THE AUDITORY CORTEX

A SYNTHESIS OF HUMAN AND ANIMAL RESEARCH

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14. DISTRIBUTED REPRESENTATION OF SOUND-SOURCE LOCATION IN THE AUDITORY CORTEX

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INTRODUCTION

Normal sound localization behavior requires an intact auditory cortex. That statement is based on clinical reports of deficits following cortical lesions (Efron et al., 1983; Greene, 1929; Pinek et al., 1989; Sanchez-Longo & Forster, 1958; Zatorre & Penhune, 2001) and on results of experimental studies in animals in which the auditory cortex has been lesioned or reversibly inactivated (e.g., Heffner, H.E. & Heffner, R.S., 1990; Jenkins & Merzenich, 1994; Lomber & Malhotra, 2003). Indeed, one of the most conspicuous behavioral deficits that follows a unilateral cortical lesion in a cat or monkey is a deficit in localization of sound sources on the side opposite to the lesion. Despite the demonstrated necessary role of the auditory cortex in localization, presently little is understood of the form in which sound-source locations are represented in patterns of cortical activity, nor is there consensus on the identity of particular cortical areas that might be specialized for processing of location-related information.

One form in which sensory space can be represented in the brain is as a point-to point "topographical" map. Such maps are well known in the visual and somatosensory systems, in which locations of stimuli in visual space or on the body surface map onto locations within visual or somatosensory cortical fields. In those sensory systems, however, locations in sensory space correspond directly to locations on the respective sensory epithelia (i.e., the retina and body surface), so the cortical maps of space might simply reflect the topography of

the sensory periphery. In the auditory system, the cochlear sensory epithelium maps sound frequency, not location. The peripheral representation of frequency is reflected in the presence in the auditory cortex of multiple topographic maps of sound frequency (i.e., "tonotopic" representations; e.g., Merzenich et al., 1975; Reale & Imig, 1980). Identification of sound-source location by the auditory system requires analysis and integration of multiple acoustical cues, including interaural differences in sound level and arrival time and direction-dependent spectral cues (reviewed by Middlebrooks & Green, 1991). That such an integration can be accomplished and locations coded in a topographical map is demonstrated by the presence of such a map in the superior colliculus (Middlebrooks & Knudsen, 1984; Palmer & King, 1982); the superior colliculus is a midbrain structure involved in initiation of orienting movements of the eyes and head to auditory, visual, and tactile stimuli. The topographical form of auditory space representation in the superior colliculus probably reflects constraints of other sensory and motor modalities, however, and might not be an appropriate example of basic auditory mechanisms.

Numerous studies over the past two decades have sought, either explicitly or implicitly, a topographical space map in the auditory cortex (e.g., Brugge et al., 1996; Imig et al., 1990; Middlebrooks & Pettigrew, 1981; Rajan et al., 1990). Those efforts have been uniformly unsuccessful. Several commonly observed properties of the spatial sensitivity of auditory cortical neurons conflict with the basic requirements of a point-to-point map. Most important, a point-to-point map would seem to require neurons with narrow, well defined spatial receptive fields. Contrary to that requirement, most neurons in all well studied auditory cortical areas have broad spatial receptive fields, generally extending throughout 180° to 360°. Often, narrower receptive fields can be measured at near-threshold sound levels, but the fields expand markedly at moderate sound levels at which animals and humans show accurate localization behavior. Also, a topographical map would require that the locations in space of receptive fields would shift systematically with shifts in cortical location, but no such systematic shifts have been observed.

The observed properties of auditory neurons that conflict with a topographical map can be seen to be ideal qualifications for an alternative, *distributed*, form of spatial representation. The broad spatial tuning of auditory cortical neurons raises the possibility that single neurons might vary their response patterns as a function of sound-source location within a broad receptive field, thereby transmitting information about source locations throughout as much as 360° of space. The expectation of a topographical representation is that the representation of a point in space is restricted to a limited portion of any auditory cortical field. In a putative distributed representation, in contrast, the representation of any particular sound source location would be widely distributed throughout an auditory cortical field. All the available data support this view, that sound-source locations are represented in a highly distributed manner in the auditory cortex.

In this chapter, we review our work that has characterized the distributed coding of source locations, we present results from cortical areas that appear to show some specialization for location coding, and we contrast location coding under anesthetized and awake-behaving conditions.

