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Spatial Receptive Fields of Inferior Colliculus Neurons to Auditory Apparent Motion in Free Field

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Ingham, Neil J., Heledd C. Hart, and David McAlpine. Spatial receptive fields of inferior colliculus neurons to auditory apparent motion in free field. *J Neurophysiol* 85: 23–33, 2001. We examined responses from 91 single-neurons in the inferior colliculus (IC) of anesthetized guinea pigs to auditory apparent motion in the free field. Apparent motion was generated by presenting 100-ms tone bursts, separated by 50-ms silent intervals, at consecutive speaker positions in an array of 11 speakers, positioned in an arc $\pm 112.5^\circ$ around midline. Most neurons demonstrated discrete spatial receptive fields (SRFs) to apparent motion in the clockwise and anti-clockwise directions. However, SRFs showed marked differences for apparent motion in opposite directions. In virtually all neurons, mean best azimuthal positions for SRFs to opposite directions occurred at earlier positions in the motion sweep, producing receptive fields to the two directions of motion that only partially overlapped. Despite this, overall spike counts to the two directions were similar for equivalent angular velocities. Responses of 28 neurons were recorded to stimuli with different duration silent intervals between speaker presentations, mimicking different apparent angular velocities. Increasing the stimulus OFF time increased neuronal discharge rates, particularly at later portions of the apparent motion sweep, and reduced the differences in the SRFs to opposite motion directions. Consequently SRFs to both directions broadened and converged with decreasing motion velocity. This expansion was most obvious on the outgoing side of the each SRF. Responses of 11 neurons were recorded to short (90°) partially overlapping apparent motion sweeps centered at different spatial positions. Nonoverlapping response profiles were recorded in 9 of the 11 neurons tested and confirmed that responses at each speaker position were dependent on the preceding response history. Together these data are consistent with the suggestion that a mechanism of adaptation of excitation contributes to the apparent sensitivity of IC neurons to auditory motion cues. In addition, the data indicate that the sequential activation of an array of speakers to produce apparent auditory motion may not be an optimal stimulus paradigm to separate the temporal and spatial aspects of auditory motion processing.

INTRODUCTION

Neuronal mechanisms that contribute to sound-source localization are likely also to contribute to the detection of sound-source motion. However, motion processing in the auditory system remains poorly understood. Two theories have been suggested to describe how the brain processes auditory motion. The first of these, often referred to as the “snap-shot” theory, suggests that auditory motion is computed from a series of successive static localization tasks, using neurons tuned to

different static spatial positions (e.g., Grantham 1986, and see Middlebrooks and Green 1991 for review). This is analogous to *phi* motion processing in the visual system. Implicit in the snap-shot theory is that neural responses to sounds originating from a point in space are independent of whether the sound source is stationary or moving. The alternate theory is that the central auditory nervous system possesses specialized motion detectors sensitive to dynamic aspects of auditory localization cues that underpin the perception of direction, velocity, and acceleration of sound-source motion. In support of this, recent studies in human extra-primary auditory cortex using neuroimaging techniques have indicated certain cortical regions that may be activated selectively by virtual motion cues (e.g., Griffiths et al. 1998). The possibility that specific auditory cortical areas might be given over specifically to the processing of sound-source motion is consistent with what is known about motion processing in the visual system. Neurons in area MT of visual cortex have been demonstrated to respond exclusively to visual motion cues in a manner consistent with populations of such neurons underpinning behavioral performance (e.g., Britten and Newsome 1998). Despite such analogies, however, there is no reason a priori why any putative motion processors in the auditory system must necessarily function in the same way as visual motion detectors. Furthermore no electrophysiological study to date has demonstrated an equivalent (to MT) cortical area dedicated to processing sound-source motion, although this obviously does not preclude the existence of such an auditory cortical area.

A number of neurophysiological studies, from brain stem to cortex, have investigated the coding of auditory motion using *real* (e.g., Ahissar et al. 1992; Sovijärvi and Hyvärinen 1974), *simulated free-field* (e.g., Wagner and Takahashi 1992; Wilson and O’Neill 1998), or *simulated closed-field* (e.g., Altman et al. 1970; Doan and Saunders 1999; McAlpine et al. 2000; Spitzer and Semple 1993, 1998; Stumpf et al. 1992) motion cues. Often the results of these studies have been inconclusive as to the exact nature of any motion-processing system. Nevertheless a consensus is developing that sensitivity to auditory motion cues emerges as the auditory system is ascended. Interaural-delay-sensitive neurons in the IC appear to be sensitive to the direction, locus, and extent of apparent motion cues produced by interaural phase modulation (IPM) stimuli (McAlpine et al. 2000; Spitzer and Semple 1993), while those

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in the medial superior olive (MSO) are not (Spitzer and Semple 1998). Additionally, Altman and his colleagues described a systematic increase in the proportion of neurons in the chloralose/urethan-anesthetized cat selective for the direction of simulated closed-field auditory motion, using interaurally delayed clicks or interaural-phase-modulated tones, from the inferior colliculus (IC) (Altman 1968), to the medial geniculate body (Altman et al. 1970) and primary auditory cortex (Altman 1987). However, the extent to which neural responses indicate the existence of specialized motion processors remains unresolved. Spitzer and Semple (1993) reported virtually all IC neurons in the barbiturate-anesthetized cat and gerbil to be sensitive to the motion cues of IPM. However, McAlpine et al. (2000), recording in the urethan-anesthetized guinea pig, suggested that response history, rather than stimulus history per se, was responsible for apparent neuronal sensitivity to the dynamic interaural phase cues of IPM. This argued for a nonspecific (to motion) mechanism of *adaptation of excitation* influencing neuronal responses to motion cues, where adaptation of excitation is defined as the reduced capacity of a neuron to respond to subsequent excitatory stimuli following presentation of a stimulus that is itself excitatory.

Here, using sequential activation of an array of free-field speakers to simulate auditory motion, we demonstrate that spatial receptive fields of IC neurons to clockwise and anti-clockwise apparent motion in azimuth are, relative to each other, skewed toward the direction from which the stimulus is moving. However, there is no evidence that these neurons exhibit selectivity for a particular direction or velocity of the motion. Overall discharge rates to the two motion directions were similar, and neurons responded to movement into the receptive field in either direction with an initially high response probability that subsequently adapted over time. Increasing the OFF time between speaker activation progressively increased the magnitude of responses to later-activated speakers in the array for either direction of motion. The consequence of this is that receptive fields to the two directions of motion converged with increasing OFF time (i.e., decreasing velocity). Thus the temporal aspects of stimulation, and the response to stimulation, appear to determine whether or not neurons are classified as showing evidence for motion sensitivity. These data have been presented previously in abstract form (McAlpine et al. 1999).

METHODS

Surgical preparation

Fourteen pigmented guinea pigs, weighing 340–420 g, were anesthetized using fentanyl citrate/fluanisone (Hypnorm, Janssen, 1 ml/kg im) and midazolam hydrochloride (Hypnovel, Roche, 2 ml/kg ip). In early experiments, animals were injected with 0.06 mg of atropine sulfate to reduce bronchial secretions. All animals were routinely administered Dopram (doxapram hydrochloride, Willow Francis Veterinary, 10 mg/kg ip), prior to surgery, to prevent respiratory insufficiency. In most cases, the animal's trachea was cannulated. Supplementary doses of anesthetic were administered as required in the form of intraperitoneal injections of an 8 ml/kg mixture of Hypnorm, Hypnovel, and water (1:1:2 parts, respectively). Animals were positioned in a minimal head holder, consisting of a nose bar and cheek supports, in which the pinnae and ear canals remain unobstructed for free-field stimulation. A heating blanket and rectal thermometer were used to maintain body

temperature at $38 \pm 1^\circ\text{C}$. A craniotomy was performed to expose the cortex overlying the right inferior colliculus (IC), and the dura was retracted to allow microelectrode access.

