

XVIII. COMMUNICATIONS BIOPHYSICS*

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A. WORK COMPLETED

These reports give summaries of S. B. theses submitted to the Department of Electrical Engineering, M. I. T. , May 1965.

1. DIGITAL CLOCK FOR THE PDP-4 COMPUTER

A variable-rate digital timing device for use with the PDP-4 computer has been designed and built. This programable clock is capable of making measurements of

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asynchronous input events with an accuracy of $\pm 5 \mu\text{sec}$. The output of the clock is buffered. By using the interrupt features of the computer, it is possible to accurately time input events while not detracting significantly from most normal computation and input-output operations. The clock will be used primarily in the study of firing patterns of single neurons.

W. H. Broadley

2. THE EFFECTS OF TEMPERATURE ON THE LOBSTER CARDIAC GANGLION

Extracellular electrodes were used to monitor spontaneous activity in isolated cardiac ganglia from the East Coast lobster, Homarus Americanus. Numerous technical difficulties have to be overcome before the relation of temperature to neural activity can be meaningfully examined.

R. E. Graves, Jr.

3. TRANSFER CHARACTERISTICS OF THE CAT'S MIDDLE EAR

Previous measurements of stapes movement as observed through a microscope led to a transfer function for the middle ear with the cavities behind the drum membrane open.¹ In the present work the effect of opening these cavities was determined by measuring the electric response recorded near the round window with the bulla first closed and then open. For frequencies up to approximately 800 cps opening the typanic cavities was found to increase the transmission approximately 6 db. Around 4000 cps, a relatively sharp resonance introduced by the cavities produces a dip of approximately 15 db in the transfer function. These effects can be interpreted in terms of a circuit analog of the acoustic system.

W. E. Mosier, Jr.

References

1. J. J. Guinan, Jr., S. M. Thesis, Department of Electrical Engineering, M. I. T., 1964.

4. COMPLEX REACTION TIMES FOR PATTERN RECOGNITION

Reaction times for recognition of lines, circles, triangles, and squares were measured on 20 subjects. The mean reaction times obtained were 413 msec (triangle), 420 msec (circle), 426 msec (square), and 436 msec (line).

When mean reaction times for each pattern were plotted as a function of the subject – in monotonically increasing order – the curves thus obtained were nearly equal point by point.

Interactions among different patterns were studied by measuring reaction times for

recognition of equalities and differences between patterns.

Further interactions were studied by differentiating distorted patterns from corresponding undistorted stimuli and by means of experiments involving color.

A simple probabilistic model describing the observed results is proposed.

L. Peusner

5. COMMUNICATION IN THE Gymnotus Carapo – A WEAKLY ELECTRIC FISH

Observations were made in two aspects of communication in the electric fish: (i) Communication with the fish's surroundings; that is, What objects can the fish locate and at what distance can an object be located? (ii) Communication with other electric fish; Is any information exchanged through the electric sense?

The first question was treated as follows: The fish's receptor system was simulated by an electrical model, and the sensitivity of the model was studied and equated to that of the electric fish. The second question involved observations of electrical behavior under different "social" circumstances; namely, the rate at which pulses are emitted in the presence or absence of another fish.

F. C. Prout

6. ANALOG SIGNAL DELAY BY PROGRAMMING THE PDP-4 COMPUTER

A program has been developed to produce an arbitrary delay of an analog signal. The signal is first sampled and stored on digital magnetic tape. The analog signal and the delayed analog signal may then be played back simultaneously by using the analog outputs of the PDP-4 computer. The sampling rate is 216 μ sec, and any delay between 0 and 0.3 sec may be obtained in steps of 8.33 μ sec. The maximum duration of the analog signal is 10 minutes.

J. A. Schafer

7. FLUCTUATIONS IN THE EXCITABILITY OF FROG SCIATIC NERVE FIBERS

Individual sensory nerve fibers frequently show a marked statistical variability in effective threshold, which appears at least qualitatively similar to the fluctuations in electrical excitability of isolated nerve fibers as observed by a number of workers.¹ This thesis was concerned with the development of equipment and techniques necessary to repeat and extend some of these earlier studies. The action potentials in individual frog sciatic-nerve fibers were recorded with gross silver electrodes and tungsten microelectrodes; but only with gross electrodes similar to those used by others were we able to obtain a sufficiently stable and reliable preparation to permit collection of quantitative data.

P. E. Strause

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References

1. See, for example, A. A. Verveen and H. E. Derksen, "Fluctuations in membrane potential of axons and the problem of coding," *Kybernetik* 2, 4, 152-160 (February 1965), which contains an extensive bibliography.

The following report is an abstract of a thesis submitted to the Department of Electrical Engineering, M. I. T. , in partial fulfillment of the requirements for the degree of Master of Science, May 28, 1965

8. ANALYSIS OF SPONTANEOUS ELECTRICAL ACTIVITY IN EMBRYONIC BRAIN EXPLANTS*

As a result of a technique developed by Dr. A. W. B. Cunningham for sustaining bits of embryonic brain tissue in culture, it has been possible to observe spontaneous electrical activity generated by the tissue. The activity takes the form of pulses, tens of microvolts high and tenths of a second long, occurring in sequences of 5 to 150, with sequences one to ten minutes apart.

It was found that the pulses usually have a sinusoidal rise portion, and invariably an exponentially decaying portion, whose period and time constant vary only slightly within a culture. These characteristic times do vary by as much as a factor of four between different cultures of a given brain area and by as much between telencephalon and cerebellum.

The pulses occur in a definite pattern within a sequence. In cerebellum, pulses tend to occur with interpulse spacing of approximately 1500 msec, almost uniformly. The interpulse spaces in telencephalon are typically 600 msec wide at the beginning of a sequence, increasing to 2400 msec.

A few measurements were taken of the peak amplitudes of the telencephalon pulses, but there is a systematic error in the method of measurement which tends to invalidate the results.

This spontaneous activity may be described mathematically in terms of a pulse that occurs with a pattern that is fixed within a brain area; the pulse rises in a nonconstant way and decays exponentially.

P. L. Marcus

B. PSYCHOPHYSICS

Work continues on theory, experimentation, and the preparation for publication of previous results. A paper describing last year's results on time-intensity relations in binaural unmasking has been completed,¹ and substantial progress has been made in the preparation of a paper on last year's results on binaural unmasking as a function of

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interaural phase shifts and time delays in the masking noise,² and a chapter summarizing all previous work on the equalization and cancellation (EC) model.³ Recent theoretical work has consisted of attempting to revise this model to account for certain results obtained when the masking noise is phase-shifted or time-delayed and of applying this model to data on just-noticeable differences (jnd's). Descriptions of the theoretical results on jnd's and of the various experiments are given in this report.

1. APPLICATION OF THE EC MODEL TO DATA ON JND'S

In the past, the EC model has been applied to data on binaural unmasking,^{1,2,4,5} and on Huggin's Creation-of-Pitch phenomenon.⁶ Recent work indicates that the model may also be useful for interpreting data on interaural jnd's.

Consider first the jnd's in interaural time delay and interaural amplitude ratio for the case in which the reference stimulus consists of signals that are identical in the two ears. Letting $s_j(\omega)$ denote the Fourier transform of the signal presented to ear j ($j=1, 2$), one can write the binaural stimuli that are to be considered as follows:

$$\text{Reference Stimulus} \quad s_j(\omega) = s(\omega)$$

$$\text{Time Stimulus} \quad s_j(\omega) = s(\omega) \exp(-i\omega\tau_j), \quad \tau_1 + \tau_2 = 0$$

$$\text{Amplitude Stimulus} \quad s_j(\omega) = a_j s(\omega), \quad a_1 a_2 = 1.$$

In these equations, $s(\omega)$ is the transform of the signal for which the time jnd and intensity jnd are being determined, τ_j are the time delays, and a_j are the amplitude factors. The time jnd, denoted τ_o , is the minimum value of $\tau = \tau_2 - \tau_1$ greater than zero for which the auditory system can distinguish between the reference stimulus and the time stimulus. Similarly, the amplitude jnd, denoted a_o , is the minimum value of $a = a_2/a_1$ greater than unity for which the system can distinguish between the reference stimulus and the amplitude stimulus.

According to the model, the auditory system attempts to distinguish between the reference stimulus and the other stimuli by subtracting $s_1(\omega)$ from $s_2(\omega)$ and observing the total energy at the output of the subtraction. For all stimuli, it is assumed that the subtraction is corrupted by random jitter in the amplitude and time alignment of the two input signals. The subject's ability to discriminate between the reference stimulus and one of the other stimuli is assumed to be determined by the ratio Q of the average output energy for the other stimulus divided by the average output energy for the reference stimulus (where the average is taken with respect to the jitter). Letting Q_T and Q_A denote the ratios for the time and amplitude stimuli, and Q_o the minimum value of Q that can be distinguished from unity (so that Q_o describes the jnd in average energy at the output of the subtractor), one sees that the jnd's τ_o and a_o can be obtained as a function of Q_o by solving the equations $Q_T(\tau) = Q_o = Q_A(a)$ for τ and a .