SPATIAL SENSITIVITY AND DISTRIBUTED CODING

Most studies of auditory spatial sensitivity in our laboratory have been conducted in cats anesthetized with α-chloralose (Middlebrooks et al., 1998). In those experiments, the cat is positioned in the center of a sound-attenuating chamber that is lined with absorbent foam to reduce sound reflections. A circular hoop, 1.2 m in radius and positioned in the horizontal plane, holds 18 loudspeakers spaced in 20° increments of azimuth. Sound stimuli are Gaussian noise bursts, 80 or 100 ms in duration. Sound levels generally vary among trials from 20 to 40 dB or more above neural thresholds. Neural responses are recorded with silicon-substrate multi-channel recording probes (Anderson et al., 1989). The probes permit simultaneous recording of spike activity from single neurons or small unresolved clusters of neurons at 16 sites positioned in a line at 100- or 150-μm intervals. The probes are inserted into the cortex, generally oriented roughly parallel to the cortical surface in the middle cortical layers.

Figure 14.1 illustrates the location of auditory cortical areas on the lateral surface of the cat's brain. Our earlier studies focused on areas A1, A2, and the anterior ectosylvian auditory area (AES) (e.g., Furukawa et al., 2000; Middlebrooks et al., 1994, 1998). Area A1 is the primary tonotopically organized field, which receives its main ascending input from the ventral
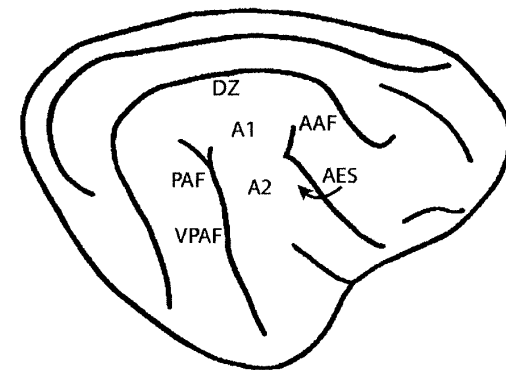
Fig. 14.1. Lateral view of the auditory areas in the cat's cerebral hemisphere. Abbreviations: A1: primary auditory cortex; A2: second auditory field; AAF: anterior auditory field; AES: anterior ectosylvian auditory area; DZ: dorsal zone of A1; PAF: posterior auditory field; VPAF: ventro-posterior auditory field.

division of the medial geniculate body. An early ablation-behavioral study indicated that area A1 might have a special role in spatial hearing (Jenkins & Merzenich, 1984), although its low-level position in cortical processing suggests that any lesion in A1 might impact function in other cortical areas. In area A2, neurons show broad frequency tuning and there is little or no tonotopic organization (Merzenich et al., 1975; Schreiner & Cynader, 1984). Psychophysical studies indicate that sounds are localized most accurately when they have broad bandwidths (Middlebrooks & Green, 1991). For that reason, it seems sensible to investigate spatial coding in an area such as A2 in which neurons appear to integrate information across broad ranges of frequency. Neurons in AES also show broad frequency tuning (Middlebrooks et al., 1998). That area is interesting for studies of auditory spatial coding because it is known to send corticofugal projections to the superior colliculus (Meredith & Clemo, 1989), which contains an auditory space map (Middlebrooks & Knudsen, 1984). Because of the differences among areas A1, A2, and AES in regard to frequency tuning and corticofugal projections, we are surprised to have found essentially no qualitative differences in the spatial sensitivity of neurons in those areas; subtle quantitative differences have been observed (Middlebrooks et al., 1998). Figure 14.2 shows examples of the spatial sensitivity of two neurons recorded from area A2. Each horizontal row of panels shows responses of one neuron, and each vertical column of panels shows responses at a particular sound level (indicated at the top of each column) relative to the neuron's threshold. The illustrated neurons are representative of the substantial majority of neurons in areas A1, A2, and AES (in the anesthetized condition) in the following respects. *First,* responses generally are restricted to a burst of spikes, ~10 to 20 ms in duration, following the onset of the noise burst. *Second,* at the lowest sound levels, neurons respond reliably to sounds located only in the frontal contralateral quadrant of azimuth. That is, there is little variation among neurons in the preferred locations of stimuli. *Third,* at more moderate sound levels, spatial receptive fields of neurons expand to encompass 360° of azimuth. Level-dependent changes in spatial sensitivity are most conspicuous at low sound levels and tend to stabilize at levels 30–40 dB above threshold. *Fourth,* response patterns of neurons vary systematically with sound-source location, particularly in the spike count, the latency to the first spike, and in some cases, in the duration of the burst of spikes. The lack of variation of preferred location and the broad spatial tuning both are inconsistent with a topographical representation. The broad spatial tuning and the location-dependent changes in spike patterns, however, both support the notion of a distributed representation.