Auditory stimulation

The animal was transferred to an anechoic chamber, with the head aligned to the center of an array of 11 loudspeakers (KEF T27A), equidistantly located 1 m from the animal's head. The array covered an arc of 225° of space, ranging from $+112.5^\circ$ left of midline (*speaker 1*; contralateral to the IC being recorded), through 0° on the midsagittal plane (*speaker 6*) to -112.5° right of midline (*speaker 11*; ipsilateral to the recording electrode). Speaker separation was 22.5° . The right IC was probed for single-unit auditory responses using parylene-coated tungsten microelectrodes (approximately 2 M Ω impedance), under semi-stereotaxic control by a Narishige micro-manipulator and manual hydraulic micro-drive. Single units were isolated using broadband noise bursts (1.2–25 kHz) presented from *speaker 5* in the array (situated $+22.5^\circ$). Neuronal best frequency (BF; the pure-tone frequency to which threshold was lowest), was determined audiovisually using 50-ms duration pure tones, again presented from *speaker 5* in the array.

Apparent auditory-motion stimuli were generated under computer control. In each case, neuronal responses were recorded to 20 repeats of each trial condition, with a 1-s interval between repeats. The stimulus used was a BF tone burst for those neurons with a defined BF, or a broadband noise burst (1.2–25 kHz) for the four neurons for which BF was not definable. Stimuli were presented through consecutive speakers in the array with a 100-ms duration at each location (with 5-ms rise-fall time), followed by a user-definable OFF interval (50–500 ms), to produce coherent motion sweeps. Stimuli were presented at a constant attenuation producing a sound level from each loudspeaker in the array, matched to within 2 dB, as recorded by a Brüel and Kjær Type 4133 microphone placed over the center of the animal's head in the center of the array. Stimuli were presented 15–20 dB above BF threshold (as recorded from stimulation at *speaker 5*, $+22.5^\circ$, in the array; or 15–20 dB above noise threshold for the 4 neurons with undefined BF). Responses to motion in the clockwise (CW, contra- to ipsilateral in our recording setup) and anti-clockwise (ACW, ipsi- to contralateral) azimuthal directions were examined. The extent and center of the motion could be controlled independently. Generally, sweeps consisted of motion through the entire array in either direction (i.e., 225° depth, centered at 0°), or short sweeps of 90° produced by activation of four consecutive speakers in the array. Angular velocity was adjusted by altering the duration of the silent interval between the stimuli at successive loudspeaker positions, from 50 up to 500 ms, producing angular velocities from 150 down to 37.5°s^{-1} .

Data acquisition and analysis

It was not possible to record responses to all possible stimulation types for each neuron isolated. Typically, neurons were held for between 20 and 60 min, often allowing only certain parameters to be recorded. Neural activity was amplified using a Neurolog System NL103 a.c. preamplifier (Digitimer). Single units were isolated using a Digitimer D130 spike processor, and the discriminated output signal was digitized using a 1401 A-D converter (Cambridge Electronic Design) at a sampling rate of 20 kHz. An event marker signifying the onset of each of the 20 stimulus trials was also digitized on the same 1401 channel to allow poststimulus time histograms (PSTHs) to be generated and analyzed off-line.

Polar plots were constructed in which the total number of spikes evoked at a particular location was plotted against the angular position of the speaker location. The polar plot therefore illustrates the auditory spatial receptive field (SRF) for the neuron in response to *dynamic stimulation* by the apparent motion sweeps (see, for

example, Figs. 1 and 2). The mean best azimuth of the SRF was calculated as the vector average of the response to each speaker location (Schnupp et al. 1995). The total numbers of discharges to full sweeps were also calculated. The borders of the SRFs, where possible, were defined as the spatial position corresponding to 50% maximum response amplitude. The *lateral* border of each SRF, irrespective of the direction of motion, was defined as the border closer to the ear contralateral to the recording site (i.e., the left ear being contralateral to the right IC). Similarly, the *medial* border was defined as the border closer to the ear ipsilateral to the recording site. A number of neurons which had SRFs located more contralaterally did not demonstrate a definable lateral border, and these were excluded from this analysis.

RESULTS

A total of 138 single neurons were isolated, 91 of which yielded sufficient data for analysis of sensitivity to apparent motion. All neurons had relatively low auditory thresholds, and 87 neurons had defined BFs, indicative of neurons in the central nucleus of the IC. Electrolytic lesions were made in two animals and were later verified histologically to be located in the central nucleus of the IC. BFs ranged from 2.5 to 16 kHz, and thresholds (measured in response to repeated presentation of 100-ms tones at 1-s intervals at *speaker 5* in the array) ranged from -12 to $+43$ dB SPL. Neurons most commonly responded to the apparent motion stimulus with onset activity, producing relatively few spikes per 100-ms stimulus. Only rarely were sustained discharge patterns observed.

Figure 1 shows responses of an IC neuron, with a BF of 13 kHz and a threshold of -4 dB SPL. The PSTH to CW motion (consecutive stimulation from *speaker 1* to *speaker 11*; Fig. 1A) indicates that an initial ON response was evoked at *speaker 1* and that this was distinct from the rest of the SRF. This ON response was not evoked by ACW motion, where *speaker 11* was the first speaker in the array, nor did stimulation at *speaker 1* evoke a response of similar magnitude in the context of the final speaker during ACW motion (Fig. 1B). Figure 1C illustrates polar plots of the dynamic SRFs for CW and ACW motion, with the ON response at *speaker 1* ($+112.5^\circ$) to CW motion clearly evident. This was followed by a marked diminution of the response at subsequent speakers (2 and 3, located at $+90$ and $+67.5^\circ$, respectively) and then increased activation as the stimulus moved through the SRF (especially *speakers 4–6*; from $+45$ to 0°). Mean best azimuth positions for the CW and ACW dynamic SRFs are indicated on the circumference of the polar plot. Note that these angles were calculated for the response of the main body of the SRF only, and do not include the response evoked by *speaker 1* for CW motion, which would have biased the best azimuth to CW motion further into the contralateral field.

In all subsequent analyses, the responses to *speakers 1* and *11* were excluded from the calculations. The rationale for excluding these responses is that their inclusion (situated as they are at the start points of the CW and ACW motion) may bias mean best azimuths toward the direction from which the stimulus was moving, particularly if responses at the beginning of the stimulus sweep were considerable. In practice, such ON responses, when they occurred, were almost wholly confined to

