NEURONS IN CAT PRIMARY AUDITORY CORTEX
SENSITIVE TO CORRELATES OF AUDITORY MOTION
IN THREE-DIMENSIONAL SPACE

by

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ABSTRACT

The primary auditory cortex (area AI) plays an important role in the localization of static sound sources. However, little is known concerning how it processes information about sound source motion. This study was undertaken to investigate the responses of single neurons in the primary auditory cortex of the cat to correlates of auditory motion in space. Diotic and dichotic changes in sound intensity presented through earphones simulated auditory motion in four directions: toward and away from the receiver along the midline, into the ipsilateral hemifield and into the contralateral hemifield. Different rates of intensity change simulated sound source velocity. Results indicate that AI neurons can be highly selective to intensity correlates of auditory motion. Three major classes of neurons were encountered: neurons sensitive to motion toward or away from the receiver, neurons sensitive to ipsilateral- or contralateral-directed motion, and monaural-like neurons. The different classes of direction-selective neurons were spatially segregated from each other and appeared to occur in clusters or columns in the cortex. In addition to their selectivity for different directions of simulated sound source motion, AI neurons also responded selectively to the rate and excursion of intensity changes, a correlate of sound source velocity. The major determinants of direction and velocity selectivity were interactions between the following response properties of AI neurons: binaural interaction type, ear dominance, on/off responses, and monotonicity of rate/intensity function. These findings suggest that neural processing of auditory motion may involve neural mechanisms distinct from those involved in static sound localization, and indicate that some neurons in the primary auditory cortex may be part of a specialized motion-detecting mechanism in the auditory system.

TABLE OF CONTENTS

ABSTRACT.....	ii
LIST OF FIGURES.....	iv
INTRODUCTION.....	1
Sound localization.....	1
Auditory system.....	4
Primary auditory cortex.....	8
The role of the primary auditory cortex in the encoding of sound source location.....	9
Real and simulated movement.....	12
Implementation and predictions.....	15
METHODS.....	18
Animal preparation.....	18
Stimuli.....	19
Calibration.....	22
Data collection.....	22
Data analysis.....	23
RESULTS.....	25
Directional selectivity.....	25
A. Motion in depth.....	27
B. Motion in azimuth.....	38
C. Monaural-like units.....	44
D. Distribution of unit types.....	48
Velocity selectivity.....	48
Effect of changing frequency.....	60
DISCUSSION.....	61
Mechanisms of direction and velocity selectivity.....	61
A. Motion in depth.....	61
B. Motion in azimuth.....	62
C. Monaural-like units.....	63
D. Velocity selectivity.....	63
E. A model for direction and velocity selectivity.....	64
Technical considerations.....	66
Analogies to vision.....	68
Specialized motion-detecting mechanisms in the auditory system?.....	69
REFERENCES.....	74

LIST OF FIGURES

Figure 1	Ascending auditory pathways.....	6
Figure 2	Binaural interaction classes.....	10
Figure 3	Stimulus conditions.....	20
Figure 4	Summary of directional preferences for population of neurons encountered.....	26
Figure 5	Post-stimulus time histograms: toward-preferring neuron.....	28
Figure 6	Polar plots: toward-preferring neurons.....	30
Figure 7	Post-stimulus time histograms: away-preferring neuron.....	33
Figure 8	Polar plots: away-preferring neurons.....	34
Figure 9	Plot of preferred direction of motion in depth versus response to binaural onset and offset.....	35
Figure 10	Plot of breadth of tuning for motion in depth versus binaural interaction.....	37
Figure 11	Post-stimulus time histograms: ipsilateral-preferring neuron...	39
Figure 12	Polar plots: azimuth-preferring neurons.....	40
Figure 13	Plot of preferred direction of motion in azimuth versus ear dominance.....	43
Figure 14	Post-stimulus time histograms: monaural-like neuron.....	45
Figure 15	Polar plots: monaural-like neurons.....	47
Figure 16	Schematic electrode penetrations.....	49
Figure 17	Polar plots and rate/intensity functions: monotonic, velocity-dependent unit.....	51
Figure 18	Polar plots and rate/intensity functions: non-monotonic, velocity-dependent unit.....	54
Figure 19	Polar plots and rate/intensity functions: idiosyncratic unit.....	56

Figure 20	Polar plots: and rate/intensity functions: velocity-independent unit.....	58
Figure 21	Model of direction and velocity selectivity.....	65

INTRODUCTION

One role of sensory systems is to convey information to living organisms about stimuli in the environment. Living organisms are equipped with receptor end-organs specialized to transduce physical stimuli of a specific sensory modality into electrical impulses; these signals from the receptor organs are then relayed to the central nervous system, where they undergo extensive processing. The result of this signal processing provides organisms with information concerning the nature of stimuli in the environment (what), and the location of these stimuli with respect to the organism (where). The focus of this research is the latter aspects of sensory processing, and more precisely on the role of the auditory cortex in the localization of sound sources moving in space.

Sound localization

The receptor organs of the visual, auditory and somatosensory systems in mammals follow a specific arrangement: retinal ganglion cells, cochlear hair cells and cutaneous receptors are organized in an orderly array or sensory epithelium. The spatial organization of the sensory epithelium in these three systems is preserved in the projections to the central nervous system, in a so-called point-to-point projection: receptors from neighboring regions of sensory epithelium project to neighboring regions of sensory cortex. In the visual and somatosensory systems, this arrangement preserves information about the location of stimuli in space. In the visual system, portions of the retina receive input from specific parts of the visual field, and in turn project to distinct areas of visual cortex; a similar arrangement exists in the somatosensory system. Therefore, spatial information is preserved in the ascending visual and somatosensory pathways and is directly available in the cortex by virtue of

retinotopic and somatotopic projections.

This does not hold for the auditory system. The sensory epithelium of the auditory system is the basilar membrane located in the cochlea of the inner ear. The basilar membrane codes for sound source frequency (pitch) along its length, and the receptor organs (the hair cells of the organ of Corti) also have an orderly spatial arrangement: hair cells located at the base of the basilar membrane respond to high frequency sound, and those located at the apex respond to low frequency sound. This arrangement is due to the mechanical properties of the membrane itself. This tonotopic organization is preserved in the projections of the auditory pathway to various brainstem nuclei and most areas of the auditory cortex. Although frequency coding provides crucial information about the nature of auditory stimuli, it gives no information about the spatial location of such stimuli because sound sources from all directions impinge on a common sensory epithelium extended in frequency rather than space. Information about sound source location must then be computed and extracted by the central nervous system.

Organisms equipped with two auditory end-organs can solve the problem of sound localization: the principal cues for sound localization are differences in the signals reaching the two ears. These binaural cues depend on the spatial location and frequency spectrum of the sound source, and on the size and shape of the receiver's head. The distance between the two ears imposes an interaural time difference (ITD) on arriving stimuli, resulting in interaural disparities in transient arrival time and in on-going phase. ITDs are important in localizing low frequency sound sources (below about 1500 Hz in humans). The acoustic shadow of the head and pinnae generate interaural intensity differences (IID) which are useful in localizing high frequency sound sources (above 1500 Hz). This so-called duplex theory of sound localization describes accurately how

mammals localize pure tones, using temporal cues for the lower portion of the audible spectrum and intensive cues for the higher portion (Stevens & Newman, 1936). Another consequence of the shadowing effect of the head and pinnae is the creation of interaural frequency disparities (IFD), which may be helpful for localizing complex broadband sound sources (Mendelson & Cynader, 1983).

The external ear (pinna) also plays an important role in sound localization. In addition to generating interaural intensity differences, the convolutions of the pinnae and the resonances in the ear canal differentially amplify or dampen certain frequencies, resulting in a transformation of the frequency spectrum from the free sound field to the eardrum (Calford & Pettigrew, 1984; Phillips, Calford, Pettigrew, Aitkin, & Semple, 1982; Shaw, 1974). This cue is especially important in localizing broadband sound with high frequency components and is thought to underlie vertical sound localization (Brown, Schessler, Moody & Stebbins, 1982; Butler, 1969; Middlebrooks, Makous, & Green, 1989) and the resolution of front-to-back ambiguities (Musicant & Butler, 1984).

All the binaural sound localization cues listed above (ITD, IID and IFD) can be generated with the head in a fixed position. However, head movements are widely used by animals attempting to locate a sound source. Head movements produce a series of changing binaural cues which limit the possible positions of a sound source relative to the receiver (Mills, 1972) and significantly improve localization accuracy in humans (Thurlow, Mangels, & Runge, 1967; Thurlow & Runge, 1967). In addition to moving the head, animals with moveable pinnae frequently use pinna movements when localizing sound sources. Because most electrophysiological and psychophysical studies focus on static localization cues, the importance of head movements in sound localization is usually overlooked.

Interaural intensity differences show marked dependence on the frequency and azimuthal location of the sound source (Irvine, 1987; Martin & Webster, 1989). The IID/azimuth function is monotonic for the frontal region of space (within about 45 degrees of the midline on either side) and is frequency dependent, being steepest at high frequencies (8 kHz in the cat). This agrees well with psychophysical data which shows that localization acuity in cats and monkeys is greatest for high frequency sounds (Martin & Webster, 1987; Casseday & Neff, 1973) and for stimuli located close to the midline (Brown et al., 1982; Heffner & Heffner, 1988). Interaural time differences are also frequency dependent although this effect is relatively independent of the pinnae. As in the case of IIDs, ITDs generated by sound sources close to the midline provide useful localization cues (Roth, Kochhar, & Hind, 1980).

