THE ACTION POTENTIAL IN FIBERS OF SLOW CONDUCTION IN SPINAL ROOTS AND SOMATIC NERVES

JOSEPH ERLANGER AND H. S. GASSER

From the Physiological and Pharmacological Departments, Washington University School of Medicine, Saint Louis

Received for publication August 16, 1929

The conducted action potential of mixed somatic nerve when recorded, after amplification, by the cathode ray oscillograph exhibits waves, the more constant and prominent of which, for the sake of convenience, have been designated alpha, beta, gamma and delta in the order of their appearance (Erlanger, Gasser and Bishop, 1924). These waves have always been confluent, with the exception of the one in the saphenous nerve of the dog, called delta, which, at sufficient distances of conduction, is separated from the waves preceding it by a stretch, labelled gamma (Erlanger, 1927), lying almost, if not quite, at the level of zero potential. With the high amplification now used it turns out that an upward convexity of this “gamma” portion of the saphenous record, when present at all, is insignificant in comparison with the other elevations of the action potential; evidently it was a mistake to dignify it with a special designation. Recently a wave spaced similarly to the “delta” in the saphenous has been found in other warm-blooded somatic nerves and in cold-blooded nerves; in addition, waves even later still have been found in the action potentials of both warm- and cold-blooded nerve, somatic (Gasser and Erlanger, 1929) and autonomic. The present paper deals primarily with the waves of slow conduction as seen in somatic nerves and spinal roots.

The waves with which we are here chiefly concerned failed until recently to appear in our records for one or more of three reasons, namely: a,

1 This delta wave was observed in our original records only occasionally; and now, in records made at an amplification of 100,000, we again find it to be quite inconstantly present. Under the circumstances it seems best for the present to disregard this wave, and consequently, in what follows, we make no attempt to account for a delta potential wave.

2 Probably the notch on the down stroke of the wave designated beta in the published records (Erlanger, 1927) marks the separation, in the dog’s saphenous action potential, between the waves homologous with the beta and gamma waves of cold-blooded action potentials.

3 A parallel investigation of nerves of the involuntary nervous system has been carried out by Heinbecker and Bishop in this laboratory (1929).
they were too low in amplitude to be discernible; b, the fibers contributing to their action potentials have such high thresholds that they were not stimulated by the shocks originally employed; and c, they are propagated so slowly that they fall outside the limits of the records as they were then made.

a. The modification of our amplifier, whereby, merely through the turning of a switch, a fourth panel can quickly be added to the three of which it originally consisted, thus making conveniently possible 100,000 fold amplification as compared with the previous limit of 6,000 to 8,000, has brought to visible amplitude the unsuspected small, slowly propagated action potential waves, some of which may have less than a hundredth the amplitude of the main deflection.

b. For the study of the initial processes of the action potential it is very desirable to use as stimuli electrical currents of very short duration. The shortest induction shock conveniently available is that supplied by the Porter inductorium with core removed; and this, therefore, was employed for the most part as the source of the stimuli heretofore used. It turns out, however, that the less irritable fibers with which the present paper is concerned may require for stimulation the strongest shocks obtainable from the coreless coil with three volts in the primary circuit. To be sure of obtaining the necessary range of stimulation strengths, it is advisable to use the cored coil.

A few words are necessary here regarding the stimuli employed. The Porter coil used throughout the research was modified by extending the ways for the secondary so that the entire range of stimulation strength could be obtained without the necessity of turning the secondary coil. The primary current was supplied usually by two or three dry cells in series, and there was a resistance, usually of about 1.5\(\Omega\), in series with the primary, and a 30\(\Omega\) shunt across the primary terminals so as to minimize an artefact that tends to distort the record. The coils begin to overlap at 6.5 cm. In order to have some notion of the relative strength of the stimuli employed under the conditions of an experiment, the heights of the shocks were measured directly on the cathode ray oscillograph at different coil positions with the primary voltage and primary and secondary resistances most commonly obtaining. From the data thus obtained a curve has been plotted of the shock height (voltage) against coil position. Though, from such a curve the absolute height of the shocks under different conditions cannot be ascertained, it is possible, when the coil position for any one response is known, to ascertain roughly the strength relative to this of the shock used for any other response from the same preparation.

With high amplification the escape from these strong shocks becomes a prominent feature and may seriously distort the base line on which the action potential is written. By using Bishop's balancing device (1926) this escape usually can be almost completely balanced out. Occasionally, however, some of it remains as a curve of unascertainable form upon which the record is written as a base line. In this connection reference should be made also to the possibility (reported at the Edinburgh Congress (1923), but not published) of there being a long lasting residual
potential upon which as a base line the successive axon action potentials would be recorded. Any such residuum and any shock distortion render impossible the exact determination of the position of the base line. In measuring amplitudes and areas of deflections, therefore, we have usually taken into consideration only transient elevations, not elevation above the zero level.

c. Our timing condenser (1 mf.) charging through 2,000 ohms and producing what we call “a 2,000 ohm line” moves the spot across the screen of the oscillograph at such a rate as to give about the most convenient intervals per sigma and total duration of deflection for the analysis of the parts of the action potential heretofore described; and in our first studies this was the speed of time line usually employed. Exact analysis is possible through about 5 to 6 σ. The wave in the saphenous nerve of the dog, heretofore designated delta (now B) (Erlanger, 1927), appears, in the lengths of nerve usually employed, something like 9 σ from start of the record; it was found in a 5,000 ω line. Lines lasting effectively longer than 9 σ were rarely employed. In cold-blooded nerve the wave which, as will be seen, corresponds with this late wave in the saphenous, requires for its demonstration a record lasting through 30 σ or more; it is obtained by a resistance of 20,000 to 30,000 ω. To permit the slowest waves to appear upon the record it has been found that the recording time may have to last 300σ or even longer, and for this a resistance of 150,000 to 200,000 ω in the condenser circuit is needed.

