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Binaural Interaction in the Superior Olivary Complex of the Cat: An Analysis of Field Potentials Evoked by Binaural-Beat Stimuli¹

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THE ACCESSORY, or medial nucleus of the superior olivary complex is the first nucleus in the classical ascending auditory pathway that receives bilateral input. Both the anatomical structure and electrophysiological responses of the accessory nucleus suggest that it is a locus of binaural signal processing. The cells of the accessory nucleus have been shown to be responsive to interaural time and intensity disparities of binaurally presented clicks (5, 6) and to the interaural phase relations of binaurally presented tones (11). The field potentials of the accessory nucleus evoked by click and pure-tone stimuli have been correlated with the anatomical distribution of synaptic input from the two ears (3, 5, 17). Evidence of binaural interaction in the slow-wave responses of the superior olivary complex to binaurally presented clicks was found by Rosenzweig and Amon (13). In the present study the field potentials of the superior olivary complex evoked by binaurally presented pure tones were analyzed to define further the mechanisms of binaural interaction.

The stimuli used in this study were binaurally presented pure tones which differed slightly in frequency, resulting in a constantly changing phase relationship between the tones. In man, this stimulus produces the percept of a beating or pulsating tone which is known as "binaural beats." The rate of beat-

ing is equal to the difference in frequency between the two tones and represents a binaural analysis of the changing interaural phase relations. The objectives of this study were: 1) to see if a periodicity corresponding to the binaural beat rate was present in the field potentials of the superior olivary complex; 2) to determine if this periodicity could be attributed to a physiological coding of interaural phase relations; and 3) to see how changes in the field potentials in response to changes in stimulus parameters corresponded to perception.

METHODS

Surgical procedures

Two types of preparations were used in 21 successful experiments: 1) cats anesthetized with sodium pentobarbital (40 mg/kg, ip) and 2) unanesthetized cats which had been decerebrated at the level of the superior colliculus. All surgical procedures were carried out with the cat in a stereotaxic apparatus with hollow ear bars. Body temperature was maintained at about 37 C with a heating pad. There was no monitoring of blood pressure or respiration. The decerebration procedure was carried out with the animals anesthetized with halothane (Fluothane, Ayerst Laboratories). The internal carotid arteries were tied, the skull exposed and a 1-inch-diameter hole was trephined in the skull overlying the colliculi. A blunt spatula (4 mm wide), fixed in a stereotaxic carrier, was lowered vertically three or four times through the brain until there was an incision extending the entire width of the trephined hole. A postmortem verification of the completeness of the decerebration was always made. In the anesthetized preparations, additional sodium pentobarbital was generally administered as needed.

Both dorsal and ventral approaches to the superior olivary complex were used. For the dorsal ap-

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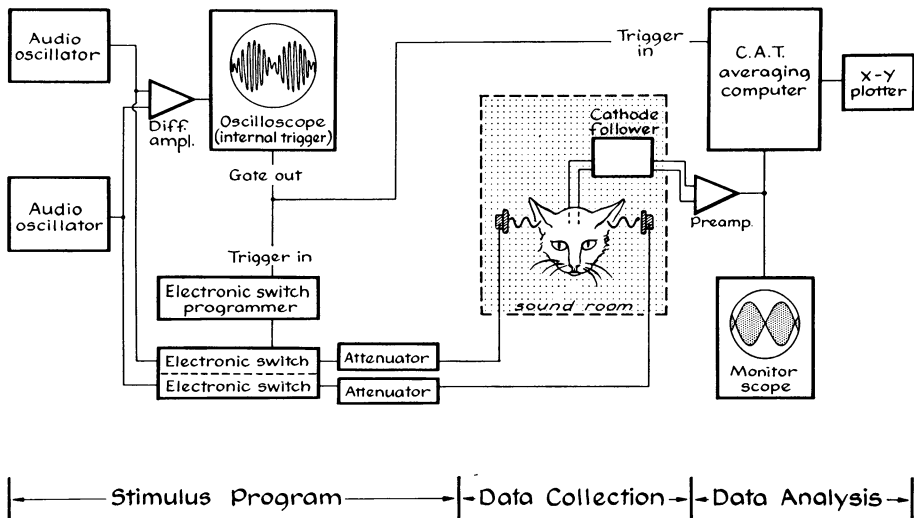


FIG. 1. Block diagram of instrumentation for presenting a binaural-beat stimulus and for recording and averaging the electrical responses to such a stimulus.

proach, the electrode was inserted stereotactically at a 30° angle from the vertical. For the ventral approach, the stereotaxic apparatus was inverted, the cat was intubated, and the bone overlying the brain stem was exposed. A hole was drilled in the midline suture and the electrode adjusted to penetrate the brain stem at a mediolateral angle of 30° . In 10 cats, a round-window electrode was inserted through a hole in the bulla and was held in place with dental cement.

Stimulus presentation

Two Hewlett-Packard (204B) audio oscillators were used to generate the pure-tone stimuli. The stimuli were gated with an electronic switch (Grason-Stadler, model 829E), amplified by a Sherwood S-9000 audio amplifier, and passed through a set of attenuators (Hewlett-Packard, model 350D) into the transducers.

The transducers were Telephonics (TDH-39) earphones which were coupled to the hollow ear bars of the stereotaxic apparatus. The system was damped to have a flat frequency response, between 200 Hz and 1,500 Hz, into a 2-cc coupler. All sound levels in this study are specified as the sound pressure level into a 2-cc coupler. The threshold for visual detection of the cochlear microphonic response at the round window to a 600-Hz tone was approximately equivalent to a sound pressure level of 40 db measured in the coupler. The system was also calibrated with a probe microphone near the tympanic membrane; these measurements were within ± 5 db of the coupler determinations.

Estimates of interaural attenuation with a stimulus frequency of 600 Hz were obtained from four animals. The method used was to record the coch-

lear microphonic potentials with a round-window electrode and note the level of the stimulus needed to produce a response which was visually detectable on the oscilloscope trace. The difference in level for detection of a contralateral and ipsilateral stimulus was the estimate of interaural attenuation. The values obtained were 32, 30, 30, and 25 db of interaural attenuation in the four cats. In one cat estimates were also made at 300 Hz and 1 kHz; the values of interaural attenuation were 25 and 40 db, respectively. Additionally, in one experiment probe microphone measurements of the sound pressure level at the tympanic membrane were made. The values of interaural attenuation obtained for frequencies between 300 Hz and 2 kHz were all greater than 45 db. Since probe microphone measurement of acoustic crossover does not include bone-conducted sound and round-window measurements do, it was concluded that the limiting factor for interaural attenuation was acoustic crossover via bone-conducted sound.

The stimuli could be presented continuously or as a train of tone bursts. The duration of the tone bursts was 100–250 msec with an interburst interval approximately equal to the duration. The rise and decay times of the bursts were 25 msec. The electronic switch was programmed so that the tone bursts had a constant preset interaural phase relationship. The stimulus frequencies were determined with an electronic counter (Hewlett-Packard, model 522B).

