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**Unit Responses in the Rat Cochlear Nucleus
to Repetitive, Transient Sounds**

By

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Abstract

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The response patterns are described of cochlear nucleus units (termed rat transient units) which only responded to a tone burst with a single discharge evoked immediately after the onset. When these cells were stimulated with bursts of repetitive clicks such units showed a marked selectivity to the click repetition rate. At a low click repetition rate one discharge was evoked for each click but this one to one relationship failed rapidly when the click rate was increased slightly above a given click repetition rate. Any additional increase in click rate resulted in only a single discharge fired immediately after the onset of a click burst and thus resembling these units' response to tone bursts. By replacing the click sounds by short bursts of pure tones presented repetitively it was shown that rat transient units were not selective to repetition rate *per se*, but rather, to the duration of silent interval between successive sounds. The activity of these units to click stimulation could be inhibited by broad band noise or by pure tones within certain frequency limits. Furthermore, these units showed a spectral selectivity which appeared when the stimulation was pure tones or band-pass filtered clicks. The spectral region of highest sensitivity varied among the individual units in the range from 5 to 20 kHz and was thus widely different from the critical repetition rate for click stimulation. The latter rate was found to vary from 200 to 800 clicks per second in different units.

These findings may thus explain why, in psychoacoustic experiments, repetitive presentation of short sounds results in a pitch perception which is dependent on the length of the silent period *between* successive sounds.

It was recently found that certain units in the cochlear nucleus of the cat only respond to the onset of tone bursts (Kiang 1965, Pfeiffer 1966). Those authors named the neurons "on units". Similar units have been encountered in an electrophysiological study of the cochlear nucleus of the rat (Møller 1969). The aim of the present paper is to critically analyze the responses of these units to different types of repetitive, transient sounds and to present new interpretations relating these neurophysiological data to certain psychoacoustical observations on pitch discrimination.

Methods

The type of experimental animal (rat) and the technical procedures have been described previously (Møller 1969). In the present study the temporal pattern of unit activity is illustrated by a "dot display" (Haapanen *et al.* 1955) and by post stimulus time histograms.

In the dot display each spike is represented by a dot placed along a horizontal time axis which is triggered when the stimulus starts. The responses to succeeding stimuli are displayed in horizontal and parallel rows and then recorded on slowly moving film (see Fig. 1). Post stimulus time histograms were computed from the responses to 256 stimuli with the aid of a TMC "Computer of Average Transients" (type 400 A). The resolution of the time scale was equal to the channel width of the analyser and usually was set at 156 μ sec. Each of the computer's 400 channels thus occupied 156 μ sec. (The channel width is often named "bin width"). The results of this type of analysis were displayed on an oscilloscope and photographed. The readability of these displays was improved by superimposing a 5 kHz triangle wave on the vertical deflection of the oscilloscope. The resultant display so obtained consisted of lines instead of dots (*cf.* Fig. 2).

As to the stimulus, repetitive click sounds were generated by applying short rectangular pulses (duration 30 μ S) from a Grass S4 stimulator to the condenser microphone (B & K 4131). The latter was used as sound source. A Wavetek type 116 generated a selected number of cycles of pure tones.

Results

On the basis of their response patterns, the recorded units (total number 214) in the rat cochlear nucleus could be divided into two groups. One group of units (170 cells—called *sustained units*) responded to continuous sounds with a sustained train of discharges which lasted as long as did the sound (when the sound intensities ranged from values slightly above to well above threshold). Another group of units (44 cells) only responded with a single discharge to stimulation with tone bursts. The discharge followed immediately after the onset of the stimulus. In the following these latter units will be called *transient units*. Both types of units showed a tone frequency selectivity. The transient units had a much higher threshold and broader tuning curves than the common sustained units. The transient units were found both in the dorsal and ventral cochlear nucleus with an apparant preponderance in the dorsal nucleus. None of the transient units showed any spontaneous activity.

The response pattern of transient units to stimulation with repetitive clicks (produced by applying 50 msec long bursts of rectangular pulses with a duration of 30 μ S to the condenser earphone) revealed certain interesting properties. Fig. 1 shows the time pattern of the discharges to click stimulation of a sustained unit (left column) and that of a transient unit (right column). The click repetition rate is shown by inserted legend numbers. Each discharge is represented by a dot and each horizontal row of dots represents one presentation of repetitive clicks. As seen, the discharges of the sustained unit fuse when the repetition rate is increased, whereas each response of the transient unit correspond in time to the click stimuli. The failure to respond to clicks with high repetition rates of this type of unit is also evident. It is seen that the precise one to one relation between stimulus and response is first lost towards the end of the stimulus presentation when the click repetition rate is slightly increased above the range where this one to one relationship exist. When the click rate is further increased the unit fails to respond during successively larger segments of the stimulus duration until only a single spike remains at the beginning of each presentation.

