

Latency of Unit Responses in Cochlear Nucleus Determined in Two Different Ways

AAGE R. MØLLER

*Division of Physiological Acoustics, Department of Physiology II,
Karolinska Institutet, Stockholm 60, Sweden*

IT HAS BEEN regarded as almost a rule that the latency of unit responses in sensory neural systems decreases with increasing stimulus intensity. This is assumed to be the result of a temporal summation either of generator potential in the receptor and/or an effect of summing EPSP in a neuron receiving synaptic input from the axon leading from a receptor cell (2).

In the periphery of the auditory system, the latency is additionally a function of the units' characteristic frequency (CF) in such a way that the latency is greater for units with low CF than for units with high CF. This dependence of the latency on CF stems from the sensory cells' location along the basilar membrane. Therefore, the time required for the mechanical deflection to travel from the base to a particular hair cell is added to the neural delay. This is naturally most prominent in the fibers of the eighth nerve where the neural delay is short. Units with CF above 2 kHz were shown to have latencies around 1.5 ms, as concerned the first peak in the PST histograms of the responses to click stimulation (4). In the cochlear nucleus, the latency of the responses of units with characteristic frequency above 2 kHz had a negligible dependence on the CF (3). Radionova (11) grouped units in the cochlear nucleus in accordance with the change in latency of their responses as a function of stimulus intensity. The stimuli were bursts of tones at the unit's characteristic frequency. In one group of units, the latency decreased markedly when intensity was increased from threshold. Units placed in the other group had latencies that were nearly independent

of stimulus intensity. At high stimulus intensity both groups had latency values between 2 and 4 ms in response to tone bursts. The latency is different in units in the different parts of the cochlear nucleus (3), values being smallest in the posterior ventral cochlear nucleus (PVCN) and largest in the dorsal cochlear nucleus (DCN). The latency of units with CF below 2 kHz, when stimulated with clicks at moderate intensities (about 1 μ B, 75 dB SPL), was found to be slightly above 2 ms in the PVCN and anterior ventral cochlear nucleus (AVCN), and 3–5 ms in the DCN of the cat (3).

The results of recent studies of the dynamic properties of units in the cochlear nucleus of the rat in response to amplitude-modulated sounds (7–9) show that the phase angle between the modulation of the stimulus and the concomitant modulation of the discharge rate is almost independent of the stimulus intensity. These units, therefore, seem to respond to a small change in amplitude with a latency that is almost independent of the stimulus intensity. In some of these studies (7, 9), the intensity of the stimulus sounds (tones at CF or broad-band noise) was sinusoidally amplitude modulated (10 or 30%) with different frequencies, after which the change in discharge frequency was evaluated from cycle histograms of the recorded discharges, locked to the modulation wave. In another study (8), tones or noise were amplitude modulated with pseudorandom noise and the modulation of the discharge frequency evaluated through statistical signal analysis.

In the present study the latency derived from poststimulus time (PST) histograms of the responses to tone bursts with rapid onset is compared with the latency of the

change in discharge frequency due to small changes in sound intensity.

METHODS

Recordings were made extracellularly from single cells in the cochlear nucleus of the rat. The surgical procedure and the arrangement of the sound stimulation have been described previously (5, 6). Therefore, only a brief description is made in this paper.

The anesthesia used in the present study was either urethan (1.5 g/kg body wt), mebumal sodium (Nembutal) (60 mg/kg body wt), or chloralose-urethan (150 and 120 mg/kg body wt, respectively). Usually no supplementary anesthesia was given during the experiments. Sounds were presented to the ipsilateral ear by a condenser microphone (Brüel & Kjaer, type 4131) operated as sound source.

Tone bursts (50 or 100 ms duration) were generated by a Wavetek (type 116) generator, the output of which was passed through a Fonema tone gate. The rise time (to 90% of maximal amplitude) was 200 μ s. Modulated sounds were produced in some instances by feeding the output of a pseudorandom noise generator (Hewlett-Packard, type 3722 A) to the amplitude control of the Wavetek (type 136) generator. In some of the experiments a Motorola (MC 1595 L) four-quadrant multiplier produced the amplitude modulation.

