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A. AUDITORY NERVE RESPONSES TO REPETITIVE ACOUSTIC STIMULATION

We have previously studied the electric responses of the auditory nerve to repeated bursts of noise (1). Formerly, our attention was focused on responses to short bursts of moderate intensity (0.1-msec duration, 35 db above threshold). We found that the way in which the neural response varies with the stimulus repetition rate can be described in terms of a gradual decrease in response size with increasing rate, together with overlapping of responses at high repetition rates. In the research reported on here, we have extended these rate studies by varying two other stimulus parameters, that is, stimulus intensity and level of background (masking) noise.

Bursts of noise (0.1 msec in duration) were delivered to a cat's ear through an earphone as previously described (1). Responses recorded from an electrode near the round window were averaged on the ARC-1 computer (2). In Fig. XVIII-1 the normalized peak-to-peak amplitude of the averaged neural response is plotted as a function of stimulus repetition rate for several stimulus intensities. The two curves for -45 db and

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Fig. XVIII-1. Peak-to-peak amplitude of averaged neural responses to noise bursts versus repetition rate. Amplitudes are normalized for each intensity so that each amplitude at 1/sec equals 100 per cent; amplitude measurement was made on the N_1 component of the response. Reference level for noise bursts, 1 volt rms; number of responses averaged, 64-2048.



Fig. XVIII-2. Averaged responses to noise bursts for several repetition rates. Intensity, -90 db re 1 volt rms = -5 db re VDL; number of responses averaged, 2048, except at 2000/sec, 8152.

-60 db are similar to those obtained before for intensities in this same range. The response amplitude decreases for rates higher than 10/sec, and a small peak occurs at 600-700/sec. In contrast, the low-intensity curve (-90 db) is relatively flat for rates below 400/sec. For this burst level, the amplitude of the averaged responses is actually greater at 600/sec and 700/sec than it is at 10/sec (Fig. XVIII-2). This low stimulus



Fig. XVIII-3. (a) Averaged responses to -60 db noise bursts for various repetition rates and masking noise levels. Reference level for masking noise, 1 volt rms into the ear phone; number of responses averaged, 1024. (b) Normalized peak-to-peak amplitude of averaged responses to noise bursts versus repetition rate for several masking noise intensities. Number of responses averaged, 64-4096. (C-523).

intensity lies in the vicinity of the visual threshold for detection of responses in single traces on an oscilloscope. (Visual detection level (VDL) was $-85 \text{ db} \pm 5 \text{ db.}$)

Amplitude-versus-rate curves (rate functions) were also measured for several levels of masking noise. Figure XVIII-3a shows the averaged responses obtained, and the



corresponding normalized rate functions are plotted in Fig. XVIII-3b. As the level of masking noise is increased, the slope of the rate functions decreases. With a relatively high masking noise level (-65 db) it is again observed that the response amplitude is greater at 700/sec than at 10/sec. Response waveforms for this masking level are given in Fig. XVIII-4 with a higher gain than that in Fig. XVIII-3a. At this masking noise level (-65 db), single responses were not visually detectable; they were detectable with -75 db masking noise.

In our previous work we have found that certain features of the rate functions can be explained in terms of overlapping of successive response waveforms. For low stimulus



Fig. XVIII-5. Comparison of experimental and theoretical responses at several repetition rates for -60 db noise bursts plus -65 db masking noise. Theoretical responses were obtained by overlapping a 50/sec response with itself. Number of responses averaged, 2048. (C-523.)



Fig. XVIII-6. Experimental and theoretical rate functions: (a) -90 db noise bursts; and (b) -60 db noise burst plus -65 db masking noise. Theoretical responses were obtained as in Fig. XVIII-5.

intensities or high masking noise levels (Figs. XVIII-2 and XVIII-4), it appears that all of the variation in the neural response with rate of stimulation might be the result of overlap. To test this hypothesis, we synthesized high-rate responses by overlapping standard low-rate responses, using the appropriate time shift for each repetition rate. The resulting waveforms are shown in Fig. XVIII-5 with the corresponding experimental results. The agreement between the computed and experimental waveforms is striking. Figure XVIII-6 shows experimental and theoretical rate functions for low-intensity bursts (left), and for the high masking noise level (right). It appears that under two conditions, in the vicinity of the absolute and masked thresholds, the neural response can be predicted very well by an overlap model.

