

Auditory cortex neurons sensitive to correlates of auditory motion: underlying mechanisms

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Summary. Neuronal response properties such as phasic vs. tonic, onset vs. offset, monotonicity vs. non-monotonicity, and E/E vs. E/I, can be shown to act synergistically suggesting underlying mechanisms for selectivity to binaural intensity correlates of auditory sound source motion. Both identical (diotic), and oppositely directed dichotic AM ramps were used as stimuli in the lightly anesthetized cat, simulating motion in four canonical directions in 3-dimensional space. Motion in either azimuthal direction evokes selective activity in cells which respond best to the onset of monaural sound in one ear and show a decreased response to binaural stimulation (E/I or I/E). In some cells specificity is increased by “off” components in the non-dominant ear. Although these cells fire only at the onset of stationary sound, they fire throughout oppositely directed AM ramps. Motion toward or away from the head evokes responses from EE cells; strong binaural facilitation increases selectivity for motion in depth. The sharpness of direction of tuning was related to the degree of binaural facilitation in E/E cells. Selectivity for sound moving away from the head is correlated with “off” responses, while “on” responses correlate with preference for motion toward the head. Most units showed a monotonic rate function as AM ramp excursion and rate was increased. One third were selective for slower rates of intensity change and may therefore encode slower rates of stimulus motion, as well as direction of movement. The findings suggest that neural processing of auditory motion involves neural mechanisms distinct from those involved in processing stationary sound location and that these mechanisms arise from interactions between the more traditionally studied response properties of auditory cortex neurons.

Key words: Auditory cortex – Motion – Depth – Binaural interaction – Cat

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Introduction

Evidence has accumulated in recent years that the visual system not only processes three-dimensional motion information, but that this analysis occurs separately from the processing of both monocular and binocular cues to static depth location (Richards and Regan 1973; Beverley and Regan 1973; Cynader and Regan 1978; Regan et al. 1979). In the visual system, motion selectivity appears to occur separately and in parallel with orientation selectivity, contrast sensitivity, and temporal frequency selectivity (Cynader and Chernenko 1976; Pasternak et al. 1985). Directionally sensitive neurons in the visual cortex have been shown to provide the physiological substrate for the behavioral discrimination of motion detection (Pasternak and Leinen 1986).

Although stimulus processing in the auditory system has been shown to have many parallels with processing in the visual system, elucidation of auditory system mechanisms has tended to lag behind that of the visual system. While progress has been made in mechanisms underlying static sound localization, the mechanisms underlying the analysis of sound source direction and speed of motion have been largely neglected. Using sounds presented through headphones it has been shown that neurons in the auditory cortex may be selectively responsive to the interaural time (ITD) (Kitzes et al. 1980), intensity (IID) (Phillips and Irvine 1981), and spectral differences (Mendelson and Cynader 1983) which would correlate with varying spatial locations. Using free-field stimuli, a neural map of physical space has been demonstrated in the superior colliculus of the cat (Middlebrooks and Knudsen 1984), but no such comparable map has been found in the primary auditory cortex of mammals. Cells in the inferior colliculus and primary cortex do however, show selectivity for the location of sound sources. (Middlebrooks and Pettigrew 1981; Moore et al. 1984; Wenstrup et al. 1986; Semple et al. 1983; Fuzesary and Pollack 1985). Middlebrooks and Pettigrew

report two classes of location sensitive neurons, hemifield and axial units, and suggest they are both inhibited by ipsilateral and excited by contralateral sound (EI units). Hemifield units have large contralateral receptive fields while axial units have smaller, more specific contralateral receptive fields. They also suggest that cortical units excited by both ears (EE units) respond to sound anywhere in front of the cat. As specific frequency bands in AI have been shown to be essential for the behavioral localization of sound (Jenkins and Merzenich 1984), it is possible that interaural difference parameters are organized within frequency bands in the primary cortex. In the inferior colliculus of the mustache bat, at least, IIDs are represented in an orderly fashion along frequency bands (Wenstrup et al. 1986).

How these neural response properties interact to produce selectivity to location in space is not yet well understood. Even less well understood are the mechanisms in cortical neurons producing directional selectivity to moving sounds. Until now reports of neural sensitivity to free field auditory motion have been largely anecdotal (Sovijarvi and Hyvarinen 1974; Evans 1968; Eisenman 1974). Sovijarvi and Hyvarinen (1974) reported four cells which responded to moving sound, but not stationary sound. Yin and Kuwada (1983) simulated the interaural phase differences of a moving sound using binaural beat stimuli by presenting tones of slightly different frequency to the two ears. Some of the motion selective units they found in the inferior colliculus would respond to sound moving in one direction, but not in the reverse direction. The results of these studies seem to imply that sensitivity to motion is not identical with sensitivity to location in space, but requires a separate, or at least additional mechanism.

Motion sensitivity at a neural level would appear to have several advantages for an organism. The obvious function is the detection of moving targets. A second role might be to compensate for the subject's own movements. A third, largely overlooked, function may be to provide the auditory system, which is most sensitive to transients, with continually changing frequency and intensity parameters as the head and pinnae are moved in space. Relative motion between the sound source and the ear could serve to sharpen spectral contrasts by providing constantly changing onsets across the frequency/intensity receptive fields of neurons. It is well known that neurons in the primary auditory cortex respond best to transients rather than constant invariant sound. It has previously been suggested that head and pinna movements may act in this way to produce a phenomenon analogous to Mach bands, but in the time, rather than spatial domain (Haftner et al. 1988).

The previous paper (Stumpf et al. 1991) demonstrates the existence of neurons in AI sensitive to the intensity correlates of the direction and velocity of moving sound sources. Dichotic (sounds which are different at the two ears) intensity changes simulated motion in azimuth and diotic (sounds which are identical at the two ears) changes simulated motion in depth toward or away from the cat. The stimuli, high frequency (2–40 kHz) pure tone AM ramps preceded and followed by stationary pla-

teaus, although presented via headphones, were designed to maximize the salience of interaural intensity differences. To a human listener these stimuli present impressions of movement of a source along the azimuth, or toward or away from the head. In a free field situation ITDs may be used to localize high frequency sounds, but the onset of the sound envelope is the most relevant cue. By embedding our ramp within a stationary plateau, we have reduced the usefulness of envelope as a potential cue. Pure tones were chosen because comparable stimuli in a free field situation would not involve shifts in spectral content which would occur with a broadband stimulus.

The present paper shows how the traditional response properties of auditory cortical neurons, such as monotonicity vs. non-monotonicity, phasic vs. tonic, on vs. off, and EE vs EI, can be shown to interact synergistically, combining to produce underlying mechanisms for selectivity to auditory motion. These results are relevant to understanding the functional principles of neural organization within the primary auditory cortex, as well as the neural mechanisms underlying sound localization behavior.