Data processing

The so-called impulse response of a system is defined as the response to an (infinitely) short impulse at the input. The impulse response (as well as the step response) fully describes the dynamic properties of a linear system in the frequency range where the input impulse can be regarded to have a uniform frequency spectrum. The step response of a system is defined as the response of the system to a step input. Since the step is a time-integrated impulse, the response of a linear system to a step consequently is identical to the time-integrated response of the system to an impulse, i.e., the time-integrated impulse response (see Fig. 1). Mathematical operations only are required to obtain, e.g., the step response or the frequency-domain transfer function from the impulse response. The frequency-domain transfer functions, also called the system's frequency response, give as a function of frequency the ratio between output and input amplitude, together with the phase relation between output and input when the input is (hypothetically) sine waves of different frequencies that cover the frequency range to be

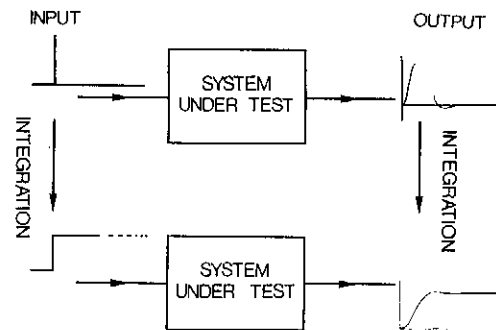


FIG. 1. Impulse response and step response of a linear system determined by applying an impulse or a step function to the input.

investigated. The shape of the impulse response is related to the frequency response of the system. The lower the frequency cutoff of a system transmitting solely low frequencies is, the wider is the impulse response and the slower is its rise and fall. A transport delay in the system will shift the response to the right by an amount of time equal to the transport delay. Inspection of the impulse response thus gives a system's delay directly.

In a study of systems such as, e.g., most man-made electrical filters that are linear over large ranges of intensities, it is convenient to observe the output when the input is a step or an impulse. The input then starts at or near zero level and rapidly increases to a level within the normal working range of the system. The shape of the responses obtained in such systems is independent of the magnitude of the applied step or impulse, as long as the input is within the range where the system operates linearly. The tone-burst stimuli frequently used in electrophysiological studies of the auditory system furnish an example of the above-mentioned method of applying a step to the input of a system when the dynamic properties are to be charted. The output is then a poststimulus time histogram of the recorded discharges. Since the tone bursts usually far exceed the linear range of the system in intensity, the PST histograms are not a valid representation of the step response of the system in normal operation.

Biological sensory neural systems, like the auditory system, in many cases can be regarded to work in a way similar to the linear system provided the input is restricted to vary slightly around a certain operating point with regard to the intensity. The derived characteristics are likely to be different for the different average intensities around which the variation is made. The discharge rate (spike density) is regarded as the output of such a system. Since the neu-

ral discharge, apart from being the result of the input stimulus to the system, contains a random component (equivalent to noise in an analogue system), some form of averaging is required. Such averaging is commonly achieved by means of poststimulus time histograms or cycle histograms.

A straightforward method to determine the step response would be to use a small repetitive step increment (or decrement) from a certain intensity of the stimulus, and then to make a histogram of the discharge pattern locked to the repetition of the step change. Application of this method does have certain drawbacks in systems like a sensory neural system, on which it is more advantageous to modulate the intensity of the stimulus continuously than to employ impulse or step increments. By continuous modulation, the variation in stimulus intensity is spread out in time compared to its location at a discrete short time interval on step or impulse stimuli. Choice of random noise as input has won considerable favor in technical fields for determining the dynamic characteristics of a variety of different systems. Statistical signal-analysis methods can then be introduced to compute the impulse response or frequency-domain transfer function. The computations of the impulse response and step response are based on the fact that the cross covariance¹ between a random input to a system and its output yields the system's impulse response in the frequency range where the input can be regarded to have a uniform frequency spectrum (see Fig. 2). If such is not the case, it is still possible to arrive at the impulse response of the system, but it takes slightly more computation. The cross covariance is a function of delay time, but when the above conditions are fulfilled and the cross-covariance function can be regarded as representing the impulse response of the system, the cross covariance is a function of time after application of a hypothetical impulse to the input of the system. As mentioned above, in linear systems, the impulse response, step response, and frequency-domain transfer functions are just mathematical transformations of each other, hence one can be computed on the basis of the other. It is equally possible to base the computation of the impulse response on the spectrum of the output relative to that of the input. That method is technically advantageous. The impulse response can then be computed on the

¹ Often the term cross correlation is used in the place of cross covariance for the lagged product of the input and output. The term cross correlation should, however, be reserved for the normalized cross covariance.