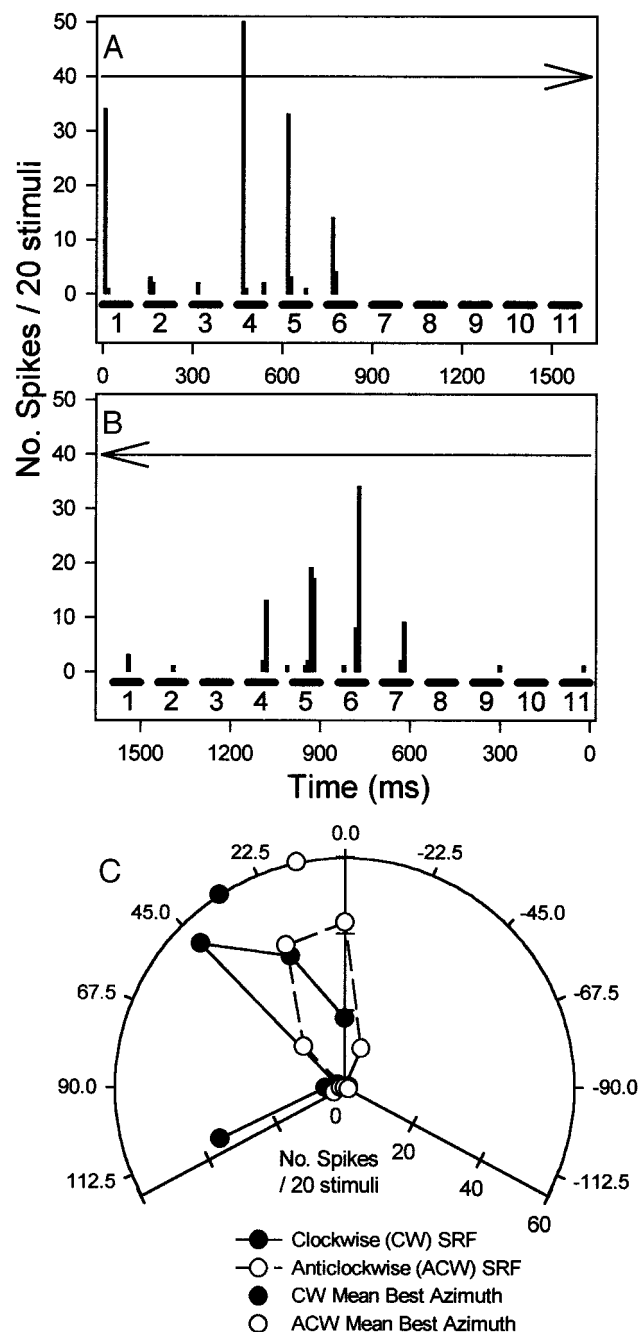


FIG. 1. Poststimulus time histograms (PSTHs) to clockwise (CW) apparent motion (A) and anti-clockwise (ACW) apparent motion (B). The 11 speaker presentations are denoted as horizontal bars under the PSTH, indicating the duration of the ON times (100 ms) and OFF times (50 ms). In A, the time axis runs left-to-right; in B, the time axis runs right-to-left, such that equivalent locations within the speaker array (but not equivalent times) line up on the PSTH plots. This emphasizes a major feature of our data: that many neurons produce partially overlapping spatial receptive fields (SRFs) to apparent motion stimuli of opposite directions. C: polar plot illustrating the dynamic SRFs recorded to CW (\bullet , —) and ACW (\circ , - - -) motion. Spike counts, plotted on the radial axes, are total number of spikes recorded during the 20 repeats of the 100 ms of stimulus at each location. The mean best azimuth for each direction of motion is plotted on the circumference of the plot; CW, \bullet ; ACW, \circ .

stimuli moving in the CW direction, i.e., starting in the contralateral field (see Figs. 1 and 2, *I–O*), and were rare for ACW motion (see Fig. 2*P*).

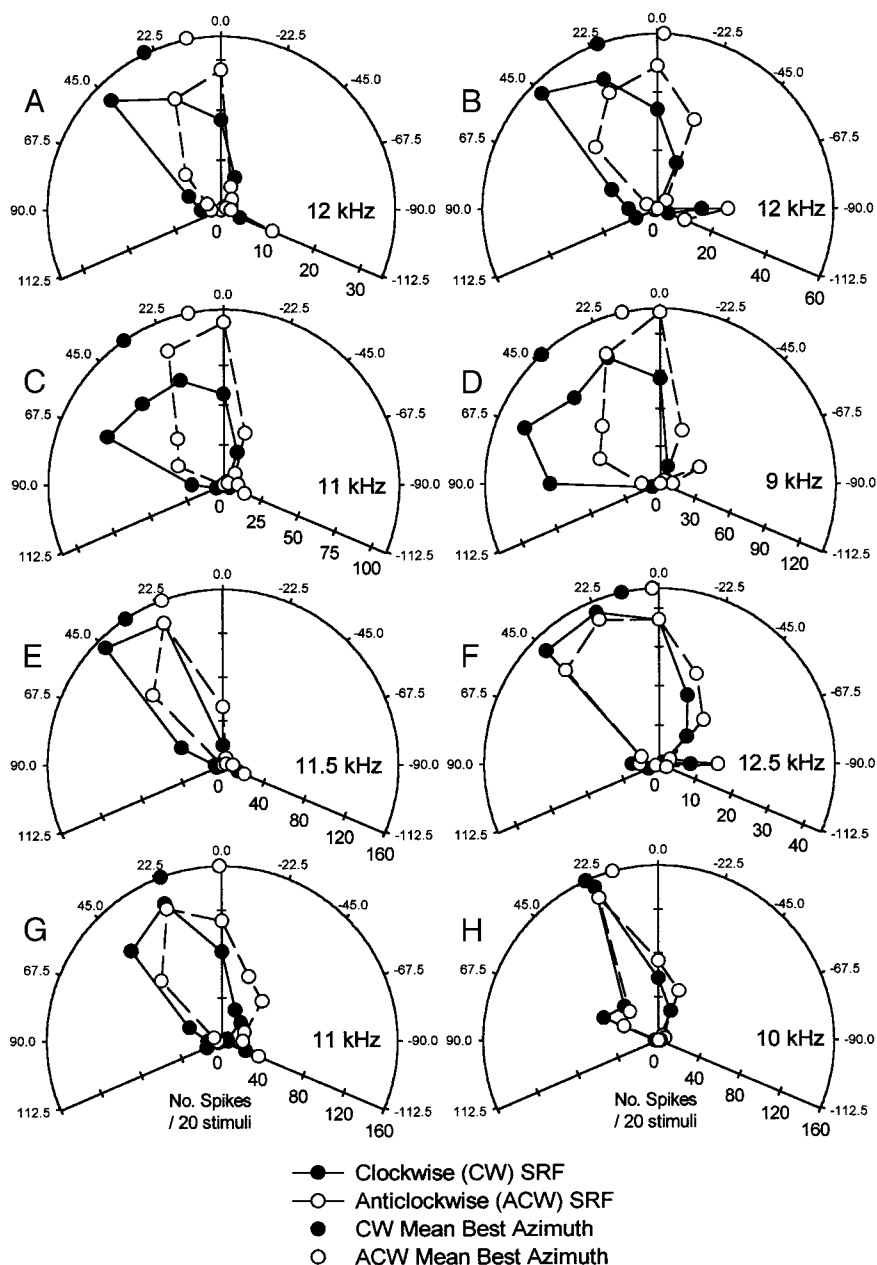


FIG. 2. A–P: dynamic SRFs of 16 inferior colliculus (IC) neurons to CW (● and —) and ACW (○ and ···) motion. Mean best azimuths calculated over *speakers* 2–10, for the 2 directions of motion, are indicated on the circumference of the plot by either ● or ○ (CW and ACW best azimuths, respectively). Unit BF is indicated on each plot. A–H: SRFs from units with little or no ON activity and that varied in the extent to which SRFs differed in response to CW and ACW motion. SRFs in F and H showed most overlap to the 2 directions, whereas those in C and D showed less overlap.

Comparison of dynamic SRFs to CW and ACW apparent motion

An obvious feature of Fig. 1C is that SRFs to the two motion directions overlap only partially. Relative to each other, they are skewed toward the direction from which the stimulus has moved with mean best azimuths for CW and ACW motion of $+33.1$ and $+12.2^\circ$, respectively. The extent to which SRFs to the two directions of motion overlapped varied considerably in different neurons. Figure 2, A–P, shows SRFs of a subset of 16 IC neurons to CW and ACW motion in response to 100-ms tone bursts, separated by 50-ms OFF times, at sequential speakers in the array. Neurons showed different degrees of disparity between SRFs to the two directions (cf. Fig. 2, H and O).

