Response of Cat Inferior Colliculus Neurons to Binaural Beat Stimuli: Possible Mechanisms for Sound Localization

Abstract. *The interaural phase sensitivity of neurons was studied through the use of binaural beat stimuli. The response of most cells was phase-locked to the beat frequency, which provides a possible neural correlate to the human sensation of binaural beats. In addition, this stimulus allowed the direction and rate of interaural phase change to be varied. Some neurons in our sample responded selectively to manipulations of these two variables, which suggests a sensitivity to direction or speed of movement.*

In order to localize the position of a sound source, the auditory system relies primarily on binaural information. For low-frequency signals ($\gtrsim 1500$ Hz for humans) a salient cue is the interaural phase difference (*1*). Neurophysiological and psychoacoustical studies of low-frequency sound localization have usually used dichotic sinusoidal stimuli in which the phase difference is achieved by delaying the stimulus to one ear with respect to the other. Rose *et al.* (*2*) found that, for some cells in the inferior colliculus of the cat, the discharge rate was a cyclic function of interaural delay with a period corresponding to that of the stimulating frequency. The cycling nature of the curve indicated that these cells were sensitive to the phase difference between the sinusoids delivered to the two ears. Similar phase-sensitive cells have been found in other parts of the mammalian auditory system (*3*). These cells are thought to be involved in sound localization.

Another way of varying the phase relationship between sinusoidal stimuli is to deliver to one ear a sine wave of frequency f which differs only slightly from the frequency $(f + f_b)$ of the sine wave delivered to the other ear. In humans, such a stimulus, which we call a binaural beat stimulus, evokes the sensation of beats at the beat frequency of f_b. The stimulus provides an orderly and continuously changing interaural phase. To our knowledge there is only one study on evoked potentials in the cat superior olive (*4*) that systematically used binaural beats as a stimulus. We now describe the response of interaural phase-sensitive cells in the cat inferior colliculus to binaural beat stimuli.

Fifteen adult cats with clean external ears were used. Cats were anesthetized with sodium pentobarbital, and the pinna and external meatus of both ears were removed. The dorsal surface of the right inferior colliculus was exposed. A chamber was mounted on the skull, filled with mineral oil, and sealed with a glass plate to which a hydraulic microdrive was attached. A metal ear-probe was inserted into each external meatus to a distance of 1 to 3 mm from the tympanic membrane. For each experiment, the sound delivery system was calibrated (under computer control) for intensity over the frequency bandwidth of interest (*5*). Gold- and platinum-plated indium microelectrodes were used to record the activity of single collicular neurons (*6*).

The response of a collicular neuron to a binaural beat stimulus with a beat frequency of 1 Hz is illustrated by a peristimulus time histogram (PSTH) (Fig. 1A). The neuron responded with three bursts during the 3-second interval in a restricted portion of each cycle of f_b. Figure 1B shows the response of the same cell to a 1000-Hz tone burst delivered to each ear, but with the onset of the stimulus to the contralateral ear (with reference to the site of recording) delayed in 100-μsec steps to a maximum of 3000 μsec; this sequence was then repeated with the stimulus to the ipsilateral ear delayed.

As in the response to the binaural beat (Fig. 1A), the interaural delay curve (Fig. 1B) shows that the cell discharge rate was modulated by changes in the interaural phase. A comparison of the responses of this cell obtained by the two methods is shown in Fig. 1C. The histogram was generated by folding the PSTH of Fig. 1A on the period of f_b (1 Hz), while the dotted line is the average delay curve generated by folding the cyclic function of Fig. 1B on the period of the stimulating frequency (1000 Hz). The cell discharged maximally when the signal to the contralateral ear led in phase by approximately 0.3 (all phase measurements are given in fractions of a cycle). The discrepancy in phase between the estimates based on the two methods is small (0.02). Thus far we have studied 53 neurons in which responses to the interaural delay and beat stimuli were compared in this fashion. Included in this sample are cells of varied response patterns, for example, onset, sustained, and pauser. More than 90 percent of these cells responded reliably to both types of stimuli; calculations of the peak phase angles determined by the two methods were highly correlated ($r = .94$) (*7*).