One of the requirements of a distributed representation, as we have presented it, is that single neurons transmit stimulus-related information throughout broad ranges of sound-source location. We tested this premise by attempting to recognize, for single neurons, the spike patterns associated with particular sound-source locations and, thereby, to estimate source locations. We have employed artificial neural networks for this task; artificial neural networks can be regarded as computer-based pattern-recognition procedures. Typically, we
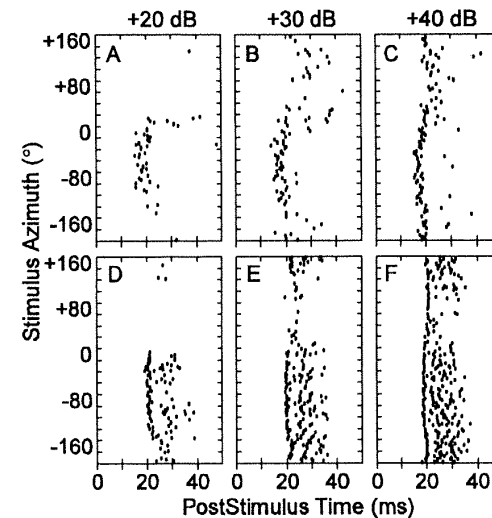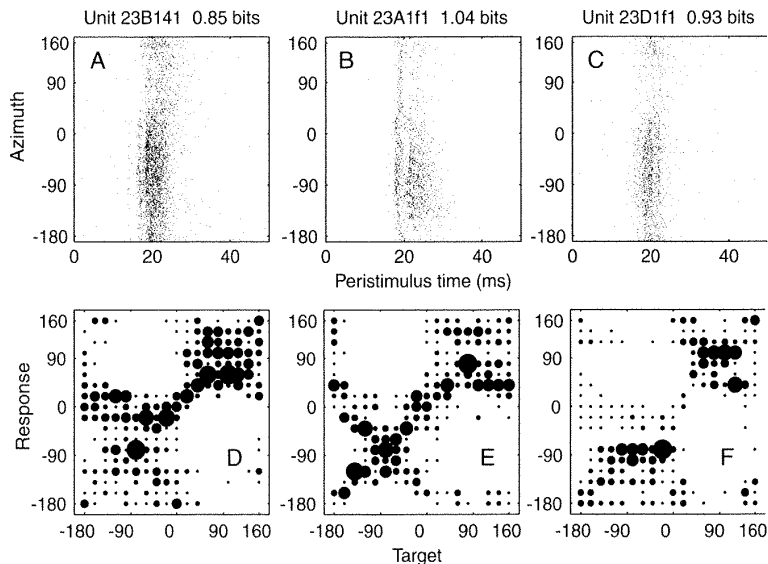
Fig. 14.2. Spatial sensitivity of two neurons recorded from area A2 (from Furukawa & Middlebrooks, 2002). Within each panel, each horizontal raster (i.e., row of dots) indicates spikes elicited by a single noise burst. The vertical position of each raster indicates the stimulus azimuth. Eight trials are represented at each azimuth. The frontal midline is plotted at 0°, and negative azimuths represent locations to the left of the midline, contralateral to the recording site. These neurons spiked only near the onset of the noise bursts; for that reason, only the first 50 ms after stimulus onset are shown.

divide a set of spike patterns into training and test sets. The training set is used to train the network, and then the trained network is used to classify the test set, resulting in estimates of the stimulus locations. Many spike patterns are classified for each stimulus location, and the distribution of estimated locations is evaluated.

