XVII. COMMUNICATIONS BIOPHYSICS

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A. A PROBABILITY MODEL FOR CORTICAL RESPONSES TO SUCCESSIVE AUDITORY CLICKS

Recent investigations (1) have provided data on responses to successive click stimuli recorded at the auditory cortex. Cortical responses to the second or conditioned click differ in several important respects from responses to these same stimuli recorded at more peripheral locations in the afferent auditory pathway. If we compare the first neural response (N_1) to the second of a pair of clicks to the response to an unconditioned click of the same intensity, we see that the shorter the interval between the first and second click, the more the N_1 component will be reduced. This component shows a gradual and monotonic increase as the interval is lengthened and returns to its unconditioned amplitude after a time interval of a few hundred milliseconds. The exact time intervals for which the conditioning click loses its influence depend upon the intensity of both clicks.

At the cortex of anesthetized cats, on the other hand, the effect of the first click is seen for intervals as long as 1500 msec, and the recovery of response amplitude is not monotonic. If the relative amplitude (the amplitude of response to the second click, divided by the amplitude of response to an unconditioned click of the same intensity) is plotted against the interval between the two clicks, the resulting curve depicts a monotonic increase modulated by a cyclic component. The apparent waveform of this cyclic component has been reported as sawtooth, sinusoidal, and even as resembling a rectified sine wave. In addition, the response is sometimes supernormal at the peaks of the cyclic variation; that is, the response to the conditioned click is greater than the response to a single click of the same intensity. The period of this cyclic component varies from 150 msec to 220 msec. A full discussion of the experimental background has been presented in reference 1. The phenomena described here are not restricted to the auditory cortex, but are also observed in other cortical areas, such as the visual cortex (2, 3).

A simple probability model has recently been developed in an attempt to account for these observations. The assumptions and procedures used in the development of this simplified model will be outlined here.

If the auditory cortex is considered to be made up of neural units, all of which are members of the same statistical population, a few simple assumptions will be sufficient

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to derive the model. These approximate the known electrophysiological facts, or assume at least plausible properties for cortical units in our present state of knowledge.

We shall assume that these units have thresholds which fluctuate randomly in time and are normally distributed with mean threshold μ. The threshold of a unit rises suddenly after firing; there follows an exponential return to normal threshold. As a first approximation we shall assume that the magnitude of the sudden rise and the time needed for recovery are independent of the intensity of the stimulus that fired the unit, and that the units obey the all-or-none law. If a certain amount of random neural activity is assumed in the cortex, it can then be shown that we may reasonably expect the thresholds of the units to exhibit a cyclic variation in time. This property has been used, in calculations of the model, by assuming the cortex divided into n subpopulations. Each of these subpopulations is randomly distributed throughout that portion of the auditory cortex that contributes to the responses investigated and the mean threshold μ of all the units in the subpopulation is a sinusoidal function of time, with the same phase angle for all units in the subpopulation. The phase angles for the different subpopulations are uniformly distributed.

In addition to these assumptions, various aspects of the experimental data make it clear that we must consider interaction between units in the cortex. The interactions seem to be of two types. In the first place, units of which some of the neighbors have fired exhibit a sudden rise in threshold followed by a quick recovery. The amount of the rise in threshold, and the time for return to normal responsiveness, are less than the corresponding quantities for units that have fired. In the second place, there is reason to believe that the firing of certain elements in a population alters the environment of the units that have not fired in such a way that when they fire to a subsequent stimulus after a short interval they will tend to do so more synchronously. Since we measure the peak-to-peak amplitude of cortical responses, this interaction will have the effect of allowing more of the units that fire in response to a stimulus to contribute to the peak, thus producing under the right conditions of anesthesia, etc., an apparent supernormality. Both interactions are assumed in calculations of the present model.

From these assumptions it is possible to develop a quantitative treatment for the amplitude of response to conditioned click stimuli. For this purpose we must estimate the mean (M) of the cyclic fluctuation of threshold and its period (a); also the standard deviation (s) of the normal distribution of thresholds, and a constant (k) that governs the time for return to normal responsiveness after firing. In practice, we have treated the response at the cortex directly in terms of the stimulus, ignoring two-click effects at intermediate points, and this procedure results in values of the time constant k (the time for recovery to a point halfway between the initial and final values) of around 200 msec. It can be shown, however, that if the intermediate synapses and the cortex are all

assumed to be composed of units with a value of k near 50 msec (which is about the value that would fit the data on N_1) the result will be an apparent cortical recovery time constant of about 200 msec when the response is considered directly in terms of the stimulus.