These results indicate that, at low intensities, changing the stimulus repetition rate has little effect on the response to each stimulus. This behavior might seem to be impossible, since single nerve cells are known to have refractory properties. However, if we consider that the gross-electrode response represents a sum of the responses of many nerve fibers, the results can be interpreted in terms of the kind of probability model suggested by Frishkopf and Rosenblith (3). If the elements of a homogeneous population of neural units are assumed to have a certain probability of responding to a given stimulus, then, for near threshold stimuli, this probability is very small. As a result, very few units of the population respond to each stimulus, and virtually the whole population is able to respond at any time. It should be pointed out that this constancy of response with changing rate cannot be explained in terms of a population of neural units with <u>fixed</u> thresholds. If that were the case, the same units would be stimulated by each stimulus, and if the units had any refractory properties, the neural response would decrease at high rates.

Addition of masking noise to moderate intensity bursts results in changes of the rate function which are similar to those obtained by decreasing the intensity of the bursts. Under these conditions, the responding units are presumably excited asynchronously by the masking noise so that the number of units capable of responding to any particular burst is reduced. At the highest masking level, it appears that the number of units available is determined entirely by the masking noise. One possible explanation is that, in a given time interval, a certain number of units becomes capable of responding after recovering from previous stimulation by the masking noise. This number is unaffected by changes in rate of the bursts, since the bursts do not add appreciably to the net power input, except at very high rates.

W. T. Peake, N. Y-S. Kiang, M. H. Goldstein, Jr.

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B. SIMULTANEOUS RECORDINGS OF SPONTANEOUS AND EVOKED POTENTIALS IN SEVERAL CORTICAL LAYERS

The exploration of electrical activity in cortical tissue has generally been accomplished by using a single electrode that is referred to a distant ground. In order to determine the spatial distribution in cortical receiving areas of effects that are due to stimulus presentation, it is usually necessary to perform a series of identical experiments, changing only the location or depth of the electrode (as, for example, von Euler and Ricci (1) have done). Such procedures yield much information about the evoked responses as a function of stimulus parameters, and can determine whether these potentials vary systematically with location. However, all information regarding temporal variations of the spatial distribution of the potentials is lost; simultaneous measurements at several locations are needed to elicit such information. This kind of work has been done by Lilly and others (2), by using a matrix electrode array (2 mm on



Fig. XVIII-7. Microphotograph of electrode array; object at right is No. 27 hypodermic needle (.016-inch diameter).

centers) at the cortical surface. These workers observed effects which they interpreted as traveling waves of activity at the surface of the cortex.

We have made some simultaneous measurements at 5 depths in the auditory cortex, paying particular attention to the observable differences in the electrical activity at different depths. Attempts to quantify these differences are beset by difficulties that will be discussed briefly.

Our electrode array consisted of parallel .0005-inch tungsten wires on .005-inch centers embedded in a Teflon ribbon (.005-inch thick). The end to be placed in the cortex was cut to make a 30° angle with the ends of the exposed tungsten wires (see Fig. XVIII-7). The wires at the other end were stripped, nickel-plated, and soldered to a connector plug.

Experiments were performed with lightly anesthetized (nembutal) cats. The multiple electrode was inserted into the Al region of the cortex; the reference electrode was in the neck muscle. Data from 5 channels were recorded on FM tape for later processing.



Fig. XVIII-8. Electrical activity observed by the extreme electrodes in the array (.045-inch difference in depth) for various stimulus conditions. Upper trace in each case is from the electrode nearest the cortical surface.

Figure XVIII-8 shows some potentials obtained from the two extreme wires of the multiple electrode under three different conditions: (a) spontaneous activity; (b) single clicks, 1/sec, VDL + 30 db; and (c) paired ($\Delta t=75$ msec) clicks, 1/sec, VDL + 30 db. The recorded traces show:

(a) Responses to successive identical stimuli as seen on a single channel (1 electrode) are not identical, even during the first 80 msec after stimulus presentation. At later post-stimulus times, there is still greater variation in response waveforms.

(b) Traces recorded on different channels (that is, at different depths) in the response to a given stimulus may also vary, but there is little difference between traces in the absence of stimuli.