Figure 14.3 shows examples of responses of neurons recorded in area A1 (top row) and shows the results of neural-network classification of spike patterns in the form of confusion matrices (bottom row). In the confusion matrices, the horizontal and vertical positions of symbols indicate, respectively, the target location and the location estimated based on the spike patterns. The area of each symbol represents the proportion of trials in which a particular location was estimated for each target location. Perfect identification of all targets would yield a line of large circles lying on the positive major diagonal. Although perfect identification never is observed, there is in many cases a strong tendency of data to clump near the diagonal. The example in Figures 14.3A and 14.3D showed quite accurate localization throughout most of the frontal hemifield (i.e., −90° to 90°), with less accuracy in the rear hemifield. The

example in Figures 14.3B and 14.3E showed many responses near the positive major diagonal plus a subset of responses lining up along the negative minor diagonal from target −180°, response 0° to target 0°, response −180°. That minor diagonal corresponds to the loci of points for which front and back locations were confused. Front/back confusions are often encountered in human psychophysical studies (e.g., Makous & Middlebrooks, 1990; Wightman & Kistler, 1989). The example in Figures 14.3C and 14.3F is representative of many neurons that accurately distinguished right from left, but showed little discrimination within each half of space.

The representation of spatial coding in the form of confusion matrices, as in Figure 14.3, leads easily to the computation of transmitted information. Transmitted information, in our application, is the information about sound-source location that is transmitted by the cat's auditory pathway, resulting in cortical spike patterns that then are interpreted by our neural-network procedure (Furukawa & Middlebrooks, 2002; Stecker et al., 2003). Perfect identification of targets that were randomly distributed among 18 possible locations would transmit ~4.2 bits of information. One bit of information could indicate perfect discrimination of two locations or could indicate somewhat imperfect


Fig. 14.3. Spatial sensitivity of 3 neurons recorded from A1. **A, B, C:** Responses of 3 units shown as raster plots. Each panel is labeled with the unit number and the amount of information (in bits) that it transmitted about sound-source location. **D, E, F:** Stimulus/response confusion matrices show the stimulus locations estimated by automated recognition of the spike patterns shown in parts A, B, and C.

identification of a larger number of locations. In the sample of neurons in areas A1 and A2 studied in the anesthetized condition, neurons typically transmitted 0.5 to 1.2 bits of information about sound-source location. As a general rule, nearly all neurons tended to transmit stimulus-related information with varying degrees of accuracy throughout as much as 360° of azimuth. We refer to this as "panoramic" coding of azimuth by single neurons (Middlebrooks et al., 1994). The finding of panoramic neurons throughout areas A1, A2, and AES leads to the inference that information about any particular source location is widely distributed throughout those areas and probably extends beyond to areas not yet explored. The accuracy of spatial representation presumably is enhanced by the combination of information transmitted by multiple neurons. For instance, we showed that a simple pattern recognition scheme based on responses of 128 cortical neurons could transmit sound locations about as accurately as a cat could localize sounds in behavioral trials (Furukawa & Middlebrooks, 2000).

Many neurons exhibit stimulus-dependent changes in the latency from the onset of the stimulus to the first spike. We attempted to quantify the information about stimulus azimuth that is transmitted by first spike latencies by disrupting the stimulus dependence of latencies and then noting the loss in total transmitted information. We eliminated the stimulus dependence of spike timing by forming a distribution of all the recorded spike times for a particular neuron, then forming "shuffled" spike patterns in which each spike pattern was replaced by a pattern containing the original number of spikes but with times drawn randomly from the distribution of all times. This had the effect of preserving the first-order distribution of spike times and preserving any information that might be transmitted by spike counts while disrupting any relationship between specific stimulus locations and spike times. Figure 14.4 compares the information transmitted by full spike patterns (plotted in the horizontal dimension) with the information transmitted by shuffled patterns (vertical dimension); data were recorded from well isolated single units in area A2 (Furukawa & Middlebrooks, 2002). One can see that most of the points lie well below the diagonal, indicating a substantial reduction in transmitted information. On average, transmitted information was reduced by 17–53% when stimulus-related temporal information was eliminated from spike patterns.