Data collection

A block diagram of the stimulating, recording, and averaging instrumentation is presented in Fig. 1. All recording was done with the cat in the

stereotaxic apparatus located in a sound-attenuating room (Industrial Acoustics Company, model 401A). A bipolar electrode was used for recording. The electrode consisted of two insulated 100- μ wires, extending about 2-3 mm from a supporting stainless steel shaft. The wires were cut at about a 45° angle so that the tips were separated in the vertical plane by approximately 0.5 mm. In one experimental series (designated by the letter M in subsequent sections of this paper), recording was monopolar using the lead electrode of the bipolar pair; the indifferent electrode was located on the frontal sinus. The electrode used for round-window recording was a 200- μ steel wire with the tip bared and coiled to a diameter of about 1 mm. The electrical activity was either led directly out of the sound room to a preamplifier (Grass, model P-511) or first passed through a cathode follower (Grass, model HIP511A).

Up to five electrode tracts, separated by at least 0.75 mm, were made in each preparation. The electrode was generally marked at the last point in its tract by passing current through the electrode. The anode was connected to the tip electrode. The electrode was withdrawn 4 mm and marked again. The cat was then sacrificed by cardiac perfusion with a 10% formalin solution containing potassium ferricyanide. For histological verification of the electrode position, 52- μ frozen sections were prepared and stained with neutral red.

Data analysis

The evoked activity was generally averaged on-line by small digital computer (Mnemotron, CAT model 400B) with as few as 10 and as many as 200 responses averaged over periods of 125 msec unless otherwise noted. The activity was averaged with respect to the phase relations of the two pure-tone stimuli. This was accomplished by mixing the two tones in a differential amplifier, triggering the oscilloscope sweep at some point in the waveform produced by the combined tones, and then triggering the computer with a gating pulse from the oscilloscope. In this manner the tones were combined for triggering purposes but were not combined in the signal channels. Activity stored in the computer was either displayed on the oscilloscope and photographed or was plotted on graph paper by a Mosely X-Y plotter.

Initial observations and necessary considerations

When the electrode was located in or near the superior olivary complex, the two types of field potentials characteristic of this region were readily seen in response to a pure-tone stimulus. These potentials have been generally referred to as the "following" response and the "slow" potentials and can be observed independently by appropriate filtering (17). The following response is a periodic

potential whose fundamental frequency is the same as that of the stimulating tone and is best between 400 and 2,000 Hz. The slow potential is essentially a base-line shift which is initiated at the onset of the stimulus and gradually decays or is brought abruptly to the initial base-line level upon termination of the stimulus. The polarity of the slow potential is dependent on the location of the electrode within the superior olivary complex.

When the binaural-beat stimulus was presented to the cat, both the following and slow potentials could readily be seen to have a periodicity corresponding to the binaural-beat rate (Fig. 2). For the following response this periodicity was present as a modulation of the envelope of the evoked potential and for the slow potential, the binaural periodicity was seen as an almost sinusoidal amplitude modulation of that potential.

Unfortunately, this periodic activity cannot be accepted, *per se*, as representing binaural interaction. There are two other possible sources of this periodicity: 1) acoustic crossover causing a physical mixing of the two tones and thus a physical beat and 2) electrical summation of the two independently evoked monaural responses producing a periodicity equal to their difference in frequency. For instance, if the two independently evoked sets of activity were recorded simultaneously at the electrode, their sum would contain a periodicity equal to the binaural-beat rate similar to that observed if the outputs of two oscillators were physically mixed. It was not necessary to control for this electrical interaction when evaluating periodicities in the slow potentials as the monaural slow-potential response is essentially a base-line shift. The summation of the two monaural responses would simply be a different base-line shift and no periodicity would result from their summation. The procedure used to differentiate summation of the monaural responses from binaural interaction is presented in the next section. The controls for acoustic crossover are presented in RESULTS.

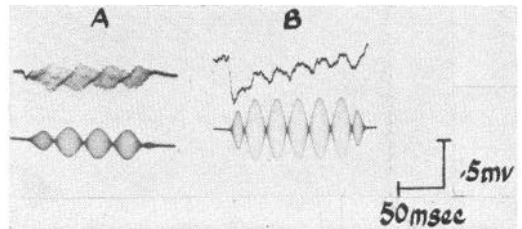


FIG. 2. Example of periodic activity evoked in the superior olivary complex by stimuli which produce the percept of binaural beats in man. Upper trace in A is following response activity and upper trace in B is slow-potential activity from a different experiment. Lower trace in each picture is an analogue of the signal. The envelope maxima of the signal analogue indicate that signals are in phase at the two ears, and the minima indicate that signals are 180° out of phase.

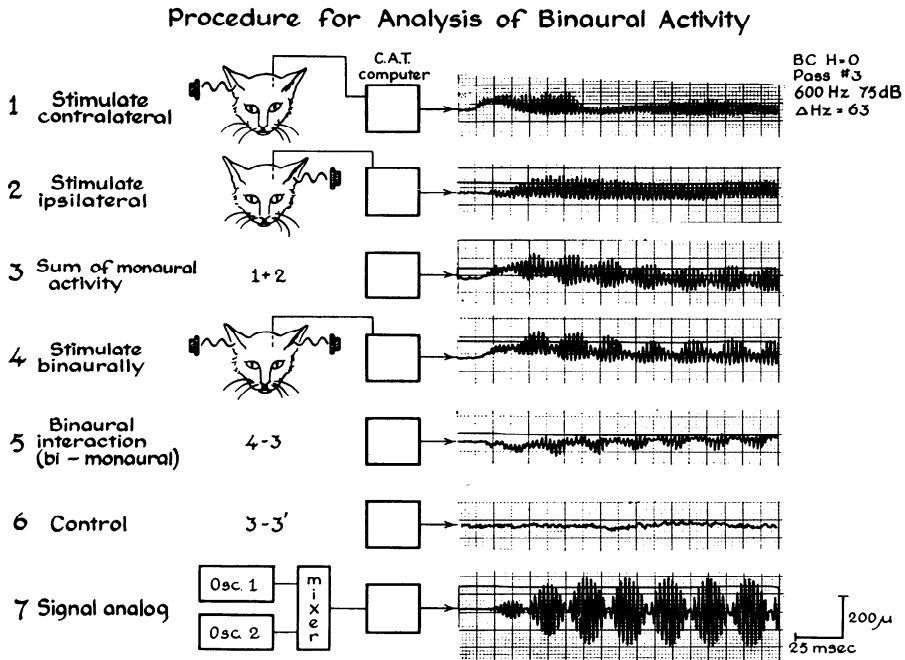


FIG. 3. Procedures for determining binaural interaction. Activity in line 3 will be referred to in the text as the monaural sum, in line 4 as the binaural response and in line 5 as binaural interaction.