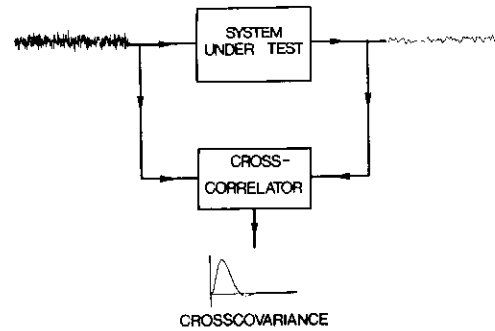


FIG. 2. Technique for determining a system's impulse response based on the system's response to random excitation.

basis of the autospectrum of the input and the cross spectrum between input and output. The mathematical background for determination of a system's dynamic properties using noise as input can be found in, e.g., ref 1 or 10.

In previous papers (7, 10) pseudorandom noise was shown to have certain advantages over ordinary noise as concerns studies of sensory neural systems. Pseudorandom noise has essentially the same properties as ordinary noise except for the fact that it repeats itself periodically. Its spectrum is a line spectrum compared to the continuous spectrum of ordinary noise.

Since the auditory receptors sense the basilar membrane vibration unidirectionally, they work functionally as rectifiers followed by low-pass filters. The neural excitation by a high-frequency tone modulated with a low-frequency signal then essentially consists of the modulation waveform. The modulation (in this case, the noise) of a high-frequency tone can be regarded to be the input to the system under test. (If the noise itself was used as input, the result of the rectification of the hair cells will be that the real input is a half-wave-rectified version of the noise.) When the frequency of the carrier tone is lower than the low-pass cutoff frequency of the receptors, the neural excitation is determined both by the waveform of the modulation and by that of the carrier tone.

The principle of the method using pseudorandom noise-modulated stimuli is sketched in Fig. 3. The stimulus is a tone (or noise) that is amplitude modulated with the noise. By varying the level of the stimulus, it is possible to determine the dynamic properties at different "operating points." The degree of modulation is kept low, usually 7 or 22% root mean square value. The dynamic property with regard to

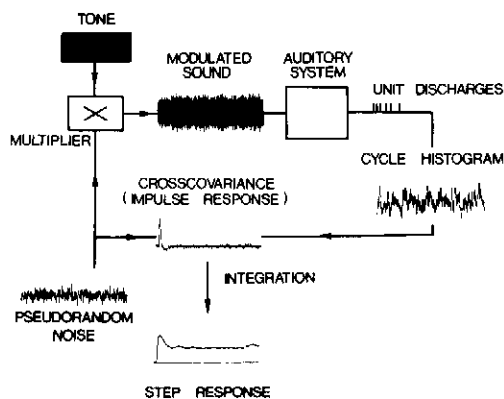


FIG. 3. Technique used to study the dynamic properties of responses of single neurons to noise-modulated stimuli.

the modulation (envelope) of the stimulus is determined by cross correlating the output, i.e., a period histogram of the recorded discharges representing the probability of firing at various times during one noise period with the input, i.e., one period of the noise used to modulate the sound. This process gives the impulse response of the system provided that the spectrum of the noise is uniform in the frequency range where the system has significant transmission. The impulse response is equivalent to the change in discharge frequency that would be the result of an increase in sound intensity for a very short time.

The noise-modulated stimuli make it possible to determine the response to a very short impulse, such as would have arisen had the system been linear, while at the same time avoiding large changes in stimulus intensities that would seriously violate linearity. The integrated impulse response, i.e., the step response, in this case corresponds to the change in discharge frequency in response to a small step increase (or decrease) in stimulus intensity.

Using cross-correlation analysis in determining the system's impulse response on the basis of noise-modulated input has additional advantages since it is an expression of the linear relationship between input and output. The impulse response computed using this method represents the linear part of the system.