When applying this model to experimental data, we estimate the value of M and s from a plot of the amplitude of cortical response to single clicks vs stimulus intensity (so-called cortical intensity function) such as that given in Fig. XVII-1, and we estimate the values of a, k, and a constant h_o which governs the relative importance of the inter-action effects from two-click data for a particular set of stimulus intensities. Once these five parameters have been set for one experimental animal at a level of anesthesia, we can use the model to generate the two-click response curves for any number of stimulus intensities, and compare the results with further experimental evidence. Three such curves are presented in Fig. XVII-2, together with the observed experi-mental points.

This model has been applied to two-click data from four different experimental ani-mals, and as many as six curves calculated for one animal and one set of values of the parameters. The agreement shown in Figs. XVII-2(a), XVII-2(b), and XVII-2(c) is representative.

We have also employed the model to predict the response amplitude to three succes-sive clicks; examples of the predicted curves and the experimental points are shown in Fig. XVII-3. These two curves come from an experimental animal for which we had previously calculated curves for the two-click case. Since the predicted curves for the three-click case were calculated on the basis of the same constants, no new fitting had to be done here.

These investigations have also led to a study of the variability of cortical responses to acoustic stimuli; these results will be reported at a later date. Figure XVII-4 illus-trates the difference in variance between responses to a click of fixed intensity at the
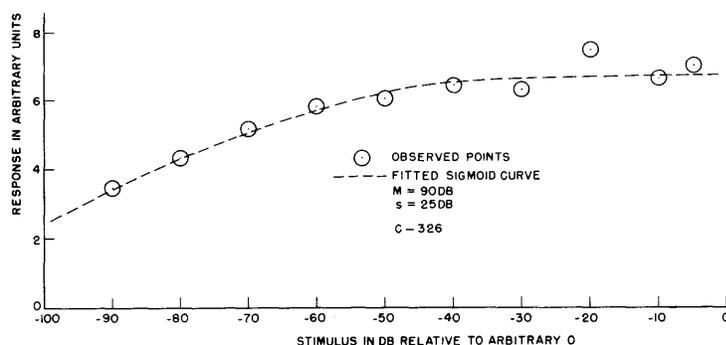
Fig. XVII-1
Intensity function for a cortical location, C-326.
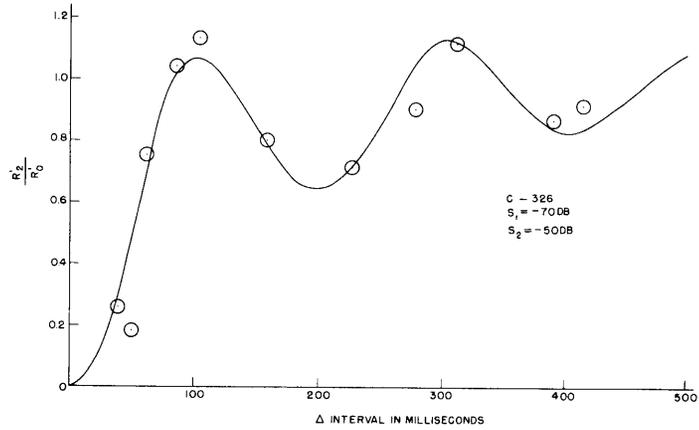
Fig. XVII-2(a)

Two-click results, C-326; for location used to
obtain Fig. XVII-1.
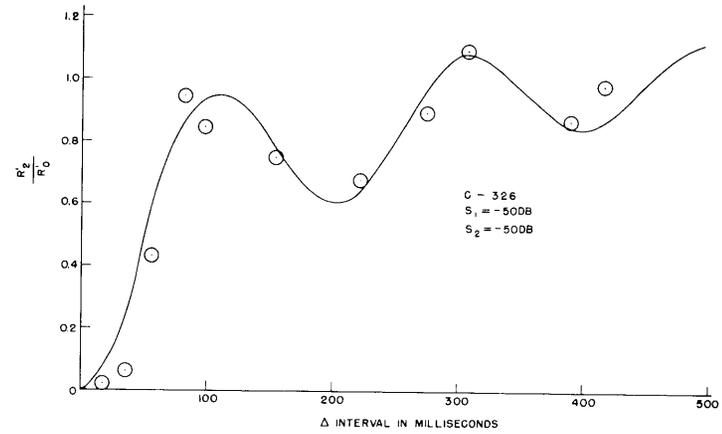
Fig. XVII-2(b)