Procedure for analysis of binaural activity

To evaluate binaural interaction, a method was devised, based on that used by Kemp and Robinson (8) and by Rosenzweig and his associates (13-15). Figure 3 illustrates the steps in this procedure. The evoked responses to binaural and monaural tone bursts were averaged, on-line, by a CAT computer. When the ipsilateral and contralateral monaural responses were summed (line 3), there was a periodicity in the envelope of the responses which corresponded to the difference in frequency between the stimulating tones. This same envelope periodicity was observed with binaural stimulation (line 4). When the sum of the monaural activities was then subtracted from the binaurally evoked activity (line 5), a difference resulted. This difference could be attributed to binaural interaction. A control was periodically run to insure that the difference obtained between binaural and monaural stimulation was not due to variability of responses over time (line 6). This was accomplished by summing the monaural responses, as in line 3, and then again stimulating each ear monaurally and subtracting the evoked activity from the stored responses. This procedure typically yielded a straight line, indicating that variability over time was not the source of binaural-monaural differences. A signal analogue was provided by mixing the two stimulus tones and averaging them (line 7). The maxima represent stimuli interaurally in phase and minima represent stimuli 180° out of phase.

Terminology

The potentials derived from a given analysis or having a characteristic feature (as in the case of slow-potential periodicity) will be referred to by the following terms:

1. Binaural activity—the “following” response activity elicited by a “binaural-beat” stimulus. An example of this activity is seen in Fig. 3, line 4.
2. Monaural sum—the sum of the two monaurally evoked following responses, as in Fig. 3, line 3.
3. Binaural interaction—the activity remaining after subtraction of the monaural sum from binaural activity, as in Fig. 3, line 5.
4. Slow potential beats—any modulation of slow potentials at the “binaural-beat” rate, as in Fig. 2, upper right-hand trace, in which the slow potential is seen with the “following” response filtered out, or in Fig. 3, line 5, in which slow-potential modulations can be seen along with binaural interaction.

RESULTS

General characteristics of binaural interaction and slow-potential beats

The difference between binaural and monaural activity (Fig. 3, line 5) can be seen to contain both slow-potential and following response components. The following response

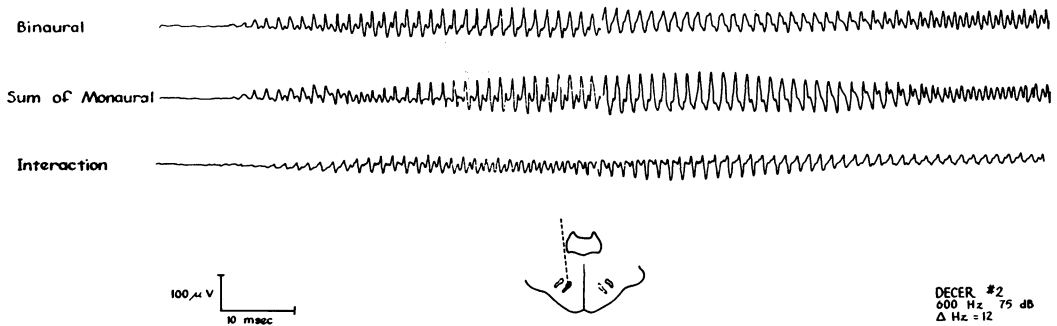


FIG. 4. Following response activity evoked by a binaural-beat stimulus. Note that the binaurally evoked response (line 1) is smaller than the sum of the monaural responses (line 2), and that there is no latency shift between the individual peaks of these two potentials. Lower trace is the measure of binaural interaction and is the difference between the upper two potentials. It has a fundamental frequency midway between the two stimulus tones and an envelope repetition rate of Δf . This activity was obtained from the anterior region of the accessory nucleus and was high-pass filtered (150 Hz cutoff) to eliminate the slow potentials. The binaural activity (line 1) is the average of 200 responses and the sum of the monaural activity (line 2) is the average of 400 responses; 200 from each ear.

activity (binaural interaction), resembles an amplitude-modulated sinusoid. It has a fundamental frequency that is about midway between the frequencies of the two stimulating tones and an envelope repetition rate equal to the frequency difference between the two tones. The slow potential has a periodicity corresponding to the binaural-beat rate (slow-potential beats). The latency of both slow-potential beats and binaural interaction from the onset of the evoked electrical activity varied between 1 and 12 msec and was usually less than 5 msec.

The prominent envelope repetition rate of binaural interaction was typical of a great many electrode locations; however, there were just as many areas where a difference between binaural and monaural stimulation was obtained without any detectable periodicity. Sometimes, slow-potential beats and binaural interaction were seen together, as in the activity seen in Fig. 3, line 5; and, at other times, at a given electrode location, only one of these potentials was present.

Binaural interaction is the difference between the binaural response and the sum of the activities produced by monaural stimulation (monaural sum) and, as such, it can either reflect an increase or a decrease of activity. This can be determined by a direct comparison of the amplitude of the binaural response with that of the monaural sum, i.e., if the monaural sum is of greater amplitude than the binaural response, then binaural stimulation has resulted in a decrease of ac-

tivity. In 12 experiments in which this determination was made, binaural stimulation resulted in a decrease in activity. This decrease typically occurred where the binaural response was of the lowest amplitude, i.e., at its envelope minima. In only one experiment, binaural stimulation resulted in a small increase in activity.

The mechanism producing this decrease in the following response during binaural stimulation could be either an amplitude change, a latency shift, or a combination of these two. These possibilities were evaluated by directly comparing the two forms of activity at a greatly expanded time scale (Fig. 4). In three such experiments binaural interaction was always the result of an amplitude difference in the following response between the binaural response and the sum of the monaural responses and no evidence of a latency shift was detected.

ANATOMICAL LOCUS OF BINAURAL INTERACTION AND SLOW-POTENTIAL BEATS. Table 1 summarizes the types of electrical activity found at different electrode locations. There were many areas in the brain stem in which the binaural response occurred with an envelope periodicity of Δf , but where binaural interaction did not result. In every experiment in which binaural interaction was found, the electrode was always within the rostrocaudal limits of the superior olivary complex. Binaural interaction was typically found from the ventromedial border of the accessory