During stimulation, considerable difference is observed between two different depths. In Fig. XVIII-8 the early classical evoked response is opposite in polarity in the two channels (the two electrodes are presumably straddling the fourth layer of cortex). At later times, after stimulus presentation, the differences between the two channels become prominent and varied.

A tentative interpretation of these observations might be that during spontaneous activity the auditory cortex is largely passive; but after stimulation, however, different time-variant local processes arise, and are observed by our multiple electrode.

Attempts to quantify these observations by crosscorrelating two channels like those seen in Fig. XVIII-8, have, thus far, not been successful. These traces exhibit small variance during the classical evoked response. Since this part of the trace contributes substantially to the crosscorrelogram, it tends to "mask" effects that arise at later post-stimulus time.

T. L. Williams, Jr., G. L. Gerstein

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C. LATERALIZATION OF CLICKS OF OPPOSITE POLARITY

If identical clicks are delivered simultaneously to the ears of a listener through earphones, he reports that he hears a single click whose apparent source is in the center of his head. By changing the timing and relative intensities of the clicks, the source can be moved laterally across the head (1,2). It has generally been assumed that lateralization judgments are based upon comparisons of the neural signal from one ear with that from the other.

The way in which the N_1 response in cats depends on the polarity of the clicks has been studied (3) recently. Although at low intensities the responses to rarefaction and condensation clicks are nearly identical, at high intensities the latency of the N_1 response to a rarefaction click is approximately 0.2 msec shorter than that for a condensation click. If a similar difference in latency occurs in man, we should be able to observe its effect on lateralization judgments when condensation clicks are presented to



Fig. XVIII-9. Block diagram of experimental apparatus.

one ear and rarefaction clicks to the other. In particular, we might predict that at high intensities the condensation click would have to occur before the rarefaction click to produce a centered apparent source. We have conducted some experiments to test this prediction.

Figure XVIII-9 shows a block diagram of the experimental apparatus. The pulse generator is triggered at a rate of 10/sec and feeds pulses into two adjustable delay units, one of which is under the control of the subject. The delayed pulses trigger pulse generators that produce rectangular pulses of 0.1-msec duration. These pulses are amplified and led through calibrated attenuators and reversing switches to the earphones. The attenuators are adjusted to give equal amplitude outputs. The reversing switches are set so that the pulses delivered by channel 1 are opposite in polarity to those delivered by channel 2. The subject sits in a soundproof chamber. In addition to the delay control, he operates a commutating switch that reverses the connection of the two channels to the earphones. If the apparent source is at the right of center, changing the position of the commutating switch moves it to the left; if the apparent source is centered, commutation produces no motion.

In our experiments the subject was instructed to adjust the delay setting until commutation produced no motion of the source. When this setting had been made, the subject signaled the experimenter, and the time interval between the two pulses was recorded. To compensate for possible unbalance between the two channels, judgments were made, first, with channel 1 delivering positive pulses and channel 2 negative pulses, and then the pulse polarities were reversed. The two measured intervals were then subtracted to eliminate any effects of unbalance. Figure XVIII-10 shows histograms of the resulting time difference for the judgments made by one subject at 6 different intensities. The mean and standard deviations of the distributions are also indicated. A significance test indicated that the sample means are significantly different from zero



Fig. XVIII-10. Histograms of time differences for judgments of source in median plane. The time difference $(\Delta t)_1$ was measured, with channel 1 producing a rarefaction click, and channel 2 a condensation click. When pulse 1 preceded pulse 2, the time interval was defined as positive. The pulse polarities were then reversed and a determination of $(\Delta t)_2$ was made with the same sign convention used. $(\Delta t)_2$ was then subtracted from $(\Delta t)_1$, and the difference was plotted along the horizontal axis. Time intervals were quantized in 10-µsec intervals. Psychophysical threshold was 0 db. (100 db corresponds to 5 volts across to the PDR-10 earphones.) (Subject: T. H.)

at the 1 per cent level for intensities 60 db and 70 db above threshold, but not for lower intensities. The sign of the time difference for high intensities is such that the condensation click needs to occur before the rarefaction click, in order to produce a centered source.

Both the direction of the time difference and its dependence on intensity agree with the prediction. There is a considerable discrepancy in the size of the time differences, however. The time difference necessary to produce a centered source for this subject is approximately 25 μ sec (half the value shown in Fig. XVIII-10), whereas the latencies of the peak of the N₁ response in cats differ by approximately 200 μ sec at high intensities.