The functional differences and similarities between the two types of units is further illustrated in Fig. 2. These "post stimulus time histograms" relate the temporal

Rat 63.6

Rat 65.1

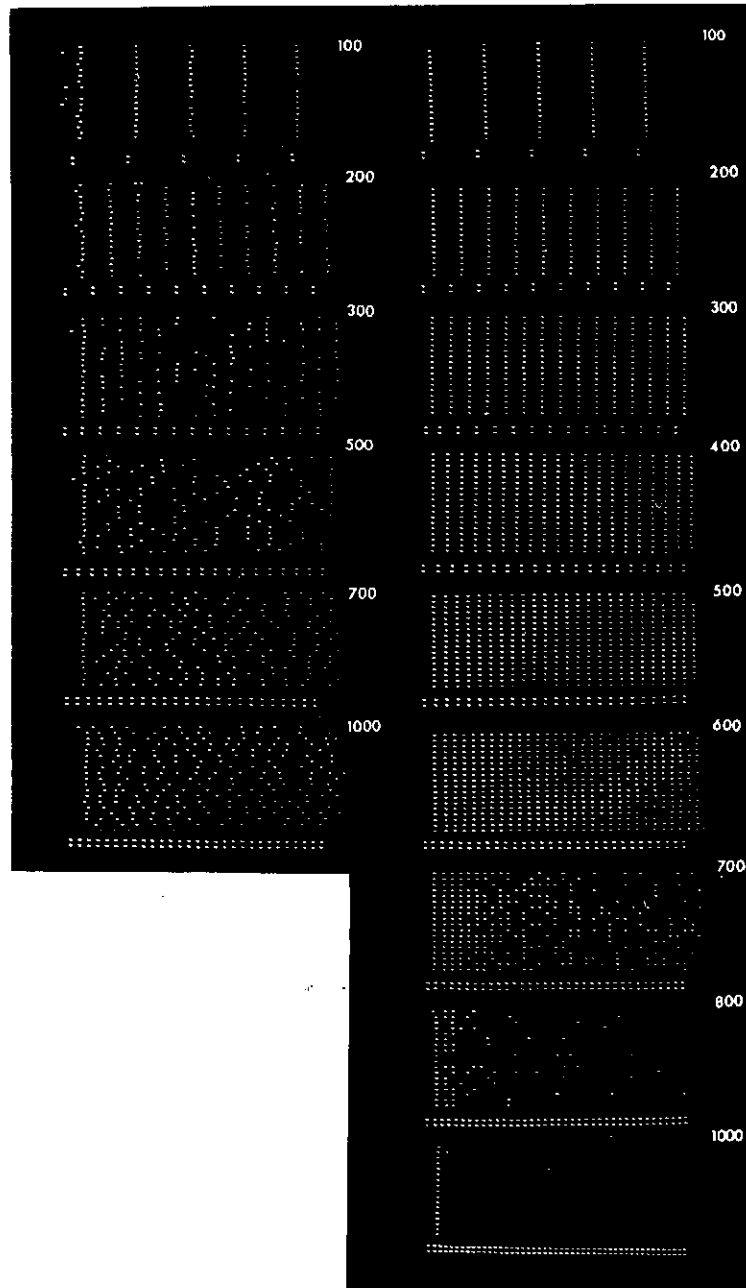


Fig. 1. Responses to 50 msec bursts of repetitive clicks of a sustained unit (left column) and a transient unit (right column). Each dot shows the occurrence of a nervous discharge. The repetition rate of the clicks is indicated by the inserted numbers and the individual clicks are shown by the double dots below each recording sequence.