In short, the advantages of pseudorandom noise over ordinary noise lie in the possibility of reducing the statistical variability of the output by the averaging brought about by the period histograms of the recorded discharge pattern. To compute the correlation between the histogram and one noise period is thus sufficient, in contrast to having to compute the cross covariance between ordinary random

noise and the discharge frequency over the entire sample length (8, 10).

The major difference between pseudorandom noise and true random noise is that the maximal delay over which the cross covariance can be computed is restricted to the duration of a period of the pseudorandom noise. The length of a pseudorandom noise period was therefore always chosen to be equal to or longer than the desired maximal delay in the computation of the cross covariance.

The noise in the present study had 4,095 steps, each 33.3 μ s long, the total length of one pseudorandom noise period being 136.4 ms. The bandwidth of the noise was 1,500 Hz. Amplitude-modulated sounds were presented in 5-s-long bursts followed by 5 s silence. Usually 5 or 10 min of data were processed for each stimulus condition.

Histograms of the recorded discharges in response to amplitude-modulated sounds were made by an Intertechnique Physioscope (DIDAC 800). The recorded discharges were converted to unit impulses by means of a level discriminator. The bin width of the analyzer was 180 μ s, its sweep being locked to the repetition of the noise. Each trigger pulse returned the sweep to its original position immediately before triggering a new sweep. The output of the analyzer was punched on paper tape and processed by a general-purpose computer (IBM 360/75), as described earlier (8).

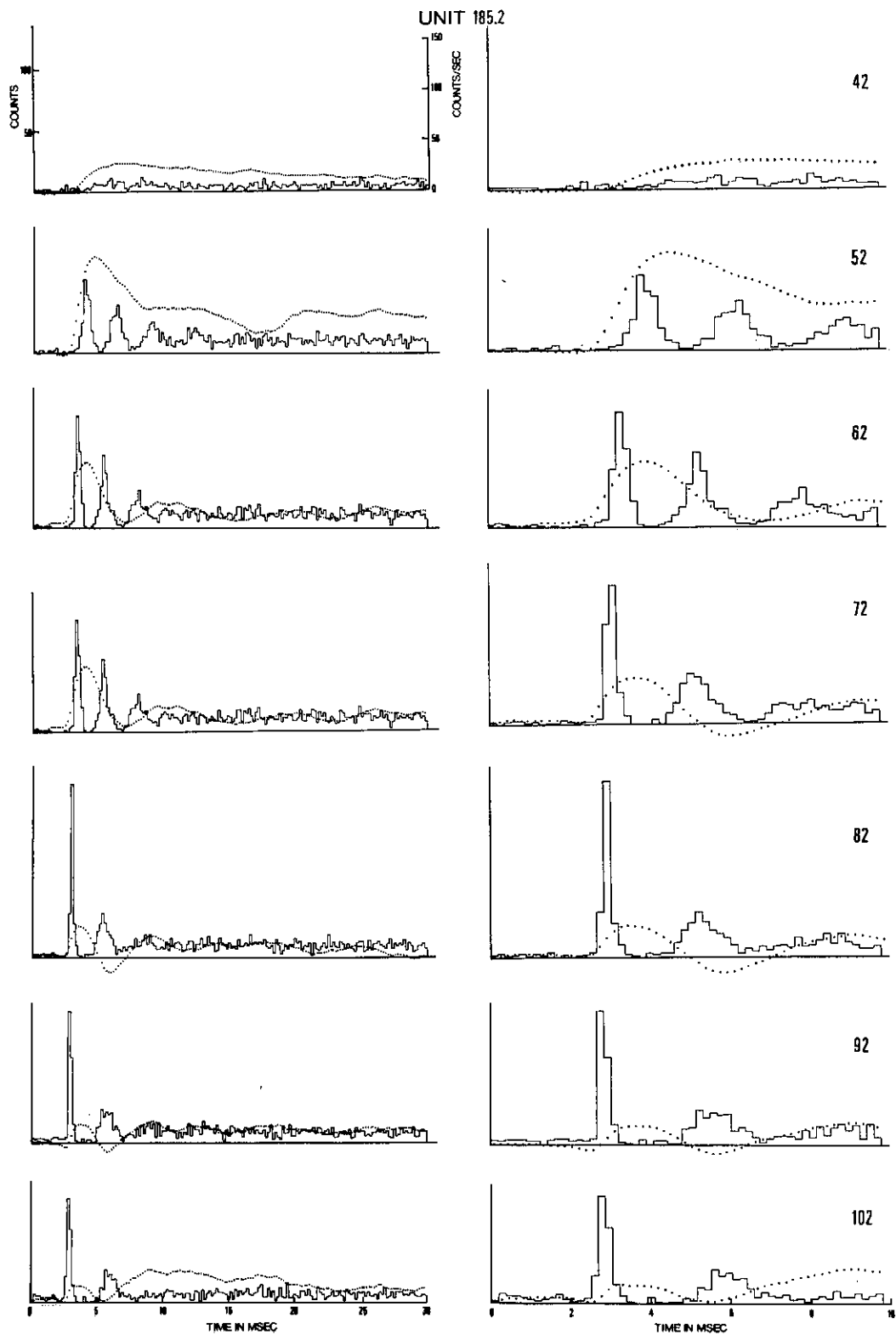
Based on the previous finding that most units in the cochlear nucleus show a cutoff frequency with regard to modulation well below 1,000 Hz (7), it can be said that the present system fully covered the bandwidth of these neurons.

