

XXIII. COMMUNICATIONS BIOPHYSICS*

Prof. W. A. Rosenblith	Dr. N. Y-S. Kiang†††	J. G. Krishnayya
Prof. M. A. B. Brazier†	Dr. T. T. Sandel††	R. G. Mark
Prof. M. Eden	Dr. Eda Berger Vidale	P. Mermelstein
Prof. M. H. Goldstein, Jr.	J. A. Aldrich	C. E. Molnar‡‡‡
Prof. W. T. Peake	R. M. Brown	Donna A. Molnar
Prof. W. M. Siebert	S. K. Burns	R. R. Pfeiffer†††
Dr. J. S. Barlow‡	R. R. Capranica	Cynthia M. Pyle
Dr. A. Cavaggioni**	Eleanor K. Chance	D. M. Snodderly, Jr.
W. A. Clark††	R. J. Clayton	G. F. Svihula
Dr. B. G. Farley††	A. H. Crist	Aurice V. Weiss
Dr. G. L. Gerstein	P. R. Gray	T. F. Weiss
Dr. François Grémy‡‡	J. L. Hall II	J. R. Welch
Dr. E. Giberman***	F. T. Hambrecht	M. L. Wiederhold
Dr. R. D. Hall		G. R. Wilde

RESEARCH OBJECTIVES AND SUMMARY OF RESEARCH

Our basic objective is a better understanding of the communication senses. Hearing, in particular, will continue to receive our major attention.

A number of experimental studies are aimed at increasing our knowledge of the neural coding of sensory stimuli. These include: recording from single nerve cells located in the accessory olive of the cat under conditions of binaural stimulation; patterns of single-unit activity in the cochlear nucleus of cat in relation to the sound stimulus and anatomical location of the unit; unit responses from the lateral geniculate body of the rat to patterns of light and shadow in the visual field. Studies of "ongoing" activity also continue to be of interest. A study of conditioning of the bullfrog's heart rate by sound stimuli is aimed at determining which sounds get coded into this animal's auditory system and at his behavioral responses to natural and unnatural sounds.

In a number of electrophysiological studies we are attempting to correlate neuroelectric activity with physiological state. These include: behavioral studies of rats with gross electrodes recording from locations on and in their sensory pathways; studies of neuroelectric activity recorded from cats in different stages of sleep and wakefulness; studies in unanesthetized cats with brain stem sections of cortical responses to shocks delivered to the sensory pathways; and studies of the olivocochlear bundle.

The development of mathematical models closely related to neurophysiological mechanisms is a major effort of the group. In this category are the following modeling studies: coding of auditory signals as patterns of neural impulses in the eighth nerve; mechanisms of some features of binaural localization; some limitations on auditory discrimination

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†Visiting Professor in Communication Sciences from the Brain Research Institute, University of California at Los Angeles.

‡Research Associate in Communication Sciences from the Neurophysiological Laboratory of the Neurology Service of the Massachusetts General Hospital.

**From the Istituto di Fisiologia, Università di Pisa.

††Staff Member, Lincoln Laboratory, M. I. T.

‡‡(Maître de Conférences, Laboratoire de Physique) Visitor from Faculté de Médecine (Paris).

***From the Department of Physics, Weizmann Institute of Science, Israel.

†††Also at Massachusetts Eye and Ear Infirmary.

‡‡‡Staff Associate, Lincoln Laboratory, M. I. T.

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implied by the nature of peripheral coding; and "ongoing" activity of single units.

Psychophysical studies form an important adjunct to the physiological and modeling work. These include studies of judgments of various binaural patterns, and of discriminability of noiselike signals.

Considerable instrumentation is involved in our experimental work, in presentation of stimuli, recording and processing of neuroelectrical signals, and physiological monitoring of the animals. Design of instruments ranging from telemetering systems to mixer-amplifiers, from real-time correlators to heart-rate meters, from digital devices for generating precisely controlled sounds to sacks for restraining cats are an important and indispensable part of our effort.

Close cooperation with the Eaton-Peabody Laboratory of the Massachusetts Eye and Ear Infirmary and with various groups at Lincoln Laboratory, M.I.T., continues to play a crucial role in our work. In particular, we anticipate a number of important applications for the LINC, a Laboratory Instrument Computer of considerable generality and utility, developed at Lincoln Laboratory under the leadership of Wesley A. Clark and with the collaboration of several Lincoln Laboratory staff members, the engineering assistance of Lt. Charles E. Molnar of Air Force Cambridge Research Laboratories, and the aid of members of the Research Laboratory of Electronics.

M. H. Goldstein, Jr., W. M. Siebert, W. A. Rosenblith

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A. BINAURAL INTERACTION IN SINGLE UNITS OF THE ACCESSORY SUPERIOR OLIVARY NUCLEUS IN CAT

There has been conjecture as to the physiological mechanisms associated with the localization of sounds in space, and a number of models have been proposed.¹⁻³ However, there were meager electrophysiological data on the behavior of single units until the work of Galambos, Schwartzkopff, and Rupert,⁴ and even that study was far from exhaustive. Psychophysical experiments with humans indicate that the difference in time of arrival of the stimuli at the two ears, the difference in intensity of the stimuli at the two ears, and the average intensity (average of intensity at left and right ears expressed in decibels) are all influential in determining the apparent position of a sound source.⁵⁻⁷ Also, these experiments indicate that human observers are capable of detecting extremely small interaural time differences (of a few microseconds),⁸ and extremely small interaural intensity differences (of a few tenths of a decibel).⁹

In an attempt to obtain electrophysiological data that are pertinent to a better

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understanding of the neurophysiology of binaural localization, we are investigating the electrical activity of single nerve cells in the accessory nucleus of the superior olive in cats under conditions of binaural stimulation. Anatomical and electrophysiological considerations indicate that this is a reasonable place in which to look. As far as is known, the accessory nucleus is the most peripheral station in the classical ascending auditory pathway to receive inputs from both ears.¹⁰ Previous electrophysiological studies have demonstrated the existence of neurons in the accessory nucleus which are extremely sensitive to small changes in interaural time difference.⁴ We have recorded from several hundred cells in the accessory nucleus, giving major attention to the question of binaural interaction. A summary of our present results is given here. A model is suggested which is in agreement with some aspects of binaural localization of sounds in both cats and humans.

1. Methods

We have used as stimuli clicks presented through earphones. Clicks have the desirable feature of being punctate in time. Earphones provide independent control of interaural time and intensity differences, which is not possible with free-field stimulation. Clicks are produced by applying 100- μ sec rectangular voltage pulses to PDR-10 earphones.

We have tried several kinds of microelectrodes and have settled on an etched stainless-steel electrode. The etching and insulating procedure is essentially the same as that described by Brown and Tasaki,¹¹ but we also plate the tip of the electrode, first with copper and then with platinum black.

An anesthetized (Dial) cat is in a soundproof, electrically shielded chamber. We position the electrode on the ventral surface of the medulla, using the rack and pinion controls of a stereotaxic instrument. The electrode is advanced by means of a hydraulic micromanipulation system from outside the soundproof chamber. As the electrode is advanced, we present the cat with a stimulus consisting of clicks at approximately -50 db relative to 4 volts across the earphones (approximately 50 db relative to visual detection level of the slow potential observed in the accessory nucleus) with an interaural time interval of 25 msec and an over-all repetition period of approximately 300 msec. At the same time, we monitor on an oscilloscope the electrical activity picked up by the electrode.

