A STUDY OF THE ACTION CURRENTS OF NERVE WITH THE CATHODE RAY OSCILLOGRAPH

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The instruments which have been used heretofore for the observation of nerve action currents have been galvanometers of the moving coil or magnet type with or without the aid of a rheotome, the capillary electrometer and the string galvanometer. Each of these instruments possesses considerable inertia. The slower galvanometers are unaffected by single action currents and give a sustained deflection when the action currents are monophasic and rapidly repeated. The size of the deflection is the mean value of the individual waves which in turn depends upon their shape and the rate at which they are repeated. As the former is not known the deflections are mainly of qualitative significance.

All of these instruments are governed by the laws of forced vibration with damping. The differential equation expressing this law is

$$M \frac{d_2 y}{dt^2} + D \frac{dy}{dt} + Cy = f(t) \tag{1}$$

which says that the applied force, $f(t)$, produces a motion which is deter mined by the mass, M, the damping, D, and another restoring force' C, the mass effect being greater when the acceleration, $\frac{d_2 y}{dt^2}$, is large; the damping increasing with the velocity, $\frac{dy}{dt}$; and the restoring force, C, increasing with the deviation of the system from equilibrium.

The string galvanometer record gives the most nearly correct picture of the action current. Unfortunately, no sufficiently accurate means are available for correcting the curve to its true form. Valuable papers on the physics of the string galvanometer have been written by Einthoven (1) and by Fahr (2). The latter is more helpful in calculating the form in which a proven function will be returned by the string than in

determining the form of the original disturbance from the photographed record.

It is obvious that the curve given by the string is the graph of the curve expressing the value of y which is the solution of the above equation. To get the true form, i.e., $f(t)$, therefore, one would have to operate on y as indicated in the first member of the above equation. Such an attempt has been made by one of us (H. S. G.). While the operation is simple in theory it presents great practical difficulties. The method of determination depends upon a comparison of the mathematical solution of the movement of the string when a constant current is applied with the curve actually produced by the string. C can be readily determined. If M and D are determined from the curve produced by a very sensitive string as suggested by Fahr (p. 110), D may be determined, but M being found in a small remainder out in the less significant figures cannot be determined with any accuracy. M and D may also be calculated, when the frequencies of oscillation of two tightly stretched strings of known tension and therefore of known values of C have been determined, from the fact that the period of oscillation equals $\dfrac{4\,\pi M}{\sqrt{4\,CM - D^2}}$. The values found by this method are in fair accord with those obtained by the former method and also with those obtained by the method of the modulus of decay. In the actual correction of an action current curve the principal difficulty lies in the determination of the acceleration with satisfactory accuracy, and if one attempts to correct such a curve one finds that the first or acceleration term plays a large part in the correction. It is this term which is responsible for the initial upward concavity of the string record of a constant current. In the case of the action current of nerve the quick portion is completed in less than 2σ, which is during the period in which the string is actually within this initial concave portion. The accuracy of the corrected curve is dependent upon the accuracy with which the rate of change of direction of this portion of the curve can be measured. How great this correction is can be seen in a comparison of the record from a string galvanometer with the true form and potential as determined immediately afterwards, by means of the Braun tube oscillograph. The record (fig. 1) was made from the sciatic nerve of the bull frog using one panel of the amplifier for the string galvanometer and three panels for the Braun tube. Figure 2 is the replica of a Braun tube tracing from the same nerve whose action current is reproduced in figure 7. The records of the action currents as made by these two means are plotted on the same system of coördinates in figure 3. The potentials

for the string galvanometer reproduction are calculated from the calibration of the string with a constant current. It is seen that the greatest distortion by the string is of potentials of very short duration. In the oscillograph record the shock (or "escape"), A, is a distinct curve and the spot returns to the base line before the action current starts. In the string galvanometer reproduction the "escape", a, is still at its crest when the action current starts, and is very much reduced in amplitude.
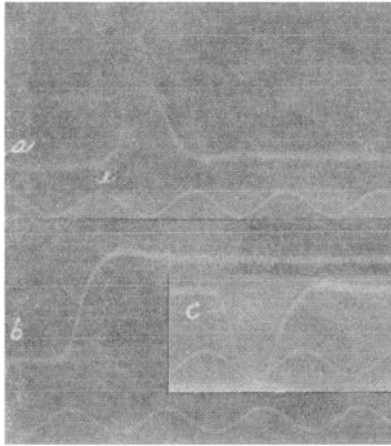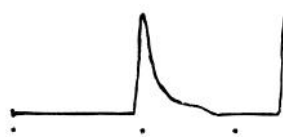

Fig. 1   Fig. 2

Fig. 1. String galvanometer records. One double vibration of the tuning fork = 10 σ. a, Action current of the sciatic nerve of the bull frog taken from the same nerve as figures 2 and 8. The short initial wave, e, is due to the shock. b, Calibration of the string and amplifier with a constant current of 3.75 mv. c, String deflection produced by a constant potential of 3.75 mv. lasting about 4.6 σ. In figure 8 is a Braun tube record of a 15 mv. potential of the same duration taken for comparison. (Reduced one-third.)

Fig. 2. Braun tube record of the shock and the beginning of the action current of the bull frog sciatic. X = 6.05 cm.; 1 mf.; 3000 $^{\omega}$ (1 $^{\omega}$ = 1 ohm); dots one sigma apart. (Natural size.)

Similarly it should be noted that it is the quick portion of the action current which is most reduced. In figure 3, C and c, are also reproduced, from figures 1 and 7, the calibration curves of the two instruments. The galvanometer string was so tense as to over-shoot slightly at the application of a constant current. Even so it did not reach its position of second equilibrium for about 4σ (1σ = 0.001 second). The gradual fall in the curve after this point is the effect of the amplifier condensers. The

curve is concave upward for most of the first two sigmas, during which
period the most rapid changes in the nerve action current take place,
and for this reason correction of string galvanometer records by the
laws of the capillary electrometer is unjustifiable. On the other
hand, a constant current produces an almost instantaneous rise of the
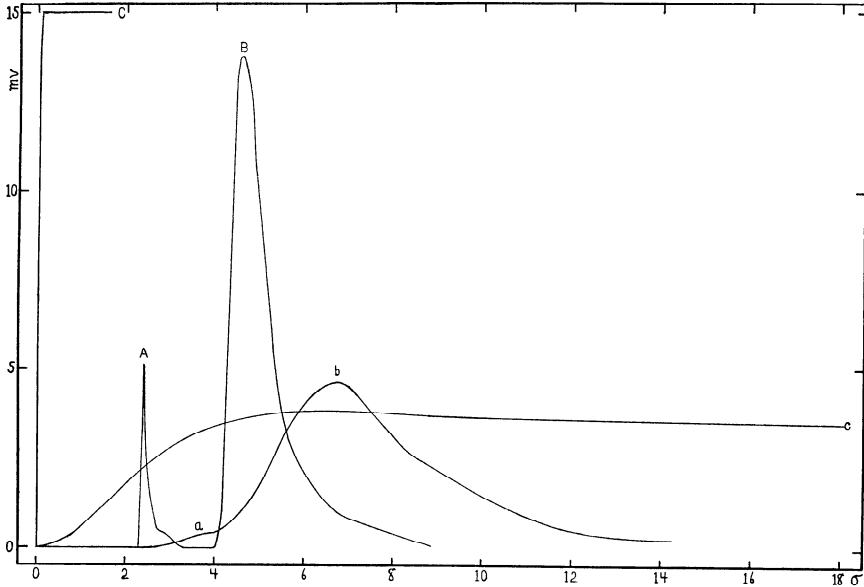oscillograph spot to its full height.

