

**Uncertainty Relations in Interaural Parameters  
of Acoustical Stimulation: An Evoked Potential  
Study of the Auditory Cortex in the  
Anesthetized Cat<sup>1</sup>**

T.W. BARRETT<sup>2</sup>

*Department of Physiology and Biophysics,  
University of Tennessee Medical Units,  
Memphis, Tennessee 38103*

The registration of acoustical stimuli of differing interaural parameters (intensity, phase and time of signal arrival), on areas AI and AII of the cortex of anesthetized cats was studied using a Laplacian electrode and tone pulses modeled on a modification of Gabor's elementary signal. An analysis of amplitude and latency ratio measures of the evoked potential, rather than absolute measures, suggests the registration of an uncertainty relation involving changes in the interaural signal amplitude spectrum and interaural time of signal arrival. Both amplitude and latency ratio measures are orthogonal representations of the same interaural information and together constitute a traveling wave of wider information representation which may be described by the following uncertainty condition:

$$(\Delta f \cdot \Delta t) \cdot \Delta I_i \cdot \Delta r_i = c,$$

where  $c$  is a constant;  $\Delta f$  is signal bandwidth;  $\Delta t$  is signal duration;  $\Delta I_i$  is interaural intensity difference and  $\Delta r_i$  is interaural time of signal arrival difference.

Differences in interaural stimulus parameters are registered uniquely at some point on the auditory cortex, i.e., for a given combination of stimulus parameters a restricted region of the auditory cortex will display a large difference in latency or ratio measures. The total effect of "unique" points of registration constitutes a traveling wave which reflects the particular stimulus parameters used.

This study also demonstrates that the phase of a binaural signal of mid-frequency, 5 kHz, is registered only at a requisite interaural difference in signal intensity. Furthermore, at about 600  $\mu$ sec of interaural signal delay, the traveling wave registration of a binaural signal is constituted by a new center of initial activity.

It has been accepted by information theorists that at the resolution limit of any system—physical or physiological—uncertainty relations exist between one stimulus parameter and another. Gabor (1946) proposed that the

<sup>1</sup>This research was supported by NIH Grant MH 18802.

<sup>2</sup>The experiments reported here were completed at Carnegie-Mellon University, Pittsburgh, Pennsylvania.

quantum or *logon* of information, based on considerations of energy distribution, is:

$$\Delta f \cdot \Delta t = 1/2, \quad (1)$$

where  $\Delta f$  is a signal bandwidth and  $\Delta t$  is signal duration. In the terms of the related but distinct theory of communication, one logon resolves one binary digit or "bit" of uncertainty.

If such a signal is confined to minimum sequential relations, i.e.,

$$f_0 \cdot t_0 = 1/2 \quad (2)$$

where  $f_0$  is signal midfrequency and  $t_0$  is signal midperiod, a nonvarying form of the signal is obtained at any midfrequency (Barrett, 1972 a-d).

In the time domain, Eqs. (1) and (2) might represent a sinusoidal signal modified by a Gaussian wave shape (Fig. 1). This form of signal has the same "bell-shaped" distribution of energy in both the time and frequency domains.

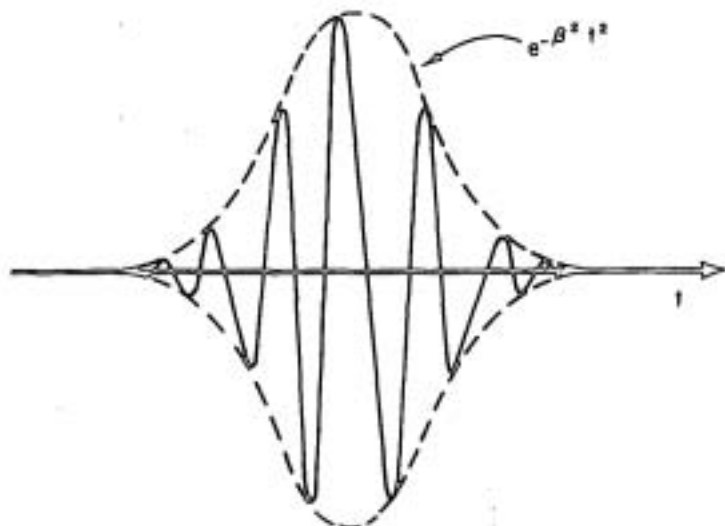


Fig. 1. The modified elementary signal of Gabor in the time domain: A sinusoidal signal modulated by a Gaussian curve. This signal satisfies the two conditions:  $\Delta f \cdot \Delta t = 1/2$  and  $f_0 \cdot t_0 = 1/2$ .

Davis (1952) first mentions using this signal in auditory research and Tunturi (1955, 1960) has made extensive use of this form of auditory pulse in electrophysiology.

It is noteworthy that Tunturi has obtained the most exact cortical center frequency representations in the dog using this elementary signal; and it would appear that other investigators have found the representation of frequency on the cortex to become fuzzier or barely discernible as the stimulus departed from the elementary signal shape (Goldstein, *et al.*, 1970; Gross and Small, 1961; Hind, 1953; Sindberg and Thompson, 1962).

The bandwidth of Gabor's elementary signal is reciprocally related to the stimulus duration. However, in most experiments tone pulses are kept at an arbitrary constant duration while the center frequency is varied, with bandwidth negligible. The resulting variety of stimuli used makes it difficult to compare the results of various investigators regarding the question of tonotopicity or the existence of an exact representation of frequency on the cortex. Yet, experiments using direct electrical stimulation of the cortex do give evidence of tonotopic registration; Woolsey and Walzl (1942) and Downman, Woolsey and Lende (1960) have demonstrated, point-to-point projection of the cochlear to the cerebral cortex of cat with electrical stimulation of small groups of nerve fibers at the edge of the osseous spiral laminae.

At variance with these experiments, microelectrode studies have failed to show a clear cortical tonotopic organization, although a trend towards one is present (Abeles and Goldstein, 1970; Erulkar, Rose and Davies, 1956; Evans, Ross, and Whitfield, 1965; Katsuki, Watanabe, and Maruyama, 1959). However, these investigators used a stimulus of constant duration and negligible bandwidth, whereas Tunturi demonstrated an *average or center frequency* ( $f_0$ ) representation of the signal bandwidth ( $\Delta f$ )  $\times$  signal duration ( $\Delta t$ ) uncertainty product of Fig. 1. Since neurons do have a bandwidth of responsiveness besides a characteristic frequency (Kiang, 1965), to view a signal of negligible bandwidth as "simpler" than the elementary signal of Fig. 1 is not supported empirically. Furthermore, as pointed out by Aitkin and Webster (1972), fibers from the medial geniculate body terminate most profusely in layer IV of the auditory cortex and not layers I and II. Thus, it is incorrect to pool data from auditory cortical neurons studied at different depths. Taken overall, the evidence seems to indicate a center frequency ( $f_0$ ) representation at the cortical level, which is associated with a minimum bandwidth ( $\Delta f$ ) if not exactly a pure tone ( $f_0$ ) or tonotopic representation with negligible bandwidth ( $\Delta f$ ).

At structures below the level of the cortex a similar representation holds. In the cat, neurons are arranged tonotopically in the dorsal and ventral nuclei of the lateral lemniscus (Aitkin, Anderson, and Brugge, 1970), in the cochlear nucleus (Rose, Galambos, and Hughes, 1959), in the superior olivary complex (Boudreau and Tsuchitani, 1970), in the medial geniculate body (Aitkin and Webster, 1972) and in the inferior colliculus (Rose *et al.*, 1963).

The form of the cortical representation will now be considered. Attempts to regard the electrical activity on the surface of the auditory cortex as a spatial representation of stimulus parameters have had some success. Lilly (1950, 1951; Lilly and Cherry, 1951, 1952, 1954, 1955) demonstrated both a "leading edge" of positive potential (velocity 0.05-0.35 m/sec) and a "trailing edge" of negative activity (velocity 0.06-0.35 m/sec) traveling across the cortex of cat at 90° to each other with velocities inversely related. The sound source in these experiments was driven by a 50- $\mu$ sec rectangular wave. Mickle and Ades (1953) also observed wavefront movements using 100- $\mu$ sec

rectangular pulses. Early investigation of the phase relations of electrical activity on the surface of the scalp (Walter and Shipton, 1951; Livanov and Anan'ev, 1955) have been extended to the exposed cortical surface; Demott (1961, 1966) using a 400-channel toposcope demonstrated voltage gradients of 0.5 mV difference across 0.5-mm areas of the cortex at frequencies of electrical activity above 50 Hz. Also, Barrett (1971a) demonstrated a traveling wave on the auditory cortex evoked by acoustical stimulation which changes its direction according to the orientation of the sound source. These observations of transcortical wave shapes are not at variance with the opinion that the cortex is constituted of vertically functioning elements. The wave shape patterning may be due to vertical potential fluctuations, without considerable horizontal voltage flow (Barrett 1969a,b).

The investigations reported in this paper extend this interest in spatial aspects of acoustical stimulus registration to changes in interaural stimulus parameters. Since the stimulus expressed by Eqs. (1) and (2) involves an uncertainty product, the question may be asked: Are there uncertainty relations in interaural differences in auditory stimulation? If so, just how are these relations registered upon the auditory cortex? Another way of asking these questions is: If the localization of a lateral sound source represents the successful transmission of unique information, are there uncertainty relations between interaural stimulus dimensions, i.e., interaural quanta comparable to the binaural signal of Eqs. (1) and (2)?

