THE PROCESSING OF AUDITORY STIMULI FOR EYE MOVEMENTS IN THE POSTERIOR PARIETAL CORTEX OF MONKEYS

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INTRODUCTION

The posterior parietal cortex has long been considered a classical association area, essential for combining information from all the senses in order to form a cognitive representation of space (Critchley, 1953; Hyvarinen, 1982; Mountcastle et al., 1975). How the various sensory modalities, which are coded in very different coordinate frames, are combined in the posterior parietal cortex has until recently not been understood. In this chapter we review experiments from our laboratory which have begun to reveal how auditory and visual signals are integrated in the lateral intraparietal area (LIP) of the posterior parietal cortex.

Area LIP was originally defined as a new cortical area in the macaque monkey based on its distinctive anatomical connections (Andersen et al., 1985). Of all the regions in posterior parietal cortex, area LIP has the strongest connections to the frontal eye fields. Moreover, area LIP projects strongly to the superior colliculus and the pontine nuclei, two brain structures that are associated with the generation of saccadic eye movements. Area LIP also receives inputs from a variety of extrastriate visual areas, including areas V2, V3, V3a, V4, and PO. These anatomical connections suggest that area LIP plays an important role in the processing of saccades to visual targets.

Our recording experiments have supported this view of the function of area LIP. A large percentage of LIP neurons respond to visual stimuli, even in the absence of saccades (Blatt et al., 1990). In addition, LIP neurons have presaccadic activity, even when eye movements are made to a remembered location instead of a visual stimulus (Gnadt and Andersen, 1988). We have also shown that microstimulation of LIP evokes saccades, and reversible lesions of LIP disrupt saccade metrics and latencies (Thier and Andersen, 1996; Li et al., 1995).

Further recording studies in our laboratory have confirmed that LIP plays a specialized role in the process of transforming visual information into saccadic eye movements. In a task

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requiring monkeys to memorize the location of a visual stimulus and then look at the remembered location after a delay (a memory saccade task), LIP neurons are tuned for particular stimulus locations and eye movement vectors (Andersen et al., 1990; Barash et al., 1991a,b). Partially overlapping populations of LIP neurons respond during three different periods: 1) during the appearance of the visual stimulus, 2) during the memory period between the disappearance of the stimulus and the eye movement, and 3) during the saccade to the location of the previously presented stimulus. The responses in all three time periods are spatially tuned, and the receptive fields during the three periods generally overlap for a given neuron. We postulate that these response properties reflect, through time, the transformation of a visual stimulus into a motor plan to saccade to that stimulus. Our studies have also shown that LIP neurons code the planned movements in motor coordinates, both during the memory period and during the saccade (Gnadt and Andersen, 1988; Barash et al., 1991b; Bracewell et al., 1996).

The sensory-motor transformation role of LIP has been further demonstrated by recent experiments from our lab showing that a component of LIP activity encodes the INTENTION to make sacccades. We trained monkeys to make two consecutive saccades to memorized locations that had been briefly cued by light flashes. We found that a majority of the memory activity in area LIP is related to the next planned movement, and not to the sensory stimulus (Bracewell et al., 1996). We also found that in animals trained to plan either eye or arm movements to visual stimuli, cells in LIP are preferentially active before eye movements (Snyder et al., 1996). Thus LIP cells code the plan to make an eye movement. Other experiments have shown that this activity is present even for plans that are not executed. If a monkey is asked to change his plan before making an eye movement, LIP neurons change their activity accordingly to code the vector of the new saccade plan (Bracewell et al., 1996).

The above experiments show that LIP neurons are active during eye movement planning. But is this planning activity only related to visually triggered saccades, or is it also present for saccades to locations specified by auditory stimuli?

AUDITORY RESPONSES IN LIP

Recent studies in our laboratory have shown that area LIP plays a role in sensorimotor transformations involving auditory as well as visual spatial information. We trained animals to perform memory sacccades to briefly presented auditory and visual targets (Mazzoni et al., 1996a). In the auditory task each animal was required to fixate a fixation light for 750 msec, at which time an auditory noise stimulus was presented for 750 msec either 10 degrees to the left or right of the fixation point. The animal was required to memorize the location of the sound, and then to saccade to the remembered location of the stimulus when the fixation point was extinguished 1250 ms after sound offset. These saccades were made in total darkness. On other trials the monkey performed the same task, but with spatial locations 8 degrees to the left or right of fixation cued by a brief visual stimulus.