Fig. 3. The action currents of the bull frog sciatic, as recorded by the Braun
tube and string galvanometer, plotted in rectangular linear coördinates. *A, B,
C,* Braun tube records; *a, b, c,* string galvanometer records. *A, a,* shock; *B, b,*
action current; *C,* calibration with a constant current of 15 mv.; *c,* with one of
3.75 mv.

On account of the tedious procedure and the accumulated error in all
the measurements involved in the correction of the string galvanometer,
the study was temporarily abandoned for the investigation of a less
cumbersome method.

While the capillary electrometer shadow is much farther from the true
form than the string galvanometer shadow, it can be very much more
readily corrected. This is due to the fact that when the electrometer
is properly made the effect of the first or acceleration term becomes
negligible and therefore the characteristic is the well-known logarithmic

curve without any initial upward concavity in the record produced by a constant current, thus making possible the simple correction as developed by Lippmann, Hermann, Burch, Einthoven and others. The best of the corrected nerve action currents have been made with this instrument.

THE CATHODE RAY OSCILLOGRAPH. The need has long been felt of an inertialess system for recording physiological currents. One would naturally think of the Braun tube in this connection, but heretofore the discrepancy between nerve potentials and the potentials necessary to deflect the cathode stream has been too great to make its use possible. In the older tubes in which the electrons were liberated from the cathode by means of a high potential, e.g., 20,000 to 30,000 volts acting between the cathode and anode, both in a vacuum, the electrons once liberated were given such an acceleration in the potential drop that large forces were necessary for their deflection. With the invention of the hot cathode and Wehnelt cathode the electron emission could be obtained much more easily; but these tubes still operated under a high anode potential to give the electron stream sufficient velocity so that the pencil of rays would not spread as the result of the mutual repulsion of its constituent electrons. In order to avoid the necessity of the high potential and velocity Johnson (3) devised a tube which contains a very small amount of gas and operates upon a 300-volt anode potential. It is this tube which has made the present work possible.[1]

The Johnson tube consists of a Wehnelt cathode heated by a current from a storage battery controlled to about 1.2 amperes by a rheostat. It is by this rheostat that the focus of the spot is controlled. About 1 mm. from the cathode is the anode which is a platinum tube (A, fig. 5). Between the anode and cathode there is a 300-volt potential supplied by "Eveready" dry cells. On account of the small amount of gas in the tube, to prevent arcing the anode and cathode are enclosed in a small inside tube. They are separated by a platinum diaphragm which prevents the positive ions formed by electronic bombardment of the gas particles from all impinging on the cathode, thereby overheating and destroying it.

The electron stream passes through the platinum anode, forming a pencil of rays which impinge upon a fluorescent screen of willemite, painted on the end of the tube, and produce a greenish spot. This spot is clearly visible to the dark-adapted eye but has a low actinic value and

is therefore not easily photographed. Contact prints on photographic films can be made in 5 to 10 seconds, depending upon the rate at which the spot is moving (fig. 4). The easiest way of making permanent records is to trace the standing wave on the end of the tube and then to transfer the record from the tube by means of transparent architect's paper.

As a means of deflecting the stream of rays two pairs of small nickel plates are inserted in the tube. When these plates are connected to a source of potential the electrons move toward the positive member of the pair and away from the negative. If there is a changing potential on only one of the pairs of plates the spot will move along a straight line perpendicular to the pair of plates but if at the same time there is also a potential change on the other pair of plates then the spot will have a motion along the two axes of rectangular coördinates and will describe a figure determined by the nature of the two potential functions. If the motions in the two directions are cyclic and synchronous a standing wave results. Unless the in-

Fig. 4. Bull frog sciatic. The action current was recorded as a contact print on photographic film. To aid the photography the nerve was cooled from 26° (aquarium tank) to 15.4° and a slow deflection of the spot along the abscissa used. X = 6.05 cm.; 1 mf.; 9000 ω; distance between dots 1 σ. Time to maximum 1.52 σ. Arrows point to first and second catacrotic notches. On account of the light from the filament, the diffuse fluorescence and the dispersion of the light from the figure, this method is not very satisfactory and gives a poor idea of the actual clearness. (Natural size.)

ternal deflecting plates are connected conductively to the anode they accumulate a charge and the spot tends to drift. A leak has to be provided, therefore, between the pairs of plates as indicated by L, figure 5.

The electron stream can also be moved by a magnetic field in which case it moves at right angles to the field. Advantage was taken of this fact in placing the zero position of the spot. Naturally the spot is at rest in about the center of the screen, its exact position depending upon its relation to the earth's field. As it is desirable to start the spot at the left of center as one faces the tube, a magnetic field is
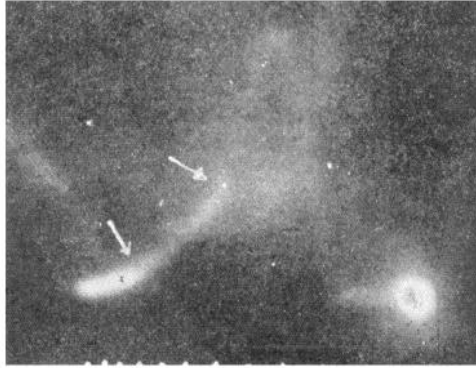
Fig. 5. Diagram of Braun tube oscillograph arranged for observation of nerve action currents. N = nerve, killed end shaded. E = non-polarizable electrodes connected through the three-stage amplifier with the horizontal plates, H, of the Braun tube, B. K = Wehnelt cathode; A = tubular anode; U = diaphragm; L = leak on horizontal plates; M = ammeter; R' = regulating resistance in filament circuit, K; R'' = resistance in anode circuit. The vertical plates, V, connect with the spreading device, O. D = discharging wheel, C = charging wheel and J = continuous contact wheel (metallic parts shaded) all connected conductively by F; R = charging resistance to 1 mf. condenser. I = rotating interrupter in primary circuit, P; S = secondary coil; T = stimulating electrodes grounded through G.   1 Ω = 1 megohm. For the intertube leaks labeled 2 Ω, 0.5 Ω was used.

produced by means of two series-connected solenoids placed one on either side of the neck of the tube. These are so placed that the field is vertical and downward, causing deflection to the left. The circuit consists of a single dry cell, the solenoid, a commutator and a small rheostat to control the strength of the field and therefore the degree of deflection.

The nerve potentials were impressed upon the horizontal or ordinate plates thus producing a vertical movement of the spot. In order to produce a movement along the axis of abscissae a device had to be made which would impress a changing potential on the vertical plates properly synchronized with that on the ordinate plates and also serve to record the time.