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For each of the three binaural stimuli above, the output of the subtraction is given by

$$Y(\omega) = (1-\epsilon_2) s_2(\omega) \exp(-i\omega\delta_2) - (1-\epsilon_1) s_1(\omega) \exp(-i\omega\delta_1),$$

where ϵ_j and δ_j represent the amplitude and time jitter. Letting $Y_R(\omega)$, $Y_T(\omega)$, and $Y_A(\omega)$ denote the output for the reference, time, and amplitude stimuli, one obtains

$$Y_R(\omega) = s(\omega)[(1-\epsilon_2) \exp(-i\omega\delta_2) - (1-\epsilon_1) \exp(-i\omega\delta_1)]$$

$$Y_T(\omega) = s(\omega) \{[(1-\epsilon_2) \exp[-i\omega(\tau_2+\delta_2)] - (1-\epsilon_1) \exp[-i\omega(\tau_1+\delta_1)]]\}$$

$$Y_A(\omega) = s(\omega)[a_2(1-\epsilon_2) \exp(-i\omega\delta_2) - a_1(1-\epsilon_1) \exp(-i\omega\delta_1)].$$

If we let Av denote the averaging operation with respect to the jitter factors ϵ_j and δ_j , the quantities Q_T and Q_A are given by

$$Q_T = \text{Av} \int_{-\infty}^{\infty} |Y_T(\omega)|^2 d\omega / \text{Av} \int_{-\infty}^{\infty} |Y_R(\omega)|^2 d\omega$$

$$Q_A = \text{Av} \int_{-\infty}^{\infty} |Y_A(\omega)|^2 d\omega / \text{Av} \int_{-\infty}^{\infty} |Y_R(\omega)|^2 d\omega.$$

Assume now (as in the binaural unmasking applications) that (a) ϵ_1 , ϵ_2 , δ_1 , δ_2 are statistically independent random variables of zero mean and variances $\sigma_{\epsilon}^2 = \sigma_{\epsilon_1}^2 = \sigma_{\epsilon_2}^2$ and $\sigma_{\delta}^2 = \sigma_{\delta_1}^2 = \sigma_{\delta_2}^2$; (b) δ_1 and δ_2 are Gaussian; (c) $s(\omega)$ is sufficiently narrow-band to allow one to regard $\exp(-\omega^2 \sigma_{\delta}^2)$ and $\cos(\omega\tau)$ as constants across the frequency span of $s(\omega)$. Letting ω_0 denote the center frequency of $s(\omega)$, one then obtains the approximations

$$Q_T(\tau) = 1 + [1 - \cos(\omega_0\tau)]/(k-1),$$

$$Q_A(a) = 1 + k[(a+1/a)/2-1]/(k-1),$$

where $k = (1+\sigma_{\epsilon}^2) \exp(\omega_0^2 \sigma_{\delta}^2)$. Solving the equations $Q_T(\tau) = Q_O = Q_A(a)$ for τ and a leads to

$$\tau_0 = \{\cos^{-1}[1-(k-1)(Q_O-1)]\}/\omega_0,$$

and

$$a_0 = \frac{Q_O(k-1) + 1}{k} + \sqrt{\left(\frac{Q_O(k-1) + 1}{k}\right)^2 - 1}.$$

In the application of the EC model to the data on the binaural unmasking of tones, it has been found that the model is most successful when the frequency of the tone is less

than 2000 cps (the frequency region for which the binaural unmasking phenomenon is most pronounced). Thus, in comparing the results above on α_o and τ_o with the data on jnd's, attention has been focused on the lower frequencies. The experimental data on τ_o and α_o in this frequency region exhibit a considerable amount of variation (depending upon the specific characteristics of the stimuli and the method of taking data); however, the bulk of these data appear to fall in the intervals $0.3 \leq 20 \log \alpha_o \leq 2.0$ and $5 \leq \tau_o \leq 50 \mu\text{sec}$. For example, according to the results of Mills, Zwislocki and Feldman, and Klumpp and Eady⁷ on tone pulses, we have approximately $20 \log \alpha_o = 0.6$ and $\tau_o = 28 \mu\text{sec}$ at 250 cps, and $20 \log \alpha_o = 1.0$ and $\tau_o = 15 \mu\text{sec}$ at 1000 cps. Making use of the values $\sigma_\epsilon = 0.25$ and $\sigma_\delta = 105 \mu\text{sec}$ (previously used in the binaural unmasking applications), and choosing $Q_o = 1.005, 1.01, 1.02$ and $\omega_o/2\pi = 250, 500, 1000$ cps, one obtains the theoretical results tabulated below.

$\omega_o/2\pi$ (cps)		250	500	1000
	k	1.092	1.185	1.642
$Q_o = 1.005$	τ_o (μsec)	19	14	13
	α_o (db)	0.25	0.34	0.54
$Q_o = 1.01$	τ_o (μsec)	27	19	18
	α_o (db)	0.36	0.49	0.77
$Q_o = 1.02$	τ_o (μsec)	39	27	26
	α_o (db)	0.50	0.69	1.09

These results indicate (at least to a crude approximation) that there exists a value of the EC energy jnd Q_o such that the values σ_ϵ and σ_δ obtained by fitting the EC model to the binaural-unmasking data lead to reasonable values for the jnd's τ_o and α_o . Obviously, if only one of these jnd's had been considered, the results would be rather meaningless, since the value of Q_o has been determined by fitting the data. The consistency of the model with the jnd data is demonstrated only to the extent that the same value of Q_o is appropriate to both τ_o and α_o simultaneously.⁸

In order to test whether or not this same value of Q_o can be used to predict other types of jnd, computations have been made for the jnd in interaural correlation, as measured by Pollack and Trittipoe.⁹ Considering again the case in which the reference stimulus consists of signals that are identical in the two ears, we can write the two binaural stimuli in this experiment as follows:

Reference Stimulus $s_j(t) = n(t)$

Correlation Stimulus $s_j(t) = \alpha m_j(t) + \sqrt{1 - \alpha^2} n(t),$

where $n(t)$, $m_1(t)$, and $m_2(t)$ are truncated versions (of relatively long duration) of statistically identical, statistically independent, white Gaussian noise signals with cutoff frequencies at 100 cps and 6800 cps. Letting $\langle \rangle$ denote the averaging operation with respect to the statistics of the noise, one sees that the crosscorrelation coefficient $\rho = \langle s_1(t)s_2(t) \rangle / \langle s_1^2(t) \rangle^{1/2} \langle s_2^2(t) \rangle^{1/2}$ is given by $1 - \alpha^2$ for the correlation stimulus (and, of course, by unity for the reference stimulus). Adapting the previous definition of Q to include the $\langle \rangle$ operation, one obtains,

$$Q = \text{Av} \int_{-\infty}^{\infty} \langle |Y_{\rho}(\omega)|^2 \rangle d\omega / \text{Av} \int_{-\infty}^{\infty} \langle |Y_R(\omega)|^2 \rangle d\omega \\ = (z - \rho) / (z - 1),$$

where $Y_R(\omega)$ and $Y_{\rho}(\omega)$ are the frequency-domain representations of the outputs of the subtractor for the reference stimulus and correlation stimulus, and z is given by

$$z = \frac{(1 + \sigma_{\epsilon}^2) \int_{-\infty}^{\infty} \langle |n(\omega)|^2 \rangle d\omega}{\int_{-\infty}^{\infty} \langle |n(\omega)|^2 \rangle \exp(-\omega^2 \sigma_{\delta}^2) d\omega}.$$

Assuming that $\langle |n(\omega)|^2 \rangle$ can be approximated by two rectangles (going from -6800 cps to -100 cps and 100 cps to 6800 cps) and making use of the same values of σ_{ϵ}^2 and σ_{δ}^2 , one obtains $z = 5.7$. Thus, the jnd ρ_0 (defined as the maximum value of ρ such that the auditory system can distinguish between the correlation stimulus and the reference stimulus) should satisfy the equation $(5.7 - \rho) / 4.7 = Q_0$. Letting Q_0 take on the same values as before, one obtains $\rho_0 = 0.98$ ($Q_0 = 1.005$), $\rho_0 = 0.95$ ($Q_0 = 1.01$), and $\rho_0 = 0.91$ ($Q_0 = 1.02$). According to the data of Pollack and Trittipoe,⁹ the value of ρ_0 determined experimentally (using 75% correct as the definition of threshold) is $\rho_0 = 0.96$.

These results indicate that the EC model may be capable of reducing a wide variety of interaural jnd's to the single jnd Q_0 hypothesized in the model. To what extent the model is capable of including the effects of power level, signal duration, bandwidth, etc., and to what extent it can be used to interpret jnd's for other reference stimuli and other interaural parameters, remains to be seen. (In all of the data above the duration of the stimuli was approximately 1 sec. For the data on tones, the sensation level was ~50 db. For the data on noise, the total power level was ~90 db SPL.) Work in this area is being continued.

N. I. Durlach

References

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2. Some of these results are described *Ibid.*, loc. cit.
3. This chapter, entitled "Binaural Signal Detection: The Equalization and Cancellation Model," will appear in a new book on hearing, edited by J. V. Tobias and E. D. Schubert (Academic Press, New York).
4. N. I. Durlach, "Equalization and Cancellation Theory of Binaural Masking-Level Differences," J. Acoust. Soc. Am. 35, 1206-1218 (1963).
5. N. I. Durlach, "Note on Binaural Unmasking as a Function of the Interaural Correlation of the Masking Noise," J. Acoust. Soc. Am. 36, 1613-1617 (1964).
6. N. I. Durlach, "Note on the Creation of Pitch through Binaural Interaction," J. Acoust. Soc. Am. 34, 1096-1099 (1962).
7. These results are discussed in A. W. Mills, "On the Minimum Audible Angle," J. Acoust. Soc. Am. 30, 237-246 (1958); A. W. Mills, "Lateralization of High-Frequency Tones," J. Acoust. Soc. Am. 32, 132-134 (1960).
8. One might also consider whether or not the value of Q_0 obtained by fitting the data is a reasonable one. The answer to this question, however, has not yet been determined.
9. I. Pollack and W. J. Trittipoe, "Binaural Listening and Interaural Noise Cross Correlation," J. Acoust. Soc. Am. 31, 1250-1252 (1959).

2. BINAURAL UNMASKING AS A FUNCTION OF THE BANDWIDTH OF THE MASKING NOISE

This report gives a summary of an S. B. thesis submitted to the Department of Electrical Engineering, M. I. T., May 1965.

It has been reported that, in the masking of low-frequency tones by random noise, the amount of binaural unmasking increases as the noise bandwidth is reduced.¹ On the other hand, it is known that in the limit of zero bandwidth (in which case the masking noise becomes a tone), the amount of binaural unmasking is relatively small.² In the present study, attempts were made to determine the effects of noise bandwidth on the masked thresholds of a 500-cps tone for two interaural configurations: (i) noise the same in both ears, tone the same in both ears (homophasic), and (ii) noise the same in both ears, tone reversed in phase at one ear (antiphasic).