Two-click results, C-326; for location used to
obtain Fig. XVII-1.
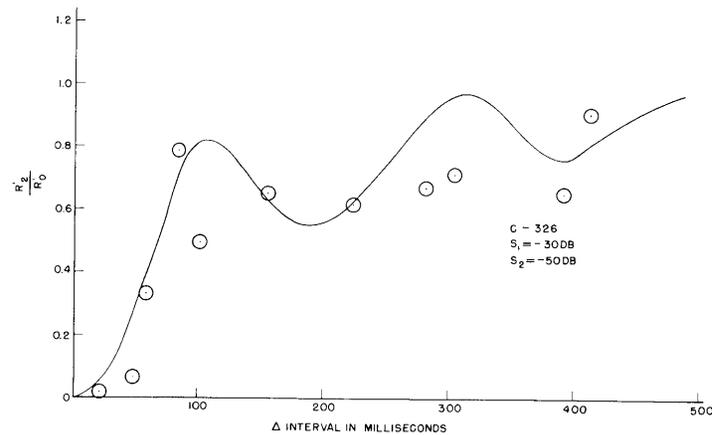
Fig. XVII-2(c)

Two-click results, C-326; for location used to obtain Fig. XVII-1.
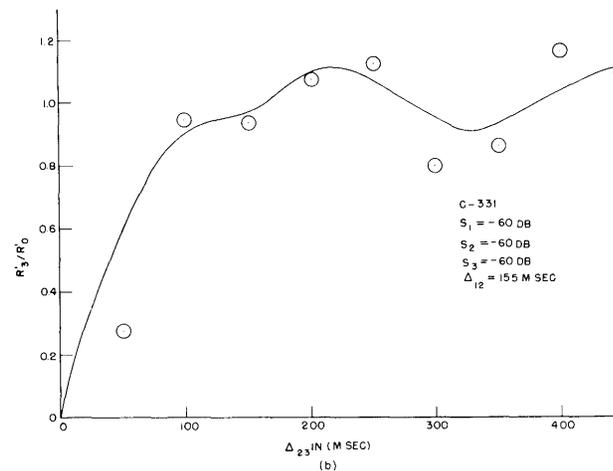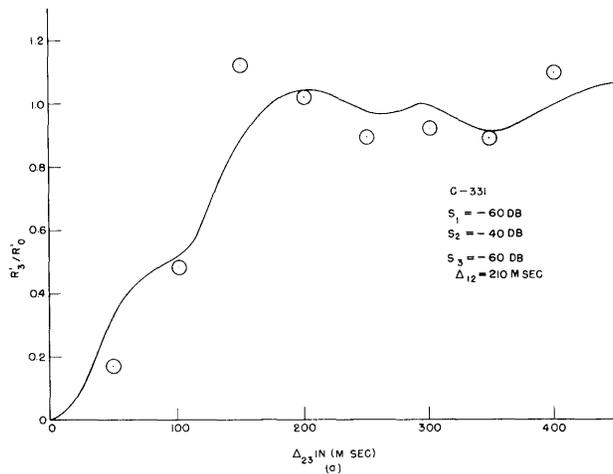
Fig. XVII-3

Typical three-click results, C-331, for the interval between S_1 and S_2 (Δ_{12}) fixed at (a) 210 msec and (b) 155 msec, and various intervals between S_2 and S_3 (Δ_{23}).
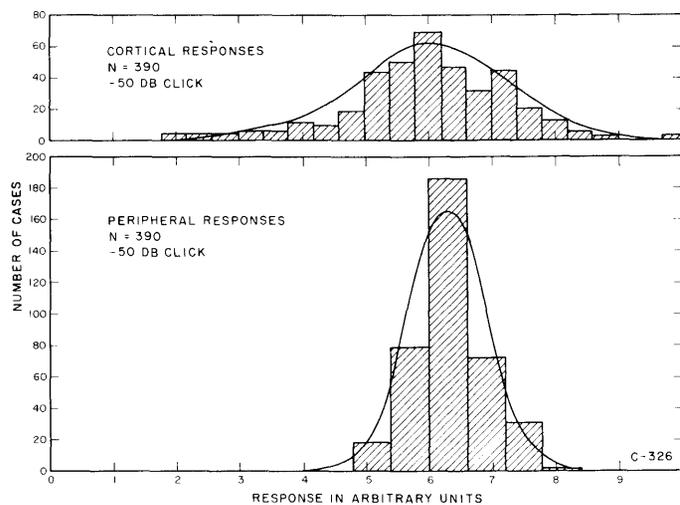
Fig. XVII-4

Distribution of response amplitude at peripheral location (near round window) and at cortical location (auditory area I); recorded simultaneously, and plotted to same scale.

cortex and at the location at which N_1 is prominent. The distributions plotted are derived from observations made simultaneously at both locations in response to 390 identical stimuli.

The model referred to above, and the development of the assumptions used, will be presented in detail in Technical Report No. 279. The relatively good agreement between the model and the experimental results invites further use and refinement of the model.

The experimental data were collected in cooperation with D. H. Raab and R. M. Brown.

J. Macy, Jr.

References

1. M. R. Rosenzweig and W. A. Rosenblith, Responses to successive auditory stimuli at the cochlea and at the auditory cortex, Psychol. Monogr. 67, No. 13 (1953).