With these slow rates of movement of the spot a single deflection suffices for a legible record, on ordinary process film, even. To obtain such a record the rate of revolution of our timing apparatus is reduced so that the nerve is stimulated at the rate of about 10 shocks per minute and the film is held against the face of the tube so as to be exposed to just one of the transits of the fluorescent spot. Legible single deflections at higher speed can be obtained by the method described by Gasser, using duplitized film (1928, a and b).

THE SLOWER WAVES IN SOMATIC NERVES: DESCRIPTION OF TYPICAL RECORDS. Figure 1, a shows the action potential in the sciatic nerve of the bullfrog, after 91 mm. of conduction, on a 5,000 ω line as we usually have recorded it, excepting that the shock is stronger. The terminal phase of the shock escape extends under the action potential, but the deformation it produces is inconsiderable. Excepting this slight deformation, the picture, with its alpha, beta and gamma waves, is quite typical of the conducted action potentials previously published. The same action potential with full four-panel amplification is reproduced as b. Homologous features in records a and b, as well as in all subsequent records, can be identified by the labelling. The increase in amplification is given by the ratio of the heights of the two gamma waves; it is about fifteen-fold. The alpha and beta waves and the down stroke of the shock escape far
exceed the limits of the record, and the spot moves so rapidly here that its impression on the film is almost illegible.

By increasing the resistance in the condenser (spot-moving) circuit from 5,000 to 19,000 ohms, the line now was prolonged so as to last effectively about 50 $\sigma$ and, without changing any other of the conditions, records c

---

**Fig. 1.** Records from bullfrog sciatic, 1/31/29 (retouched). Conduction distance 9.1 cm. Temp. 21°C. In this and in all other records $S =$ shock artefact; $I =$ start of $A$ elevation, $S =$ start of $B$ elevation, $S =$ start of $C$ elevation. $\times 3/5$ approx. In all figures, unless otherwise specified, the time in $\sigma$ is indicated by dots below each record, zero (sometimes ahead of record) being the start of the induction shock.

- a, 3 panels, 5,000 ohms, 1 mf. (1 mf. in all other records unless other capacity is mentioned). Stimulus maximum for $B$, coil at 7.5 cm.
- b, 4 panels, otherwise same as a.
- c, 3 panels, 19,000 ohms, otherwise same as a.
- d, 4 panels, otherwise same as c.
- e, 4 panels, 149,000 ohms. Stimulus maximum for $C$, coil at 3.9 cm. Conduction rates of $A$, $B$ and $C$ are 42.0, 4.36 and 0.56 m.p.s., respectively.

and d were made with three- and four-panel amplification, respectively. The shock escape and the alpha-beta-gamma group of waves now are further forward and closer together spatially, but not temporally. Toward the end of the line in c close examination reveals (at 2) a slight upward undulation ($B$); in d this is magnified into a wave 9 to 10 mm. high, becoming a
prominent feature of the record. At this amplification the estimated height of the A elevation is about 174 mm. The intervals between the shock and the start, crest and end of the B elevation are 20.89, 30.06 and 53.53 \( \sigma \), respectively. Between the end of gamma and the beginning of B the potential is low and steadily declining, but how much of this is due to newly arriving axon potentials and how much to displacement and deformation of the base line by shock escape and residual potentials it is impossible to say.

For a, b, c and d of figure 1, the strength of the stimulus was so chosen as to elicit a just maximal B wave; the coil position was 7.5, that is to say, the secondary was 7.5 cm. from home. The threshold position of the coil for the alpha wave was 25.5 cm. and for the B wave 11.8 cm.

Finally, the movement of the spot across the face of the tube was slowed still further by raising the resistance in the condenser circuit to 149,000 \( \Omega \), thereby obtaining a line lasting usefully through something over 300 \( \sigma \), and the strength of the shock was increased by moving the secondary coil to 3.9 cm. The shock escape now (fig. 1, e) is at the beginning of the line and indistinguishably fused with A; the alpha-beta-gamma (A) complex is completed in the first 10 mm. of the record, but is so quick that only the end of it becomes visible, and it is succeeded by the B wave. Following this, and lasting about 0.1 second, there is a long, practically horizontal, stretch of record a trifle below the base line. This depression of the base line is attributed partly to the shock artefact and partly to the diphasic artefact. A strictly monophasic action potential is impossible of attainment (Bishop, Erlanger and Gasser, 1926) and the slower the propagation of an action potential wave the shorter must be the distance between the leads in order to mask diphasic effects. For this reason, the B wave, and especially the C wave, are apt to exhibit diphasicity even when A appears to be monophasic. These displacements render impossible the exact determination of the intermediate potentials. In this case, we may assume, however, without introducing any great error, that the B- to -C potentials, were it not for these artefacts, would have recorded a trifle above the base line. The record is terminated by a low wave labelled C. The start, crest and end of this wave follow the shock 183.8, 203.3 and 314.0 \( \sigma \), respectively. The shock strength used was just maximal for this C wave. The threshold position of the secondary coil for the C wave was about 7.6 cm.