Methods

Single unit recording was carried out in the primary auditory cortex of cats using experimental techniques described in greater detail in the previous paper (Stumpf et al. 1991). Pinna resection and craniotomy were carried out under surgical anaesthesia induced with sodium thiopental (10 mg/kg i.v. plus supplemental doses to maintain areflexia). Atropine sulfate (0.2 mg i.v.) and dexamethasone (0.5 mg i.m.) were administered and all wounds infiltrated with bupivacaine hydrochloride 2.5%. Cats were then paralyzed (Flaxedil 20 mg/kg i.v.) and artificially respired through an endotracheal tube with nitrous oxide and oxygen in a 70:30 ratio. A continuous intravenous infusion of Flaxedil (10 mg/kg/h), sodium pentobarbital (1 mg/kg/h) and lactated dextrose in Ringer's (10 ml/h) was maintained. End tidal CO₂, heart rate, blood pressure and EEG were continuously monitored and rectal temperature was maintained at 38° C. A sealed sound delivery system was fixed in each auditory canal.

Stimuli and sound delivery system

Small speakers (Pioneer WXX-172) housed in Teflon adapters were fitted with a custom-designed aluminium sound delivery system which was snugly inserted in the transected auditory canal close to the tympanic membrane. A microphone (IVIE 1300) probe tube was inserted in the delivery system close to the eardrum. Sound pressure levels were monitored in situ throughout each experiment. Fast Fourier transforms of the sound spectra were produced by a Data Precision 6000 waveform analyzer. The entire sound system was calibrated with a B&K pistonphone. Pure tone sinusoids were generated by a Wavetek 110 function generator and led through an analog multiplier and amplifier. Stimulus intensity, duration and repetition rate were controlled by a PDP/11 computer.

The stimuli employed consisted of amplitude modulation correlates of sound moving in four canonical directions relative to the center of the cat's head. Identical tones (interaural phase always 0°) increasing or decreasing in intensity in both ears simulated sound moving directly toward or away from the head. In this case a 295 ms plateau was preceded or followed respectively by a 250 ms AM ramp. Sound level increasing in one ear while decreasing in the other

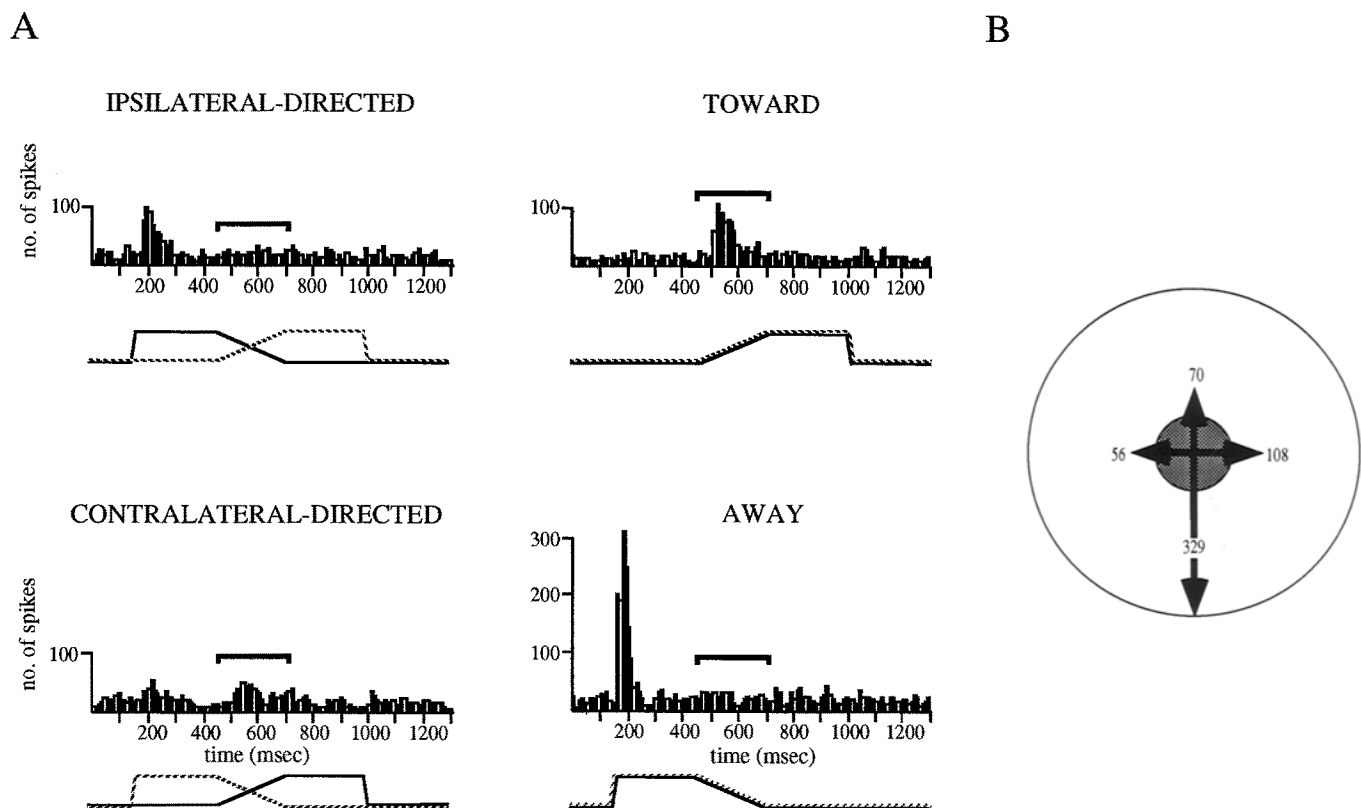
simulated azimuthal motion. In this case, stimulus rise/fall time was 5 ms, followed by a 295 ms stationary plateau, then a 250 ms AM ramp simultaneously in both ears, another 295 ms stationary plateau and then offset; 650 ms elapsed before the next stimulus, yielding a 1500 ms repetition rate. Each of the 4 directional correlates was presented at 4 different intensity levels (over an 18 dB range). The initial level of the plateau was presented approximately 20 dB above each cell's threshold at CF, and was increased in 6 dB steps. Each individual condition was presented 40 times for a total of 640 ($4 \times 4 \times 40$) computer randomized presentations.

Data collection and analysis

Recordings were carried out in a sound-attenuating chamber (IAX Controlled Acoustic Environments) with all life-support equipment located outside. Glass insulated platinum-iridium microelectrodes (1–1.5 M Ω at 1 kHz) were advanced perpendicularly to the surface of the ectosylvian gyrus using a remote controlled microdrive. Signals were amplified and filtered (0.5–12 kHz) with a BAK preamplifier and monitored visually and acoustically throughout the ex-

periment. Spikes were discriminated using a window trigger. Data collection display, and stimulus presentation were controlled by a PDP/11 computer with an IBM PC acting as an intelligent terminal.

Pure tones and white noise were used as search stimuli. When a unit was encountered the characteristic frequency was determined and the stimulus series was then presented at CF with the plateau portion at four different intensities ranging from approximately 20–38 dB above threshold (four intensities in 6 dB steps). Some cells were also tested at other frequencies. Post-stimulus time histograms (PSTH) were generated for each stimulus condition. The average level of spontaneous activity was determined from the intertrial intervals. Spike counts were generated for the plateau and ramp intervals of each stimulus condition and adjusted for spontaneous rate. Ear dominance and binaural interaction were determined by comparing the onset response to the plateau in the contralateral ear, the ipsilateral plateau, and the simultaneous plateau in both ears. The spike counts for the four intensity conditions were compared to determine intensity functions both for the stationary plateau periods and the AM ramps. Spike counts for AM ramps were compared for each simulated direction of motion and plotted as vectors relative to the center of the head.