This discrepancy is not too surprising. Psychophysical experiments have suggested (1,2) that the lateralization judgment involves much more than a simple measurement of the latency difference for peaks of N_1 , and the electrophysiological data (3) show that although the N_1 latency difference is the most striking phenomenon, high-intensity condensation and rarefaction click responses differ in several other ways. Also, there is no reason for assuming that the differences in neural latencies are exactly alike in feline and human cochleas.

Our experiment will be repeated on several subjects.

R. C. Beal, T. N. Hastings, J. L. Hall II, W. T. Peake

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D. THE LATENCY OF THE HUMAN ELECTROMYOGRAM IN RELATION TO REACTION TIME

The time required for a subject to respond to sensory stimuli (reaction time) might be divided into components as follows:

(a) Time from onset of stimulus to onset of an evoked cortical response;

(b) time from onset of evoked cortical response to onset of cortical activity leading to muscular activity – this may be called the central information processing time;

(c) time from onset of this motor cortical activity to onset of electrical activity in the muscles involved in the motor response; and

(d) time from onset of the electrical activity in the muscle to the instant at which the motion begins.



Fig. XVIII-11. Scheme for dividing reaction time into component intervals.



- Fig. XVIII-12. Muscle potential of extensor digitorum communis. Trace starts at onset of the stimulus. (a) Stimulus 65 db above threshold.
 (b) Stimulus 15 db above threshold. (c) Stimulus 5 db above threshold. The behavioral response consists of raising and lowering the index finger. The second deflection in the traces results from lowering the finger.
- Fig. XVIII-13. Muscle potential and time markers for EMG and motor response. Trace starts at onset of stimulus. (a) Muscle potential. (b) Stepmarking onset of EMG. (c) Step-marking finger movement (leading edge). The curve of EMG latency versus stimulus intensity is approximately parallel to the curve of reaction time versus intensity.

These intervals can be represented symbolically as shown in Fig. XVIII-11. In the work reported here we have studied the time interval, d.

In our experiments the subject was instructed to respond to auditory stimuli (clicks) by lifting his finger. The finger motion was detected by a photocell that triggered a pulse generator. The electromyogram (EMG) was measured in the extensor digitorum communis with Disa bipolar electrodes (model 13K13). The time interval between the onset of the EMG response and the photocell pulse was measured for various stimulus conditions. These measurements were in the range 20-80 msec, which is of the same order of magnitude as that reported by other workers (1, 2). This time interval is an appreciable fraction of the total reaction time and is about equal to the afferent delay <u>a</u>.

The length of interval \underline{d} was measured as a function of click intensity (3). The subject was stimulated by the clicks at five different intensity levels (above threshold) that were randomly distributed in time and intensity. Preliminary results indicate that the interval \underline{d} is not a function of intensity. Figure XVIII-12 shows averaged responses for three different click intensities. Averaging was done on the ARC-1 computer. Figure XVIII-13 shows the steps generated at the onset of the EMG, and by the photocell pulse generator in relation to the EMG waveform.

D. Sashin, J. Allen

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E. EFFECT OF MASKING ON THE PITCH OF PERIODIC PULSES

[This report is a summary of an S. M. thesis submitted to the Department of Electrical Engineering, M.I.T., May 1960. The experiment was performed in the Visual and Acoustics Research Department of Bell Telephone Laboratories, Inc., Murray Hill, New Jersey, under the supervision of J. L. Flanagan and N. Guttman, and under the auspices of the Cooperative Course in Electrical Engineering.]

It is well known that the pitch perception of complex periodic stimuli is related to both the spectral distribution and the temporal characteristics of the signal. It has been demonstrated by a number of experimenters that a judgment of low pitch associated with the periodicity of a stimulus can be elicited, even if there is no spectral energy present in the stimulus at this low frequency.