The position of the electrode tip relative to the accessory nucleus is determined by one or more of the following methods: (a) We measure the depth of penetration of the electrode from the surface. (b) We measure the position of the electrode relative to the depth at which the slow-wave potential reverses polarity (see below). (c) In some cases we have marked the electrode position by passing a current through the electrode, with subsequent histological control. As far as we have been able to determine, the

nerve cells that exhibit binaural interaction are located in or near the accessory nucleus.

We have taken as a measure of unit activity the percentage of stimulus presentations to which the unit responds at least once. We determine this by presenting a given number of stimuli (usually 50) and counting the number of stimulus presentations to which the unit responds. In most of the cases this has been on-line by means of a level discriminator and electronic counter. In a few cases we have recorded the responses on magnetic tape.

2. Results

As the electrode is advanced, we see two distinct kinds of electrical activity. One is what Galambos and his co-workers have termed the "slow-wave" potential⁴; the other is spike responses from individual nerve cells. The slow-wave potential follows the pattern described by Galambos, and others. Ventromedial to the accessory nucleus, stimulation of the contralateral ear evokes a negative-going slow wave, and stimulation of the ipsilateral ear evokes a positive-going slow wave. Dorsolateral to the accessory nucleus, the polarities are reversed. While this slow wave may, in some sense, represent the excitation for cells in the accessory nucleus, we have not attempted to study in detail the interaction between slow wave and unit activity. We have been interested in the slow wave only insofar as it provides an indication of the position of the electrode relative to the accessory nucleus.

We have observed firing patterns of cells showing many sorts of binaural interaction. We shall mention briefly two kinds of interaction. Some cells show summation, in that

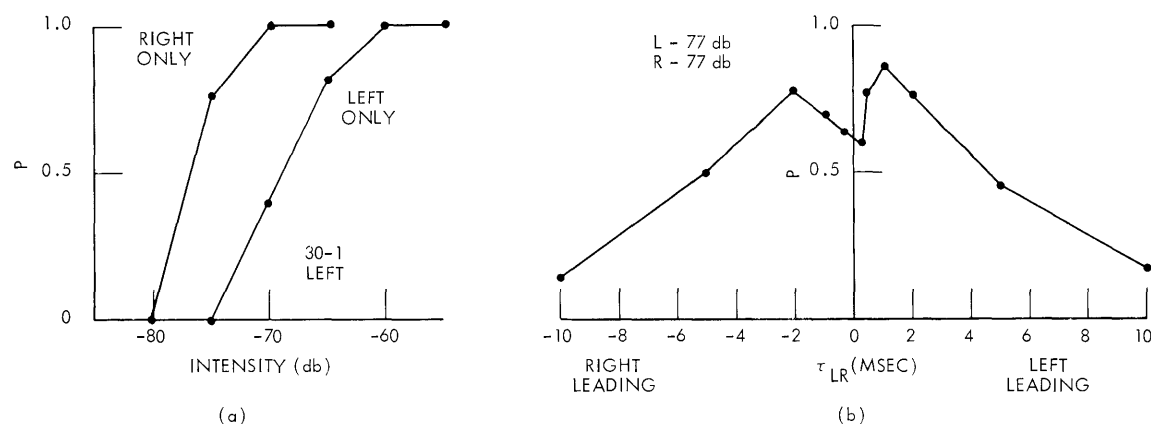


Fig. XXIII-1. Cell showing summation of stimuli to two ears. (a) Monaural intensity series. (b) Effect of interaural time difference. P is relative frequency of firing measured over 50 stimulus presentations at a rate of ~ 3 per second; τ_{LR} is time difference between clicks in left and right ears.

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if the stimuli are presented simultaneously to the two ears they respond more than they respond to stimulation of either ear alone. This summation may extend over several milliseconds, as shown in Fig. XXIII-1, or over a few hundred microseconds, as in Fig. XXIII-2. This property has been observed in approximately 20 cells.

Other cells have the cyclic behavior shown in Fig. XXIII-3. As the interval between the clicks to the two ears is varied, the unit shows several successive peaks of excitability. We have seen three such cells, all with a time between adjacent peaks of approximately 1 msec.

The group of cells in which we are most interested shows the properties summarized in Fig. XXIII-4. These cells respond to monaural stimulation of the contralateral ear,

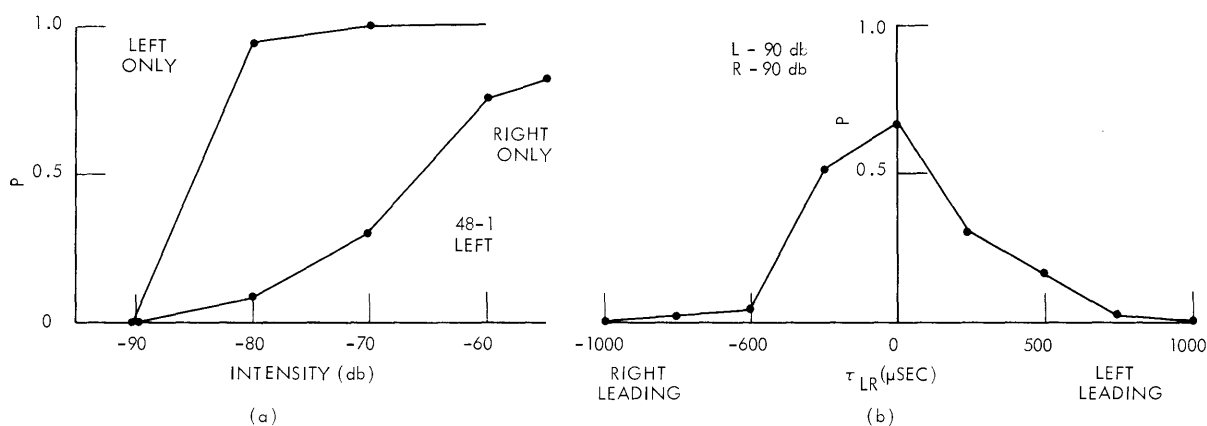


Fig. XXIII-2. Cell showing summation of stimuli to two ears. (a) Monaural intensity series. (b) Effect of interaural time difference.

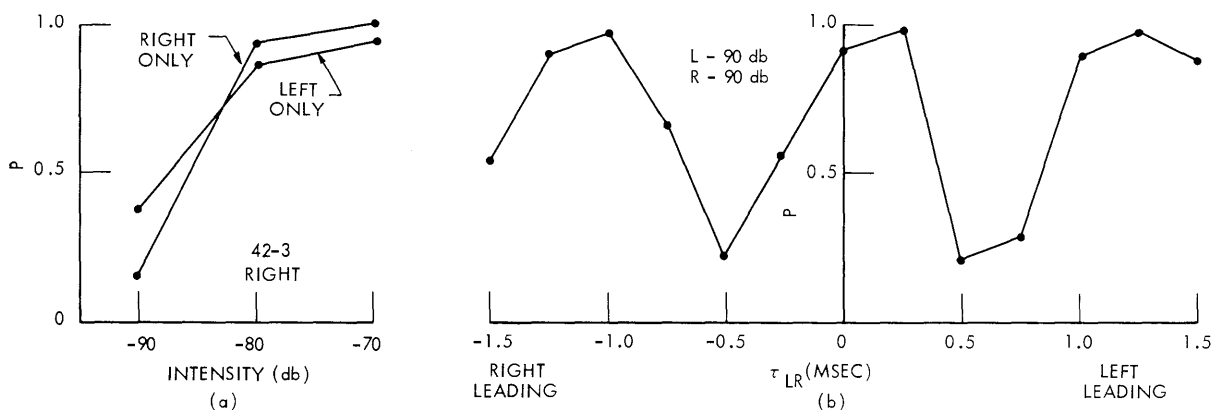


Fig. XXIII-3. Cell showing cyclic interaction of stimuli to two ears. (a) Monaural intensity series. (b) Effect of interaural time difference.