## METHODS

Eighteen cats, chosen after visual inspection of the tympanic membrane, were anesthetized with thiopental sodium 15 mg/kg. The amount of anesthesia might be termed "moderate" with the reticular formation affected and the medial geniculate body to some degree. The radial vein was cannulated and 1 cc of atropine sulphate administered to reduce body fluids. To stop movements of the brain due to respiration, the dura of the spinal cord at the base of the occiput was cut and the cerebrospinal fluid released. A caudal approach was made to the auditory bulla of the right side and a hole drilled so that a small stainless steel electrode bent in a loop could be placed touching the round window. In this way the cochlear microphonic responses were monitored. The electrode was then cemented to the bulla. The skull was resected over the right side and the dura reflected over areas, AI, AII and Ep.

A rectal telethermometer in conjunction with a heating pad maintained temperature at 38° C when recordings were not being made. The cortex was maintained in a moist state by periodic application of mineral oil heated to body temperature.

Tone pulses modeled on a modification of the elementary signal of Gabor (1946) were generated by delivering rectangular pulses from two

stimulators (American Electronic Laboratories 104A) of appropriate duration through half-octave filter sections of two filter sets (Krohn-Hite 3700). [This method was first used by Tunturi (1955).] The duration of the rectangular pulses was one-half the period of the center frequency of the half-octave filter section selected. These tone pulses were led to separate attenuator sets (Hewlett-Packard 350D) and the contralateral stimulus line only was led through a delay network (Universal Ad-Yu Electronics 802E). Both stimuli lines were then led to separate earphones (TDH-39) covered by plastic tubes directing the sound at each ear. A yarn was placed within the tubes to dampen resonance. The earphones have a flat frequency response until the 8-10 kHz region. The sound pressure level at each source was determined (with a Bruel and Kjaer 1/2-in. condenser microphone and an artificial ear) as 40 db prior to the use of the attenuators. All the results obtained are for elementary signals which gave a cochlear microphonic of 5 kHz—a frequency above the usually ascribed range of application of the volley theory of nervous conduction. The cochlear microphonic was used as a physiological indicator of the physical stimulus innervating the earphones. All recordings took place in a sound and electrically shielded room.

A sketch was made of the cortical surface on which electrode placements were later recorded. A stable stainless steel electrode was placed at the edge of area AI to compare evoked potentials as the preparation declined. Most recordings were made in the 3-hr period after the surgery was completed and no noticeable decline in the preparation was ever observed.

A five-point stainless steel Laplacian electrode, 2 mm square around the outer four points, with tips of approximately  $300\mu$  diameter was used to record evoked potential activity (Perl and Casby, 1954). This electrode differs from the widely used concentric electrode in that at the center, recorded potentials are amplified with respect to the *average* of the surrounding potentials rather than the *sum* of the surrounding potentials. Thus, the potentials arising from deeper structures are recorded rather than transcortical potentials. The recordings are, therefore, 2-mm squares of cortical surface. Using a Kopf Instrument, moveable adjustment, recordings were taken at 2-mm steps on the cortical surface. Minimum surface pressure was maintained.

At each cortical recording position, five contralateral ear signal delays were used: 0, 300, 600, 900, and  $1200\mu$ sec. At each delay, five ipsilateral ear signal attenuations were used: 0, 10, 20, 30 and 40 db. Twenty-five stimulus records were thus obtained at each recording site. Sufficient records were taken with each stimulus condition for later averaging, the data being collected on magnetic tape. Usually only activity above 50 Hz was recorded, although some recordings (Fig. 3A-D) include all frequencies. Using a D.E.C. PDP-9 computer, analog to digital conversion and averaging was achieved. The averaged response was then converted back again into an analog form and relayed to an A.E.I. 680 analog computer. Records were then made on graph paper by an *x-y* plotter. The plot achieved was of such size ( $25\mu$ /in. and

5  $\mu\text{sec/in.}$ ) that high-accuracy measurements of evoked potential latency and amplitude could be made.

Interesting results were obtained when, instead of "absolute" latency and amplitude measures being used, "amplitude ratios" and "latency ratios" of first positive peak to second positive peak were calculated. The use of ratio measures rather than absolute measures was dictated by the consideration that a measure referencing succeeding activity is more appropriate than a measure referencing an unrelated and distant activity (the rationale being that a distant potential is the summed result of many dipole layers and thus a meaningless measure). The ratio measure provides "contrast" for signal registration. These ratio measurements were calculated only in records of activity above 50 Hz.

## RESULTS

This study is based on 70 recordings from areas AI and AII in 18 cats. I shall begin by describing the noticeable changes occurring in cortically recorded measures of electrical potential when the stimuli at the two ears are separated by a 600- $\mu\text{sec}$  delay or more. As sounds are delayed about 29  $\mu\text{sec/cm}$  at the farther ear with respect to the cat's interpinnae distance, a 600- $\mu\text{sec}$  delay represents a period signalling two sounds rather than one fused localized sound. A plot of the amplitude ratios of the first positive and negative peaks in many cases indicated that at a 600- $\mu\text{sec}$  delay at the contralateral ear, a difference in cortical registration of interaural delay occurs (Fig. 2A,B,C) when there are no interaural intensity differences. In Fig. 2A and 2B, notice the decline of the graph lines at between 600 and 900  $\mu\text{sec}$  contralateral delay—with the exception of the plots of latency of the first negative trough in Fig. 2B, which indicate a noticeably fast reaction of the negative trough at 600  $\mu\text{sec}$  contralateral delay. In Fig. 2C, notice the steepness of the graph lines at between 300 and 600  $\mu\text{sec}$  contralateral delay. Averaging has indicated the significance of these differences. It appears that interaural delays less than 600  $\mu\text{sec}$  are registered differently on the cortex of cat at some locations. This conclusion is born out by other indicators mentioned below in the discussion of Fig. 4A-G.

Whether amplitude or latency measures are taken, there is a registered effect when only the interaural delay at the contralateral ear is changed, and the interaural intensity difference remains constant (Fig. 3A-D). Notice the change in shape of the averaged evoked response in Fig. 3A-D. These results were obtained for all frequencies of electrical activity at the cortex in the anesthetized cat.

At frequencies of electrical activity above 50 Hz, the reaction of changing potential inputs to the cortex, indicated by positive going peaks, to stimuli *greater* than 600  $\mu\text{sec}$  interaural delay, appear to mirror the reaction of potentials to stimuli *less* than 600  $\mu\text{sec}$  interaural delay (Fig. 4A-G).

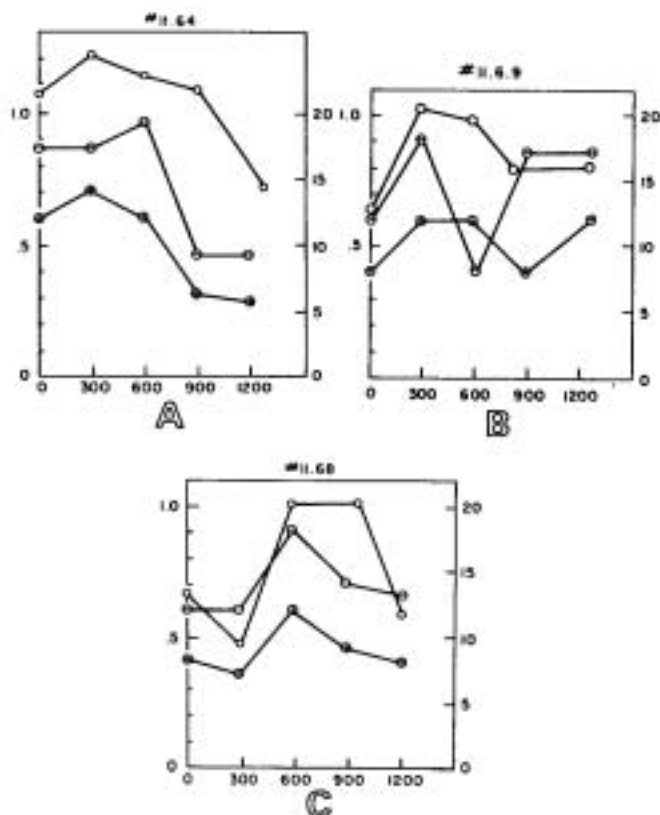


Fig. 2A-C. Three examples from different subjects of measures of evoked responses to a binaural 5-kHz elementary signal with contralateral delays in time of signal arrival. Left ordinate refers to the intensity ratio of the amplitude of the first positive peak to the amplitude of the second positive peak (open circles) of averaged (30) evoked responses in area AI of cat auditory cortex. Right ordinate refers to the latency in msec of the first positive peak (circles with inscribed plus) and of first negative trough (circles with inscribed minus) of the same averaged data. Delays in microseconds are shown on the abscissa. Frequencies of electrical data: 50 Hz and above.

In Fig. 4A, notice that the peak labeled "1" decreases through the conditions 0, 300, and 900  $\mu$ sec contralateral delay, but increases at 900 and 1200  $\mu$ sec contralateral delay.

In Fig. 4B, notice that the peak labeled "1" increases through the conditions 0, 300 and 600  $\mu$ sec contralateral delay but decreases at 900  $\mu$ sec contralateral delay and increases again at 1200  $\mu$ sec contralateral delay.

