

**DYNAMIC PROPERTIES OF
THE RESPONSES OF SINGLE NEURONES IN THE
COCHLEAR NUCLEUS OF THE RAT**

BY AAGE R. MØLLER

*From the Division of Physiological Acoustics, Department of Physiology II,
Karolinska Institutet, S-104 01 Stockholm, Sweden*

(Received 11 September 1975)

SUMMARY

1. The dynamic properties of unit responses to amplitude-modulated tones were studied using modulation with pseudorandom noise and described by cross-covariance and integrated cross-covariance functions between the discharge rate and the modulation. Under the experimental conditions used, these two functions are valid approximations of the system's impulse and step response functions respectively.

2. On the basis of their impulse response functions units could be classified into two groups, Type I with a low adaptation and Type II with a large degree of adaptation as well as a damped oscillation in their impulse response functions.

3. The response pattern of the Type II units is most likely the result of a negative feed-back striving to keep the discharge rate at a nearly constant level.

4. The cross-covariance functions are shown to remain unchanged during long duration recordings from the same unit.

INTRODUCTION

Since the intensity of natural sounds varies more or less rapidly with time, it is of interest to study how such changes are processed by the ear and the auditory nervous system. The responses of sensory neural systems are in general non-linear, but in many cases non-linear systems behave similarly to linear systems, provided the input is allowed to vary only a little around a certain operating point. The dynamic properties of a sensory neural system at a certain stimulus intensity can then be obtained by varying the stimulus intensity in such a way around the operating point.

As regards the auditory system, sinusoidally amplitude-modulated sounds have been utilized in investigations of the dynamic properties of

single units in the cochlear nucleus (Møller, 1973*b*, 1974*a*). Since the haircells in the inner ear function like half-wave rectifiers followed by a lowpass filter, they transform a high frequency sound in such a way that its envelope becomes the signal determining neural excitation. The dynamic properties of the system following the haircells are best studied by designating the envelope of a suitable sound as the input test signal.

By varying the intensity of the sound while maintaining a constant depth of modulation, the dynamic properties of the auditory system were observed at different stimulus levels, i.e. at different operating points (Møller, 1972, 1973*b*, 1974*a*). The modulation of the rate of unit discharges, recorded extracellularly, was determined from period (cycle) histograms locked to the modulation. The ratios between the depth of sinusoidal modulation of the discharge rate and the amplitude of the sinusoidal modulation of the stimulus intensity were determined, together with their phase relationships, at a number of different frequencies. Plotting these two measures as a function of modulation frequency completely describes the frequency domain transfer function of a linear system. In cases in which the system can be regarded as functioning like a linear system, the output in response to any input signal is the input filtered by this transfer function. Consequently the output which will result from any given input can be computed from a knowledge of the transfer function of the system and the spectrum of the input.

The above-mentioned experiments (Møller, 1972, 1973*b*, 1974*a*) generally have shown that the depth of modulation of the neurone discharge rate is greatest when the stimulus sound is modulated at a certain frequency. This frequency varies from unit to unit but is for the most part independent of the intensity and the spectral composition of the sound that is modulated. It usually lies between 50 and 200 Hz.

The impulse response function is another relationship commonly employed to describe the dynamic properties of a linear system. This function consists of the response to a hypothetical impulse with an infinitesimal duration but with a finite energy.

Mathematically, the impulse response function of a linear system is the inverse Fourier transform of the system's frequency domain transfer function. The impulse response is thus the time domain counterpart of the frequency domain transfer function. These two functions can be derived from each other by mathematical operations. When the impulse response or the frequency domain transfer function of a linear system is known, the output resulting from any given input can be predicted.

The step response function of a linear system is defined as the response to a step input. Since the time derivative of a step is an impulse, the impulse response function of a linear system is also the time derivative of