When the frequencies of tones to the two ears are interchanged in the binaural beat stimulus, the direction of the interaural phase change will be reversed. In addition, the rate of change of phase can be increased by using higher f_b. Figure 2A shows a commonly seen response of an inferior colliculus neuron to the dif-
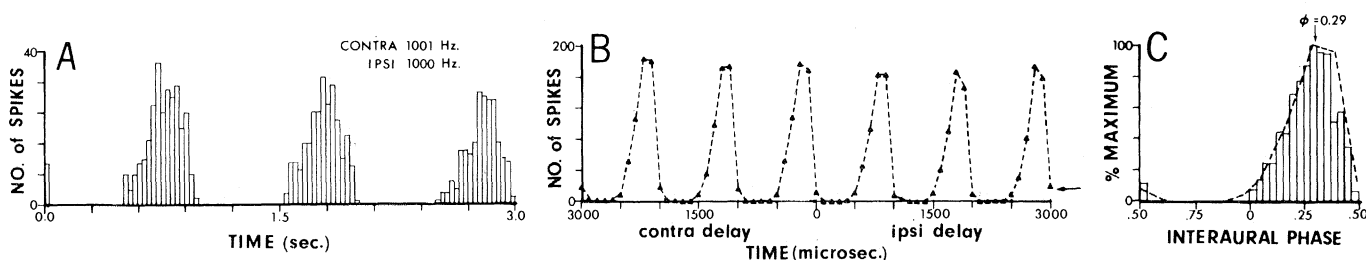

Fig. 1. (A) Peristimulus time histogram of the response of a collicular neuron to a binaural beat stimulus. The intensity of the tone was 50 dB sound pressure level (SPL) (with reference to 0.0002 dyne/cm²) to both ears. The stimulus consisted of five presentations, 3 seconds on, repeated every 3.5 second. (B) Interaural time delay curve for the same cell. Each point shows the total number of impulses discharged by the cell during the stimulus as a function of the interaural delay. On the left are the points obtained when the contralateral ear was delayed from 3000 to 0 μsec, and on the right when the ipsilateral ear was delayed from 0 to 3000 μsec in 100-μsec steps. The arrow on the right shows the discharge when the contralateral ear was stimulated alone. All stimuli were 1000 Hz, 50 dB SPL, of 1 second duration, and presented once. (C) Period histogram of the binaural beat response and the averaged delay curve, normalized so that comparisons of their shapes can be made. Since the stimuli were turned on 180° out of phase, the abscissa has been shifted by a half a cycle. Thus, in this and all subsequent period histograms, $\phi = 0$ corresponds to the time at which the stimuli are exactly in phase. The peak phase angle ($\phi = 0.29$) was calculated from the period histogram (*7*).

ferent directions and rates of change of interaural phase. The discharge rates of this cell were similar for all f_b up to 10 Hz and were independent of the direction of phase change. As f_b increased, however, the peak phase angles of the period histograms shifted systematically. For most cells, this shift in phase was a linear function of f_b, which suggests that it resulted from a time delay. Because of this phase shift, the optimal interaural phase sensitivity of a cell should be best estimated when the difference between the frequencies delivered to the two ears is smallest. In the right-hand columns of Fig. 2, A and B, the interaural phase sequence was reversed; thus the abscissas of the period histograms have also been reversed. The majority of the cells we have studied are similar to the one illustrated in Fig. 2A, although from one cell to another there was considerable variation in the shapes of the period histograms, their peak phase angle, and their ability to follow high rates of change. We have studied cells that continue to show reliable locking to beat frequencies of up to 80 Hz.