Figure 1 shows a typical response for an LIP neuron in this task. This particular neuron preferred stimuli presented to the right of the fixation point, and was even slightly inhibited by stimuli to the left. The neuron showed essentially the same behavior for the auditory and visual stimuli. During the stimulus period the activity increased for rightward locations, and remained elevated throughout the memory period. Once the saccade was made the cell ceased to respond.

Of 80 neurons tested 44 were found to have auditory responses in either the stimulus, memory, or both periods. The majority of neurons with auditory responses showed the same properties as illustrated in Fig. 1; the cells usually also responded to visual stimuli, and the

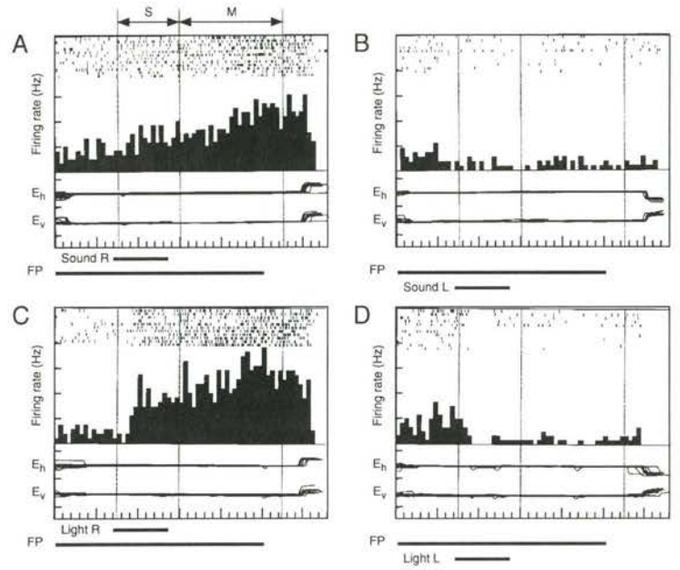

Figure 1. Activity of a neuron with auditory and visual stimulus-period (S) and memory-period (M) responses in the auditory and visual memory saccade tasks. In each of the four panels, time is plotted on the abscissa. Rows of ticks (one row per trial) indicate the occurrences of spikes. Below the ticks in each panel is a histogram indicating the average firing rate across different trials. The two traces below the histogram represent the horizontal (E_h) and vertical (E_v) components of eye position (up represents right, down represents left). The spike rasters, histogram, and eye position traces for each trial are horizontally aligned on stimulus onset. Double arrows above **A** indicate the stimulus (S) and memory (M) periods of the memory saccade task. Thick horizontal lines below each panel indicate the presentations of the stimuli: FP, fixation point; Sound R, sound presented on the right; Sound L, sound presented on the left; Light R, light spot presented on the right; Light L, light spot presented on the left. **A:** Auditory memory saccade to the right. **B:** Auditory memory saccade to the left. **C:** Visual memory saccade to the right. **D:** Visual memory saccade to the left. Scales are 100 ms per horizontal division, 10 Hz (impulses/s) per vertical division (firing rate), and 15 degrees per vertical division (eye position). [From Mazzoni et al., 1996a.]

preferred direction of the auditory and visual responses were usually the same. Thus LIP neurons are multimodal in this task, and they appear to have overlapping receptive fields when the animal is initially fixating straight ahead. The preferred direction for auditory or visual stimuli was toward the contralateral side in a majority of the cells tested.

A majority of the cells also had saccade responses occurring just before the saccade. Figure 2 shows one of these neurons, which had a saccade response for leftward eye movements to locations cued by either auditory (Fig. 2A) or visual (Fig. 2B) targets. Most LIP neurons showed this behavior; if a saccade response was present it was found for both modality cues and the preferred direction was the same.

We also examined the latency of stimulus onset response for those cells that became active during the stimulus period. Figure 3 shows the distribution of latencies for auditory and visual stimulus responses. Latencies of the auditory response ranged from 30 to 250 msec with a median value of 155 msec (Fig. 3A), and latencies of the visual response ranged from 60 to 210 msec with a median value of 125 msec (Fig. 3B). Thus the auditory and visual latencies were rather similar across the population. This similarity can be seen more directly in Fig. 3C, in which visual latencies have been subtracted from auditory latencies within individual cells. The distribution ranged from -90 to 190 msec with a median of 0 msec.