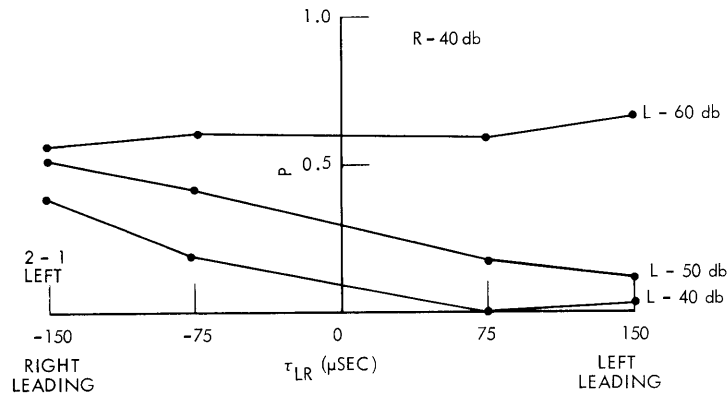


Fig. XXIII-4. Effect of interaural time difference, interaural intensity difference. Cell on left side.

but not to monaural stimulation of the ipsilateral ear. For all of these cells, the percentage of stimulus presentations to which the unit responds can be decreased either by making the stimulus to the ipsilateral ear more intense while holding interaural time difference constant or by making the stimulus to the ipsilateral ear arrive earlier while holding interaural intensity difference constant.

There is a striking parallel between the properties of cells of the type shown in Fig. XXIII-4 and results of psychophysical experimentation in humans. The responsiveness of these cells (we have recorded from approximately 50 of them) is a function of interaural time difference, interaural intensity difference, and average intensity. These parameters are also involved in determining the apparent location of a sound source with humans. This parallel of physiological and psychophysical data has led us to suggest the following model for the process of binaural localization: Binaural stimuli excite cells in the left and right accessory nuclei. If the stimulus at the left ear is more intense or arrives earlier than that at the right, more cells will be excited in the right accessory nucleus, and vice versa. Because of the sensitivity of these cells to both interaural time and intensity difference, time and intensity differences can be made to offset each other at the level of the individual cell. The psychophysical judgment of sidedness comes about as a result of any imbalance of the number of cells excited at the left and right accessory nuclei. This schema is similar to one proposed recently by van Bergeijk,³ and, as pointed out by van Bergeijk, it has a great deal in common with a model proposed in 1930 by von Békésy.¹ A simplified diagrammatic representation of our model is shown in Fig. XXIII-5.

In our model we assume that each cell that we observe is representative of a population of cells, and that the system is symmetrical; that is, there are similar populations of cells in the left and right accessory nuclei. Although we are restricted to

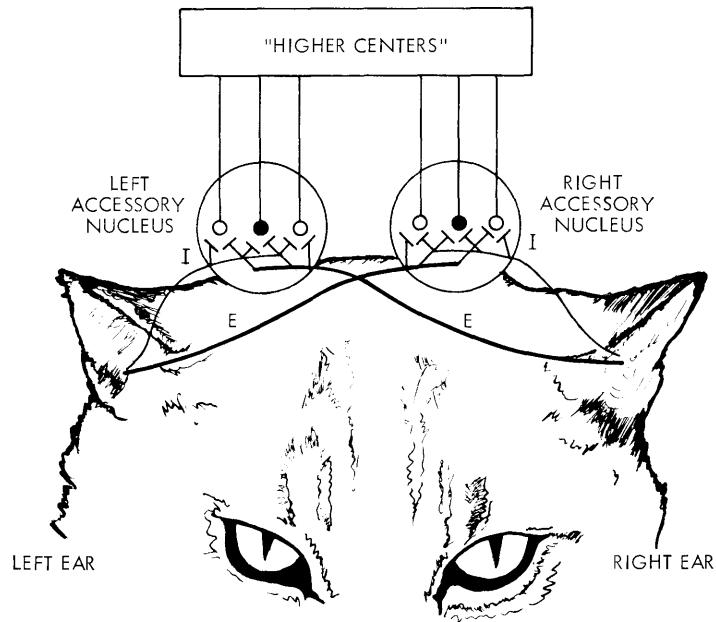


Fig. XXIII-5. Cells in both left and right accessory nuclei are innervated by excitatory inputs from the contralateral ear and inhibitory inputs from the ipsilateral ear. Ascending fibers from both accessory nuclei go to hypothetical "higher centers." The psychophysical judgment of sidedness is related to the relative number of cells responding at the two sides. The two solid cells are intended to indicate that the system is symmetrical, that is, in the model each cell on one side has its counterpart on the other.

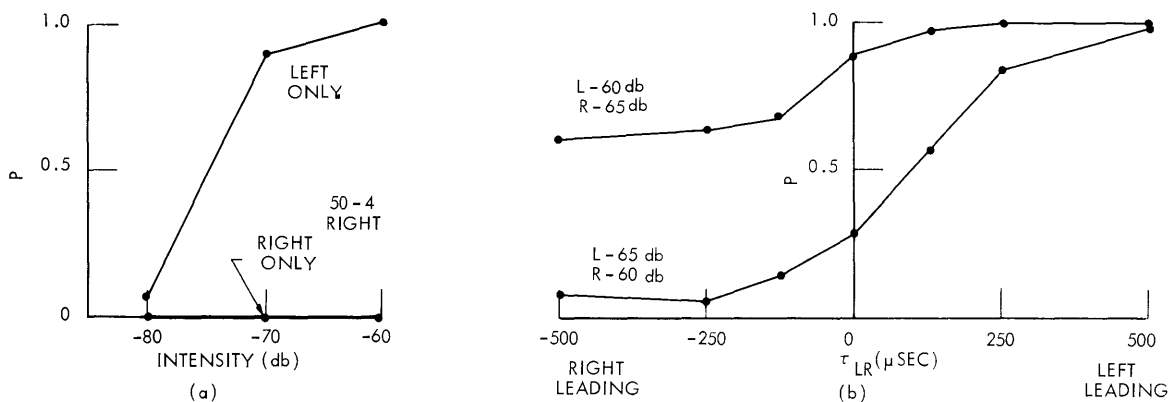


Fig. XXIII-6. (a) Monaural intensity series. (b) Effect of interaural time difference and interaural intensity difference. Cell on right side.

observing cells on only one side at a time, we can infer the behavior of corresponding cells on the opposite side by this assumption. A typical example is shown in Fig. XXIII-6. This cell was situated on the right-hand side of the cat. We observed the activity of the cell over a range of interaural time differences from plus to minus 500 μsec , where positive numbers indicate that the stimulus to the left ear is leading, and negative numbers indicate that the stimulus to the right ear is leading. Two intensity conditions are illustrated: left -60 db, right -65 db; and left -65 db, right -60 db. In order to infer the behavior of a hypothetical symmetrical cell on the left side, we interchange "left" and "right," both for time difference and for intensity difference, for one of these two curves. The resulting plot for the condition left -60 db, right -65 db is shown in Fig. XXIII-7.