THE SPREADING DEVICE. It takes about 23 volts to produce 1 cm. of deflection along the abscissa, therefore 140 to 150 volts are necessary to produce the desired total deflection. Our earliest device, a diagram of which was published in the Proceedings of the American Physiological Society (4), was a rotating potentiometer. A circular resistance was made in segments to each one of which was attached a loop of chromel wire. Across the resistance was a 140-volt drop. One end of the resistance was connected to one of the vertical plates, the other plate was connected to a rotating brush operating on the shaft of a motor with a maximum velocity of 1800 r.p.m. Since the tangential velocity is constant the movement of the spot was linear. As the brush moved along the circular resistance the spot moved linearly to the right; as the brush jumped the gap between the ends of the resistance it came back to zero practically instantaneously, the process being repeated 30 times per second. This spreading device had the advantage that the time was a linear function of the distance along the X axis. It had the disadvantage that the velocity of the spot was determined by the speed of the motor, which therefore had to be recorded. The resistance was easily worn out by the rapid movement of the brush and the speed was limited. At 30 r.p.s. the movement of the spot was 2 M.p.s.

After considerable experimentation with various devices it was found that the most satisfactory scheme was one in which the movement of the spot was controlled by the charge of a condenser. This device has the great advantage that the velocity of the spot is independent of the speed of the motor being dependent only upon the capacity of the condenser and the resistance through which it receives its charge. The condenser being constant the speed is easily varied by changing the resistance. The apparatus has the following construction: a motor is mounted on a

heavy iron base and connected to a shaft in such a way that the shaft may be removed for the setting in place of contact wheels as desired. The motor speed is controlled through a rheostat.

If the inductive reactance is negligible, when a constant potential is impressed across the terminals of a condenser whose initial charge is zero, the potential of the condenser plates at any instant is determined by the expression

$$e - e \, \epsilon^{-\frac{t}{RC}} \tag{2}$$

where e is the impressed potential, ϵ, the base of the natural system of logarithms, t, the time in seconds, R, the resistance in ohms, and C, the capacity in farads. From this expression the desired resistance and capacity may be calculated for the necessary impressed potential of 140 volts. Such a calculation showed that ordinarily a 2-microfarad condenser charged through 1000 to 2000 ohms would give the proper rates of deflection.

The alternate charge and discharge of the condenser is effected by a rotating commutator mounted on the motor shaft. The wheels are made of hard rubber with conducting segments of phosphor-bronze inserted into the periphery. The exact construction can be seen by reference to this portion of the diagram in figure 5. The two large wheels are screwed together and their metallic parts are connected to each other and to the small continuous metallic wheel, J. About one-third of the charging wheel, C, is metallic and about two-thirds of the discharging wheel, D. The conducting segments are so placed that the brushes operating on the periphery are both in contact with the non-conducting rubber for a short segment between the charge and discharge. During the period in which the wheel, C, is making contact, current is flowing into the condenser at a rate determined by the 140-volt battery and the size of the resistance. The plates in the Braun tube are directly connected to the condenser plates and therefore have the same potential as the latter. The spot is thereby deflected at a rate determined by the second term in expression (2), the velocity being greatest at first and then falling off logarithmically. In recording potential changes which are also most rapid at the start, such as the action currents of nerve, this is an advantage. As the commutator wheel rotates, the charging is stopped when the brush runs over onto the rubber, then after a very brief interval the condenser plates are connected through the discharge wheel, D. To prevent sparking as the result of a too rapid discharge, a resistance of 100 ohms is inserted in this circuit; this still allows a

return of the spot to its zero position so rapidly as not to be visible. The process is repeated 20 times per second at the usual motor speed used. The condenser used in the earlier experiments was a 2-mf. paper condenser made by the Western Electric Company for telephone service. The capacity of this condenser was calibrated as follows: The charging time was determined from the rate of rotation of the motor and the length of the conducting segment of the charging wheel. Known high resistances or small intervals were employed which would not allow complete charging and therefore shortened the deflection; then knowing the total potential and the potential attained in the interval, the value of C in expression (2) can be calculated. For the value of the total potential the deflection of the spot when the condenser is fully charged was employed. This involves the assumption that the deflection is a linear function of the impressed potential which practically holds for the amounts of deflection involved.

It then follows from (2) that

$$C = \frac{t}{R \log_\epsilon \dfrac{X}{X - x}} \tag{3}$$

where X is the total length of the line when the condenser is fully charged, and x is the length of the line for the chosen values of t and R. After proving the accuracy of the method by obtaining in separate determina-

TABLE 1

RESISTANCE	X	x	CALCULATED CAPACITY
ohms			*microfarads*
7,000	5.78	3.7	22.08
10,000	5.65	2.9	21.82
20,000	5.65	1.7	22.08
30,000	5.65	1.2	22.10

tions with different values of R, values of 1.003, 0.995, 0.996 and 1.035 mf. for a 1-mf. condenser whose accuracy is guaranteed by the maker to be within $\frac{1}{4}$ per cent, the condenser used was calibrated. The results are given in table 1. They show that the capacity is a constant when calculated with the aid of different resistances, as is demanded by the theory; therefore when the capacity is known, the value of the time at any point on the abscissa may be obtained.

To render the calculation simple no leak is inserted between the vertical plates of the Braun tube. Such a leak is not necessary as any

accumulation of potential on these plates can pass off through the commutator wheel and the spot has no tendency to drift in the horizontal direction when this is running. In calculating the capacity of the condenser it is necessary to determine the internal resistance of the source of potential as this is added to the known resistance in delaying the filling of the condenser. This value was found to be about 50 ohms. The correction could have been obviated by using the condenser discharge but unfortunately this was not desirable because the spot loses its preciseness of contour when maximally deviated and potential changes occurring on the ordinate plates at the beginning of the discharge of the condenser, when the movement of the spot is fastest, do not produce as clear a figure. As any change in resistance in any part of the condenser circuit particularly at the brush contacts would introduce an error into the time values, the value of C is checked up as a matter of routine at each experiment. In later experiments a precision one microfarad mica condenser was used.

THE AMPLIFIER. As a potential of about 26 volts on the ordinate plates is necessary for a deflection of 1 cm., nerve potentials which lie in the range from 5 to 25 millivolts must be considerably amplified to produce a satisfactory deflection. The amplifier in its present form is shown as a skeleton diagram in figure 5. It was built to embody some improvements suggested by the experiments with the apparatus built by Newcomer and employed by Gasser and Newcomer (5) in a previous investigation. The panels are mounted in separate compartments in a heavy steel box 106 × 34 × 34 cm. in dimension. This rests on a thick cotton mattress and is surrounded by the same material. Each steel compartment is lined with cotton mattresses. The apparatus of each panel is mounted on steel plates about 1 cm. in thickness which rest on rubber sponges lying on the mattress on the floor of the compartment. The plates are grounded to the wall of the box and to them are connected the grid leaks and the negative sides of the filaments. The vacuum tubes are mounted on spongy rubber, so that as the combined result of the damping devices vibration is effectively eliminated. All wires are as short as possible. The connections to the A and B batteries pass directly downward through glass conduits to the battery compartment placed underneath the amplifier proper. Switches are so inserted in each panel that the amplifier may be used as a single panel, a two- or three-tube cascade or as two amplifiers of one tube each, or of one and two tubes. Some changes have been made since the diagram previously

published (4). One A battery supplies the first two panels since separate batteries were found to be unnecessary. The third panel has been modified so as to make the dynamic characteristic more nearly linear. The tubes used are designed with an amplification constant of 28 and for a maximum input voltage of two volts. When potentials of the order of those in nerve are applied to the input of the first tube the input potential to the third tube is higher than that for which the tube is designed and in the former system of connection the characteristic deviated from a straight line at input potentials to the amplifier of -5 and $+10$ mv. As no other type of vacuum tube, designed for a high maximum input voltage and having at the same time a high amplification constant, is available it was necessary to increase the negativity of the filament and then to increase the voltage of the plate battery to 300 volts. Accordingly a 3-volt battery was placed in the grid circuit. The negative side of the filament is given a potential of $+1.3$ volts by the resistances in series with it and thus the grid is given a total bias of -4.3 volts.