Figure 3A compares mean best azimuths for CW and ACW motion calculated over *speakers* 2–10 (i.e., from $+90$ to -90°) for the 91 neurons. Across most neurons, dynamic SRFs to CW motion were skewed toward relatively more contralateral best

azimuths compared with dynamic SRFs to ACW motion. Virtually all of the points lie below the line representing equivalence. The averaged mean best azimuth was $+31.4 \pm 15.5^\circ$ (mean \pm SD) for CW motion, and $+14.9 \pm 16.1^\circ$ for ACW motion. Mean best azimuths for CW motion were significantly more contralateral than those for ACW motion (ANOVA, $P < 0.0001$). Differences in mean best azimuth for individual neurons ranged from -13.1° (contralateral re. ipsilateral) to $+50.1^\circ$. Only four neurons showed more contralaterally positioned best azimuths for ACW motion than for CW; i.e., a negative difference. When *speakers* 1 and 11 were included in the calculation of mean best azimuth, a similar trend was observed, albeit with more scatter (i.e., CW dynamic SRFs were skewed to more contralateral positions; data not shown). The averaged mean best azimuths for CW and ACW motion when *speakers* 1 and 11 were included in the analysis, were $+42.2$ and $+14.3^\circ$, respectively, with the individual differ-

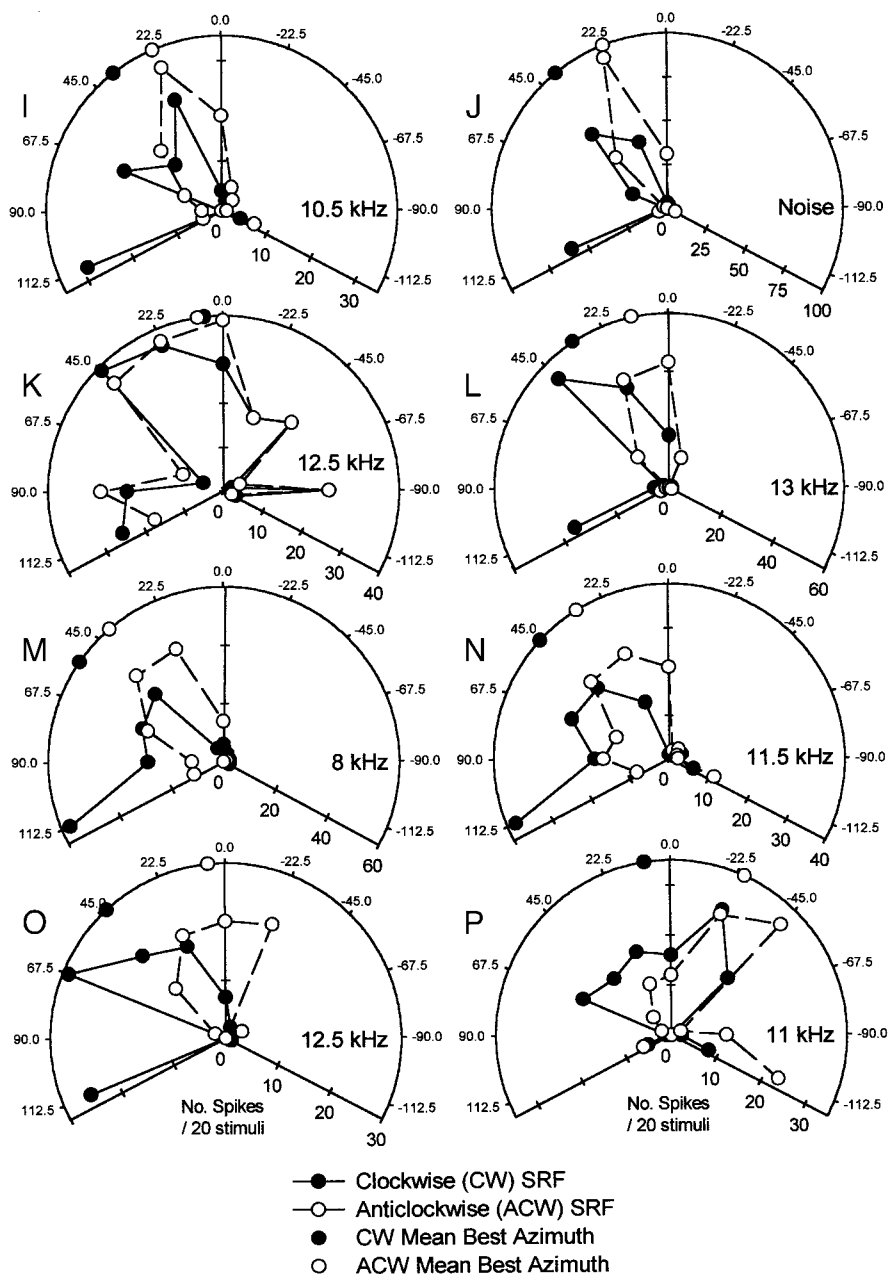


FIG. 2 (continued). I–L: SRFs for 4 units with ON activity that was generally distinct from the main body of the dynamic SRF. For these units, the main body of the SRFs to the 2 directions were largely overlapping, resulting in similar best azimuths. The SRF in J was from 1 of 4 neurons that responded preferentially to broadband noise, and did not, therefore show a BF. The SRF in K demonstrated a less commonly observed broad SRF with a more complex pattern. While the ON response is separated from the main body of the SRF, it may be that there is a secondary lobe of the response stretching into contralateral space from $+90^\circ$ and extending beyond the range of the speaker array. M and N: SRFs of 2 units with ON activity, which in the CW direction (●), appears to form part of the main body of the SRF. The best azimuths for CW motion are generally more contralateral than generally observed, even when the activity at *speakers 1* and *11* is omitted from the calculation (see RESULTS). O: the SRF of a unit with ON response to CW motion distant to the remainder of the dynamic SRF, which shows less overlap with the SRF for ACW motion. P: a rare ON response at *speaker 11* for ACW motion. For this neuron, the best azimuths to either direction of motion are shifted more toward and into the ipsilateral hemisphere compared with most other neurons sampled.

ences ranging from -18 to $+84.6^\circ$. Including the ON responses shifted CW best azimuths further into contralateral space ($+31.4$ to $+42.2^\circ$) but had no effect on ACW best azimuths ($+14.9^\circ$ compared with $+14.3^\circ$ for *speakers 2–10*), thus supporting our rationale for exclusion of responses to *speakers 1* and *11* from the analyses.

Comparison of discharge rates to CW and ACW motion

The dependence of SRFs of individual neurons on the direction of the stimulus motion could be taken to indicate that IC neurons are sensitive to motion direction per se as has been suggested for a proportion of neurons in the barn owl IC (Wagner and Takahashi 1992). However, an equally plausible, and perhaps simpler, explanation is that the effect of repeated stimulation over time and, in this case, over different spatial positions produces adaptation of the response during the course

of the motion sweep. Thus later speakers in the motion sweep evoke fewer spikes, irrespective of the direction of motion. A consequence of this explanation is that responses to the two motion directions might be expected to be similar in terms of the total number of spikes elicited by either direction of motion. This indeed appears to be the case. Figure 3B compares the total number of discharges evoked over the 20 trials of ACW motion, with the total number evoked over the 20 trials of CW motion, when *speakers 2–10* only are included, and indicates that total evoked discharges were, in fact, very similar for apparent motion in the two directions. Ratios of ACW to CW discharges for 89/91 neurons were in the range 0.81 to 1.63, suggesting that they were not selective for one direction of motion over the other. Selectivity for motion direction is often defined as a discharge ratio of 2:1 for one direction over the opposite direction (e.g., Stumpf et al. 1992). The remaining