For purposes of the model, we are interested in the relative number of cells firing at the two sides. We have taken as a measure of this $\mathcal{R}_L = P_L / (P_L + P_R)$, where P_R is the probability that the cell on the right will fire to a given stimulus presentation, and P_L is the probability that the hypothetical cell on the left will fire to a given stimulus presentation. This measure is bounded between 0 (corresponding to activity on the right and no activity on the left) and 1 (corresponding to activity on the left and no activity on the right), and is symmetrical about 0.5. That is, since $\mathcal{R}_L = 1 - \mathcal{R}_R$, where $\mathcal{R}_R = P_R / (P_L + P_R)$, the curve of \mathcal{R}_R is the curve of \mathcal{R}_L reflected about the 0.5 level.

If we had a homogeneous population of cells, we would be able to generalize directly from the behavior of a single cell to the total number of cells responding. Although we do not have a homogeneous population, it is still possible to set bounds on over-all activity from our data. As an example, consider the situation in which the stimulus to the left ear is more intense than the stimulus to the right ear, and the two stimuli are

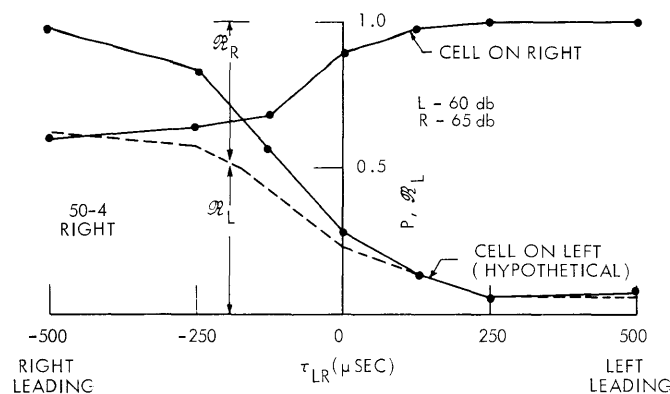


Fig. XXIII-7. Same cell as in Fig. XXIII-6, with "left" and "right" interchanged for original condition (left, -65 db; right, -60 db). Dashed line shows $P_L / (P_L + P_R) = \mathcal{R}_L$.

presented simultaneously. While \mathcal{R}_L is not necessarily the same for any two cells, \mathcal{R}_L is less than 0.5 for all cells that we have observed. Therefore we are justified in saying that, on the average, more cells respond to this particular stimulus configuration in the right population than in the left population.

Figure XXIII-8 summarizes the behavior of a typical cell. In this plot, \mathcal{R}_L is shown on the ordinate and interaural time difference is shown on the abscissa. Interaural intensity difference is held constant at 5 db, and average intensity is the parameter. Keeping in mind that (a) the data are from cats and (b) the model is highly simplified, we can compare predictions of the model and psychophysical results from humans. The effects of interaural time and interaural intensity difference are in qualitative agreement. With zero interaural time difference and the stimulus to the left ear more intense, we have $0 \leq \mathcal{R}_L < 0.5$, corresponding to "image to the left." If interaural intensity difference and average intensity are held constant and the stimulus to the left ear is made to arrive earlier, \mathcal{R}_L decreases, corresponding to movement of the image to the left.

Interaural time difference can offset the effect of interaural intensity difference for individual cells in terms of the model, just as it can in human centering experiments.^{5, 6} At point A in Fig. XXIII-8, for example, the stimulus to the left ear is 5 db more intense but lags the stimulus to the right ear by 120 μsec , and $\mathcal{R}_L = 0.5$, corresponding to equal firing probabilities at the two sides. In this sense an interaural intensity difference can be said to be "equivalent" to an interaural time difference, and we can define a time-intensity trading ratio in microseconds per decibel. The time-intensity trading ratio for point A would be 120 μsec per 5 db, or 24 μsec per db.

In Fig. XXIII-9, this time-intensity trading ratio is plotted as a function of average intensity for 12 cells that we have observed. The dashed lines indicate the range of time-intensity trading ratios obtained from human subjects presented with clicks with

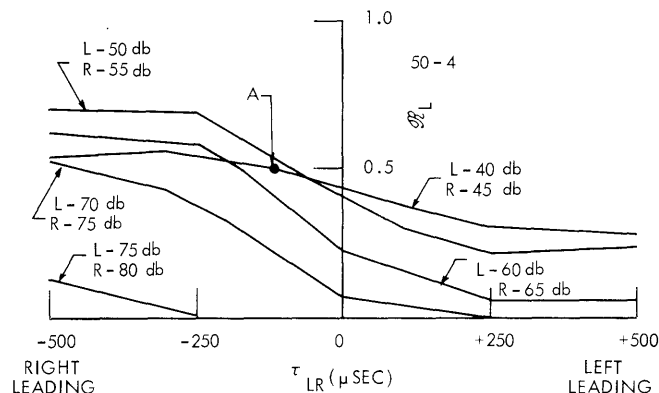


Fig. XXIII-8. Effect of interaural time difference and average intensity on \mathcal{R}_L . Interaural intensity difference, 5 db.

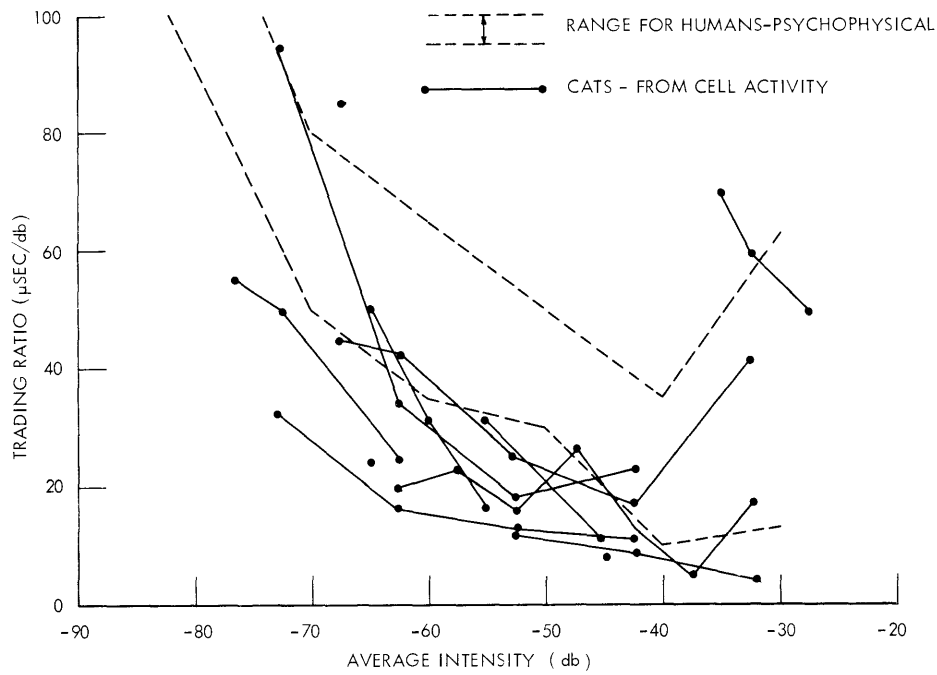


Fig. XXIII-9. Time-intensity trading ratio for human beings compared with that computed on the basis of the model. The dashed lines indicate the range of time-intensity trading ratios for humans (see E. E. David et al.⁶). Solid points represent time-intensity trading ratios computed from single units on the basis of the model. Points from the same cell at different intensities are joined by a solid line. Not shown on this graph are two points computed from a single low-threshold cell: -99.5 db, 430 μ sec/db; -101.5 db, 330 μ sec/db.