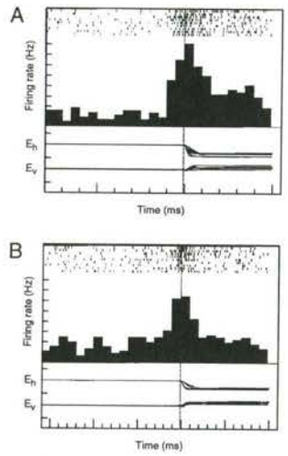

Figure 2. Activity of a neuron with directionally tuned saccade-related activity during (**A**) a memory saccade cued by a sound on the left and (**B**) a memory saccade cued by a light on the left. The spike rasters,Äfiring rate histogram, and eye position are plotted as in Fig. 1, except that all events are horizontally aligned on the beginning of the saccade. Scales are as in Fig. 1. [From Mazzoni et al., 1996a.]

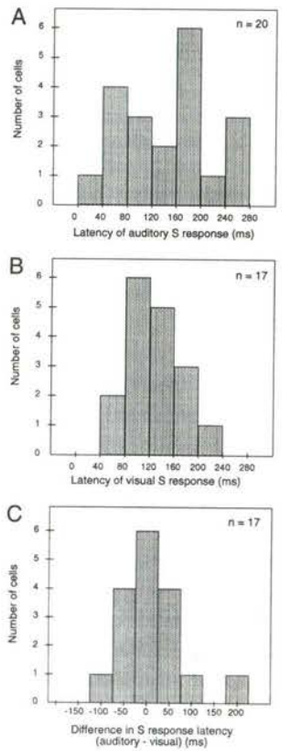

Figure 3. Latencies of onset of stimulus-period responses of neurons with clear stimulus responses. **A:** Latencies of auditory stimulus-period responses. **B:** Latencies of visual stimulus-period responses. **C:** Differences between auditory and visual latencies (auditory minus visual) for cells with both auditory and visual stimulus-period responses. [From Mazzoni et al., 1996a.]

There was no systematic difference in latencies, some cells having earlier auditory responses and others having earlier visual responses.

THE NATURE OF MULTIMODAL INTEGRATION IN LIP

We were surprised to find auditory responses in LIP so similar to the visual responses in spatial tuning and latency. In early studies Hyvarinen et al. (1982) and Mountcastle et al. (1975) tested several posterior parietal neurons with auditory stimuli and found no responses. The neurons tested may have been outside of LIP, which had not yet been described at that time. In the early days of our experiments we tried auditory stimuli and found no response for area LIP neurons (unpublished observation). However, several authors (Koch and Fuster, 1989; Sakata et al., 1973; Seal et al., 1983) have reported auditory responses for neurons in the posterior parietal cortex. Interestingly these authors found responses only when the auditory stimuli were cues for movement. These observations led us to examine whether area LIP neurons respond to auditory stimuli when monkeys are not engaged in, nor trained to perform, auditory memory saccade tasks.

We examined LIP auditory and visual responses when an animal was trained to fixate a fixation point for his reward, and ignore the presentation of auditory and visual stimuli in the periphery. Remarkably, area LIP neurons showed strong spatially tuned responses to visual stimuli but not to auditory stimuli (Linden et al., 1996). The auditory responses in our earlier memory-saccade study could be a result of training the animal in the auditory memory saccade task, or alternatively, auditory signals in LIP are target representations which appear only when the animal is required to use them for planning saccades.

Figure 4 illustrates two possible explanations for the finding of auditory responses in LIP in the memory saccade experiments (Mazzoni et al., 1996a), but not in the sensory mapping experiments (Linden et al., 1996). Figure 4A illustrates that the auditory signals may arise in LIP as a result of auditory memory saccade training. This model would hold that normally LIP is involved only in visual-motor processing, but that training initiates permanent changes which cause LIP neurons to develop auditory responses. This finding would demonstrate that training monkeys to perform saccade tasks can alter brain areas to a significant extent. Auditory processing in area LIP might therefore serve as an interesting paradigm for studying how neural properties change as a result of learning.