Some conception of relative stimulation strengths at the coil positions given above is obtainable by reference to the curve we have plotted of coil separation against shock amplitude. At separations of 25.5, 11.8, 7.5 and 3.9 cm. the relative shock heights are 1, 2.8, 16.7 and 152, respectively.

The entire picture in one record, but of another, and shorter, bullfrog sciatic, is seen in figure 2. The stimulus was a single shock that was
maximal for the $C$ wave, the record being made at full four-panel amplification by a single transit of the spot across the screen at a rate determined by $200,000 \omega$ in the timing circuit. The retention of the A and B potentials deforms the base line. The arbitrarily assumed zero line has been drawn into the figure in a form that would give to this record about the configuration of other, less deformed, records. The action potential obviously is made up of three main elevations, $A$, $B$ and $C$, of which $A$ together with the shock artefact can be recognized merely as an interruption in the deflection; the $A$ amplitude far exceeded the limits of the film. Some idea of the voltages of the elevations can be obtained by taking the sensitivity of the tube in round numbers as 10 volts equals 1 cm. at three-panel amplification (6,000 times). Then the $A$, $B$ and $C$ deflections in figure 1 subtend 23.2, 1.3 and 0.5 millivolts, respectively.

Figure 3 shows the action potential of the bullfrog sciatic (data derived from the records of fig. 1) drawn into a linear coordinate system from the logarithmic time coördinates of the records by joining with straight lines the points representing the starts, crests and ends and notches of the several waves. The height of the connection between $A$ and $B$ is taken directly from the record, the stretch connecting $B$ with $C$ has arbitrarily been placed a trifle above zero level. In the figure thus obtained the $A$ elevation, made up of the alpha, beta and gamma waves, is seen to form a
Fig. 3. The action potential of figure 1 transferred to linear coordinates by joining the points indicating the starts, crests, ends and notches of the $A$, $B$ and $C$ waves, the start of $A$ resting on zero. Abscissae, time in $\sigma$; ordinates, amplitude in millimeters.

Fig. 4. Records, retouched, from bullfrog skin nerve, 11/20/28; slightly diphasic. Distance of conduction 0.9 cm. Temp. 22°C. 4-panel amplification. $\times 3/4$.

a, 5,000$\sigma$, stimulus maximum for $B$.

b, 45,000$\sigma$, stimulus maximum for $C$. A third record of the series taken at less amplification shows that the height of $A$ on the scale of these records is 152 mm. The conduction rates of $A$, $B$ and $C$ are 20, 3.4 and 0.35 m.p.s.
Fig. 5. The action potentials of figure 4 (bullfrog skin nerve) transferred to linear coordinates as in figure 3.
very high narrow spike at the left edge of the chart, the C elevation a low broad lift far to the right, while the B elevation consists of a peak of intermediate height and width a little to the right of the alpha-beta-gamma (A) spike.

Three elevations, comparable with these sciatic waves as regards rates of conduction and relative irritabilities, are exhibited by all cold-blooded somatic nerves we have examined. These include the dorsal skin nerve in the bullfrog (figs. 4 and 5), the sciatic and the branch of the sciatic to the gastrocnemius muscle in the green frog, and the sciatic of the turtle (Heinbecker4). Waves, presumably comparable, have been observed also in the tibial, peroneal and saphenous nerves in the dog (see figs. 6 and 7) and cat. In warm-blooded muscle nerves the B elevation may be small, as in muscle branches of the dog's femoral (see fig. 6), or practically absent, as in the phrenic nerve of the dog. The significant data from many of these observations are collected in table 1. The B and C waves often are double, particularly the C elevation, and then the position of the cleft is not constant in the different preparations. The C elevation may have the form of a plateau which may be level or slightly undulating, and often is higher at the late end than the front. The very strong shocks needed to stimulate the C fibers rapidly cause deterioration of the nerve under the electrodes, and it is, therefore, difficult to obtain exactly comparable successive records of C. The height of the B and C waves in a given nerve depends in part upon the distance of conduction; like the A elevation (Erlanger, Gasser and Bishop, 1924), they become lower and longer as they move away from the site of their origin.