In Fig. 4C, notice that the peak labeled "2" decreases through the 0, 300 and 600  $\mu$ sec contralateral delay conditions to a minimum at 900  $\mu$ sec contralateral delay but greatly increases again at 1200  $\mu$ sec contralateral delay.

In Fig. 4D, notice the decrease of the peak labeled "1" at 600 and



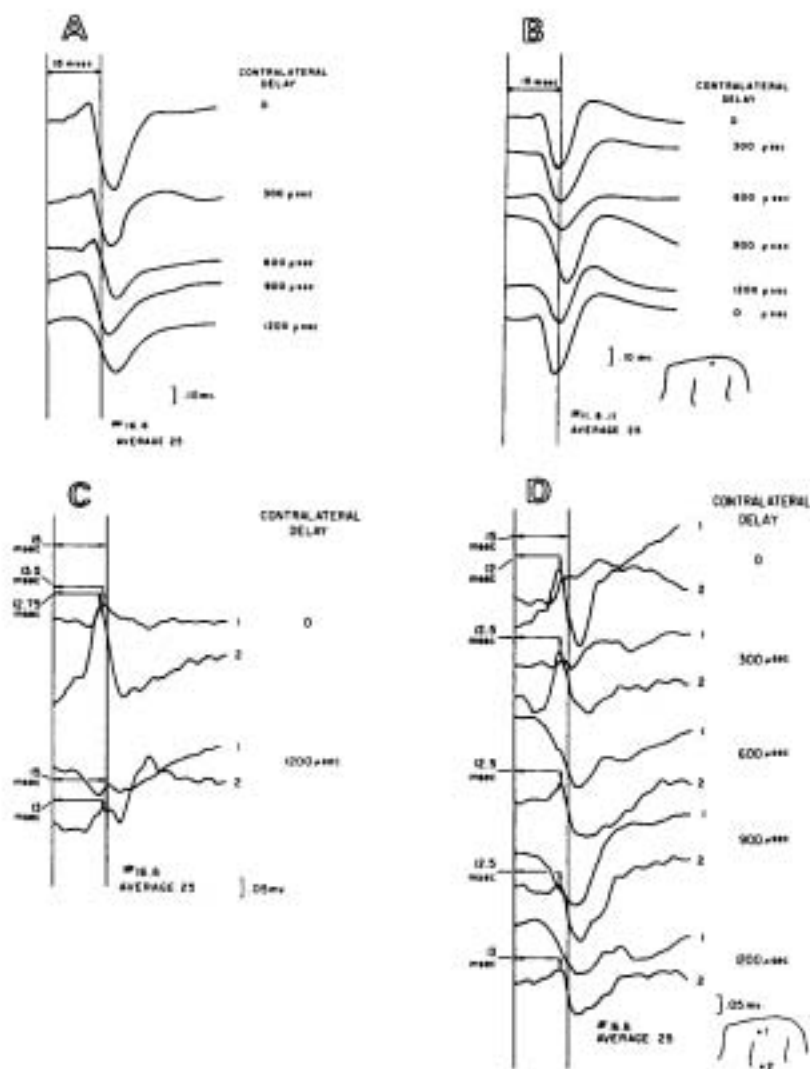


Fig. 3A,B. Two examples of averaged evoked potentials from area AI of cat auditory cortex. Frequencies of electrical data: all frequencies.

Fig. 3C,D. Two examples of averaged evoked potentials from (1) area AI and (2) area AII of cat auditory cortex. Frequencies of electrical data: all frequencies.

900  $\mu$ sec contralateral delay and the slight *increase* at 1200  $\mu$ sec contralateral delay.

In Fig. 4E, notice the *increase* of the peak labeled "2" at 0,300, and 600  $\mu$ sec contralateral delay and the *decrease* at 900 and 1200  $\mu$ sec contralateral delay.



In Fig. 4F, notice the peak labeled "I" occurs only at 900 and 1200  $\mu$ sec contralateral delay.

In Fig. 4G, notice the decrease of the peak labeled "I" at 300 and 900  $\mu$ sec contralateral delay.

These figures indicate that an apparently changing latency of the first peak of positive potential is more properly the dropping out of the faster first peak and the heightening of a slower second peak, or vice versa. The separate but overlapping cortical representations of the input from the two ears, established statistically (Rosenzweig, 1951), are shown as separate peaks in Fig. 4A-G, where the first 50 Hz of electrical activity has been filtered out.

Figure 5A shows the cortical electrode positions for the data representations of Fig. 5B-L, which are latency ratio (left figure) and intensity ratio (right figure) measurements to interaural intensity differences at various interaural delays. In over 90% of the 70 placements studied *there occurs only one maximum peak or trough in the graph line for a particular delay.*

In Fig. 5B-L notice the following peaks (P) and troughs (T) at the various contralateral delays (CD) and interaural intensity differences with the signal attenuated at the ipsilateral ear (II).

TABLE I

Latency Ratio and Intensity Ratio Measures

		Latency Ratio Measures	Intensity Ratio Measures
Fig. 5B	At	0 $\mu$ sec (CD) P at 30db & 10db (II)	P at 40db (II)
	At	300 $\mu$ sec (CD) P at 20db (II)	P at 20db (II)
	At	600 $\mu$ sec (CD) T at 20db (II)	
	At	900 $\mu$ sec (CD) T at 30db & 10db (II)	
	At	1200 $\mu$ sec (CD) P at 20db (II)	
Fig. 5C	At	0 $\mu$ sec (CD) T at 10db (II)	T at 20db (II)
	AT	300 $\mu$ sec (CD) P at 20db (II)	T at 20db (II)
	At	600 $\mu$ sec (CD) P at 10db (II)	T at 20db (II)
	At	900 $\mu$ sec (CD) P at 10db (II)	T at 20db (II)
	At	1200 $\mu$ sec (CD) P at 0db (II)	T at 20db (II)
Fig. 5D	At	0 $\mu$ sec (CD) P at 30db (II)	
	At	300 $\mu$ sec (CD) P at 20db (II)	
	At	600 $\mu$ sec (CD) P at 10db (II)	
	At	900 $\mu$ sec (CD) P at 0db (II)	
	At	1200 $\mu$ sec (CD) P at 20db (II)	
Fig. 5E	At	0 $\mu$ sec (CD) P at 20db (II)	P at 10db (II)
	At	300 $\mu$ sec (CD) P at 30db (II)	P at 20db (II)
	At	600 $\mu$ sec (CD) P at 20db (II)	P at 40db (II)
	At	900 $\mu$ sec (CD) P at 30db (II)	P at 30db (II)
	At	1200 $\mu$ sec (CD) P at 20db (II)	P at 30db (II)
Fig. 5F	At	0 $\mu$ sec (CD) P at 10db (II)	P at 40db (II)
	At	300 $\mu$ sec (CD) P at 20db (II)	P at 20db (II)

Table 1—(Cont'd)

	Latency Ratio Measures		Intensity Ratio Measures
Fig. 5F	At	600 $\mu$ sec (CD) P at 30db & 10db; T at 20db (II)	P at 10db (II)
	At	900 $\mu$ sec (CD)	P at 10db (II)
	At	1200 $\mu$ sec (CD)	P at 30db (II)
Fig. 5G	At	0 $\mu$ sec (CD) T at 30db (II)	P at 40db (II)
	At	300 $\mu$ sec (CD) P at 20db (II)	P at 10db (II)
	At	600 $\mu$ sec (CD) P at 20db (II)	P at 10db (II)
	At	900 $\mu$ sec (CD) T at 20db (II)	T at 10db (II)
	At	1200 $\mu$ sec (CD) T at 30db (II)	P at 20db (II)
Fig. 5H	At	0 $\mu$ sec (CD) T at 30db & P at 10db (II)	P at 20db (II)
	At	300 $\mu$ sec (CD) P at 30db (II)	P at 10db (II)
	At	600 $\mu$ sec (CD) P at 10db & T at 30db (II)	P at 10db (II)
	At	900 $\mu$ sec (CD) P at 20db & T at 30db (II)	P at 10db (II)
	At	1200 $\mu$ sec (CD) P at 0db & T at 30db	P at 30db (II)
Fig. 5I	At	0 $\mu$ sec (CD) P at 40db (II)	P at 30db (II)
	At	300 $\mu$ sec (CD) P at 30db (II)	P at 30db (II)
	At	600 $\mu$ sec (CD) P at 40db (II)	P at 30db (II)
	At	900 $\mu$ sec (CD) P at 30db (II)	P at 0db (II)
	At	1200 $\mu$ sec (CD) P at 10db (II)	P at 40db (II)
Fig. 5J	At	0 $\mu$ sec (CD)	
	At	300 $\mu$ sec (CD) P at 30db (II)	
	At	600 $\mu$ sec (CD) P at 30db (II)	
	At	900 $\mu$ sec (CD)	
	At	1200 $\mu$ sec (CD)	
Fig. 5K	At	0 $\mu$ sec (CD) P at 0db (II)	P at 40db (II)
	At	300 $\mu$ sec (CD) T at 30db (II)	P at 30db (II)
	At	600 $\mu$ sec (CD) P at 10db (II)	P at 0db (II)
	At	900 $\mu$ sec (CD) P at 20db (II)	P at 10db (II)
	At	1200 $\mu$ sec (CD) P at 40db (II)	P at 30db (II)
Fig. 5L	At	0 $\mu$ sec (CD) P at 20db (II)	P at 10db (II)
	At	300 $\mu$ sec (CD) P at 30db (II)	P at 10db (II)
	At	600 $\mu$ sec (CD) P at 10db (II)	P at 20db (II)
	At	900 $\mu$ sec (CD) P at 30db (II)	P at 30db (II)
	At	1200 $\mu$ sec (CD) P at 40db (II)	P at 20db (II)

The peaks vary according to both the delay and the position of the electrode on the cortex. Since an average signal frequency ( $f_0$ ) representation occurs as a position of maximum firing on the cat cortex (tonotopicity), and the average frequency ( $f_0$ ) in this study was kept constant at 5 kHz, it would appear that these peaks and troughs are the result only of (a) the interaural difference in time of signal arrival, and (b) the interaural difference in signal intensity.