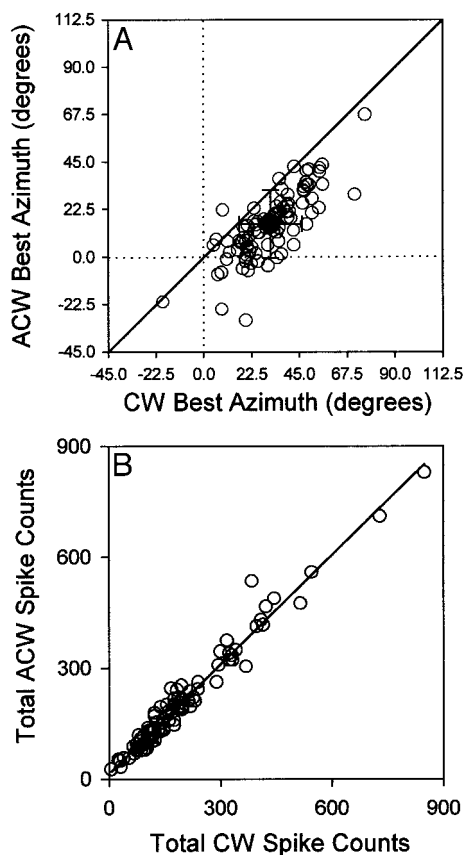


FIG. 3. *A*: mean best azimuths calculated over $\pm 90^\circ$ (*speakers 2–10*) for CW and ACW motion. —, equivalence. *B*: total number of counts (spikes per 20 stimuli) plotted for ACW motion plotted as a function of discharge rate for CW motion (spike counts relate to *speakers 2–10* only). Linear regression analysis of these data indicated a correlation coefficient, r , of 0.963, which was significant at the level of $P < 0.0001$ (ANOVA of the regression analysis data).

two neurons had ratios of 2.04 and 4.33 respectively. However, these neurons had very low numbers of evoked spikes (fewer than 1 spike evoked for each of the 20 motion sweeps in the CW direction). Thus IC neurons were not selective for the direction of sound-source motion, at least for the motion paradigm here described.

Motion-direction-dependent shifts in SRF borders

Consistent with the notion that adaptation of neural responses over time contributes to the relative skewing of SRFs for CW and ACW motion, the position of the borders of SRFs depended on motion direction. The positions of dynamic SRF lateral and medial borders were calculated at 50% maximum response amplitude for both directions of motion (defined in METHODS) over *speakers 2–10*. The azimuthal positions of these borders, along with the best azimuth for each neuron with definable borders (64 of the 91 units recorded), are shown in Fig. 4, *A* and *B*, for CW and ACW motion, respectively. Clockwise borders (Fig. 4*A*) were more contralaterally positioned than ACW borders (Fig. 4*B*). With one exception, CW border positions (medial or lateral) were *always* more contralateral than the equivalent ACW border positions. The azimuthal distance covered by the SRFs at 50% maximum response ranged from 38.4 to 189.0° for CW motion, and from

27.0 to 194.6° for ACW motion. The mean 50% spread for CW motion was $81.9 \pm 28.9^\circ$ and for ACW motion was $80.0 \pm 30.4^\circ$. There was no significant difference between the values of 50% spread for CW and ACW motion (ANOVA, $P = 0.713$). There was no significant correlation between the 50% spread of the SRF and the mean best azimuth position (CW motion: $R^2 = 0.045$, $P = 0.091$; ACW motion: $R^2 = 0.018$, $P = 0.288$; $R^2 =$ correlation coefficient, P value from ANOVA of the regression analysis data). Average displacement of the border position from CW to ACW motion was $+18.6 \pm 16.2^\circ$ (mean \pm SE; range -3.5 to $+76.5^\circ$) for the lateral border and $+17.8 \pm 12.3^\circ$ (range 0.0 to $+58.5^\circ$) for the medial border. There was no significant difference between the lateral and medial border displacements (ANOVA, $P = 0.737$).

The remaining 27 neurons could not be classified as having these borders as their SRFs tended to be more contralaterally positioned and, as such, a lateral border position could not be calculated for the CW SRF and often for the ACW SRF.

Effects of changing the velocity of apparent motion

If adaptation of excitatory responses contributes to differences in SRFs to the two motion directions, then for slower

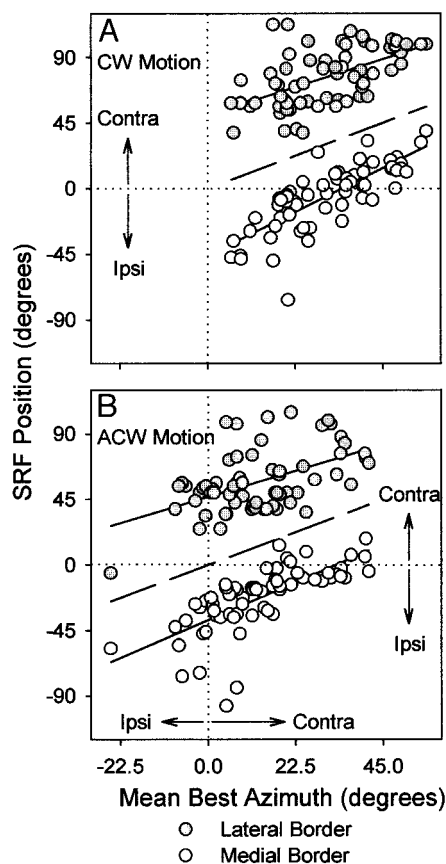


FIG. 4. The positions of lateral (\bullet) and medial (\circ) borders at 50% maximum response amplitude, plotted as a function of the mean best azimuthal position. *A*: border positions of SRFs in response to CW apparent motion. *B*: border positions of SRFs in response to ACW apparent motion. A linear regression line is fitted to the border position data on each graph. The remaining (---) line plots equivalent point on either axis, and indicates that the lateral border positions are found further into contralateral space than the mean best azimuth, whereas the medial border positions are found further toward ipsilateral space.