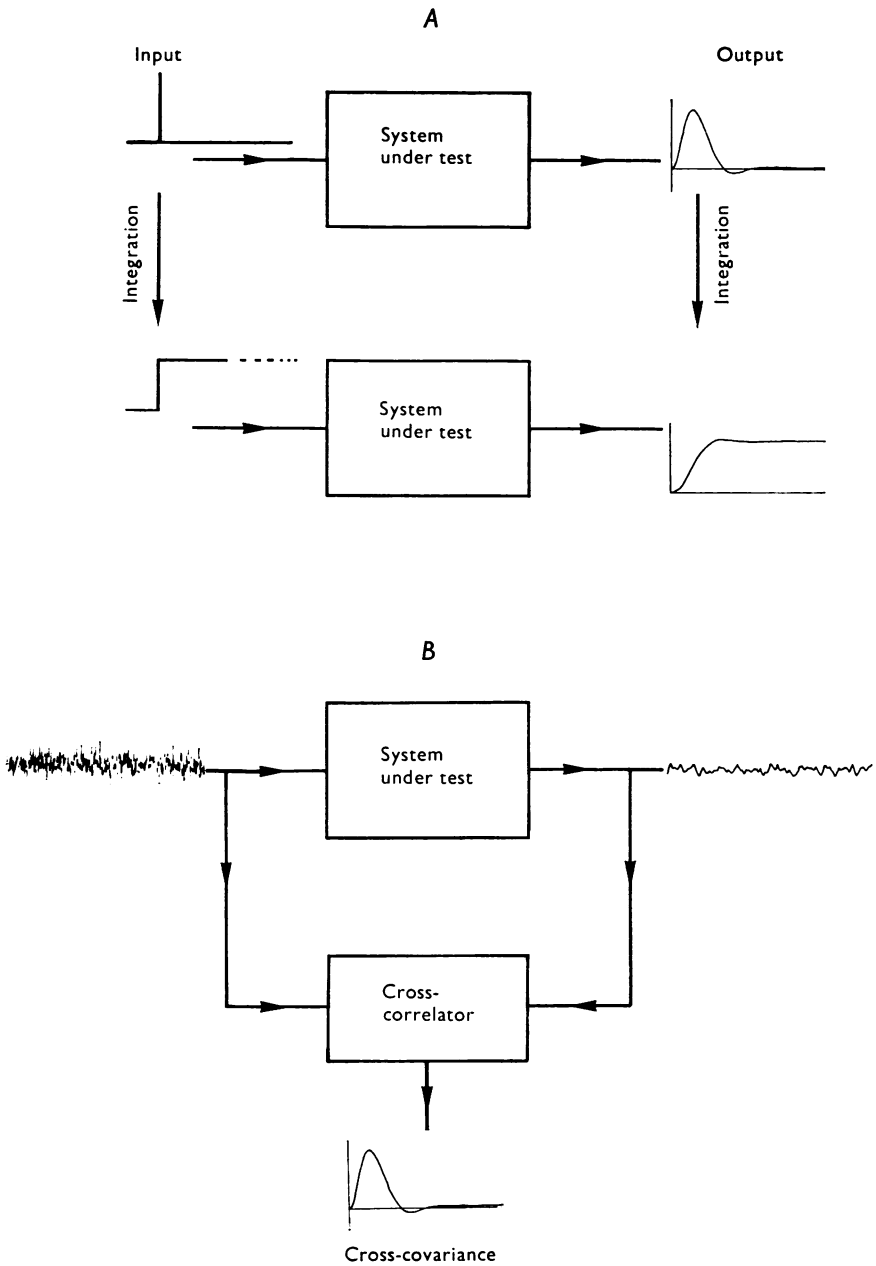


Fig. 1. Illustration of principles according to which a linear system's dynamic properties can be described by: *A*, the system's impulse response function; and *B*, step response function.

the system's step response (Fig. 1A). The impulse response function of a linear system can be computed from the system's step response function, a procedure often employed in the study of engineering systems.

In a sensory neural system the impulse response function can rarely be determined directly. A step increase in stimulus intensity could be utilized for determination of the system's step response function, but as regards a neural system some practical difficulties emerge, making other methods more suitable.

One method makes use of random noise as input to the system being tested. The dynamic properties of a linear system in response to random noise can be computed by cross-correlating the input with the output (Lee, 1960; see also Bendat & Piersol, 1966). If the spectrum of the random noise is uniform over a range of frequencies exceeding that within which the system being tested has significant transmission, the cross-covariance as a function of the delay between input and output is a valid approximation of the system's impulse response function. If the cross-covariance is computed for positive lags it then represents the response of the system to an (hypothetical) impulse applied to its input at a time corresponding to zero delay. The positive delays represent time after application of the impulse. Since the time-integral of an impulse is a step, the step response function of a linear system is the time-integrated impulse response function of the system. Consequently, the time-integrated cross-covariance function is equivalent to the system's step response function (Fig. 1).

In cases in which the cross-covariance function is a valid approximation of a linear system's impulse response, the system's frequency domain transfer function can be computed from the cross-covariance function since the transfer function is the Fourier transform of the system's impulse response function. In systems containing amplitude non-linearities, this operation yields the impulse response function or transfer function of the linear part of the system.

In many systems, the output is not only a filtered version of the input but also contains a certain amount of noise produced in the system itself. In the nervous system this noise is manifest in the statistical variability of the neural firing frequency at a constant level of excitation. This variability affects the estimates of the transfer function and of the impulse response function. In order to obtain an estimate of the response with sufficient confidence, some form of averaging over a certain length of time must be performed. The required time, i.e. duration of recording, depends on: the amplitude of the inherent noise and the required statistical confidence; the amplitude of the test input signal; and the efficiency of the averaging technique.

In systems in which the input must be kept small due to non-linearities,

it is particularly important to have an optimal averaging technique on hand.

When the input is periodic, the statistical variability of the firing frequency can be reduced satisfactorily by temporal averaging in the form of period histograms of the recorded discharges. Such histograms are locked to the input wave form.

When noise is used as input, the cross-covariance function must be computed over lengthy samples in order to reduce the influence of the variability. Since the analysis is most conveniently performed on digital computers, the input and the output signals have to be sampled and digitized. The usual precautions have to be taken against aliasing (by which is meant the fact that power at frequencies higher than half the sampling rate is represented in the sampled version as though the power were located at lower frequencies) by choosing a sufficiently high sampling rate. Cost of computation therefore renders this direct method generally unfeasible in systematic studies of the dynamic transmission properties in neural systems.

These difficulties can largely be overcome by replacing the random noise with pseudorandom noise. Pseudorandom noise has the same properties as true random noise with the important difference that pseudorandom noise repeats itself periodically. True random noise has a continuous spectrum but pseudorandom noise has a line spectrum with the frequency difference between the lines equal to $1/T$ where T is the length of a noise period. Pseudorandom noise, generated digitally, is usually better defined than true random noise generated by analogue devices.

Since a pseudorandom noise repeats itself periodically, averaging of the responses can be performed by setting up period histograms of the neural firing, the histograms being locked to the period of the noise. The statistical variability of the firing frequency can thereby be reduced to a satisfactory level. Since this averaging can be performed on line during the experiments by a readily available signal analyser, this method is far less expensive than computing the cross-covariance function between true random noise and the recorded neural responses.

The cross-covariance function between the noise during one period and these histograms is an approximation of the system's linear impulse response function in the same way as the cross-covariance function computed from the response to true random noise.

In the calculation of the cross-covariance between one period of the pseudorandom noise and a histogram of the neural discharges, these two functions are treated as circular functions (see Møller, 1974*b*). The maximal frequency resolution with which the spectra and the transfer functions can be obtained is thus equal to $1/T$ where T is the length of one noise

period. It is assumed that no correlation exists between the stimulus and the firing frequency at negative delays, in which cases a certain stimulus could influence the response before it is applied. A schematic view of the system is shown in Fig. 2.

This method, described in detail elsewhere (Møller, 1974*b*), has been applied to studies of the dynamic properties of single neurones in the cochlear nucleus (Møller, 1973*a,b*, 1974*a*, 1975*a,b*, 1976) in which tones (or noise) were amplitude- (or frequency-) modulated with pseudorandom noise.

When the step response function is to be determined, this method is generally more efficient than averaging the responses to step modulation of the stimulation. The reason is that the system studied mainly responds to changes in stimulus intensity. In the case of noise modulation changes in stimulus intensity are spread evenly over time whereas the changes in the case of a step-modulated stimulus are concentrated to short discrete periods, the interval between which cannot be reduced below a certain interval. To obtain the same enhancement of the response when step modulation is used a longer observation time is required compared with deriving the step response function from the responses to noise. In studies of the dynamic properties of systems in which the input can be allowed to vary only little around a certain operating point, noise is therefore preferable to impulses or steps as an input. Furthermore, the tendency of many neural systems to synchronize their responses to an abrupt stimulus change may result in unwanted effects. When noise-modulated sounds serve as input, such effects are avoided.

One further advantage inherent in noise (or noise-modulated stimuli) as input is that it permits computation of the coherence spectrum (Bendat & Piersol, 1966). This spectrum is a measure of the relative dependence of the input upon the output. Low values mean that the output to a great extent consists of noise generated inside the system itself or that the system is non-linear.