CORTICAL SPECIALIZATION FOR SPATIAL REPRESENTATION

Studies of cortical areas A1, A2, and AES in the anesthetized condition have demonstrated spatial sensitivity that qualitatively is quite similar among areas. The observation of rather uniform spatial sensitivity among those areas has led us to speculate that auditory spatial processing is largely complete within the auditory brainstem and that the special role of the cortex in spatial processing is restricted to routing spatially coded information to cortical areas that might have more or less spatial functions (Middlebrooks et al., 2002). That speculation was founded partially on the premise that knowledge of the location of sound

Transmitted Information (bits)
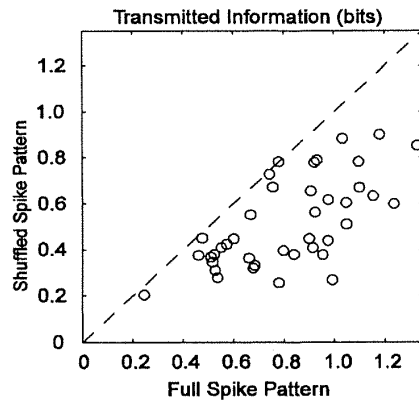
Fig. 14.4. Stimulus-related information transmitted by full spike patterns (horizontal dimension) and by spike patterns in which spike timing was degraded (from Furukawa & Middlebrooks, 2002).

sources is beneficial for many auditory tasks, including those that are explicitly spatial in nature (e.g., discrimination of source locations; orientation toward sound sources) and others that are less so (e.g., recognition of communication sounds amid spatially distinct distracters). We recently have obtained data that conflict with the notion that spatial sensitivity is uniform across all the auditory cortical areas (Stecker et al., 2003; Stecker & Middlebrooks, 2003). We find rather distinctive spatial sensitivity in the posterior auditory field (PAF) and in the dorsal zone (DZ) of area A1.

Area PAF is located posterior to the posterior ectosylvian sulcus, extending onto the bank of that sulcus (see Fig. 14.1). In previous studies in the anesthetized cat (Phillips & Orman, 1984), PAF has been shown to have a larger proportion of neurons that show non-monotonic rate-level functions. That finding is pertinent to studies of spatial representation because, at least in area A1, non-monotonic neurons tend to show the most restricted spatial tuning (Barone et al., 1996, Imig et al., 1990). Also, neurons in PAF tend to show relatively complex frequency response areas (Heil & Irvine, 1998; Loftus & Sutter, 2001). Such complexity might reflect a specialization for processing spectral cues for the vertical and front/back locations of sounds.

Neurons recorded from PAF show a greater variety of spatial tuning than that encountered in other areas studied in anesthetized conditions (Stecker et al., 2003). Figure 14.5 shows three examples. The neuron in Figure 14.5A showed two strong temporally discrete bursts of spikes (latencies ~25 and 35 ms) to sound sources restricted to a contralateral quadrant, and a later, more diffuse, burst to ipsilateral sounds. The neuron in Figure 14.5B had a spatial receptive field sharply bounded within the ipsilateral half of space. The neuron in Figure 14.5C showed spatial tuning centered about 80° contralateral to the frontal
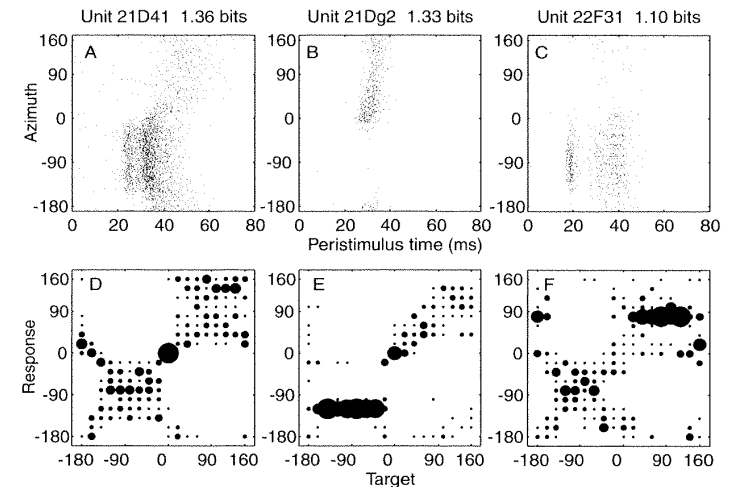
Fig. 14.5. Spatial sensitivity of 3 neurons recorded from PAF. Same format as Figure 14.3 (adapted from Stecker et al., 2003).

midline compared to neurons in areas A1, A2, and AES studied in the anesthetized condition, PAF neurons showed greater modulation of spike counts by sound-source location and showed narrower tuning width. Moreover, the distribution of spatial preferences in PAF covered space more uniformly than that measured in A1, A2, or AES.