It was initially expected that some correlation would exist between the intensity and latency ratio measures of Fig. 5B-L. However, neither a significant positive nor negative correlation was found ( $r = \pm 0.5$ ), which suggests that the intensity and latency ratio measures of information registration above 50 Hz are orthogonal or independent functions of the same variables. Furthermore, the registration, in both left and right figures, of a particular interaural delay at a particular interaural intensity, suggests the existence of an uncertainty relation or reciprocal relation between interaural delay and interaural signal intensity differences. Thus, the unique peak registration can be considered a dependent variable to two independent variables (of interaural time of signal arrival difference and interaural signal intensity difference). The suggestion is, therefore, that the uncertainty condition of these two independent variables is registered on the cortex by the tracking of the curves shown in Fig. 5B-L.

### DISCUSSION

At low frequencies the phase of a stimulus can be a cue to the localization of a sound in space. At higher frequencies there is an ambiguity in the interpretation of the phase of the stimulus with respect to auditory angle. However, the registration of the phase angle of the signal is a function not only of frequency and interaural differences in time of signal arrival but also of interaural differences in signal intensity, i.e., the phase angle of the signal is only registered at a certain interaural intensity difference, then the ambiguity no longer exists. The results shown in Fig. 5B-L suggest that this is the case. I will now discuss the significance of this result.

Some confusion can arise in the use of the term "signal phase." Because of the refractory period of axonal discharge (1 msec) and the size of nerve fibers provide boundary conditions to mean pulse rate, the volley principle (Wever, 1949) of nerve impulse conduction no longer applies with stimuli above about 4 kHz. The volley principle describes a form of mean pulse rate modulation which, when the number of spikes is counted in discrete intervals of time, is a form of amplitude modulation of those counts. I shall call the frequency of this modulation:  $f_m$ . The frequency of the modulated signal,  $f_c$ , is generally assumed to be registered at the basilar membrane by a place principle (Von Békésy, 1960, 1965). At frequencies below 4 kHz, either principle might register the frequency of a signal and frequency modulation could no longer occur. When the amplitude modulating frequency,  $f_m$ , and the carrier frequency,  $f_c$ , overlap at signal frequencies below 4 kHz, the physical signal is presented twice—by pulse rate modulation ( $f_m$ ) and by a place principle ( $f_c$ ). The stimulus used in the present study gave a cochlear microphonic of center frequency 5 kHz. The interaural phase angle generated when the stimulus was delayed at one ear was thus a function of 5 kHz ( $f_c$ ); I shall call this form of phase angle:  $\phi_c$ . The phase angle generated as a function of  $f_m$  I shall call:  $\phi_m$ .

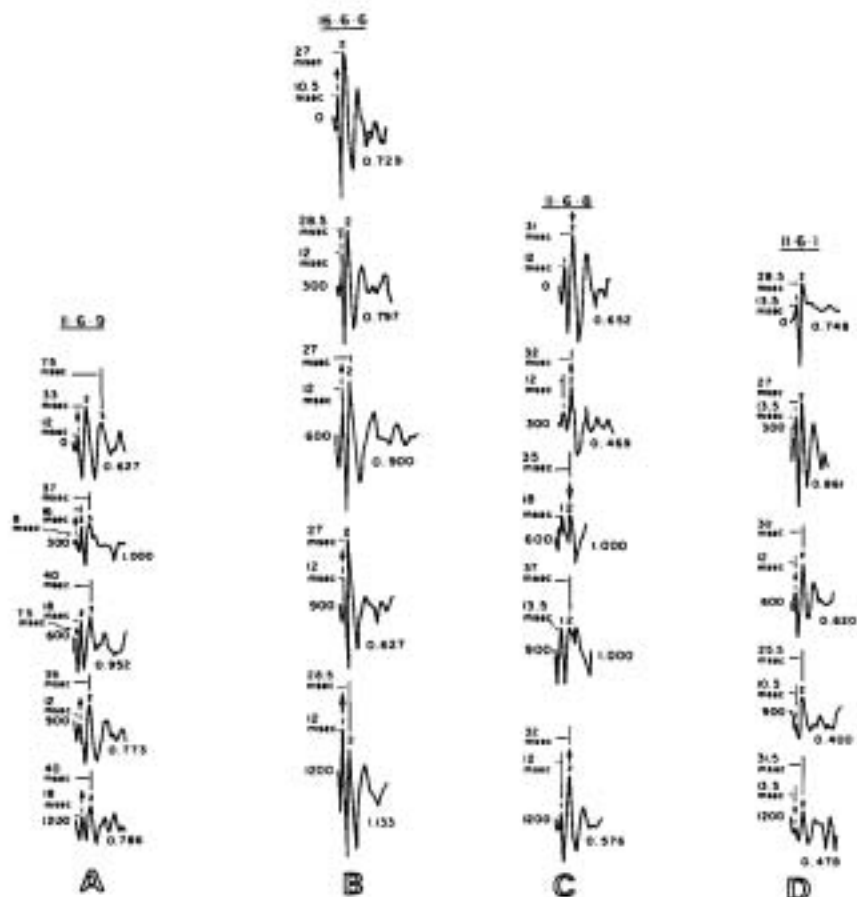
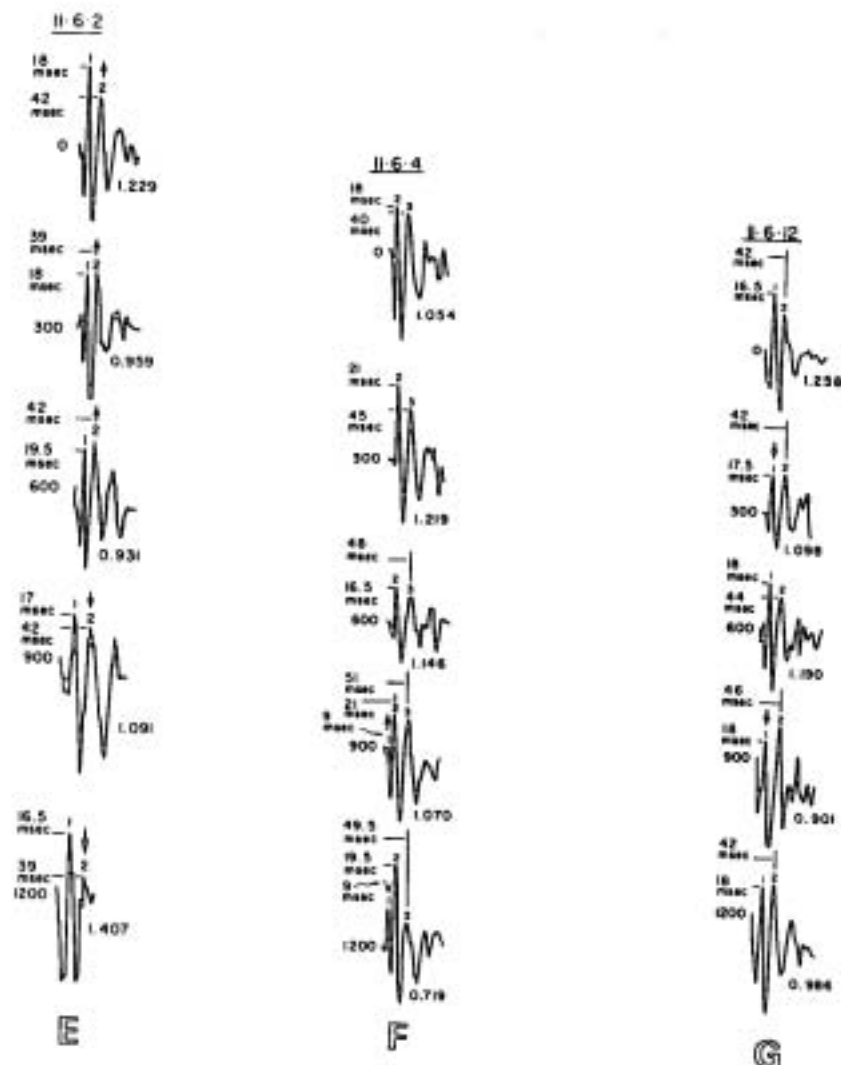


Fig. 4A-G. Averages of 30 evoked potentials from area AI of cat auditory cortex to interaural delays of 0, 300, 600, 900, and 1200  $\mu$ sec reading from top to bottom. Numerals on the right of each averaged response refer to the ratio of the first appearing peak to the next. Frequencies of electrical data: 50 Hz and above. (A) Peak 1 decreases from 0 through 300 and 600  $\mu$ sec delay, and then begins to regain its height (arrow);

#### Investigations of $\phi_m$

Cortical neurons are responsive to interaural phase differences for tones below 2400 Hz (Brugge, Dubrovsky, and Rose, 1964; Brugge *et al.*, 1969). The number of action potentials in the response to a binaural stimulus is a