The results obtained in this study may be summarized as follows.

1. If the total noise power is held constant at 90 db SPL and the bandpass of the noise is centered on 500 cps and confined to widths in the region 1000-7 cps, the homophasic threshold rises monotonically as the bandwidth decreases, whereas the antiphasic threshold first rises and then falls.
2. The ratio of homophasic threshold to antiphasic threshold increases monotonically with decreasing bandwidth and varies from approximately 9 db at 1000 cps to

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approximately 24 db at 7 cps.

3. Although equipment difficulties and time limitations prevented the completion of tests in which the spectral level (rather than the total power) of the noise was held constant, it appears that essentially the same results would hold if the spectral level were held constant. In other words, the increase in the ratio caused by narrowing the bandwidth appears to dominate the decrease in the ratio caused by lowering the total power.³

According to the results of this study, even higher values for the ratio may be obtainable with bandwidths less than 7 cps. How narrow the bandwidth must be before the ratio begins to decrease and approach the values obtained for tonal maskers is still undetermined.

M. J. Riezenman

References

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3. For data on the effect of the total noise power, see I. J. Hirsh, "Binaural Summation and Interaural Inhibition as a Function of the Level of Masking Noise," *Am. J. Psychol.* 56, 205-213 (1948), or "The Influence of Interaural Phase on Interaural Summation and Inhibition," *J. Acoust. Soc. Am.* 20, 536-544 (1948).

3. BILOCAL CUTANEOUS UNMASKING

An attempt has been made to analogue the phenomena of binaural unmasking on the skin. Von Békésy¹ has outlined a series of experiments that indicate that many auditory phenomena, including some binaural ones, can be successfully modeled in the cutaneous sense. These experiments (plus certain puzzling results in binaural unmasking) served as the primary motivation for the present work.

In the present experiments, the stimuli were presented through two identical Goodmans V-47 vibrators and contactors approximately 3 mm in diameter. The signals presented to the vibrators consisted of the sum of random noise (with a flat spectrum and bandwidth of 80-500 cps) and a tone of frequency 100, 200, or 400 cps.

In one set of experiments, the contactors were placed on opposite sides of the tip of the middle finger of one hand, the noise signals were identical in the two vibrators, and the tone had the same frequency and amplitude in the two vibrators. A study of the masked threshold for a tone frequency of 100 cps and a noise level of 45 db SL as a function of the intervibrator phase, ϕ , of the tone showed that the threshold is smallest when $\phi = \pi$ and largest when $\phi = 0$, the difference being approximately 12 db. In general, the data obtained in this study were found to be similar to the corresponding data on hearing.

A study of the difference in thresholds between the $\phi = 0$ and $\phi = \pi$ stimuli as a function of frequency and level showed that the difference decreases as the frequency increases from 100 cps to 400 cps, or as the noise level increases from 45 db SL to 60 db SL. In hearing, the difference decreases as the frequency increases, but increases as the level increases.

In addition to placing the contactors on opposite sides of the tip of the middle finger of one hand, in which case the stimuli interact mechanically in the volume of flesh and bone constituting the finger, a few experiments were performed in which the two contactors were placed on the tips of the middle fingers of both hands. Von Békésy¹ and Sherrick² have reported considerable cutaneous interaction in experiments in which the mechanical interaction can safely be ignored. For example, Sherrick has reported that the threshold for a 100-cps tone applied to one fingertip can be raised approximately 29 db by the application of noise at 45 db re 0.1 micron to the contralateral fingertip. He has also reported that applying the noise to the contralateral fingertip produces only ~5 db less masking than applying the noise to the same fingertip (and through the same vibrator) that receives the tone. Attempts to repeat Sherrick's findings have indicated that the amount of contralateral masking is only approximately 6 db (as opposed to 29 db), and that the difference between the contralateral and ipsilateral masking is approximately 20 db (as opposed to 5 db). No explanation of this very large divergence in the two sets of data has yet been discovered. The idea that mechanical interaction is an important (and perhaps necessary) condition for achieving substantial interaction in masking on the skin was further substantiated by the finding that the intervibrator phase difference ϕ for the tone had negligible effect on the masked threshold when the two contactors were moved from opposite sides of the same middle finger to the two contralateral middle fingers. Experiments in which the contactors are placed on the same side of the body, but in which the mechanical interaction is negligible, have yet to be performed.

L. Braida

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4. CEREBRAL DOMINANCE AND THE PERCEPTION OF VERBAL STIMULI

This report gives a summary of an S. B. thesis submitted to the Department of Electrical Engineering, M. I. T., June 1965.

It has been hypothesized that the ear contralateral to the locus of the "speech center" in the brain is more efficient in the perception of speech than is the ipsilateral ear. Kimura¹ attempted to test this hypothesis by presenting different digits to the two ears simultaneously and recording the number of correct identifications for each ear. The results of Kimura's experiments were consistent with this hypothesis; however, the magnitude of the effect was extremely small. In the present work, efforts were made to modify the experimental technique in such a way that the dominance effect (if it exists) would be more apparent. Although a number of different modifications were employed, and certain tests revealed asymmetries for certain subjects, no convincing evidence was obtained that the contralateral ear is more efficient.

J. F. Dyro

References

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C. DISPLAY OF THE CUMULATIVE BEHAVIOR OF EVOKED RESPONSES

In recent years displays of average responses from gross electrodes have become quite common. The assumptions underlying the legitimacy of the averaging operation have not always been sufficiently stressed. The average evoked response is defined as an ordered set of averages $\{M_n(t_k)\}_k$, where

$$M_n(t_k) = \frac{1}{n} \sum_{i=1}^n x(T_i + t_k)$$

n = number of responses

T_i = instant of time of occurrence of the i^{th} stimulus

t_k = time interval following delivery of i^{th} stimulus

It is assumed that the data are stationary; that is, that the set $\{x(T_i + t_k)\}_i$ are identically distributed for each T_i . Experimentally, it is apparent that data recorded during many conditions are not stationary. Experimental situations involving behaving animals, sleeping subjects, and anesthetized preparations often yield systematic changes in average evoked response waveforms with time. Such changes often occur slowly with respect to the time span that is necessary to obtain an average response. To avoid the difficulties that accompany state changes, many workers use a small number of individual responses to obtain an average evoked response.

It is the purpose of this report to examine the quasi-secular changes in average

evoked response wave forms in order to test the validity of the proposition that small samples characterize meaningfully electrical activity in a changing organism and constitute the basis for a useful data reduction scheme.

Most averaging techniques involve determination of sums $Y_k = \sum_{i=1}^n x(T_i+t_k)$, the cumulative evoked response, which are related to the average by a multiplicative scale factor. If $\{x(T_i+t_k)\}_i$ comes from a population with mean μ_{kx} (which itself is not necessarily invariant with time) and standard deviation σ_{kx} , then the statistic y_k will have mean $\mu_{ky} = n\mu_{kx}$ and standard deviation $\sigma_{ky} = \sqrt{n} \sigma_{kx}$. If we plot the statistic y_k against n , we expect the points to be centered about a straight line with slope μ_{kx} and bounded by confidence limits proportional to $\sqrt{n} \sigma_{kx}$. Notice that the standard deviation of this statistic y_k increases only as \sqrt{n} , while the statistic itself increases as n . If μ_{kx} should change once during the averaging to some new value, we expect the data to be centered about some new straight line having slope μ_{kx} , and that it will exceed confidence limits based on μ_{kx} and σ_{kx} , if we take a sufficiently large sample after the change. One can thus test the hypothesis that the data are stationary by observing the extent of fluctuations of y_k , the cumulative evoked response. Note that such a test fails if μ_{kx} changes several times in the course of a given averaging operation. A new set of confidence limits must be established each time there is a long-term change in μ_{kx} .

A computer program has been developed (for the TX-0 computer) to determine the cumulative evoked response, y_k , and plot it against the number of responses, n . Two examples of data processed by using this program are included in this report.

Figure XVIII-1 summarizes data recorded from the auditory cortex of a dog. Clicks

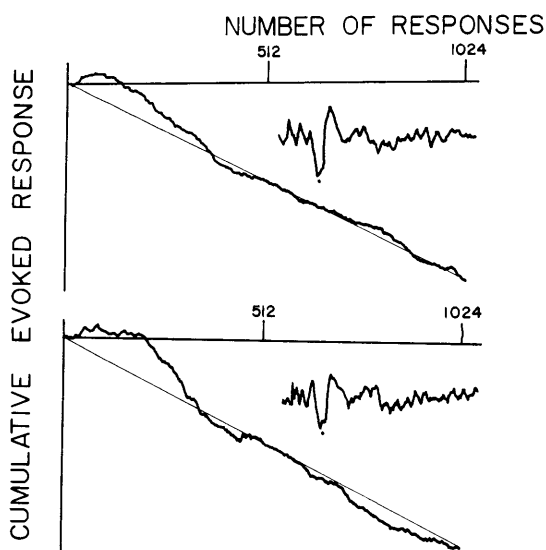


Fig. XVIII-1.

Cumulative evoked response display from data recorded from a dog's auditory cortex during changes in the dog's environment. Samples taken simultaneously with the instant of stimulus presentation (upper trace) show much smaller variation from a straight line than do samples taken at the peak of the evoked response (lower trace). The sampling time is indicated by a dot beneath the averaged evoked response waveform.

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were presented once every two seconds through a speaker placed in the animal's cage. The recording session was divided into 11 epochs. Just before epoch 1, the door of the animal's cage was opened, thereby allowing it to see another cage. The door was closed immediately before epoch 2, opened before epoch 3, closed before epoch 4, and so forth. Averages of the first 100 responses in each epoch were computed in an effort to determine the effect of this "changing environment" on the evoked responses. These averages are displayed just below each epoch in Fig. XVIII-1. A reasonable initial interpretation was to assume that the change in the average was being caused by the change in the environment. This view is confirmed by the behavior of the cumulative evoked response. (which changes as the door is opened just before epoch 1). Without the cumulative evoked response display, it would also seem reasonable to interpret the change in the average of epoch 8 as being caused by the closing of the cage door immediately before epoch 8. The slope of the cumulative evoked response does not change with the environmental change, however, and this suggests that there is no causal relationship but simply on-going changes in the animal's state which are not particularly related to the experiment.