A striking feature of responses in PAF is their long latencies and the strong modulation of first-spike latency by stimulus location. The median of first spike latencies in PAF is 29 ms, compared to 18 ms in A1. The median value of the range of first-spike latencies across all stimulus locations is 10.7 ms in PAF compared to 3.2 ms in A1. We compared areas A1 and PAF in regard to the location-related information transmitted by spike count alone or by the latency to the first spike (Stecker et al., 2003). Figure 14.6 shows that for both cortical areas, first-spike latency transmits more information than does spike count (i.e., the majority of data points lies above the diagonal). The relative importance of latency is considerably greater in PAF, however, in which the ratio of information transmitted by latency versus spike count was 1.7:1 compared to 1.3:1 in A1. The difference between A1 and PAF is most pronounced in respect to neurons that transmit the largest amount of information. In A1, many of the most informative neurons transmitted more information by spike count than by latency (i.e., many points on the right half of the left panel of Fig. 14.6 lie below the diagonal) whereas in PAF it was a general trend that first-spike latency tends to transmit more information than does spike count.

Area DZ is found at the dorsal margin of area A1, near the ventral bank of the suprasylvian sulcus. Similar to more ventral regions of A1, DZ receives a
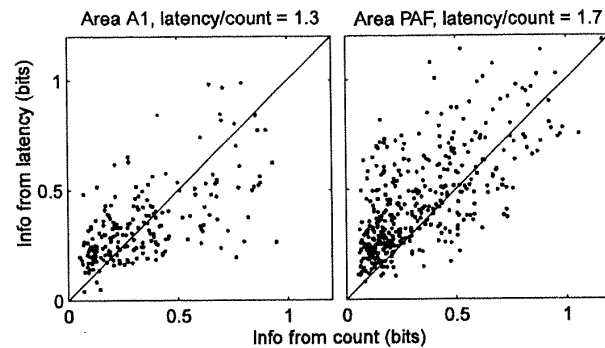
Fig. 14.6. Stimulus-related information transmitted by first-spike latency (vertical axis) or spike count (horizontal axis) computed from A1 (left panel) or PAF (right panel).

strong thalamic input from the ventral division of the medial geniculate body, but in the case of DZ the source of that input is restricted to the dorsal cap of the ventral division (Middlebrooks & Zook, 1983). Compared to more ventral regions of area A1, neurons in DZ show broad frequency tuning that is biased toward high frequencies, and many DZ neurons respond only to sounds presented simultaneously to both ears (Middlebrooks & Zook, 1983). The latter property suggests that DZ might show a preponderance of tuning for locations near the midline.

In recent studies of spatial sensitivity in DZ, we have found examples of spatial tuning that is more restricted than that usually seen elsewhere in A1 or in A2 (Stecker & Middlebrooks, 2003). A distinctive characteristic of spatial sensitivity in DZ is that nearly half of the neurons show spatial tuning centered in the ipsilateral half of space. Often, along a recording penetration in DZ, we encounter a sequence of several neurons tuned to contralateral locations, then tuning abruptly shifts to ipsilateral tuning, then back to contralateral, and so on.

Figure 14.7 shows examples of sequences of recordings in DZ. In the figure, each neuron is represented by an azimuth "centroid" which is a spike-count-weighted center of mass of a spike-count-vs-azimuth function. The spatial sensitivity seen in PAF and DZ suggests that those cortical areas might play a more important role in spatial representation than do areas A2, AES, or A1 ventral to DZ. In the case of PAF, that suggestion is supported by a recent study that demonstrated following reversible inactivation of PAF a striking deficit in sound localization performance in cats (Lomber & Malhotra, 2003). That study also showed that inactivation of the anterior auditory field (AAF) produced a deficit in a task requiring identification of a temporal pattern but produced no localization deficit. The latter result is consistent with our unpublished physiological observations that AAF seems to show no particular specialization for location coding.
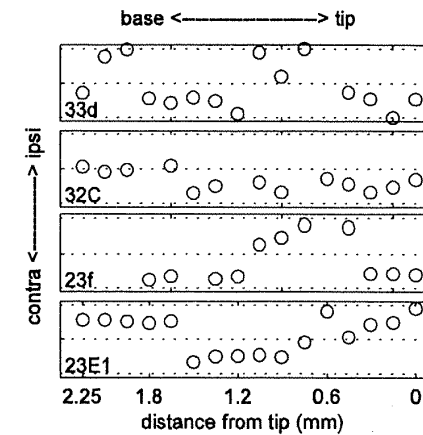
Fig. 14.7. Preferred locations as a function of recording position for 4 electrode penetrations in DZ. Each open circle shows the azimuth preference of a single neuron represented by its azimuth centroid, the spike-count-weighted center of mass of spatial tuning. Electrode penetrations were oriented from lateral to medial down the ventral bank of the suprasylvian sulcus. The vertical axis plots the location of the azimuth centroids in the contra- or ipsilateral hemifields (from Stecker & Middlebrooks, 2003).