(B) The height of peak 1 fluctuates at 900  $\mu$ sec delay; (C) An increase in the intensity ratio measures at 600 and 900  $\mu$ sec delays; (D) A diminution of the first peak after 600  $\mu$ sec delay; (E) The second peak reaches a maximum value at 300  $\mu$ sec delay and then declines; (F) A first peak appears at 900 and 1200  $\mu$ sec delay; (G) The first peak dips at 300 and 900  $\mu$ sec delay.

function of the interaural time delay, and the time between peaks of this function corresponds to the frequency period of the tone employed. The amplitude of the cortical evoked response is also dependent upon the interaural phase angle of stimuli below 2 kHz (Hirsch, 1968). Finally, to

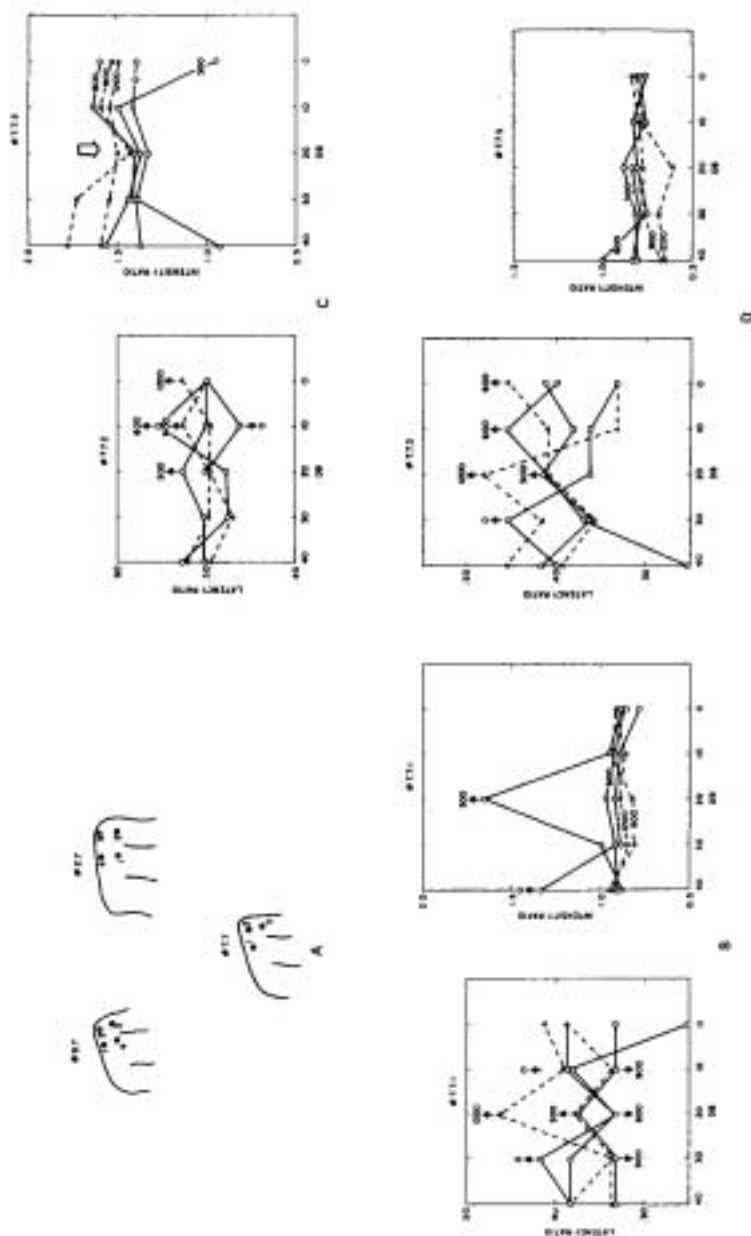


Fig. 5A. Positioning of electrodes on cat auditory cortex and from which the data shown in Fig. 5B-L were obtained. Upper line refers to the suprasylvian sulcus. Vertical lines refer to the posterior and anterior ectosylvian sulci. Brains face to right.

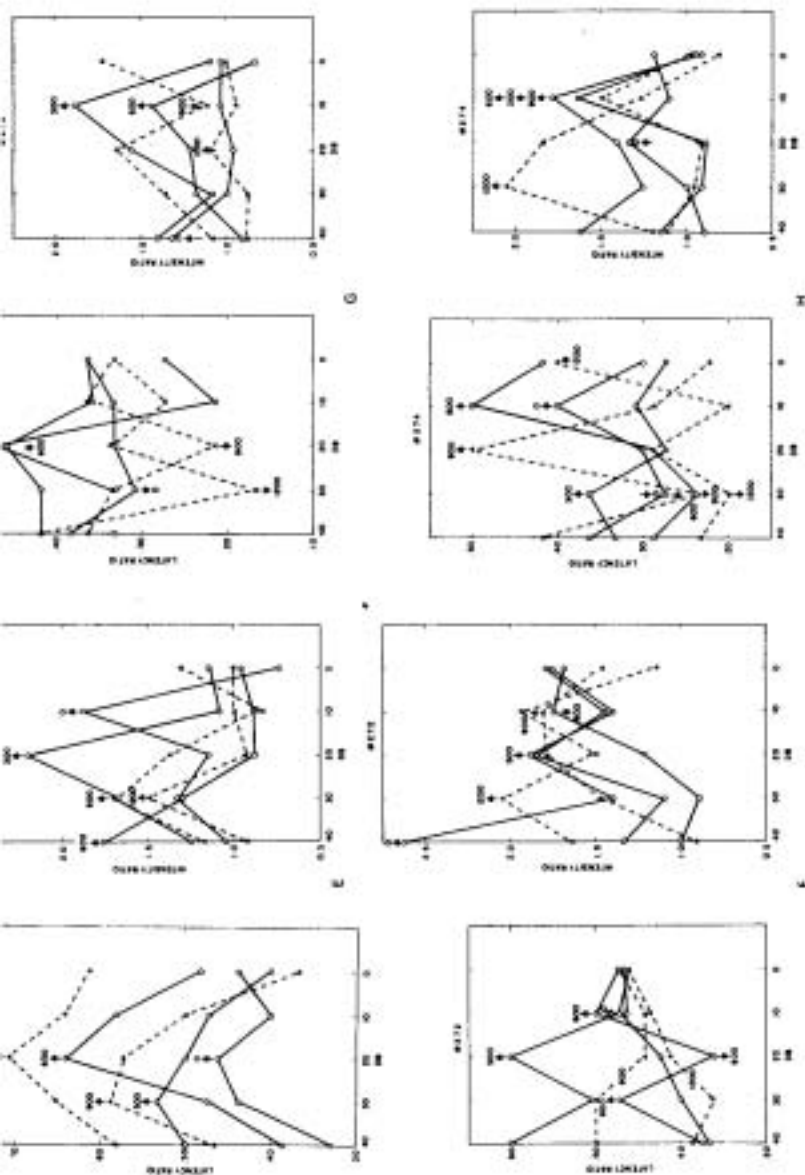
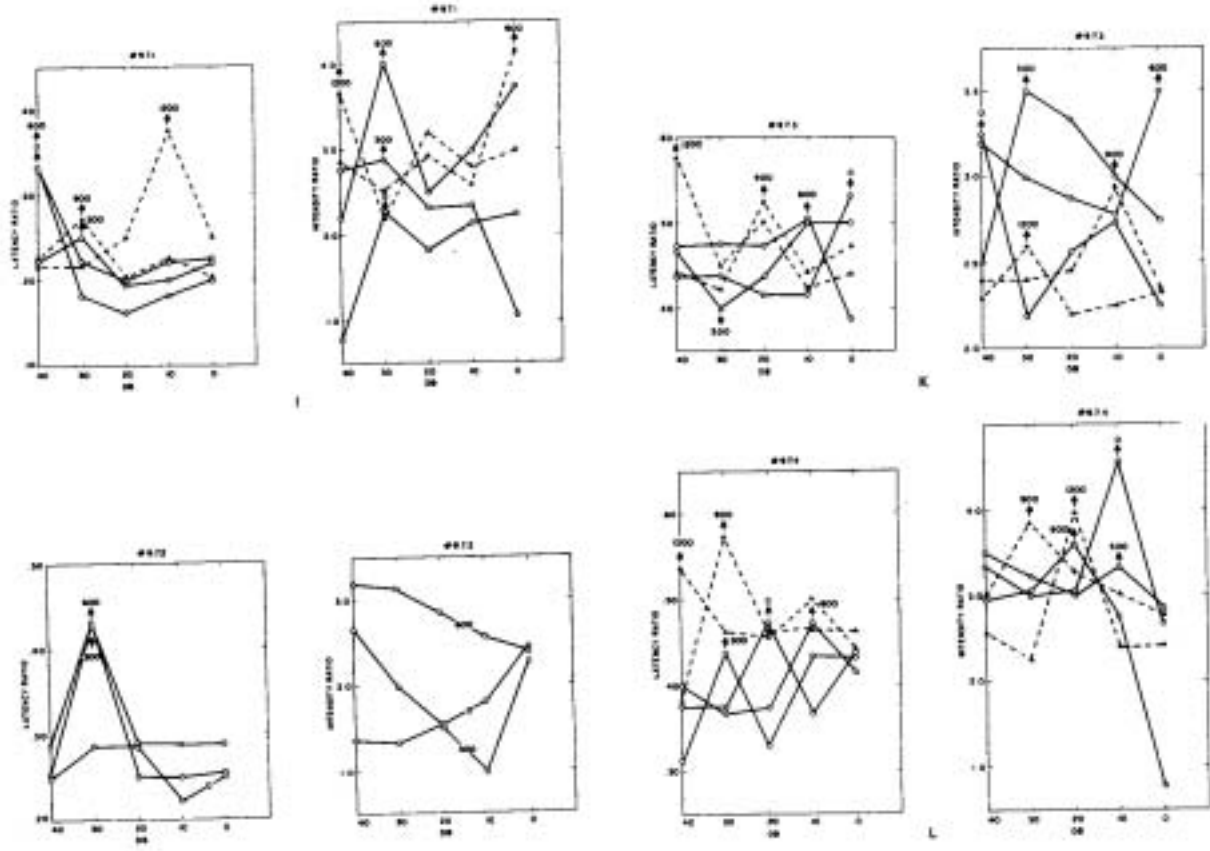