TABLE 1. *Relation of electrode location to binaural activity*

Exp	Electrode Tract	Activity Obtained			Electrode Location
		BR	BI	SP beats	
<i>Anesthetized preparations</i>					
B	1	x	x	s l o w	ASO
C	1	x	.	w	ASO
D	1	x	x	p o t e n t i a l s	ASO and S seg
E	1	.	.	c e n t r a l	Lat to ASO
F	1, 2	.	.	t e r m i n a l	Post to SOC
G	1	x	.	a	Post to SOC
	2	x	x	l s	ASO and S seg
H	1	x	.	f i l t e r e d	Post to SOC
	2, 3	x	x		ASO and S seg
	4	.	.		Post to SOC
J	1	x	x		SOC
K	1	x	x		ASO
L	1	x	x	o u t	ASO
A.A.	1	x	x	x	ASO
<i>Decerebrate preparations</i>					
P	1	x	.	.	S seg
	2, 3	x	.	.	Post to SOC
Q	1	x	.	x	Ant to SOC
	2	x	x	.	ASO
BC	1	x	.	.	Med to SOC
	2	x	x	.	Med to SOC
	3	x	x	x	Med to SOC
	4	x	x	x	Med to SOC
MA	1	x	x	x	S seg and ASO
MB	1, 2	x	x	x	ASO and S seg
	3	x	x	.	S seg and Med to ASO
MC	1, 2	x	.	.	Med to SOC
	3	x	x	x	Med to S seg and ASO
	4	x	x	x	ASO and S seg
	5	x	.	.	Post to SOC

Small x denotes presence of indicated activity. In experiments B, C, L, and A.A., the electrode was lowered to point of maximal following response. In all other experiments, the electrode was lowered in 0.5-mm steps from point of first evoked response. Monopolar recording was used in experiments MA, MB, and MC; in all others bipolar recording was used. BI = binaural interaction; BR = binaural response; SP beats = slow-potential beats; ASO = accessory nucleus; S seg = S segment of superior olivary complex; SOC = superior olivary complex; Lat = lateral; Med = medial; Post = posterior; Ant = anterior.

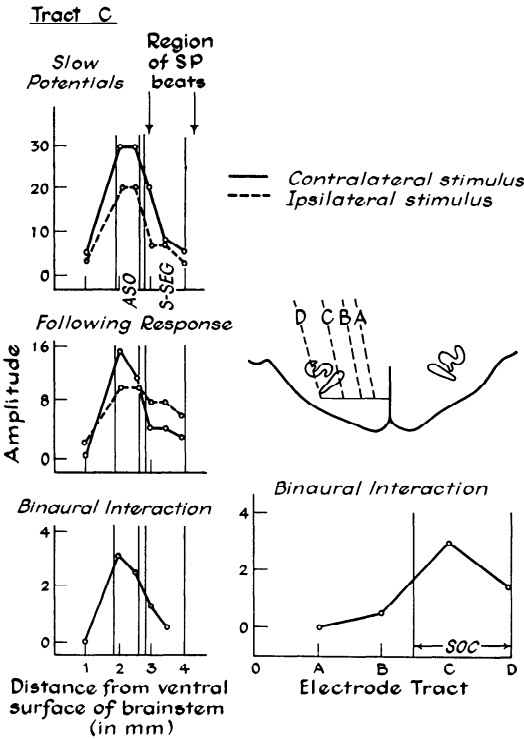


FIG. 5. Relative amplitude of potentials at different electrode locations in experiment MC. Graph on right presents maximum amplitude of binaural interaction for four tracts 1 mm apart in lateral plane. Three graphs on left present relative amplitude of potentials for tract in graph on right which was 3 mm from the midline (tract C). In the graph on upper left is the dorsoventral area over which slow-potential beats were seen. Note that all potentials were maximal in the accessory nucleus except slow-potential beats, which were only seen in vicinity of S segment. ASO = accessory nucleus; s-seg = S segment of superior olivary complex; soc = superior olivary complex.

nucleus to the dorsal extent of the S segment and was maximal in the accessory nucleus. The anatomical locus yielding maximal slow-potential beats was dorsal to the region of maximal binaural interaction, but in the same rostrocaudal plane.

The graphs in Fig. 5 illustrate the relations of the potentials obtained from a typical experiment. In this experiment four electrode tracts were made in the lateral plane in 1-mm steps. The maximum amplitude of binaural interaction in each of these tracts is graphed in the right-hand column in Fig. 5. Two tracts were medial to the superior olivary complex (tracts A and B). In these tracts, following activity without binaural interac-

tion or slow-potential beats was seen. Tract C was medial to the S segment but went through the accessory nucleus. In this tract there was both binaural interaction and slow-potential beats. The most lateral tract (tract D) traversed both the S segment and the accessory nucleus. The activity obtained in this tract was similar to that in tract C except that binaural interaction was smaller. The three graphs in the left-hand column of Fig. 5 illustrate, respectively, the amplitudes of the slow potentials, following response, and binaural interaction along tract C, which traversed the center of the accessory nucleus. Binaural interaction, the slow potentials, and following potentials were of maximal amplitude in the accessory nucleus, whereas slow-potential beats were seen only in the region of the S segment. Thus, the locus of maximal slow-poten-

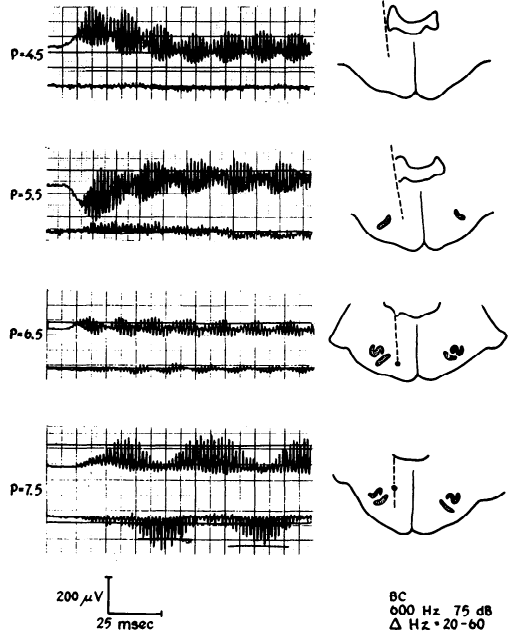


FIG. 6. To show activity obtained from four electrode tracts in experiment BC. Upper trace in each picture is the binaural response and lower trace is binaural interaction. Electrode tracts were separated by 1 mm; top picture represents the most anterior of the tracts. Note that all tracts were medial to the superior olivary complex. Activity at P=7.5 was obtained from the location indicated by the black dot in insert diagram. Activity at P=6.5 was recorded just medial to S segment and not at position of black dot. Note that binaural interaction was of largest amplitude at P=7.5, the only location where monaural contralateral stimulation did not evoke any following activity.

tial beats was different from the locus of both slow potentials and binaural interaction.

There was only one instance in which binaural interaction and slow-potential beats were detected beyond the bounds of the superior olivary complex. In experiment BC four electrode tracts were made in 1-mm steps in the anterior-posterior plane with all of the electrode tracts medial to the superior olivary complex. Examples of the obtained activity are presented in Fig. 6, along with reconstructions of the electrode location. It can be seen that in each tract a periodic envelope was evident in the activity evoked by binaurally presented tones (the top trace in each picture) and except for the tract which was anterior to the entire superior olivary complex, binaural interaction was obtained (the lower trace in each picture). Binaural interaction was maximal in the most posterior tract. It is of interest that there was essentially no following response from stimulation of the contralateral ear at this location. At all other electrode locations in this animal, contralateral stimulation did evoke a response, but binaural interaction was much smaller.

