DIRECT RECORDING OF THE ACTION CURRENTS OF THE NERVE TRUNKS AND A QUANTITATIVE ASSESSMENT OF NERVOUS ACTIVITY

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In physiological experiments there is frequently need to record the electrical activity in nerve trunks together with other processes and to compare the functions quantitatively. The experimenter then encounters considerable difficulties.

The first is due to the impossibility of recording the electroneurogram (ENG) on ten recorders; these recorders are widely used and are in many ways convenient, but they have a frequency cut-off below 100 cycles and are not well suited to recording rapid processes. It is on this account, as in other cases where high-frequency potentials are to be recorded, that for electroneurography photographic methods of recording are required; however, it is known that they show a number of shortcomings. The inconvenience of the string oscillograph or cathode ray tube is felt in particularly acute form if during the experiment a long continuous recording is required where there is a need for immediate comparison of the changes in the ENG with other indices (for example the EKG, EEG, blood pressure, respiration, etc.).

The second difficulty concerns the approach to a quantitative evaluation of complex neurograms obtained in leads from nerve trunks or from more or less thick bundles of nerve fibers. This estimate is often very approximate and made "by eye" or by use of laborious graphical methods of visual measurement of the "amplitude" and counting the "frequency" of the different impulses making up the neurogram. Often this count can be made only at high sweep speeds (of the order of 100 cm or more per second), and even then is extremely coarse; the high scanning speed is often very inconvenient and frequently incompatible with simultaneous recording of slower processes. Also when a visual estimate of the neurogram is made it is difficult to find a criterion which effectively reflects the "electrical activity" of the nerve and the amount of information transmitted.

Indeed, according to modern views, the function of each separate nerve fiber is to transmit information in terms of a sequence of separate pulses, each pulse having identical shape and amplitude. Evaluation of the "activity" of a single nerve fiber does not involve any major difficulties: an objective judgement of the amount of information transmitted over any interval of time may be made from a simple count of the number of isolated impulses recorded on the corresponding section of the electroneurogram.

However the position is different when the potentials are led off from a nerve trunk consisting of a mass of fibers of various diameters, and when the impulses from the separate nerve fibers reach the electrodes they are changed to a considerable extent according to their position in the nerve and the position of the electrodes, and on many other factors. Therefore from the point of view of the observer the complex neurogram represents the combined effect of impulses of random amplitude occurring at random times and therefore the instantaneous value of the neurogram itself has a randomly determined value.

On this account it appears that what is required is to employ some statistical criterion of the electrical neurogram which is related only to the number of impulses transmitted along the nerve trunk in an interval of time τ*. It is easy to see that neither the amplitude nor the "frequency" of the net impulses is itself such a criterion. A certain number of unit impulses falling on the pick-up electrode may form either a low-amplitude or a long "net"

*Strictly speaking we are interested only in the amount of information transmitted along the nerve in a time τ. However, it can be shown that in a system transmitting information (a code) in terms of unit impulses (binary code) the amount of information is directly proportional to the number of impulses transmitted.

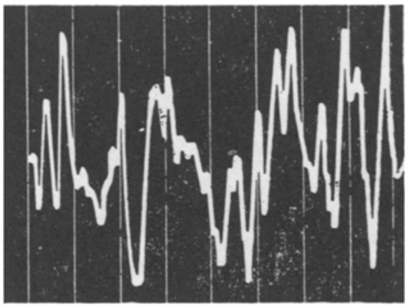

Fig. 1. Neurogram of the phrenic nerve of a rabbit. Part of a respiratory volley. Photograph from screen of oscillograph, Scan speed 200 cm/second.

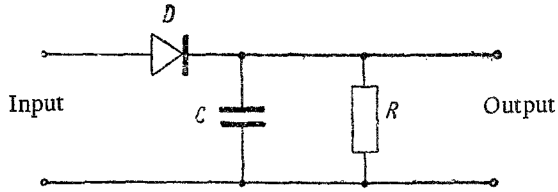

Fig. 2. Circuit of a diode detector.

pulse, or else a high-amplitude short pulse according to their temporal and spatial distribution. In just the same way the "frequency" of the net signal is inevitably related to the frequency of the unit impulses.