Localization of sound sources implies extracting information about the spatial location of stimuli largely from the binaural cues generated by that source. However this process can be reversed: presenting binaural sound localization cues through earphones produces a fused auditory image located within the head instead of in the free acoustic field, and listeners can locate the sound source accordingly. This task is called lateralization (in contrast with the usual task of localization). The binaural temporal and intensive disparities that are thought to underlie sound localization of pure tones can be used to lateralize tonal stimuli; localization and lateralization acuity are similar, suggesting that similar mechanisms underlie localizing internal and external sound sources (Jeffress & Taylor, 1961). Moreover, the lateralization acuities of cats and humans are comparable (Wakeford & Robinson, 1974; Yost, 1974).

Auditory system

The organization of the central auditory system is more complex than that

of other sensory systems: in contrast with the somatosensory system where information can reach the cortex with as few as two synapses, or the visual system where there is only one major relay nucleus, information from the hair cells in the inner ear passes through several nuclei before reaching the auditory cortex, and the interconnections between the various nuclei are intricate. Several distinct auditory areas exist at the level of the cortex. In addition, parallel descending pathways add to the complexity of this system.

A simplified scheme of the ascending auditory pathway is shown on figure 1. Neurons with cell bodies in the spiral ganglion synapse with the hair cells of the organ of Corti; the axons form the auditory nerve (the auditory part of the eighth cranial nerve) and terminate in the dorsal and ventral divisions of the cochlear nucleus. From the cochlear nucleus, fibers ascend in the dorsal acoustic stria (stria of Monakow) and the intermediate stria of Held to the contralateral lateral lemniscus and inferior colliculus, sending collaterals along the way to brainstem nuclei. Fibers from the cochlear nucleus also ascend in the trapezoid body, sending collaterals to the superior olivary complex of the brainstem before synapsing contralaterally in the lateral lemniscus and/or the inferior colliculus. The medial superior olive is particularly noteworthy: it is the first nucleus in the ascending auditory pathway which receives input from both ears. Fibers from the superior olivary complex project bilaterally to the lateral lemniscus and the inferior colliculus. The latter is the midbrain auditory area; it sends fibers to the thalamic auditory nucleus (the medial geniculate body), which in turn projects to the auditory cortex. Although ascending projections from the cochlear nucleus are largely contralateral, there are significant crossed connections from the level of the lateral lemniscus upward, that the inferior colliculus, the medial geniculate body and the auditory cortex all receive binaural information. Ascending projections preserve the tonotopic organization of the

Figure 1. Schematic representation of the mammalian ascending auditory pathways. DCN: dorsal cochlear nucleus; VCN: ventral cochlear nucleus; LSO: lateral superior olive; MSO: medial superior olive; NTB: nucleus of the trapezoid body; LL: lateral lemniscus; IC: inferior colliculus; MG: medial geniculate nucleus of the thalamus; SH: stria of Held; SM: stria of Monakow (from Moller, 1983).

cochlea so that frequency coding is present at all levels of the auditory pathway.

The auditory cortex is made up of several distinct auditory areas. In the cat, as many as eight distinct fields have been identified, and about a third of the auditory cortex is non-tonotopically organized (Reale & Imig, 1980). The most prominent are the primary and secondary auditory fields (AI and AII), the anterior auditory field (AAF), and the posterior and ventroposterior auditory fields (PAF and VPAF). Contrary to what its name may imply, the primary auditory cortex is not the only site receiving direct thalamic input; rather, several parallel projections run from the medial geniculate body to the different auditory fields so that all fields receive equally direct thalamic input. There are two largely segregated thalamocortical auditory projection systems in the cat: a tonotopic projection to AI, AAF, PAF and VPAF, and a non-tonotopic projection to AII and other secondary regions (Andersen, Knight, & Merzenich, 1980). In addition, various intracortical and interhemispheric connections also exist (Brugge & Imig, 1978; Matsubara & Phillips, 1988).

All nuclei of the ascending pathway receive input from higher levels. The descending auditory pathway is made up of two systems: the corticothalamic system which terminates in the medial geniculate body, and the corticocochlear system which is a widely distributed network of connections to all nuclei of the ascending pathway, extending to the cochlear hair cells (Harrison & Howe, 1975). The descending pathways are thought to exert an inhibitory influence on the activity of the ascending pathway.

A salient feature of signal processing in the auditory system (which is probably true of other sensory systems as well) is its increasing complexity as one ascends the auditory pathway. The many nuclei of the ascending auditory pathway are not mere relays; signals from the cochlear hair cells are extensively processed. In the inner ear and auditory nerve, one can record the cochlear

microphonic, an electrical potential which faithfully reproduces the waveform of a sound with little distortion. Neurons at lower levels of the pathway respond throughout the length of the stimulus; these sustained responses are gradually replaced by transient responses at higher levels, and are virtually absent from the cortex. Brainstem auditory neurons show phase-locking; again, these responses gradually disappear at the level of the midbrain and are absent in the thalamus and cortex. In the auditory cortex, rapidly adapting neurons predominate; transient excitatory responses are common and responses to sound offset also appear. Cortical neurons also respond well to frequency and amplitude modulated sound (Mendelson & Cynader, 1985; Phillips, Mendelson, Cynader, & Douglas, 1985; Schreiner & Urbas, 1988). Overall, neurons in lower auditory centers show little adaptation; in higher centers and especially in the cortex, neurons show more adaptation, giving more transient responses, a greater variety of response patterns and strong excitatory and inhibitory responses. Cortical neurons respond best to change and show rapid adaptation; the increasing complexity in signal processing in the ascending auditory pathway allows these neurons to enhance change, and in turn, neuronal adaptation saves channel capacity in the cortex (Moller, 1983).

Primary auditory cortex

Information about sound source frequency is preserved in the primary auditory cortex. Area AI is tonotopically arranged: isofrequency bands run dorsoventrally, with high frequencies located rostrally and low frequencies more caudally (Merzenich, Knight, & Roth, 1975; Phillips & Irvine, 1981a). Neurons in area AI are sharply tuned to sound frequency; in addition, neurons found within the same perpendicular penetration show similar frequency tuning, which is evidence for some form of columnar organization in the auditory cortex with

respect to frequency (Merzenich et al., 1975). There is also a gradient for breadth of frequency tuning in AI: neurons in the dorsal part show narrower frequency tuning and those in more ventral locations are more broadly tuned (Schreiner & Cynader, 1984). The rate/intensity functions of the responses of primary auditory neurons can be monotonic or non-monotonic, although the latter are less frequent (Phillips & Irvine, 1981a).

Most neurons in AI respond well to stimulation of the contralateral ear, and respond differently to monaural and binaural stimulation. The responses of AI neurons to binaural stimulation can be classified in one of three functional categories: 1- EE units (excitatory/excitatory) in which the response evoked by stimulation of the dominant ear is facilitated by simultaneous stimulation of the other ear; 2- EI and IE units (excitatory/inhibitory and vice versa) in which the response evoked by stimulation of the dominant ear is inhibited by simultaneous stimulation of the other ear; 3- EO units (monaural) in which the response evoked by stimulation of one ear is unaffected by binaural stimulation (Imig & Adrian, 1977; figure 2). Neurons found along the same electrode penetration tend to display similar binaural interactions, suggesting that area AI is organized in vertical binaural interaction columns. These columns are grouped together in bands which are oriented orthogonal to the isofrequency bands (Middlebrooks, Dykes, & Merzenich, 1980).

The role of the primary auditory cortex in the encoding of sound source location

Three kinds of experiments have attempted to delineate the role of the primary auditory cortex in sound localization: electrophysiological experiments using sealed systems to present binaural sound localization cues, electrophysiological experiments using free-field stimuli, and studies of sound localization behavior following selective cortical lesions. The first type of

Figure 2. Binaural interaction classes of primary auditory cortex neurons. EE: excitatory/excitatory (binaural facilitation); EI: excitatory/inhibitory (contralateral-ear-dominated with binaural inhibition); IE: inhibitory/excitatory (ipsilateral-ear-dominated with binaural inhibition); EO: monaural (no binaural interaction).

experiments has demonstrated that neurons in the primary auditory cortex of the cat are sensitive to binaural sound localization cues (IIDs, ITDs, and IFDs) corresponding to the frontal and contralateral regions of auditory space (Brugge, Dubrovsky, Aitkin, & Anderson, 1969; Kitzes, Wrege, & Cassady, 1980; Mendelson & Cynader, 1983; Phillips & Irvine, 1981b; Reale & Kettner, 1986). The selectivity of AI neurons to interaural time, intensity and frequency differences is related to binaural response category. Preferences for IIDs and ITDs seem to result from the interaction of excitatory and/or inhibitory events evoked by stimulation of each ear; the binaural response in such cells is dependent on the timing of the sequence of excitatory and inhibitory events at the site of interaction, which in turn depends on stimulus intensity (Brugge et al., 1969; Kitzes et al., 1980).

Free-field studies have demonstrated that AI neurons are sensitive to the spatial location of pure tone and noise stimuli. Again, AI neurons seem to respond best to sound sources located in the frontal and contralateral sound fields (Eisenman, 1974; Benson, Hienz, & Goldstein, 1981). Middlebrooks and Pettigrew (1981) have proposed that primary auditory neurons can be classified in one of three classes of spatial receptive fields based on their sensitivity to stimulus location: hemifield units, which respond to sound in the contralateral sound hemifield; axial units, which respond to sound in the acoustic axis of the contralateral pinna; and omnidirectional units, which respond to sound from any direction in front of the animal. These auditory spatial receptive fields are computational: they are not derived from a point-to-point map from the inner ear to the cortex but are computed from comparisons of the signals at the two ears. However, despite the existence of location-sensitive units in the primary auditory cortex of the cat, there is no indication of a systematic map of auditory space in area AI (Middlebrooks & Pettigrew, 1981).