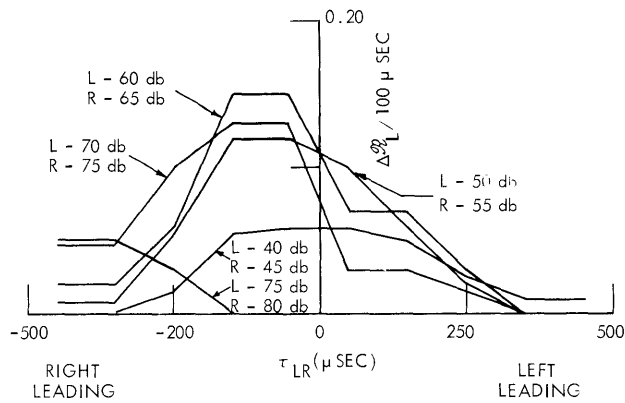


Fig. XXIII-10. Slope of curves in Fig. XXIII-8. Ordinate is the change in R_L resulting from a 100- μ sec change in interaural time difference.

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a given interaural intensity difference and asked to obtain a centered image by adjusting the interaural time difference (see David et al.,⁶ Fig. 5, impulse). The two sets of results are in close agreement, considering that they refer to two different species, etc., and they both show a trend downward with increasing intensity.

The range of interaural time differences over which a change in interaural time difference produces a change in unit activity is consistent with reasonable assumptions about the cat's localization behavior. The sensitivity of a unit to changes in interaural time difference as measured by the slope of the curves in Fig. XXIII-8 is greatest for values of interaural time difference near zero, and it shows a sharp decrease for values of interaural time difference greater than 200-300 μ sec. The slope of the curves in Fig. XXIII-8 is plotted as a function of interaural time difference in Fig. XXIII-10. The slopes are not symmetrical about zero interaural time difference because of the presence of an interaural intensity difference.

These curves can be related to a psychophysical parameter known as the Hornbostel-Wertheimer constant. This parameter is defined as the interaural time difference beyond which change in interaural time difference produces little change in position of the sound image. In humans this is approximately 500 μ sec.¹ Since the distance between the ears is smaller for cats than it is for humans, and therefore the maximum interaural time difference that could occur in free-field stimulation is smaller, it is perhaps not unreasonable to assume that the Hornbostel-Wertheimer constant for cats, if such a thing could be measured, would also be smaller.

A particularly interesting feature of the model is that the minimum interaural time difference that can be discriminated in terms of the model compares favorably with the minimum interaural time difference that the cat is capable of discriminating behaviorally. We can obtain an estimate of the precision afforded by the model by making the following assumptions: (a) There is in each accessory nucleus a homogeneous population of n cells. (b) Each cell on the left fires to a given stimulus presentation with probability P_L and does not fire with probability $Q_L = 1 - P_L$. Similarly, each cell on the right fires with probability P_R . (c) Firings of individual cells are mutually independent.

We define random variables X_L and X_R as the number of cells on the left and right sides, respectively, which respond to a given stimulus presentation. From our assumptions, the means and variances of these random variables are

$$E(X_L) = m_L = nP_L, \quad \sigma^2(X_L) = \sigma_L^2 = nP_LQ_L \quad (1)$$

$$E(X_R) = m_R = nP_R, \quad \sigma^2(X_R) = \sigma_R^2 = nP_RQ_R. \quad (2)$$

We define a third random variable, X_D , as the difference between X_L and X_R .

$$X_D = X_L - X_R. \quad (3)$$

It follows that

$$E(X_D) = m_D = m_L - m_R = n(P_L - P_R), \quad (4)$$

and from the assumption of independence that

$$\sigma^2(X_D) = \sigma_D^2 = \sigma_L^2 + \sigma_R^2 = n(P_L Q_L + P_R Q_R). \quad (5)$$

We now ask the question, For a given number of cells n , what is the smallest difference ΔP between P_L and P_R which will result in X_D being greater than zero with probability at least 0.75? (If the higher centers in our model made a "forced-choice" decision of right or left of center based simply on whether X_L was greater than or less than X_R , the choice of 0.75 probability would mean that three out of four stimulus presentations would result in the judgment "right of center." The choice of 0.75 is arbitrary. It is chosen as a convenient level midway between 0.5, corresponding to pure chance, and the asymptotic value 1.0. While it is chosen on much the same basis as the 0.75 level is chosen in psychophysical experiments, it should not be construed as corresponding to a behavioral just-noticeable difference.) If n is large, we can use the normal approximation to the binomial, so that X_D can be approximated by a normal distribution, and from a tabulation of the normal distribution we find that

$$P(X_D > 0) > 0.75 \text{ if } m_D > 0.7\sigma_D. \quad (6)$$

Setting $m_D = 0.7\sigma_D$ and substituting from Eqs. 4 and 5, we have

$$n(P_L - P_R) = 0.7 \sqrt{n(P_L Q_L + P_R Q_R)} \quad (7)$$

$$P_L - P_R = \Delta P = 0.7 \sqrt{(P_L Q_L + P_R Q_R)/n}. \quad (8)$$

Since we are interested in small differences between P_L and P_R , we can set $P_L Q_L + P_R Q_R = 2(P_L Q_L)$. Finally, we have

$$\Delta P = \sqrt{(P_L Q_L)/n}. \quad (9)$$

Let us, for the moment, set $n = 5000$. This estimate is based on the density of cells in the accessory nucleus and the size of the accessory nucleus³ and on the assumption that one-fourth to one-half of the cells in the accessory nucleus are of the type that can be included in the model. It is probably conservative. Referring to Fig. XXIII-7, we see for this particular cell and this particular stimulus configuration that $P_L = 0.7$, $Q_L = 0.3$, when P_L and P_R are equal. Substituting these numbers in Eq. 9, we have

$$\Delta P = \sqrt{(0.7 \times 0.3)/5000} = 0.006.$$

In order to determine the change in interaural time difference to which this corresponds, we observe from Fig. XXIII-7 that a change in interaural time difference of 50 μ sec results in a difference between P_L and P_R of ~ 0.12 . Therefore $\Delta P = 0.006$ corresponds to a change in interaural time difference of $0.006/0.12 \times 50 \mu$ sec, or 2.5 μ sec. This value is typical of the cells that we have observed and is of the same order of magnitude as the minimum change in interaural time difference that the cat is capable of discriminating behaviorally.¹²

While our assumptions of homogeneity and independence are gross simplifications, we have an indication that the model potentially may be capable of discriminations of the right order of magnitude.