Changes in binaural interaction and slow potential beats resulting from changes in stimulus parameters

CHANGES IN INTERAURAL FREQUENCY DIFFERENCES (Δf). A Δf series was run in five experiments in which values of Δf ranging from 1 to 320 Hz were presented most often at a base frequency of 600 Hz. Each Δf value was usually presented at three signal intensities: 65-, 75-, and 85-db SPL; or 75-, 85-, and 95-db SPL.

Data from one of these experiments are presented in Fig. 7 to illustrate the results typically obtained in a Δf series. Both binaural interaction and slow-potential beats, with a periodicity at the rate of Δf , occurred over a wide range of Δf values. In these results there was no trend in the amplitude of either binaural interaction or the slow-potential beats with changes in Δf . In the cases where a trend was detected, it was found to depend upon electrode location, such that a movement of the electrode by as little as .5 mm to a new location might reverse this trend. In one experiment (Fig. 8), values of Δf larger than 100 Hz were used and two modes of binaural interaction were evident. When the two tones were

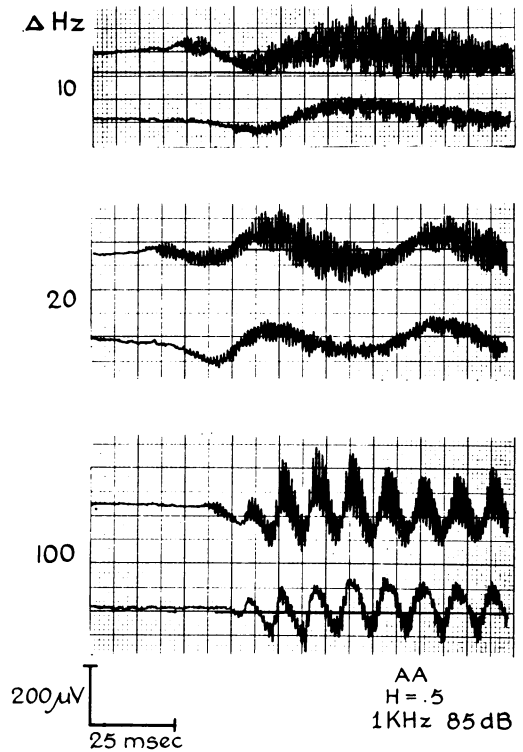


FIG. 7. Changes in binaural response, binaural interaction, and slow-potential beats with changes in Δf at a base frequency of 1 kHz. Upper trace in each picture is binaural response, lower trace is binaural interaction and slow-potential beats.

close in frequency (<100 Hz), binaural interaction was represented as a periodic suppression of activity. When Δf was >200 Hz, there was only a generalized suppression of activity without any periodicity.

CHANGES IN STIMULUS FREQUENCY. The limiting factor on the size of binaural interaction with changes in frequency was that the frequency used had to evoke a following response. Within these limits, no definite trend in the size of binaural interaction with changes in frequency could be determined. Different electrode locations in an experiment would yield maximum binaural interaction at different frequencies. The data in Fig. 9 illustrate the changes in the binaural response, binaural interaction, and slow-potential beats that result from changes in base frequency. Binaural interaction was maximal at 1 kHz and at 600 Hz and there was little binaural interaction at 300 Hz, 800 Hz, and 2 kHz. The amplitude of the slow-potential beats was smallest both at

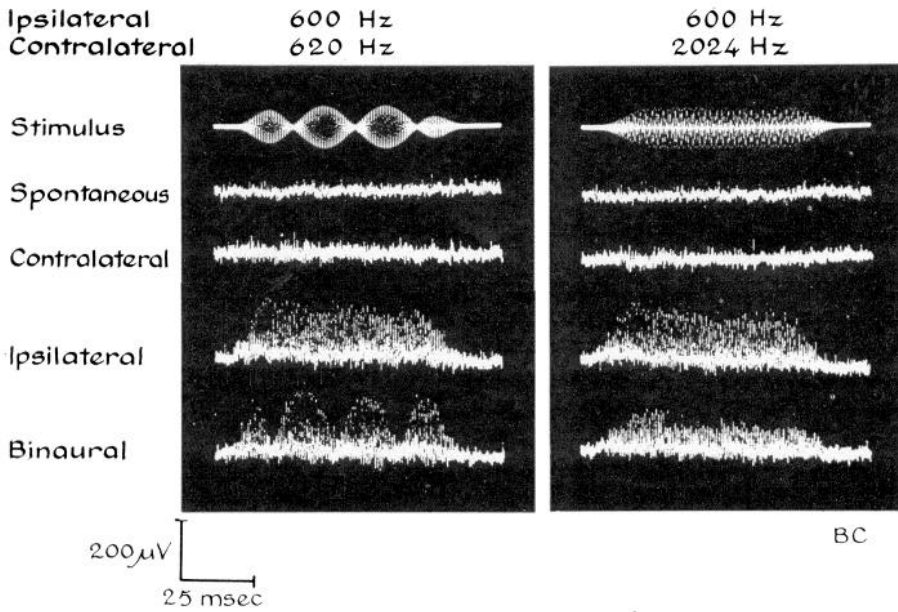


FIG. 8. Binaural interaction in the absence of an excitatory monaural contralateral response. Top trace in each picture is stimulus analogue. Stimulus intensity was 75-db SPL. Note periodic suppression of activity which occurs during binaural stimulation when the two stimulus tones are close in frequency (bottom trace in left picture) and general suppression of activity which occurs when stimulus tones are far apart in frequency (bottom trace in right picture). Electrode was located medial to the S segment.