Lesion to the primary auditory cortex spare intensity and frequency discrimination abilities but produce permanent sound localization deficits in the sound field contralateral to the lesion. This conclusion has been reached in studies with cats (Jenkins & Masterton, 1982), dogs (Heffner, 1978) and monkeys (Heffner & Masterton, 1975). Comparisons between lesions to area AI and to other auditory cortical fields indicate that among other auditory cortical fields, integrity of area AI is necessary and sufficient for normal binaural sound localization behavior. Area AI in each hemisphere contributes primarily to location representation in the contralateral sound field (Phillips & Gates, 1982; Jenkins & Merzenich, 1984).

The sensitivity of auditory neurons to binaural sound localization cues and to the spatial location of sound sources, and the importance of the primary auditory cortex for accurate sound localization indicate that area AI of the auditory cortex plays an essential role in directional hearing.

Real and simulated auditory movement

All of the research cited above has been carried out using stationary sound sources, or correlates of such sounds. Yet, a conspicuous feature of auditory stimuli in the environment is their motion with respect to the receiver. Despite this prominence, auditory movement as a stimulus feature has largely been overlooked by most investigators of the psychophysics and neurophysiology of sound localization. Although much progress has been made in understanding static sound localization, little is known about how the auditory system extracts information about stimulus motion.

As sound sources move across the auditory field, they provide the auditory system with a series of changing binaural disparities. In particular, movement of a sound source in azimuth produces modulations of interaural differences in

intensity, on-going phase and frequency spectrum; the rate of change in these binaural cues is a correlate of sound source velocity. Therefore it is possible to simulate sound source movement without actually providing real motion, by presenting correlates of motion (modulated IIDs, ITDs and IFDs) to a listener via earphones or speakers; dichotic modulations of both ITDs and IIDs can produce simulated auditory motion, and subjects can lateralize such stimuli. Briggs and Perrott (1972), and Perrott (1974) demonstrated auditory apparent movement by presenting human subjects with dichotic noise stimuli of varying interstimulus onset. At optimal interstimulus onset, subjects perceived two sounds as one continuous moving sound; these findings concerning auditory motion perception coincided with those obtained from free-field studies. However, the temporal disparities used in this study to simulate auditory motion (tens or hundreds of milliseconds) were not faithful representations of the actual temporal cues used by the auditory system for sound localization, which are in the order of tenths of milliseconds. Altman and Viskov (1977) used continuous modulations of interaural phase differences in a dichotic paradigm (click trains of varying interaural time delays) to simulate auditory motion; these stimuli were derived from actual ITDs generated by sound sources moving in azimuth. Such stimuli produced a fused auditory image (FAI) which moved within the head, and evoked a distinct sensation of auditory motion in human subjects. In addition, subjects could make velocity discriminations based on perceived FAI movement. Grantham (1984, 1986) came to similar conclusions by presenting subjects with amplitude modulated narrow-band noise via distant speakers to simulate horizontal auditory motion.

In an attempt to delineate the role of the auditory cortex in localizing moving sound sources, Altman and Kalmykova (1986) lesioned the auditory cortex of dogs and tested their subsequent ability to lateralize signals simulating

auditory movement. Bilateral lesions completely eliminated the ability to discriminate the direction of simulated auditory motion, and unilateral lesions produced a lateralization deficit on the side contralateral to the lesion. These lesion effects parallel those found with static stimuli (Jenkins & Masterton, 1982; Heffner, 1978; Heffner & Masterton, 1975). However, because different regions of auditory cortex were not selectively lesioned, no conclusions could be drawn regarding which auditory field in particular is involved in processing of information about stimulus motion. Although these findings have not been replicated in free-field situations, they still highlight the importance of the auditory cortex for dynamic sound localization.

Because neurons in the primary auditory cortex are sensitive to the location of sound sources but show rapid adaptation to static stimuli, one might expect that some neurons in area AI would respond well to sound source movement within their spatial receptive fields. Also, given the fact that AI neurons are sharply tuned to binaural disparities corresponding to certain sound source locations, and given the propensity of auditory cortical neurons for change, one could presume that the direction and rate of change of binaural disparities (which are correlates of direction and velocity of auditory motion, respectively) could evoke strong responses from these neurons. Surprisingly, there are few reports of sensitivity to movement of sound sources by neurons of the auditory cortex. Sovijarvi and Hyvarinen (1974) presented continuous pure tones moving horizontally and vertically in a free field situation, and found neurons in the primary auditory cortex of the cat which were sensitive to the direction of sound source movement. Altman (1987) studied the responses of AI neurons to modulations of interaural phase disparity in a sealed system, and found neurons which responded selectively to the direction of phase change, a correlate of sound source motion in azimuth. These two reports were the first to

point to the existence of motion detecting mechanisms in the auditory cortex. However, in neither report was the degree of directional selectivity quantified or further analyzed in terms of possible underlying mechanisms. In addition, relatively few motion-sensitive units were reported, an indication that such units in the primary auditory cortex of the cat may be relatively rare, as opposed to the more common location-sensitive units (Middlebrooks & Pettigrew, 1981).

The aim of this study is twofold: to confirm and assess the existence and prevalence of motion-sensitive neurons in the primary auditory cortex of the cat, and to investigate the mechanisms underlying this sensitivity to auditory motion in terms of known response characteristics of auditory cortical neurons.

Implementation and predictions

As previously mentioned, moving sound sources produce a series of changing binaural disparities. One correlate of auditory motion in space is modulation of sound intensity at the receiver's ears. When a sound source moves toward or away from the receiver along the midline, the two ears receive correlated (diotic) increases or decreases in sound intensity. When a sound source moves across the receiver's auditory field along the horizontal plane, the two ears receive opposite-directed (dichotic) changes in sound intensity: sound intensity increases in one ear and simultaneously decreases in the other ear. Presenting these diotic and dichotic changes in intensity at the two ears through earphones produces a simulation of auditory motion: a fused auditory image appears to move within the head, as was produced by Altman and Viskov (1977) with modulations of interaural time delay. To determine the sensitivity of auditory neurons to modulated IIDs, one can present this correlate of sound source motion directly into the ears of an animal and simultaneously record the electrical activity of AI neurons evoked by this stimulus.

Presenting modulated interaural intensity differences through earphones can simulate motion of real world sound sources without actually providing that motion. This paradigm has advantages and shortcomings. One obvious limitation of using earphones instead of free-field stimuli is the fact that the modifying effects of the head and pinnae on the incoming signal are bypassed altogether. This results in a stimulus containing less information, because some sound localization cues normally present in the free sound field are missing. Another limitation is due to the signal itself: modulations of IIDs as the only auditory motion cue is an incomplete stimulus. Using the same paradigm but adding other motion cues to the stimulus (modulations of frequency spectrum, time of arrival and on-going phase) would produce a more accurate simulation of auditory motion. In turn, a more complete stimulus may help uncover a neural mechanism specialized to detect moving sound sources by providing additional information to such a system. The limitations of this paradigm may result in perceptual ambiguities: for example, it is impossible for a receiver to distinguish between the intensity changes associated with sound source movement toward or away from the receiver and actual modulation of the intensity of a stationary sound source. On a more positive side, modulations of IIDs produce an appropriate (albeit simplified) simulation of sound source movement that can be easily implemented in a calibrated, sealed sound delivery system. In addition, presenting only one motion cue eliminates possible interactions among stimulus parameters and facilitates the interpretation of results.

Aside from responses to intensity correlates of auditory motion, other response characteristics of AI neurons will be investigated: aural dominance, binaural interaction category, transient on and off responses, and monotonicity of the rate/intensity function. From these response characteristics, some predictions can be made regarding selectivity to direction of auditory motion: 1-

neurons will prefer simulated auditory motion into the hemifield corresponding to the dominant ear; 2- neurons with facilitatory binaural interactions will prefer simulated auditory motion toward the receiver; 3- neurons with inhibitory binaural interactions will prefer simulated auditory motion in azimuth, away from the ear producing inhibition and toward the ear producing excitation; 4- neurons with off responses will prefer simulated auditory motion in directions opposite those specified above; 5- a neuron's preference for slow or fast simulated auditory motion will depend on the monotonicity of its rate/intensity function. These predictions will be verified, along with possible interactions among the response characteristics of the units encountered and their resulting sensitivity and selectivity to direction of simulated auditory motion.

METHODS

Animal preparation

Acute experiments were performed on 7 healthy adult cats. Surgical anesthesia was induced with sodium pentothal (10 mg/kg i.v. initially); additional doses were administered during surgery to maintain areflexia. To prevent excessive salivation and respiratory difficulties, a single dose of atropine sulfate (0.2 mg, i.v.) was administered. Dexamethasone (0.5 mg, i.m.) was administered to prevent brain edema.

A tracheotomy was performed and an endotracheal tube inserted. The animal was supported by a head-holder which left the skull and pinnae free from obstruction. The skull and auditory meatuses were cleared of surrounding tissue. A 5-mm diameter hole was drilled in the skull overlying the left ectosylvian gyrus (area AI), and the intact dura was covered with petroleum jelly to keep it from drying. The auditory meatuses were transected and the pinnae reflected anteriorly to allow insertion of the stimulus delivery system (hollow aluminum acoustic couplers) directly into the ear canals. All wounds and pressure points were infiltrated with a long-acting local anesthetic (bupivacaine hydrochloride 2.5%). When surgery was completed, sodium pentothal anesthesia was discontinued. The animal was paralyzed (gallamine triethiodide 20 mg, i.v.) and artificially respired with a 70:30 mixture of nitrous oxide and oxygen. The animal was maintained on a continuous intravenous infusion of gallamine triethiodide (10 mg/kg/hr), sodium pentobarbital (1 mg/kg/hr) and 5% lactated dextrose (10 ml/hr) in Ringer's. End-tidal CO₂, heart rate, blood pressure and EEG were monitored continuously. Rectal temperature was maintained at 38°C using a feedback-controlled heating blanket; expired CO₂ was maintained at about 4% by adjusting the rate of the respiration pump.