A few cells in our sample were also sensitive to the direction or the rate of change of interaural phase, or both (Fig. 2B). The period histograms were markedly asymmetrical when the stimuli to the two ears were interchanged. Thus, when the stimulus to the ipsilateral ear was at a frequency higher than that to the contralateral ear (right column), the cell discharged vigorously in a phase-locked manner up to $f_b = 10$ Hz. When the stimulus to the contralateral ear was at a higher frequency, however (left column), the response of the cell was drastically reduced. We have also observed a few cells which responded much more vigorously at high than at low f_b, or vice versa, indicating a sensitivity to rates of change of phase.

The results (Fig. 2, A and B) can be understood if we interpret the binaural beat stimulus to simulate a moving sound source. The basis for this interpretation rests on the presumption that a tone moving along the azimuth will generate a continuously changing interaural phase similar to that created by the binaural beat stimulus (Fig. 2, C and D). When the stimuli to the two ears are in phase, the sound will be localized in the middle of the head. We have defined this point of zero phase difference as $\phi = 0.0$, or equivalently 1.0. In this example, the stimulus to the ipsilateral ear is lower in frequency, and the two sinusoids start in phase. The sound is assumed to be initially localized in the middle of the head

and to move gradually toward the contralateral ear, which is leading in phase ($0 < \phi < 0.5$). At the interaural phase equivalent to a half cycle, the perceived tone will jump to the ipsilateral ear although there may be a period of ambiguity during which the tone is not well localized. The degree of lateralization will depend on the interaural distance and the wavelength of the signal (8). As the interaural phase changes to $0.5 < \phi < 1.0$, the phase of the signal to the ipsilateral ear is now leading, simulating a movement of the source from the

ipsilateral ear back toward the midline. This movement is repeated for each complete phase change. Thus, for each cycle of f_b, there will be a simulated movement of the sound source from the ipsilateral to the contralateral ear. Neurons, such as those illustrated in Figs. 1 and 2, are most sensitive to a particular interaural phase and will respond each time during the cycle that that interaural phase occurs. Interchanging the frequencies of the signals delivered to the two ears reverses the direction of simulated movement, and increasing f_b mimics an
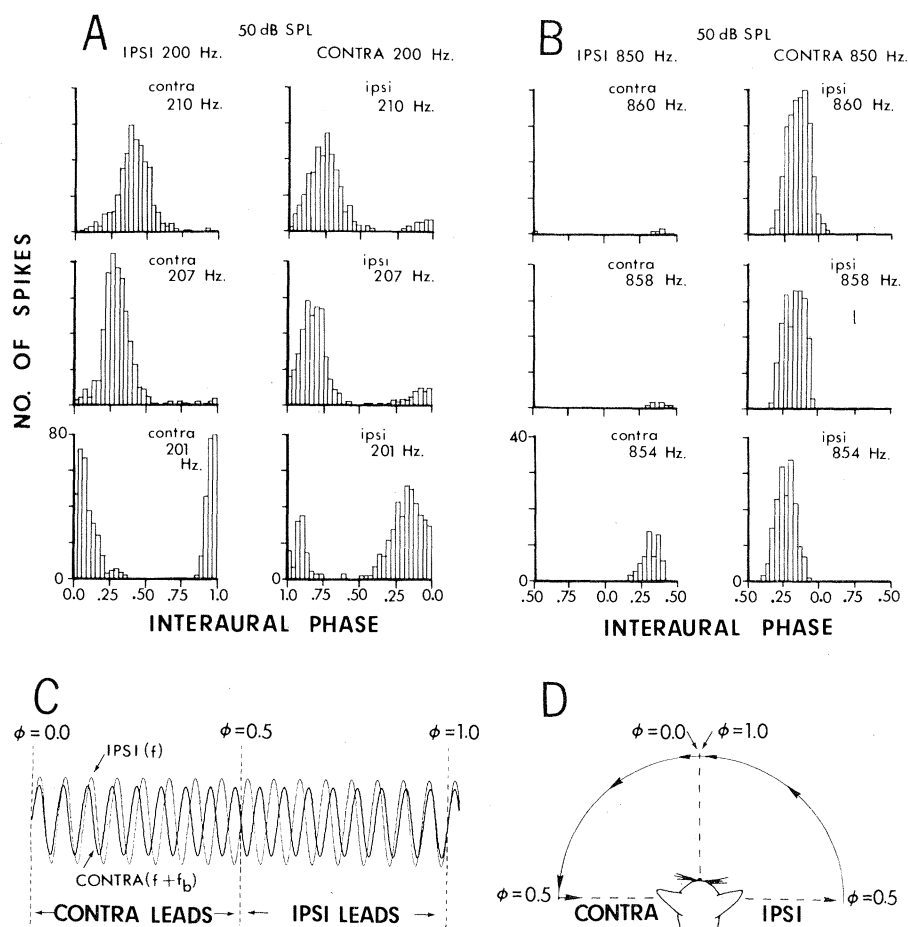