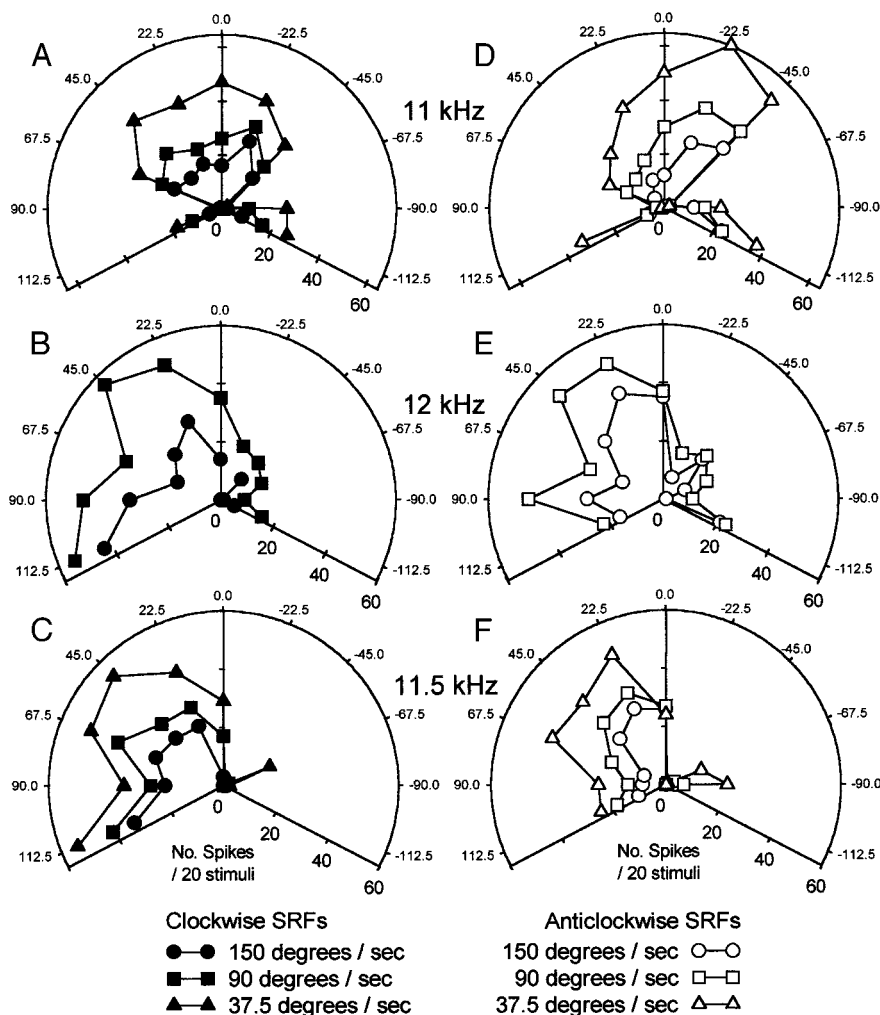


FIG. 5. A–C: SRFs to CW motion; D–F: SRFs to ACW motion for the same 3 neurons. Different velocity apparent motion are indicated by different symbols; circles, squares, and triangles represent velocities of 150, 90, and $37.5^\circ \text{ s}^{-1}$, respectively. For clarity, only 3 different angular velocities are indicated on these polar plots.

motion velocities, i.e., where the OFF time between successive speaker presentations is increased, differences to the two directions should be less marked, as the increased recovery time between each speaker activations will enable neural excitability to recover from the effects of prior excitatory stimulation. Specifically discharge rates to both directions of motion might be expected to increase with decreasing motion velocity, and this increase should be greater for later-activated speakers in the array for either direction of motion. This should have the consequence that SRFs to the two directions of motion become more similar with decreasing stimulus velocity.

The angular velocity of apparent motion was varied by altering the duration of the silent interval between successive speaker activations, to produce angular velocities of 37.5, 64.3, 75, 90, 112.5, and 150° s^{-1} . Responses of 28 neurons were examined using some or all of the various speeds, to both the CW and ACW directions. Figure 5 shows the effect of increasing stimulus OFF time between consecutive speaker presentations for three typical IC neurons. In general, as stimulus OFF time was increased, reducing the motion velocity (a result of decreasing stimulus repetition rate), the magnitude of the response at each location within the unit's receptive field increased, and the SRF broadened. The increase in discharge rate with increasing OFF time is shown in Fig. 6A. Using motion sweeps with a 50-ms OFF time (150° s^{-1} velocity) as the control

condition (i.e., 100% discharge rate), there was an increase in discharge rate, from 137% of the control rate at $112.5^\circ \text{ s}^{-1}$ (100-ms OFF time), to 212% of the control rate at $37.5^\circ \text{ s}^{-1}$ (500-ms OFF time).

Figure 6, B–D, illustrates the azimuthal angles of the border positions and the mean best azimuths for different motion velocities for the 16 (of 28) neurons that demonstrated definable borders. The effects of decreasing stimulus velocity (by increasing gap duration) on mean best azimuth and borders were identical for CW and ACW motion. Dynamic SRFs to both directions of motion expanded on their *outgoing* side (Fig. 6, B and D), indicating a broadening of the receptive field and, as a consequence, best azimuthal positions to the two directions converged (Fig. 6C). The average difference in mean best azimuth fell from $20.9 \pm 11.0^\circ$ at 150° s^{-1} to $6.5 \pm 4.4^\circ$ at $37.5^\circ \text{ s}^{-1}$ (mean \pm SD; Fig. 6F). For the 16 neurons with definable border positions, the lateral and medial SRF borders for CW and ACW motion become more similar with decreasing velocity (Fig. 6, E and G), producing dynamic SRFs to opposite directions of motion overlapped that were more spatially similar. This is reflected in the expansion of the angular spread of the SRFs (as measured at the 50% maximum response level) which increased progressively as the angular velocity decreased from 150 to $37.5^\circ \text{ s}^{-1}$ for both CW and ACW motion (see Fig. 6E).