Stimuli

Pure tone sinusoids were generated by a Wavetek model 110 function generator. Signals to the speakers were controlled by two digital-to-analog converters of the PDP/11 computer, and fed through an analog multiplier and an amplifier (Technics SU-700 stereo integrated amplifier). The stimulus delivery system consisted of two loudspeakers (Pioneer WXX-172) connected to hollow aluminum acoustic couplers which fitted snugly into the transected auditory meatuses.

The stimuli employed were amplitude modulated pure tones which simulated auditory motion in four canonical directions. Like-directed changes in sound intensity at both ears simulated movement toward or away from the head along the midline; opposite-directed changes in sound intensity simulated sound moving along the azimuthal plane, toward one ear and away from the other, and vice versa (figure 3A, B). Since the duration of the AM ramp was constant at 250 msec, AM ramp rate and excursion in these experiments are correlates of sound source velocity: increased ramp excursion and rate correspond to higher velocities of sound source motion. Each of the four simulated directions of motion was presented at four different rates of rise of the AM ramp; the four different intensity levels spanned 24 dB, in four 6 dB increments (figure 3C).

The stimuli were shaped with envelope generators to produce rise and fall times of 5 ms; interaural phase was always zero. Stimulus time course is shown on figure 3D. Stimulus onset occurred at 150 msec and was followed by a 295 ms plateau; the AM ramps simulating auditory motion occurred between 450 and 700 msec, and were followed by another 295 ms plateau and stimulus offset at 1000 msec. Total data collection time was 1300 ms, with a 200 ms wait time between each stimulus presentation. There were 40 presentations for each condition, for a total of 640 stimulus presentations (4 directions of motion x 4

Figure 3. Representation of stimuli used to simulate auditory motion in space. Pure tones are presented to the two ears through a sealed system. **A:** Correlated increases or decreases in sound level at the two ears simulate auditory motion in depth. **B:** Opposite-directed changes in sound level at the two ears simulate auditory motion in azimuth. **C:** Four different ramp rates and excursions corresponding to the four velocity conditions. **D:** Stimulus time course.

ramp excursions x 40 presentations) for each unit.

Calibration

A probe microphone (IVIE 1300) was inserted in the acoustic couplers for *in situ* measurement of sound pressure levels near the tympanic membrane. A waveform analyzer (DataPrecision Data 6000) produced fast Fourier transforms of the sound spectra. The output of a Brüel and Kjaer pistonphone (124 dB at 250 Hz) was used to convert relative intensity measurements into sound pressure level (dB SPL re 20 $\mu\text{N/m}^2$). Variations in sound intensity at different frequencies were corrected with reference to the output of the waveform analyzer. Sound levels were calibrated at the beginning of each experiment and monitored on-line throughout the experiment.

Data collection

The animal was located in a sound-attenuating chamber (IAC Controlled Acoustic Environments). Except for the sound delivery system, microdrive, stereotaxic apparatus, table and animal, all of the equipment used (infusion pump, respirator, computer, etc.) was located outside the chamber. The responses of single neurons in area AI were recorded extracellularly using glass-insulated platinum-iridium microelectrodes with impedances of 1-1.5 M Ω at 1 kHz (Wolbarsht, MacNichol, & Wagner, 1960). Electrodes were advanced perpendicularly through the dura and cortex using a remote controlled microdrive. Signals from the electrode were bandpass filtered (500 Hz to 12 kHz), amplified (1000x), discriminated with a window discriminator and monitored on an oscilloscope and an audio monitor (Grass AM8). Stimulus presentation and on-line data collection and display were controlled by the PDP/11 computer via an IBM PC serving as an intelligent terminal.

White noise and pure tone bursts were used as search stimuli. When a unit was encountered, its characteristic frequency (CF) was determined. Stimulus presentation was done at CF, although additional frequencies were sometimes used. The 16 stimulus conditions delineated above were individually interleaved and presented in a randomized order. This process was repeated for a total of 40 trials at which point data collection for an individual unit terminated.

The total length of an experiment was 2-3 days; recording time was 12-36 hours. When recording was completed, the animal was killed with an intravenous injection of sodium pentobarbital (100 mg/kg). The skull was opened to verify electrode placement using anatomical landmarks and previous maps of the auditory cortex surface (Schreiner & Cynader, 1984).

Data analysis

The computer generated post-stimulus histograms and spike counts for all stimulus conditions. Aural dominance and binaural interaction category were determined by comparing responses to stimulation of the contralateral ear alone, stimulation of the ipsilateral ear alone and stimulation of both ears during stimulus onset. Responses to stimulus offset were examined in a similar way.

Responses to correlates of the four different directions of motion were determined by analyzing responses during the AM ramps. Preferred direction of movement in depth was determined by comparing responses to simulated sound source movement toward and away from the receiver (correlated binaural increases and decreases in sound levels, respectively); similarly, preferred direction of movement in azimuth was determined by comparing responses to ipsilateral- and contralateral-directed simulated sound source movement (increasing sound level in one ear and decreasing sound level in the other ear, and vice versa). Units which gave weak responses to AM ramps (less than one

spike per sweep) were classified as insufficiently responsive and not evaluated further. A 2:1 ratio between responses to opposed directions of motion along one dimension (depth or azimuth) was taken as the criterion for directional selectivity. In addition, responses to simulated auditory motion in one dimension had to be at least 1.5 times stronger than those evoked by simulated auditory motion in the other dimension. For all analyses, spontaneous activity was subtracted from the spike counts and response latencies were taken into account.

RESULTS

Data were obtained for a total of 80 neurons. Nineteen neurons did not respond well to the AM ramps and will not be described further. The characteristic frequencies of the remaining 61 units ranged from 2 to 44 kHz. In general, sharp stimulus onsets (5 msec rise times) typically produced strong transient responses; the discharge elicited by the AM ramps was more sustained.

Directional selectivity

Three-quarters (61/80) of the units encountered responded to correlates of auditory motion. The majority of these AM-sensitive units (54/61) responded selectively to the direction of auditory motion and were classified according to preferred direction of simulated sound source motion. Three broad categories of directional selectivity were observed: 1- selectivity for correlates of auditory motion in depth (toward or away from the receiver), 2- selectivity for correlates of auditory motion in azimuth (ipsilateral- or contralateral-directed), and 3- selectivity for auditory motion directed both toward the receiver and in azimuth (monaural-like responses). A small number of units ($n=7$) responded to AM ramps but did not show any selectivity for a particular direction of motion. The distribution of units falling into each of the major groups is summarized in figure 4. In this figure the perspective is from above the head of the animal and the receiver is positioned at the bottom of the figure. The horizontal axis represents azimuth; the vertical axis represents depth. Recordings were made from the left hemisphere; hence the left ear is ipsilateral to the recording site, and the right ear contralateral. The length of each arrow is proportional to the number of units preferring a particular direction of simulated sound source

Figure 4. Summary of directional preferences for all direction-selective units encountered (n=54). The perspective is from directly above the head of the animal. The vertical axis corresponds to depth; the horizontal axis corresponds to azimuth. Recordings are assumed to be made from left hemisphere. The length of each arrow is proportional to the number of units preferring a particular direction of simulated sound source motion; the numeral next to each arrow indicates the number of such units that were encountered. Oblique arrows refer to monaural-like units; these units showed equal preference for increases in sound level in both ears and in one ear alone. Units not included in this figure were those which did not show any directional preference (n=7), and those which did not respond to correlates of sound source motion (n=19).

motion; the accompanying numeral indicates the number of units in each category. Oblique arrows refer to units which responded equally well to motion directed toward the receiver and in one azimuthal direction (monaural-like units; see section C). Not included in this figure are seven units which showed no directional preference, and nineteen units which did not respond to AM ramps.

A. Motion in depth

Units preferring simulated sound source motion in depth comprised 37% (23/61) of all motion-sensitive units sampled. Many more of these units responded selectively to increases than to decreases in sound level (more toward- than away-preferring units were found; see figure 4). Toward-preferring units gave transient responses to binaural stimulus onset and sustained responses during AM ramps in both ears. Figure 5 shows post-stimulus time histograms depicting the timing of a toward-preferring neuron's discharge in relation to the time course of the stimulus (shown below each histogram), for the four directions of simulated auditory motion. This neuron responds well to monaural stimulus onset in the contralateral ear (top left panel) but gives weak responses to stimulus onset in the ipsilateral ear (bottom left panel). The response to binaural stimulus onset is stronger than the sum of both monaural responses (bottom right panel), indicating strong facilitation (EE binaural interaction type). On each histogram, a horizontal line marks the responses to intensity correlates of auditory motion. There is virtually no response above background for ipsilateral-directed auditory motion, when the stimulus increases in amplitude in the ipsilateral ear and decreases in the contralateral ear (top left panel); the reversed condition, in which sound level increases in the contralateral ear and decreases in the ipsilateral ear, produces a weak response (bottom left panel). By contrast, the

Figure 5. Post-stimulus time histograms showing the responses of a single neuron in relation to the time course of the stimuli, for the four direction of auditory motion. Responses are collapsed across the four values of ramp excursion; bin width is 10 msec. A horizontal line indicates the responses during the AM ramp; these responses are subject to further analysis. This unit is defined as a toward-preferring unit because the responses during correlated AM ramps in the two ears (top right panel) are the strongest.

response obtained during *correlated* increases in stimulus amplitude in the two ears (top right panel) is quite vigorous, and contrasts markedly with the lack of response observed with correlated decreases in amplitude in the two ears (bottom right panel).