Flanagan and Guttman (1) have recently performed pitch-matching experiments. Their stimuli were periodic trains of rectangular pulses having various repetition rates and polarity patterns. In their experiments, an A signal, fixed in repetition rate and polarity pattern, is presented to a listener through headphones. A B signal is also presented to the listener; this signal has a fixed polarity pattern but variable repetition rate. The listener is required to match the pitch of B to that of A by varying the repetition rate of B. A similar experiment was performed in which the A signal was fed through a highpass filter so as to reject the fundamental. For pulse repetition rates below approximately 150 pps, listeners essentially match the pulse repetition rate of B to that of A. For fundamental frequencies higher than approximately 150 cps, listeners match the fundamental frequency of B to that of A, even if the fundamental has been removed from A by filtering. There are thus two kinds of judgments, based on periodicity properties of the signal. The first set of pitch judgments seems to be based on pulse rate, while the second set seems to be dependent on what might be called "pattern rate." When the fundamental of B is higher than approximately 800 cps, listeners match it to the lowest component present in A. For repetition rates in the transition region between matches based on pulse rate and matches based on pattern rate, listeners find it difficult to made a judgment.

The present experiment is concerned with the following phenomenon: The pitch of an A signal whose repetition rate is in the transition region can be altered by partially



Fig. XVIII-14. Pulse patterns and associated line spectra. The pulses are nearly rectangular across the earphones (Permoflux PDR-8). The pulses are maintained at 20-µsec half-amplitude width to ensure uniform spectral height, at least up to the earphone cutoff (approximately 7000 cps).

masking the signal. Highpass noise (1000 cps) will mask the "buzz" quality of A associated with the pulse-rate judgment, and favor a pattern-rate judgment. Conversely, lowpass noise (1000 cps) will mask the "tonal" quality of A associated with the patternrate judgment, and favor a pulse-rate judgment. The masking stimulus need not be highpass or lowpass noise. Under certain conditions, narrow bands of noise and sinusoids are equally effective. The most effective maskers seem to lie in the vicinity of 5000 cps for masking pulse-rate pitch, and in the vicinity of 500 cps for masking patternrate pitch. Narrow bands of noise, or sinusoids, centered below 200 cps, seem to have little masking effect.

The principal experiment used in the study of this phenomenon involved 4 subjects, a significant number of stimuli, and a variety of experimental conditions. To limit the complexity of the experiment, only highpass and lowpass noise bands were used as maskers. The pulse patterns and their spectra are displayed in Fig. XVIII-14. The pulses are presented at a constant amplitude that corresponds to a sensation level between 30 db and 35 db. The following combinations (Fig. XVIII-14) are used for each stimulus condition:

Pattern combination 2-2 is included as a control.

Pulse repetition rates are chosen so that the A signals produce judgments in the region of transition between pulse-rate and pattern-rate matches under the condition of no masking. The repetition rates are listed below.

Pattern 2		Pattern 3		
Pulse Repetition Rate (pps)	Fundamental Frequency (cps)	Pulse Repetition Rate (pps)	Fundamental Frequency (cps)	
102	51	164	41	
164	82	262	65.5	
262	131	419	104.75	
419	209.5	671	167.75	

The following stimulus conditions were studied:

I. No noise.

II. No noise – fundamental of A rejected.

III. Highpass, lowpass. Noise added to A so that a signal-to-noise ratio, defined as the ratio of the rms level per component of the signal to the spectrum level of the noise, remains constant.

IV. Highpass, lowpass. Noise added to A at a constant rms level.

V. Highpass, lowpass. Noise added to A at a constant rms level – fundamental of A rejected.

VI. Highpass, lowpass. Noise added to both A and B at a constant rms level.

The bandpass noise alone has a sensation level of approximately 40 db for the constant rms level of conditions IV, V, and VI. In condition III, the noise level remains within ± 10 db of 40-db sensation level. There are 16 stimuli per stimulus condition, which gives a total of 160 stimuli. Each subject makes 4 judgments per stimulus.

Despite the variety of stimulus conditions, the results do not vary significantly except with respect to the major masking conditions – no noise, highpass noise, and lowpass noise – and with respect to different pattern combinations. In general, the results are just as described in the introductory paragraph. However, whether a masker is used to bias the judgments or not, it appears that pattern-rate matches cannot be made for pattern rates below 50 cps, and pulse-rate matches cannot be made for pulse rates above 300 pps. The effect of masking, showing the extent of the bias, can be seen in the scatter plots of Fig. XVIII-15. This figure gives results for pattern combination 2-1 under stimulus conditions I, IV (Lowpass), and IV (Highpass). It should be emphasized that rejection of the fundamental of A had no observable effect on the results within the range of experimental stimuli used.