The upper trace in Fig. XVIII-1 is derived from the same data as the lower one, but

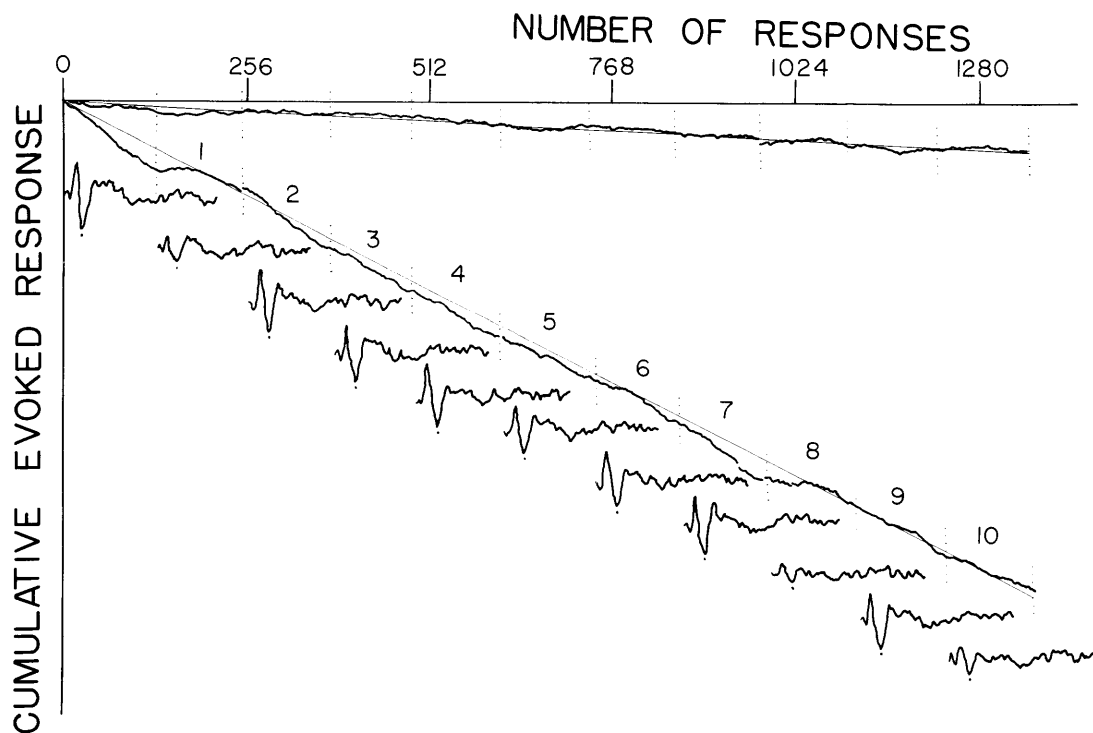


Fig. XVIII-2. Cumulative evoked response from data recorded from the scalp of a human subject who is falling asleep. The lower trace is from the same subject who has been awakened and is again falling asleep. The sampling time is indicated by the dot beneath the averaged evoked response.

is computed for a time interval $t_k = 0$, a time interval that is supposedly too small to show any effect of the stimulus. Superposed on these data is a small, negative constant, $-\epsilon$. The upper trace has a slope $-\epsilon$. Notice that variations from a straight line are considerably smaller than variations occurring in the lower trace. While this might be (circularly) explained by the greater over-all variance of the lower trace as compared with the upper trace, studies¹ have shown that variance estimated over short terms is in fact smaller during the larger deflection of an evoked response than it is before or after these portions of the response. This suggests that a piecewise linear approximation with several break points is a better characterization of the mean than a single, constant value, and thus the changes that we see in the cumulative record are caused by changes in the mechanism producing the response rather than by greater additive stationary background noise.

The upper trace in Fig. XVIII-2 comes from data recorded from the scalp of a human subject who is falling asleep. Clicks are presented to the subject once every two seconds. The lower trace is from the same subject after he has been awakened and is again falling asleep. It is quite apparent that the mean of the data is changing considerably during this averaging operation: initially it is positive; it then becomes quite negative, and finally approaches a less negative, but steady, value. The cumulative evoked response seems to provide a way of characterizing the temporal characteristics of a person falling asleep in a rather nice, compact form and may be as useful as an average. It, at least, provides information about the time when a meaningful average can be determined.

S. K. Burns

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D. ON EVOKED RESPONSES IN RELATION TO TEMPORAL CONDITIONING TO PAIRED STIMULI IN MAN

This report is based on a collaborative investigation with Dr. Frank Morrell and Dr. Lenore Morrell, carried out during a working visit to the Division of Neurology of Stanford University Medical School, in July 1964.

These experiments were carried out in a search for possible electrical manifestations of intrinsic timing mechanisms of the brain, as monitored by EEG recordings from scalp electrodes. In additional experiments, intrinsic timing mechanisms of the brain, as indicated by measurements of distributions of motor reaction times (key pressing), were explored under several different experimental conditions.

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The experiments were carried out while subjects, with eyes closed and comfortably seated in a dark, soundproof room, were presented at irregular intervals (2.1-3 sec, average interval 2.5 sec) with click-light pairs of stimuli separated by fixed intervals (200-700 msec). The clicks (1 msec in duration) were presented by a loudspeaker at such an intensity as to be comfortably audible; the visual stimulus was a flash of 4-msec duration from a noiseless glow discharge tube, located 6 inches in front of the subject at the level of the eyes. The EEG (9 or 10 channels) and stimulus pulses were recorded simultaneously on paper and on magnetic tape. Averages of evoked responses were computed by means of a LINC computer.

For the initial part of this experiment, the stimulus pairs were always presented together (total of 100 pairs). In the second part of the experiment, the visual stimuli were omitted in a randomized manner, on an average of 2 out of 15 stimulus pairs. In the final part of the experiment, click stimuli alone were presented.

A summary of the results from one subject (the author) with whom extensive studies were carried out are shown in Fig. XVIII-3. For these recordings, the click-flash separation was 700 msec. The curves in Fig. XVIII-3, for which the sweep length of the computer was 2 sec, have been traced from Polaroid photographs of averages of 100 responses each. The averages were computed from monopolar EEG recordings, linked ears being used as the common reference.

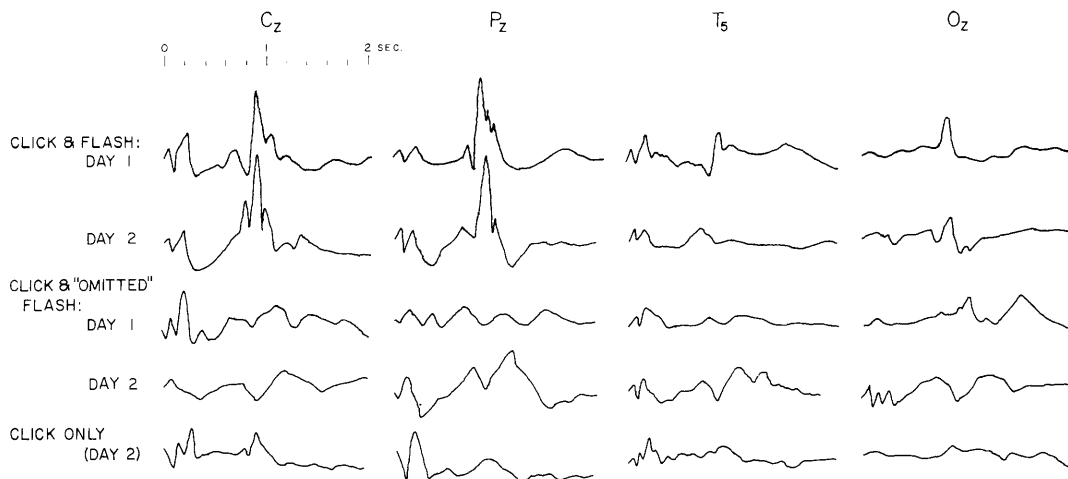


Fig. XVIII-3. Averaged responses for various types of stimuli. Click-flash interval, 700 msec; number of responses averaged, 100. Electrode Locations: C_z vertex; P_z midline parietal; T_5 posterior temporal; O_z midline occipital. Reference electrode, linked ears.

For each of the active electrode locations (vertex, midline parietal, left posterior temporal, and midline occipital, respectively) the results of experiments for two different days are shown. The first two rows in the figure represent averages for 100 click-flash pairs, the trace beginning with the presentation of the click. In the results for both days, and in all leads, but especially at the C_z and P_z electrode locations, the average responses evoked by the clicks and by the flashes are clearly evident. Moreover, the forms of the responses for the two days are generally similar. In the third and fourth rows are shown the results of averages for 100 instances in which only the clicks were presented, these trials being interspersed at random among the 700 trials in which both clicks and flashes were presented. For these trials, therefore, the flashes were "limped," that is, omitted. Of interest from the results of both days is a positive deflection in the averages which occurs at very nearly the same time at which the evoked response complex to flashes appears, in the trials when the flashes were actually presented (rows 1 and 2 in Fig. XVIII-3). The negativity just described is most clearly demarcated in the C_z and P_z leads, being less in evidence for the T_5 and O_z linkages.