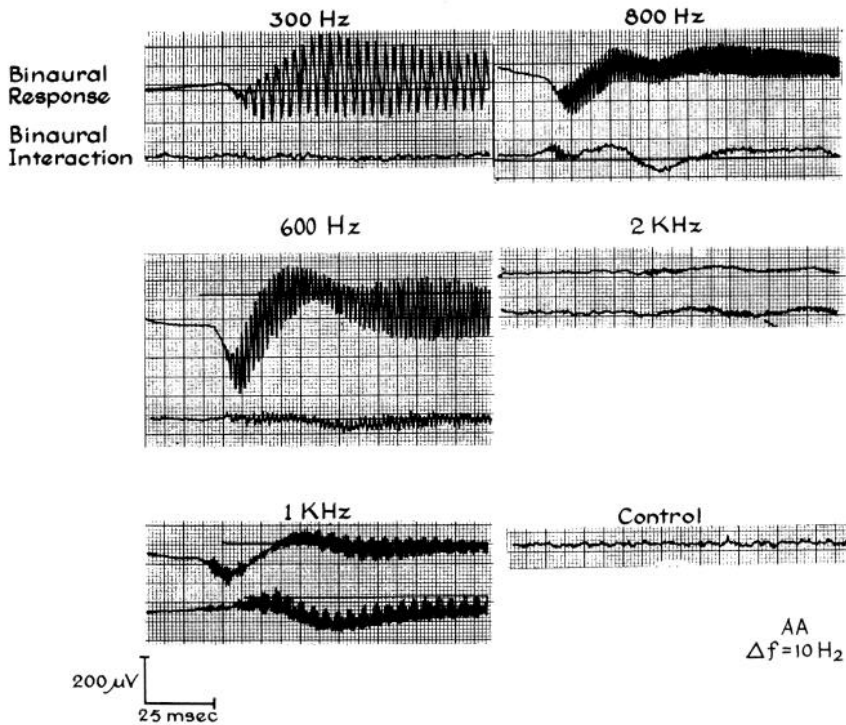


FIG. 9. Changes in binaural response, binaural interaction, and slow-potential beats with changes in base stimulus frequency at a constant Δf . Upper trace in each picture is binaural response, lower trace is binaural interaction and slow-potential beats.

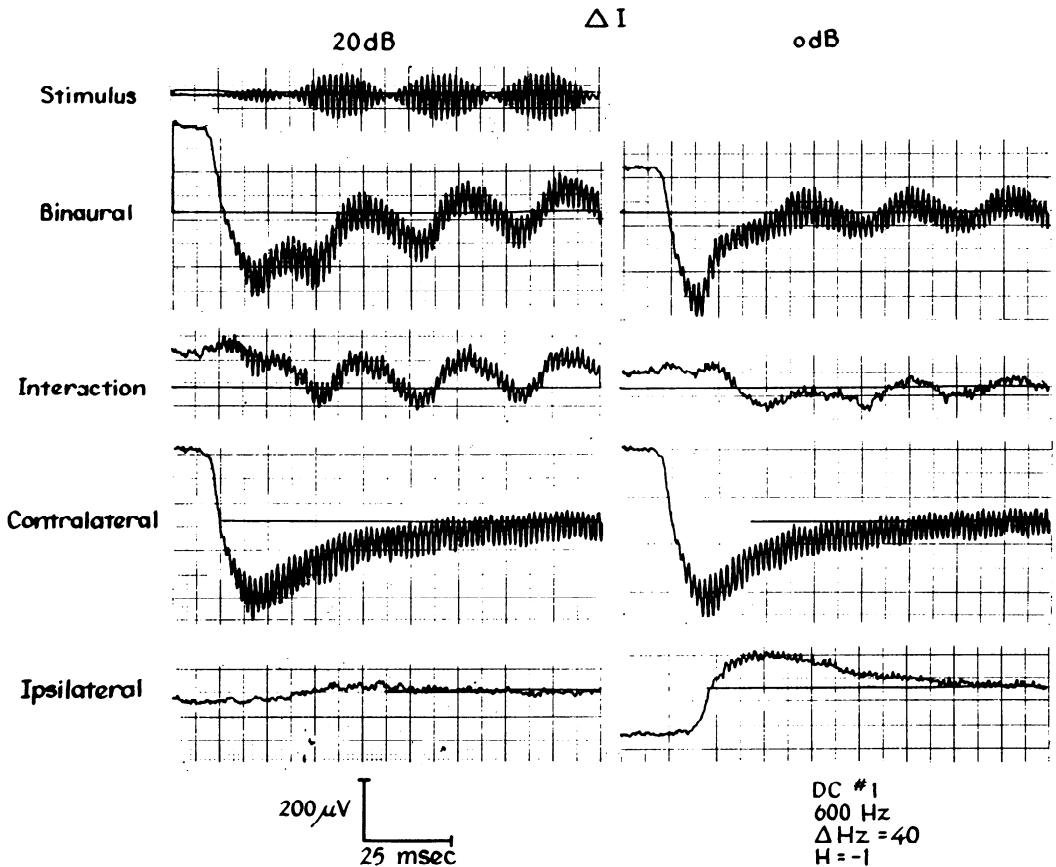


FIG. 10. Effects of changing the interaural intensity differences (ΔI). Potentials shown were taken from experiment MA, were maximal with an interaural intensity difference of 20 db. Recording was monopolar. Note that there is essentially no monaural response to the ipsilateral stimulus when $\Delta I = 20$ -db condition, and yet binaural interaction is evident. Negativity is upward.

the lowest (300 Hz) and at the highest frequencies used (2 kHz). The lack of binaural interaction at 2 kHz can be attributed to the fact that there was very little following at this frequency.

In one other animal the changes in slow-potential beats with changes in frequency were studied. With Δf held constant at 20 Hz, slow-potential beats were present, at about the same amplitude, for frequencies of 600 Hz, 1 kHz, and 2 kHz, but were not observed when the stimulus frequency was 4 kHz. The results of these two studies indicate that slow-potential beats decrease in amplitude at high frequencies (above 1–2 kHz).

CHANGES IN INTERAURAL INTENSITY DIFFERENCES (ΔI). The effects of ΔI on binaural interaction and slow-potential beats were investi-

gated in five animals. In three of these experiments binaural interaction and slow-potential beats were seen over a ΔI range of 30–50 db and were maximal when the tones were of equal intensity. In the other two experiments, however, both slow-potential beats and binaural interaction were maximal when the tones were mismatched by 20–30 db.

Figure 10 shows the activity evoked in one of these preparations when ΔI was equal to 0 db and when ΔI was equal to 20 db. Both binaural interaction and slow-potential beats were greater when ΔI was equal to 20 db, even though the monaural responses were of equal amplitude when ΔI was equal to zero. The occurrence of maximal slow-potential beats with an interaural intensity mismatch was characteristic of this entire electrode tract, independent of base frequency and Δf value.

EFFECTS OF VARIABILITY AND ANESTHESIA. The amplitude of slow-potential beats was fairly stable over time; however, the amplitude of binaural interaction could sometimes change dramatically. When this occurred, binaural interaction was greater at all stimulus parameters. These changes were not correlated with either the level of spontaneous activity or the level of anesthesia. These abrupt changes in the amplitude of binaural interaction were also seen in nonanesthetized, decerebrate preparations. The relationship of binaural interaction to the binaural response was independent of the level of anesthesia. Though the amplitude of the binaural response decreased as anesthesia deepened, binaural interaction remained a constant percentage of the binaural response.