Individuality of A, B and C Elevations. The elevations we have designated A, B and C, like the alpha, beta and gamma waves of A, unquestionably are produced by a grouping of conduction rates in as many different sets of fibers composing the nerve. The only other possibility is that they are successive waves started in the same fibers by the strong shocks needed to elicit the slower waves. Repeated stimulation of the same fibers by a single shock, sometimes at the cathode, sometimes at the anode (Heinbecker, 1928), occasionally does occur, but repetitive waves usually are readily recognizable as such in the oscillograph picture. That the B and C elevations are not repeating action potentials can be demonstrated by the crucial test that supplied the proof of the individuality of the fibers producing the alpha, beta and gamma waves (Erlanger, Gasser and Bishop, 1924). When an action potential, started from one end of a nerve by a

4 The C wave in mixed nerve was found independently by Heinbecker while working on the cervical sympathetic nerve of the turtle under the direction of one of us. Elevations corresponding, presumably, to B and C of somatic nerves have been described by Heinbecker and Bishop (1929) as occurring in the cervical sympathetic and vagus nerves of both cold- and warm-blooded animals.
<table>
<thead>
<tr>
<th>Preparation</th>
<th>Conduction Distance</th>
<th>Conduction Rates in M.P.S. of Fibers of</th>
<th>Relative Amplitudes</th>
<th>Time to Maximum</th>
<th>Duration</th>
<th>Remarks</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>A</td>
<td>B</td>
<td>C</td>
<td>A</td>
<td>B</td>
<td>C</td>
</tr>
<tr>
<td>1. Green frog peroneal 11/13/28</td>
<td>4</td>
<td>—</td>
<td>—</td>
<td>2.6</td>
<td>1.04</td>
<td>0.45</td>
</tr>
<tr>
<td>2. Green frog peroneal 1/5/29</td>
<td>36.1</td>
<td>18.4</td>
<td>—</td>
<td>3.08</td>
<td>1.26</td>
<td>0.47</td>
</tr>
<tr>
<td>3. Green frog peroneal 3/21/29</td>
<td>2.8</td>
<td>0.6</td>
<td>—</td>
<td>3.33</td>
<td>1.71</td>
<td>0.57</td>
</tr>
<tr>
<td>4. Bullfrog sciatic 11/13/28</td>
<td>4.0</td>
<td>—</td>
<td>—</td>
<td>4.2</td>
<td>1.4</td>
<td>0.71</td>
</tr>
<tr>
<td>5. Bullfrog sciatic 11/13/28c</td>
<td>3.3</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>6. Bullfrog sciatic 11/20/28b</td>
<td>5.8</td>
<td>18.7</td>
<td>13.8</td>
<td>5.3</td>
<td>1.8</td>
<td>0.66</td>
</tr>
<tr>
<td>7. Bullfrog sciatic 11/20/29c</td>
<td>6.4</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>8. Bullfrog sciatic 1/29/29</td>
<td>7.4</td>
<td>55.3</td>
<td>11.9</td>
<td>4.48</td>
<td>1.38</td>
<td>0.54</td>
</tr>
<tr>
<td>9. Bullfrog sciatic 1/31/29</td>
<td>9.1</td>
<td>42.0</td>
<td>18.0</td>
<td>4.40</td>
<td>1.73</td>
<td>0.56</td>
</tr>
<tr>
<td>10. Bullfrog skin nerve 1/10/28</td>
<td>0.9</td>
<td>20.0</td>
<td>5.5</td>
<td>3.05</td>
<td>1.39</td>
<td>0.35</td>
</tr>
<tr>
<td>11. Bullfrog skin nerve 1/5/29</td>
<td>1.53</td>
<td>23.3</td>
<td>6.53</td>
<td>3.42</td>
<td>1.19</td>
<td>0.39</td>
</tr>
<tr>
<td>12. Dog femoral 11/2/28</td>
<td>9.0</td>
<td>88.7</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
</tbody>
</table>