In the present study the impulse and step response functions of single neurones in the cochlear nucleus are determined on the basis of the responses to tones amplitude-modulated with pseudorandom noise. Sounds of different intensities provide the stimulation and the resulting temporal patterns are compared in different units.

METHODS

White Sprague-Dawley rats weighing 200–300 g were used. The anaesthesia given was urethane (1.5 g/kg body weight). Unit potentials were recorded extracellularly with KCl-filled micropipettes. The surgical procedure and sound stimulation system have been described in detail earlier (Møller, 1969*a*, 1971).

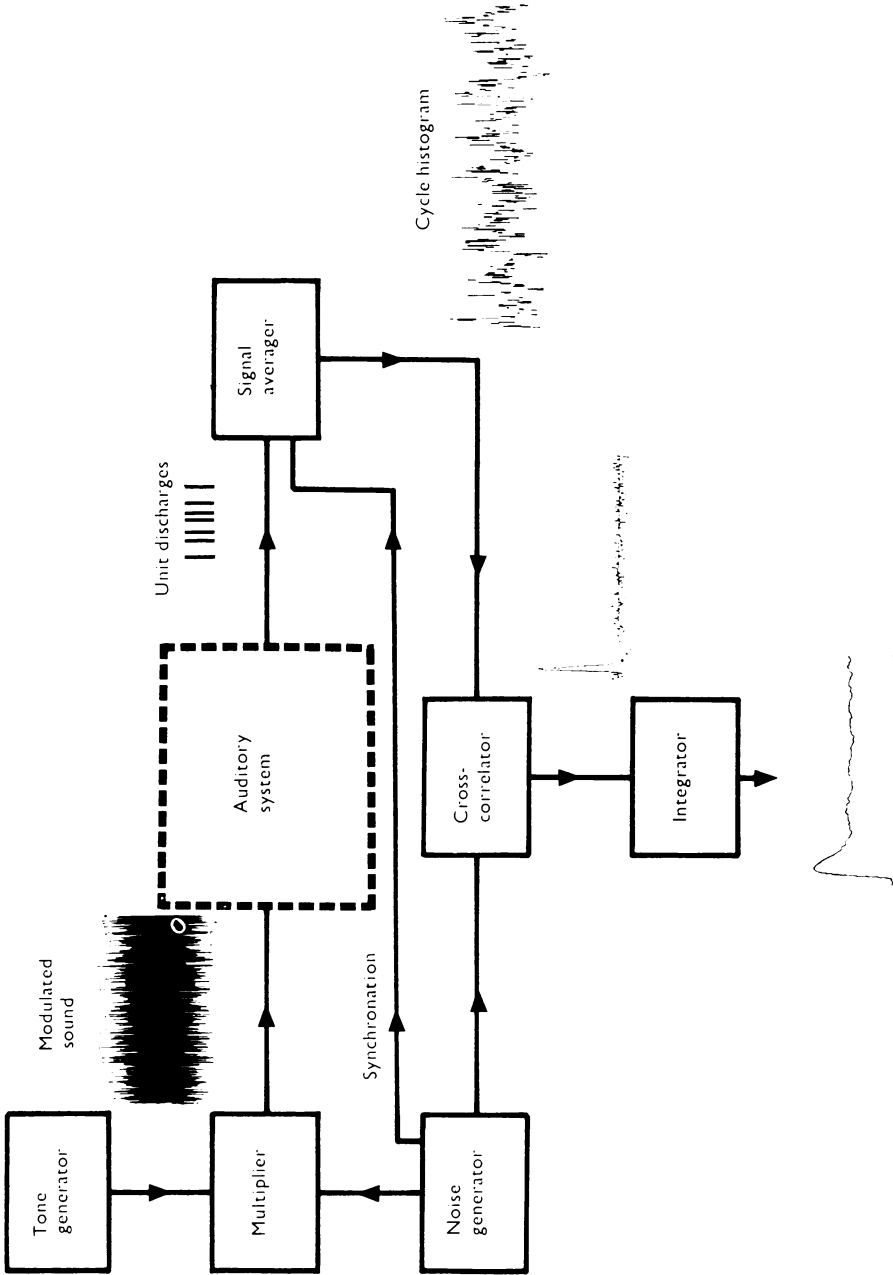


Fig. 2. Schematic block diagram illustrating the method of data processing.

Either one or both of two Wavetek (type 136) generators were amplitude-modulated by pseudorandom noise generated by a Hewlett-Packard (type 3722A) pseudorandom noise generator operated at a clock period of 33.3 μ sec. Each noise sequence consisted of 4095 points, corresponding to a length of 136.4 msec. The bandwidth of the noise was 1500 Hz and the modulation depth of the sound was usually 22% RMS (root mean square), corresponding to approximately ± 2 dB.

After suitable high and lowpass filtering, the recorded unit responses were fed to a level discriminator, the output of which was led to an Intertechnique Physioscope (DIDAC 800) set to produce cycle histograms (bin width 0.18 msec). These histograms were punched on paper tape and read into a general purpose computer where circular cross-covariance functions between one noise sequence and these histograms were computed (see Møller, 1974*b*). The principles for stimulus generation and for data processing are shown in Fig. 2. The stimuli were presented during 5 sec followed by 5 sec of silence in order to reduce fatigue. Under each stimulus condition (2.5 min effective stimulation time) 5 min of data were usually processed. Discharges were recorded during stimulus presentation only.

Peristimulus time histograms were made of the responses to 50 msec tone bursts by the Intertechnique Physioscope.

The use of the present method rests on the assumption that the system under test can be regarded as functioning in the way a linear system does under the stimulus conditions used. The results of earlier studies (Møller, 1973*a*) suggest that so is the case provided that the modulation is kept within the range given above and provided that the sound level at the carrier frequency is kept above threshold. A situation where that may not be the case is when the carrier is located outside the response area, e.g. at a frequency above the unit's response area. To understand this contradiction, the modulation sound should be viewed from its spectrum which can be described as a carrier with two broad sidebands each of a width equal to the bandwidth of the lowpass filtered noise serving as modulation. If these sidebands, but not the carrier, extend within the response area of the unit, the unit consequently is excited in accordance with the extent of the sidebands. When the carrier is located above the unit's response area, the threshold is exceeded by parts of the low-frequency sidebands that correspond to the high-frequency components of the noise. The recording will thus contain information about the time at which such high-frequency components in the noise occur. This information is not likely to be related to the correlation of the temporal pattern of the noise as would be the case if the noise was passed through a linear system. Since the noise repeats itself these high-frequency components will have the same location within a noise period. This type of non-linearity may result in a correlogram in which significant energy occurs at long lags. This type of non-linearity is easily recognized by the distribution of energy over a large range of delays and from the coherence spectrum (see Møller, 1973*a*, 1974*b*) that in such cases has low values.