SE06.015
16 kHz

Fig. 1. A Post-stimulus time histograms showing the responses of a single neuron in relation to the time course of the stimuli for the four directions of simulated auditory motion. Responses are collapsed across the four values of ramp excursion; bin width is 10 msec. The darkened portions are the responses during the AM ramps which simulate auditory motion. This unit is a toward-preferring unit because the response during correlated increasing AM ramps in the two ears is the strongest (top right panel). **B** Polar plot representation of the responses of the same unit during AM

ramps simulating four directions of auditory motion. 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)

Results

The data sample consists of the same population of cat primary auditory cortex neurons reported in the previous paper (Stumpf et al. 1991). Of 80 neurons sampled, 61 showed sensitivity to correlates of auditory motion (amplitude modulated pure tones); 54 of these 61 AM-sensitive neurons also exhibited directional selectivity and are the subject of further analysis.

Directional selectivity

A 2:1 ratio of responding between opposed directions of motion along one axis (depth or azimuth) was the criterion for directional selectivity. Three classes of directional selective units emerged: depth-preferring units, azimuth-preferring units and monaural-like units.

Motion in depth. Units preferring simulated sound source motion toward or away from the receiver comprised 37% (23/61) of all motion-sensitive units sampled. Fig. 1A shows post-stimulus time histograms depicting the timing of a toward-preferring neuron's discharge in relation to the time course of the stimulus, for the four

directions of motion used in this experiment. The darkened bins highlight the response evoked by the AM ramps simulating auditory motion. Note that the transient response to binaural sound onset (bottom right panel) is stronger than the response evoked by sound onset in either ear alone (top and bottom left panels), indicating a facilitatory binaural interaction. The responses evoked by AM ramps are represented in the form of a polar plot in Fig. 1B. The AM stimulus condition which produces the strongest response in this EE unit is a correlated increase in sound level at both ears (Fig. 1A, top right panel; Fig. 1B, downward pointing arrow).

Figure 2 shows post-stimulus time histograms (A) and polar plot (B) for an away-preferring neuron. Monaural and binaural sound onset evoke weak responses (left panels, bottom right panel). In contrast to Fig. 1, note the 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 3 is a plot of the preferred direction of motion in depth versus the response to binaural sound onset and offset, for the population of depth-preferring units. We derived a "depth motion index" in which the preferred

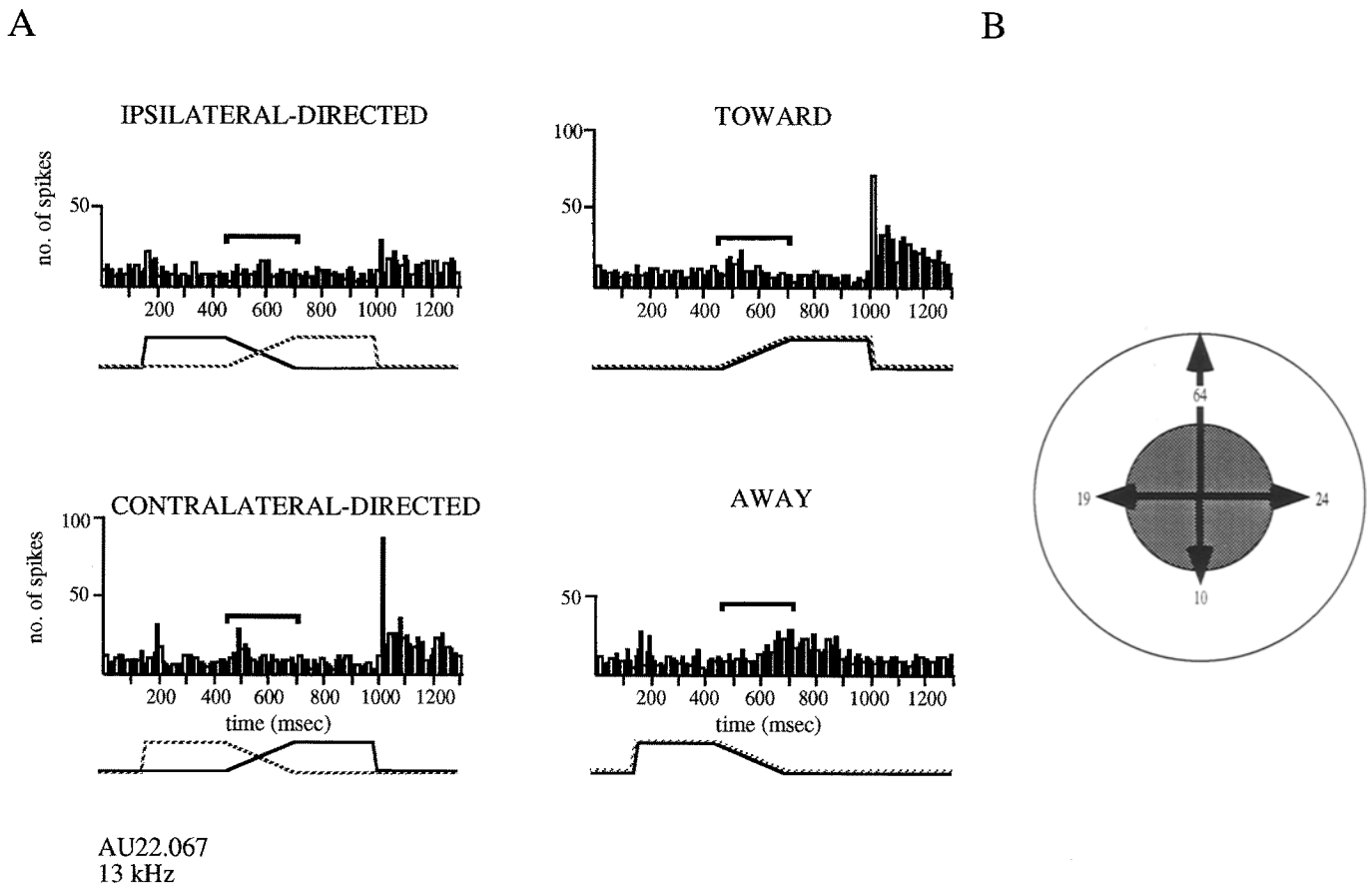


Fig. 2A, B. Conventions are the same as for Fig. 1. **A** Post-stimulus time histograms showing the responses of an away-preferring neuron, for the four directions of auditory motion. This unit is an away-preferring unit because the response during correlated de-

creasing AM ramps in the two ears is the strongest (bottom right panel). **B** Polar plot representation of the responses of the same unit during AM ramps simulating four directions of auditory motion