TABLE 1

Notch of C 0.23 m.p.s. Maxima, B 11.5, C 3 cm. Duration to notch 44.0
Maxima, B 7.4, C 0.8 cm.
Notch of C 0.46 m.p.s.
Constant current; conduction rates not determinable
Maxima, B 9.4, C 5.2 cm.
Maxima, B 8.8, C 5.2 cm.
Thresholds, A 25.8, B 11.6, C 7.6 cm. Maxima, B 7.5, C 3.9 cm.
B notch 1.7 m.p.s. Duration to notch 2.25
Maxima, R 20.2, R 7.8, C 0.5 cm.
|   | Dog femoral 11/10/28 | Muscle | 6.7 | 89.7 | — | — | — | — | — | — | — | — | — | — | — | — | No B in muscle-nerve |
|---|---------------------|--------|-----|------|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
|   | Saphenous           | 70.9 68.2 | 13.1 | 10.2 | — | — | — | — | — | — | 22.0 | 1 | — | — | 1.09 | — | — | — | 2.3 |
| 14. | Dog femoral 11/14/28 | Muscle | 4.4 | 77.0 | — | — | — | — | — | — | — | — | — | — | 0.92 | — | — | — | 1.06 |
|   | Saphenous           | 58.7 36.4 | 11.2 | 8.33 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| 15. | Dog femoral 11/14/28, Saphenous | 4.9 | 77.0 | 49.0 | — | 13.9 | 10.1 | — | — | — | — | — | — | — | — | — | — | — | — |
|   | Trace of B in muscle-nerve | 77.0 | 82.7 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| 16. | Dog femoral 11/14/28, Saphenous | 12.0 | 80.0 | 35.2 | 16.8 | 13.2 | 1.04 | 0.8 | 79.5 | 14.0 | 1 | 1.09 | 14.4 | 2.51 | 2.53 | 34.4 |       |
|   | Trace of B in muscle-nerve | 61.0 | 60.3 | 14.3 | 11.6 | 8.0 | 0.18 | 0.7 | 8.5 | 1 | — | — | — | — | — | — | — | — | — |
| 17. | Dog femoral 11/26/28, Saphenous | 12.0 | 83.8 | 34.7 | 13.1 | — | 1.28 | 0.57 | 61.7 | 9.5 | 1 | — | — | — | — | — | — | — | — |
|   | Trace of B in muscle-nerve | 62.8 | 34.7 | 13.9 | 10.98 | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| 18. | Dog femoral 1/30/29 | Muscle | 6.05 | 89.6 | 55.2 | Trace | Small | 0.94 | 0.07 | 32.8 | 4.3 | 1 | — | — | — | 1.19 | — | — | — | — |
|   | Saphenous           | 73.2 | 47.6 | 20.0 | 15.3 | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| 19. | Cat 5/1/29 Saphenous | 1.55 | 67.0 | ? | 14.6 | 0.22 | 1.10 | 0.64 | 6.0 | 1 | — | — | — | — | — | — | — | — | — |
| 20. | Cat 5/1/29 Saphenous | 5.5 | 88.5 | 37.7 | 30.6 | 16.8 | 1.46 | 1.63 | 5.4 | 1 | — | — | — | — | — | — | — | — | — |
| 21. | Cat peroneal        | 2.9 | 93.0 | ? | 32.3 | 10.4 | 1.59 | 0.82 | 20.0 | 1 | — | — | — | — | — | — | — | — | — |
| 22. | Dog phrenic 4/16/27 | Muscle | 3.75 | 55.2 | — | 11.07 | 1.13 | — | 18.07 | 0.07 | 1 | — | — | — | — | — | — | — | — |

**Somatic Nerve Fibers of Slow Conduction**

---

For more details or analysis, please refer to the original publication or related studies.
stimulus just below the threshold, of the B elevation, for instance, is made to meet an action potential consisting of both the A and the B elevations started from the other end of the nerve by a stimulus of appropriate strength, the A elevation of the latter is blocked while the B elevation passes on without modification. Or, by stimulating a nerve first with a shock that is maximal for C and again, at the same place, after the A fibers have recovered from their refractory state, with a shock maximal for A one can start one or more A waves that will overtake the C wave and beat it to the lead. The configurations of the waves, A and C, are unaffected by this interesting process.

Survey of the relation of axon conduction rate to the configuration of the action potential. The positions taken by the three elevations, A, B and C, in the records, and their durations, are, of course, determined mainly by the propagation rates of the contributing fibers and by the distance of conduction. The rate of movement of the head of a wave is determined by the rate of conduction in the fastest fiber contributing to the potential of that wave. Our method of determining it, namely, as the time intervening between the shock and the beginning of the elevation, is subject to two errors; it fails to take cognizance either of the utilization period of the shock, which, however, is so short as to be almost negligible even in the case of the fast moving A elevation (Erlanger, Gasser and Bishop, 1924), or, when superthreshold shocks are used, of the spread of the stimulus. With threshold shocks the spread will be negligible, but with strong shocks it may, in the case of the most irritable fibers, extend out a distance of 1 cm. or more (Erlanger, Gasser and Bishop, 1924). When, as in many of the present experiments, the rates have been derived from records obtained by stimulation strong enough to elicit the C elevation it is obvious that the deduced conduction rates of B, and especially of A, may be somewhat too fast, relatively. Only, however, when the conducting distance is short will the error from this source become considerable.

The conduction time of the slowest fiber contributing to a wave can be arrived at approximately by deducting from the conduction time of the end of the wave the duration of the axon action potential. It has been assumed, in doing this, that the potentials in the axons contributing to the B and C elevations have the same duration as in those contributing to the alpha, beta and gamma waves, namely, 0.9 and 0.6 σ in cold- and warm-blooded nerve, respectively (Gasser and Erlanger, 1927). Should it eventuate, as Heinbecker's preliminary observations seem to indicate (1929), that the action potentials of some or all of the slower fibers are longer, the corrections necessitated would not materially affect the deductions we are making; for the slower elevations, excepting warm-blooded B,
<table>
<thead>
<tr>
<th></th>
<th>A</th>
<th>B</th>
<th>C</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>First</td>
<td>Last</td>
<td>First</td>
</tr>
<tr>
<td>Sciatic, bullfrog</td>
<td>Rate</td>
<td>42</td>
<td>13 to 10</td>
</tr>
<tr>
<td></td>
<td>Size</td>
<td>20</td>
<td>6 to 5</td>
</tr>
<tr>
<td>Skin nerve, bullfrog</td>
<td>Rate</td>
<td>30</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Size</td>
<td>14</td>
<td></td>
</tr>
<tr>
<td>Peroneal, green frog</td>
<td>Rate</td>
<td>30</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Size</td>
<td>14</td>
<td></td>
</tr>
<tr>
<td>Femoral preparation, dog</td>
<td>Rate (M*)</td>
<td>82.8</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Size (M)</td>
<td>17</td>
<td>ave. (10) 38.91</td>
</tr>
<tr>
<td></td>
<td>Size (S)</td>
<td>13.5</td>
<td>ave.† 7.98</td>
</tr>
<tr>
<td>Femoral preparation (P), dog, 1/30/29</td>
<td>Rate (M)</td>
<td>89.6</td>
<td>47.6</td>
</tr>
<tr>
<td></td>
<td>Rate (S)</td>
<td>73.2</td>
<td>20.0</td>
</tr>
<tr>
<td></td>
<td>Size (M)</td>
<td>17</td>
<td>13.9</td>
</tr>
</tbody>
</table>