Poststimulus time histograms of the responses to tone bursts were produced by the same analyzer and the analyzer was triggered at the beginning of the tone stimulus.

RESULTS

The results to be presented here are based on recordings from 59 units in 30 animals. Units frequently could be kept in good condition for 2 h or more, occasionally up to 8 h. Only units that were kept for more than 30 min are included in the present account.

Figure 4 shows PST histograms of responses to tone bursts compared with the step response computed from the responses to a tone at CF modulated with pseudorandom noise in the way described above. Results from stimulation with tones in the intensity range from 42 to 102 dB SPL are depicted. In each graph the tone bursts and



the amplitude-modulated tones had the same intensity. The two sets of graphs (*A* and *B*) show the same data on different time scales.

The latency of the step response undergoes no or only a very small decrease as the stimulus intensity is raised. The latency of the PST histograms, on the other hand, decreases when the intensity of the stimulus is increased.

Inspection of Fig. 4 also reveals that the step response is smoother than the PST histograms. The temporal resolution of the step response is the same as that of the PST histograms, meaning that its smoother appearance is not due to a difference in temporal smoothing between the two recordings, but rather is a result of a lower statistical variability, the efficient observation time being longer than in the case of the responses to tone bursts.

The latencies of the responses of two typical neurons are plotted as a function of stimulus intensity in Fig. 5. The latency of the step response is observed to be almost independent of the stimulus intensity, while the latency of the response to tone bursts is observed to approach the latency values of the step response asymptotically as stimulus intensity is increased.

In these units the latency to the step response at any stimulus intensity is, thus, a good measure of the latency value of the response to tone bursts at high-stimulus intensity.

The response characteristics depicted in Figs. 4 and 5 are typical for units encountered in the entire cochlear nucleus complex. There were no recognizable differences with regard to the features described above between the responses of units from animals anesthetized with urethan compared with urethan-chloralose or light barbiturate anesthesia.

In the superficial dorsal layer of the DCN, units did appear that responded in a different way from those described above;

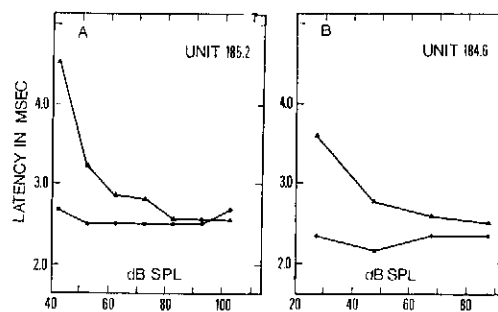


FIG. 5. Latency for two units as a function of stimulus intensity for PST histogram (triangles) and for the step response computed from the response to noise-modulated tones (filled circles). The frequency of tones was equal to the CF of units. In the unit depicted in *A*, the CF was 10.7 kHz and it had a threshold of 37 dB SPL. The unit in *B* had a CF at 31.5 kHz and a threshold at 20 dB SPL. The anesthesia was urethan.

namely, by having a higher threshold and much longer latency on tone-burst stimulation. The PST histograms of the responses to tone bursts of these units have a gradual onset, whereas the units described above have a fast onset. Figure 6 illustrates the responses of two such units in the same way as Fig. 4. These two units had, as is usual for their type, a much higher threshold than the ordinary type of units and they had no spontaneous activity.