Motion in depth versus binaural on off response

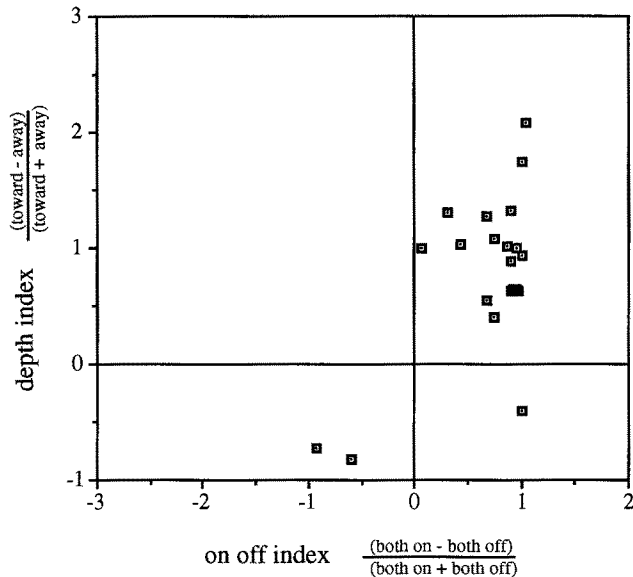


Fig. 3. Plot of the preferred direction of motion in depth versus the response to binaural sound onset and offset, for the population of depth-preferring neurons. Units with positive abscissa values prefer motion toward the receiver, and units with negative abscissa values prefer motion away from the receiver. Similarly, units with positive ordinate values give stronger transient on responses, and units with negative ordinate values give stronger transient off responses. Toward-preferring units are also “on” units; away-preferring units can be both “on” or “off”

direction of motion in depth is evaluated by dividing the difference between the “toward” and “away” responses by the sum of these responses:

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

In Fig. 3, units with positive abscissa values have stronger “toward” responses than “away” responses, and vice versa for units with negative values. Preference for binaural onset or offset is evaluated in a similar way by dividing the difference between the responses to binaural onset and offset by the sum of these responses:

$$\text{on off index} = (R_{\text{onset}} - R_{\text{offset}}) / (R_{\text{onset}} + R_{\text{offset}}).$$

Units with positive ordinate values have stronger transient “on” responses than “off” responses, and conversely for units with negative values. All units which gave transient responses to binaural stimulus onset also preferred correlated increases in sound source intensity at the two ears (simulated sound source motion toward the receiver). Units which responded to binaural 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 follow this pattern and did not respond to sound offset.

Most depth-preferring units had facilitatory (EE) binaural interactions: the response to stimulation of both ears together was greater than stimulation of either ear alone. This holds both for the sharp stimulus onsets and the AM ramps; responses to increases in sound level in

Breadth of tuning for motion in depth versus binaural interaction

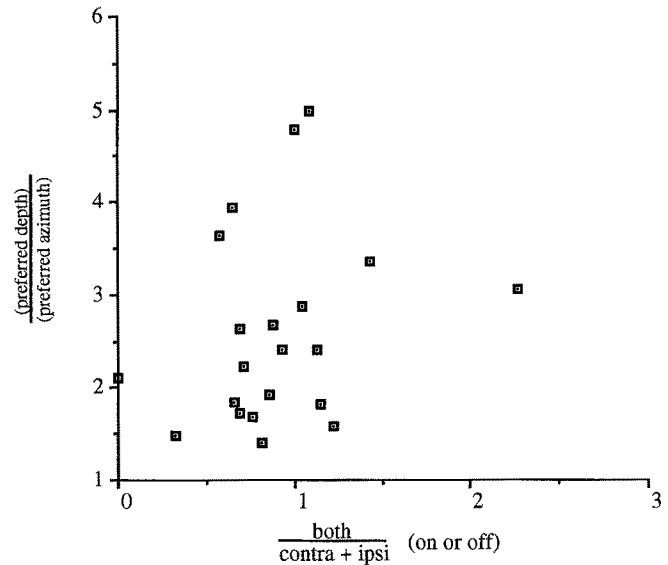
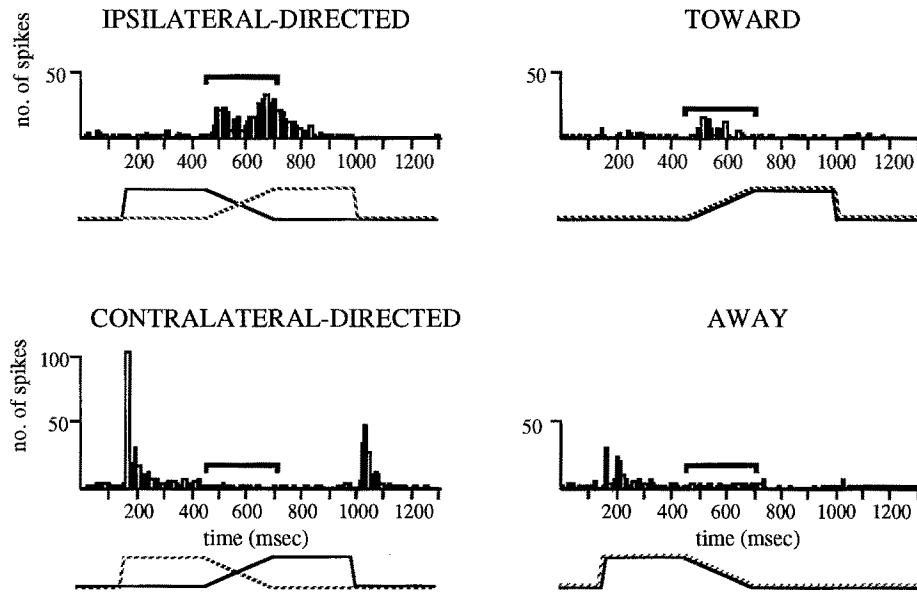


Fig. 4. Plot of the breadth of tuning to simulated motion in depth versus the degree of facilitatory binaural interaction, for the population of depth-preferring neurons. Breadth of tuning is calculated by dividing the strongest response to depth by the strongest response in azimuth. Binaural interaction is calculated by dividing the binaural response to sound onset by the sum of the monaural responses

both ears together is greater than response to increases in either ear alone. 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 4 shows that units with strong binaural facilitation tended to show greater selectivity for depth motion than did weakly facilitatory units.

Azimuth units. Units which responded exclusively to simulated sound source motion in azimuth comprised 10% of our sample (6/61). Most of these units (4/6) had inhibitory (EI or IE) binaural interactions. All units preferred motion toward the dominant ear. All units gave transient responses to sound onset in the dominant ear; a few units (3/6) also gave transient responses to offset in the non-dominant ear. Figure 5 shows post-stimulus time histograms (A) and a polar plot (B) for an ipsilateral-preferring unit. This unit is ipsilateral-ear-dominated: contrast the strong transient response evoked by sound onset in the ipsilateral ear (lower left panel) with the absence of response evoked by onset in the contralateral ear (top left panel). The greatly diminished response to binaural sound onset (bottom right panel) is indicative of inhibitory binaural interaction. In addition, note the transient response evoked by sound offset in the non-dominant ear (bottom left panel). From the ear dominance, on/off transient responses and binaural interaction type of this unit, one would predict that

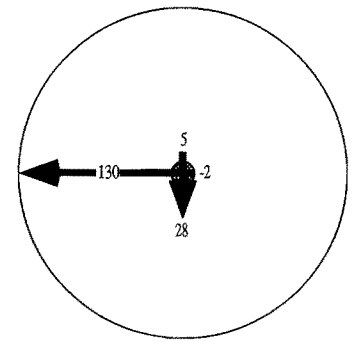
A



AU22.026

Fig. 5A, B. Conventions are the same as for Fig 1. **A** 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 response during opposite-

B



directed AM ramps increasing in the ipsilateral ear and decreasing in the contralateral ear is the strongest (top left panel). **B** Polar plot representation of the responses of the same unit during AM ramps simulating four directions of auditory motion

it would respond most strongly to increases in sound level in the ipsilateral ear *and* decreases in sound level in the contralateral ear. This is precisely what was found.