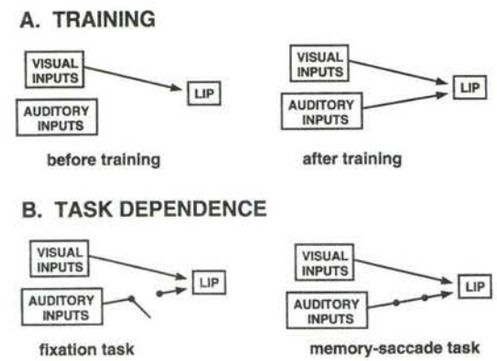

Figure 4. Possible explanations for the presence of auditory responses in LIP in memory saccade experiments but not in sensory mapping experiments. **A:** Training hypothesis. Training the animal to perform auditory memory saccades causes LIP neurons to develop auditory responses. **B:** Task dependence hypothesis. Neurons in area LIP respond to auditory stimuli only if the auditory information must be used to plan a saccade.

The second possibility, illustrated in Fig. 4B, is that there is a dynamic switch which allows auditory signals into LIP only when they are necessary for eye movements. This switch represents much more than an attentional modulation of the gain of sensory signals (Maunsell, 1995; Desimone and Duncan, 1995). According to this model, the decision to make a saccade gates auditory signals into LIP; area LIP is therefore "multimodal" only in a dynamic sense. The hypothesized switch of Fig. 4B implies that even responses during the stimulus period are already dependent on the behavioral function of the sensory signals. If the monkey must ignore an auditory stimulus, no auditory response arises in LIP; if the monkey must use the stimulus to determine the target location for a future saccade, then responses appear in LIP. Perhaps signals in LIP are best considered saccade plans, independent of the modality that specifies the saccade target.

We are currently performing experiments to distinguish between the two mechanisms diagrammed in Fig. 4. These experiments should resolve the issue of what (and when) auditory information appears in area LIP.

COORDINATE TRANSFORMATIONS IN LIP

Another important issue is HOW auditory information is represented in area LIP. In other words, what is the coordinate frame in which auditory information is coded? Visually triggered signals in area LIP have been shown to be in eye-centered coordinates (Gnadt and Andersen, 1988; Barash et al., 1991b), which are convenient coordinates for coding saccades since they specify the metrics of a saccade to foveate a visual target. These signals are also modulated by eye position, and a population of gain-modulated neurons can be used to represent the head-centered locations of stimuli. Thus the visual information in LIP has the interesting property of representing both eye- and head-centered frames of reference. Is auditory spatial infomation represented similarly? Auditory locations are coded in head-centered coordinates in the early auditory pathway; the receptive fields are synthesized from head-referenced interaural time and intensity cues. Do auditory locations remain coded in head-centered coordinates in LIP? Since visual locations are coded in eye-centered coordinates, the existence of head-centered auditory coding would mean that visual and auditory signals would be represented in completely different coordinate frames in the same area. Or are auditory signals converted to eye-centered coordinates at the level of LIP, so that the two modalities share the same coordinate representation? And are the auditory receptive fields modulated by eye position, enabling them to code in more than one coordinate frame in the distributed representation?

We examined the coordinate frame of the auditory signals within area LIP using a task, illustrated in Fig. 5, which allowed us to measure auditory response tuning curves at three different eye positions (Stricanne et al., 1996). The animal made memory saccades from the different eye positions to five speakers in complete darkness and with the head fixed. The speakers were arranged horizontally, since primates are better at discriminating sound locations in azimuth than in elevation (Brown et al., 1980; Brown et al., 1982). Cells were examined only if they had activity during the delay period.

The delay activity was tuned for spatial location, such that for saccades starting from a particular eye position one of the five speakers produced the greatest response and the magnitude of responses progressively decreased for locations further away from the preferred speaker location. Tests at different eye positions revealed three categories of responses. For some cells, the eye displacement in the saccade determined the response, regardless of which combination of fixation lights and speakers was used; these cells responded in eye-centered coordinates. In other cells, only the speaker location determined the response; these cells

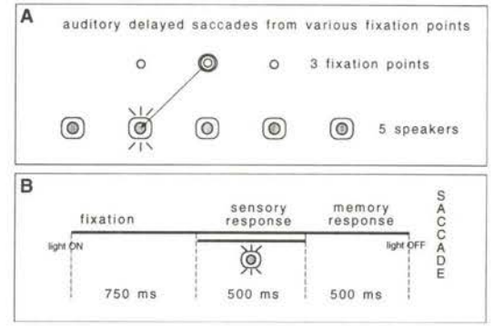

Figure 5. Schematic representation of the experimental paradigm. **A:** The stimulation apparatus consisted of five speakers displaced horizontally, centered straight ahead of the monkey and separated by 12 degrees. A round fixation light was back-projected on a translucent screen 10 degrees above one of three central speakers. **B:** The monkey fixated for a total of 1750 ms. After the first 750 ms of fixation, a 500-ms noise burst was emitted from one speaker. After an additional delay of 500 ms, the fixation spot was extinguished, and the monkey made a saccade to the remembered sound location. [From Stricanne et al., 1996].