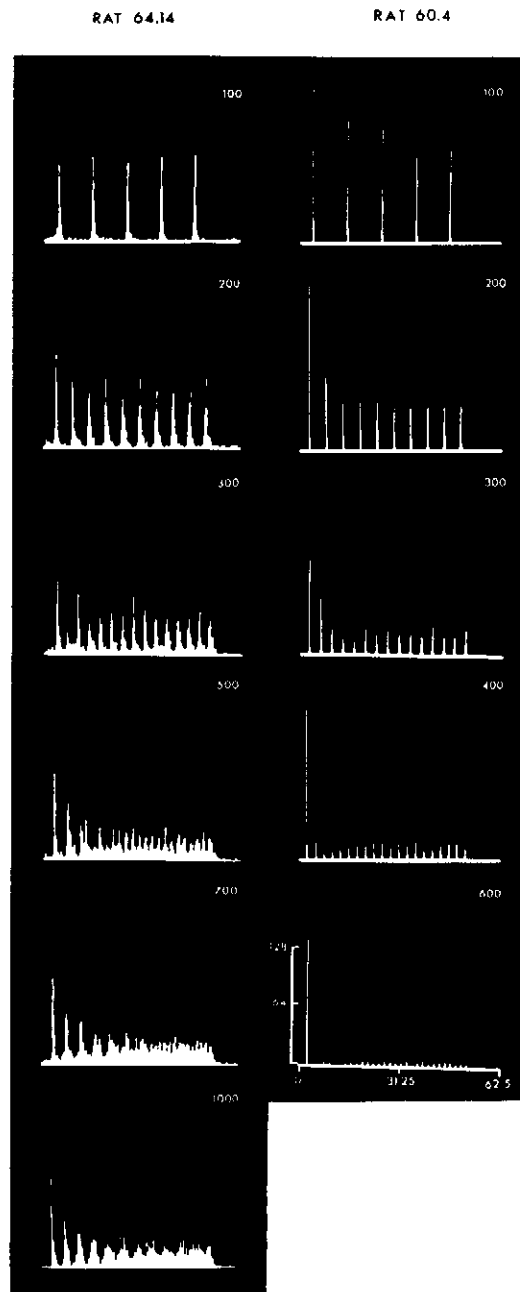


Fig. 2. Post stimulus time histograms of responses to 50 msec bursts of repetitive clicks with various repetition rates. As in Fig. 1, the left column of recordings is from a sustained unit and the right column are recordings from a transient unit. The click repetition rate is indicated by inserted legend numbers on each graph. The scale in the lower right recording gives the time in msec on the horizontal axis and the number of spike counts are given on the vertical axis. Each histogram represents the responses to 256 stimulus bursts.

distribution of spikes in response to clicks of various repetition rate obtained from a sustained unit (left column) and that of a unit of the transient type (right column). The click repetition rate is given by legend numbers. Similarities between the two types were noted when both were stimulated with clicks of low repetition rates, whereas the responses differ markedly when higher click rates are used. As seen there is a precise timing of the responses of the transient unit whereas the responses of the sustained unit fuses above a certain click repetition rate. The majority of the responses of the transient unit falls within one channel of the analyser or is shared between two channels, while the responses of the sustained unit is spread out over several channels.

The "repetition rate selectivity" of four typical transient units is illustrated in Fig. 3 A—D. The stimulus consisted of repetitive clicks with various repetition rates delivered in bursts of 50 msec duration. The responses to the same type of stimulation of two sustained units is shown in Fig. 3 E and F. In all six graphs the average number of discharges during the stimulus duration was plotted as a function of click repetition rate. The individual curves for each unit represent different sound intensities with 10 dB between each curve. The dashed lines in Fig. 3 A and B show what the response would be if each click evokes one discharge. The discharge rate of all the transient units (A—D in Fig. 3) is seen to depend strongly on the repetition rate of the stimulus clicks. The firing rate of these units equalled the click rate up to a certain click rate. Above this rate, (which varies among individual units), the discharge rate falls rapidly. The rate of decrease in firing rate also varies somewhat in different units. The figure also indicates that the "repetition rate selectivity" becomes less marked when the stimulus intensity is lowered. The firing rate of the sustained units, however, are but dependent on the click rate (Fig. 3 E—F) and the discharge rate only increases slightly with increasing click rate.

The repetitions rate selectivity to clicks of the transient units could be equally well demonstrated by the use of continuous trains of clicks instead of clicks delivered in bursts. The range within which each click is followed by a single discharge is, however, smaller when using continuous trains of clicks than when the clicks are presented in 50 msec bursts. The graphs in Fig. 4 show the mean discharge frequency as a function of click frequency for stimulation with a 10 sec long train of clicks (open circles) and for thirty-two 50 msec long bursts of clicks (filled circles). In both cases the sound intensity was the same (15 dB above threshold).

No difference in response could be seen when the polarity of the electrical pulses applied to the condenser microphone was shifted in order to change the stimulus from compression to rarefaction clicks. Nor was a change in the response pattern obtained when alternating click polarity was used.