Fig. 2. (A and B) Period histograms of two neurons illustrating their responses to different beat frequencies and in the two directions of interaural phase change. (A) A cell that responded about equally in both directions and for different beat frequencies. The tones were turned on in phase so that the abscissa begins at $\phi = 0$. The stimulus was as in Fig. 1A. (B) A cell sensitive to the direction of interaural phase change. The cell responded preferentially when the stimulus to the ipsilateral ear was higher in frequency (right column). For phase changes in the opposite direction (left column), the cell responded with a few impulses, but was still phase-locked to the beat frequency. The stimulus consisted of ten presentations, 3 seconds on, repeated every 3.5 seconds. (C) Binaural beat stimulus. In this example, the stimuli were turned on in phase and the frequency of the sinusoid delivered to the ipsilateral ear was slightly lower than that delivered to the contralateral ear. For purposes of illustration, the amplitudes of the two sine waves are different and the frequencies of the tones are much lower than those used. This illustrates the manner in which the interaural phase slowly shifted from the signal to the contralateral ear leading ($0 < \phi < 0.5$) to the ipsilateral signal leading ($0.5 < \phi < 1.0$), through one complete cycle of the beat frequency. (D) Schematic diagram of the assumed movement of the sound source. The sound would actually be perceived to be within the head, but for simplicity we have drawn it as if it were projected into space. During the first half cycle, when the signal to the contralateral ear leads, the sound moves from the midline toward the contralateral ear. At $\phi = 0.5$, the sound will move to the ipsilateral ear [possibly with a period of ambiguity if the stimulating frequency is low (8)]. As the signals come back into phase during the last half cycle, the sound will move from the ipsilateral ear toward the midline.

increase in the speed. The response properties in Fig. 2B would be consistent with those of a cell exhibiting directional selectivity for sound sources moving from left to right at high velocities. There are other reports of directional sensitivity of auditory neurons using free-field or dichotic click stimuli, but the interaural phase sensitivities of the cells in these studies are not known (9).

The observation that most of the cells in our sample responded periodically at the rate of the beat frequency provides a possible neural correlate for the human psychoacoustic phenomenon of binaural beats (10). Human listeners report the sensation of beats up to $f \cong 60$ Hz. At very low beat frequencies ($f_b < 2$ Hz) subjects have reported a sensation of the tone moving in the head from one ear to another at the rate of f_b, in line with our interpretation that the binaural beat stimulus can simulate a moving sound source.

Although the binaural beat stimulus simulated the changing phase of the signals arriving at each ear for a naturally moving sound source, it cannot simulate the interaural intensity changes. These intensity differences are small for low-frequency sounds, but may still be a significant cue for sound localization. Furthermore, the pinna and external meatus play an important role in the natural situation. Nevertheless, the common symmetrical response to binaural beat stimuli (Fig. 2A) contrasts sharply with the more unusual asymmetrical responses when the frequencies to the two ears are interchanged (Fig. 2B), or when f_b is increased. This result at least implies a difference in sensitivity to direction or speed, or both.