The Braun tube operates by the potential on its plates and its internal resistance is practically infinite so that it is a very much more favorable instrument for the amplifier to work into than is the string galvanometer. To keep the output resistance as high as possible the leak between the ordinate plates is a small one of 1 megohm. This not only allows a high voltage amplification in the last panel but helps to keep the dynamic characteristic straight.

The voltage amplification of each panel is about 20, making a total between 7,000 and 8,000 depending upon the time the tubes have been in use. The amplification was determined as follows. A dry cell of 1.502 volts was inserted in a circuit interrupted by a tuning fork one hundred times per second, the interruption being necessary on account of the condensers. Connected in this circuit through a commutator was a potentiometer which consisted of a 100,000-ohm resistance box, fractions of which could be led to the input. The tuning fork was adjusted so that the contact period was equal to the open circuit period. This was shown by the fact that the deflection of the beam in the Braun tube appeared as two equally bright spots at the ends of the line. The contact period was therefore 5σ and of sufficient duration to eliminate any effect on the values by the capacity of the resistance box. The deflections in the tube were then compared with the deflection which was produced by an unamplified potential similarly applied to the output condenser, the latter being identical with the deflection produced by the same potential applied to the tube directly. The results of the

calibration showed that a 1 cm. deflection of the spot was produced by 26.4 volts applied directly; by 1.43 volts when amplified by one tube; 0.079 v. by two tubes and 0.00357 v. by three tubes. This means amplifications of about 18.4, 334 and 7400 respectively for one-, two- and three-stage amplifiers, the amplification in the second and third panels being, therefore, 18.1 and 22.1.

For potentials up to 15 millivolts it is convenient to connect the nerve directly to the input. It frequently happens, however, that the nerve develops a potential considerably higher than this, causing the spot to go beyond the limits of the screen. It is also desirable for other reasons to keep the deflection small as corrections are necessary for large deflections. The amplification is decreased too much by the elimination of the third panel of the amplifier, but the desired deflection can be obtained by fractioning the input potential. When this was done by setting up a potentiometer with the 100,000-ohm resistance box used for determining the amplification, the potentials calculated from the fractioned wave regularly proved to be less than those from the unfractioned. This was finally traced to the resistance box. The latter is wound bifilar and therefore presumably has little inductance but an appreciable capacity, and the effect of the latter is to decrease the height of the waves. When the resistance box was replaced by a non-reacting resistance the potentials obtained by calculation from the fractioned waves agreed with those obtained from the direct input. A lavite resistance of 47,500 ohms made by the Western Electric Company is used. It is mounted as a shunt across the input (R', fig. 6) and can be put into use by closing a key.

As the internal resistance of the nerve is by no means negligible with respect to that of the 47,500-ohm shunt, it must be measured. This is done by means of a Kohlrausch bridge made with a non-reacting resistance of two 47,500-ohm units which used either singly or together give the proper resistance in the known arm for the range of nerve resistances. The source of current is a microphone hummer giving 1000 double vibrations per second and a balance is obtained with an appropriate double telephone receiver. The bridge is permanently set up (fig. 6) with a lead easily attached to the nerve connection through a double-pole switch, S', so that determination of the resistance of the nerve and electrodes is only a matter of a few seconds. The potential, E_n, in millivolts at any point on the action current curve can then be calculated from the formula

$$E_n = yV \frac{R_n + 47500}{47500} \tag{4}$$

where y is the ordinate, V is the number of millivolts per centimeter of deflection, and R_n is the resistance of the nerve. In these determinations the only grid leak from the first tube is through the potentiometer.

The dynamic characteristic of the amplifier working into the Braun tube was determined using the same input potentiometer arrangement as was used for determining the amplification. The results are plotted in
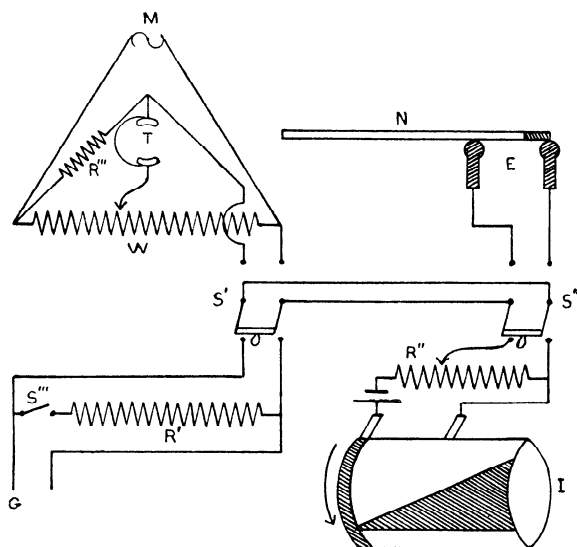

Fig. 6. Diagram of the arrangement of the input apparatus. The nerve, N, is connected directly by the electrodes, E, to the amplifier input, G, by closing the switches, S'' and S', toward the nerve and amplifier and opening the switch, S'''. When S''' is closed the nerve is shunted by R'. Calibration is effected by throwing switch, S'', toward the potentiometer circuit consisting of the resistance, R'', the contact maker, I, and a dry cell. By throwing S'' and S' toward the nerve and the Kohlrausch bridge, the resistance of the former may be measured. M = microphone hummer; R''' = non-reacting resistance; W = slide wire and T = telephone.

figure 7. The linear portion of the characteristic extends from -15 mv. to $+25$ mv. In this experiment the A battery of the first two amplifier panels had been in use for some time and the amplification was 7460. In another determination in which the amplification was 8320 the linear portion of the characteristic was found to be somewhat shorter, especially for negative input potentials. In each instance the characteristic is linear for a longer range of potentials when the input is positive

than when it is negative.   The input to the grid of the tube in the third
panel has the same sign as the input to the first panel.   The grid of the
third panel is therefore set farther from the bend produced by saturation
and by absorption of current by the grid circuit, due to grid positivity,
than it is from the bend due to high internal resistance, as the results of
grid negativity.   In accord with this finding the nerve preparations are
always connected with the cut
end to the grid and with the side
to the ground.   The potential
range is from 0 to +15 mv. and
therefore on the best portion of
the characteristic.