In the last row in Fig. XVIII-3 are shown averages computed for the last part of the experiments in which only the click stimuli were presented. It is of interest that in the last instance, a negativity is apparent whose latency from the click is about the same as that for the large negativity of the flash-evoked responses when the flashes were presented (rows 1 and 2 in Fig. XVIII-3). Although this finding was not fully explored (with control recordings at the beginning of the experiment, and with recordings of sufficient length to explore the extinction of the response), it does appear to suggest a conditional response to click stimuli, when these had been preceded by a large number of click-light pairs. In contrast with the latter electrical sign of conditioning, the traces in columns 3 and 4 suggest an electrical sign of conditioning of the opposite polarity, for the trials in which the flash was "expected" but actually was omitted. In contrasting ways, therefore, both of these electrical manifestations of conditioning suggest that intrinsic brain timing mechanisms may have been activated to result in these different manifestations of temporal conditioning to the time interval between pairs of stimuli.

In another experiment, also with the same subject (JB), electrical manifestations of conditioning were explored for flashes (only) delivered periodically at a flash rate of 1/sec, 2 out of every 15 flashes being omitted in an unpredictable manner. Averages for 100 traces of these "limped" presentations were preceded by 100 presentations of the flash in which no flashes were omitted. The results from this experiment are shown in Fig. XVIII-4. In Fig. XVIII-4(A), the trace length is 2 sec; in the lower part of this figure, the average of 100 sequences in which no flashes were omitted is shown and hence the response evoked by flash appears twice; in the upper part of this figure, the computer was triggered by pulses marking the omission of flashes, and hence the real evoked response to flash appears only once in the trace, after a delay of 1 sec. Although the

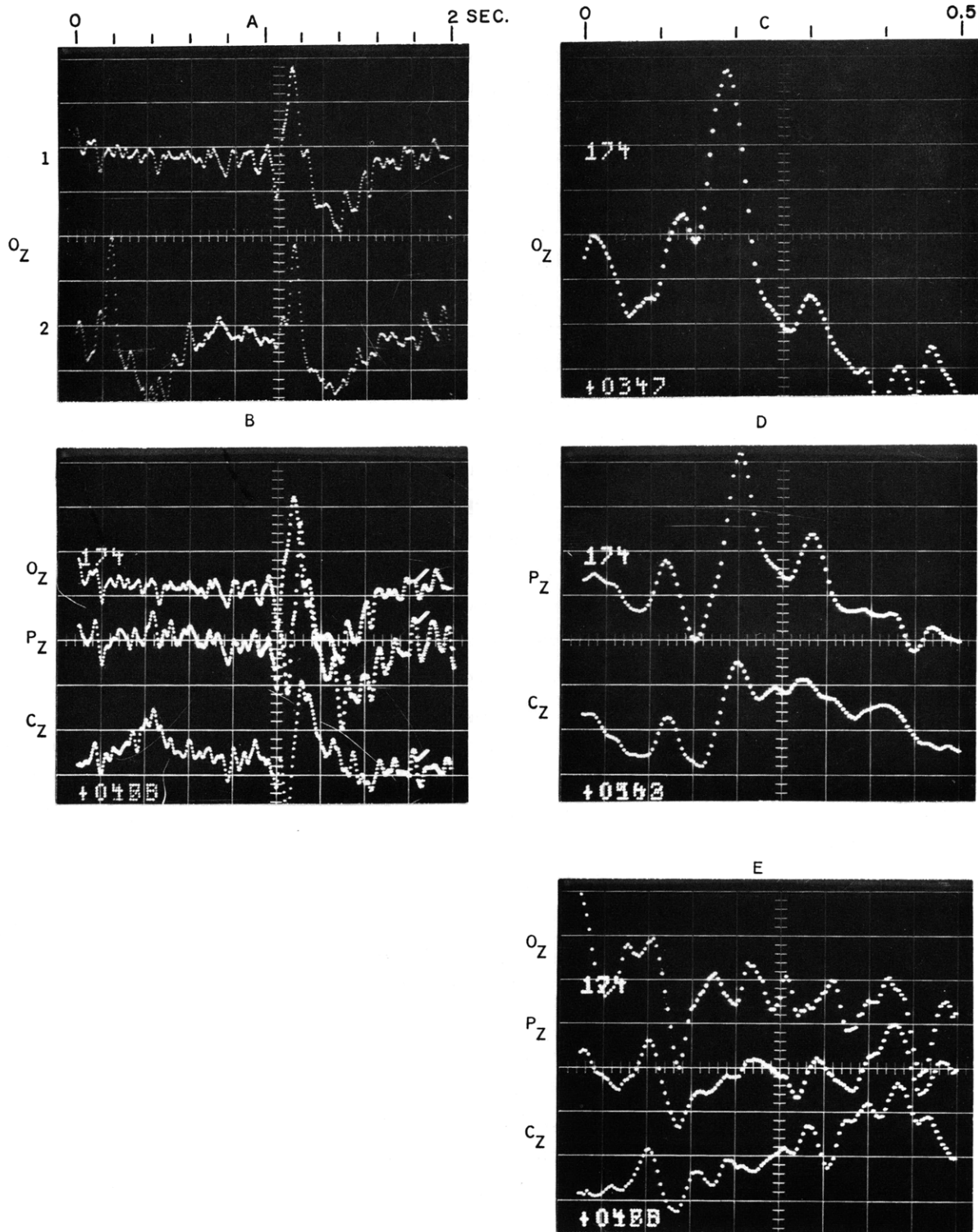


Fig. XVIII-4. Evoked responses for 1/sec flashing. Computer triggered by "limped" flashes in A-1, B, and E. (For C and E (P_z and C_z) computer gain is up by a factor of 2, for E (O_z only) by a factor of 4, in comparison with gain for A and B.

effect is not very clearly defined, of interest is the suggestion in this instance of "limping" of the flash of a positive deflection in the trace at approximately the same time when the evolution of the real evoked response to flash would have begun (the latter being apparent in the trace immediately below in Fig. XVIII-4(A)). It is perhaps also of interest that this suggestive positive deflection is of opposite polarity to the corresponding component in the real evoked response, a finding that was noted in the results presented in Fig. XVIII-3. Also interesting is the fact that the initial part of the average evoked response immediately following the "limped" flash is somewhat different in form than is the case when the preceding flash has not been "limped," the latter being evident in the lower trace in Fig. XVIII-1(A).

Traces from the "limped" presentations for the O_z linkage are repeated in Fig. XVIII-4(B) in the upper trace, the middle and lower traces in the figure representing similar computations at the same gain for electrodes P_z and C_z , the last suggesting a somewhat similar event for the "limped" flashes.

The results for the trials in which the flashes were actually presented are compared with those in which they were omitted, on a faster time base (a 500-msec sweep) in Fig. XVIII-4(C-E). In Fig. XVIII-4(C), the real evoked response, at O_z , to flash is shown, and in Fig. XVIII-4(D), average responses for flash stimuli recorded from P_z and for C_z , respectively, are shown. Averages for the "limped" or omitted flashes are shown in Fig. XVIII-4(E), for electrodes O_z , P_z , and C_z , respectively. (For the averages for electrode O_z , the gains of the computer were increased for Fig. XVIII-4(C) by a factor of 2, and for Fig. XVIII-4(E) by a factor of 4, in comparison with the gains employed in Fig. XVIII-4(A and B); for the averages for electrodes P_z and C_z in Fig. XVIII-4(E), the gain of the computer has been increased by a factor of 2, in comparison with that used in Fig. XVIII-4(B). In these traces on an expanded time base, the positive deflection in the average response for electrode O_z , which begins at approximately 100 msec, is more clearly depicted, and it is seen that this event is opposite in direction to the component of the actual response evoked by flash beginning at about the same time, shown in Fig. XVIII-4(C). These time relationships are not so well defined for the averages for electrodes P_z and C_z , respectively.

In the experiments that were carried out in the second experimental day (Fig. XVIII-3, day 2), additional recordings of motor responses (key pressing) were carried out in order to examine the distributions of the latter for various paradigms. Brief pulses corresponding to the closing of the key contact were recorded on a separate channel of the magnetic tape recorder, and the distribution of these pulses was examined with the LINC computer. It may be remarked parenthetically that the addition of these motor responses in the experiments of the second day were without noticeable effect on the form of the average responses for that day, in comparison with those from the previous day, in which no motor responses were carried out (compare traces 1 and 2, and traces 3 and 4

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of Fig. XVIII-3).

The results of the observations on the distribution in time of motor responses are shown in Fig. XVIII-5. In Fig. XVIII-5(A and B), the subject was attempting to make the instant of the pressing of the key to be subjectively simultaneous with the occurrence of the flash, the latter being presented 700 msec after the presentation of the click, the traces in Fig. XVIII-5(A and B) being initiated by the click pulse. In trace 1 of Fig. XVIII-5(A), the results represent those for the preliminary presentation (after an initial pair of 10) of 100 click-flash pairs, no flashes being omitted. In trace 2, the distribution represents attempted synchronization during presentation of the first 100 click-flash pairs, in which flashes were occasionally omitted. The third trace in Fig. XVIII-5(A) represents attempted synchronization for the instances in which all of the flashes were omitted. The fourth trace indicates the distribution for the last 100 click-flash pairs for the run in which occasional flashes were omitted.

These results are repeated in the successive traces in Fig. XVIII-5(B), except that a four-point running average has been utilized, in order to effect a smoothing of the data. It is apparent from comparison of the four traces for the different conditions, that the distributions are very much the same and appear to be distributed in a skewed manner about a mode of approximately 700 msec (the running average program in these traces also inverts the form of the distribution).

Figure XVIII-5(C) shows the distribution of 100 reaction times to flashes, the latter being invariably presented after an interval of 700 msec from the warning click that initiates the traces, the lower trace in the figure representing the smoothed data. The distribution is seen to be rather symmetrically distributed about a mode of 900 msec, a result that indicates a compound reaction time to the flash (the click being the warning stimulus) of approximately 200 msec. The distribution is notably narrower than the distributions in Fig. XVIII-5(B).