J. L. Hall II, Cynthia M. Pyle

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B. POSTAURICULAR ELECTRIC RESPONSE TO ACOUSTIC STIMULI IN HUMANS

Many investigators have reported that acoustic stimuli alter the electric activity recorded from the scalp of humans. Several of these reports describe evoked responses

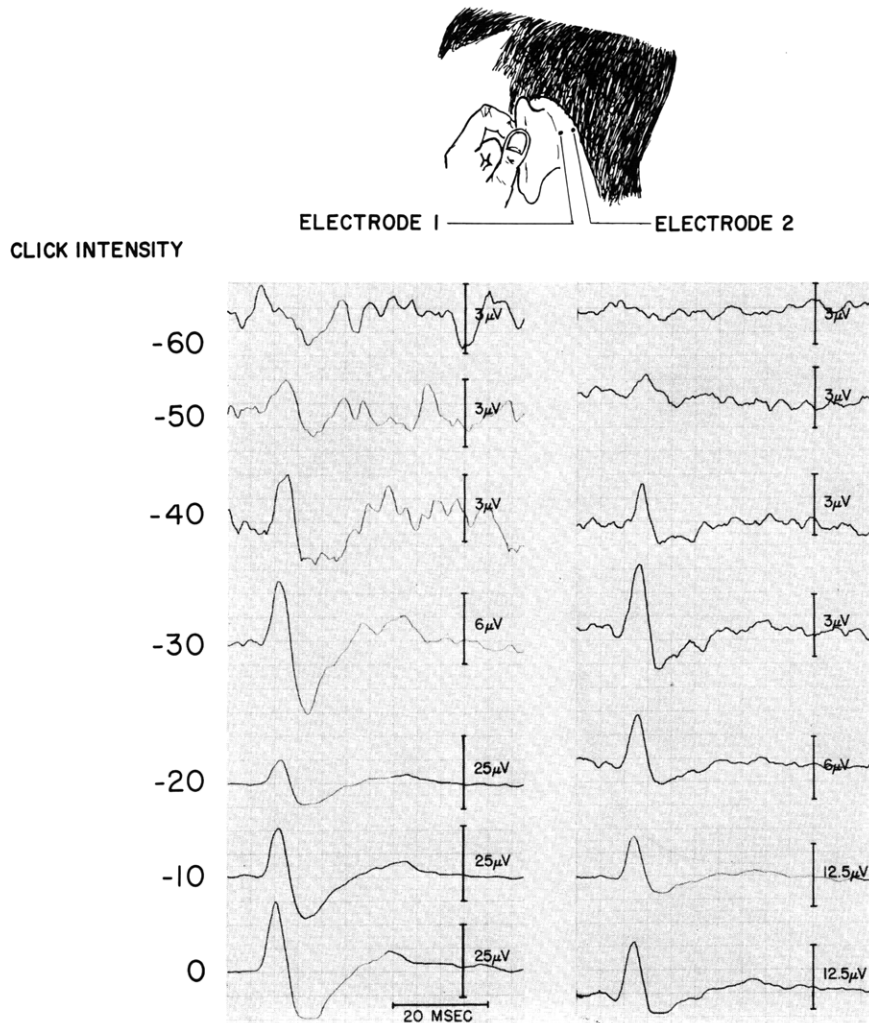


Fig. XXIII-11. Averaged responses to clicks for two electrode locations behind the left ear. The electrodes were stainless-steel needles. The reference electrode was clipped to a saline-moistened cotton pad on the right earlobe. Negative polarity for the active electrodes is plotted upward. Responses are shown for 7 stimulus intensities. Clicks were produced by applying a 10- μ sec rectangular pulse to the terminals of an Altec 1-755A loud-speaker that was located \sim 4 feet in front of the subject seated in a soundproof room. Clicks were presented at a 10/sec rate; reference level (0 db) = 13 volts into the speaker. With this stimulus arrangement the psychophysical threshold was approximately -65 db for this subject. (The beginning of each trace in this and subsequent figures marks the instant at which a monitoring microphone placed near the ear detects the arrival of the click.) Number of responses averaged for each trace, $N = 1000$. Recording session 1 on this subject (N. Y-S. K., 1/12/62).

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with latencies of less than 70 msec.¹⁻⁶ We have recently found a short latency response localized behind the external ear (auricle) which does not appear to have been previously reported. Some of the characteristics of this response are sufficiently unusual to warrant a brief report.

The postauricular response has been recorded both from needle electrodes thrust into the skin posterior to the attachment of the ear (Fig. XXIII-11) and from wick electrodes curled over the attachment of the ear. Since the responses are not visually detectable in single traces except at high stimulus intensities, it was necessary to compute⁷ averaged responses on the ARC.

Figure XXIII-11 shows responses recorded from two electrodes located behind the ear. The distance between the electrodes was 1.5 cm. The responses from electrode 1 show a peak approximately 11 msec after the acoustic stimulus arrives at the ear. This

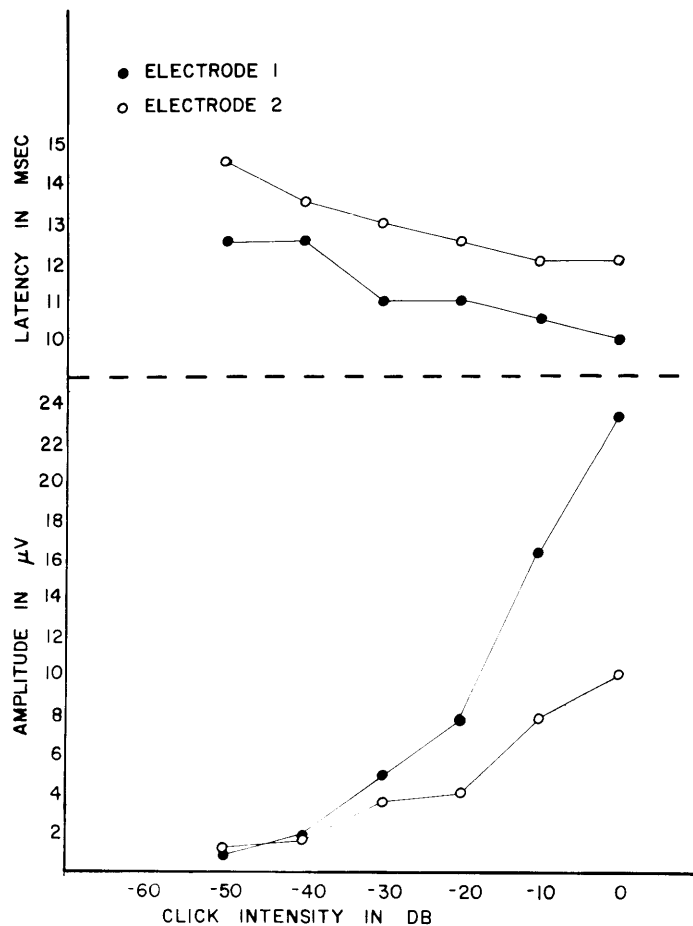


Fig. XXIII-12. Latencies and amplitudes of the negative peaks in the traces of Fig. XXIII-11 as functions of click intensity. Latencies are measured from the beginning of each trace; amplitudes are measured from base line to peak.

negative peak is followed approximately 7 msec later by a positive peak that is less prominent in the recordings from electrode 2. In general, the waveform of the responses can vary considerably with location of the electrode, although the most prominent deflections occur with latencies in the 10-20 msec range. For a specific location on any one subject, the response waveform seems to be quite repeatable except as noted below.

Figure XXIII-12 shows that the latency of the negative peak decreases and its amplitude increases with increasing click intensity. There is a relatively constant difference of approximately 2 msec between the latencies of the responses from the two electrodes. Note also that the amplitude of responses is smaller for electrode 2. This is consistent with our observation that the responses are largest in the region near the attachment of the external ear.