When the click stimulation was replaced by a series of short tone bursts delivered at a low repetition rate the transient units responded to each burst with a single discharge. When repetition rate was increased or the duration of the individual bursts prolonged above a certain limit the firing ceases. This selectivity is illustrated in Fig. 5 A which shows the firing rate of a transient unit to short bursts of pure

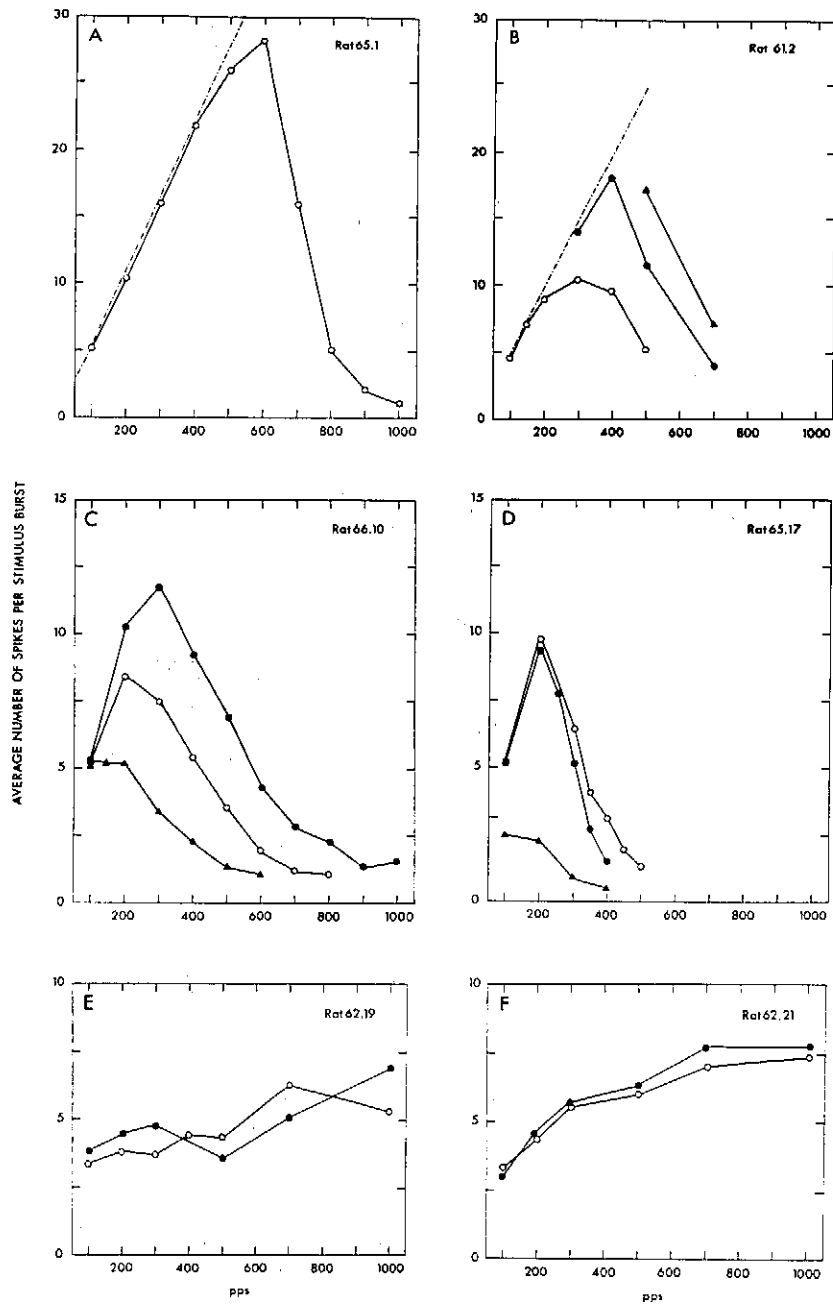


Fig. 3 A—D. Spike counts per stimulus burst as a function of repetition rate for 4 transient units. The average number of discharges is shown as evoked by stimulation with thirty-two 50 msec bursts of repetitive clicks. The individual curves in B, C and D show responses to clicks with different intensity (10 dB difference between each curve). The straight dashed line in the two upper graphs shows the number of discharges which corresponds to one discharge per click.

E and F are similar plots of recordings from two sustained units.