*M = Muscle branch, S = Saphenous.
† End of first large deflection.
are relatively long in duration, and their ends cannot be located with any great precision. The rates in the fastest and slowest fibers of A, B and C thus determined in certain of the nerves are included in table 1 and summarized in table 2. The limiting conduction rates of the A elevation have not been determined as a routine in the present investigation. For the purposes of this paper the numerous determinations we have made in previous studies are available.

In the *bullfrog sciatic* the normal rate of conduction, at room temperature (usually 23–25°C.), in the axons forming the head of the first, or A, elevation may be taken as 42 m.p.s., though rates as high as 48 m.p.s. are occasionally observed, and of the end of *gamma*, a rather indefinite point, as 13 to 10 m.p.s. For the B elevation the corresponding values are, start, 5.4 to 4.0, end, 1.8 to 1.26 m.p.s.; and for the C elevation start, 0.71 to 0.46, end, 0.37 to 0.23 m.p.s. On the basis of proportionality of fiber diameter to conduction rate (Gasser and Erlanger, 1927), if 20μ be taken as the diameter of the largest fiber in the bullfrog’s sciatic, the diameters of the fibers conducting at the other rates would be (see table 2), in the order above used, A, end, 6μ; B, start, 2.6 to 1.9, and end, 0.9 to 0.6 μ; C, start, 0.34 to 0.22, and end, 0.18 to 0.11 μ. Since myelinated fibers practically never are less than 1.5μ in diameter and rarely less than 2μ, it follows that the fibers producing the C elevation certainly, and the B elevation probably, fail to obey the fiber-size rule.

Similar analysis of the action potentials of the other nerves examined leads to the same conclusion. Thus, a *skin nerve of the bullfrog* ordinarily conducts at rates ranging between 26 and 35 m.p.s. and its largest fiber measures something like 14μ (Erlanger, 1927). The diameters of the fibers determining the limiting rates of its slower waves, taking 30 m.p.s. as the rate in a 14μ fiber, become, on the basis of the present data, for the B elevation, start, 1.59 to 1.42μ, and end, 0.55μ; for the C elevation, start 0.18 to 0.14μ, and end, 0.11 μ. Since myelinated fibers practically never are less than 1.5μ in diameter and rarely less than 2μ, it follows that the fibers producing the C elevation certainly, and the B elevation probably, fail to obey the fiber-size rule.

In the case of the B elevation of the *sciatic nerve of the green frog* the limiting fiber sizes taking the conduction rate in the largest fiber (14μ) as 30 m.p.s. (Gasser and Erlanger, 1927), on the basis of our data would be, start, 1.5 to 1.2μ, end, 0.6 to 0.4μ. For the C elevation the fiber diameters would be, start, 0.22 to 0.13μ, and end, 0.07 to 0.05μ.

Of warm-blooded nerves the *saphenous and muscle branches of the femoral nerve of the dog* have been singled out for a more complete study of the relation of fiber-size to conduction rate. This has been done because, by using as the preparation the trunk with attached saphenous nerve and some one muscle branch, and by recording from each of these two branches separately the action potential started by stimulation of the trunk, exactly comparable records can be obtained from a purely cutaneous nerve and a purely muscle nerve (Erlanger, 1927). The femoral nerve itself is so short
and thick that a good mixed-nerve action potential at a sufficient distance from the site of stimulation cannot be obtained from it for comparison with the separate action potentials of its branches. There is every reason for

believing, however, that the femoral action potential is formed by a combination of action potentials similar to those of these two of its branches. Records from longer mixed nerve, the peroneal of the cat, for example, show that this is the case (see table 1).

![Fig. 6. Records from a femoral, saphenous and muscle-branch preparation, 1/30/29 (retouched). Distance of conduction 6.95 cm. Temp. 37.5°C. Stimulus to femoral nerve in all cases. × 3/4 approx.](http://ajplegacy.physiology.org/)

- a. Saphenous. 3 panels, 2,000\omega. Stimulus maximum for B, coil at 13.4 cm.
- b. Saphenous. 4 panels, otherwise same as a.
- c. Saphenous. 4 panels, 4,000\omega. Stimulus maximum for B, coil at 14.8 cm.
- d. Saphenous. 4 panels, 92,000\omega. Stimulus maximum for C, coil at 7.1 cm.
- e. Muscle branch, otherwise same as a.
- f. Muscle branch. 4 panels, otherwise same as a.
- g. Muscle branch, otherwise same as c.
- h. Muscle branch, otherwise same as d. Conduction rates: A of muscle branch 89.6, of saphenous 73.2; B of muscle branch (?), of saphenous 20.0; C of muscle branch 4.44 (?), of saphenous 1.5 m.p.s.
The data derived from the femoral nerve of the dog are summarized in table 2. The values there averaged include all excepting those obtained from the nerve of the experiment dated 1/30/29. The latter nerve (for the sake of convenience, it will be referred to as P) is treated separately because the conduction rates derived from it are decidedly the fastest of the series. Whether, on this account, they are to be regarded as the nearest to normal is a question that must be left open. All that can be said is that in every other respect the records from this preparation are typical; those of them that are required for a complete story, given in the legend, are included in figure 6. Rates in the saphenous of the cat often are as high as in this case.

