

XII. COMMUNICATIONS BIOPHYSICS

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A. RESPONSES FROM THE AUDITORY CORTEX TO TONE PIPS AND BURSTS OF NOISE – AN INTERPRETATION IN TERMS OF THE PLACE AND FREQUENCY PRINCIPLES

Electric recordings from the auditory nerve indicate that a low-frequency pure tone gives rise to synchronous bursts of neural firing at the frequency of the tone ("frequency-following") and that there is also specificity of individual auditory nerve fibers (place). Tonotopic organization has been demonstrated in the auditory cortex of many animals for evoked responses to the onsets of tone bursts. The question may be asked: Does the tuning for pure tones at the level of the auditory cortex reflect both mechanisms, i. e., frequency-following and place that are found in lower parts of the auditory nervous system?

A pure tone has only one frequency component in its spectrum. Its "repetition rate" is the frequency of this single component; therefore changing the frequency necessarily changes both the spectrum and the repetition rate. Since it is difficult to study the place and frequency mechanisms independently with a tonal stimulus, we have also used other types of periodic stimuli, namely, bursts of white noise and bursts of chopped noise. All these stimuli had identical envelope shape, rise-fall times of 10 msec, and a burst duration of 200 msec (see Fig. XII-1).

When the stimulus is a burst of chopped noise and the recording electrode is placed near the round window, synchronized neural impulses are recorded in response to each blip of noise within the burst envelope. Thus our requirement that the auditory nerve respond at the chopping rate of the noise is met.

In order to obtain sharply tuned response curves for low-frequency locations in the auditory cortex, we used Tunturi's method (1) of recording from small strychninized filter-paper patches placed on the cortex with the evoked strychnine spike as criterion for response. The intensity at which responses are evoked for 50 per cent of the

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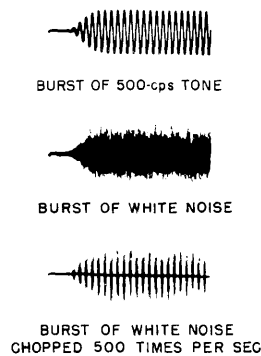


Fig. XII-1. Onset of stimulus waveforms: burst of tone, burst of noise, and burst of chopped noise; rise time, 10 msec.

stimulus presentations is taken as the threshold intensity.

There are two distinct low-frequency areas in the cat's auditory cortex. Both these areas were studied by comparing the threshold-versus-frequency curves for tonal and chopped noise stimuli. (See Fig. XII-2.) The flat response curves for chopped noise indicate that there is no "tuning" for repetition rate at either the A I or the A II locations. Since the spectral distribution of noise is unchanged by chopping, these results indicate that the frequency mechanism

does not play a role in the "tuning" for pure tones at the level of the auditory cortex. In another experiment, threshold curves were first obtained for responses from a low-frequency A II location to both bursts of tone and bursts of chopped noise (Fig. XII-3a). Then with unchopped noise as the stimulus, threshold curves were run for different frequency settings of a high-pass filter (Fig. XII-3b). As the spectral components in the frequency range that is capable of eliciting the response are attenuated, the threshold rises. Thus the threshold remains unchanged when the repetition rate is varied but is markedly affected when the relevant spectral components are attenuated.

The preceding results demonstrate that if "place pitch" and "periodicity pitch" for low frequencies are brought together at one place in the nervous system, it is probably not at a stage leading to the auditory cortex. There is actually no a priori reason to assume such a simple correspondence between pitch judgments and neural events.

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References

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B. PITCH JUDGMENTS FOR REPEATED BURSTS OF TONE AND NOISE

Recently, much interest has been shown in the study of pitch judgments for complex auditory stimuli (1, 2, 3, 4). In the present investigation, four subjects were instructed to judge which of a pair of stimuli sounded higher in pitch. A choice was required following each pair. One stimulus, the standard, of every pair had a repetition rate of 200/sec; the variable stimulus had a repetition rate that ranged from 175/sec to

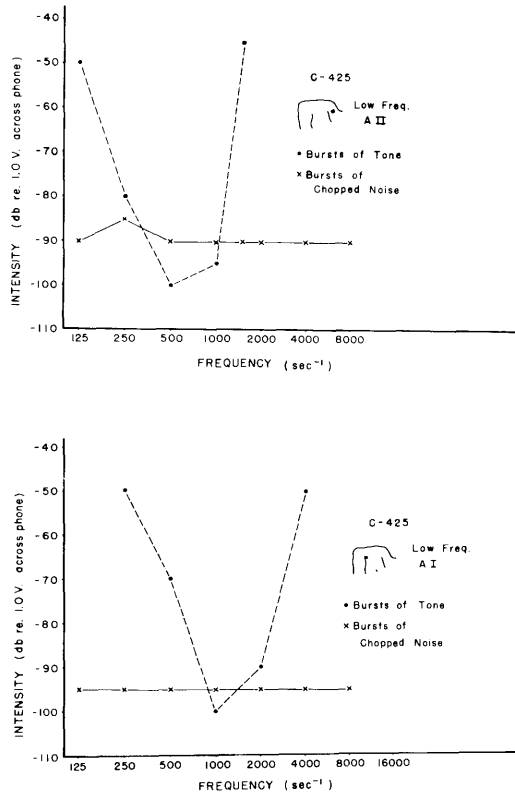


Fig. XII-2. Response curves for two low-frequency areas, using onsets of pure tones and chopped noise. Inset shows electrode location on cortex. The upper half is for a low-frequency A II region; the lower half is for a low-frequency A I region.