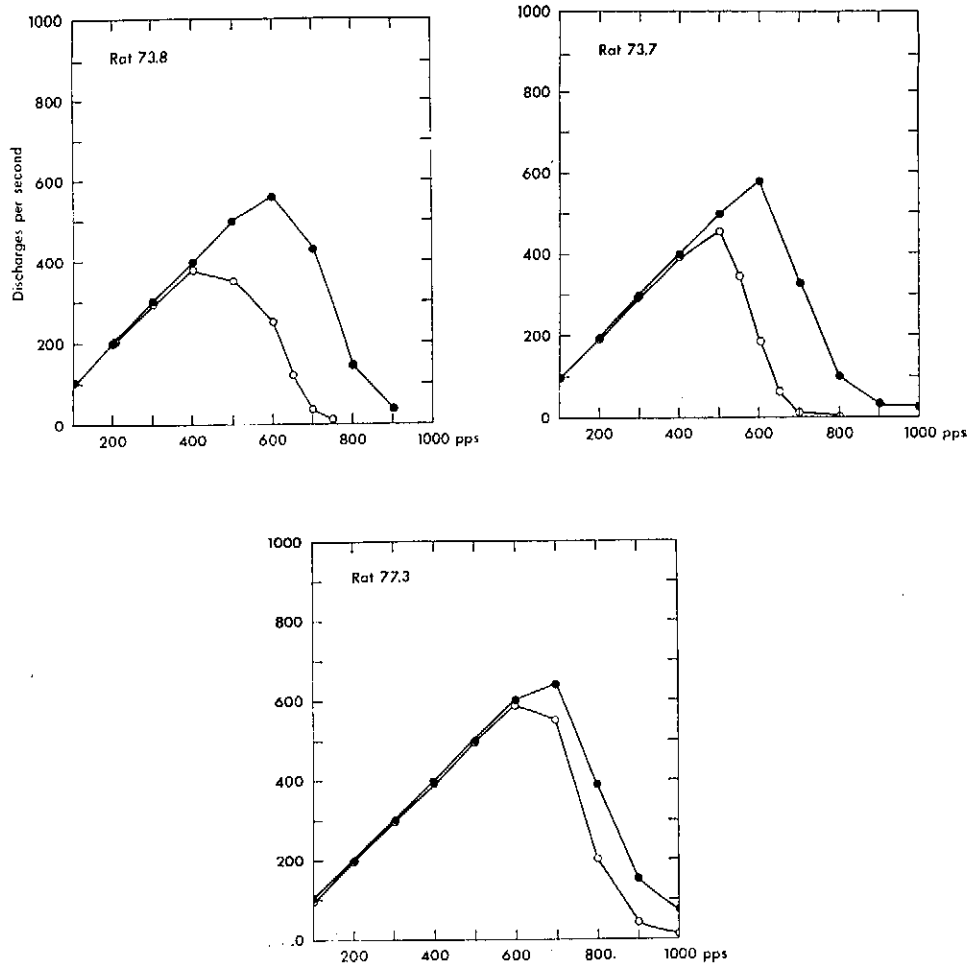


Fig. 4. Response of three transient units to clicks presented in 50 msec bursts (filled circles) and to a 10 sec burst (open circles). The average discharge frequency is shown as a function of the click repetition frequency.

tones presented repetitively as a function of repetition rate with the duration of the sound as parameter. The frequency of the tone was 15 kHz and the duration of the sounds are expressed by the number of full sinewaves which each burst consisted of (8, 16, 32 and 64 waves). The intensity of the sound was 15 dB above threshold.

When the duration of the sound was increased the range of repetition rate in which each sound evoked one discharge decreased. Fig. 5 B shows the average number of discharges which each toneburst evoked as a function of the reciprocal length of the silent period between the individual sound burst. For comparison the responses to click stimulation is also shown (filled circles) and connected with