Most azimuth-sensitive units responded to the plateau with sharp onset peaks usually about 20 ms wide. However, the response to the AM ramps tended to be much broader, in some cases continuing throughout most or all of the ramp. This was in contrast to the ramp responses of both depth and monaural-like units which tended to be shorter and more nearly similar to the phasic onset responses which almost all units gave in response to the plateau.

For all units responding well to sideways motion (including monaural-like units; see next section), there was a strong relationship between the transient response to sound onset in the dominant ear and the preferred direction of simulated sound source motion in azimuth: units with strong “on” 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-prefering units. Figure 6 is a plot of preferred direction of simulated auditory motion in azimuth versus 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 with the sum of these responses:

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

Motion in azimuth versus ear dominance

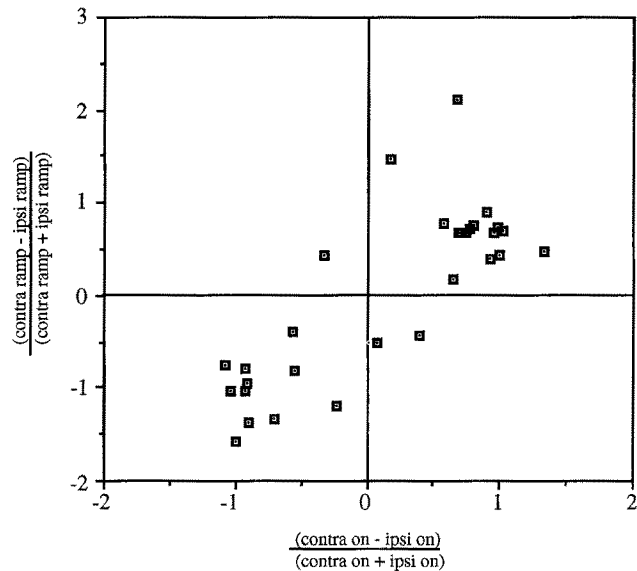
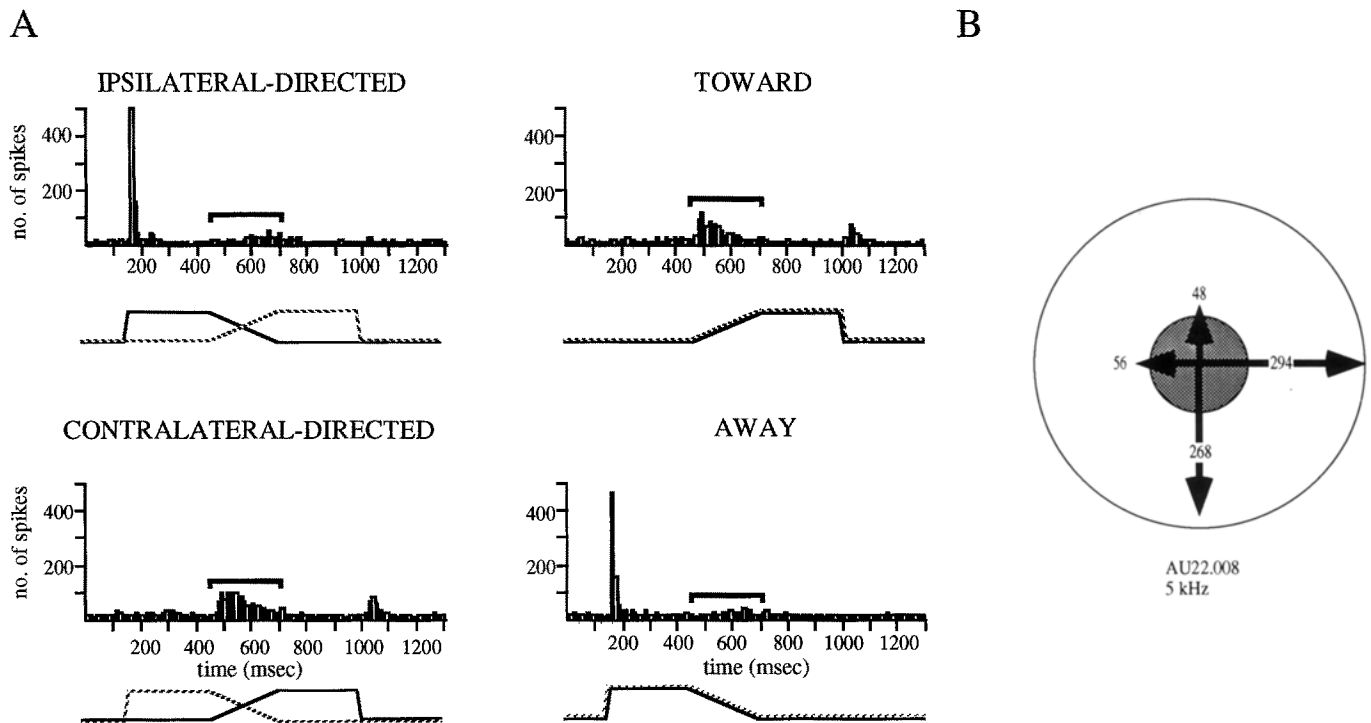


Fig. 6. Plot of preferred direction of simulated azimuthal auditory motion versus ear dominance (measured using both responses to monaural sound onset), for all units displaying selectivity for one direction of motion in azimuth (including monaural-like units). Units with positive abscissa values prefer 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



AU22.008
4.5 kHz

Fig. 7A, B. Conventions are the same as for Fig. 1. **A** Post-stimulus time histograms showing the responses of a contralateral-dominated, monaural-like neuron, for the four directions of auditory motion. This unit is a monaural-like unit because the response during increasing AM ramps in the contralateral ear is the same,

regardless of the input from the ipsilateral ear (top right and bottom left panels). **B** Polar plot representation of the responses of the same unit during AM ramps simulating four directions of auditory motion

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:

$$\text{ear dominance} = (R_{\text{contra on}} - R_{\text{ipsi on}}) / (R_{\text{contra on}} + R_{\text{ipsi on}}).$$

Units with positive ordinate values give stronger responses to contralateral onset 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.

Monaural-like units. These units were the most numerous, comprising 41% of our sample (25/61). Monaural-like units exhibited strong directional preferences along both axes (depth and azimuth). They 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 7A 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. The response to an increase in sound level in the contralateral ear is the same whether it is accompanied by a corresponding increase or decrease in sound level in the ipsilateral ear (compare the bottom left and top right panels). 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. Figure 7B is a polar plot of the response during the AM ramps for the same unit; this unit responds equally well to increases in sound level in the contralateral ear alone and in both ears together, the intensity correlates of auditory motion toward the contralateral ear and directly toward the receiver, respectively. The responses in 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.