In a separate recording, clicks alone were presented in irregular succession, and the distribution of simple reaction times to these are shown in Fig. XVIII-5(D), in their unsmoothed (upper trace), and smoothed (lower trace) forms. Although the mode of the reaction times is seen to appear at approximately 190 msec, there is a suggestion in the smoothed data of a multimodal distribution, with additional peaks occurring 100 and 200 msec later. The distribution of simple reaction times in another recording in which flashes alone were presented in irregular sequence is shown in Fig. XVIII-5(E). In the smoothed data, shown in the lower trace, the mode is seen to appear at 200 msec, and the distribution is quite narrow.

It is apparent from comparison of the results shown in Fig. XVIII-5(A and B) with those shown in Fig. XVIII-5(C and E) that the distribution of both simple and compound (that is, after a warning click) reaction times to flashes are appreciably narrower than

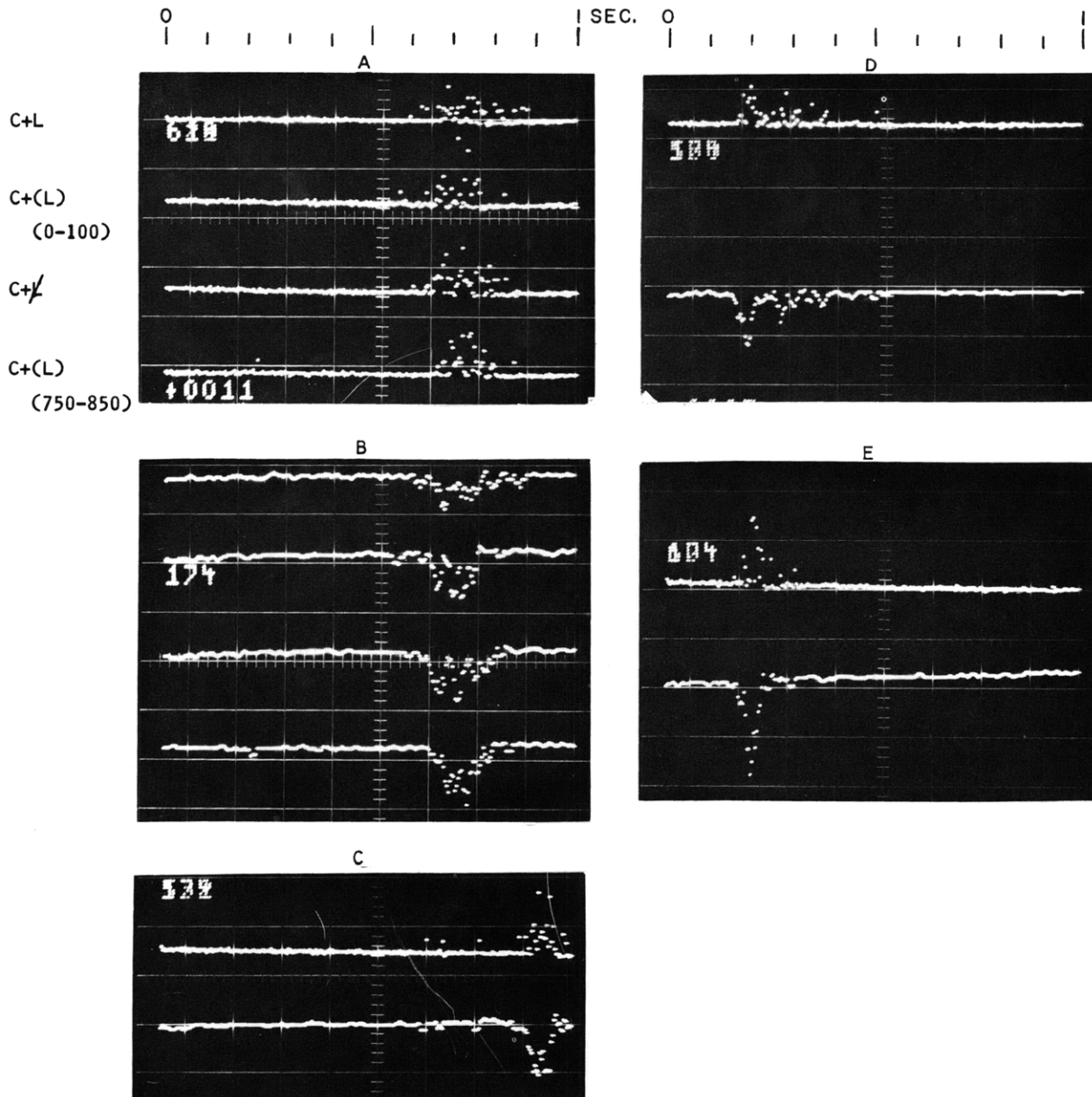


Fig. XVIII-5. Distribution of motor response times: A. For subjective simultaneity with flashes C+L, click invariably followed by light after 700 msec; C+(L) (0-100), first 100 trials of series of click followed by light in the run of 850 trials in which the light was occasionally omitted; C+(L) (750-850), same, except last 100 of click-light pairs; C+L, average of 100 trials interspersed in the series of 850 in which light was omitted. B. Same, after smoothing (4-point running average). (The smoothing program also inverts the trace.) C. Upper trace: reaction times of the click-flash pairs; lower trace, same, after smoothing. D. Reaction times to clicks alone. E. Reaction times to flashes alone.

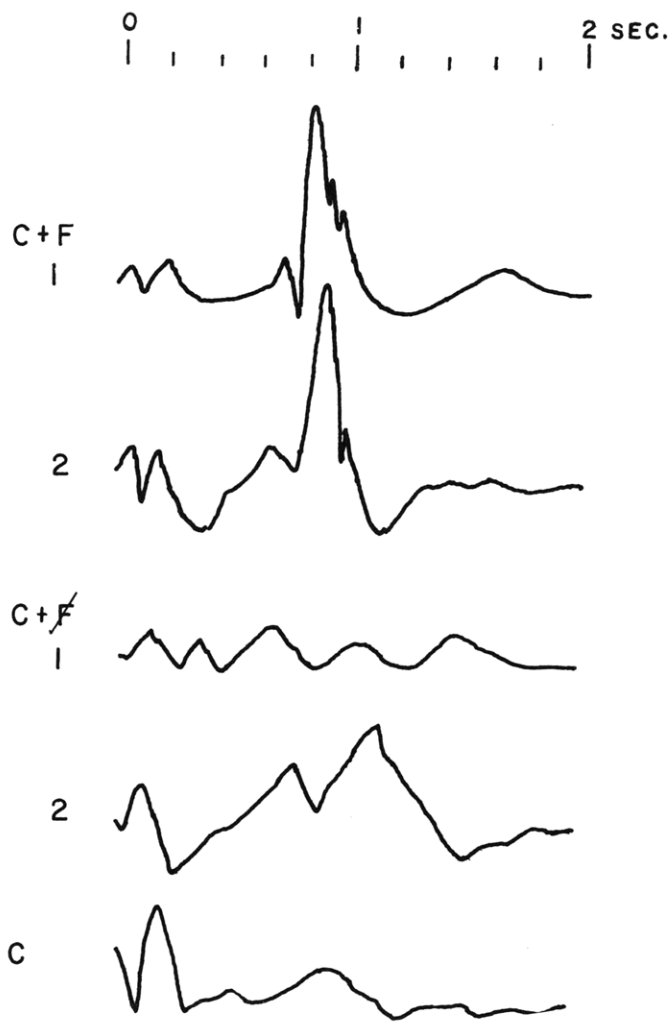
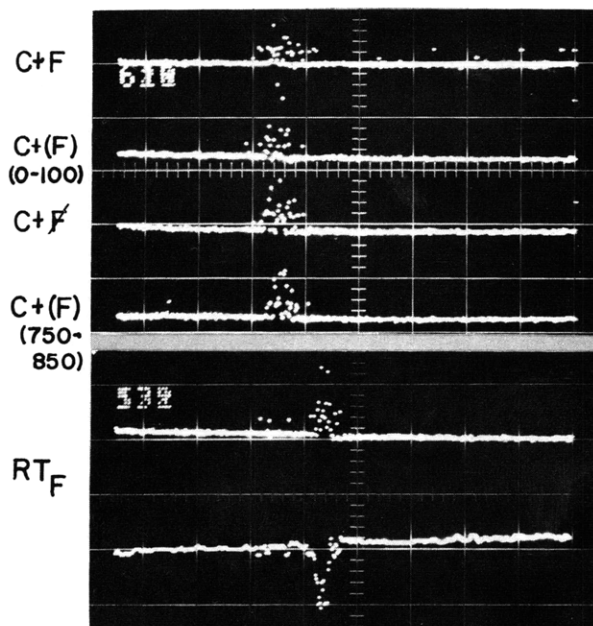


Fig. XVIII-6.

Comparison of averaged responses at P_z (midline parietal electrode) with distribution of motor responses. Notation same as in Fig. XVIII-5, except F (flash) instead of L (light). RT_F = reaction times to flash of click-flash pairs.



the distributions of motor responses that were made in such a manner as to be subjectively simultaneous with the perception of the flashes. It should be pointed out, however, that the role of practice effects in these experiments has not been specifically examined.

The unsmoothed distributions of the motor responses for which the subject was attempting to make them subjectively simultaneous with the actual (or expected, in the case of the "limped") flashes are repeated on a 2-sec time base in Fig. XVIII-6 for comparison with the averaged evoked responses, which are reproduced from Fig. XVIII-3 for electrode P_z . (Remember that the clearest electrical suggestion of temporal conditioning to the "limped" flashes was apparent in the EEG recordings from electrodes P_z and C_z .) From a comparison of these data in Fig. XVIII-6, it is evident that the mode of the motor responses, at 700 msec, is almost coincident with the beginning of the evolution of the electrical responses evoked by the flashes, in those instances in which the latter were actually presented; the mode is also coincident with the onset of the positive deflection in the averaged responses for the instances in which the flashes were omitted.

Also shown, in the lower part of Fig. XVIII-6, are the distributions of compound reaction times to flashes which have been preceded by the warning click stimuli. The mode of the distribution (apparent from the smoothed data shown in the lower trace) is seen to be coincident with the late components of the responses evoked by the flashes.