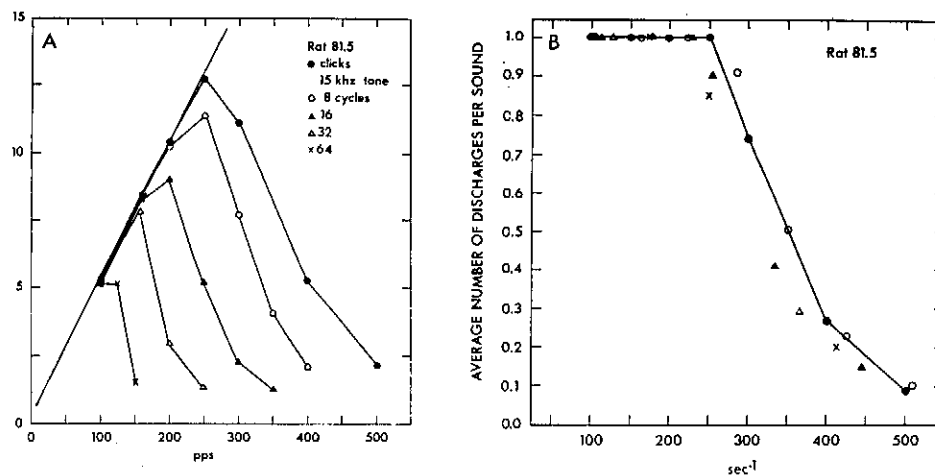


Fig. 5 A. Response to tone bursts of various durations compared to that of clicks. The sounds were presented in 50 msec bursts in the same way as in Fig. 4 and spike counts per burst are shown as a function of repetition rate.

B. The same data as in A but the average number of discharges per each sound is shown as a function of the reciprocal of the length of the silent period between the individual sounds. The same symbols as in A are used. The data points for click stimulation are connected by straight lines.

straight lines. The symbols indicating the durations of the sounds are the same in Fig. 5 A and B. It is apparent that the range in which the unit responded with one discharge depends on the length of silence between successive sounds and this range is almost independent of the repetition rate. Thus these units are not selective to the repetition rate *per se* but rather to the duration of the silent period between successive stimulus sounds.

The responses of the transient units to clicks can be completely inhibited by noise and by pure tones in certain frequency ranges. More specifically pure tones with a frequency immediately below or above the best excitatory spectrum are usually most effective.

Low frequency pure tones (below 1000 Hz) could not elicit any response in transient units nor could tones in which the amplitude was sinusoidally modulated at a frequency in the range in which click bursts elicited a response. It should also be noted that the maximal firing rate of some of these units was more than 700 discharges per sec while the maximal firing rate of sustained units was never more than 400/sec.

Discussion

The units in the rat which only respond to transient sounds are similar or identical to those described by Kiang (1965) and by Pfeiffer (1966) for the cochlear nucleus of the cat. Those investigators, however, did not systematically study the response

to transient sounds. Consequently they did not observe the specificity of these units to the repetition rate of transient sounds (or rather to the interval between individual sounds). Observations on the response pattern of rat transient units are valuable since they may elucidate the mechanisms underlying our ability to discriminate the pitch of certain sounds. It is an open question whether the ability to discriminate pitch is always due to spectral analysis like the one performed by the frequency selectivity of the basilar membrane (place theory) or if, under certain circumstances, it is based on some time pattern analysis accomplished by the nervous system (volley theory). Numerous psychoacoustic investigations indicate that pitch discrimination of at least some sounds cannot be explained by spectral analysis. Thus, for instance, removal of the fundamental frequency of a train of repetitive clicks does not change the judged pitch of the sound (Schouten 1960). This procedure obviously removes the primary prerequisite for a pitch discrimination on a spectral basis, although the distance between individual harmonics still conveys information about the repetition rate of the clicks. Furthermore, recent psychoacoustic investigations have shown that the pitch of periodic clicks of a certain duration is, under some circumstances, related to the duration of silence between these pulses rather than the periodicity of the pulses (McClellan and Small 1965, Rosenberg 1965, Zwillocki 1967). Although the duration of silence may have some weak spectral correlates, other factors make it difficult to explain the phenomenon on the basis of spectral analysis similar to that performed by the basilar membrane. Of additional interest to our findings is that this particular pitch phenomenon is only present at low repetition rates. The rat transient units display response patterns similar to the psychoacoustic finding regarding this particular type of pitch perception. The repetition rate selectivity of rat transient units is not a result of spectral analysis and shows that the discrimination is due to a time pattern analysis. This statement is supported by the fact that shifting the polarity of every second click in a train consisting of clicks of the same polarity did not change the response pattern. The precise timing of the transient units (Fig. 1 and 2) makes it further plausible that these units play an active rôle in the perception of the periodicity of sounds.

There may be a widespread distribution of this type of units through the entire animal kingdom. Roeder (1966) has found similar units located in the mesothoracic ganglion of certain nocturnal moths. He found that some of these "pulse marker" units only respond once for each stimulus and that they needed a certain period of silence before a new response could be evoked. In this context it should be mentioned that in the somatic sensory cortex of cats Mountcastle, Davies and Berman (1957) found a similar type of unit. They called these unit "cut-off" units since they followed the repetitive peripheral stimulation up to a certain rate above which they ceased to respond.

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