RESULTS

The results of the present study are based on recordings from fifty-five units in twenty-eight animals. The characteristic frequency of the units ranged from 2 to 45 kHz. Units were often kept in good shape for several hours. Only units that: functioned well for more than 30 min; responded with a sustained train of discharges to a continuous tonal stimulation; and had a cross-covariance function latency of less than 5 msec, are included in this account.

Fig. 3 shows a typical cross-covariance function (continuous line) between a cycle histogram of the discharges and the envelope (modulation) of the stimulus sound. The stimulus consisted of a tone at the unit's characteristic frequency, amplitude-modulated with pseudorandom noise. The cross-covariance at a certain delay t represents the firing rate that can be expected at a time equal to t after a hypothetical brief increase in the

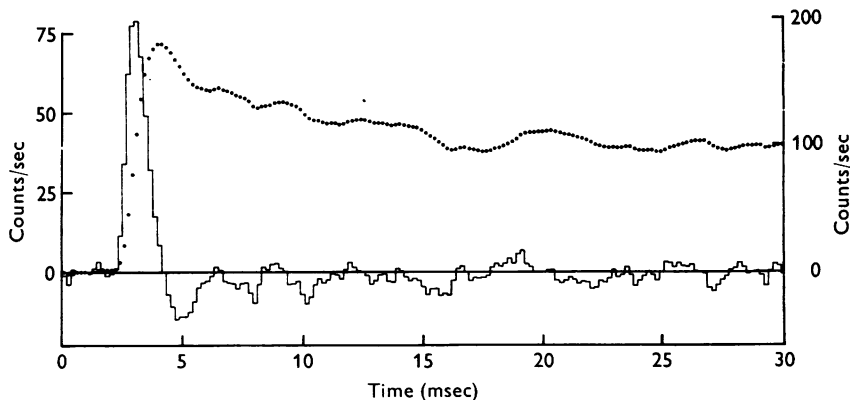


Fig. 3. A typical cross-covariance function (continuous line and left hand scale) computed from the responses to stimulation with a tone that is amplitude-modulated with pseudorandom noise. The dots (and right scale) show the integrated cross-covariance function corresponding to the step response of the system under test. The stimulus was a 32.0 kHz tone equal to the unit's characteristic frequency with an intensity of approximately 20 dB sound pressure level, SPL (10 dB above threshold). The curves are based on 4 min of data. The stimulus was on during half that time (2 min). The modulation was 22% RMS, and the average discharge rate was 190 discharges/sec (unit 224.2).

stimulus intensity. An upward deflexion indicates that an impulse increase in stimulus intensity results in an increased discharge rate. Correspondingly, a downward deflexion means a decrease in probability of firing in response to an impulse increase in stimulus intensity. The base line represents the firing rate without modulation. The right vertical scale gives the change in discharge rate that a square wave modulation of the same energy as the noise would give rise to if the system under test was an ideal linear system. Correspondingly the left scale refers to the cross-covariance and gives the change in discharge rate that would occur if the system was an ideal linear system and the input was modulated with an impulse with the same energy as the noise. The integrated cross-covariance function shown in Fig. 3 (filled circles) is an approximation of the system's

step response function, i.e. the discharge rate that can be expected after applying a hypothetical step increase to the stimulus intensity.

The integrated cross-covariance function shows an increase in firing rate that undergoes a brief period at a high value and then decreases to a lower value. This decrease in firing rate indicates that the response to the small hypothetical step increase in the stimulus intensity is adapting. The adaptation, having its lowest value for stimulus intensities immediately above the unit's threshold, increases with stimulus intensity. In some units, under special stimulus conditions, the integrated cross-covariance may adapt to a value that is close to its initial value, indicating that there is little or no increase in discharge rate for a steady increase in stimulus intensity.

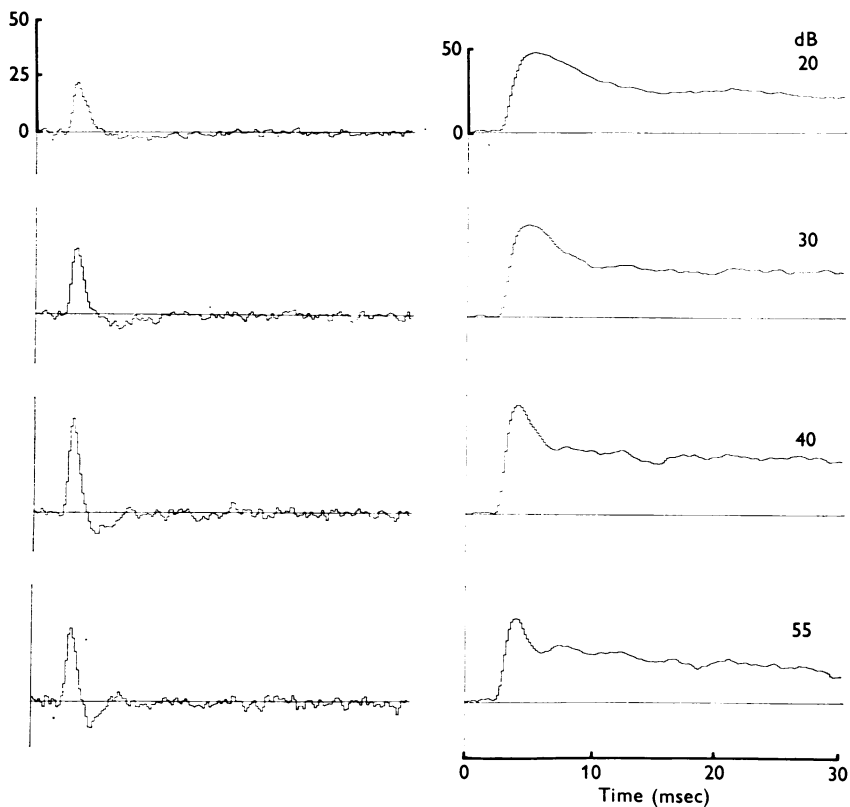


Fig. 4. Typical impulse responses and step responses of a type I unit determined at different stimulus intensities. The unit's characteristic frequency was 20.1 kHz and the modulation was 13% RMS. Each graph represents 10 min of data. The average discharge rate in pulses/sec was: at 20 dB, 77; 30 dB, 110; 40 dB, 169; 55 dB, 204 (unit 162.1).