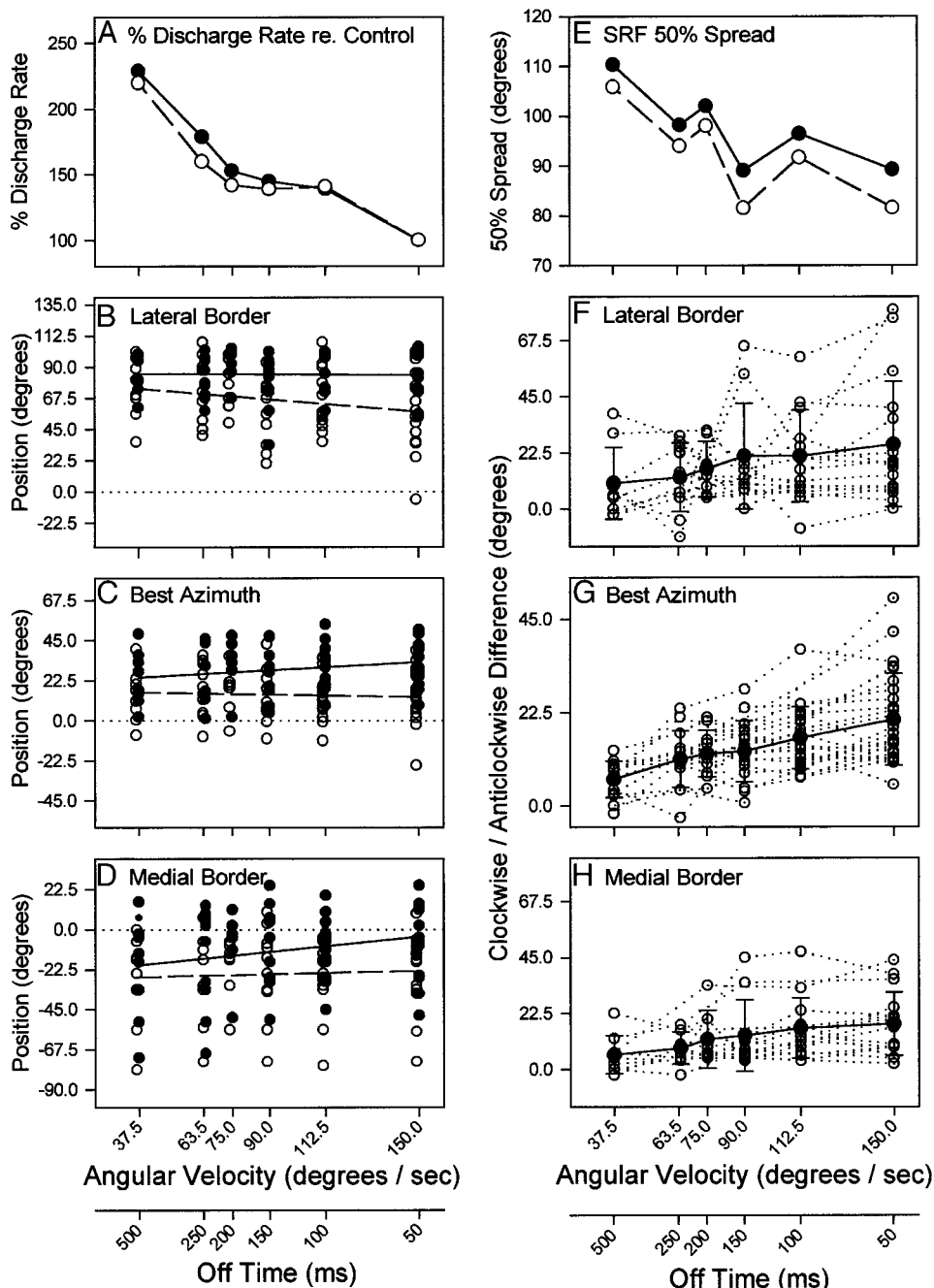


FIG. 6. A: comparison of the numbers of discharged spikes at different angular velocities. The ordinate indicates the numbers of spikes evoked by the submaximal velocity stimuli (over speakers 2–10) compared with that evoked by stimulation under “control” conditions of 100-ms stimuli duration separated by 50-ms OFF times (150°s^{-1}). This is expressed as a percentage of the control spike count, and plotted as a function of angular velocity (i.e., OFF time). ●, CW motion; ○, ACW motion. B–D: the positions of the lateral border B, best azimuth C, and medial border D for 16/28 neurons with definable border positions at different velocities. ●, CW SRF positions; —, regression line; ○, ACW SRF positions; - - -, regression line. E: comparison of the 50% spread of SRFs at different angular velocities; ●, CW motion; ○, ACW motion. F and H: displacement (CW to ACW dynamic SRF) of the lateral border position F, for each neuron at the different velocities (○, ···), ● and —, the mean \pm SD. G: difference in the best azimuths for CW and ACW motion, plotted as a function of angular velocity. ○, individual neurons’ results; ●, the mean difference for each velocity (\pm SD).

Responses to partial motion sweeps

For 11 neurons, we also examined the responses of IC neurons to partial motion sweeps in which only 4 of the 11 speakers were activated sequentially. Consistent with the adaptation-of-excitation hypothesis, higher discharge rates were evoked when motion sweeps were initiated at speakers further into a neuron’s SRF than were evoked by the same speakers when they were presented in the context of following speakers that evoked relatively strong excitatory responses.

Figure 7, A–D, compares responses of four neurons to full motion sweeps in which all 11 speakers were activated, with responses recorded when only four consecutive speakers in the array were activated. The angular velocity of these full and short motion sweeps was held constant at 150°s^{-1} . In most

cases, these partial sweeps elicited response profiles which for some spatial locations did not overlap completely the responses to full sweeps. Of the 11 neurons examined with partial sweeps, 9 demonstrated such responses (Fig. 7, A–C). The remaining two neurons showed response profiles to partial sweep stimuli, which were much more similar (overlying) to those of the complete sweep stimuli (e.g., Fig. 7D).

The partial motion sweeps, which began outside, and moved into, the SRF, elicited responses of a similar magnitude at a given position to those elicited by the complete motion sweep. For short sweeps beginning after the peak of the SRF, however, the responses to the partial sweeps were often larger than those to full sweeps at some locations, at least until the stimuli moved well outside the main body of the SRF. Additionally, at

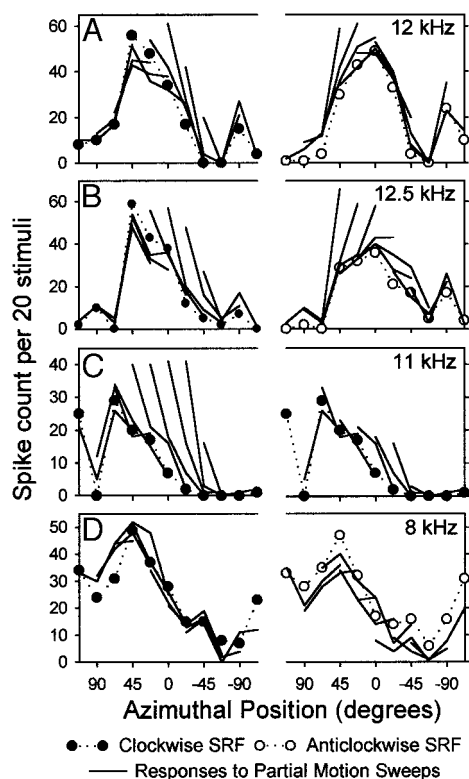


FIG. 7. A–D: comparisons of responses to full (225°) and partially overlapping (90°) sweeps. Full motion sweeps are indicated by the symbols joined by lines; \bullet and \circ , CW and ACW motion respectively. Lines without symbols indicate responses to partial motion sweeps, in either direction (on the appropriate graph). A, B, and D indicate data recorded for 3 neurons to CW (left) and ACW (right) stimuli. C: data recorded for CW motion sweeps (full and partial) only for 1 neuron. Left: the data for all 4 speakers contributing to the partial sweeps. Right: the same data, with the response to the 1st speaker in the partial sweeps excluded (to remove the possible influence of an ON response for this neuron).

later positions in a partial sweep, responses could be reduced compared with those from the same locations when elicited earlier in a partial sweep (Fig. 7C).

It might be argued that the first response for each short sweep is significantly elevated by an ON response. However, similar patterns are seen in neurons demonstrating such an ON response (for example, Fig. 7C) and those without this feature (for example, Fig. 7, A and B). Even if the response at the first stimulus locations for the short sweeps is excluded, a similar pattern holds for the remaining data (Fig. 7C, right).

DISCUSSION

The major finding of this study is that SRFs of IC neurons are influenced by the temporal features of apparent-motion stimuli in which the percept of motion is achieved by discrete and sequential activation of speakers positioned in azimuth around the animal's head. With slow velocities, SRFs to CW and ACW motion were similarly spatially tuned, both in terms of the sharpness of their tuning and in terms of their mean best azimuth. As velocity was increased, however, by reducing the duration of the off interval between successive presentations in the speaker array, SRFs sharpened and were increasingly skewed toward the direction from which the sound source appeared to move. These results, therefore, demonstrate that

there is an interaction between the location of a sound source, a neuron's prior history of stimulation, and the temporal pattern of that stimulation. However, no neurons were observed to respond preferentially to one particular direction of motion. In all cases, spike counts to opposite motion directions, for the same motion velocity, were similar, consistent with Wilson and O'Neill's (1998) recent study in the moustached bat in which a similar motion paradigm was used. We interpret our observation of a "skewing" in SRFs toward the direction from which the sound appears to move as consistent with "directional-sensitivity" rather than "directional-selectivity." Again this accords with the data of Wilson and O'Neill (1998) in the bat, although differences in SRFs to CW and ACW motion were smaller in their study than in the present study. This is consistent with a nonspecific mechanism for motion processing and accords with the more robustly controlled of previously-published experiments (e.g., Ahissar et al. 1992), in which there is also no evidence of motion-specialized cells but, rather, of spatially-tuned neurons being influenced by the direction or rate of motion.

Mechanisms responsible for motion-influenced SRFs

We believe the simplest mechanism that could account for our data are related to the fact that neuronal excitation producing these responses adapts over time with repeated stimulation. Since movement through the SRF in one direction or the other evokes activity over a number of speaker positions, neuronal firing will adapt as the stimulus moves further through the SRF. For stimuli of opposite directions, this produces *partially overlapping* dynamic SRFs, which are relatively more tightly tuned to auditory space, and therefore in one sense, relatively more "sensitive" to the direction of the sound. As the stimulus velocity is reduced (by increasing the OFF time between successive stimulus presentations), however, the neuron initiates its response at the same spatial position, but the longer recovery time between successive presentations enables it to recover from the effects of adaptation. Discharge rates are therefore higher at spatial positions further into the sweep expanding the outgoing border of the SRF. Thus with decreasing velocity, neurons become increasingly responsive to a larger portion of space; i.e., they become relatively less tightly tuned, spatially. Since this occurs for both directions of motion, it has the effect that the SRFs to the opposite directions converge to overlap almost completely, and therefore show less "sensitivity" to the direction of motion. An interesting issue, which was not addressed in the current study, is how neurons might have responded to a continuous sound rather than a series of discrete sounds. Information at stimulus onset appears to dominate the perceived location of a sound (Buell et al. 1991). It might be speculated that the discrete, sequential nature of the stimuli used in the present study provided information for processing motion cues that would otherwise have been absent in a continuously-moving sound even if that information constituted simply information concerning stimulus onsets.