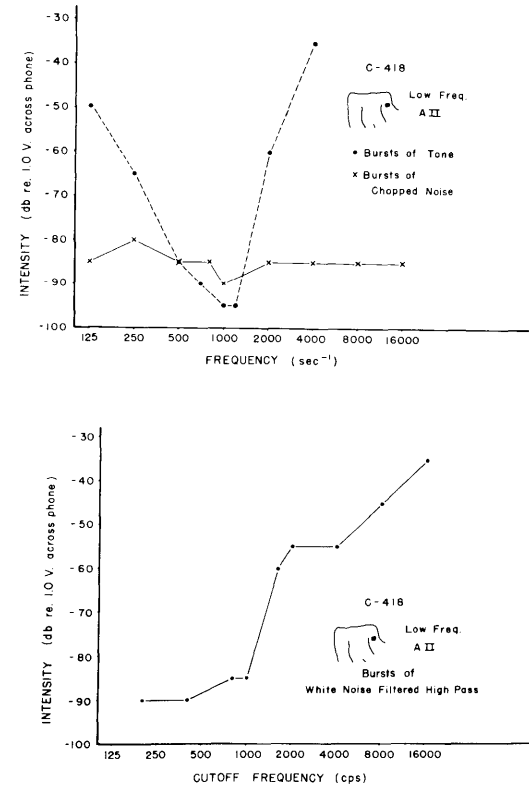


Fig. XII-3. Threshold as a function of the filter setting. In the upper half: threshold versus frequency curves for a low-frequency A II point. Inset shows electrode location on cortex. In the lower half: threshold-versus-cutoff frequency of high-pass filter. Stimulus is filtered unchopped white noise. Electrode location is the same as for Fig. XII-3a.

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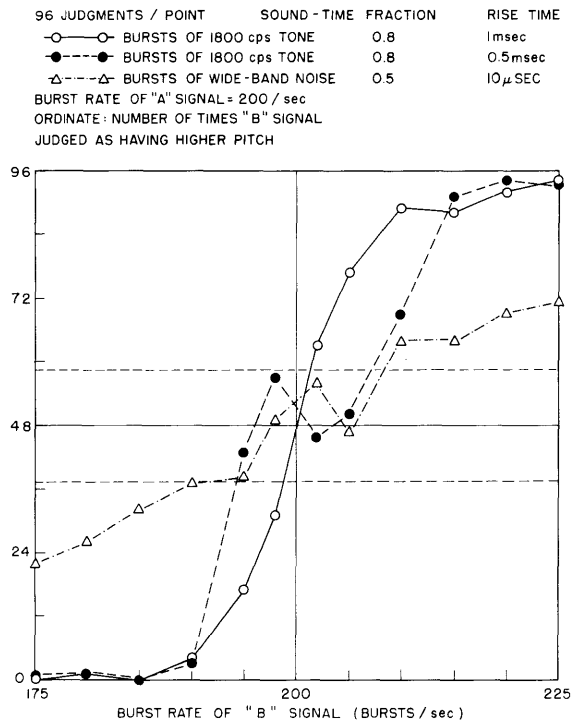


Fig. XII-4. Total of judgments from four subjects in "forced-choice" experiments concerning pitch of repetitive bursts of tone and noise. If judgments were produced by a series of Bernoulli trials, the alternate judgments having 0.5 probability, the probability of points falling outside the dashed lines is less than 1 per cent.

225/sec. Within a given pair the stimuli differed with respect to modulation rate. The results of three experiments are reported: in two experiments the stimuli were bursts of 2000-cps tones with different rise times; the third experiment involved bursts of wideband noise. For repetition rates in the vicinity of 200/sec, the difference limen for burst rate is smaller for bursts containing tonal stimuli than for bursts of wideband noise. The summed judgments of four subjects are given in Fig. XII-4.

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References

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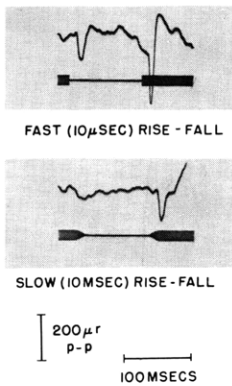


Fig. XII-5. Cortical "off" responses and stimulus decay time. The sweep is adjusted so that the end of the stimulus burst is displayed at the beginning of the trace; this is followed by a period without stimulation, followed by the onset of another burst. "Off" responses are thus seen at the left of each trace, followed by an on-response at the right. The top traces in each pair represent the electrocortical activity, while the bottom trace represents the stimulus waveform. Stimulus conditions are: intensity, -70 db re 1 volt across phone; duration, 900 msec; repetition rate, 1/sec; frequency of pure tone, 4 kc. (Optimum tuning frequency of cortical point, 4 kc.)