The PST histograms illustrate how the latency of the response to tone bursts of these dorsal layer units is very much longer than the latency of the step response. Figure 7 shows the latency values in response to tone bursts and that of the step response as a function of stimulus intensity for two dorsal layer units. Similar to the units with the short latency (Figs. 4 and 5), the latency of the step response of these units is almost independent of stimulus intensity, but it is longer than that of the units depicted in Fig. 5.

Thus, these latter-mentioned units respond with a rather slow increase in discharge rate on stimulation with a tone

FIG. 4. Poststimulus time histograms (solid lines) in response to tone bursts of various intensities compared with the step responses (dots) computed from responses to noise-modulated tones of the same intensity as the tone bursts. Data are shown on two different time scales. The modulation was 22% root mean square. Stimulus intensity is given by legend numbers (in decibels SPL). The frequency of the tones was equal to the unit's CF (10.7 kHz). The unit's threshold to tone-burst stimulation was 37 dB SPL. Urethan anesthesia.

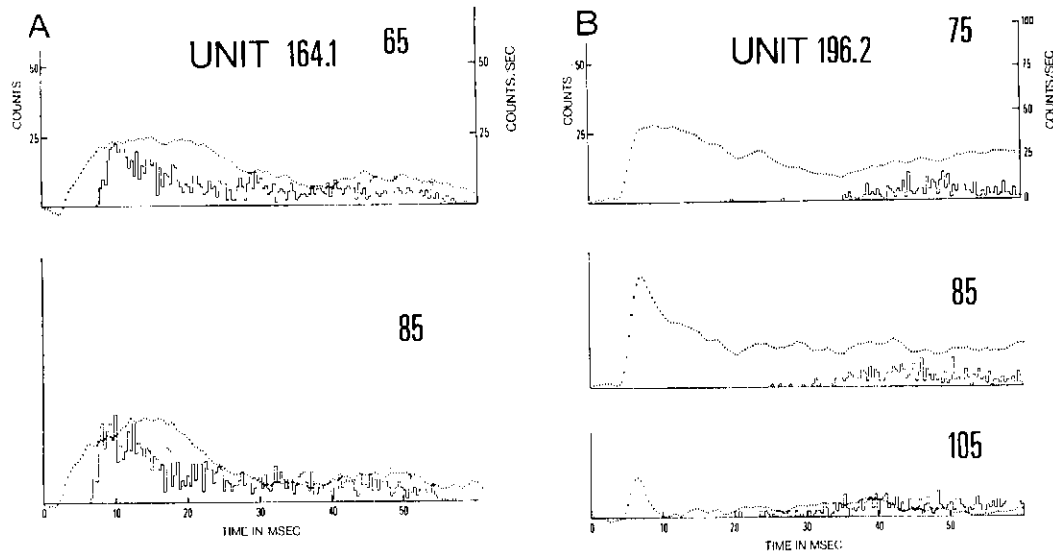


FIG. 6. Poststimulus time histograms (solid lines) of the response to tone bursts compared with the step responses (dots) determined from responses to noise-modulated tones for two long-latency units. The modulation was 22% root mean square. The frequency of tones was equal to the CF of units. Legend numbers show stimulus intensity in decibels SPL. The CF's of units were in *A*: 5.0 kHz and in *B*: 7.8 kHz, and their thresholds were 50 and 70 dB SPL, respectively. Durations of the tone bursts were in *A*: 50 ms and in *B*: 100 ms. The anesthesia was in *A*, Nembutal and in *B*, chloralose-urethan.

burst, but when presented with noise-modulated stimuli, they display a step response similar to that of the units that have a rapid onset of their PST histograms.

The type of unit depicted in Figs. 6 and 7 is usually only found in animals under light barbiturate anesthesia or in animals anesthetized with chloralose-urethan.