It should be stressed that monaural-like units are not necessarily monaural (hence the term "monaural-like"); at certain intensity levels some of these units respond *as*

A

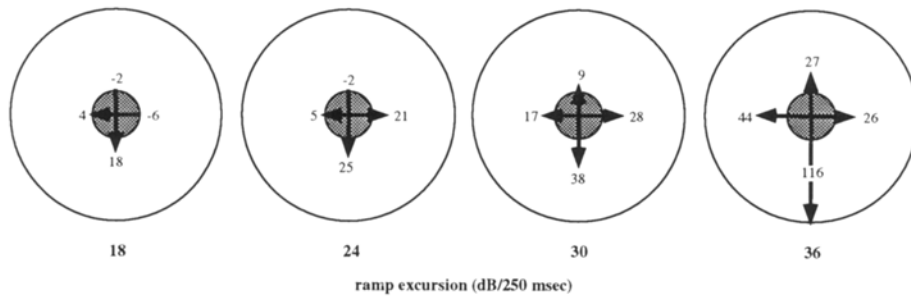
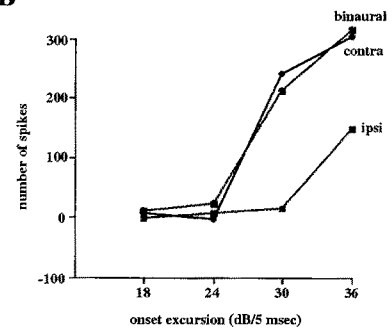
SE06.024
15 kHz

Fig. 8A, B, Polar plot representations of the responses during the AM ramps at the four values of ramp excursion (A), and the rate/intensity functions of the same neuron for the monaural and binaural transient “on” responses (B). 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

B



excursion per 250 ms is printed below each plot. This unit is a monotonic unit: increases in ramp excursion produce stronger responding in the preferred direction of motion. The rate/intensity function is also monotonic and parallels the response to increasing AM ramps

A

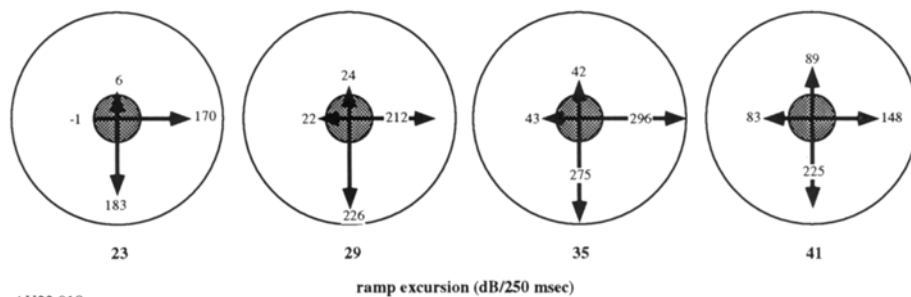
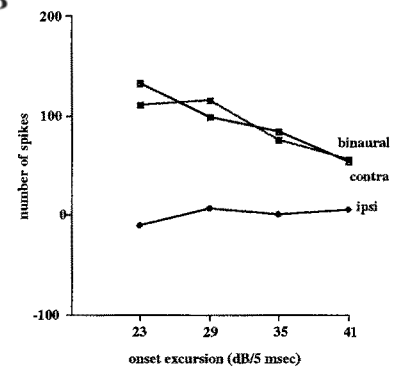
AU22.018
5 kHz

Fig. 9. Conventions are the same as in figure 8. Non-monotonic unit. A particular value of ramp excursion (35 dB/250 msec) produces the strongest response; increases or decreases in ramp

B



excursion diminish responding. The rate/intensity function for the transient “on” response is also non-monotonic but does not exactly parallel the response to the AM ramp in the preferred direction

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 from the non-dominant ear and no binaural interaction (EO units) 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 units had strong binaural interactions; when present, input from the non-dominant ear was usually slightly facilitatory.

Velocity selectivity

Most of the direction-selective neurons encountered responded best at one particular ramp excursion. The majority (41/61) responded best to the highest ramp excur-

sion (monotonic units). Figure 8 shows polar plots of the responses during AM ramps at the four velocity conditions (A), and the monaural/binaural rate/intensity functions for the transient “on” response at four intensity levels (B), for a monotonic toward-preferring unit. Note the stronger responses to AM ramps with greater ramp excursion and the monotonicity of the rate/intensity function. A small number of units (10/61) gave non-monotonic responses to increased ramp excursion and preferred one particular ramp excursion; smaller or greater ramp excursions produced weaker responses. Figure 9 shows polar plots of the responses during AM ramps (A), and the monaural/binaural rate/intensity functions for the transient “on” response (B) for a non-monotonic monaural unit. The intensity functions and the response to the AM ramp are both non-monotonic (for the range of intensity tested) but peak at different intensity levels. The remaining ten units gave responses which were independent of ramp excursion or idiosyncratic, sometimes with changes in preferred direction. Figure 10 shows the polar plots (A) for a neuron which

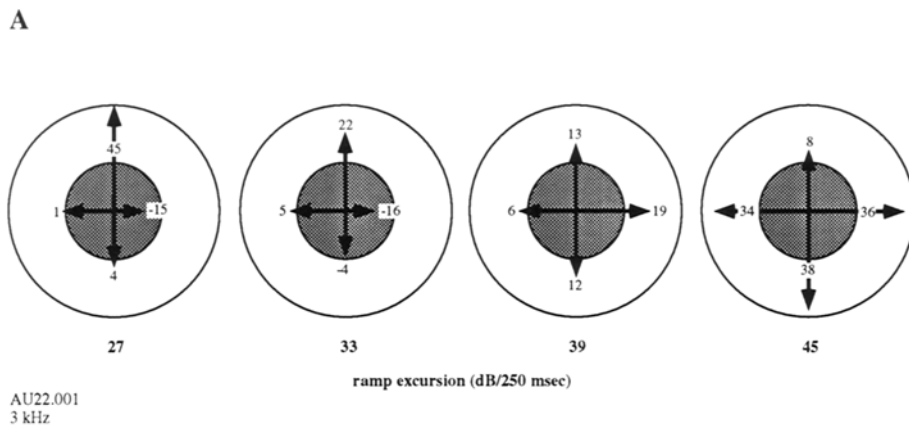
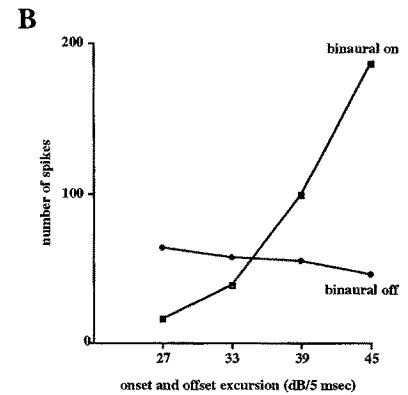