Fig. 5B-L. Latency and intensity ratio measures to ipsilateral signal attenuation. Lateral signal commences at 40 db and is progressively attenuated to 0 db. Five lateral delays (ipsilateral stimulus leads) of 0, 300 and 600  $\mu$ sec (heavy lines); 900 and 0  $\mu$ sec (dotted lines). Peaks indicated by (†); troughs by (‡).





low-frequency tones single auditory fibers of the squirrel monkey give a phase-locked response (Rose *et al* 1967; Brugge *et al.*, 1969; Rose *et al.*, 1969).

#### *The Present Investigation of $\phi_c$*

The results summarized in Fig. 5B-L suggest that in the anesthetized preparation:

(1) The registration of  $\phi_c$  is present in cortical macropotential activity above 50 Hz.

(2) The registration of  $\phi_c$  is indicated by a maximum ratio measure (i.e., peak or trough in Fig. 5B-L), rather than an "absolute" value of the evoked potential amplitude or latency.

(3) The registration of  $\phi_c$  is a function not only of interaural differences in time of signal arrival and signal frequency ( $f_0 = 5$  kHz), but also of interaural intensity differences.

Point (3) warrants further discussion. The phase angle of a modulating signal ( $\phi_m$ ), if the component frequencies lie within approximately 20% of each other, is audible. A change of the central components with respect to the side bands is also audible (Mathes and Miller, 1947). A monaural phase detection also occurs when the differences in phase spectra are *nonlinear* with respect to frequency (Ronken, 1970). However, a shift in the phase angle of the components are *not* detected normally when the shift is by amounts linearly dependent upon frequency (de Boer, 1961). Thus, if:

$$\phi(f) = a + bf, \quad (3)$$

Then a change in  $b$  gives a linear shift or time delay and a change in  $a$  gives a uniform phase shift for all components. Neither shift ( $\phi_c$ ) is audible. The present results are not at variance with these facts.

On the other hand, the results of the present study demonstrate the registration of phase,  $\phi_c$ , to be dependent upon *both* differences in interaural time of signal arrival *and also* upon differences in interaural signal intensity. Thus, the registration of the interaural phase demonstrated here is *nonlinear* with respect to the signal center frequency (5 kHz), being also dependent upon the two variables already mentioned. If the interaural difference in signal intensity is not systematically varied, there is no registration of  $\phi_c$ .

In this vein, Helmholtz (1877) wrote:

the quality of the musical portion of a compound tone depends solely on the number and relative strength of its partial simple tones, and in no respect on their differences of phase (page 126).

It is, however, sometimes forgotten that this statement was qualified by:

When the musical tone is accompanied by unmusical noises, such as jarring, scratching, coughing, whizzing, hissing, these motions are either not to be considered as periodic at all, or else correspond to higher upper partials, of

nearly the same pitch, which consequently form strident dissonances. We were not able to embrace these in our experiments, and hence we must leave it for the present doubtful whether in such dissonating tones difference of phase is an element of importance. Subsequent theoretic considerations will lead us to suppose that it really is (page 127).

The nonlinearity of the  $\phi_c$  registration with respect to frequency demonstrated in Fig. 5B-L agrees with Helmholtz's suppositions. The distinction between  $\phi_c$  and  $\phi_m$  registration as well as that between  $f_c$  and  $f_m$  places the result of this study within the explanatory framework of Licklider's (1951, 1956) triplex theory of pitch perception. Emphasis on place registration here is also in agreement with previous theories (Bowker, 1908; Jeffress, 1948).

#### *The Registration of $\phi_c$ and Its Relation to Tonotopicity*

The representation on the cortex of the center frequency ( $f_0$ ) of a tone pulse in which the duration ( $\Delta t$ ) and bandwidth ( $\Delta f$ ) are reciprocally related [Tunturi's center frequency ( $f_0$ ) representation], implies that a change in electrode position is similar to a change in location on a two-dimensional frequency representation map with a constant center frequency ( $f_0$ ) input in this study of 5 kHz. Figures 5B-L demonstrate that for various positionings on this map a maximum peak or trough in the ratio measures corresponds to specific interaural differences in time of signal arrival and signal intensity. The uniqueness of this peak registration on a two-dimensional frequency representation map can be summarized in the following equations:

$$\Delta i_i \cdot \Delta \tau_i \cdot (\Delta f \cdot \Delta t) = c, \quad (4)$$

where,  $\Delta i_i$  is interaural differences in signal intensity (power difference spectrum of the signal);  $\Delta \tau_i$  is interaural differences in time of signal arrival;  $\Delta f$  is signal bandwidth; and  $\Delta t$  is signal duration.

The center or average frequency ( $f_0$ ) associated with the signal bandwidth  $\Delta f$ , is defined by the following equation:

$$f_0 = \frac{\int f \psi \psi^* df}{E} = \frac{1}{2\pi j} \int \frac{X \frac{dX^*}{dt} dt}{E} \quad (5)$$

where  $\psi \psi^*$  and  $XX^*$  are the spectral energies of the signal in the frequency and time domain, respectively, and  $E$  is signal energy.

The binaural trading ratio of  $\Delta \tau_i$  to  $\Delta i_i$  is a measure of the relative effectiveness of these two interaural parameters in permitting sound localization. The existence of a  $\Delta \tau_i$ - $\Delta i_i$  trade is well documented in the psychophysical literature, although such a trade may be (i) incomplete and (ii) the relative usefulness of the two interaural parameters may be idiosyncratic to the individual listener (Hafer and Carrier, 1972).

*The Orthogonality of Amplitude and Latency Ratio Measures*

At low frequencies an interaural difference in time of signal arrival can be compensated by an interaural intensity difference in judging the localization of a sound source (Licklider, 1951). On the other hand, with low-frequency stimulation, phase (a periodic variable), and not the interaural difference in signal time of arrival (which is not a periodic variable), is registered on the cortex in both evoked potential (Hirsch, 1968) and action potential (Brugge, Dubrowsky, and Rose, 1964; Brugge *et al.*, 1969) form. The uncertainty conditions underlying these two facts can be summarized in the following equations:

$$\phi \cdot \Delta t_i = c \quad (6)$$

$$\Delta t_i \cdot \Delta I_i = c, \quad (7)$$

where  $c$  is a constant;  $\phi$  = interaural phase differences;  $\Delta I_i$  = interaural intensity differences;  $\Delta t_i$  = interaural time of signal arrival differences. The opposing proposals are illustrated in Fig. 6. A translation between the two proposals is possible, as center frequency,  $f_0$  (a periodic measure), is also represented positionally on the cortex as a related signal dimension. The confrontation of the two proposals need not occur if one signal dimension is always represented with the other; and this actually is the case if all signal dimensions have a related cortical representation. A place principle for center frequency ( $f_0$ ) representation on the cat cortex has been demonstrated (Tunturi, 1960); phase (a periodic measure of frequency) also has a spatial representation (Hirsch, 1968); and time of signal arrival differences at the two ears have a representation at right angles to the surface, i.e., by means of the height and latency of the evoked potential (demonstrated here in Figs. 4 and 5). This overall conception is illustrated in Fig. 7.

The representation of interaural differences in time of signal arrival and interaural intensity differences in the signal by amplitude and latency ratios (Figs. 4 and 5)—both measures of activity at right angles to the surface of the cortex—thus favors the trading relation of Eq. (7) and not (6) and yet is compatible with a surface representation of center frequency and phase.