CONTROL PROCEDURES

Round window. To test whether binaural interaction measured in the superior olive reflected binaural effects at the cochlea, either from a cochleocochlear pathway (4) or from acoustic crossover, determinations of binaural interaction in cochlear microphonic potentials were made. These measures were made in three cats and in no case was a difference between binaural and monaural stimulation noted. In one determination of binaural interaction, the value of interaural attenuation was first obtained, as previously described, and was found to be 30 db. The stimulus at the ear contralateral to the electrode was then set 30 db more intense than the stimulus to the ipsilateral ear. Since this was the amount of interaural attenuation, the contralateral and ipsilateral stimuli were physically present at approximately equal amplitudes at the cochlea from which the activity was recorded. This produced a physical beat which was reflected in the cochlear microphonics. No difference between binaural and monaural stimulation was noted even in this extreme condition, thus indicating that the contribution of cochleocochlear connections or acoustic crossover to binaural interaction as measured in the superior olive was negligible.

Physical beat control. In order to evaluate the possibility that slow-potential beats recorded in superior olivary complex resulted from physical beats generated by acoustic crossover, physical beats were introduced as stimuli and the responses were compared to

those evoked by the same two tones presented binaurally. Physical beats produced a modulation of the slow potentials at a rate of Δf , as did the binaurally presented stimuli, but the potentials produced by physical beats were approximately 180° out of phase with those produced by the binaural-beat stimuli.

Binaural interaction and slow-potential beats at higher auditory stations

Some preliminary observations have been made at the level of the inferior colliculus and at the auditory cortex. Binaural interaction and slow-potential beats were found in the inferior colliculus. Binaural interaction in the inferior colliculus tended to be a greater percentage of the following response than in the superior olive. More observations of these potentials in the inferior colliculus are needed to determine their anatomical loci within that nucleus and to determine their behavior relative to the potentials arising in the superior-olivary complex. At the auditory cortex, no periodic activity was found corresponding to the binaural-beat rate.

DISCUSSION

Sources of binaural interaction and slow potential beats other than binaural interaction

SUMMATION OF THE MONAURALLY EVOKED RESPONSES. The results of this study show that stimulation with a binaural-beat stimulus will evoke a periodicity in the potentials of the superior olivary complex of the cat that corresponds to the binaural-beat rate. The possibility that the periodicity seen in the following response was the result of the summation at the electrode of the two independently generated monaural responses was handled by subtracting the monaurally evoked activity from the binaurally evoked activity and attributing the binaural-monaural difference to binaural interaction. This analysis yields a conservative estimate of binaural interaction as it is possible that the binaurally evoked response (binaural response) is attributable to binaural processing but is essentially equal to the sum of the monaural responses. This would be indistinguishable from the situation where binaural interaction did not exist and where the binaurally evoked response was solely the sum of the monaural activity. Binaural interaction was, in general, character-

ized by an envelope periodicity equal to the binaural-beat rate. The absence of such a periodicity reflected a condition in which binaural interaction was present but was independent of the interaural phase relations of the signals. Since the sum of the monaurally evoked slow potentials did not contain a periodic component, the presence of slow-potential beats was taken to reflect binaural processing.

ACOUSTIC CROSSOVER. It was noted previously that the periodicities seen in slow-potential beats and in the envelope of binaural interaction could arise from the production of physical beats via acoustic crossover. The results of round-window recording showed that acoustic crossover did not influence binaural interaction. Slow-potential beats were shown to exist over a wide range of interaural intensity differences (0–40 db) with very little change in amplitude. If these modulations of the slow potential resulted from physical beats produced by acoustic crossover, they would exist over a much smaller range of ΔI , since the production of a well-defined physical beat requires that the two signals be of approximately equal amplitude. When physical beats were introduced as stimuli, a modulation of the slow potential similar to that evoked by binaural stimulation was seen; however, this modulation was 180° out of phase with slow-potential beats. This indicates that these are two separate potentials and, thus, slow-potential beats cannot be attributed to acoustic crossover. It also suggests, however, that observations of slow-potential beats, with respect particularly to changes in ΔI , might be biased by acoustic crossover; for as the value of ΔI approaches the value of interaural attenuation, physical beats will result and produce their own modulations of the slow potentials.

CHANGES IN IMPEDANCE. It has been suggested that binaural interaction might be attributed to a monaurally induced impedance change at the electrode. Unless this impedance change was solely in the resistive component of the impedance, which seems unlikely, a latency shift between binaural and monaural stimulation should result. Since no latency shifts between the binaural response and the monaural sum were observed, the probability that binaural interaction resulted from an impedance

change is low. Also, the possibility that monaurally evoked impedance changes would result in a periodicity at the Δf rate seems unlikely.

Anatomical locus of binaural interaction and slow-potential beats

Binaural interaction and slow-potential beats were found in the accessory nucleus and in the S segment of the superior olivary complex. In addition, in one experiment, both binaural interaction and slow-potential beats were found at a point about 1 mm medial to the S segment. Since recording was bipolar with the electrodes closely spaced and binaural interaction and slow-potential beats, when found, existed only in a small area, it appears unlikely that these were volume-conducted potentials originating from distant generators. Binaural interaction and slow-potential beats were not always found together. In experiments where both potentials were found in separate loci, binaural interaction was found in the accessory nucleus and slow-potential beats were found in the S segment. This would suggest that two independent generators of binaural activity exist. This concept is supported by the findings that changes in frequency and Δf did not always evoke corresponding changes in binaural interaction and slow-potential beats. When ΔI was varied, however, binaural interaction and slow-potential beats behaved in a similar fashion. This would indicate that there is some degree of dependence between the generators of binaural interaction and slow-potential beats. The finding that slow-potential beats were largest in an area distant from the region in which slow potentials themselves were maximal suggests that slow-potential beats are generated independently of the slow potentials, rather than by direct modulation of the slow-potential source.

Correspondences between electrophysiological results and perception

Although it is not known if cats perceive binaural beats, it is reasonable to assume that the neurophysiological mechanisms processing interaural phase differences in cats are similar to those in man. The periodicity of the binaurally evoked potentials corresponds to the binaural-beat percept in man. The ampli-

tude of binaural interaction and slow-potential beats was found to vary with changes in frequency and interaural intensity differences in the same manner as the binaural-beat percept (9, 16). However, the changes in these potentials, with respect to changes in Δf , did not correspond to perception. Binaural beats are heard only over a small range of Δf values, from about 2 to 25 Hz (9), whereas binaural interaction and slow-potential beats were found over a much larger Δf range. Furthermore, the latency for the perception of binaural beats is about 120 msec (1), whereas the latency of both binaural interaction and slow-potential beats, relative to the onset of the evoked response, was typically less than 5 msec.

The short latency of binaural interaction and slow-potential beats, relative to the binaural-beat percept and the effects of Δf changes on these potentials, indicate that they are not direct correlates of binaural beats. These differences indicate that there is, probably, additional transformation of this information at other levels of the brain. The study of Masterton and Diamond (10) indicates that one additional transform, permitting the perception of a "fused" image to binaurally presented sounds, takes place at the cortex. The presence of binaural interaction and slow-potential beats at high Δf values may reflect aspects of binaural interaction other than the binaural-beat percept. An example of a perceptual manifestation of binaural interaction at high Δf rates is provided by von Békésy (2).