Fig. 10. Conventions are the same as in figure 8. Idiosyncratic unit. At lower ramp excursion, this unit prefers “away”; as ramp excursion increases, this unit gradually changes directional preference and prefers “toward”. This change in preferred direction with increasing ramp excursion can be explained by the rate/intensity



functions for the binaural “on” and “off” transients: the “off” transient diminishes gradually with increasing intensity, while the “on” transient is weak at low intensities and becomes progressively stronger at higher intensities

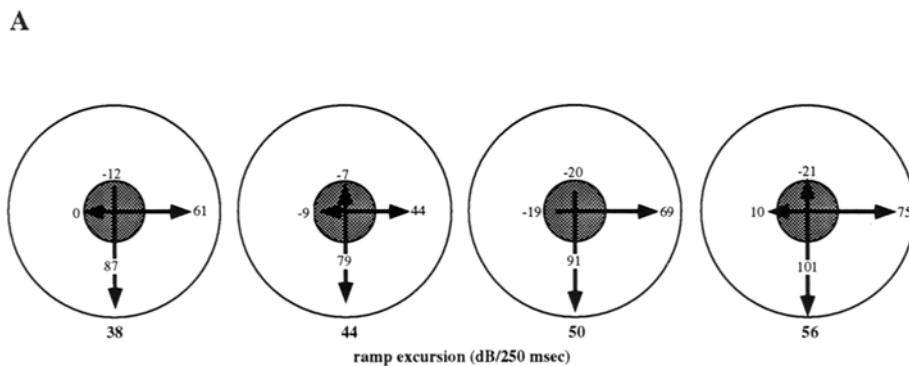
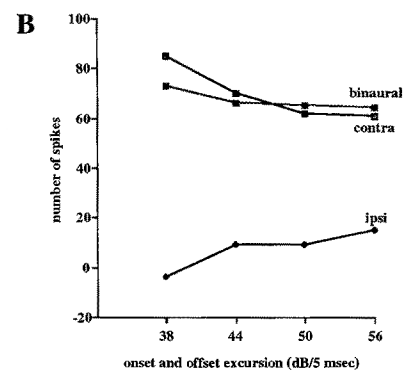


Fig. 11. Conventions are the same as in Fig 8. Velocity independent unit. The responses to AM ramps are independent of ramp excursion,



and the rate/intensity function for the transient “on” response is relatively flat

prefers “away” at the smallest ramp excursion but whose directional selectivity changes as ramp excursion increases. The accompanying graph (B) shows the monaural/binaural transient “on” and “off” responses. The “off” transient is strongest at low ramp excursion and progressively decreases with increasing ramp excursion; the “on” transient is weak at low ramp excursions and gradually becomes stronger. Therefore this unit prefers increases, rather than decreases in sound level, at higher ramp excursions. Figure 11 shows polar plots (A) and rate/intensity functions (B) for a unit which showed no preference for any particular ramp excursion (velocity independent unit).

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 at different intensity levels. This is particularly true of most toward-preferring neurons in which the responses to sharp and gradual binaural sound onset across intensity levels are similar and usually monotonic. The remaining units had intensity functions for the ramp

and sharp onset which differed and the preferred ramp excursion could not be predicted from the intensity function. This was especially true of units which gave non-monotonic, speed-independent or idiosyncratic responses to increased ramp excursion.

Discussion

Directional selectivity

The results presented here indicate that the traditionally studied response properties of cortical neurons (monotonicity vs. non-monotonicity, phasic vs. tonic, “on” vs. “off” and E/E vs. E/I) can be shown to act synergistically, providing mechanisms for selectivity to the binaural correlates of auditory motion. Several examples drawn from our data indicate how these interrelated mechanisms may function. Figure 12 summarizes the relationships between the various response properties, showing the selectivity for direction and velocity which these mechanisms

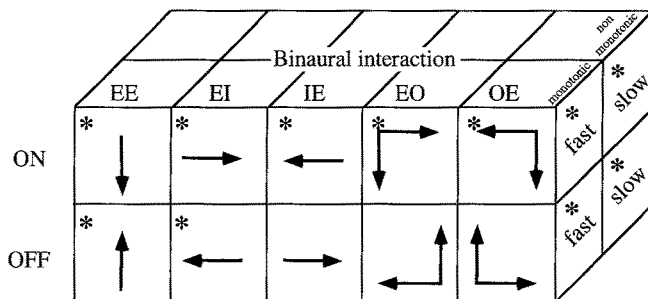


Fig. 12. A model of direction and velocity selectivity for auditory movement, based on interactions of response characteristics of neurons in the primary auditory cortex. The major determinants of the direction selectivity of AI neurons are interactions between binaural interaction type, ear dominance 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, and whose responses to simulated auditory motion could be predicted from response characteristics listed above

would provide for a given neuron. The key features of Fig. 12 are as follows: The responses of a neuron to onset vs. offset of stimuli combined with its binaural interaction class determine the neuron's preferred direction of motion in 3-dimensional space. The shape of the spike rate vs. intensity function is related to the preferred velocity of the moving sound. Thus E/E cells prefer motion either toward or away from the organism depending on the strength of their onset vs. offset responses. Note that EE cells which gave both onset and offset responses would be expected to show an axial form of direction preference with responses to stimuli moving toward or away from the organism, but not to sideways motion. E/I cells prefer sideways motion either toward the contralateral or ipsilateral hemifield, depending on the relative strength of their "on" vs. "off" responses. I/E cells respond to motion in the opposite directions to E/I cells and their preferred direction is likewise dependent on relative strength of their "on" vs. "off" responses. In both I/E and E/I cells with equal "on" and "off" responses one would expect a preference for axial sideways motion with weak responses to motion in depth. Monaural cells dominated by input from one ear alone would still show characteristic preferences depending on the dominant ear and the relative strength of their "on" and "off" responses. Monaural cells with equal "on" and "off" responses should respond equally well to all directions of sound source motion.

Cells sensitive to motion in depth. Facilitatory E/E cells respond best to the diotic intensity changes corresponding to motion directly toward the head. The degree of binaural facilitation seen in depth sensitive cells extended

all the way from very strong interactions ("and gate" cells), to cells which responded to sound in each ear alone, but showed no binaural facilitation at all (occlusive cells). The degree of directional specificity was correlated with the amount of binaural facilitation, with strongly facilitatory cells being most highly selective. E/E cells with "off" responses respond as well to motion away from the head.

The high percentage of neurons (39%) responding best to 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 and Irvine 1981). Thus sounds near the midline would receive the largest representation in the cortex.

Cells sensitive to motion in azimuth. E/I cells with phasic onset responses to sound in the contralateral ear respond best to intensity correlates of motion in azimuth toward the contralateral side. Sound source motion toward the ipsilateral side evokes selective responses from I/E cells which respond phasically to sound onset in the ipsilateral ear. While these response properties are sufficient to confer selectivity to these cells, some cells showed an additional characteristic, namely "off" responses in the non-dominant ear. This feature would enhance selectivity for the detection of motion in one azimuthal direction.