The effect of the reactance of
the coupling condensers is the
same as previously described (5).
The effect of the reactance of the
output condenser is much less due
to the high output resistance.
The capacity of the output con-
denser is 20 mf., the resistance in
series with it is the 1-megohm
leak on the ordinate plates.   In
such a circuit the impedance
angle is less than 1° for fre-
quencies of 0.5 (per second) and
higher, or if a constant potential
is impressed on the condenser it
takes 0.2 second for a 1 per cent
decrease in the potential differ-
ence between its plates.   Corre-
sponding figures for the intertube
condenser circuits are f = 10, and
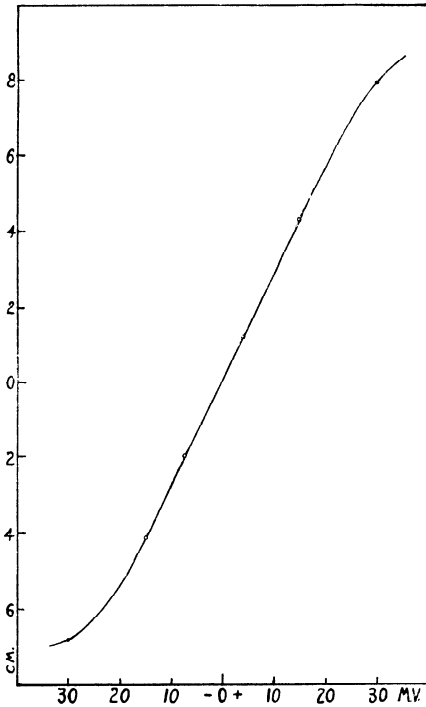0.01 second.   It can therefore be
seen that the condensers are with-

Fig. 7. Dynamic characteristic of the
3-stage amplifier and Braun tube.   Ab-
scissa: input in millivolts; ordinate: de-
flection of spot in centimeters.

out effect on the form of the functions for which the circuit is designed
and the ease of manipulation gives a great advantage over non-react-
ing circuits.

The amplifier is built as free from inductance as possible by means of
short straight wires but any circuit has some inductance, and this will
tend to delay the jump in potential at the moment the circuit is made.

Expression (2) does not hold for very small values of t, otherwise the current would jump instantly to its full value which would necessitate the impossible condition of a non-reacting circuit. When a current is impressed upon an electric circuit a finite time elapses during which energy is stored in the electric field. In the original arrangement of the apparatus the amplifier was placed at some distance from the spreader and oscillograph to protect its input from their influence. This involved long connecting wires and the delay in the rise of the calibration curve was longer than that shown in figure 8, due mainly to their inductance. To eliminate this effect the elements of the apparatus were brought closer together and the decreased separation was compensated by better shielding. In the calibration by a constant potential (fig. 8) the potential rises to its full value in 8.8×10^{-5} sec., and to 91.3 per cent and 97.3 per cent of its full value respectively in 3×10^{-5} and 4.5×10^{-5} seconds. This residuum of delay of the rise is due, as has been explained above, to the capacity of the resistance box. As this is not used in the direct connection of the nerve to the input, there is even less distortion than the calibration curve indicates.

THE INPUT. An electrically heated incubator is used as the chamber for the nerve. The atmosphere is kept saturated by wet filter paper plastered against its walls. The temperature can be kept constant at 37° for mammalian nerve by means of the thermoregulator and low temperatures are maintained by filling the jacket with water at the desired temperature. The electrodes used are non-polarizable ones of the Zn-$ZnSO_4$-NaCl type. The nerve employed was usually the sciatic nerve of a large bull frog. The connections to the electrodes are at the cut end and the side, the nerve being killed between the electrodes by means of heat. The nerve is of such a length that there are still left five or six centimeters between the stimulating electrodes and the proximal lead. Connection is always made with the cut end to the grid. The lead to the grid is a lead-sheathed insulated copper wire. Both the sheath and the incubator wall with which it is connected are grounded. This was necessary because the input often picked up extraneous disturbances especially the one produced in the spreader circuit containing the abscissa plates. This disturbance, synchronized with the abscissa, amplified and connected to the ordinate plates, caused the line to deviate from horizontal in such a way that the deviation was greatest at first, returning logarithmically to the horizontal position. The presence or absence and the size of these extraneous disturbances depend upon the size of the leak from the first grid. The nerve connection as can be seen in figure 5

is in effect a grid leak and the disturbances are much less when the nerve is in place than when the only leak is the two megohms. The size of these disturbances undergoes variations not under our control, at times being very small. In an actual experiment the undeflected abscissa line is absolutely still and straight. The input connection to the ground is with ordinary annunciator wire. The connections are made through a double-pole-double-throw switch (S'', fig. 6), so that just after a record is traced a calibration curve can be made.

Calibration is effected by a constant current of short duration. A dry cell whose potential is 1.502 volts is connected in series with a 100,000-ohm resistance box and a rotating contact maker. The latter is the one used by Erlanger and Garrey ((6) and see I, fig. 6) in which a V-shaped conductor in a cylindrical wheel produces the desired current duration, the latter depending upon the rate of deflection of the spot. A fraction of the potential drop across the resistance box is led to the input through the double-throw switch (S', fig. 6) so that potentials of $+5$, $+10$ and $+15$ mv. may be impressed upon the grid. The contact maker is mounted on the shaft with the commutator wheel for producing the deviation along the abscissa and may be adjusted to the proper portion of the abscissa line. Due to its connections both to the commutator wheel and to the input it is apt to carry the logarithmic disturbance from the former to the latter. When this is the case the disturbance can usually be eliminated by using a lower resistance potentiometer, for instance one of 5,000 or 10,000 ohms instead of 100,000 ohms.

Another source of trouble has been the leads from the induction coil which, presumably acting as antennae, pick up extraneous disturbances. This was particularly true when long leads were used at the time that the elements of the apparatus were placed considerable distances apart. These disturbances can be eliminated by grounding one side of the secondary of the induction coil. The stimulus is the break induction shock from a Harvard (Porter) coil applied with platinum electrodes so placed that the stimulus starts at the pole nearest to the proximal lead. The break shock of this coil was found by Erlanger and Garrey (6) to be faster than that of any of the models studied by them.

OPERATION OF THE OSCILLOGRAPH. Since the life of a Wehnelt cathode is short in a tube containing gas the Braun tube is kept in operation only during the period of observation. Both the anode potential circuit and the filament circuit are connected through a double-pole-single-throw switch. To prevent arcing a 2,000-ohm resistance (R'', fig. 5) is inserted in series with the anode and the current in the

filament is built up slowly by means of an adjustable resistance whose intensity is measured by an ammeter. This adjustable resistance also is used to make the spot definite for definition is a function of the temperature of the filament. The filament current is increased until the spot becomes sharp. When any further increase is made the spot again spreads. The adjustment is very delicate and one hand is kept on the controlling rheostat during an observation.

In order to interpret properly the figures traced upon the screen of the tube an investigation of its coördinate system was necessary. In this investigation it soon became apparent that it would be necessary to differentiate between what we may call static coördinates and dynamic coördinates. As the latter are the only ones which are of use, they alone will be described.

It was first determined that in the range of the screen utilized the deflection of the spot both along the abscissa and the ordinate is a linear function of the potential. The central portion of the screen is the surface of a sphere whose center is in the region of the deflecting plates. The distances are measured on the surface of the tube and hence are segments of meridians of this sphere, equal in length for like potentials. When by means of impressing the spreader potential upon the horizontal plates ordinate potential lines are plotted at various points upon the X axis, they are found to be straight and at right angles to the latter in the working range but outside of this range they begin to diverge. In like manner when abscissae are plotted at the various ordinates, there is considerable convergence from left to right, increasing as the line deviates from the X axis. It is principally in this respect that the dynamic coördinate system differs from the static. The reason for the convergence has not been determined, it probably is dependent in some way upon the working connections of the tube. It can be seen in the calibration curve in figure 8.

As the deflection along any ordinate is linear, within the limits of the characteristic, the value of the potential at any point can be determined by means of the following expression:

$$e = \frac{y\,E}{Y - x\,tan\,\alpha} \tag{5}$$

where x and y are the coördinates, Y is the length of intercept of the calibration line upon the Y axis; α is the angle which the line makes with the X axis and E is its potential.