A widely cited hypothesis (Rauschecker & Tian, 2000) asserts, by analogy with the primate visual system, that the primate auditory cortex contains two hierarchically organized auditory processing streams. One of the hypothetical pathways, the "what" stream, is said to lie anterior to the primate area A1 and to be specialized for identifying sounds. The other, "where" stream, lies posterior to A1 and is hypothesized to specialize in processing of spatial aspects of sounds. It is difficult to draw homologies between cortical areas in cats and primates. Nevertheless, because of the lateral expansion of the temporal lobe in the primate, the anterior-posterior locations of cortical areas in primates seem to be reversed relative to those in cats. That means that area PAF in the cat, which appears to show some specialization for localization, is more likely to correspond to an anterior area in the primate. Indeed, the Rauschecker group has speculated that PAF is part of a putative feline "what" pathway and AAF part of a "where" pathway (Tian & Rauschecker, 1998). Our present results in the cat, and the behavioral results from the Lomber group (Lomber & Malhotra, 2003), conflict with that assignment of PAF and AAF, respectively, to what and where streams. Because of uncertainty in cortical-field homologies in cats and primates, our present results cannot be said to refute conclusively the dual stream hypothesis as stated for the primate, but neither do our results support that hypothesis.
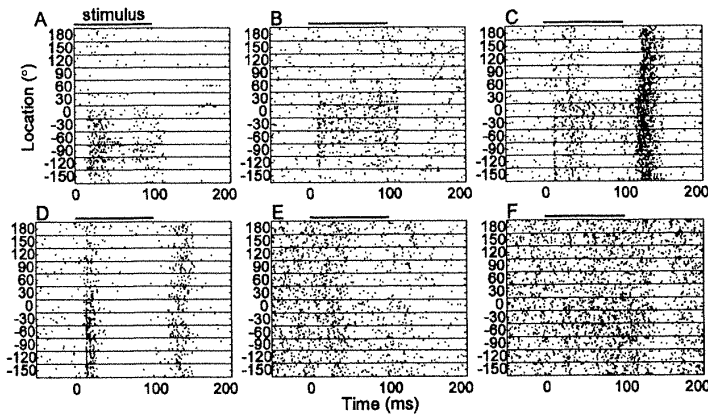
Fig. 14.8. Spatial sensitivity of 6 neurons recorded from A1 in awake cats (from Mickey & Middlebrooks, 2003).

SPATIAL REPRESENTATION IN AN AWAKE PREPARATION

With few exceptions (Ahissar et al., 1992; Benson et al., 1981; Eisenman, 1974; Recanzone et al., 2000), studies of spatial sensitivity in the auditory cortex have used anesthetized preparations. The use of anesthesia offers many advantages in experimental design, but one always must be concerned that the true nature of the cortical representation of auditory space might be masked by the presence of anesthetic agents. We recently have begun to study spatial representation in the auditory cortex of unanesthetized cats (Mickey & Middlebrooks, 2003). In our protocol, the cat is only loosely restrained. The cat's head is free to move. The cat performs a simple auditory discrimination, in which it is rewarded by discriminating a periodic 200-Hz click train from an ongoing sequence of broadband noise bursts that vary in location. The purpose of the auditory task is simply to insure that the cat is listening to sounds. There is no reward contingency related to the locations of the sounds. The cat is implanted with a 16-channel recording probe similar to that described above. During recording sessions, the cat has a tracking device attached to its head that permits measurement of the orientation of the head relative to the loudspeaker array. All stimulus locations are corrected for head orientation, yielding stimulus locations in head-centered coordinates. The cats generally maintain their pinnae in a forward position while doing the auditory task, so variation in pinna position adds only minimal uncertainty to the interpretation of results. Our present data set in the awake preparation is limited to recordings in area A1.