Two general classes of units can be discerned on the basis of their impulse and step response properties: one having a moderate degree of adaptation (Type I) and another having much greater adaptation and possessing impulse and step response functions with damped oscillations (Type II).

Fig. 4 gives typical examples of the first class of units. The impulse response functions have a single peak followed by only one (small) negative deflexion. The corresponding step response shows only a moderate depression after its initial peak. Adaptation increases only slightly with increasing stimulus intensity.

The unit depicted in Fig. 5 is a typical example of the second class of units. Its degree of adaptation is high and several oscillations appear in

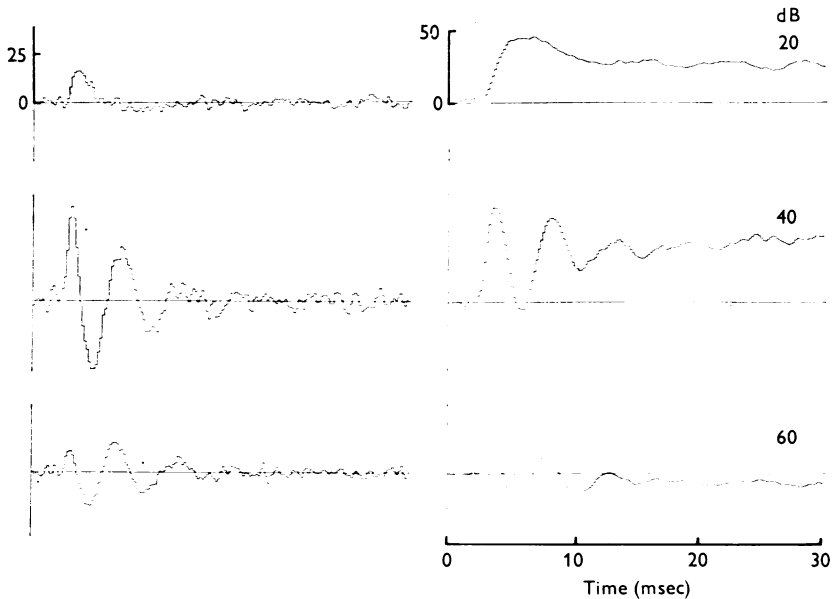


Fig. 5. Typical impulse responses and step responses of a type II unit at different stimulus intensities. The characteristic frequency of the unit was 13.5 kHz and the modulation was 22% RMS. Each graph represents 5 min of data. The average discharge rate in pulses/sec was: at 20 dB, 75; 40 dB, 195; 60 dB, 79 (unit 185.1).

the impulse and step response functions, except at the lowest stimulus intensity.

When the stimulus intensity is increased the amplitude of these damped oscillations usually increases and the oscillation damps out more slowly. In contrast, the frequency of the oscillations is almost independent of the

stimulus intensity as illustrated in Fig. 5. The step response function in this group of units reveals that the initial increase in discharge rate following the hypothetical increase in stimulus intensity is in turn followed by a reduction to a value lower than before the step was applied.

Examination of the cross-covariance functions of Type II units shows that the initial increase in discharge rate by and large has a much shorter duration than the succeeding opposite deflexion (adaptation), although in a few units the responses are nearly symmetrical. The following waves of the oscillation in the cross-covariance function invariably have a duration that is very close to that of the first negative deflexion.

In some units the step response's initial peak becomes narrower with increasing stimulus intensity and consequently its entire area decreases with increasing stimulus intensity. The result manifested in the step response function is a decrease in the initial deflexion with increasing sound intensity.

In many Type II units the area of the brief negative deflexion in the impulse response function that follows the initial positive deflexion becomes larger than that of the positive deflexion at certain stimulus levels (Fig. 5).

The peak amplitude of the integrated cross-covariance function is influenced rather little by the average stimulus intensity regardless of unit class. This observation shows that a certain proportional step change in stimulus intensity gives rise to almost the same change in discharge rate over a rather wide range of stimulus intensities. In other terms, small rapid changes in stimulus amplitude are transmitted over a large range of average stimulus intensity independently of whether or not the average discharge rate changes as a function of stimulus intensity.

Inhibitory effects

The above described characteristics were obtained in response to stimulation with a single tone at the unit's characteristic frequency. In most units of the cochlear nucleus the activity driven by a tone at characteristic frequency can be inhibited by a second tone within certain ranges of frequencies. It has been shown earlier that cross-covariance has almost the same shape when two tones, one excitatory and one inhibitory, are presented simultaneously, one or both being modulated (Møller, 1975*a*, 1976).

A tone immediately above the unit's response area is usually the most efficient inhibitory stimulus. Fig. 6 shows examples of the cross-covariance and integrated cross-covariance functions from an exemplary Type II unit when two tones were presented simultaneously, one excitatory at the unit's characteristic frequency and one inhibitory at the unit's best inhibitory frequency. Either the excitatory tone or the inhibitory tone was modulated. The response to modulation of the inhibitory tone is seen to exhibit

damped oscillations almost the exact inverse of those of the response to modulation of the excitatory tone.

Fig. 7 shows similar recordings from a unit that does not show any damped oscillation in its impulse response function (Type I). The