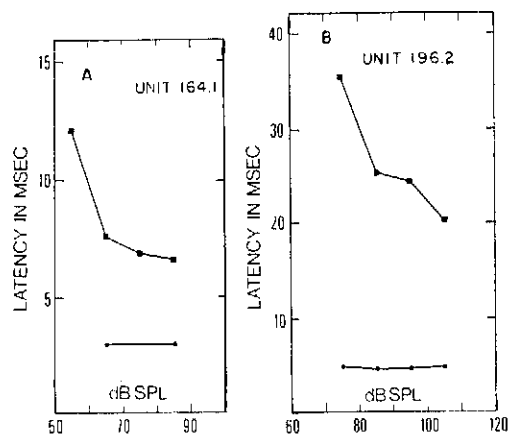


FIG. 7. Latency as a function of sound intensity for the two long-latency units depicted in Fig. 6 measured from PST histograms (squares) and from the step response (filled circles).

The latency of the response to modulation of broad-band noise and to sounds consisting of two tones shows the same properties as evidenced above. The step response determined from the responses to two tones presented simultaneously, one being excitatory and the other being inhibitory, and one or both being modulated, gives rise to similar results with regard to latency, as does modulation of a single excitatory tone at CF.

The distribution of latencies for different units determined from the step response in the way described in the present paper groups narrowly around certain values, as is illustrated in Fig. 8. It is seen that the majority of the investigated neurons had latencies around 2.8 ms. There is a second peak in the histogram at 4.7 ms; one reason for the narrow peaks in the histogram of latencies of the step response is the relative independence between the latency values and the stimulus intensities.

DISCUSSION

The results of the present study show that the latency of the step response to sounds that are amplitude modulated with

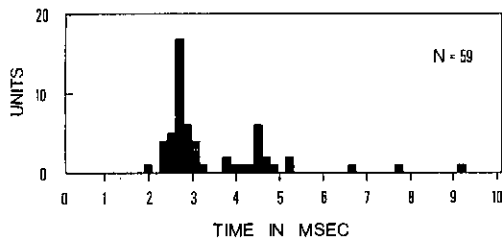


FIG. 8. Histogram of the latency of units in the cochlear nucleus measured from the step response determined from the response to tones at CF modulated with noise. The CF of units ranged from 1.4 to 36 kHz and only three units had CF below 2.5 kHz. The binwidth is 180 μ s.

noise is relatively independent of the stimulus intensity. The latency of the response to tone bursts determined from PST histograms, however, decreases in the same units when sound intensity is increased to a greater or lesser degree from unit to unit. In most units, the latency of the PST histograms approaches the latency of the step response as stimulus intensities are increased.

The latency of the response to a stimulus that reaches its full intensity rapidly from zero such as, e.g., a tone burst is assumed to be the sum of 1) mechanical travel time in the cochlea, 2) propagation time in the axons and dendrites involved, 3) synaptic delay, and 4) degree of temporal summation of EPSP needed to reach a certain (small) probability of firing. The two first-mentioned sources of latency are relatively independent of the stimulus intensity whereas the third, the gradual buildup of an EPSP, will occur at a rate that is dependent on the intensity of the stimulus. In this regard, how far the EPSP has to travel before it reaches the firing level of the neuron will ultimately be the determining factor which, in turn, depends on the threshold of the neuron and on the stimulus intensity. No or very little temporal summation of neural events is needed to increase the probability of firing in response to a small increment in intensity of a continuous stimulus well above threshold. The reason is that the EPSP already has a certain (high) probability of reaching firing level. The latency of a change in firing rate in response to a change in stimulus intensity becomes relatively independent of the mean stimulus

intensity from which the change in intensity is made. It consequently takes a long time to reach the firing level of the membrane potential from far below threshold. The higher the stimulus intensity is, the sooner it reaches a certain firing probability. The difference between the latency of the step response and of that of the response to tone bursts is understandably larger in the units with high threshold than it is in units with low threshold. In the latter, little temporal summation is needed in order to reach firing level for moderate or high sound intensities. The higher the stimulus intensity is, the faster the EPSP rises, thereby decreasing the latency.