*A Traveling Wave as an Unambiguous Measure of All Parameters of Acoustical Signals*

This study has presented evidence indicating that cortical intensity and latency ratio measures both register the uncertainty relations of interaural differences in time of signal arrival and interaural intensity differences (Fig. 5). Such measures on a two-dimensional surface, orthogonal, yet measuring the same signal dimensions, constitute a traveling wavefront which is an unambiguous measure of all parameters of stimulation considered

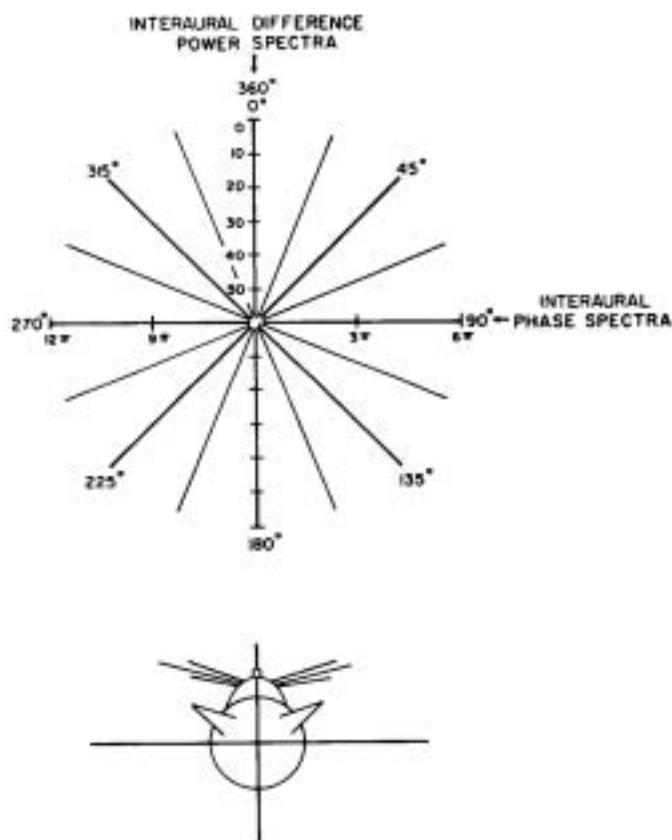
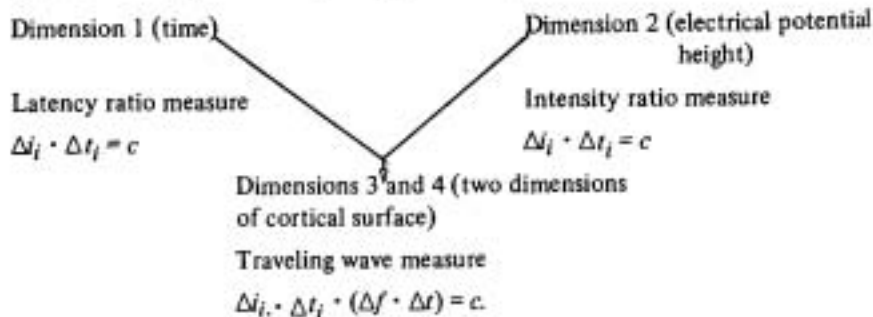
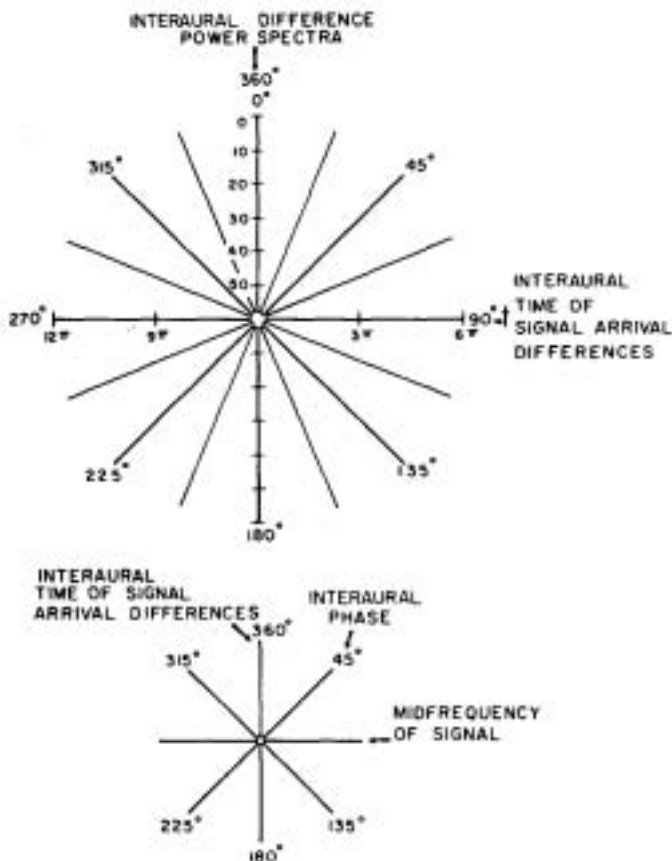


Fig. 6. Left (this page) and right (opposite page) top figures: two theories of information concerning sound lateralization registration. The left top figure plots auditory angle in terms of (i) the interaural difference power spectrum  $\Delta t_i$  and (ii) the interaural phase spectrum ( $\phi$ ). This theory corresponds to Eq. (6) in the text. The right top figure



Thus, the present study suggests that the registration of interaural "quanta" of acoustical stimuli ( $\Delta t_i \cdot \Delta t_i = \text{some minimum value}$ ), together with



plots auditory angle in terms of (i) the interaural difference power spectrum ( $\Delta f_i$ ) and (ii) the interaural time of signal arrival differences ( $\Delta t_i$ ). This theory corresponds to Eq. (7) in the text. The one theory may be translated into the other by the use of a signal average frequency ( $f_0$ ) representation—a representation shown on the lower right.

the modified Gabor quantum,  $\Delta f \cdot \Delta t = 1/2$ ;  $f_0 \cdot t_0 = 1/2$ , occur as a traveling wave. The effect of such a signal on a single unit activity has already been demonstrated (Barrett, 1971b, 1972f), as well as the multiple use of local cortical areas (Barrett, 1972e). The registration of the minimum value of the interaural quantum, rather than the dimensions of interaural differences in time of signal arrival or signal intensity specifically, suggests that these dependent signal parameters might be registered by the central nervous system at resolution limits far below the value one would ascribe from a knowledge of the refractory period of a neuron: A very small  $\Delta f_i$  can be registered if  $\Delta t_i$  is large; conversely, a very small  $\Delta t_i$  can be registered if  $\Delta f_i$  is large. A question to be answered by further research is thus: What is the minimum value of the interaural quanta?

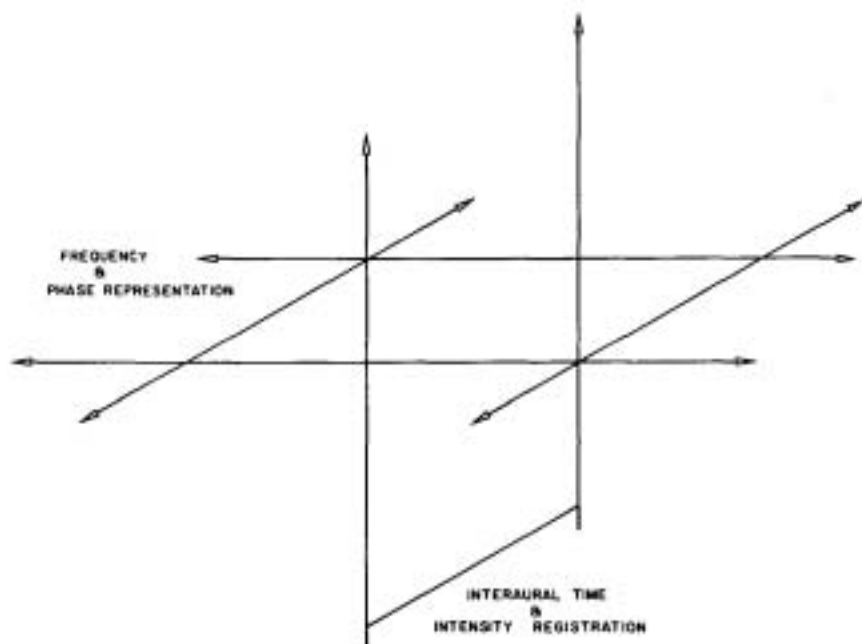


Fig. 7. Simplified scheme of binaural and interaural information registration. The frequency and phase of the binaural signal are registered positionally on the cortical surface. The interaural intensity and time of signal arrival differences are registered in a plane at right angles to the cortical surface by the height and timing of the evoked potential. The evoked potential thus exists as a spatiotemporal patterning on the cortical surface—a patterning in which potential height, position, and temporal relations are meaningful in defining uniquely the particular binaural and interaural parameters of the stimulus.

## REFERENCES

- Abeles, M., and Goldstein, M. H. (1970). Functional architecture in cat primary auditory cortex: Columnar organization and organization according to depth. *J. Neurophysiol.* 33, 172-187.
- Aitkin, L. M., Anderson, D. J., and Brugge, J. F. (1970). Tonotopic organization and discharge characteristics of single neurons in nuclei of lateral lemniscus of the cat. *J. Neurophysiol.* 33, 421-440.
- Aitkin, L. M., and Webster, W. R. (1972). Medial geniculate body of the cat: Organization and responses of tonal stimuli of neurons in ventral division. *J. Neurophysiol.* 35, 365-378.
- Barrett, T. W. (1969a). The cortex as interferometer: The transmission of amplitude, frequency and phase in cortical structures. *Neuropsychologia* 7, 135-148.
- Barrett, T. W. (1969b). The cerebral cortex as a diffractive medium. *Math. Biosci.* 14, 311-350.
- Barrett, T. W. (1971a). Cortical wavefront movements to a changing sound source. *Brain Res.* 27, 271-280.



