regarded as specific detectors for those features; rather the cells respond to the basic acoustic elements of the stimuli.
6. Behavioural studies of the auditory cortex, in which auditory performance is tested before and after cortical lesions, have shown that the

auditory cortex is implicated in many tasks. However, it is often very difficult to work out the functions underlying the deficits. Frequency discrimination, for instance, was once thought to be impossible after complete lesions of the auditory cortex. Later it was shown that frequency discrimination was possible after cortical lesions if the animals had to detect changes in the frequency of an ongoing series of tone pips, and this led to hypotheses either that lesioned animals were only able to respond to stimuli on the basis of change, or that they had difficulty in inhibiting inappropriate responses. Now however, lesioned animals have been shown to respond in ways which contradict both theories, and we have to resort to explaining the results in terms of task difficulty. Cortical lesions upset performance on these tasks only if the initial learning was difficult.

7. The auditory cortex seems to be necessary for normal sound localization. AI is necessary for the localization of sounds on the contralateral side of the head. Sound locus is coded in a frequency-specific way, such that each iso-frequency strip is involved in coding the source locus for sounds of that frequency.
8. Cortical lesions upset tasks where the animals have to utilize the temporal dimension of auditory stimuli, and when they have to detect or discriminate very short stimuli. This suggests that the auditory cortex may be necessary for auditory short-term memory, and for prolonging the effects of short stimuli.
9. The auditory cortex seems to affect the ability to attend to sounds in the contralateral ear.
10. Hypotheses as to the function of the auditory cortex suggest:
 - (i) that it may be necessary for the analysis of complex sounds;
 - (ii) that it subserves sound localization and the representation of "auditory space";
 - (iii) that it is necessary for selective attention to auditory stimuli on the basis of source position;
 - (iv) that it serves to inhibit inappropriate motor responses;
 - (v) that it serves to identify stimuli on an absolute basis;
 - (vi) that it is necessary for the discrimination of auditory temporal patterns;
 - (vii) that it is necessary for short-term memory when one auditory stimulus has to be related to another later in time;

(viii) that it is necessary for auditory tasks that are difficult.

F. Further Reading

The anatomy of the auditory cortex is reviewed by Brugge and Reale (1985) and Seldon (1985). Neuronal responses are reviewed by Goldstein and Abeles (1975) and Brugge and Reale (1985). Earlier behavioural studies are reviewed by Neff *et al.* (1975) and Ravizza and Belmore (1978), and some of the more recent ones by Pickles (1985c). Sound localization is reviewed by Phillips and Brugge (1985). Auditory cortical function in man is reviewed by Pinheiro and Musiek (1985).

8. The Centrifugal Pathways

The centrifugal auditory pathways run from the higher stages of the auditory system to the lower. One pathway, the olivocochlear bundle, runs from the superior olivary complex to the hair cells of the cochlea. The central auditory nuclei are targets for other centrifugal pathways. It has been suggested that the pathways are organized into a chain, running from the cortex to the cochlea. In this chapter, electrophysiological and behavioural experiments on centrifugal pathways will be described, and some hypotheses as to the function of the pathways discussed.

A. Introduction

So far we have considered the auditory pathway as one in which information is handed exclusively from the lower to the higher levels of the nervous system. Such a view is, however, far from that of the whole picture. In particular, the auditory system possesses a large number of nerve fibres running in the reverse direction, from the higher levels of the nervous system to the lower. The fibres run close to, but not generally within, the tracts carrying the ascending information. In this way the activity of the lower levels of the nervous system can be influenced by the complex responses of the highest. We might also expect the central state of the animal to affect the sensory responses of the early stages of the auditory pathway. Centrifugal pathways have been known since the end of the nineteenth century (e.g. Held, 1893); however, the more recent interest in centrifugal pathways was triggered by Rasmussen's description in 1946 of the olivocochlear bundle, running from the superior olive to the hair cells. Interest was also triggered by the possibility that the centrifugal pathways could modify the sensory input during processes such as attention.