Panel A of figure 6 illustrates the responses of the unit described in figure 5 in the form of a polar plot. In this panel the perspective is from above and the receiver is positioned at the bottom of the open circle. Directional conventions are the same as in figure 4. The filled inner circle represents the spontaneous activity of the unit. The length of each arrow is proportional to the response evoked by the AM portion of the 40 stimulus presentations; the accompanying numeral refers to the actual number of spikes (minus spontaneous activity). For this unit, 329 spikes above spontaneous activity were evoked during correlated increases in sound level at the two ears and only 70 spikes were evoked by correlated decreases in sound level at the two ears. Markedly weaker responses were evoked when sound level increased in one ear and decreased in the other ear (corresponding to ipsilateral- or contralateral-directed azimuthal motion), indicated by the shorter side arrows. The breadth of tuning for this correlate of direction of sound source motion could vary from neuron to neuron. Panels B-D of figure 6 show the responses of two other toward-preferring units, both of which responded most vigorously during correlated increases in stimulus amplitude in the two ears. In some neurons like that illustrated in panel B, responses to the other directions of motion tested (aside from directly toward the receiver) were less than spontaneous activity, indicating inhibition below spontaneous levels in the non-preferred directions. The neuron in panel C showed responses that were much more broadly tuned than those of the cells of panels A and B, but responses to other directions of motion were still clearly weaker than those evoked by simulated motion toward the receiver.

Figure 6. Plots of spike counts during AM ramps simulating four directions of auditory motion. Each plot refers to a different unit. The perspective is from directly above the head of the animal; the filled inside circle indicates spontaneous activity. The vertical axis represents depth (toward/away), and the horizontal axis represents azimuth (ipsilateral/contralateral). The ipsilateral ear is on the left side in all cases. The length of each arrow is proportional to the spike count during the AM ramp for each direction of motion; the accompanying numeral refers to the number of spikes evoked during the same period (minus spontaneous activity). These four toward-preferring units have different breadths of tuning for simulated motion toward the receiver. **A:** Polar plot for the unit shown in figure 5. **B-D:** Toward-preferring units with different breadth of tuning for motion toward the receiver. The added response to sideways motion becomes more apparent in more broadly tuned units (D).

A

SE06.015
16 kHz

B

SE13.004
44 kHz

C

JL13.002
5 kHz

JL24.013
20 kHz

As illustrated in figure 4, neurons preferring simulated auditory motion away from the animal were relatively less common than those preferring motion toward the animal. Figure 7 shows post-stimulus time histograms for an away-preferring neuron. Note the absence of response to monaural or binaural sound onset and the transient response to sound *offset* in the ipsilateral ear (top left panel), in the contralateral ear (bottom left panel) and in both ears (top right panel). Most away-preferring units responded to sound offset in both ears more vigorously than did the population of toward-preferring units. Figure 8 shows polar plots representing the responses of two neurons that responded most vigorously to simulated motion directed away from the receiver; panel A illustrates the responses of the unit described in figure 7. For away-preferring neurons, the degree of selectivity also appeared to vary in strength from neuron to neuron. The neuron in panel A of figure 8 showed almost no response to motion toward the animal while the neuron in panel B was more broadly tuned for motion in depth.

Figure 9 plots the preferred direction of motion in depth against the preference for binaural sound onset or offset, for the population of depth-preferring units. A quantitative index of the motion in depth preference is obtained by dividing the difference between the toward and away responses by the sum of these responses:

$$\text{motion in depth index} = (\text{toward} - \text{away}) / (\text{toward} + \text{away})$$

Thus, in figure 9, units with positive abscissa values have stronger toward responses than away responses, and conversely for units with negative values. Similarly, preference for binaural onset or offset is measured by dividing the difference between the responses to binaural onset and offset by the sum of these responses:

$$\text{on off index} = (\text{binaural on} - \text{off}) / (\text{binaural on} + \text{off})$$

Figure 7. Conventions are the same as in figure 5. Post-stimulus time histograms showing the responses of a single neuron in relation to the time course of the stimuli, for the four direction of auditory motion. This unit is defined as an away-preferring unit because the responses during correlated AM ramps in the two ears (bottom right panel) are the strongest.

Figure 8. Conventions are the same as in figure 6. Polar plots of spike counts during AM ramps simulating four directions of auditory motion for two away-preferring units.

Motion in depth versus binaural on off response

Figure 9. Plot of the preferred direction of motion in depth versus the response to binaural sound onset and offset, for the population of depth-prefering neurons. Units with positive abscissa values prefer motion toward the receiver, and units with negative abscissa values prefer motion away from the receiver. Similarly, units with positive ordinate values give stronger transient on responses, and units with negative ordinate values give stronger transient off responses. Toward-prefering units are also on units; away-prefering units can be both on or off.

Units with positive ordinate values greater have stronger transient on responses than off responses, and conversely for units with negative values. The plot shows that all units which gave transient responses to stimulus onset in both ears also preferred correlated increases in sound source intensity at the two ears (simulated sound source motion toward the receiver). Units which responded to sound offset preferred correlated decreases in sound source intensity at the two ears (simulated sound source motion away from the receiver); one away-preferring neuron did not respond to sound offset and did not follow this pattern. Because relatively few away neurons were encountered it was not possible to quantify the relationship between preferred direction of motion in depth and binaural on/off response beyond the obvious relationship noted in figure 3.

Most depth-preferring units have facilitatory (EE) binaural interactions: the response to stimulation of both ears together is greater than stimulation of either ear alone. This holds for the sharp stimulus onsets as well as the AM ramps: responses to increases in sound level in both ears together is greater than response to increases in either ear alone. The degree of binaural facilitation seen in depth-sensitive units ranged all the way from units with very strong facilitatory interaction to units which responded to sound in each ear alone but showed no binaural facilitation at all (termed occlusive cells by Imig and Adrian, 1977). The strength of binaural interaction was related to the breadth of directional tuning for simulated motion in depth: units with very strong facilitatory binaural interactions responded exclusively to motion toward the receiver; units with medium or weak binaural interactions showed broader tuning, responding to sideways motion in addition to motion toward the receiver. Figure 10 plots the breadth of tuning against the degree of facilitatory binaural interaction for all depth-preferring units. Breadth of tuning for motion in depth is calculated by dividing the strongest response to depth by the strongest response

Figure 10. Plot of the breadth of tuning for motion in depth versus the strength of binaural interaction, for the population of depth-preferring units. Breadth of tuning of measured by taking the ratio of the strongest responses to simulated motion in depth and in azimuth. Binaural interaction is measured by dividing the binaural response by the sum of both monaural responses. For toward units, this ratio is calculated using the onset responses; for away units, response offset are used instead.

in azimuth. The strength of binaural interaction is calculated by dividing the binaural response by the sum of both monaural responses. For toward units, this ratio is calculated using the transient onset response; for away units, the response to sound offset is used. Although the scatter between these two measures is rather broad ($r=0.21$), there is a general trend for units with weaker binaural interactions to show broader tuning for movement in depth.

B. Motion in azimuth

Units which responded exclusively to simulated sound source motion in azimuth comprised 10% of our sample (6/61). Units selective for azimuthal motion appeared relatively more rare than units preferring motion toward the animal (see figure 4) and tended to be characterized by inhibitory binaural interactions (EI or IE cells) and strong excitatory responses via only one of the two ears. Azimuthal selective neurons gave transient responses to sound onset in the dominant ear, sometimes accompanied by transient responses to sound offset in the non-dominant ear. All units preferred motion directed toward the dominant ear. Figure 11 shows post-stimulus time histograms for a unit preferring ipsilateral-directed auditory motion. This unit gives strong transient responses to stimulus onset in the ipsilateral ear (lower left panel) and does not respond at all stimulus to onset in the contralateral ear (top left panel). Binaural sound onset produces a diminished response (bottom right panel), indicating inhibition (IE binaural interaction type). In addition, this neuron responds to stimulus *offset* in the *contralateral* ear (bottom left panel). The strongest response during the AM ramps is elicited by an increase in sound level at the ipsilateral (dominant) ear and a simultaneous decrease in sound level at the contralateral (non-dominant) ear (bottom left panel).

Figure 12 shows polar plots illustrating the responses of four neurons

Figure 11. Conventions are the same as in figure 5. Post-stimulus time histograms showing the responses of an ipsilateral-prefering neuron, for the four directions of auditory motion. This unit is an ipsilateral-prefering unit because the responses during opposite-directed AM ramps increasing in the ipsilateral ear and decreasing in the contralateral ear are the strongest (top left panel).

Figure 12. Conventions are the same as in figure 6. Polar plots of spike counts during AM ramps simulating four directions of auditory motion, for four units preferring azimuthal motion. **A-B:** Units preferring ipsilateral-directed motion. **C-D:** Units preferring contralateral-directed motion.

A

AU22.026
10 kHz

B

AU22.028
10 kHz

C

AU22.075
2 kHz

D

SE13.003
16 kHz

which responded most vigorously to contralateral-directed simulated sound source motion (panels A and B) and ipsilateral-directed simulated sound source motion (panels C and D). The degree of directional selectivity among azimuth-preferring units showed some variability. In some cases, responses to the opposite direction of motion could be either non-existent or less than spontaneous activity. In other cases, responses to the opposite direction of motion could be fairly vigorous.