- Barrett, T. W. (1971b). The response of auditory cortex neurons in cat to various parameters of auditory stimulation. *Brain Res.* 28 579-581.
- Barrett, T. W. (1972a). Octave ratio as the absolute measurement unit of sensory communication in the cerebral cortex. *J. Theor. Biol.* 34, 87-97.
- Barrett, T. W. (1972b). On vibrating strings and information theory. *J. Sound Vibration*, 20, 407-412.
- Barrett, T. W. (1972c). Conservation of information. *Acustica*, 27, 44-47.
- Barrett, T. W. (1972d). Definition precedence of signal parameters. Sequential versus simultaneous information. *Acustica*, 27, 90-93.
- Barrett, T. W. (1972e). The multiple use of the auditory cortex: Interaction at a single point. *Exp. Neurol.* 34, 1-15.
- Barrett, T. W. (1972f). Interaural stimulation: Effects on the  $Q$ -value of tuning curves and post-stimulus time histograms of cat auditory cortex neurons. *Exp. Neurol.* 34, 484-496.
- Boudreau, J. C., and Tsuchitani, C. (1970). Cat superior olive S-segment cell discharge to tonal stimulation. In W. D. Neff (Ed.), "Contributions to Sensory Physiology," Vol. 4, p. 143-213. New York:Academic Press.
- Bowler, T. J. (1908). On the factors serving to determine the direction of sound. *Phil. Mag.* 15, 318-332.
- Brugge, J. F., Anderson D. J., Hind, J. E., and Rose, J. E. (1969). Time structure of discharges in single auditory nerve fibers of the squirrel monkey in response to complex periodic sounds. *J. Neurophysiol.* 32, 386-401.
- Brugge, J. G., Dubrovsky, N., and Rose, J. E. (1964). Some discharge characteristics of single neurons in cats' auditory cortex. *Science* 146, 433-434.
- Brugge, J. F., Dubrovsky, N., Aitkin, L. M., and Anderson, D. J. (1969). Sensitivity to single neurons in auditory cortex of cat to binaural tonal stimulation; effects of varying interaural time and intensity. *J. Neurophysiol.* 32, 1005-1024.
- Davis, H. (1952). Information theory: 3. Applications of information theory to research in hearing. *J. Speech Hear. Disord.* 17, 189-197.
- de Boer, E. (1961). A note on phase distortion in hearing. *Acustica* 11, 182-184.
- Demott, D. W. (1961). An inexpensive multi-channel, electrophysiological recording system. *Electroencephalogr. Clin. Neurophysiol.* 13, 467-470.
- Demott, D. W. (1966). Cortical microtoposcopy. *Med. Res. Eng.* 5, 23-29.
- Downman, C. B. B., Woolsey, C. N., and Lende, R. A. (1960). Auditory areas I and II and Ep: Cochlear representation, afferent paths and interconnections. *Bull. Johns Hopkins Hosp.* 106, 127-142.
- Erulkar, S. D., Rose J. E., and Davies, P. W. (1956). Single unit activity in the auditory cortex of the cat. *Bull. Johns Hopkins Hosp.* 99, 55-86.
- Evans, E. F., Ross, H. F., and Whitfield, I. C. (1965). The spatial distribution of unit characteristic frequency in the primary auditory cortex of cat. *J. Physiol. (London)* 179, 238-247.
- Gabor, D. (1946). Theory of communication. *J.I.E.E. (London)* 93, 429-457.
- Goldstein, M. H., Abeles, M., Daly, R. L., and McIntosh, J. (1970). Functional architecture in cat primary auditory cortex. *J. Neurophysiol.* 33, 188-197.
- Gross, N. B., and Small, H. M. (1961). Frequency correlates of the cat brain. *Exp. Neurol.* 3, 375-387.
- Haftner, E. R., and Carrier, S. C. (1972). Binaural interaction in low-frequency stimuli: The inability to trade time and intensity completely. *J. Acoust. Soc. Amer.* 51, 1852-1862.
- Helmholtz, H. L. (1877). "On the Sensations of Tone." New York: Dover Publications (1954) of the translation of the fourth and last German edition.
- Hind, J. E. (1953). An electrophysiological determination of tonotopic organization in auditory cortex of cat. *J. Neurophysiol.* 16, 475-489.

- Hirsch, J. E. (1969). Effect of interaural time delay on amplitude of cortical responses evoked by tones. *J. Neurophysiol.* 31, 916-927.
- Jeffress, L. A. (1948). A place theory of sound location. *J. Comp. Physiol. Psychol.* 41, 35-39.
- Katsuki, Y., Watanabe, T., and Maruyama, N. (1959). Activity of auditory neurons in upper levels of brain of cat. *J. Neurophysiol.* 22, 343-349.
- Kiang, N. Y.-S. (1965). "Discharge Patterns of Single Fibers in the Cat's Auditory Nerve." Research Monograph No. 35, Cambridge, MA: M.I.T. Press.
- Licklider, J. C. R. (1951). Basic correlates of the auditory stimulus. In S. S. Stevens (Ed.), "Handbook of Experimental Psychology." p. 985-1039. New York: Wiley.
- Licklider, J. C. R. (1956). Auditory frequency analysis. In C. Cherry (Ed.), "Information Theory-Third London Symposium, Royal Institution, Sep 12-16, 1955." p. 253-68.
- Lilly, J. C. (1950). Moving relief maps of the electrical activity of small areas of the pial surface of the cerebral cortex. *Electroencephalogr. Clin. Neurophysiol.* 2, 358.
- Lilly, J. C. (1951). Equipotential maps of the posterior ectosylvian area and acoustic 1 and 11 of the cat during responses and spontaneous activity. *Fed. Proc.* 10, 1.
- Lilly, J. C., and Cherry, R. (1951). Travelling waves of action and of recovery during spontaneous activity in the cerebral cortex. *Amer. J. Physiol.* 167, 806.
- Lilly, J. C., and Cherry, R. (1952). New criteria for the division of the acoustic cortex into functional areas. *Fed. Proc.* 11, 1.
- Lilly, J. C., and Cherry, R. (1954). Surface movements of click responses from acoustic cerebral cortex of cat: Leading and trailing edges of a response figure. *J. Neurophysiol.* 17, 521-532.
- Lilly, J. C., and Cherry, R. (1955). Surface movements of figures in spontaneous activity of anesthetized cerebral cortex: Leading and trailing edges. *J. Neurophysiol.* 18, 18-32.
- Livanov, M. M., and Anan'ev, V. M. (1955). An electrophysiological study of spatial distribution of activity in the cerebral cortex of a rabbit. *Fiz. Zh.* 41, 461.
- Mathes, R. C., and Miller, R. L. (1947). Phase effects in monaural perception. *J. Acoust. Soc. Amer.* 19, 780-797.
- Mickle, W. A., and Ades, J. W. (1953). Spread of evoked cortical potentials. *J. Neurophysiol.* 16, 608-633.
- Perl, E. R., and Casby, J. V. (1954). Localization of cerebral electrical activity: the acoustic cortex of cat. *J. Neurophysiol.* 19, 500-512.
- Ronken, D. A. (1970). Monaural detection of a phase difference between clicks. *J. Acoust. Soc. Amer.* 47, 1091-1099.
- Rose, J. E., Brugge, J. F., Anderson, D. J., and Hind, J. E. (1967). Phase-locked response to low frequency tones in single auditory nerve fibers of the squirrel monkey. *J. Neurophysiol.* 30, 769-793.
- Rose, J. E., Brugge, J. F., Anderson, D. J., and Hind, J. E. (1969). Some possible neural correlates of combination tones. *J. Neurophysiol.* 32, 402-423.
- Rose, J. E., Galambos, R., and Hughes (1959). Microelectrode studies of the cochlear nuclei of the cat. *Bull. Johns Hopkins Hosp.* 104, 211-251.
- Rose, J. E., Greenwood, D. D., Goldberg, J. M., and Hind, J. E. (1963). Some discharge characteristics of single neurons in the inferior colliculus of the cat. I. Tonotopic organization, relation of spike counts to tone intensity, and firing patterns of single elements. *J. Neurophysiol.* 26, 294-320.
- Rosenzweig, M. R. (1951). Representation of the two ears at the auditory cortex. *Amer. J. Physiol.* 167, 147-158.
- Rosenzweig, M. R., and Rosenblith, W. A. (1953). Responses to successive auditory stimuli at the cochlea and at the auditory cortex. *Psychol. Mon.* 67, No. 13, 1-26.

- Sindberg, R. M., and Thompson, R. F. (1962). Auditory response fields in ventral temporal and insular cortex of cat. *J. Neurophysiol.* 25, 21-8.
- Tunturi, A. R. (1955). Analysis of cortical auditory responses with the probability pulse. *Amer. J. Physiol.* 181, 630-8.
- Tunturi, A. R. (1960). Anatomy and physiology of the auditory cortex. In G. L. Rasmussen and W. F. Windle (Eds.), "Neural Mechanisms of the Auditory and Vestibular Systems." p. 181-200. Springfield, Ill: Thomas.
- von Békésy, G. (1960). "Experiments in Hearing." New York: McGraw-Hill.
- von Békésy, G. (1965). Cochlear mechanics. In T. H. Waterman and H. J. Morowitz (Ed.), "Theoretical and Mathematical Biology." p. 172-197. New York: Blaisdell.
- Walter, W. G., and Shipton H. W. (1951). A new toposcopic display system. *Electroencephalogr. Clin. Neurophysiol.* 3, 281-292.
- Wever, E. G. (1949). "Theory of Hearing." New York: Wiley.
- Woolsey, C. N., and Walzl, E. N. (1942). Topical projection of nerve fibers from local regions of the cochlea to the cerebral cortex of the cat. *Bull. Johns Hopkins Hosp.* 71, 315-344.

NLP-84 <sup>micro</sup>file

Separated for copying  
add no. of pp.

(3) for binding 4 reg. format

NOTICE: This material may be protected  
by copyright law. (Title 17 U.S. Code)