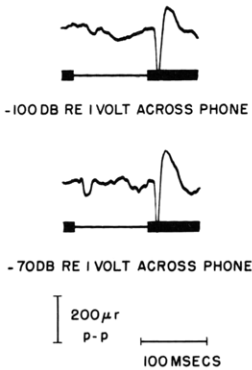


Fig. XII-6. Cortical "off" responses for two stimulus intensities. The recording and stimulating conditions are substantially the same as in Fig. XII-5, except for stimulus intensity, which is being varied, and rise-fall time, which is abrupt.

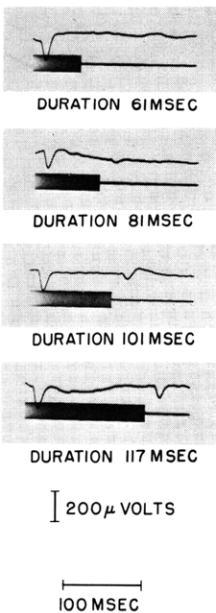


Fig. XII-7. Cortical "off" responses for different stimulus durations. In these pictures, the onset of the stimulus coincides with the start of the sweep. Stimulus conditions are: intensity, -70 db re 1 volt across phone; rise-fall time, fast; repetition rate, 1/sec; frequency of pure tone, 4 kc. (Optimum tuning frequency of cortical point, 1250 cps.)

C. "OFF" RESPONSES IN THE AUDITORY NERVOUS SYSTEM OF ANESTHETIZED CATS

When acoustic stimuli of more than 0.1-sec duration are turned off, electric responses at cortical and peripheral locations are frequently recorded. Several observations suggest that these "off" responses are related to acoustic transients. Certain conditions under which cortical "off" responses to transients occur were determined.

When the stimuli are bursts of tone and the recording electrode is located on the auditory cortex, the following stimulus parameters were found to influence the occurrence of "off" responses: (a) stimulus decay time (Fig. XII-5); (b) stimulus intensity (Fig. XII-6); (c) level of masking noise; (d) stimulus duration (Fig. XII-7); and (e) frequency of the pure-tone stimulus as related to the particular location of the electrode (Fig. XII-8). These results can be interpreted in terms of the refractory characteristics of groups of neurones. Since the auditory cortex is tonotopically organized, a weak pure tone of a given frequency stimulates only a restricted portion. A large proportion of the available auditory cortical neurones remains inactive throughout the burst and is therefore in a responsive state when the transient, with its wide spectral distribution, occurs at the end of the burst. Masking noise tends to reduce the number

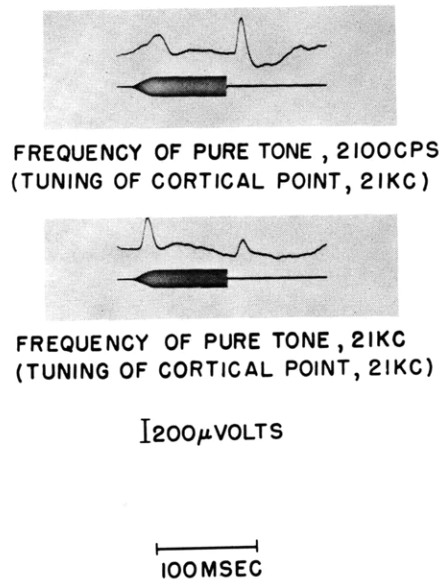


Fig. XII-8. Cortical "off" responses and frequency of pure tone stimulation. To demonstrate this effect of frequency, it was necessary to use a concentric electrode whose tip penetrated 2.2 mm into the cortex while the sleeve rested on the surface of the cortex. Stimulus conditions are: intensity, -60 db re 1 volt across phone; rise time, 20 msec; fast fall; duration, 100 msec; repetition rate, 1/sec.

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Fig. XII-9. "Off" responses to noise. We have not been able to obtain "off" responses to noise. Note the prominent on-response. Stimulus conditions are: intensity, -70 db re 0.355 VRMS across phone; rise time, 200 msec; fast fall; duration, 100 msec; repetition rate, 1/sec; burst of white noise.

of available neurones. This interpretation is strengthened by the fact that bursts of noise under all conditions that were examined result in no "off" responses (Fig. XII-9). Presumably, noise activates most of the available neurones in the auditory cortex, leaving few in a nonrefractory state at the time at which the "off" transient occurs.

When these tone bursts are presented to human listeners, a click is heard under those stimulus conditions that are accompanied by an "off" response in some part of the auditory cortex in cats. No click is heard when bursts of noise are turned off.

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