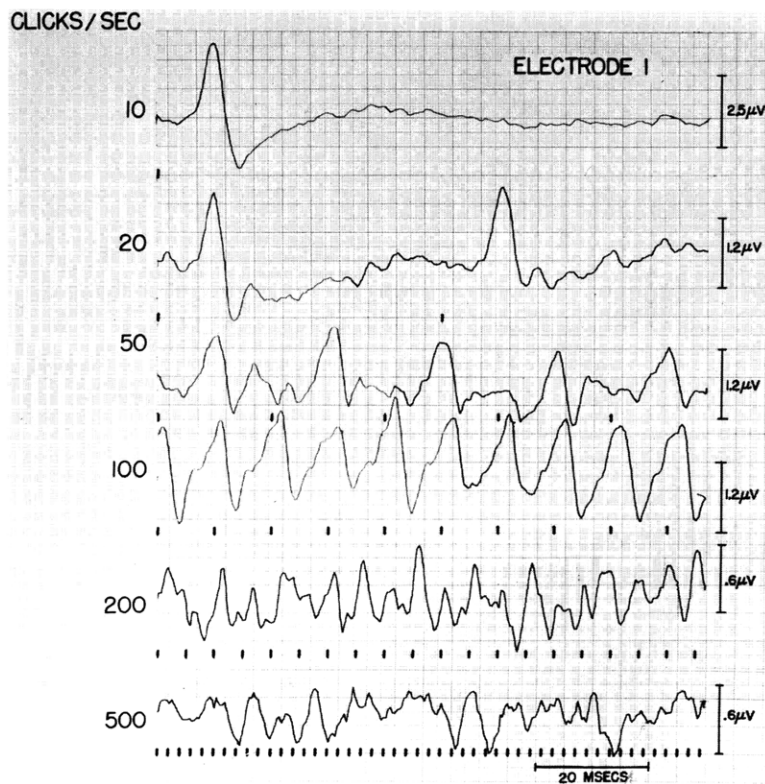


Fig. XXIII-13. Averaged postauricular responses for several click rates. The marks under each trace denote the times of arrival of the clicks at the ear. The electrode was placed in the same location as electrode 1 of Fig. XXIII-11. The reference electrode was on the right earlobe. Clicks were produced by 10- μ sec rectangular pulses delivered to the loud-speaker terminals. Click intensity, -10 db re 7 volts into loud-speaker; N = 1000. Recording session 2 on this subject (N. Y-S. K., 1/24/62).

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Figure XXIII-13 shows the postauricular response for six different click rates. The responses at 200 clicks/sec and 500 clicks/sec are complicated by the overlap of responses to successive clicks. However, it is clear that some responses are synchronized with clicks, even at the 200/sec rate.

These results might seem to suggest that the relationship of these responses to the stimulus parameters can be easily described. However, this appears to be so only for the first few recording sessions. One of the exasperating aspects of working with this

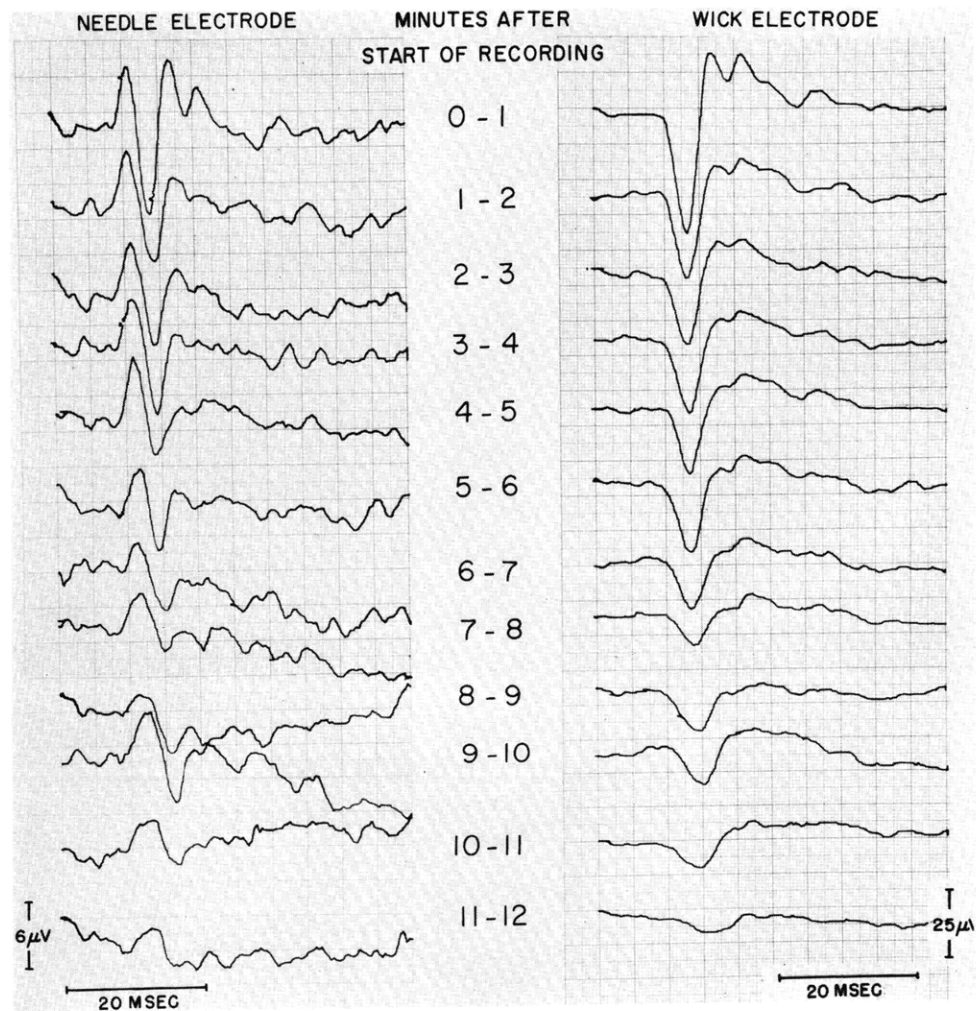


Fig. XXIII-14. Averaged postauricular responses as a function of time after the start of stimulation. Averages of responses recorded simultaneously from both a needle electrode and a wick electrode. Reference electrode on nose. Clicks were produced by 100- μ sec rectangular pulses. Click intensity, -20 db re 17 volts; repetition rate, 10/sec; N = 500. Recording session 4 on this subject (N. Y-S. K., 3/20/62).