2. H. Gastaut, Y. Gastaut, A. Roger, J. Corriol, and R. Naquet, Etude électro-graphique du cycle d'excitabilité cortical, EEG clin. Neuro-physiol. 3, 401-428 (1951).

3. H.-T. Chang, Changes in excitability of cerebral cortex following single electric shock applied to cortical surface, J. Neurophysiol. 14, 95-112 (1951).

B. MASKING AND VARIABILITY OF NEURAL RESPONSES TO CLICKS

The effect of noise on the click intensity function recorded at the round window of the cat was described in the Quarterly Progress Report, January 15, 1954. Additional experiments have been carried out to determine the threshold characteristics of the neural units comprising the peripheral auditory nervous system, using clicks and noise as stimuli. In particular, the hypotheses of fluctuating threshold and two populations were investigated further. A detailed statistical analysis of the resulting data was attempted in the hope that the extent of data variability would shed some light on the size and number of the neural populations involved and on their threshold distributions. It appeared, however, that the sample size was too small to provide statistically signifi-cant results. This line of investigation has been carried further in recent experiments in which long sequences of responses to fixed stimuli were recorded from paired simul-taneous locations near the round window of the cat. The long runs (fifty or more responses at each location for each stimulus value) provide significant results con-cerning the variance of the data as a function of stimulus intensity. It is hoped that crosscorrelation of the data from paired locations will provide an indication of the source of the variability, in particular the extent to which it is neural in origin. This analysis is still in progress.

L. S. Frishkopf

C. A NEURAL LATENCY MONITOR

The neural latency monitor (NLM) was constructed and put into working order. This device was designed to measure automatically the delay time (latency) between a certain physiological stimulus (such as an acoustic click) and a certain phenomenon in the neuroelectrical response that is evoked. Such a signal is picked up by an electrode located near the round window of the animal's cochlea (see Fig. XVII-5(a)).

One part of the NLM system generates pips that occur when the waveform of the "peripheral" response exhibits points of zero slope (see Fig. XVII-5(c)). Since the response signal is gated so that only the part containing the neural is transmitted, there results, in response to a click, a series of pips the last of which corresponds in time to the peak of the neural (point n in Fig. XVII-5). The rest of the NLM system receives these pips and automatically measures the difference in time between the stimulus and the last pip in the subsequent series of pips. This time difference is called the latency of the neural.

The system is effective in choosing the point of maximum excursion in the neural, in the presence of interfering noise and "microphonics." These interfering signals are always present in varying degrees in the response signal. The device has a resolution time of 50 μsec, and presents the data in decimal form by means of neon lights. The accuracy of measurement is within plus or minus one time level or 50 μsec.

In order to use commercially available equipment for the recording of latency data, the present indicator system is being modified. A "tree" of relays will be used to translate the binary count given by the storage circuits to a decimal count.

(a)   TYPICAL PERIPHERAL RESPONSE SIGNAL

(b)   GATED SIGNAL

(c)   COINCIDENCE PIPS
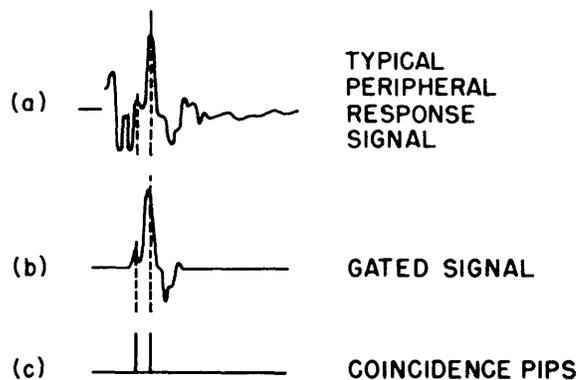
Fig. XVII-5
Waveforms in the neural latency monitor.

Since the NLM was designed to measure latencies of neurals in "peripheral" responses, its operating range covers approximately 3 msec. The device could be modified for the measurement of latencies in cortical responses. Such an extension of specifications would require a change in the oscillator frequency from 20 kc/sec to 10 kc/sec, thereby increasing the resolution time to 100 μsec. The range of measurement would have to be extended to about 30 msec.

A. K. Hooks

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Within the report period Professor Wolfgang Köhler (Swarthmore College), Dr. Karl Pribram (Institute of Living at Hartford, Connecticut), Mr. D. O'Connell (Harvard University), and W. A. Rosenblith have carried out a series of experiments on slowly varying cortical potentials in monkeys and cats. Such "dc type" of potentials of different polarity were recorded in response to prolonged visual and auditory stimuli from the projection areas and from several other sharply defined locations on the cortex.

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