The value of the time at any point is determined by a rearrangement of (3), viz.,

$$t = C R \log_\epsilon \frac{X}{X - x} \tag{6}$$

Just after the tracing has been made of an action current a calibration by means of the constant current of short duration is made with the deflection in the same portion of the screen as the action current. After the tracing has been transferred by means of transparent paper, the
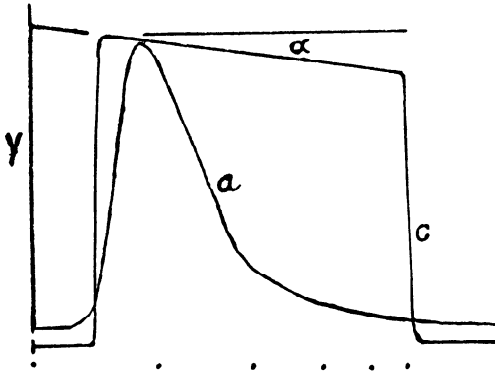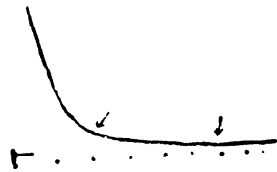

Fig. 8.   Fig. 9

Fig. 8. Braun tube record. Action current, a, from bull frog's sciatic. Temperature $= 25.2°$; $X = 6.05$ cm.; 1 mf.; 3000 $^\omega$; dots 1 σ apart. Calibration curve, c, with a constant current; $Y =$ its intercept on the Y axis $= 4.26$ cm.; $\alpha =$ the angle the calibration curve makes with the X axis; $\tan \alpha = 0.1428$. Same nerve as figures 1 and 2. (Natural size.)

Fig. 9. End of the action current of figure 8; 1 mf.; 10,000 $^\omega$; dots 1 σ apart; first arrow at second notch, second arrow at end.

coördinates of the points on the curve are determined by mounting the transfer under a pointer carried on a mechanical stage of a type designed for microscopes. With the aid of the vernier the coördinates can then be read to 0.1 mm. The accompanying table (2) gives in detail the data necessary for plotting the action current in rectangular linear coördinates of potential-time. The data were obtained from the tracing reproduced in figure 8. As the end of the action current comes too near the end of the line in the record of figure 8, another record was made by setting the stimulus earlier and slowing the movement along the abscissa by inserting 10,000 ohms in the condenser circuit. Since the current has a

very gradual ending, an aid in locating the deviation from the base line is repeatedly to interrupt the stimulus, noting the point at which the base line changes its direction. It is from figure 9 that the data for the duration of the action current between the second notch (described below) and the end were obtained. The data are plotted in figure 10.

TABLE 2

$X = 6.05$ cm.	$R = 3050$ ohms
$Y = 4.26$ cm.	$C = 1$ mf.
$E = 15$ mv.	$tan\ \alpha = 0.1428$

ABSCISSA	$\log_\epsilon \dfrac{X}{X-x}$	$1000\ RC \times \log_\epsilon \dfrac{X}{X-x}$	ORDINATE	$x \tan \alpha$	$Y-x \tan \alpha$	$\dfrac{y}{Y-x \tan \alpha}\times 15$
		(time in σ)				millivolts
0	0	0	0	0	4.26	0
0.47	0.081	0.247	0	0.07	4.19	0
0.62	0.108	0.329	0.03	0.09	4.17	0.11
0.75	0.131	0.399	0.15	0.11	4.15	0.54
0.85	0.151	0.460	0.49	0.12	4.14	1.77
1.05	0.190	0.580	1.82	0.15	4.11	6.58
1.15	0.210	0.640	2.73	0.16	4.00	10.24
1.20	0.221	0.674	3.12	0.17	4.09	11.44
1.28	0.237	0.723	3.58	0.18	4.08	12.86
1.38	0.258	0.787	3.73	0.20	4.06	13.78
1.51	0.286	0.872	3.64	0.21	4.05	13.48
1.60	0.307	0.936	3.46	0.23	4.03	12.88
1.85	0.365	1.114	2.89	0.26	4.00	10.84
2.15	0.438	1.336	2.12	0.31	3.95	8.06
2.45	0.519	1.584	1.45	0.35	3.91	5.56
2.65	0.576	1.757	1.02	0.38	3.88	3.93
2.81	0.624	1.904	0.77	0.40	3.86	2.99
3.05	0.701	2.139	0.60	0.44	3.82	2.36
3.50	0.863	2.631	0.37	0.50	3.76	1.47
3.83	1.002	3.057	0.22	0.55	3.71	0.89
4.16	1.163	3.548	0.17	0.59	3.67	0.69
4.91	1.668	5.087	0	0.70	3.56	0

THE ACTION CURRENT. The start of the action current is gradual; there is no evidence of a sudden or explosive change although the initial acceleration is very great. Heretofore this form of start has been obscured by the slowness and inertia of the recording mechanisms and by the small size of their deflections. Boruttau (7) in figure 3, plate II, pictures without comment such a start of the action current as recorded

by means of Hermann's rheotachygraph. A similar form of start appears in capillary electrometer records of the larger and slower muscle action currents.

To determine whether this form of start represents the process under the electrode only, an experiment was performed in which, in a nerve showing a large action current, a short heat block was produced just proximal to the proximal electrode. As a result of this procedure all trace of the action current disappeared; therefore there is no reason to believe that the current from the advancing wave of negativity contrib-
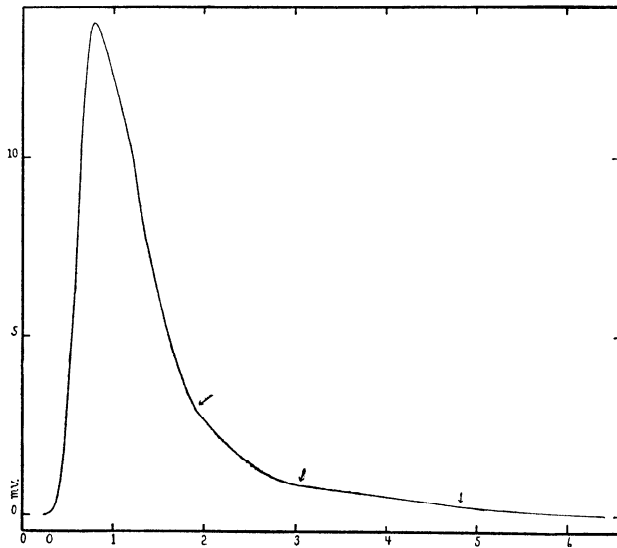

Fig. 10. The action current of figures 8 and 9 and table 2 plotted in rectangular linear coördinates. Abscissa: time in σ; ordinate: potential in millivolts. Arrows show the position of the three notches.

utes anything to the phenomenon until the process starts under the electrode.

The rising phase of the action current is smooth. The crest is reached in 0.54σ (fig. 8). In other nerves at about the same temperature the phase lasts from 0.54σ to 0.72σ (table 3). These are considerably longer durations than those obtained with the capillary electrometer. For instance, Gotch and Burch (8) found that the crest was reached in frog nerve in 0.5σ at 6° and Adrian (9) places the crest at 0.7σ at 13° in figure 5, and at 1.06σ and 0.47σ respectively at 6° and 16° in figure 6.

We thus find durations at temperatures close to 25° slightly longer than those of Adrian at 13° to 16° and of Gotch and Burch at 6°. At about 16° we have found values of about 1.5σ.