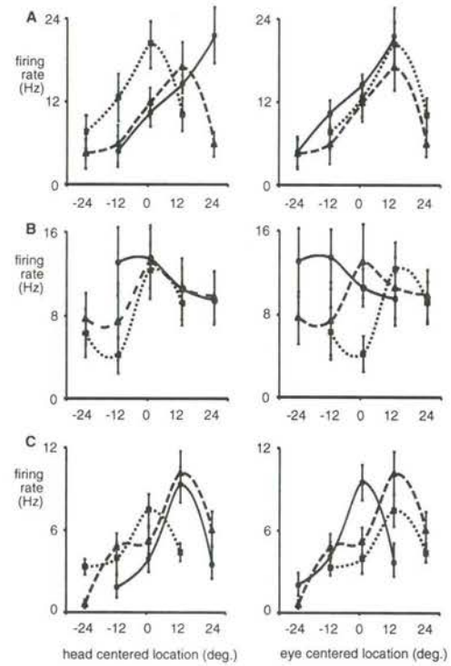

Figure 6. Tuning curves for three representative LIP neurons. Mean response averaged over the last 400 ms of the memory period is plotted with standard errors against head-centered location of the sound (left column) or horizontal component of motor error (right column). The three lines in each plot correspond to the neural response obtained from a given starting eye position: solid line, 12 degrees right fixation; dashed line, central fixation; dotted line, 12 degrees left fixation. **A:** Neuron with an eye-centered response field. Curves obtained for the three different fixations are aligned in the right column but not in the left column, indicating that the strongest response occurred when the animal was planning a saccade to a location 12 degrees to the right regardless of the initial fixation point. **B:** Neuron with a head-centered response field. Curves are now aligned in the left column but not in the right column, indicating that the strongest response occurred for saccades to the central speaker. **C:** Neuron with an intermediate response field. Here the curves are partially aligned in both columns. [From Stricanne et al., 1996.]

coded the target location in head-centered coordinates. In a final class of cells both the eye displacement and the speaker location affected the response; these cells can be operationally defined as coding locations in an intermediate coordinate frame. Figure 6A shows an example of a cell coding in eye-centered coordinates. The plot on the left shows the response to the five speaker locations with the three curves obtained from the three different initial eye positions. These three tuning curves shift with initial eye position. The graph on the right replots these same data in eye coordinates. The alignment of the curves in this plot shows that the shift was equal to the difference in eye position and that this neuron responds most when the animal is planning an eye movement 12 degrees to the right, independent of the initial eye position. An example of a cell coding auditory locations in head-centered coordinates is shown in Fig. 6B. The fact that the curves align in the left plot but not the right plot shows that the cell maintains similar responses for particular speaker locations, independent of the initial eye position. Figure 6C shows an example of a cell with intermediate coding, with the three curves partially aligned in both plots.

We used a statistical analysis to separate the population of LIP cells into these three cell types. Of 43 cells tested, 44% had receptive fields in eye-centered coordinates, 33% in head-centered coordinates, and 23% in intermediate coordinates. For all three types of cells, initial eye position was also found to introduce a gain on the response. Figure 7 shows a cell with eye-centered coding which is modulated by eye position. The alignment of the curves on the left plot shows the receptive field is eye-centered. The modulation of the amplitude of the cell's response by eye position is indicated by the vertical shift of the tuning curves.

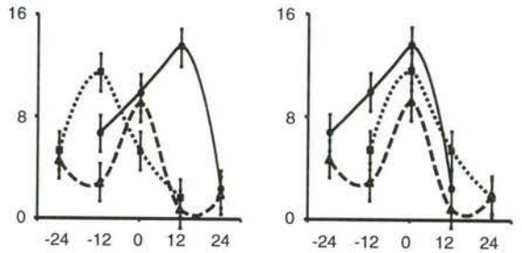

Figure 7. Neuron with an oculocentric response field modulation. Changing initial eye position modulates amplitude of neural response. Indeed, the 3 curves are aligned on the right only, with strongest response for downwards saccades for all 3 fixation positions, but intensity of the response is strongest for fixation on right.