Relevance of results to single-unit activity

The first level of the auditory pathway at which interaural phase-sensitive units have been found is in the accessory nucleus of the superior olivary complex (11). The results of this study provide support for this finding by showing that the electrical activity of the superior olivary complex contains a periodicity in both the following and slow-potential responses dependent on stimulus-phase relations. It is also indicated that the elements generating these electrical responses have a relative decrease in activity to binaural stimulation, when compared with responses to monaural stimulation similar to the phase-sensitive unit in the accessory nucleus reported by Moushegian and Rupert (11) that

discharged less frequently to binaural stimulation than it did to monaural contralateral stimulation.

The discharge rate of phase-sensitive units in the inferior colliculus studied by Rose and his associates (12), varied as a function of the interaural phase relations of tonal stimuli below 3 kHz. This is comparable to the upper frequency limit at which binaural interaction and slow-potential beats were found in the present experiments.

RESPONSES OF SINGLE UNITS TO A BINAURAL-BEAT STIMULUS. A few studies (7, 11) have used the binaural-beat stimulus paradigm to determine how a unit would react to different frequencies in each ear. In these studies the analysis of unit discharges was not related to the interaural phase relations of the binaural stimuli and, thus, no analysis was made of periodicities in the unit discharge. Some preliminary experiments were carried out to find out if units would respond periodically to a binaural-beat stimulus. Such units were found in both the superior olive and the inferior colliculus.

The binaural-beat stimulus is an excellent paradigm for studying unit sensitivity to interaural phase relations as it provides an almost instantaneous record of a unit's behavior over the entire range of interaural phase differences. This is an advantage over using two tones of the same frequency and obtaining a measure of the units' responses at numerous discrete phase relationships, as has been done in previous studies investigating phase-sensitive units (11, 12).

SUMMARY

Electrical activity in the superior olivary complex of decerebrate or pentobarbital-anesthetized cats was recorded with bipolar electrodes during the presentation of binaural tones differing slightly in frequency. This stimulus produces the percept, in man, of a single tone which appears to pulsate or beat in the center of the head at a rate equal to the difference in frequency between the tones. This percept is known as "binaural beats" and is related to the constantly changing interaural phase relations of the stimuli.

A periodicity at the binaural-beat rate was seen in both the "following" response and slow potentials of the superior olivary complex. To determine what portion of the bin-

aurally evoked following response was due to binaural interaction, the activity evoked by the sum of the two monaural stimuli was subtracted from the binaural response by a small digital computer. A difference between monaural and binaural stimulation (binaural interaction) was restricted to the region of the accessory nucleus and the ventral region of the S segment of the superior olivary complex. Binaural interaction was the result of an amplitude change in the following response and resembled an amplitude-modulated sinusoid. It had a frequency of approximately $(f_1 + f_2)/2$ and an envelope periodicity corresponding to the binaural-beat rate. It almost always represented a relative decrease in the following response evoked by binaural stimulation when compared with the responses evoked by monaural stimulation.

Binaural interaction in the slow potentials

evoked by the binaural-beat stimulus was represented as a modulation of the slow potentials at the binaural-beat rate. This slow-potential periodicity was generally found throughout the S segment and was not maximal in the same region as the binaural component of the following response or the slow potentials themselves.

Changes in the binaurally evoked potentials with changes in base frequency, interaural frequency differences, and interaural intensity differences, were determined and related to the effects of similar stimulus changes on the binaural-beat percept in man.

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REFERENCES

- ANTONELLI, A. R. AND MOSCIARO, O. A hypothesis about the site of origin of binaural beats. *Intern. Audiology* 2: 63-64, 1965.
- BÉKÉSY, G. VON. *Experiments in Hearing*, translated and edited by E. G. Weaver. New York: McGraw, 1960, p. 318-319.
- BIEDENBACH, M. A. AND FREEMAN, W. J. Click-evoked potential map from the superior olivary nucleus. *Am. J. Physiol.* 206: 1408-1414, 1964.
- GALAMBOS, R., ROSENBLITH, W. A., AND ROSENZWEIG, M. R. Physiological evidence for a cochleo-cochlear pathway in the cat. *Experientia* 6: 438-440, 1950.
- GALAMBOS, R., SCHWARTZKOPFF, J., AND RUPERT, A. Microelectrode study of superior olivary nuclei. *Am. J. Physiol.* 197: 527-536, 1959.
- HALL, J. L. II. Binaural interaction in the accessory superior-olivary nucleus of the cat. *J. Acoust. Soc. Am.* 37: 814-823, 1965.
- HIND, J. E., GOLDBERG, J. M., GREENWOOD, D. D., AND ROSE, J. E. Some discharge characteristics of single neurons in the inferior colliculus of the cat. II. Timing of the discharges and observations on binaural stimulation. *J. Neurophysiol.* 26: 321-341, 1963.
- KEMP, E. H. AND ROBINSON, E. H. Electric responses of the brain stem to bilateral auditory stimulation. *Am. J. Physiol.* 120: 316-322, 1937.
- LICKLIDER, J. C. R., WEBSTER, J. C., AND HEDLUN, J. M. On the frequency limits of binaural beats. *J. Acoust. Soc. Am.* 22: 468-473, 1950.
- MASTERTON, R. B. AND DIAMOND, I. T. Effects of auditory cortex ablation on discrimination of small binaural time differences. *J. Neurophysiol.* 27: 15-36, 1964.
- MOUSHEGIAN, G., RUPERT, A., AND WHITCOMB, M. Brain-stem neuronal response patterns to monaural and binaural tones. *J. Neurophysiol.* 27: 1174-1191, 1964.
- ROSE, J. E., GROSS, N. B., GEISLER, D. C., AND HIND, J. E. Some neural mechanisms in the inferior colliculus of the cat which may be relevant to localization of a sound source. *J. Neurophysiol.* 29: 288-314, 1966.
- ROSENZWEIG, M. R. AND AMON, A. H. Binaural interaction in the medulla of the cat. *Experientia* 11: 498-499, 1955.
- ROSENZWEIG, M. R. AND SUTTON, D. Binaural interaction in lateral lemniscus of cat. *J. Neurophysiol.* 21: 17-23, 1958.
- ROSENZWEIG, M. R. AND WYERS, E. J. Binaural interaction at the inferior colliculi. *J. Comp. Physiol. Psychol.* 48: 426-431, 1955.
- TOBIAS, J. V. Application of a "relative" procedure to a problem in binaural-beat perception. *J. Acoust. Soc. Am.* 35: 1442-1447, 1963.
- TSUCHITANI, C. AND BOUDREAU, J. C. Wave activity in the superior olivary complex of the cat. *J. Neurophysiol.* 27: 814-827, 1964.