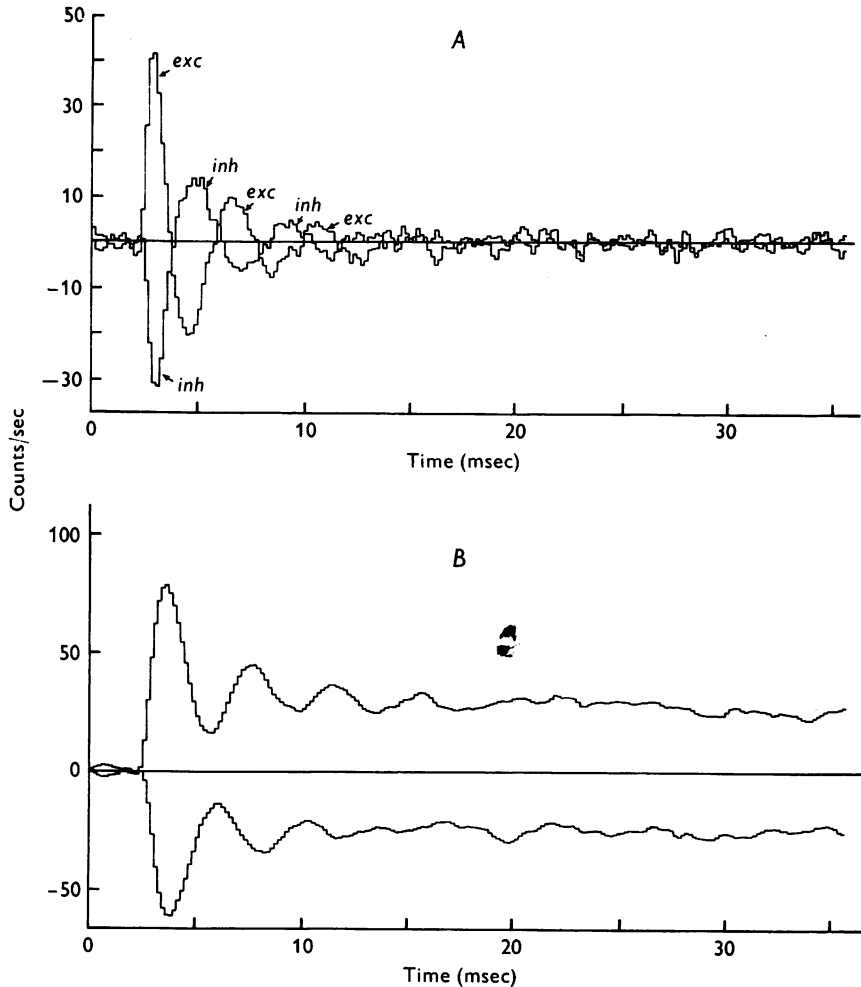


Fig. 6. *A*, cross-covariance and *B*, integrated cross-covariance of a type II unit stimulated with two tones, one excitatory and one inhibitory. Results upon modulation of the excitatory tone are indicated by an initial upward deflexion in the cross-covariance function (*exc*) and those upon modulation of the inhibitory tone are indicated by an initial downward deflexion (*inh*). The excitatory tone had a frequency of 18.9 kHz and the inhibitory of 20.9 kHz. Both tones had intensities of 75 dB SPL. Each graph represents 10 min of data and the average discharge rate was 220 pulses/sec. The modulation depth was 22% RMS (Unit 162.2).

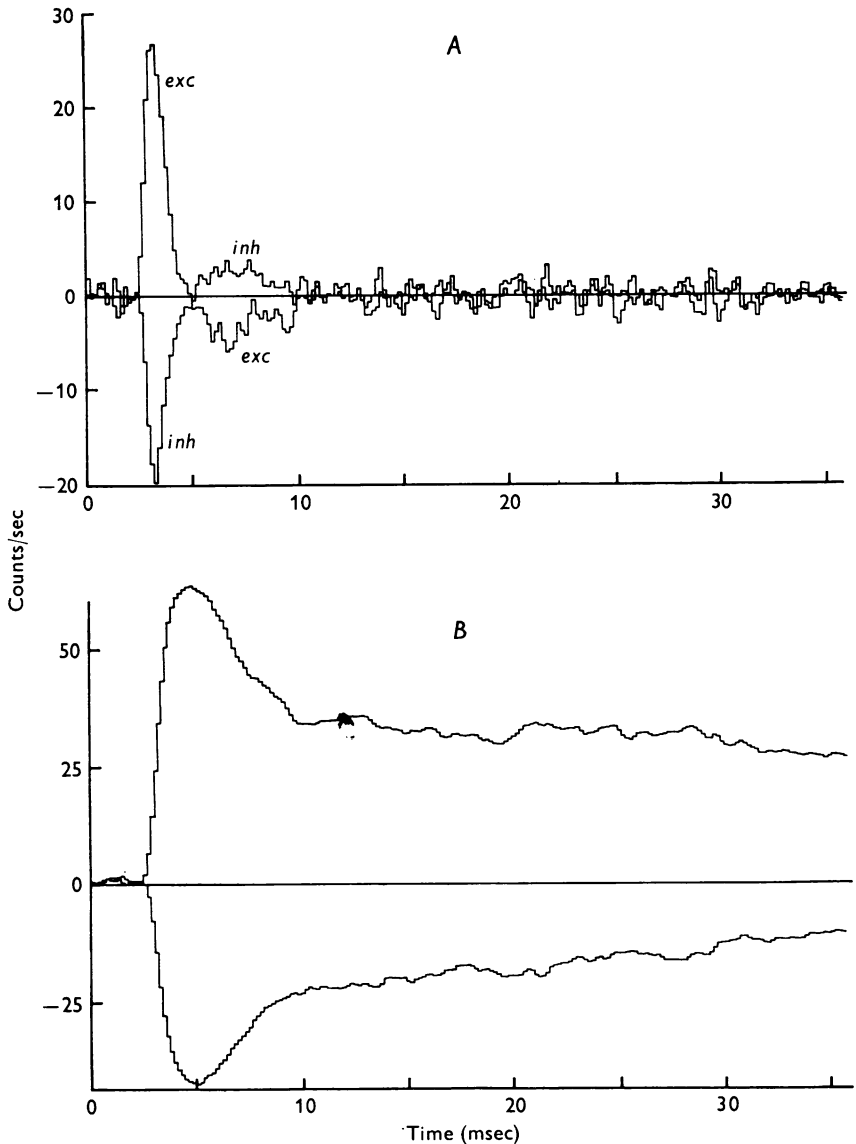


Fig. 7. Similar graph to Fig. 6 but from a Type I unit. The excitatory tone had a frequency of 20.1 kHz and the inhibitory of 22.25 kHz. Their intensities were 45 and 50 dB SPL respectively. Each graph represents 10 min of data and the average discharge rate was 110 pulses/sec. The modulation was 13% RMS (Unit 162.1).

adaptation in the response to an intensity change of the excitatory tone is seen to resemble closely the adaptation in the response to an intensity change in the inhibitory tone.

Thus, in both types of units, adaptation for inhibition and for excitation follows by and large the same time course.

Of fifty-five units (in twenty-eight rats) that were studied in detail, twenty-nine had pronounced damped oscillations in their impulse and step response functions (Type II) whereas twenty-six had no oscillations (Type I). Of these latter units, nineteen had a low degree of adaptation as judged from the small negative swing in their impulse response function whereas seven had a higher degree of adaptation. However, these seven showed only a single rather negative swing in their impulse response function, and thus no oscillations. A word of caution may be appropriate here. Micro-electrodes are no doubt biased with regard to the morphological properties of units. The distribution of units encountered by a certain electrode may thus not be a true picture of the real distribution of units in the entire cochlear nucleus.