Both the delay curves and the binaural beat period histograms suggest a mechanism for the center-surround organization described in the presumed avian homolog of the inferior colliculus of the owl (11). For most cells, the trough of the delay curve and period histograms is below the level of discharge that would be evoked by the contralateral ear alone (Fig. 1B). Hence there must be some inhibitory process that is active when the interaural phase relation corresponds to these troughs. When these curves are transformed into auditory space, one would expect the peaks to correspond to an excitatory receptive field with a limited spatial extent, bordered on both sides of the azimuth by inhibitory flanks.

As a technique for studying binaural interaction, the use of binaural beat stimuli is both efficient and practical. The strong correlation between response patterns generated by varying the interaural

delay and the binaural beat stimulus demonstrates the reliability of the method for studying interaural phase sensitivity while also providing information about the dynamic phase properties of the cells.

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6. By histological verification, all electrode tracks were found to traverse the central nucleus of the inferior colliculus.
7. The peak phase angles were found by calculating the phase of the first Fourier coefficient of the period histograms (binaural beat stimuli) or averaged delay curves (interaural delay stimuli).
8. In reality, only one frequency will have a period perfectly matched to the maximum interaural delay. For example, for an interaural distance of 8.3 cm (that is, an interaural delay of 250 μsec) and a sine wave of 2000 Hz (whose period is 2 × 250 μsec), the sound will presumably just be lateralized to one ear when the stimuli are 180° out of phase. For $f < 2000$, $\phi = 0.5$ corresponds to a delay longer than 250 μsec. During the time that the delay exceeds the physiological interaural delay, there will be an ambiguity as to the ear to which the source is lateralized. For $f > 2000$, ϕ will be 0.5 before the signal to one ear can lead the other by 250 μsec, so the sound never completely lateralizes to that ear. At increasingly higher frequencies the source will move smaller distances from the midline.
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12. We thank T. Buunen for suggesting the use of the binaural beat stimulus for simulating a moving sound source and J. E. Rose, J. E. Hind, and our colleagues in the Department of Neurophysiology for critical reviews of our manuscript. Supported by NIH grants NS 12732 (to J. E. Hind) and EY02606 (to T.C.T.Y.).

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Moment of Inertia:

Psychophysical Study of an Overlooked Sensation

Abstract. *The distribution of mass in an object held in the hand, as described by its moment of inertia, is a fundamental and potent but largely unrecognized contributor to the object's "feel." A limited set of experiments has produced Weber fractions for human differential sensitivity to this property in the approximate range of 1/5 to 1/3, which is about ten times the Weber fraction reported for lifted weights.*

Designers of hand-held tools and commercial products must often improve the "feel" of the object as part of improving its overall performance. It is possible to enumerate and test many obvious properties contributing to feel, such as weight and balance, and sensitivities to them can be found in standard references or obtained by relatively simple psychophysical tests. However, a fundamental property of a body—its moment of inertia (*I*)—has been largely overlooked both as a decided contributor to the feel of an object and as a sensation in its own right (*1*).

The *I* of a body is a measure of its inertial resistance to rotational acceleration just as the mass (*M*) is a measure of inertial resistance to translational acceleration (*2*). Unlike *M*, however, *I* depends upon the axis chosen for the angular rotation and has the dimensions of mass × (distance)². As the dimensions suggest, *I* can be increased by increasing *M* or by spreading the same mass out farther from the axis of rotation, just as the variance of a probability distribution increases as values depart from the mean. Therefore, with control over the shaping of a body of mass *M*, the three quantities, *M*, *I*, and *CG* (center of gravity), can be independent as long as no geometric restrictions are imposed. This independence still holds within limits as constraints such as length and diameter are placed on the body. Thus, two otherwise visually identical objects can have, for example, identical *M* and *CG* but different *I* values.

A simple experiment can demonstrate moment of inertia sensations. Tape a quarter to each end of a new unsharpened lead pencil, and, while holding it in the center between thumb and index finger in a horizontal position (for convenience), "twiddle" it like a rapid seesaw. Retape the quarters near the center of the pencil and twiddle it again. Now try to verbalize the difference between the two sensations.

Even subjects with scientific training attempting to describe the difference in