For all units responding well to sideways motion (including monaural-like units; see section C), there was a strong relationship between the transient onset response in the dominant ear and the preferred direction of simulated sound source motion in azimuth: units with strong onset responses in the contralateral ear preferred increases in sound intensity in the contralateral ear and simultaneous decreases in the ipsilateral ear, and vice versa for ipsilateral-preferring units. Figure 13 plots the preferred direction of simulated auditory motion in azimuth against the response to sound onset in the ipsilateral and contralateral ear (a measure of ear dominance) for all units displaying selectivity for one direction of motion in azimuth. Preferred direction of motion in azimuth is measured by dividing the difference between the ipsilateral- and contralateral-directed responses during the AM ramps by the sum of these responses:

$$\text{motion in azimuth index} = (\text{contra AM} - \text{ipsi AM}) / (\text{contra AM} + \text{ipsi AM})$$

Units with positive abscissa values have stronger contralateral-directed responses than ipsilateral-directed responses, and conversely for units with negative values. The ordinate values refer to ear dominance, which is measured by dividing the difference between both transient monaural responses to sound onset by the sum of these responses:

$$\text{ear dominance} = \text{binaural on} / (\text{contra on} + \text{ipsi on})$$

Units with positive ordinate values give stronger responses to contralateral onset

Motion in azimuth versus ear dominance

Figure 13. Plot of preferred direction of simulated azimuthal auditory motion versus ear dominance (measured using both responses to monaural sound onset), for all units displaying selectivity for one direction of motion in azimuth, including monaural-like units. Units with positive abscissa values prefer contralateral-directed motion, and units with negative abscissa values prefer ipsilateral-directed motion. Similarly, units with positive ordinate values give stronger transient responses to contralateral sound onset, and units with negative ordinate values give stronger transient responses to ipsilateral sound onset. There is a strong linear relationship between the two measures ($r=0.81$).

and units with negative ordinate values give stronger responses to ipsilateral onset. The relationship between preferred direction of azimuthal motion and ear dominance is strongly linear, with a correlation coefficient of 0.81.

C. Monaural-like units

It is important to understand the response of a neuron with no binaural interaction under the stimulus conditions used in this experiment. If a neuron prefers stimulus onset in the contralateral ear (and therefore responds to increasing stimulus amplitude via that ear) and has no input at all from the ipsilateral ear, then that neuron will respond well in two of the four conditions employed. These include the conditions in which stimuli increase in amplitude in both ears (because of the increase in amplitude in the contralateral ear) and the azimuthal motion condition in which the stimulus increases in amplitude in the contralateral ear and decreases in the ipsilateral ear.

Monaural-like units were the most numerous, comprising nearly 41% of our sample (25/61). These units exhibited strong directional preferences along both axes (depth and azimuth), and responded equally well to increases in sound source intensity in one ear alone or in both ears together; the response to simulated sound source motion toward the receiver and the preferred ear were often indistinguishable. Figure 14 shows post-stimulus time histograms depicting the timing of a monaural-like unit's discharge in relation to the time course of the stimulus. The transient response to sound onset in the contralateral ear (top left panel) and in both ears together (bottom right panel) is essentially the same, hence there is no binaural interaction (EO binaural interaction type). Increasing AM ramps in the contralateral ear produces strong responses regardless of the input of the ipsilateral ear: the response to an increase in stimulus amplitude in the contralateral ear is the same whether it is

Figure 14. Conventions are the same as in figure 5. Post-stimulus time histograms showing the responses of a contralateral-ear-dominated, monaural-like neuron, for the four directions of auditory motion. This unit is defined as a monaural-like unit because the response during increasing AM ramps in the contralateral ear is not influenced by the input from the ipsilateral ear (top right and bottom left panels).

accompanied by a corresponding increase or decrease in stimulus amplitude in the ipsilateral ear. The responses during the AM ramps in the bottom left and top right panels of figure 14 are essentially the same. Figure 15A is a polar plot representation of a contralateral-dominated monaural-like unit (the same unit as in figure 14). This unit responds equally well to increases in sound level in the contralateral ear alone and in both ears together; the responses to the two preferred directions of motion are similar in magnitude. Two arrows of equal length for azimuthal and radial motion are the signature of a monaural-like unit. A ipsilateral-dominated monaural-like unit is shown in figure 15B; the response to ipsilateral-directed azimuthal motion is virtually the same as that directed directly toward the receiver.

All monaural-like units preferred increases in intensity rather than decreases; no monaural-like away units (units preferring decreases in intensity) were encountered. Nine units preferred simulated sound source motion directed toward the receiver and the ipsilateral ear, and 16 units preferred simulated sound source motion directed toward the receiver and the contralateral ear (refer to figure 4).

It should be stressed that monaural-like units are not necessarily entirely monaural; at certain intensity levels these units respond *as though* they receive input from one ear only, and therefore respond well to sound level increases in the dominant ear regardless of what happens at the other ear. About half of the monaural-like units (12/25) were truly monaural, with no response evoked by the non-dominant ear and no binaural interaction (EO binaural interaction type) at any of the intensity levels tested in our study; the remaining 13 units had unequal thresholds and intensity functions for the two ears, producing monaural-like responses at certain intensity levels. All units showed strong ear dominance and preferred increases in sound level in the dominant ear. Few of these units had

Figure 15. Conventions are the same as in figure 6. Polar plots of spike counts during AM ramps simulating four directions of auditory motion. **A:** Polar plot for the unit shown in figure 13. **B:** Ipsilateral-ear-dominated monaural-like unit. In both cases, the responses to simulated sound source motion toward the receiver and in the preferred azimuthal direction are approximately equivalent.

strong binaural interactions; when present, input from the non-dominant ear was slightly facilitatory. The parameters influencing the strong preference of monaural-like units for correlates of azimuthal motion were examined in section B.

D. Distribution of unit types

A total of 21 penetrations, roughly normal to the cortical surface, were made. Neurons found along most electrode penetrations normal to the surface of the cortex showed similar directional preferences, which indicates that units with constant responses to simulated sound source motion may occur in clusters or columns within the cortex. Four schematic reconstructed penetrations are shown on figure 16. Each polar plot illustrates the directional preference of a different unit. Neurons encountered along penetrations A and B responded best to simulated sound source motion toward the receiver; some units also responded to sideways motion as well, to varying degrees. Neurons encountered along penetration C responded best to simulated ipsilateral-directed sound source motion. Neurons encountered along penetration D preferred simulated motion toward the receiver and ipsilateral-directed (monaural-like). Although no histological information is available to confirm that penetrations were orthogonal to the cortical surface, this clustering of units with similar directional preferences is an indication of possible columnar organization in the primary auditory cortex with respect to preferred direction of sound source motion.

Velocity selectivity

Most AM-sensitive neurons also showed selectivity for the speed and amplitude of AM ramp excursion. These are intensity correlates of sound source velocity. The majority of units (41/61, or 67% of all motion-sensitive units

Figure 16. A-D: Schematic reconstruction of 4 electrode penetrations made roughly normal to the cortical surface in area AI, showing units encountered and their directional preferences. Each polar plot corresponds to one unit; directional conventions are the same as in previous figures.

Figure 17. A: Polar plots representations of the responses during the AM ramps at the four values of ramp excursion. The four plots refer to the responses of one unit at four different ramp excursions. Ramp excursion increases from left to right; the corresponding ramp excursion in dB per 250 msec is printed below each plot. **B:** Monaural and binaural rate/intensity functions of the same neuron for the transient onset response. This unit is defined as a monotonic, velocity-dependent unit: increases in ramp excursion produce stronger responses in the preferred direction of motion. The rate/intensity function is also monotonic and parallels the response to the AM ramp in the preferred direction.

A **B**

SE06.024
15 kHz

sampled) responded best to the highest ramp excursion used and were termed monotonic, velocity-dependent units. Figure 17 shows polar plots (A) of the responses during AM ramps at the four values of ramp excursion (printed below each plot) for a monotonic, toward-preferring unit, and the rate/intensity function (B) of the same unit for the monaural and binaural responses evoked by sharp stimulus onsets at four different intensity levels. The responses to AM ramps increase with greater ramp excursions, and louder binaural stimulus onset also evokes a stronger response. The two measures are monotonic and parallel each other. Such units are called monotonic, velocity-dependent units. A small number of units (10/61 or 16%) preferred one particular ramp excursion, and smaller or greater ramp excursions evoked weaker responses. These units were termed non-monotonic, velocity-dependent units. Figure 18 shows polar plots of the responses during AM ramps (A), and the rate/intensity function (B) for monaural and binaural onset response for a non-monotonic, monaural-like unit. The intensity functions and the response to the AM ramp are both non-monotonic (for the range of intensity tested). The remaining ten units (16%) gave responses which were either independent of ramp excursion or idiosyncratic, sometimes with changes in preferred direction. Figure 19A shows the polar plots for a neuron which prefers away at the smallest ramp excursion but whose directional selectivity changes as ramp excursion increases. The accompanying graph (figure 19B) show the rate/intensity functions for the binaural onset and offset responses. The binaural offset response is strongest at low intensity levels and progressively diminishes at higher intensities; the onset response is weak at low intensities and gradually becomes stronger as stimulus amplitude increases. Therefore this unit prefers decreasing AM ramps (away) at lower ramp excursions and increasing AM ramps (toward) at higher ramp excursions. Figure 20 shows polar plots (A) and rate/intensity functions (B) for a

Figure 18. Conventions are the same as in figure 17. **A:** Polar plots representations of the responses during the AM ramps at the four values of ramp excursion. **B:** Monaural and binaural rate/intensity functions of the same neuron for the transient onset response. This unit is defined as a non-monotonic, velocity-dependent unit: a particular ramp excursion produces the strongest response; increases or decreases in ramp excursion diminish responding. The rate/intensity function is also non-monotonic but does not parallel the response to the AM ramp in the preferred direction.