The neurons whose responses are shown in Figs. 4 and 5 are probably secondary neurons, although the above reasoning is also valid for higher order neurons. It is likely that the difference between the two ways of measuring latency discussed will be greater when observing higher order neurons since temporal summation will have an additive effect on the latency in response to tone bursts, while only the additional propagation delay adds to the latency in the step response. The units whose responses are depicted in Figs. 6 and 7 may be taken as exemplifying higher order neurons. Their latency in response to tone bursts is much longer than that presented by ordinary units, and it is highly dependent on the sound intensity. It is clear from these recordings, however, that it would not have been possible to come to any conclusion about the number of neurons along the pathway just by looking at the responses to tone bursts. On the other hand, the latency of the step response of these units (4.7 ms) does make it quite clear that they are of higher order. That is also supported by the facts that these units only are found in lightly anesthetized animals and that they are located in the dorsal surface of the DCN. In addition they have a high threshold.

The fact that the latency determined from the step response shows no or very little dependence on stimulus intensity makes it a considerably more suitable measure of transmission delay in the nervous system than the conventionally used stimuli

that abruptly attain a high (suprathreshold) value from a subthreshold value such as, e.g., tone bursts. The change in latency with intensity may, in fact, be regarded as a result of the rather unnatural character of tone bursts as stimuli of the auditory system. In contrast, the temporal pattern of more natural sounds, having far less drastic intensity changes, may be preserved in the discharge pattern; that is to say, the pattern is rather uninfluenced by the overall intensity of the stimuli. The superiority of determination of latency from the step response is supported by the narrow peaks in the histogram for latency of different units (Fig. 8). It is seen here that the units group themselves distinctly with regard to latency. Since widely different types and degrees of anesthesia have been used in this study, the narrowness of the peaks furthermore indicates little influence on the latency determined from the latency of the step response.

The results of the present study thus show that neurons represent small changes in sound stimulus intensity by a latency that is practically independent of the mean stimulus level from a few decibels above threshold to the highest intensities studied (70–80 dB in most units). This finding has a particular practical implication in the auditory system where much information is coded in rapid small changes in amplitude of sounds. Directional hearing is, e.g., highly dependent on correct information about the temporal difference between the sound reaching the two ears. Temporal information in general is usually coded in the envelope of natural sounds as rather small changes in amplitude. An example is voiced speech that can be regarded as an amplitude-modulated high-frequency sound. The modulation is the fundamental (vocal cord) frequency and the "carrier" is a mixture of higher frequencies representing formant frequencies (vocal tract resonances). On the other hand, drastic changes involving an elevation in sound intensity from below threshold to its maximal value in a very short time do not represent a natural situation. Tone bursts that are commonly used in auditory physiology represent such unnatural changes.

It is interesting to ponder whether such a phenomenon as the dependence of latency

on stimulus intensity may be a product of the use of an overly idealized stimulation, i.e., a stimulus that reaches its value rapidly from below threshold. Such type of stimulation rarely occurs in real life. It should be considered whether such might be the case in neural transmission in general.

SUMMARY

The latency revealed by poststimulus time histograms of the responses of single units in the cochlear nucleus to tone bursts was compared with the latency of the change in discharge frequency in response to small increments in the amplitude of the stimulus. The latter was derived on the basis of statistical signal analysis of the discharge pattern in response to tones amplitude modulated with pseudorandom noise. The "step response" of the system was computed by time integration of the cross covariance between modulation and spike density. The following observations can be made:

1. The latency of the responses to tone bursts always decreased with increasing sound intensity, whereas the latency of the step response was almost constant for intensities from immediately above threshold to the highest intensity used (60–70 dB above threshold).
2. In most units the latency revealed by the PST histogram of the responses to tone bursts approached the value of latency of the step response asymptotically.
3. In some units with longer latency, the latency of the response to tone bursts was many times greater than the latency of the step response, even at high sound intensities.
4. A histogram of latency values of the step response of the units studied showed narrow peaks at 2.8 and 4.7 ms.
5. On the basis of the present results it is concluded that the latency values of the step response represent the true sum of synaptic and axon dendritical propagation delay, whereas the latency of the responses to tone bursts also includes the temporal summation at the synaptic level.

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