Linearity

The shape of the computed impulse or step response function is largely independent of the modulation depth as long as the depth does not reach the value above which the effect of the non-linearities becomes significant. Fig. 8 shows the impulse response computed from the responses obtained with two different degrees of modulation, 22 and 13 % RMS. The amplitude scale has been corrected in accordance with the different degrees of modulation. A lower modulation depth calls for a longer time of averaging data in order to ensure a certain statistical stability. In the two graphs in Fig. 8 the observation time was the same (5 min) and therefore the recording obtained at the lower modulation depth is somewhat more noisy than that obtained at a higher modulation.

Stability

The impulse and step response functions determined from the responses to noise-modulated tones from the same unit show a good stability over long periods of time. Fig. 9 displays the step response recorded shortly after the unit was encountered, and 1.5 and 3 hr later. The response function did not change significantly, indicating that the dynamic properties of the unit were not influenced by the sound exposure or by the presence of the recording electrode. Such a stability of the dynamic properties over a long time is a constant finding. The spontaneous activity occasionally changes during a recording session, but the shape of the impulse or step response changes rarely. Even in units in which the

discharge rate in response to a tone of a certain intensity varies from time to time, the step response function as a rule is constant during recording over a long time. The dynamic properties of these units are found to have a strong resistance to fatigue and other changes such as the irritating effect of the electrode that may occur during recording for several hours from the same unit.

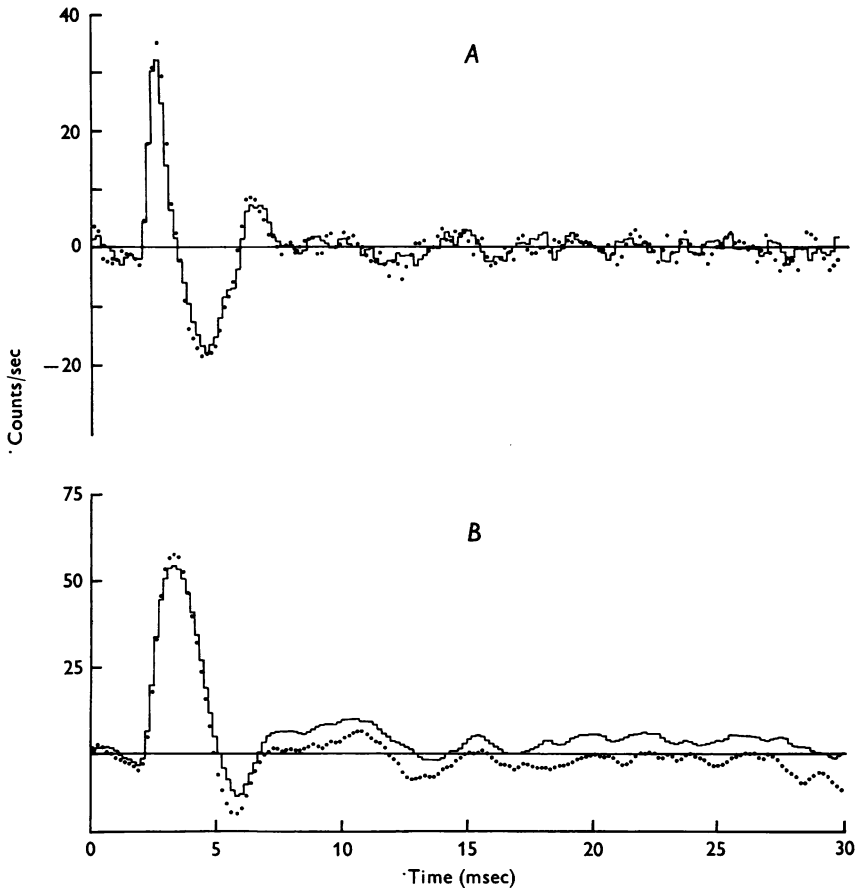


Fig. 8. *A*, Impulse responses and *B*, step responses computed from the responses to an amplitude-modulated tone at two different modulation depths, 22% (dots) and 13% (continuous line). The vertical scale refers to the graph showing the response to a 22% modulation tone. The values of the other curve have been multiplied by 1.69 to facilitate comparison of the shape of the curves. Each curve represents 5 min of data. The stimulus tone had a frequency of 33.3 kHz and an intensity of 30 dB SPL. The average discharge rate was 187 pulses/sec (Unit 172.2).

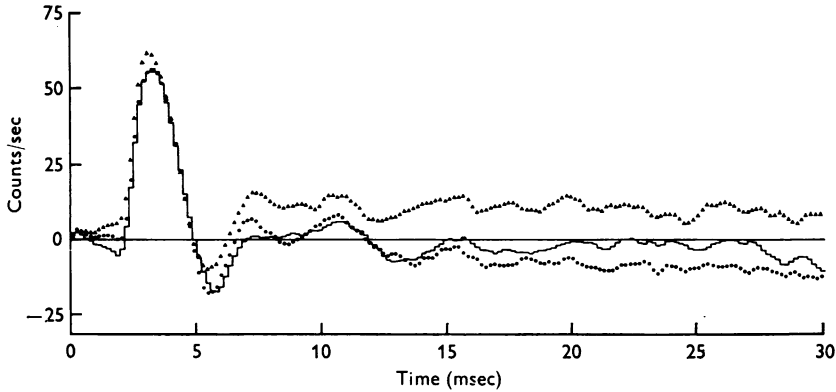


Fig. 9. Step response functions obtained at three different times during recording from a unit. Directly after the unit was encountered (continuous line), 1.5 hr later (filled circles) and 3 hr later (triangles). Each curve represents data obtained over 5 min (2.5 min of stimulation). The average discharge rates were 187, 213, 213 pulses/sec. The intensity of the tone was 30 dB SPL (20 dB above threshold), its frequency equal to the unit's characteristic frequency (33.3 kHz) and the modulation was 13% RMS (Unit 172.2).

DISCUSSION

The step and impulse response functions determined in the manner described in the present investigation provide a general description of the dynamic properties of neurones responding to a continuous sound stimulation with a sustained train of discharges, under conditions of small changes in stimulus intensity. The responses showed no systematic dependence on the unit's characteristic frequency for characteristic frequencies ranging from 2 to 45 kHz.