Figure 19. Conventions are the same as in figure 17. **A:** Polar plots representations of the responses during the AM ramps at the four values of ramp excursion. **B:** Binaural rate/intensity functions of the same neuron for the transient onset and offset responses. This unit is defined as an idiosyncratic, velocity dependent unit: at lower ramp excursion, this unit prefers away; as ramp excursion increases, this unit gradually changes directional preference and prefers toward. This change in preferred direction with increasing ramp excursion can be explained by the rate/intensity functions for the onset and offset transients: the offset transient does not vary with changes in intensity, while the onset transient is weak at low intensities and becomes progressively stronger at higher intensities.

A

AU22.001
3 kHz

B

Figure 20. Conventions are the same as in figure 17. **A:** Polar plots representations of the responses during the AM ramps at the four values of ramp excursion. **B:** Monaural and binaural rate/intensity functions of the same neuron for the transient onset response. This unit is defined as a velocity-independent unit: changes in ramp rate and excursion have little or no influence on the strength of responding or on the directional preference of this unit.

A

B

AU22.052
5 kHz

velocity-independent neuron. This neuron showed little selectivity for AM correlates of stimulus velocity, over the range of ramp excursion employed; the four ramp excursions evoked similar responses.

For about half of all direction-selective units, the preferred value of ramp excursion could be predicted from a unit's rate/intensity function for sharp sound onset. This is particularly true of most toward-preferring neurons in which the responses to sharp and gradual (AM) binaural sound onset across intensity levels usually monotonic. The remaining units had intensity functions for the ramp and sharp onset which differed and the preferred ramp excursion could not be directly predicted from the rate/intensity function for sound onset. This was especially true of non-monotonic, velocity-independent, and idiosyncratic units.

Effect of changing frequency

Several units were examined at a variety of frequencies. A total of 33 cells were tested at best frequency plus one or more additional frequencies. All four magnitudes of ramp excursion were used at each frequency tested. Although this parameter was not systematically investigated for all neurons encountered, directional preference seemed to a first approximation independent of the frequency used for testing. Only four of these 33 cells appeared to clearly change directional preference over this admittedly limited range of frequencies. However, some of these cells changes binaural interaction class at different frequencies, and as might be expected, rate/intensity functions were could be different at different frequencies. In addition, for the entire population of direction-selective units, there was no overall effect of frequency on directional preference, i.e., units with high or low characteristic frequencies were not confined to a particular class of directional preference.

DISCUSSION

The results of these experiments indicate that single neurons in the primary auditory cortex of the cat can be highly sensitive to at least one correlate of auditory stimulus motion, namely relative modulation of sound intensity at the two ears of the receiver. These neurons are quite common, constituting three-fourths of our sample. They respond selectively to certain directions of simulated sound source motion and can be classified according to their preferred direction of motion. Depth-selective units respond best to correlated increases or decreases in sound source intensity at the two ears; azimuth-selective units prefer opposite-directed changes in sound source intensity at the two ears. Monaural-like units respond equally well to changes in sound intensity in one ear alone or in both ears. Direction-selective neurons are spatially segregated from each other and may occur in clusters within the cortex. These units also respond selectively to AM ramps of different speeds and excursions, a correlate of sound source velocity and range of movement.

Mechanisms of direction and velocity selectivity

The responses of AI neurons to simulated sound source motion can be explained in terms of response characteristics which are normally studied separately, but which interact to produce selectivity to the correlates of direction and velocity of sound source motion in space.

A. Motion in depth

Neurons with facilitatory binaural interactions (E/E cells) respond best to the diotic intensity changes corresponding to motion directly toward the head. Neurons preferring motion directly toward the receiver gave strong responses to

binaural sound onset and to diotic increasing AM ramps. The degree of directional selectivity is correlated with the amount of binaural facilitation, with strongly facilitatory cells being the most selective. E/E neurons with off responses respond to motion away from the head; binaural facilitation of offset components may also be present and increases selectivity in the preferred direction.

The high percentage of neurons (39%) responding best to simulated motion in depth may be a reflection of the fact that the majority of cortical neurons give their greatest response when IID is very small or equal to zero (Phillips & Irvine, 1981b). Thus sound sources located near the midline would receive the largest representation in the cortex. The more transitory nature of the response (compared with the azimuth units) may be a reflection of the fact that IIDs do not unambiguously code for movement in space but also signal intensity changes in a stationary sound source.

B. Motion in azimuth

Neurons with inhibitory binaural interactions (E/I and I/E cells) respond best to the dichotic intensity changes corresponding to azimuthal auditory motion. Ear dominance determines the preferred direction of azimuthal motion. E/I units which give transient responses to sound onset in the contralateral ear respond best to intensity correlates of motion in azimuth directed toward the contralateral ear. Sound source motion directed toward the ipsilateral ear evokes selective responses from I/E units which give transient responses to sound onset in the ipsilateral ear. While these response properties are sufficient to confer selectivity to these neurons, some units also give responses to sound offset in the non-dominant ear; this feature enhances selectivity for the detection of azimuthal motion.

C. Monaural-like units

Many cells with little or no binaural interaction, either facilitatory or inhibitory, responded equally well to sound becoming louder in both ears and to sound becoming louder in the dominant ear. The contralateral ear dominated in 64% of these units and the ipsilateral ear in 36%. Monaural-like units comprised the largest group of neurons in this study (41% of direction-selective units). Most behaved as if they were only influenced by one ear; a few responded weakly to sound in the non-dominant ear, but the binaural response was equal to the response evoked by the dominant ear alone. These units appeared monaural but it is likely that some of them would have shown binaural interactions with varied IID levels. In this study, all stimulus presentation was performed at a reference IID level of 0 dB, with both ears receiving equally loud stimulation. However, since many E/I and I/E cells show binaural interactions only when the input to the non-dominant ear is louder than that to dominant ear, presenting stimuli with different sound levels in the two ears may reveal stronger, more specific binaural interactions in this neuronal population.

D. Velocity selectivity

Most units exhibited monotonic rate/intensity functions over the range of AM ramp excursions used in this study. This reflects the monotonic rate/intensity functions for the onset portion of the stimulus; monotonic cells prefer faster velocities of auditory motion where the higher ramp excursions begin to resemble sharp onsets. About one-third of the units were selective for one of the smaller AM ramps; these cells would be suitable for encoding specific velocities of moving sound. By and large, the responses to sharp sound onsets (5 msec rise time) and ramps simulating auditory motion (250 msec rise time) were similar across intensity levels. Monotonic units responded well to the

highest ramp excursions and non-monotonic units preferred lower ramp excursions. However, the preferred velocity could not always be predicted from the rate/intensity function for the onset responses; additional temporal response characteristics may account for this discrepancy.

E. A model for direction and velocity selectivity

The results of this experiment show that the selectivity for sound source motion reported in this study can be related to particular combinations of monaural and binaural response properties that have been studied extensively (in isolation) by other workers. These response properties of neurons in the primary auditory cortex can be shown to act synergistically, providing an underlying mechanism for selectivity to the binaural intensity correlates of auditory motion. Figure 21 illustrates how the response characteristics of cortical neurons interact to produce response selectivity for the direction and velocity of moving sound sources. The main determinants of direction selectivity are binaural interaction class, on/off responses and ear dominance; monotonicity of rate/intensity function for sound onset (and offset, to a lesser extent) determines velocity selectivity. Several generalizations from this hypothetical mechanism arise from these data: 1- Neurons with facilitatory binaural interactions prefer motion in depth: neurons with on responses prefer motion toward the receiver, and neurons with off responses prefer motion away from the receiver. 2- Neurons with inhibitory binaural interactions respond best to motion in azimuth, directed into the hemifield corresponding to the dominant ear: neurons with contralateral on responses and/or ipsilateral off responses prefer motion into the contralateral hemifield (and vice versa for ipsilateral-on and/or contralateral-off neurons). 3- Neurons with no binaural interaction (monaural) prefer motion directed toward the receiver and into the hemifield corresponding

Figure 21. A model of direction and velocity selectivity for auditory movement, based on interactions of response characteristics of neurons in the primary auditory cortex. The major determinants of the direction selectivity of AI neurons are interactions between binaural interaction type, ear dominance and transient onset and offset responses. Directional preferences resulting from these interactions are indicated by arrows; the vertical axis represents depth, and the horizontal axis represents azimuth. Arrows pointing down and up represent auditory motion directed toward and away from the receiver (along the midline), respectively; arrows pointing to the right and left represent auditory motion directed into the contralateral and ipsilateral hemifield, respectively (assuming recordings are made from the left side). The monotonicity of the rate/intensity function determines preference for velocity of auditory motion. Asterisks refer to classes of direction- and velocity- selective neurons encountered, whose responses to simulated auditory motion could be predicted from response characteristics listed above.

to the dominant ear; neurons with off responses prefer the opposite directions of motion (away from the receiver and into the hemifield corresponding to the non-dominant ear). 4- Neurons with monotonic rate/intensity functions prefer higher velocities; neurons with non-monotonic rate/intensity functions respond best at lower velocities. The asterisks in figure 21 refer to classes of direction- and velocity-selective neurons that were encountered in this study, and whose responses to intensity correlates of auditory motion could be predicted from the previously listed responses characteristics and/or combinations of these responses characteristics.