MODEL FOR COORDINATE TRANSFORMATIONS

How might a transformation of auditory signals from head-centered to eye-centered coordinates be accomplished in area LIP? Previous modeling studies from our lab have suggested that eye position gain modulation of retinal receptive fields could be used to transform signals from retinal (eye-centered) coordinates to head-centered coordinates. Gain modulation of the auditory signals implies that a similar gain mechanism might be operating to transform head-centered auditory signals into eye-centered coordinates for the purpose of making saccades to auditory targets. We have recently trained a neural network to make this transformation (Xing et al., 1994). The inputs to this network are eye position, auditory stimulus position in head-centered coordinates, and visual stimulus position in retinal coordinates. The output of the network codes motor error for making saccades to auditory and visual targets. The hidden layer units develop many properties similar to those found in LIP neurons. These similarities include auditory and visual fields, gain modulation, and auditory receptive fields in head-centered and intermediate coordinate frames. The output units of the network are similar to the eye-centered auditory receptive fields found in some LIP neurons. The similarities between the model and physiological data suggest that area LIP participates in the transformation of auditory signals to oculomotor coordinates for the purpose of making saccades.

CONCLUSIONS

The above experiments suggest an interesting role for auditory signals in area LIP. Area LIP would normally be considered a visual extrastriate area which plays a critical role in the planning of eye movements to visual targets. However, it is also an auditory area, but only under certain behavioral conditions. Those conditions are when the monkey needs to use auditory information to plan saccades. Furthermore, the finding of head-, intermediate- and eye-centered encoding of auditory signals in LIP suggests that LIP participates in, or is the source of, the transformation of auditory spatial information from head-centered coordinates into oculomotor coordinates for the purpose of making saccades.

Does area LIP also play a role in transformation of spatial information from other sources into oculomotor commands? Will non-spatial, cognitive signals also have gated access to LIP for particular eye movements? What happens in LIP when, for instance, an increase in the rate of optical flow as we drive inspires us to look down at the speedometer? The saccade to the speedometer is determined by cognitive rather than spatial information. Perhaps LIP receives many signals from numerous parts of the brain for this type of learned eye movement behavior. The simultaneous input of all these signals may overwhelm the LIP machinery, requiring dynamic switching of specific signals based on the particular task being processed. Answering these and related questions will make for exciting experiments in the years to come.

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LOCATION CODING BY AUDITORY CORTICAL NEURONS

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INTRODUCTION

The auditory cortex is essential for normal sound localization behavior. In humans, unilateral temporal lobe lesions result in deficits in the ability to point to a sound source presented on the side contralateral to the lesion (Greene, 1929; Wortis and Pfeiffer, 1948; Sanchez-Longo and Forster, 1958; Klingon and Bontecou, 1966). In cats, experimental ablation of the auditory cortex results in an inability of the cat to walk to the source of a contralateral sound (Jenkins and Masterton, 1982; Jenkins and Merzenich, 1984).

In contrast to these behavioral results showing the importance of auditory cortex for sound localization, physiological studies generally have been unsuccessful in identifying a systematic cortical representation of sound-source location. Physiologists in several laboratories (e.g., Middlebrooks and Pettigrew, 1981; Imig et al., 1990; Rajan et al., 1990; Ahissar et al., 1992; Clarey et al., 1994; Brugge et al., 1996) have explored the cortical representation of sound-source location by presenting stimuli sequentially from loudspeakers in an anechoic chamber and recording the number of single-unit spikes elicited as a function of sound-source location in the horizontal plane (i.e., as a function of azimuth). Whether stated explicitly or not, the goal of such experiments appears to have been to discover a topographical representation of auditory space in which single neurons are selective for a particular "best area" and in which locations in the sound field are represented by restricted foci of maximal cortical activity. Such maps have been found, for instance, in the optic tectum of the barn owl (Knudsen, 1982) and in the superior colliculus of mammals (Palmer and King, 1982; Middlebrooks and Knudsen, 1984). In the mammalian auditory cortex, depending on the particular cortical area that is studied and on the particular defining criteria that are used, roughly half of units are location selective in the sense that their spike counts are modulated by more than about 50% by the location of the sound source. The spatial sensitivity of units, however, tends to be quite broad, such that many spatially selective neurons respond with greater than half of their maximum response to stimuli presented almost anywhere within half of the sound field. Moreover, the tuning of most units broadens considerably as

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