These results appear to suggest that the perception of stimuli, since the time of their occurrence is indicated by the timing of motor responses that are subjectively simultaneous with the perception of stimuli, occurs rather early in time with respect to the elaboration of the electrical responses evoked by the stimuli as monitored from scalp electrodes. These findings are in agreement with previous results¹⁻³ which indicated that the event of perception occurs, on the average, quite early (perhaps less than 50 msec) after the presentation of stimuli, motor responses, in reaction-time experiments, appearing much later (compare Fig. XVIII-6(A and C)). These findings also provide some indications of electrical concomitants of temporal conditioning in the brain in man to paired sensory stimuli, which may perhaps be a reflection of the processes that are concerned with the timing and execution of motor responses.

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E. PRELIMINARY STUDIES: MACROELECTRODE AND MICROELECTRODE RECORDINGS OF AUDITORY RESPONSES FROM THE CAT'S CEREBELLUM

In contrast to the wealth of information available concerning evoked responses at various levels of the classical auditory pathway, relatively limited information is available about cerebellar responses to different acoustic stimuli.¹⁻³ It appears, in particular, that no previous attempts have been made to analyze different response patterns in the cerebellum as a function of stimulus parameters.

Such information might be expected to contribute to an understanding of the role that the cerebellum plays in the analysis of afferent sensory activity, the cerebellum's dynamic range of response and its resolving capacity.

We have attempted to carry out some preliminary studies in cats, employing tone bursts and single- and double-click stimuli in a manner similar to studies that have been done on the cerebral cortex.⁴⁻⁶

Twenty-six unanesthetized succinylcholine-maintained encéphale isolé cats were studied. Posterior vermis including lobules simplex, folium and tuber vermis (lobules VI, VIIa and VIIb in Larsell's classification) were studied with gross surface electrodes, in conjunction with 3 M NaCl-filled micropipettes at a depth of 200-400 μ below the cerebellar surface, the depth depending upon the angle of penetration.

1. Macroelectrode Studies

A few experiments were undertaken to investigate responses that are recordable from the surface, at different locations within the auditory projection area of the posterior vermis. In these locations clicks or tone bursts readily evoke typical positive-negative responses whose latency ranges from 5 msec to 20 msec and whose duration varies between 20-40 msec.

Initial studies indicated that differences in waveform and amplitude resulted from either changes in the location of the recording electrodes or variation of the frequency and intensity of the tone bursts. Some examples are given in Fig. XVIII-7a which shows

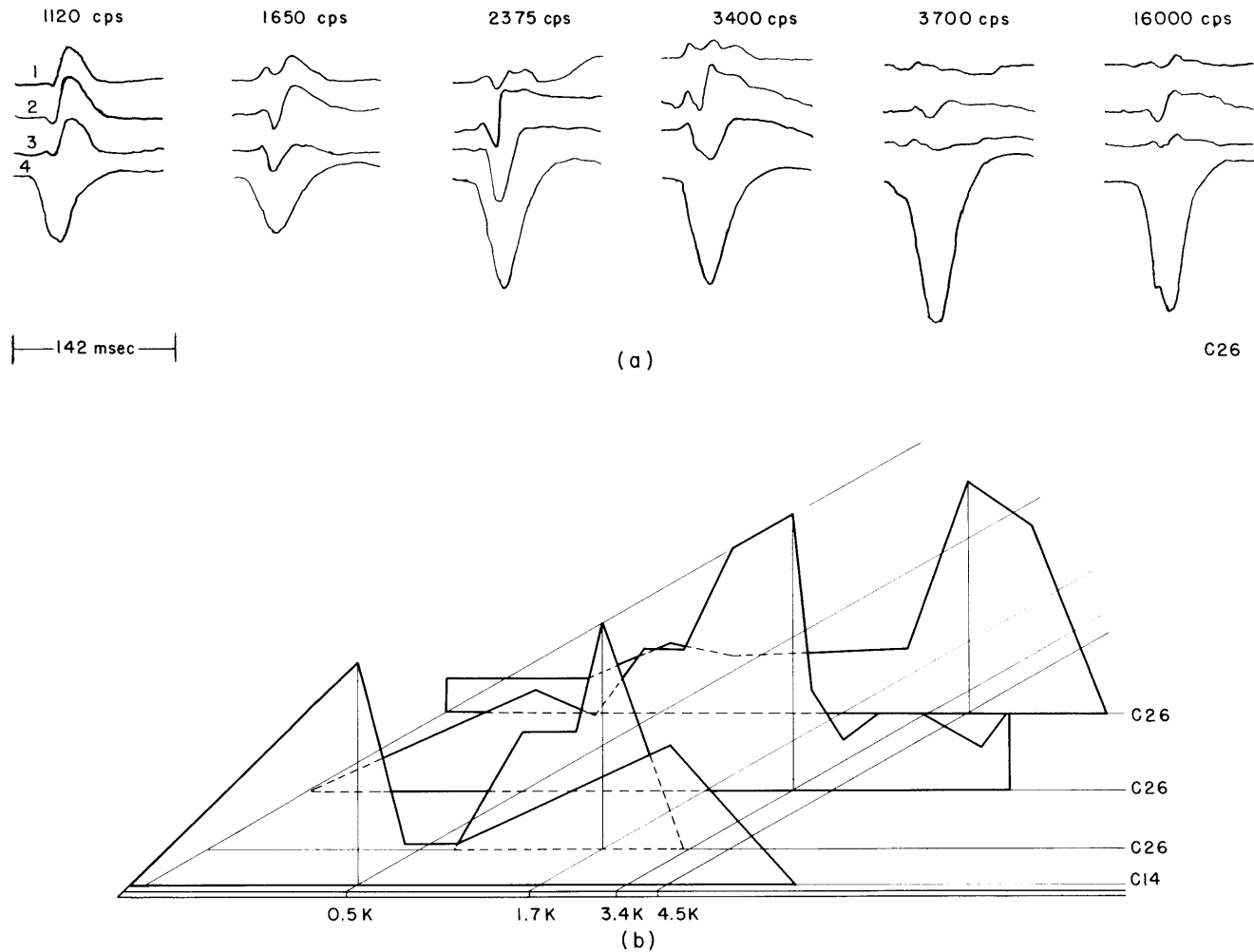


Fig. XVIII-7. (a) Averaged gross responses recorded simultaneously from 4 locations on the surface of lobule VII to tone bursts of varying frequency, constant intensity, 100-msec duration, and 10-msec rise and fall times. Each average represents 20 responses. (b) Each of the 4 curves demonstrates the amplitude of averaged evoked response at a given cerebellar location as a function of tone-burst frequency where intensity was kept constant. Data were obtained from 2 animals as indicated, but are representative for a number of cats.

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averaged responses to tone bursts of different frequencies and constant intensity simultaneously recorded from four sites on lobule VIIa, with 2-3 mm separations between the gross recording electrodes.

In Fig. XVIII-7 each row (numbered 1 to 4) contains responses from one recording location. Among the number of differences that can be seen, emphasis is to be placed on the following: the amplitude of the surface positive component for a given row seems in general to be enhanced for certain frequency ranges of the tone burst and attenuated for others. The stimulus frequency that evokes a maximal response, however, may differ for individual recording sites, as indicated by comparing rows 3 and 4.

In a number of locations in different cats frequency-dependent amplitude changes were seen and several curves are shown in Fig. XVIII-7b where, for convenience, the peak-to-peak amplitudes of responses are plotted against the frequency of tone bursts.

2. Microelectrode Studies

Most of our experiments dealt with the evoked activity of cerebellar units. Virtually all units studied showed some degree of spontaneous activity, although many of these had complex burstlike activities with sudden onset and cessation of spike discharges at variable rates up to 200/sec.

Studies of the effect of tone bursts on single-cell responses are illustrated in Fig. XVIII-8a; photographs of unit activity for several levels of stimulus intensity are shown. It is apparent that two easily identifiable amplitude levels are present for unit discharges in these records; the smaller amplitude presumably represents more "distant" units. The behavior of the larger amplitude spikes – with regard to incidence and rate of firing – appears to differ from the lower amplitude spikes. At the highest stimulus intensity the activity is confined to the stimulus duration. Figure XVIII-8b gives PST histograms for the unit having the larger spikes in Fig. XVIII-8a at corresponding intensity levels with increase in stimulus intensity. The unit fires more frequently throughout the duration of the tone burst.

In a number of other units similar stimulus conditions produced a response pattern that was considerably different. In these, following the onset of the tone burst, the preferred firing time for evoked discharges occurred 20-30 msec later than that in Fig. XVIII-8b, as indicated by their PST histograms which showed a commensurate delay preceding the time of peak activity. Moreover, these peaks were further elevated by increasing the stimulus intensity, although little change in the level of activity took place during the rest of the stimulus interval.