Without the accumulation of many data on frogs from various sources, and at different seasons of the year, it is difficult to make a comparison of one set of data with another. The longer anacrotic limb which we find must be due in part to the nature of the start of the wave. In previous methods this slow start being less apparent, the measurements were probably made from a point higher up on the rising wave. For example, in the nerve of figure 8 the rise from one-tenth of maximum to maximum is 0.36σ and in a nerve at 15° whose rising phase lasted 1.7σ the time from one-tenth of maximum to maximum is 1σ. The frogs used

TABLE 3

BULL FROG	TEMPER-ATURE	TIME TO MAXIMUM	MAXIMUM POTENTIAL	TIME TO FIRST NOTCH	TIME TO SECOND NOTCH	DURATION
	degrees	σ	mv.	σ	σ	σ
1	23.7	0.603	11.6	1.25	2.33	
2	11.0	2.03	6.1			
3	20.9	0.946	11.2			
4	15.0	1.71	15.36			
5	16.4	1.26	16.45	2.21	3.6	
6	26.4	0.598	14.6	1.27	1.889	7.86
7	25.0	0.721	14.3	2.38	3.87	
8	25.2	0.540	13.8	1.657	2.81	6.17
9	15.4	1.52	12.14	3.26	6.4	
Green frog						
1			23.6			
2			22.9			

in these experiments are accustomed to a warm climate. Their source is the region of New Orleans. The room temperature in St. Louis at the time of the experiments was 25° to 26°, the temperature of the water in the aquarium being about the same.

Garten (10) made string galvanometer records from four sciatic nerves of Rana esculenta. He made a rough correction of these curves according to the laws of the capillary electrometer. While this form of correction, as he realizes, is not justifiable, it gives results which are closer to the facts than the record itself, and which are in closer agreement with our results than the capillary electrometer data. He obtained at 18° a time to maximum of 0.9σ and at 32° of 0.55σ. We feel that our data on this point exceed in accuracy any previous data on account of

the large size of the deflections, the great rapidity of the movement along the abscissa and the freedom from distortion by inertia.

The maximum potential developed in the nerve of the bull frog (Rana catesbiana) has been found to be from 13.8 mv. to 16.45 mv. at temperatures of 16° to 25°. In the nerve of the green frog (Rana pipiens) the highest potential seen has been 23.6 mv. The potential recorded is, of course, not necessarily the potential developed at the seat of activity because the nerve can be considered as consisting of an active portion, or generator with high internal resistance, and of an inert portion which acts as a parallel conductor, thereby cutting down the potential drop across the leads.

The falling phase of the action current is much slower than the rising phase and its course is usually not smooth. The rising phase ends rather abruptly and it takes a definite short period for the decline in potential to attain its maximum velocity. The wave therefore is not symmetrical, but the peak is situated well over toward the side of the rising phase. There are quite regularly upon the curve of the decline of the wave points of more rapid change of direction, tending to produce notches, and in some nerves the intervals between these notches manifest themselves as definite waves with new maxima. There are quite regularly three such waves; in two instances we have seen evidences of a very small fourth wave. We have also seen these waves in the tibial nerves of the cat and rabbit, but never in the phrenic nerve of the dog. They cannot be attributed to a reduplicated stimulus by a shattered break because the records of the shocks show that they are single. Frog nerves vary considerably as to the degree in which they show this phenomenon. The waves appear in action currents from sub-maximal stimuli but are made more definite by increasing the strength of the stimulus. Figures 8 and 11 were taken in sequence from the sciatic nerves of different frogs but otherwise under as identical conditions as possible. In figure 8 the phenomenon is just developed; in figure 11 definite waves appear. A number of records were taken from the latter nerve using shocks of different strengths. In figure 12 the tracings obtained are drawn with their coördinate systems superimposed. With the weakest shock (curve with the dotted line) the notches are barely visible. The position of the first notch is indicated by the arrow. The stimulus as usual was the break shock of a Harvard induction coil operated by a single dry cell and, in this case, the secondary of the coil was set at the end of the slide and turned but a few degrees from vertical. Strengthening the shock by turning the secondary coil a few degrees

further from vertical accentuated the notches, and when the coil was turned to 60° from vertical the waves were well developed. The escape now lasted until the beginning of the action current and the first wave in this instance decreased in size. The total duration of the disturbance is not much increased by increasing the strength of the stimulus. It will be noted that the crests of the action currents come progressively earlier as the strength of the induction shock is increased. This probably means that the excitation process is completed sooner by the stronger and therefore steeper shocks.

The use of the Braun tube renders a study of the effect of the strength of shock upon the size of the action current very simple, because the escape does not alter the position of the crest of the action current. This has not been investigated in any detail but a number of observations
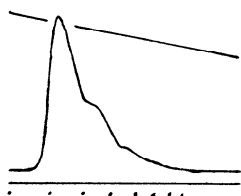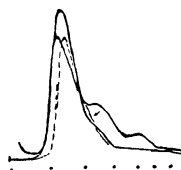

Fig. 11   Fig. 12

Fig. 11. Braun tube record. Bull frog's sciatic showing well-developed catacrotic waves from a weak break shock. Calibration line at 15 mv. (Reduced one-half.)

Fig. 12. Three records of the same action current with different strengths of stimulation to show development of the catacrotic waves. Constants for figures 11 and 12: 1 mf.; 5000 $^{\omega}$; dots 1 σ apart; temperature 25°. (Reduced one-half.)

indicate that over a very short range of stimuli the size of the action current increases with the size of the shock. After this, no further increase in the size of the action current takes place, although the size of the escape becomes progressively larger. It encroaches higher and higher upon the rising phase of the action current, but the position of the crest does not change. These findings therefore confirm the conclusions which had been reached on this point from experiments made under more difficult conditions by Gotch (11) and particularly by Forbes and Gregg (12).

It is questionable whether the wavelets under consideration correspond to anything that has been previously described. It is now a well-known fact that muscle and nerve respond with rhythmical currents to stimulation by the make or break of strong constant currents. It has

further been found that the induction shock (6) may last so long that a nerve might respond with a second stimulation (Garten (12) and Forbes and Gregg (11)). We have one record made from the tibial nerve of a rabbit which was not responding normally, which shows a second wave and a shock of sufficient duration to produce it. This curve has the general form of Garten's figure 17 and Forbes and Gregg's figure 3B3, but not the form of the waves under discussion. There are other reasons for believing that these waves are not reduplications of the main wave.

a. In the first place they may be produced in some nerves in a well developed form by very weak shocks while in the phrenic nerve of the dog they did not appear after very strong shocks. *b*. Referring again to figure 2, which is the reproduction of the action current of a frog's sciatic, and the shock which produced it, the total duration of the shock as indicated by the escape is only 1σ and its effective duration must be much less. The current it produces reaches its crest in 0.54σ. In the light of Adrian's (9) observations on the relation of the refractory period to the action current it is highly improbable that the nerve could again discharge during the duration of the shock; nevertheless the waves in question are present though poorly developed. In other records, not reproduced, the duration of the shock is less than the rising phase of the action current. When the nerve is cooled the catacrotic notches are present although the ratio of the duration of the action current to the shock duration is higher.

c. When the intrinsic rhythm in nerve appears the individual waves have about the same period (Garten (13)). No evidence is found in our data that the waves have a common period. The time from the start to the first notch is always considerably longer than the time from the first notch to the second, even when the error in setting an exact location of the notches is discounted (table 3). The third wave is much longer than either the first or second but as it might be considered as the sum of two undifferentiated waves it is not justifiable to compare it with the former.

d. The double action current recorded by Garten was obtained with a make induction shock. Forbes and Gregg, likewise, state that deformation occurs at more remote coil distances with the make shock than with the break shock. Our waves are obtained with break shocks and the corresponding make to many of the breaks we are calling "stronger" is subminimal.

e. The extra wavelets appear more conspicuously in cold blooded nerve, although the refractory period is longer and the shock, due to

higher secondary resistance, is shorter. *f.* While the wavelets become more marked in preparations losing their irritability and in which the strength of shock is increased, some of our best instances were obtained in fresh and very irritable nerves with weak shocks.