In these femoral preparations the beginning of the muscle branch action potential has traveled at rates ranging between 85.7 and 77.0 m.p.s., the average being 82.8 (in P the rate was 89.6). In the case of the saphenous branch the rates have ranged between 80.0 and 58.4 m.p.s., the average being 65.6 (in P, 73.2). The slowest axon action potential of the A elevation travels at rates that have ranged between 55.2 and 29.3 m.p.s., with an average of 38.9 (in P, 47.6). Taking $17\mu$ as the diameter of the largest fiber of the femoral nerve (Erlanger, 1927), the smallest fiber of the A elevation is found by calculation to range between 11.3 and 6.2\mu, with the average at $7.98\mu$; the smallest A fiber in P would measure $9.04\mu$. The slowest fiber contributing to the main elevation of the saphenous action potential reconstructed by Erlanger (1927) has an estimated diameter of $7.25\mu$. 

---

**Fig. 7.** The saphenous action potentials of figure 6 transferred to linear coordinates as in figure 3.
range of axon conduction rates of the fastest fiber of the B elevation is 16.8 to 11.2 m.p.s. (average of 10 determinations, 13.8, and in P, 20 m.p.s.), of the slowest fiber, 13.2 to 8.3 m.p.s. (average of 8, 10.5, and in P, 15.3); the range of axon conduction rates of the C elevation is, fastest, 1.28 to 0.82 (average of 8, 0.98, and in P, 1.54), and of the slowest, 0.80 to 0.33 (average of 8, 0.58, and in P, 0.67). The fiber sizes calculated from these rates are for B, largest, 3.45 to 2.30μ (average 2.83, and in P, 3.80), smallest, 2.71 to 1.70 (average, 2.16, and in P, 2.90); and for the C elevation, largest, 0.26 to 0.17 (average, 0.20, and of P, 0.29), smallest, 0.16 to 0.078 (?) (average, 0.12, and in P, 0.13). Here again the result of calculation is such as to force the conclusion that proportionality of conduction rate to fiber diameter cannot possibly hold in the case of the fibers forming the C elevation and probably does not in the case of the fibers forming the B elevation.

Relation of the B and C Potential Waves to the Morphology of the Nerve. The problem is to find on histological examination the fibers serving as the source of the potential. The method of approach is to take the fiber distribution, found on analysis, and attempt to reproduce the potentials recorded, using the assumptions which were successful in the reconstruction of the A wave, namely, that the axon potential has the same form and duration in all fibers, that the velocity of conduction is in linear relationship to the fiber diameter, and that the fibers affect the recording instrument as their cross-sectional areas (Gasser and Erlanger, 1927). This necessitates a complete analysis of the small fibers in the nerve. The only nerve in which this had previously been done was the skin nerve of the frog, although the small fibers in the saphenous of the dog had been counted (Erlanger, 1927). In most nerves the measurements had stopped in the region of 3–5μ, and it was, therefore, necessary to complete them.

Since our most complete data have been derived from the saphenous nerve of the dog this will be considered first. The saphenous nerve contains so many fibers that to map it completely is a stupendous task and since “the large myelinated, the small myelinated and the unmyelinated fibers are not uniformly distributed” (Laugley, 1922) anything short of a complete analysis of a nerve may fail to produce a reliable picture of the whole.

In an effort to meet this difficulty we have completely analyzed a small branch of the saphenous nerve (1/30/29) from which the records of figure 6, a, b, c and d, were obtained. This branch arose about 1 cm. beyond the point from which the lead was taken; it was placed in osmic acid at the time the nerve was mounted for observation. It contained 341 myelinated fibers and a considerable amount of unmyelinated material (possibly half the area of all the fibers), all beautifully prepared. The measurements, made on a photograph enlarging the fibers over 2,000 times, were controlled by
measurements with an eyepiece micrometer and an oil immersion lens. In comparing this analysis with the action potential it is assumed that the branch is a fair sample of the trunk and would yield a wholly comparable action potential.

The action potential reconstructed from the values obtained from the measurement of the fibers of this nerve as of 69.5 mm. of conduction, that is, the conducting distance at which the records of figure 6 were obtained, is shown in figure 8. Onto this figure have been transferred as triangles the waves of figure 6 in correct time and height relations.