In most cases (if not always), with appropriate amplification and a sufficiently rapid scan this effect may readily be seen on recordings of the total complex electroneurogram (Fig. 1). It is understandable that the "amplitude of the impulse" and the "frequency of the impulses" cannot be used in an attempt to evaluate such records visually (thus, for example, the term "impulse" loses its definite physical significance and ceases to correspond to its physiological equivalent).

Statistical methods may be used to show that the mean value of the total neurogram* represents the required quantity corresponding to the frequency of the random unit impulses.

Thus in many cases instead of a record of the electroneurogram itself it may be more advantageous to record only its mean value, a procedure which is advantageous from the point of view of method and greatly extends the experimental practicability**. Because the mean value of the electroneurogram alters comparatively slowly it may readily be recorded by the ordinary writing heads, and the record obtained may easily be evaluated quantitatively.

The practical realization of the principle just described of recording the electroneurogram is based on well-known laboratory procedures, and requires practically no additional apparatus. The simplest circuit for obtaining a mean value is a diode detector (Fig. 2). The diode D rectifies the applied signal converting it into a direct voltage. The rectified signal is fed to a RC circuit. If a time constant τ = RC is chosen so that τ is considerably greater than the duration of the longest impulse in the total neurogram, then at the output of the circuit a voltage will be produced whose instantaneous value at a moment t will be approximately equal to the mean value of the signal at the output over the period τ (i.e., the average value will be found for the period extending from $t-\tau$ to t).

From what has been said above it can be seen that the instantaneous value of the voltage at the output of the detector is proportional to the amount of information transmitted along the nerve during the time τ = RC preceding the moment of observation. The whole area enclosed by the graph of voltage at the output of the detector up to time t_1 is proportional to the information transmitted along the nerve in time $t_1 - t$, less some constant related to the amount of noise and stray pick-up.

In order to record relatively rapid changes in the mean value of the neurogram the averaging time (i.e., τ = RC) must be sufficiently small in relation to the time of rise (or decay) of the mean value. In practice it is sufficient if the condition: RC < T/3-5 is fulfilled, where T is the least time for a threefold change in the mean value. Thus the time constant RC of the circuit must be chosen so as to satisfy the condition: $t_2 \ll RC \ll T$, where t_2 is the duration of the longest impulse of the electroneurogram***. In choosing the values of R and C it must be remembered

*By mean value of the function $y = f(t)$ over a period τ is understood the quantity

$$y_\tau = \frac{\int_{t^0-\tau}^{t^0} f(t)\,dt}{\tau},$$

or from the geometrical point of view the area contained between the curve $y = f(t)$, the axis t, and the verticals $t - t^0$ and $t = t^0 - \tau$, divided by τ.

**It will be understood that recording the mean value of the electroneurogram may be convenient in many cases for a study of the activity of separate nerve fibers.

***In most experiments we use a circuit with τ = 0.1 seconds (R = 50 kohm; C = 2μF).

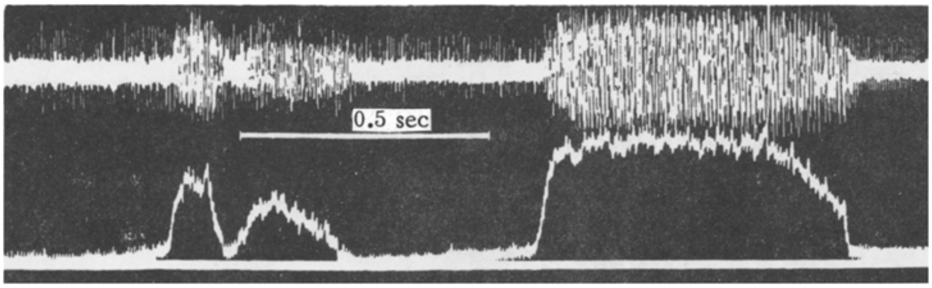

Fig. 3. Parallel recording on a string oscillograph of the electroneurogram of the phrenic nerve of a rabbit (1) by the usual method and (2) by use of an averaging circuit. Two respiratory volleys are recorded at a film speed of 3 cm/second.