Partial masking of a periodic pulse signal in the transition region produces pitch



Fig. XVIII-15. Scatter plots showing effect of masking: (a) no noise; (b) lowpass noise (1000 cps); and (c) highpass noise (1000 cps). Each group of columns represents a stimulus; each column represents a subject; each point represents a single judgment. A horizontal line segment represents an ideal match for the scatter of judgments associated with it. Diagonals are drawn to connect a class of ideal matches. The two classes shown are pulse rate (PR), and pattern rate (f_1) .

judgments that depend on the frequency of the masker. We conclude, then, that for this range of stimuli a reasonable model associates significant pattern-rate pitch information with low-frequency "auditory channels," and associates significant pulse-rate pitch information with high-frequency "auditory channels." The "residue" phenomenon, described by Schouten and others, identifies the high-frequency auditory channel with the perception of the "residue" pitch. In the present experiment, this associated with pattern-rate pitch. However, these lower frequencies lie above the fundamentals of these signals.

A. E. Rosenberg

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F. CORTICAL RESPONSES TO AUDITORY STIMULI IN THE GUINEA PIG

Responses from the auditory cortex of the guinea pig have been studied in order to provide basic data for future work with this animal, and for cross-species comparisons. A series of experiments was performed in which stimulus parameters were systematically varied, and some studies were undertaken to develop techniques for future work with anesthetized and unanesthetized guinea pigs.

The animals used were young guinea pigs, each of which weighed approximately 250 grams. Dial anesthesia (0.5 cc/kg), or nembutal (35 mg/kg), was administered intraperitoneally. In the guinea pig there is only a narrow margin between surgical anesthesia and death; hence great care must be taken in administering the drugs. Stimuli were delivered to an earphone coupled to the animal by a tube inserted loosely into the external auditory meatus, contralateral to the exposed cortex. Responses were recorded from the intact dura with the use of macroelectrodes (either monopolar or coaxial). Since cortical responses are variable in amplitude, it was necessary to average many responses to make quantitative amplitude measurements, and to detect small evoked responses in the presence of background activity.

The presentation of an intense click to the ear of the guinea pig results in a large evoked response at the auditory cortex that is clearly distinguishable from background activity. This response varies with respect to location on the cortex, physiological state of the animal, and stimulus parameters. These responses, when recorded from the dura, have a well-known waveform: a surface-positive component followed by a surface-negative component. The peak-to-peak amplitude of the largest responses recorded was approximately 1.5 mv. The latency of the surface-positive peak from the



Fig. XVIII-16. Averaged cortical responses for several stimulus intensities.



Fig. XVIII-17. Averaged responses for several levels of masking noise.



Fig. XVIII-18. Averaged responses to two clicks for several values of Δt .

instant of delivery of the electric pulse to the earphone was approximately 15 msec. These latencies are similar to those observed in the cat, but the amplitudes exceed those observed in the cat by a factor of 2 or 3.

The large voltages of these cortical responses suggested that suitable records could be obtained from the intact skull (1). In this way, cortical damage can be avoided, and a preparation obtained that permits detection of responses to auditory stimuli from the intact animal. Such records were actually obtained from one guinea pig.

The amplitude and latency of cortical responses varied systematically with the intensity of the click stimulus. Figure XVIII-16 shows superimposed responses to clicks for several intensities. Each trace represents an average of 64 responses. The amplitude decreases and the latency increases when the stimulus intensity is decreased; this has been found previously for the cat and other mammals (3).

Figure XVIII-17 demonstrates the effect of masking noise on responses to intense clicks. Note that again, as in the cat, both amplitude and latency are affected (2).

Using pairs of clicks as stimuli, we studied the responses to the second click as a function of the interval Δt between the clicks. Specifically, we were interested in the amplitude of the response to the second click as a function of Δt . To ensure reasonable independence of responses to successive pairs, the rate of presentation chosen was 1 pair every 2 seconds; Δt ranged from 25 msec to 200 msec. Superimposed traces of the responses, demonstrating the growth of the second response as Δt increases from 80 msec to 200 msec, are shown in Fig. XVIII-18. No response to the second click was detectable for Δt less than approximately 80 msec.

This study has demonstrated that virtually all of the phenomena found for evoked cortical responses in the cat are present in the guinea pig.

R. G. Mark

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