Two distinct classes of units with respect to adaptation have become apparent: Type I, in which the cross-covariance function has a single peak and Type II, in which the cross-covariance has damped oscillations following an initial peak. The oscillations in the step response functions of Type II neurones are indicated to be a result of an automatic gain control system (servo system) that tends to keep the average discharge rate as close as possible to a constant value. A small change in the stimulus sound level such as a brief impulse or a step increase or decrease in stimulus intensity gives rise to an 'error signal' that regulates the discharge rate back to its normal value. The discharge rate in response to a step increase in stimulus intensity can increase appreciably before the delayed and rather slow feed-back system acts to return the discharge rate to its original value. The response to a step change in excitation thus is a damped

oscillation around a certain value before a new, stable value is obtained. In many units the regulation has a certain overshoot and decreases the discharge rate for a short period to a level below the value it had before the step increase. The result may be several oscillations as are seen in the Type II neurones described in this paper. Similar responses are seen in many other biological control systems (Ratliff, Knight, Toyoda & Hartline, 1967; Ratliff, Knight & Graham, 1969; Enroth-Cugell & Shapley, 1973) and have been suggested to exist in the cochlear nucleus by Allanson & Whitfield (1956). The response of such a feed-back system is governed by the gain and the phase shift (delay) around the feed-back loop. A damped oscillation will appear whenever the loop gain in a negative feed-back system has a value below but close to one at the frequency at which the loop phase shift is 180° . If the gain is precisely one, the system will produce a maintained oscillation; if it is above one the system will be unstable and oscillate with increasingly higher amplitude until reaching saturation.

The damped oscillation in the impulse response function implies that sinusoidal changes in stimulus intensity are transmitted best in a narrow frequency band around the frequency of the damped oscillation. Higher as well as lower frequencies are attenuated to an extent related to the degree of damping of the oscillations in the impulse response function. The relative transmission of amplitude modulation plotted as a function of modulation frequency (frequency transfer function) thus shows a peak at the frequency equal to that of the damped oscillation (cf. Møller, 1972, 1973*a*, 1974*a*). The peak is narrower at high stimulus intensities than at low ones and near threshold the transfer function may have a lowpass character corresponding to the situation where there is no oscillation in the impulse response function.

In Type I units the response functions reveal either little adaptation or a moderate degree of such. No damped oscillation is seen in the impulse or step response functions indicating that these units possess no such regulation. Consequently the frequency domain transfer functions of the units with regard to modulation are lowpass functions.

The responses to tone bursts as revealed by the peristimulus time histograms are different from the step response functions computed from the responses to amplitude-modulated tones. Thus the oscillations often seen in such peristimulus time histograms are not identical to the damped oscillations in the impulse and step response functions. Such oscillations in the peristimulus time histograms of the responses to tone bursts, seen in neurones with a fairly regular discharge rate, result from the tendency to synchronize discharges with the onset of a tone burst. The oscillations in the peristimulus time histograms in response to tone bursts

are thus peculiar to the situation in which the stimulus abruptly attains a high suprathreshold value from below threshold. A continuous background stimulus slightly above threshold greatly diminishes these oscillations, in most cases totally abolishing them.

The latency of the response to tone bursts usually decreases with sound intensity whereas the latency of the response to noise-modulated tones is almost independent of sound intensity (Møller, 1975*b*), this being another important difference between the two.

The similarity between the transfer functions obtained using noise-modulated tones and sinusoidally modulated tones (Møller, 1972) indicates that the properties described throughout this paper are operating on different types of sounds.

It should also be noted that the above classification concerns units that respond to continuous sounds with a sustained train of discharges. There is a third group of units in the cochlear nucleus that responds only to transient sounds (transient units; Møller, 1969*b*). In such a classification this group could be named Type III units.

This work was supported by the Swedish Medical Research Council (Project No. 04X-90 and P-3251). Computer time was made available by the Karolinska Institute.

REFERENCES

- ALLANSON, J. T. & WHITFIELD, I. C. (1956). The cochlear nucleus and its relation to theories of hearing. In *Third London Symposium on Information Theory*, ed. CHERRY, C., pp. 269–284. London: Butterworth.
- BENDAT, J. S. & PIERSOL, A. G. (1966). *Measurement and Analysis of Random Data*. New York: Wiley.
- ENROTH-CUGELL, C. & SHAPLEY, R. M. (1973). Adaptation and dynamics of cat retinal ganglion cells. *J. Physiol.* **233**, 271–309.
- LEE, J. W. (1960). *Statistical Theory of Communication*. New York: Wiley.
- MØLLER, A. R. (1969*a*). Unit responses in cochlear nucleus of the rat to pure tones. *Acta physiol. scand.* **75**, 530–541.
- MØLLER, A. R. (1969*b*). Unit responses in the cochlear nucleus of the rat to repetitive, transient sounds. *Acta physiol. scand.* **75**, 542–551.
- MØLLER, A. R. (1971). Unit responses in the cat cochlear nucleus to tones of rapidly varying frequency and amplitude. *Acta physiol. scand.* **81**, 540–556.
- MØLLER, A. R. (1972). Coding of amplitude and frequency modulated sounds in the cochlear nucleus of the rat. *Acta physiol. scand.* **86**, 223–238.
- MØLLER, A. R. (1973*a*). Statistical evaluation of the dynamic properties of cochlear nucleus units using stimuli modulated with pseudorandom noise. *Brain Res.* **57**, 443–456.
- MØLLER, A. R. (1973*b*). Coding of amplitude modulated sounds in the cochlear nucleus of the rat. In *Basic Mechanisms in Hearing*, ed. MØLLER, A. R., pp. 593–619. New York: Academic Press.
- MØLLER, A. R. (1974*a*). Responses of units in the cochlear nucleus to sinusoidally amplitude-modulated tones. *Expl Neurol.* **45**, 104–117.

- MØLLER, A. R. (1974*b*). Use of stochastic signals in evaluation of the dynamic properties of a neuronal system. *Scand. J. Rehabil. Med.* suppl. 3, 37-44.
- MØLLER, A. R. (1975*a*). Dynamic properties of excitation and inhibition in the cochlear nucleus. *Acta physiol. scand.* **93**, 442-454.
- MØLLER, A. R. (1975*b*). Latency of unit responses in the cochlear nucleus determined in two different ways. *J. Neurophysiol.* **38**, 812-821.
- MØLLER, A. R. (1976). Inhibition and excitation in the cochlear nucleus studied using amplitude modulated tones. *Expl Brain Res.* (in the Press).
- RATLIFF, F., KNIGHT, B. W., TOYODA, J.-I. & HARTLINE, H. K. (1967). Enhancement of flicker by lateral inhibition. *Science, N.Y.* **158**, 392-393.
- RATLIFF, F., KNIGHT, B. W. & GRAHAM, N. (1969). On tuning and amplification by lateral inhibition. *Proc. natn. Acad. Sci. U.S.A.* **62**, 733-740.