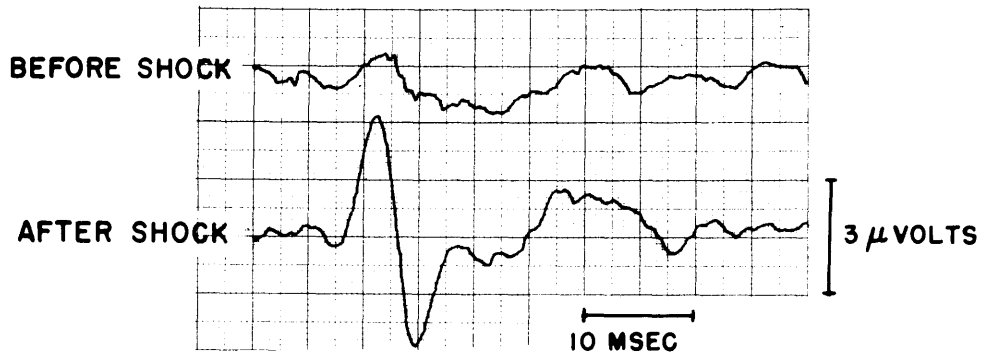


Fig. XXIII-15. Averaged postauricular responses from a subject before and after the delivery of electric shock to the bare feet. The responses of the subject to steady clicks had decreased steadily with time from the start of the session. After the responses had declined to the level shown in the trace marked "before shock," the shock was delivered. The first 100 seconds of response activity were then processed to give the trace labeled "after shock." Responses recorded between a wick electrode and reference on nose. Stimulus conditions identical with those of Fig. XXIII-14; $N = 1000$. Session 5 for this subject (E.C.T., 4/5/62).

particular response is illustrated in Fig. XXIII-14. On the fourth recording session for this subject, responses were recorded for more than 12 minutes during which time click stimuli were delivered at the rate of 10/sec. Both needle and wick electrodes were used for this run. The wick electrode was in contact with almost the entire posterior line of attachment of the external ear. The responses recorded by the needle electrode are smaller than those in Fig. XXIII-11 because the needle could not be placed in the same locations with the wick in place. The waveforms of the responses from the two electrodes are quite different, particularly in that the initial negative peak is absent in the wick recordings. The later components in the responses recorded by the two electrodes seem to be comparable in latency, and they decline in amplitude in a similar way. This gradual decrease in response amplitude does not occur in initial recording sessions and occurs more rapidly in later recording sessions. For some of our more "experienced" subjects, responses that had been stable in the initial sessions decreased rapidly in amplitude after the first few responses in later sessions. In sessions in which the amplitude had become small, various instructions to the subjects, such as "count the clicks," "relax," and "read," did not result in an increase in amplitude. Also, changes in room illumination or click intensity and repetition rate did not bring back the response. One instance in which the responses did become large again momentarily is shown in Fig. XXIII-15. Electric shocks to several of our subjects resulted in a spectacular increase in response amplitude with subsequent rapid decrease. After the shocks were repeated several times they, too, ceased to have significant effects.

The position of the head also seems to be a factor in the appearance of the

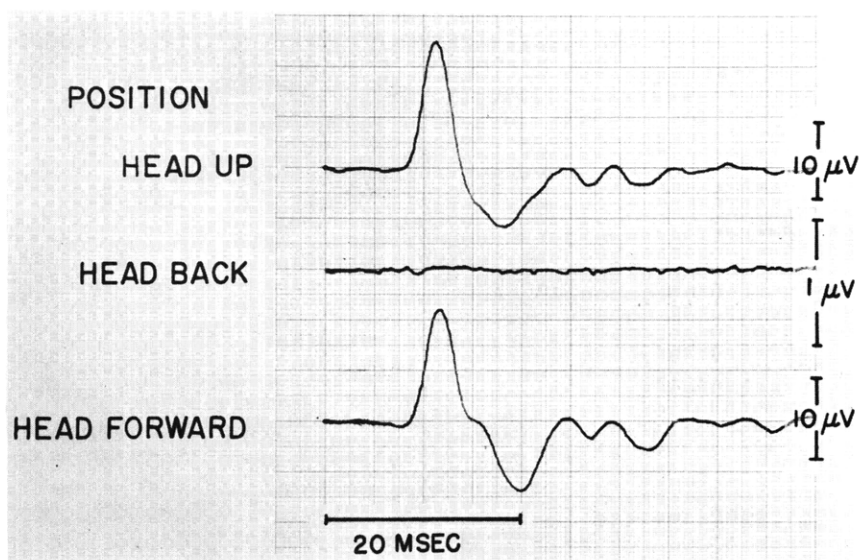


Fig. XXIII-16. Postauricular responses influenced by head position. The head was first oriented in an upright position. Then the head was allowed to fall back until it rested comfortably on a support. Finally, the head was brought forward in a bending position. Changes in head position often had dramatic effects on the responses, but at other times did not. Checks of the recording arrangement were always made to ensure that no electrical connections were disturbed as a result of head movements. Stimulus conditions are identical with those of Fig. XXIII-14. $N = 1000$ for the top and bottom traces; $N = 500$ for the middle trace. A needle electrode behind the left ear was used in these recordings with the reference electrode on the right earlobe. Session 4 for this subject (E. C. T., 3/26/62).

postauricular response. For most of our subjects an upright position or forward bend of the head resulted in larger responses than tilting the head back. The effect is not always as dramatic as that illustrated in Fig. XXIII-16, even for the same subject. A similar phenomenon has been previously reported for a longer latency response to auditory stimuli.⁸

A few miscellaneous facts can also be noted. The postauricular responses are obtainable with other transient stimuli, such as bursts of tone or bursts of noise. They are obtainable bilaterally, even by using earphones to stimulate only one ear. Clear responses were obtained from 8 of 10 subjects. Of these eight, four were male and four female. All subjects were less than 40 years of age and healthy. No responses could be detected in records obtained from two subjects with severe hearing losses.

The ease of recording postauricular responses invites further experimentation to determine their origin. The lability of the response challenges the ingenuity of the experimenter. This lability resembles the behavior of certain responses recorded from the brains of unanesthetized cats.⁹ In particular, a decrease in amplitude with prolonged

stimulation is characteristic of some components of the cortical responses in cats. It is difficult, however, to make direct comparisons between these two sets of data recorded in different ways from different species.

Despite the synchrony of the postauricular responses with stimuli at high rates (Fig. XXIII-13), it is possible that the response arises from activity of either ear or neck muscles. The sensitivity of the response to changes in electrode location and the effects of head position support such a view. The response is unlikely to be the result of stapedius muscle activity in the middle ear, since a clear response was obtained in a subject who had undergone stapes surgery with resultant severing of the muscle.

N. Y-S. Kiang, A. H. Crist, M. A. French, A. G. Edwards
(Dr. A. G. Edwards is a Resident at the Massachusetts Eye and Ear Infirmary.)

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C. RESPONSES OF A NEURONLIKE NET TO PAIRED STIMULI

We have reported previously that the response to the second of a pair of stimuli to a neuronlike net goes through damped "cycles" of alternate "enhancement" and "depression" as a function of the length of the interval between the two stimuli.¹ Other work on such "recovery curves" has confirmed and extended this result.

The variance of these recovery curves was found to be considerable, seldom being

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less than 20-30 per cent of the amplitude of the cyclic oscillation, and sometimes exceeding it. The explanation for this variability lies in the fact that the stimulus pair never re-encounters identical conditions, since the net is spontaneously active.

We found that the intervals between the peaks in the recovery curves increase when the time constant that represents the refractory property of the neuronlike elements is increased. This effect was expected, since the periods for spontaneous oscillations show a similar dependence.

Finally, we found that the "enhancement-depression" cycle varies in prominence as a function of the intensity of the stimuli. If the two stimuli are of equal intensity, there is one intensity level that produces the effect with greatest prominence. At high intensities (for which a large proportion of the elements is stimulated), the activity of the net dies, or nearly dies, after the first stimulus, since most of the elements are simultaneously refractory: the cycle vanishes under these conditions. At low stimulus intensities, "spontaneous" firings occur so frequently that the responses are small compared with the total activity; thus the effect vanishes into the noise level.

A detailed account of these results has been given in R. B. Keim's thesis.²

R. B. Keim, B. G. Farley

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