While reduplication of the action current cannot be absolutely ruled out as the explanation, the evidence does not point in that direction. This being the case one must inquire into such possibilities as the summed effect of nerve components of different characteristics, or the production of the current itself by more than one process.

The total duration of the action current was determined in two nerves with considerable accuracy by placing the stimulus so early that the action current ended on the earlier and better portion of the line. The durations found were 7.86σ at $26.4°$ and 6.17σ at $25.2°$. Many other slightly less accurate determinations agree with these. It is, however, difficult to compare them with the values obtained by other methods because of the various conditions of the experiments. The differential rheotome figures for the duration of the action current in frogs' nerve are as follows: Bernstein (14), 0.56σ to 0.8σ; Hermann (15), uncooled nerve, 5.03σ, cooled, 13.2σ; Head (16), winter frogs, 24σ, spring frogs, 7.90σ; Boruttau (7), 5σ to 7σ at $10°$ to $12°$. With the capillary electrometer Gotch (11) obtained 9σ at $1.5°$ and Adrian (9), 9σ to 12σ at temperatures ranging from $6°$ to $16°$. The many determinations obtained with the aid of the string galvanometer whether uncorrected or corrected by the capillary electrometer method while interesting cannot, for reasons mentioned above, be regarded as accurate. Considering the temperature at which our observations were made, it would seem that in general our durations are somewhat longer than others recorded in the literature. As the ending is very gradual and as its location can be determined definitely only with special precautions, it is likely that we have followed out the declining phase farther than these observers.

Since the impulse producing figure 8 traveled 5.6 cm. in 1.69σ, measuring from the beginning of the shock which is slightly previous to the excitation, the impulse was travelling at about 33.1 meters per second. The wave length, or the length of nerve in activity at any instant, is therefore 20.3 cm. and the crest of the wave is 1.77 cm. behind its start.

MAMMALIAN NERVE. A few records have been made from mammalian nerves. These were isolated, thoroughly freed of fascia, and mounted in the incubator which was maintained at a temperature of $37°$ and ventilated with oxygen. The whole process was carried out rapidly to keep the nerve as nearly normal as possible.

A rabbit tibial nerve was obtained immediately after death from con-
cussion of the cervical cord.   Figure 13 is a tracing of a submaximal
action current.   The end of the shock appears in the record.   The wave
has the same general form as the cold blooded action current except for
the notches, but traces of these appeared with a very strong shock.   The
time to maximum is 0.24σ and the duration 2.05σ, although the end
point is not precisely determined.   The sharp bend on the declining
phase comes at 1σ.   A record of a maximal action current was made
with a more rapidly moving spot (1 mf., 1000 ohms).   The time to
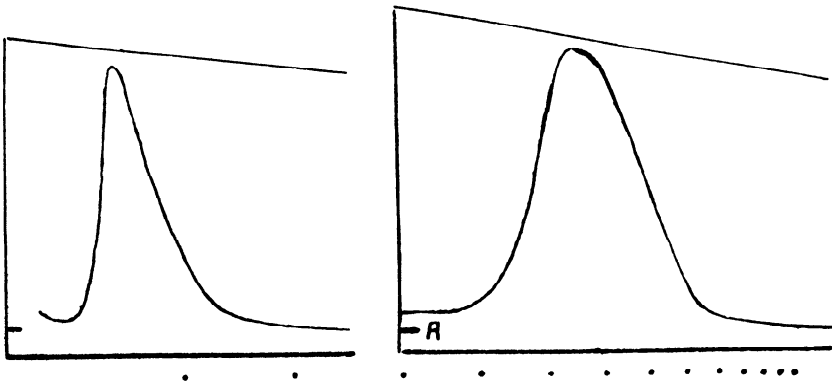maximum was 0.25σ.   These values of the time to maximum are con-

Fig. 13   Fig. 14

Fig. 13. Braun tube record of rabbit's tibial nerve. 1 mf.; 2000 $^{\omega}$; dots 1 σ
apart; temperature 36.6°; calibration line 15 mv.   (Natural size.)

Fig. 14. Dog's phrenic nerve. 1 mf.; 1000 $^{\omega}$; dots 0.2 σ apart; double dots
1 σ apart.   The distance between the line, A, and the start of the shock is the
initial value of the logarithmic disturbance.

siderably shorter than Garten's approximations from string galvan-
ometer records.   He gives 0.5σ at 35° for the rabbit's sciatic and 0.7σ
at 36° for the dog's sciatic.

The conduction time in this nerve as measured from the beginning of
the shock was 81 meters per second.   As excitation does not take place
until somewhat after the beginning of the shock, the rate of propagation
must be faster than this and approach the region of normal.   The
wave length is 16.6 cm. on the basis of the above figures and the crest
of the wave is 1.94 cm. from the start.

A record from a phrenic nerve taken from a dog under paraldehyde
anesthesia has the same general form as the tibial record except that

the notches did not appear with any strength of stimulus (fig. 14). In this record no trace of the producing shock is visible; the slant of the line is the logarithmic disturbance which we have described as being transmitted to the ordinate plates. The great speed of the spot makes this disturbance more evident than a similar disturbance would be in a slower record. Measurement can, however, be made from this line as a base line. The conduction time is 51.9 meters per second and the time to maximum is also slower than that of the tibial, being 0.36σ. Whether or not this is a physiological difference we are not prepared to say. The ratio of the two times to maximum practically equals the ratio of the conduction times.

SUMMARY

The low voltage cathode ray oscillograph offers a means by which nerve action currents can be easily and accurately recorded. A description is given of the apparatus by which this may be accomplished. It consists essentially of a three-stage amplifier, giving 7,000- to 8,000-fold amplification, working into a Braun tube. The method is possible because nerve action currents can be repeated with great precision twenty times per second and the record appears as a standing wave on the screen of the tube, where it may be drawn or photographed.

A description is given of apparatus for synchronizing the nerve potential changes recorded on the ordinate with the movement along the abscissa. The rate of movement along the abscissa is controlled by a condenser and resistance, and can be made very fast. The action current of mammalian nerve has been recorded in the range of velocities between 50 and 20 meters per second.

The method employed for connecting the nerve to the input is described; also the methods for calibration of the amplifier and Braun tube and for measuring the internal resistance of the nerve.

Records of frog and mammalian nerve are presented with data as to potentials and time relations.

The action current has a gradual start, a steep smooth anacrotic limb and a more gradual catacrotic limb. The latter like the former shows a period of great initial acceleration so that the crest is situated near the anacrotic side. In frog nerve and some mammalian nerves there are secondary waves on the catacrotic limb. Suggestions are made as to the cause of these waves.

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