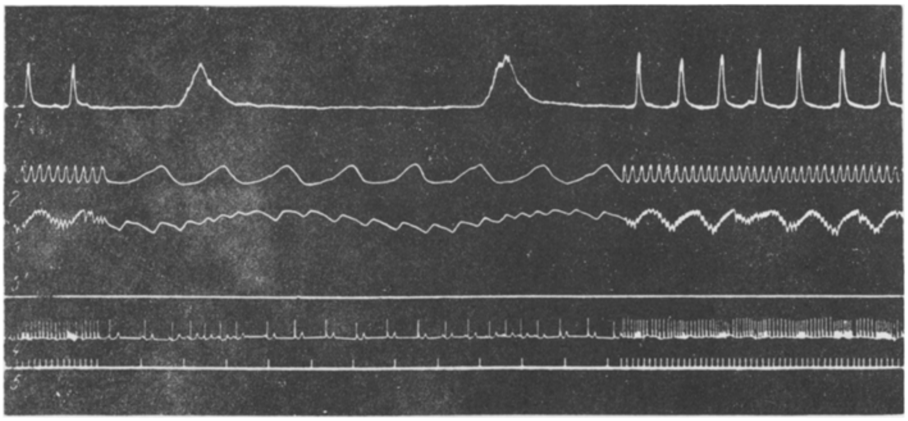

Fig. 4. Simultaneous recording on an ink-writing electroencephalograph of (1) the averaged electroneurogram from a canine vagus, (2) movements of air in the trachea during artificial respiration, (3) arterial pressure, and (4) the electrocardiogram. 3') Baseline of arterial pressure; 5) time marker (1 second). Left and right portions of the drawing were recorded at a speed of 2 mm/second, middle portion at a rate of 15 mm/second.

that the resistance of the circuit from the input side $R_i = R/2$, while the input resistance of the apparatus following the circuit must be 5-10 times greater than R.

The signal from the output circuit is best amplified by a DC amplifier. Then changes in the level of activity of the nerve of any frequency however low may be recorded. It is understandable that by appropriate setting of the baseline of the pen the average noise of the apparatus may be eliminated, and in cases when the only interest of the experiment is the increase of activity of a nerve above a certain steady level (for example respiratory volleys along the vagus) this "background activity" may be excluded from the record. If this is done, by increase of amplification the signals of interest in the experiment may be separated from the total electroneurogram; in this way their correlation with changes in other recorded quantities will be facilitated.

If the output signal from the detector is applied to a AC amplifier only those changes in the neurogram will be amplified whose frequency exceeds a certain threshold set by the low-frequency cut-off of the amplifier.

As far as the input to the detector the amplifier need amplify a band of only relatively high frequencies (for example from 100 cycles upwards). If this were not the case, slow potentials due to polarization of the electrodes and so forth, which need not be taken into account and which are not related to the neurogram, would reach the input to the detector. Such slow waves would be passed by the detector and might give rise to considerable artefacts. Various solutions to this problem will be applied according to the apparatus in use: if necessary a filter may be placed after the second pre-amplifier stage and before the input to the main amplifier; also additional filters in some intermediate stage of the main amplifier may be incorporated, etc.

It will be appreciated that if the main amplifier by itself possesses the necessary characteristics no further devices apart from the integrating circuit will be required.

For normal operation of the diode the amplitude of this signal at the input to the detector must be of sufficient amplitude (for example, for a germanium diode D-2 it must be of the order of 1 v).

Figure 3 shows an example of a parallel recording of a normal and of an average electroneurogram displayed on a string oscillograph.

Figure 4 illustrates a simultaneous ink recording of an averaged electroneurogram and other physiological processes. This sample volley was derived from an experiment on a dog under conditions of complete muscular relaxation while hypoventilation was maintained by artificial respiration. There is clearly no correlation between the respiratory volleys from the nuclei of the vagus (the electroneurogram was recorded from its central end) and the forced movements of the thoracic cage. On the other hand there is a very evident relationship between the vagal volleys, oscillations of the pulse and main arterial pressure (recorded from an electromanometer), and changes of the heart rate.

SUMMARY

A method is suggested which allows the electroneurogram from a bundle of nerve fibers or nerve trunks to be recorded on an ink-writing or other kind of instrument with electromagnetic heads having the usual frequency response of up to about 100 cycles per second. For this purpose rectification and integration of the signals of the neurogram was carried out by use of a simple diode detector whose output voltage was supplied to a DC amplifier feeding into a recording device.

It was shown that the values recorded in this way are proportional to the quantity of information (in a binary code) transmitted along the nerve.

The record obtained from the averaged electroneurogram facilitates objective quantitative assessment of nervous activity.