A similar mechanism of adaptation of excitation as we propose here was suggested by McAlpine et al. (2000) to account for the responses of IC neurons to interaural phase modulation (IPM), a stimulus in which the motion paradigm is one of continuous movement back and forth around a center interaural phase disparity (IPD). With IPM, IC neurons re-

spond to movement toward favorable IPDs with higher discharge rates than to movement away from favorable IPDs, irrespective of the direction of motion. Such responses had previously been interpreted as evidence for motion sensitivity in IC neurons (Spitzer and Semple 1993, 1998). However, as McAlpine et al. (2000) suggest, Spitzer and Semple's data can be explained satisfactorily by a mechanism of adaptation-of-excitation hypothesis, whereby a neuron's *response* history rather than the stimulus history per se determines the subsequent responsiveness.

One final issue that needs to be addressed is the occasional presence of ON responses to the first speaker in the CW motion sweep (*speaker I*). This was usually not evoked by the first speaker in the ACW motion sweep (*speaker II*). A possible explanation for the appearance of this response is that when stimulation of the ipsilateral ear precedes that of the contralateral ear an (early) inhibitory event suppresses this component of the response. Stimulation of the contralateral ear before the ipsilateral ear produces excitation before the onset of any inhibitory event, and thus produces an ON response to the first speaker. Although neurons in the IC fall into many classes of binaural interaction (e.g., Irvine 1992) depending on their relative excitation or inhibition by contralateral and ipsilateral inputs, the free-field stimulation paradigm used in this study does not allow the determination of specific neuronal binaural interaction, normally assessed using monaural stimuli. As all our neurons have BFs in the range of 2.5 to 16 kHz, we assume that most will be either EI or EO neurons. Finally, it should be noted that studies of the responses of low-frequency neurons to dynamic interaural phase cues routinely disregard up to the several *seconds* of the response to remove the effects of ON responses (e.g., Spitzer and Semple 1993; Takahashi and Keller 1992; Yin and Kuwada 1983).

Comparison with previous neurophysiological studies

Evidence for neurons involved in auditory-motion processing has been presented in a number of studies, using real (e.g., Ahissar et al. 1992; Sovijärvi and Hyvärinen 1974) and simulated closed-field (Altman et al. 1970; Doan and Saunders 1999; Gordon 1973; Spitzer and Semple 1993; Stumpf et al. 1992) motion. Sovijärvi and Hyvärinen (1974) reported a small number of auditory cortical neurons (8/25) selective to the direction of sound source movement in a free-field situation using continuous sounds presented with a manually-moved speaker. Subsequently, Altman (1987) reported primary auditory cortical (A1) neurons to respond selectively to the direction of phase change of dynamically varying interaural phase disparities. Toronchuk et al. (1992), using AM ramps presented either dichotically or diotically, observed sensitivity to both azimuthal and radial motion in primary auditory cortex, while Doan and Saunders (1999) similarly demonstrated motion-sensitivity in rat auditory cortex to azimuthal and radial motion using a fully reconstructed virtual space stimulus.

We can postulate at least three reasons for our failure to observe motion-sensitivity in the responses of IC neurons. First, it may be related to the relatively small proportion of neurons in the IC that are sensitive to auditory motion cues, as reported previously (e.g., Altman 1968; Wagner and Takahashi 1992; Yin and Kuwada 1983), compared with thalamus (Altman et al. 1970) or primary auditory cortex (Ahissar et al.

1992; Altman 1987). Altman et al. (1970) described almost half of cells (22/50) in the medial geniculate body of the cat as being directionally selective in response to dichotic clicks on the basis that they showed a much stronger response to one direction of movement than the other. This was compared with just 10/79 neurons in the IC (Altman 1968). This suggests an increased prevalence for motion detectors at successively higher stations in the central auditory pathway.

Second, differences between stimuli used in the various studies of motion sensitivity may contribute to the differences in neuronal responses reported. Spitzer and Semple (1993) reported the vast majority of IC neurons to be sensitive to the dynamic interaural phase cues of IPM, a stimulus they described as "more physiologically realistic" than other motion paradigms such as binaural beats. A possible interpretation, therefore of the current study, and previous studies (e.g., Wagner and Takahashi 1992; Wilson and O'Neil 1998), is that sequential activation of an array of speakers does not resemble closely enough a moving sound source. Only Wagner and Takahashi (1992) reported neurons in the barn owl IC that showed markedly different discharge rates to CW and ACW motion. Even then the proportion showing such behavior was small, and these neurons tended to be located in the external nucleus, rather than the central nucleus, of the IC. In common with Wilson and O'Neill's (1998) observations, differences in discharge rate for opposite directions of motion in the current study were small, and are unlikely to provide any significant basis for directional selectivity/sensitivity.

A final possible reason lies in the interpretation of what constitutes motion sensitivity in the responses of auditory neurons. Thus while Spitzer and Semple (1993) argued that many IC neurons were highly motion sensitive, McAlpine et al. (2000) ascribed the effects observed to neuronal response history rather than to any specific element of the motion stimulus.

Motion sensitivity using static spatial processors

The psychophysical evidence for the existence of a specialized system for motion processing remains controversial. Evidence suggesting specialized motion detection does exist. For example, thresholds for spatial resolution in motion detection are independent of thresholds for spatial resolution per se (Perrott and Musicant 1981), while the existence of auditory motion aftereffects (Grantham 1989, 1998), suggesting fatigue of motion detection mechanisms, appears to indicate the presence of an auditory-motion analysis system at some level in the auditory pathway above the level of binaural integration. Perrott and Marlborough (1989) described reduced minimal audible movement angle thresholds for sounds played continuously throughout a motion sweep compared with those recorded when the sound marked the endpoints only of the motion trajectory. Conversely Grantham's (1986) demonstration that thresholds for angular movement detection depend on the angular extent of the motion rather than the simulated velocity or stimulus duration suggests that judgements of motion derive from comparison of sound source position at the beginning and end of its trajectory. Similarly, Perrott and Tucker (1988) demonstrated evidence that both static and dynamic spatial discrimination are dependent on the same underlying mecha-

nism, suggesting that additional hypothetical mechanisms, such as specialized motion detectors, were not required.

As with neurophysiological studies, at least part of the difficulty lies in the nature of the stimulus and whether it may be considered sufficient to enable a distinction to be made between the effects of static and dynamic spatial cues. It remains incumbent on researchers to demonstrate unequivocally that the motion cue per se is the determining factor in either a subject's or a neuron's response to auditory motion. Until such time as this issue is addressed, the effort to ascribe motion sensitivity in the auditory system to a process that is separate to, and distinct from, static localization (e.g., Perrott and Marlborough 1989; Perrott and Musicant 1981) may not be possible. Of potential concern also is the seeming desire to create a dichotomy between static and dynamic motion processing where none may be required, particularly as, on balance, the majority of neurons reported in neurophysiological studies respond to both static stimuli and dynamic stimuli. This suggests that static motion processing at least contributes to the perception of a moving sound source, and indeed may even dominate it, compared with the contribution of a specialized motion processing system. As such, a more fruitful exercise might be to attempt to explain how neurons responsive to static sound sources may contribute to the percept of motion.

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