Figure 14.8 shows examples of responses of 6 neurons (or clusters of neurons) in area A1 in the awake condition. In contrast with responses in the anesthetized condition which usually are restricted to a short burst of spikes near the stimulus onset, these responses show a variety of temporal patterns. The illustrated examples include responses primarily near the stimulus onset (Fig. 14.8A), responses sustained throughout the stimulus duration (Fig. 14.8B), responses that were strongest after the stimulus offset (Fig. 14.8C), and responses to both stimulus onset and offset (Fig. 14.8D). In some cases, neurons showed relatively high rates of spontaneous activity that was suppressed either by stimulus onset (Fig. 14.8E) or offset (Fig. 14.8F).

As in the anesthetized preparation, spatial receptive fields of neurons in the awake condition generally were broad, typically 150° to 180° wide in azimuth. Also like the anesthetized condition, there was no indication of spatial topography. Those two observations, while somewhat disappointing, reassured us that previous failures to demonstrate point-to-point auditory space maps in A1 were not simply a consequence of the use of anesthesia. Several other properties of spatial sensitivity in area A1 were quite different between the anesthetized and awake conditions. *First*, the modulation of spike counts by sound-source location generally was greater in the awake condition and spatial tuning was sharper, largely because of suppression of spontaneous activity at non-optimum locations. *Second*, there was a greater diversity of temporal spike patterns, as indicated above. *Third*, the awake condition showed a greater diversity of preferred stimulus locations, including spatial tuning centered throughout the contralateral hemifield, in the ipsilateral hemifield, and on the midline in the front and in the back. In A1 in the anesthetized condition, in contrast, most neurons show tuning centered in the frontal contralateral quadrant, in front of the axis of greatest sensitivity of the contralateral pinna (Middlebrooks & Pettigrew, 1981). *Finally*, spatial tuning in the awake condition was considerably less sensitive to changes in stimulus level. Across the population sampled in the awake condition, there was little or no systematic increase or decrease in spatial tuning width or in the amount of stimulus-dependent modulation of spike count. (Mickey & Middlebrooks, 2003). In contrast, neurons in A1 in the anesthetized condition consistently react to increases in stimulus level with a decrease in the modulation of spike counts by stimulus location and an increase in the breadth of spatial tuning (Stecker et al., 2003).

The present data in the awake condition were obtained while the cats were engaged in a task that demanded only minimal attention to sound. In future studies, it will be of interest to test the degree to which the demands of the behavioral task influence the cortical representation of space. For instance, might we expect the sharpness of spatial sensitivity to increase under conditions in which the animal must attend to the locations of sounds? If reward is paired with a particular sound source location, how might that affect the representation of rewarded and of unrewarded locations?

SUMMARY AND CONCLUSIONS

In all auditory cortical areas studied so far, spatial receptive fields tend to be broad, although somewhat sharper spatial tuning and narrower spatial receptive fields are seen in PAF and DZ than in ventral A1, A2, or AES. In none of these areas is there consistent evidence of point-to-point spatial topography.

Response patterns of neurons vary systematically with source location, such that neurons can be said to code space "panoramically". The accuracy of panoramic coding appears to be considerably greater in PAF and DZ than in ventral A1, A2, and AES, at least under anesthetized conditions. In PAF and DZ, panoramic location coding is particularly conspicuous in the form of modulation of spike latencies by stimulus location. By inference, the representation of any point in auditory space is distributed across widespread neural populations, within and among cortical fields. There is some indication of specialization for spatial processing in PAF and, perhaps, in DZ, but any of the cortical areas studied so far display considerable capacity for spatial representation.

In the awake condition, neurons in A1 show sharper spatial tuning and greater diversity of temporal spike patterns than in the anesthetized condition. Even so, spatial receptive fields in the awake condition often occupy nearly 180° of azimuth, and there is no indication of point-to-point spatial topography. The model of distributed coding developed in the anesthetized preparation appears to apply equally to the awake condition.

The greater diversity of spatial tuning observed in PAF (in the anesthetized condition) and in A1 in the awake condition indicates that coordinated activity of even small numbers of neurons in those areas potentially could signal sound-source location with accuracy comparable to reported behavioral performance. In ongoing studies, we are eager to evaluate spatial sensitivity in area PAF to test the hypothesis that it is particularly adapted for distributed representation of sound-source location.

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