Technical considerations

It is important to recognize the limitations of the conditions used in this experiment to simulate of sound source movement. In the free-field case, changes in interaural time differences and in spectral content would accompany the alterations in stimulus intensity that were used in this study. In addition, the patterns of interaural intensity changes used in this experiment are not entirely unique with regard to particular directions of motion. A full account of the relationship between alterations in relative aural amplitude and the direction of motion of a sound source of constant strength in three-dimensional space has been provided by Zakarauskas and Cynader (1990). They have carried out a mathematical analysis of the set of amplitude modulations associated with motion of a constant intensity sound source moving in three dimensions. This analysis has revealed that certain changes in sound level at the two ears are not necessarily associated with *one* specific sound source trajectory but may also result from a variety of other stimulus conditions. It is possible, for instance, that correlated increases in sound level are associated with stimuli moving tangentially to the receiver as well as directly toward her, resulting in possible

perceptual ambiguities. In addition, the stimuli used in this experiment do not represent the full set of binaural intensity modulations produced by sound sources moving in azimuth or in depth. The analysis cited above demonstrated that unlike the AM ramps used in this study to simulate auditory motion, the rates of intensity change associated with sound source movement are not necessarily linear, nor do intensity changes occur at the same rate at the two ears (in the case of auditory motion in azimuth). In spite of this, stimuli with constant rates of change and with similar binaural time courses were used because they produce an appropriate simulation of sound source movement that can be easily implemented in a sealed sound delivery system. One must be well aware of the unavoidable limitations and ambiguities inherent in efforts to simulate motion of real world sound sources without actually providing that motion. This study deals only with binaural sound intensity modulation; it is by no means the only cue available to a neural system detecting moving sound sources.

A striking result that can be derived from the acoustic analysis described above (Zakarauskas & Cynader, 1990) is that the rate of change of monaural intensity function is found to be directly proportional to the velocity scaled by the distance of a sound source for omnidirectional sources of constant intensities. This emphasizes the importance of a system that uses amplitude modulation as a component of a specialized motion detection system. This contention is supported by the neurophysiological evidence presented in this study indicating that in addition to responding selectively to the correlates of direction of motion, auditory neurons also show selectivity to correlates of sound source velocity. In this neuronal population, some neurons seemed to be sensitive to different rates of intensity change in the two ears. Some neurons preferred low rates of change, while others preferred higher rates of change, corresponding to faster motion.

There was a distinct preponderance of neurons that responded best to the highest rates of AM that were employed. This is in agreement with psychophysical evidence that shows that low rates of change of amplitude are poorly resolved by human receivers (Small, 1977).

Analogies to vision

This study has provided evidence for specialized systems dealing with correlates of auditory motion in three-dimensional space. It is interesting to note that similar mechanisms appear to exist in vision and that like the auditory system, both systems appear to operate by dynamically comparing parameters of the stimuli in the paired end organs. Abundant psychophysical evidence indicates that the human visual system contains specialized channels for dealing with three-dimensional motion and that these channels are distinct from those that process static depth (Beverley & Regan, 1973, 1975; Regan, Beverley & Cynader, 1979; Richards & Regan, 1973). In addition, neurophysiological studies have shown that single cells in cat visual cortex can be highly sensitive to the direction of stimulus motion in three dimensional space (Cynader & Regan 1978, 1982). In the visual system, the relative velocity of the two retinal images has been shown to be a sensitive cue to the direction of stimulus motion in three dimensional space (Beverley & Regan, 1973, 1975; Regan, Beverley & Cynader, 1979) and visual cortex neurons (Cynader & Regan, 1978) show differential sensitivity depending on relative stimulus velocity. This provides a striking parallel with the mechanisms that we have uncovered here in which single cells in the *auditory cortex* appear sensitive to the relative rate of change of *intensity* in the two ears. It appears that both sensory systems use similar principles to extract three dimensional motion. The neurophysiological parallels between the two systems are supported by psychophysical evidence indicating that the

resolving capacities of the visual and auditory systems for stimulus motion are strikingly similar (Perrott, Buck, Waugh & Strybel, 1979; Waugh, Strybel & Perrott, 1979). Perception of stimulus motion in the visual and auditory modalities appear to depend on similar central mechanisms of motion detection.

Specialized motion-detecting mechanisms in the auditory system?

Considerable, highly specific information is available to the auditory system concerning the trajectory of a moving sound source. Obviously, there is a survival advantage for an organism in detecting movement in its environment as quickly and efficiently as possible. Aside from their obvious utility for avoiding collisions and compensating for self-generated movements, motion detection mechanisms may be important for extracting information about the form of a sound source. In principle, one can imagine two different methods to infer sound source motion from the signals at the two ears. One method would be to simply use the same system which is used to localize stationary sound sources, to register the position of the sources at different times, and then compare them to extract direction and velocity of motion. In this case, specialized systems for detecting motion are not needed or employed, but such a system requires extensive sequential processing of changing binaural patterns to extract motion information. The other method would be to use a specialized motion channel, working in parallel with mechanisms extracting information about stimulus position. One advantage of calculating sound source velocity from position is economy of specialized hardware, because the same neural mechanisms are involved in extracting information about stimulus position and motion. On the other hand, there is a distinct survival disadvantage for an organism to have to explicitly calculate sound source position before knowing whether or not a sound source is moving, since this method is likely to be slower than a parallel,

dedicated auditory motion channel.

Several investigators have gathered psychophysical data suggesting that the human auditory system infers motion without the use of specialized motion-detecting mechanisms. According to this view, the binaural auditory system is relatively insensitive to motion, and position and distance are more salient cues than motion and velocity (Grantham, 1986). Psychophysical studies have compared the ability of the auditory system to resolve position and motion of sound sources, by measuring the smallest angular separation between two sound sources that a listener can detect (minimum audible angle or MAA) and the minimum arc swept by a moving source which can be detected as moving (minimum audible movement angle or MAMA). The argument against the necessity of specialized motion detecting mechanisms is based on the observation that performance of human subjects in detecting sound source motion varies in the same way as in static sound localization when stimulus frequency, duration or velocity are varied: the MAA and MAMA are affected by these stimulus parameters in similar, predictable ways (Altman & Viskov, 1977; Grantham, 1984, 1986; Perrott & Musicant, 1977; Perrott & Tucker, 1988). Therefore the MAMA is only a blurred estimate of the MAA, a measurement error on the part of the receiver caused by movement of the sound source. In addition, because a serial system of position comparison has a limited capacity to process changing inputs, a minimum integration time is necessary to resolve sound source motion, resulting in larger MAMAs with increasing stimulus velocity because the system is approaching its upper processing limit. According to a serial method of extracting motion information, one can generalize directly to the dynamic sound field from known parameters defining static auditory localization. Therefore both static and dynamic sound localization depend on the same underlying mechanism, and there is no need to postulate specialized

motion detectors in the auditory system.

On the other hand, psychophysical and neurophysiological evidence point to the existence of specialized motion-selective mechanisms in the auditory system, i.e., that the detection of auditory motion involves more than the coding of successive localization judgements. Harris and Sergeant (1971) found that the monaural MAMA was almost as good as the binaural MAMA for slowly moving sound sources. In the monaural mode, the auditory system can only use frequency and intensity information to detect motion; the binaural cues normally used by the auditory system to infer sound source position are unavailable, and horizontal sound localization acuity is poorer (Butler, 1969). Nevertheless, subjects were able to detect auditory motion in the monaural mode, indicating that specialized motion detecting mechanisms can use monaural information to detect motion. This is an indication that the auditory system uses time history, and possibly the time derivative of sound intensity, to detect motion (Zakarauskas & Cynader, 1990). In addition, range (or distance) cannot be calculated directly from binaural disparities, and motion of a source moving directly toward or away from the receiver cannot be inferred by a position comparison system. Hence, mechanisms specialized for detecting motion would be the only ones available to an organism in this case.

Perrott and Marlborough (1989) found that sound localization performance of moving broadband free-field stimuli is superior to that which would be predicted if the subject were simply comparing the location of the sound source at signal onset and offset. MAMAs obtained when the sound source was actually moving were significantly lower than when only the end-points of the arc of travel were marked. Therefore MAMA discrimination is not solely based on successive comparisons of sound source location at onset and offset. Although this finding does not necessarily confirm the existence of specialized motion

detecting mechanisms, it indicates that such mechanisms cannot be reduced to simple position comparators. Perrott and Musicant (1981) measured the MAA under dynamic conditions by asking subjects to estimate the position of a moving sound source at onset. The dynamic MAA was almost independent of sound source velocity, and almost as good as for stationary sources, indicating that localization precision is not affected by motion of the source, and pointing to a possible distinction between the coding of auditory spatial position and motion. Waugh et al. (1979) measured the capacity of listeners to subjectively estimate suprathreshold auditory velocity in the dark, and found that the ability to discriminate sound source velocity is a well defined feature of the dynamic binaural system. In addition, auditory and visual velocity judgement capabilities were nearly identical. This degree of similarity in the perception of velocity by the visual and auditory systems is quite surprising, given the fact that the spatial resolving power of the visual system is much higher than that of the auditory system. These findings suggest that velocity judgements are drawn from similar specialized central motion-detecting mechanisms (Perrott et al., 1979; Waugh et al., 1979).

Neurophysiological studies have provided some support for the notion that auditory neurons respond selectively to sound source motion or correlates of such sounds. Neurons which appear to detect motion of sound sources and which could be part of specialized motion-detecting mechanisms in the auditory system have been found in the inferior colliculus (Altman, 1968), the medial geniculate body (Altman, Syka, & Shmigidina, 1970), the superior colliculus (Altman, 1971), the cerebellum (Altman, Bechterev, Radionova, Shmigidina, & Syka, 1976; Bechterev, Syka & Altman, 1975) and the auditory cortex (Altman, 1987; Sovijarvi & Hyvarinen, 1974). The data presented in this thesis also points to the existence of motion-detecting mechanisms in the primary auditory cortex.

Future research should investigate the parameters governing the activity of specialized motion-detecting channels in the auditory system, and the role of these channels in the processing of motion information in the free sound field. The interrelations between location-, motion- and velocity-sensitive auditory units are also of interest. Presumably, information about sound source motion is integrated with other types of spatial information from the auditory, visual and somatosensory systems, and combined with vestibular, proprioceptive and motor information to produce an integrated and cohesive perception of reality, and if David Marr was around he'd probably take up audition as a hobby and solve all our problems.

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