When frequency is the variable parameter, the patterns of response are somewhat more complex. Figure XVIII-9a shows tone bursts at the frequencies indicated. Intensity is 50 db above the VDL with respect to the gross response at the best frequency, 3 kcps. Here, the preferred period of unit discharge begins and lasts throughout the

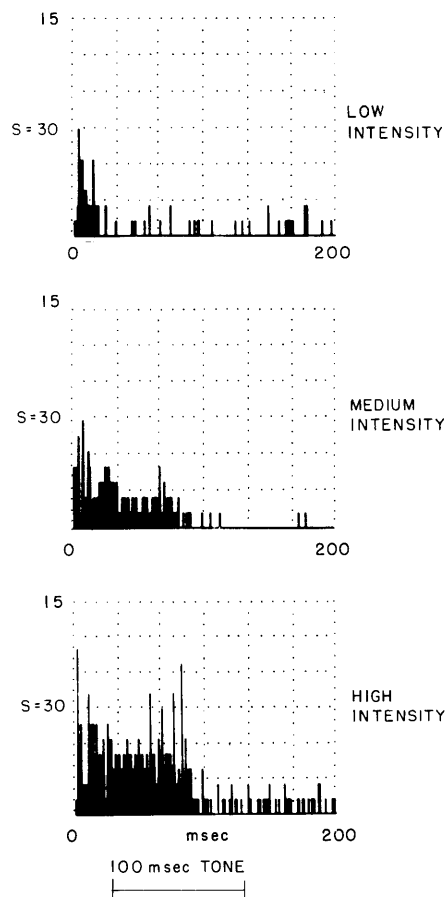
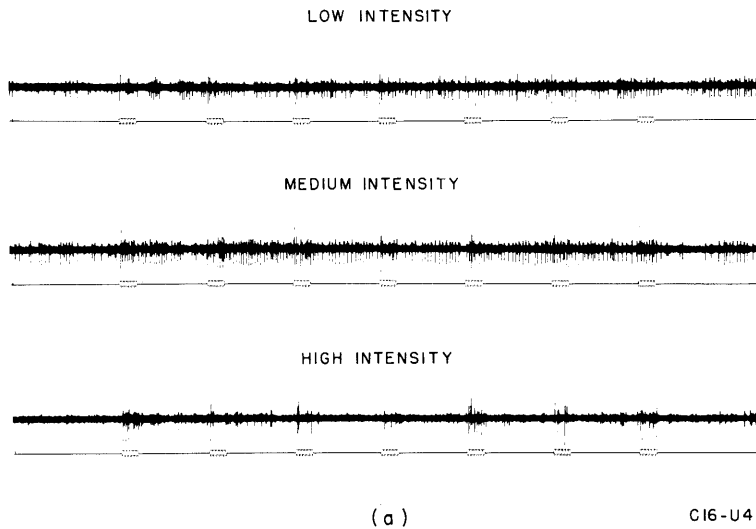


Fig. XVIII-8. (a) Sample of unitary responses to tone bursts of 100-msec duration with 5-msec rise and fall times; tone burst frequency, 300 cps. Seven bursts (1/sec) were followed by 6 sec of silence. Three traces are for low (upper), medium (middle), and high (lower) stimulus intensities, respectively.

(b) PST histograms of response to tone bursts specified in Fig. XVIII-7a for three intensity levels. 30 responses were taken for each histogram (S=30).

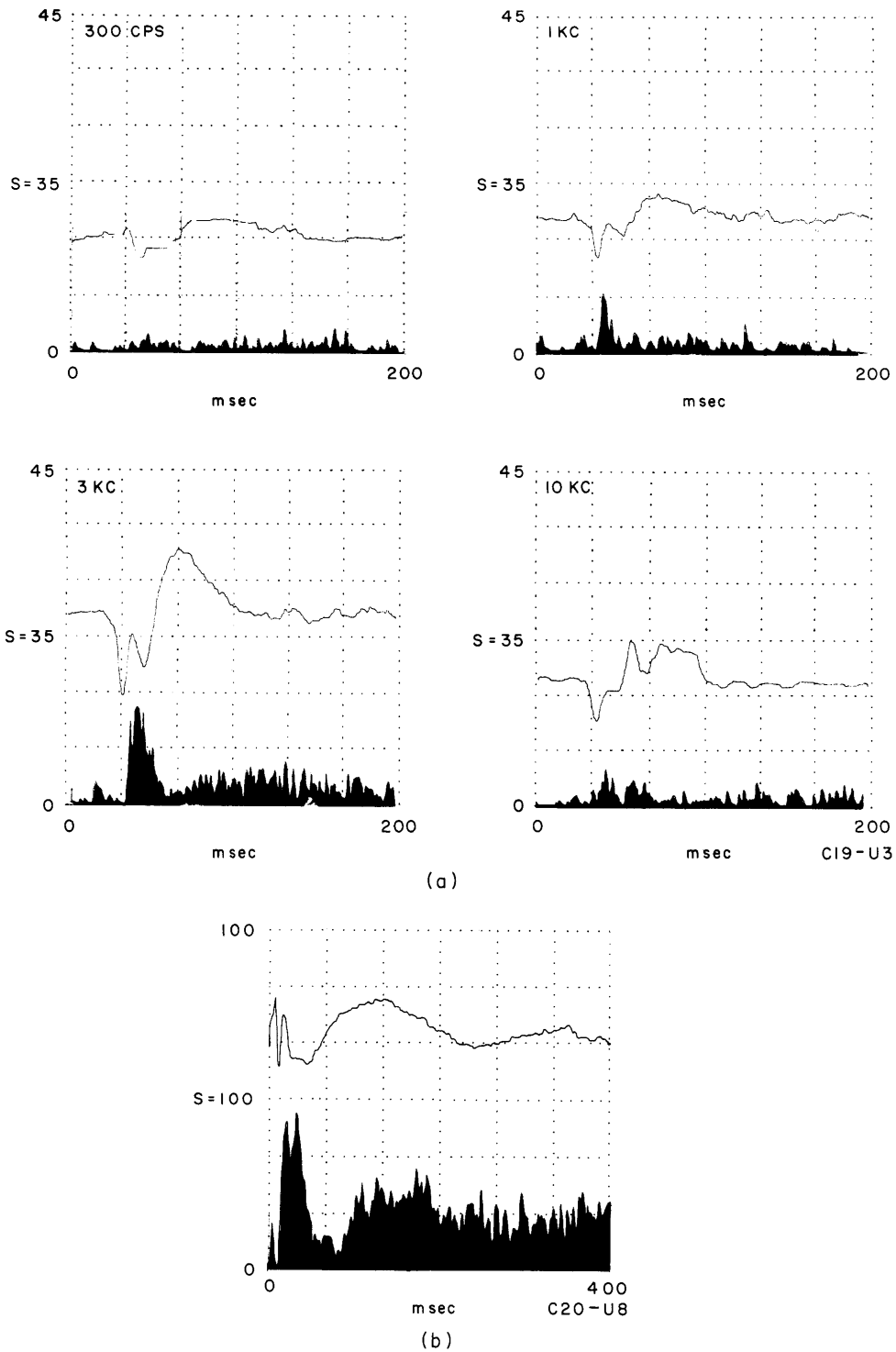


Fig. XVIII-9. (a) PST histograms for single-cell responses to tone bursts of different frequencies and constant intensity (50 db above VDL). Tone burst duration, 100 msec; rise and fall times, 10 msec. Trace starts 20 msec before stimulus delivery. (b) PST histogram of unit response to click. Upper trace shows averaged gross evoked response recorded simultaneously from the surface close to the location of the microelectrode.

rising phase of the positive component of the corresponding surface response.

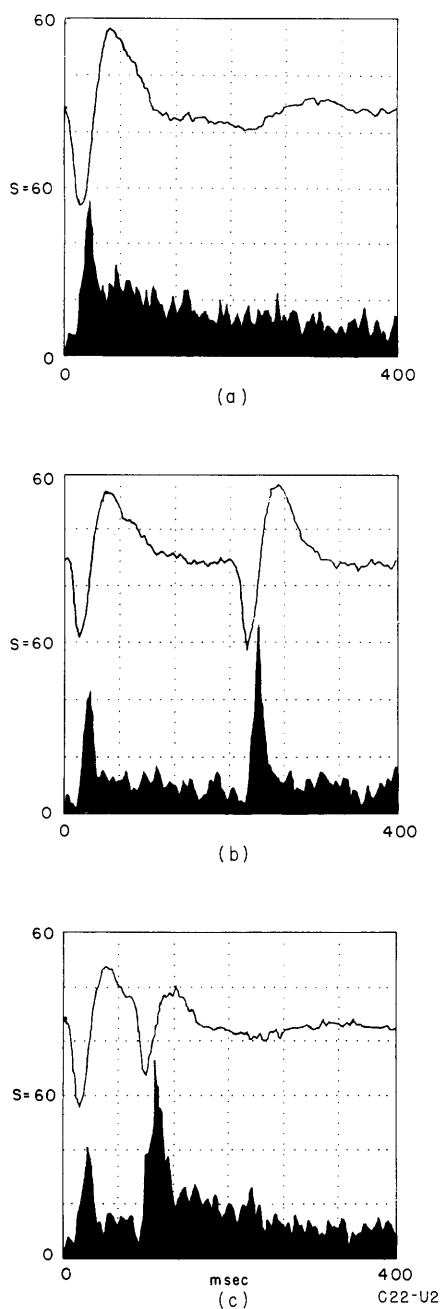


Fig. XVIII-10.

PST histogram and averaged gross response to 1/sec single (a) and paired-click (b, c) stimuli. Click intensity, 50 db above VDL.

In some other units the preferred time for the discharge is just preceding the onset of the surface response recorded from the adjacent cerebellar surface.

Unit responses for single clicks are relatively less complicated (Fig. XVIII-9). Single sharp peaks sometimes followed by periods of inhibition up to 50-60 msec characterize click PST histograms. Presentation of two identical clicks separated by varying short duration intervals, however, produces complex interactions that affect responses to the first, as well as to the second, click.

Figure XVIII-10 demonstrates the effect of moderately strong identical, paired clicks (S_1 and S_2) on the amplitude of gross surface responses (R_1 and R_2) and on the height of corresponding peaks (P_1 and P_2) of the simultaneously obtained histograms relative to the single-click control response.

For $\Delta t = 200$ msec, where Δt is the interval between S_1 and S_2 ,

$$\begin{aligned} R_1 &= 80\% & R_2 &= 95\% \\ P_1 &= 80\% & P_2 &= 120\% \end{aligned}$$

and for $\Delta t = 80$ msec,

$$\begin{aligned} R_1 &= 80\% & R_2 &= 55\% \\ P_1 &= 70\% & P_2 &= 125\% . \end{aligned}$$

These findings indicate that presentation of paired clicks in the

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manner described give rise to interactions affecting the first response, as well as the second.

Reductions of R_1 and P_1 and also the reduction of R_2 have been regularly seen in our studies and suggest an inhibitory mechanism evoked by the second click. The increase of P_2 in the example shown here is an unusual finding and cannot be further commented upon until its generality has been ascertained.

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