"Monaural-like" cells. Many cells with little or no binaural interaction, either facilitatory or inhibitory, respond equally well to sound becoming louder in both ears or to sound becoming louder in the dominant ear. The contralateral ear dominated in 64% of these units and the ipsilateral ear in 36%. The largest group of neurons in this study (41%), they were either dominated or influenced by only one ear. A few responded weakly in the non-dominant ear, but binaural response was roughly equal to the response in the dominant ear alone. These units appeared monaural with our testing methods, but it is likely that some of them would have shown binaural interaction with varied IID levels. All simulated motion here was performed at a reference IID level of 0 dB. Since many E/I cells (Brugge and Imig 1978) show binaural interactions only when non-dominant ear input is louder than that for the dominant ear, a different stimulus regime may well reveal stronger, more specific binaural interactions in this neuronal population.

Velocity sensitive cells. Most units exhibited monotonic rate/intensity functions over the range of AM ramp excursions used in our study. This probably reflects their monotonic rate/intensity functions for the step portion of the stimulus. These cells would, therefore, be expected to have greater responsivity to the larger ramp excursions. About one third of the units encountered were selective for one of the smaller AM ramps; these cells would be suitable for encoding specific velocities of moving sound. By and large, there was a good correlation between responses to the initial step and to the simulated motion stimuli. Monotonic cells responded well to the highest speeds/excursions and non-monotonic

cells often preferred lower speeds/excursions of the AM ramps. However the best velocity could not always be predicted from the step responses and that suggests that additional temporal response characteristics may come into play. Note that the step response rises to its plateau level over 5 ms while the ramp duration is 250 ms. Similarly, Phillips (1988) found that neurons with monotonic rate-intensity functions at 5 and 10 ms rise times tended to remain monotonic at slower rise times (up to 50 ms in his study), whereas cells which were non-monotonic at 5 ms typically became less non-monotonic or even monotonic as the rate of rise was decreased.

Comparisons with other studies

Comparing our results with those reports using stationary sound or its IID correlates reveal some contrasts. Phillips and Irvine (1981) report that both EI and strong EE units are selective for location of sound. In our population the strong E/E units do not seem to be involved in azimuthal motion, but "on" E/E cells do respond to simulated motion directly toward the head, while "off" units are more likely to favor motion away from the head. Middlebrooks and Pettigrew (1981) reported two classes of cortical neurons sensitive to free-field speaker location—low frequency hemifield neurons with large receptive fields and high frequency axial neurons with smaller more circumscribed receptive fields. Both types responded only at the onset of stimuli. Axial units are highly influenced by the directionality of the pinnae, as would be expected from free-field measurements of IIDs at higher frequencies (Martin and Webster 1989). We would not recognize units with properties similar to axial units in our population, because the sound delivery system circumvented directionality introduced by the pinnae at high frequencies. It is also unclear whether our units can be compared to hemifield units, because our stimuli represent a sound source moving from one ear through both hemifields to the opposite ear. Although the methods employed here are very different from theirs, our results also differ from those of Sovijarvi and Hyvarinen (1974) in that we have found some units which appear to respond continuously as a source passes through both hemifields from one ear to the other.

Using low frequency binaural beat stimuli, Yin and Kuwada (1983) report that 10% of the cells they recorded in the inferior colliculus, responded with directional selectivity to stimuli moving towards either the contralateral or ipsilateral side, but not in the reverse direction. Most of these selective cells favored ipsilateral motion, with the remaining 90% responding equally well to both directions. These cells, however, did not fire throughout the entire stimulus, but showed phase-locking with the beat frequency, which was in turn related to the preferred interaural phase difference. This represents an entirely different mechanism for motion sensitivity than we have studied for cortical cells reported here. Nevertheless, either or both these mechanisms would enable a cell to display directional sensitivity. Perhaps the mechanism

studied by Yin and Kuwada would be used more by low frequency-following units, which show good phase locking, while the rate of intensity change cue that we describe here would relate more to high frequency preferring neurons. It would be interesting to examine the effect of combining the two cues on the responses of azimuth-motion selective cortical units. On the basis of both neural response characteristics (Middlebrooks and Pettigrew 1981) and behavioral ablation studies (Jenkins and Masterton 1982) it has been suggested that the primary auditory pathway rostral to the superior olivary complex plays a role in localization of stationary sound sources within contralateral space (Phillips and Irvine 1981; Phillips and Brugge 1985). Because we did not test movement in each hemisphere independently, further studies are needed to determine whether azimuthally sensitive cells prefer motion in one hemifield or whether both hemifields are equally effective.

Acoustical considerations

In detecting the location of a sound source in space the auditory system uses, not only IIDs but also ITDs and the so-called "monaural cues" provided by spectral differences. In the present study motion was simulated using IIDs alone. A theoretical study carried out by Zakarauskas and Cynader (1991) has shown that the first derivative of the IID may provide powerful cues to localize sound. Because our stimuli consisted of pure tones, differences in spectral content would not have played a role had we used free-field stimuli although we recognize that small Doppler shifts would occur during movement in both depth and azimuth. In addition, because recording was confined to AI, where units are relatively sharply tuned, the comparison of the relative intensities of various frequencies would have provided a less salient cue for the neurons in this study. According to the duplex theory of sound localization, high frequency sounds are localized using intensity cues and low frequencies using time and phase cues. Characteristic frequencies of units found in this study ranged from 2 kHz to 44 kHz, a range in which IIDs would be most salient. In humans, ITD and phase do not influence the lateralization position of sinusoids above 1.2 kHz (Yost and Hafter 1987). Due to smaller head size, the region of cross-over from mechanisms using ITD to IID should be 3–4 kHz in the cat. ITDs contained in the envelope of the waveform may also be used to localize high frequency sounds (Henning 1974); however, in the present experiment, the AM ramps simulating motion were preceded and followed by a 300 msec stationary plateau in order that the onset and cessation of the stimuli would not provide relevant cues. None of the cues described above could apply, of course, to stimuli moving directly *toward* or *away* from the head.

IID is a function of both spectral components and location in space. In the cat in a free sound field, intensity differences between the ears may range from a maximum IID of 10 dB at 2 kHz to a maximum of 20–40 dB at higher frequencies (Martin and Webster 1989). The plateau region of the sound stimuli used in our experiments consisted of sound in the approximate range of 20–38 dB

above threshold in one ear and 0 dB in the other ear, an IID which would be within the actual physiological range at frequencies above 8 kHz, and somewhat greater than the physiological range at frequencies between 2 and 8 kHz. In a free-field situation with the pinnae intact, intensity levels do not actually rise in one ear and fall in the other in constant linear relationship as a sound moves azimuthally at a constant velocity. The actual pattern of the intensity change is dependent on frequency response and location of the pinnae and tends to be linear below 12 kHz, but may be quite non-monotonic at higher frequencies (Martin and Webster 1989). Our stimuli are, therefore, approximations of the intensity changes of moving sound and, at least at high frequency, may not always represent azimuthal movement at a constant unchanging velocity. Movement in depth in a free-field environment also produces at times slightly non-linear intensity changes due to the changing angle of reflection from the head and pinnae. Nevertheless, given these limitations, our stimuli provide a plausible representation of the salient changes in intensity that would occur as a sound source moves in space.

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