![Fig. 8. Reconstruction of the dog's saphenous action potential (crosses) as of 6.95 mm. conduction, based on the histological analysis of a branch of the nerve from which the saphenous action potentials of figure 6 were obtained. Zero lag is that of the fastest axon action potential of the femoral, saphenous and muscle-branch preparation. The recorded saphenous action potential is superimposed in the same scale by joining with straight lines the dots marking its significant points, the recorded \( \beta \) being given the same height as the reconstructed \( \beta \); the heights of other waves are drawn relative to this. The arrow indicates the position of the end of \( A \) in the average saphenous action potential. The average position of \( B \) is indicated by dotted elevation, \( B' \).

As has always been the case the main, or \( A \), wave of the reconstruction and of the record are essentially alike, the times to maximum being respectively 0.48 (±0.15) and 0.39 \( \sigma \), and what may be taken as the duration, 1.2 (±0.1) and 1.11 \( \sigma \), respectively. But beyond this the agreement, as heretofore, ceases. The reconstruction fails to bring out any other elevation than \( A \), showing merely a very definite flattening of the decline beginning with what we take to be the end of the main wave, coincident with the position of the triangle representing the 6.25\( \mu \) fiber. The recorded \( B \) elevation of nerve, \( P \), travels at about the theoretical rate of a 3.75\( \mu \) fiber, and the \( B \) elevation (dotted), traveling at the mean saphenous \( B \) rate moves at the rate of a 2.75\( \mu \) fiber.

This reconstruction is quite in accord with the previous one in which
the small fibers were only counted (Erlanger, 1927). To produce an elevation simulating \( B \) the nerve would have to exhibit an accumulation of fibers between 3.45 and 1.7μ with a mean at 2.8μ. Such is not the case. All sizes of fibers are represented while there is a gap in the recorded potential.

The skin nerves of the bullfrog are so small—they may contain fewer than 150 fibers measuring more than 3μ in diameter—that to map completely all of the fibers is not a particularly arduous task. The main

Fig. 9. Reconstruction of the bullfrog's sciatic action potential (the one shown in figures 10 and 11, Gasser and Erlanger, 1927) as of 9.1 cm. conduction, zero being the position taken by the start of the fastest axon action potential (traveling 42 m.p.s. in a 20.7μ fiber). Superimposed on this is the action potential of figure 1 as straight lines joining the significant time points. If \( \alpha, \beta, \gamma \) and \( B \) of the recorded action potential are produced by the fibers of \( \alpha', \beta', \gamma' \) and \( B' \) of the reconstruction it would follow that conduction in the \( \gamma \) fibers is slightly out of accord with the fiber-size rule, and in the \( B \) fibers entirely out of accord. The area of \( A \) is about the same as that of \( A' \), but the area of \( B \) is more than twice that of \( B' \).

difficulty here, inexplicably, has been in getting a preparation with uncrenated fibers. The best preparation we have succeeded in obtaining, after several attempts, is the one used as the basis of the chart and reconstruction already published (Erlanger, 1927, figs. 7 and 8). On account of the increased interest the smaller fibers have assumed, the smaller myelinated fibers of this section have been remeasured as accurately as the crenation would permit, this time not only from the enlargement but also with an oil immersion lens and eyepiece micrometer. The result has been not to alter materially the distribution of the myelinated fibers in the chart. If
the last three triangles in the chart be omitted, there remain only those
which represent myelinated fibers. Accordingly a reconstruction was
made of the potential, which would be produced by myelinated fibers
alone. In this reconstruction a wave developed resembling $B$, in figure
4, but it was in such a position as to indicate a velocity of 6.5 m.p.s.
instead of the observed velocity of 3.4 m.p.s. This discrepancy is too
great to be accounted for by an error in either measurement involved.

Analysis of the data derived from the sciatic and peroneal nerves of the
bullfrog and of the green frog leads to much the same result. The prepara-
tion on which figure 10 (Gasser and Erlanger, 1927) was based was very
suitable for further analysis. Consequently the measurements were com-
pleted so as to include all the small myelinated fibers in the area examined;
and the measurements, as in the case of the other nerves, were subjected
to microscopic control.

The result of this analysis is included in figure 9 in such a way as to make
possible comparison between the reconstructed action potentials (crosses)
and the action potential of figure 1 (dots). As has always been the case
the correspondence as regards alpha and beta is very close indeed; the cor-
respondence with gamma is rather poor, but there is an indication of such
a wave in the reconstruction, and the resemblance would probably be still
better if the alpha and beta potentials had been drawn with the retention
of potential which follows the fast part of the axon potential represented
by the triangles. The gamma potential would then be found on a higher
base line than appears in the reconstruction. A comparison of the gamma
wave and the third pile of fibers in the distribution curve brings out one
point of considerable importance. The wave can at best utilize only a
small part of the third pile. The area of the fibers is too great and their
potentials appear too late in the theoretical reconstruction.

Now, can the fibers not needed for the gamma wave be made to account
for the $B$ wave? Certainly not without departing from the assumptions
made at the beginning of this section. The recorded wave, $R$, begins 12 $\sigma$
later than the only elevation, $B'$, in the reconstruction that could be
assigned to $B$. In fact, the recorded $R$ actually begins later than the
arithmetically derived action potential in the slowest myelinated fiber of
the nerve.

The foregoing observations show clearly that the velocity of conduction
in the small fibers is slower than the one calculated on a size basis from the
velocity in the fastest fibers. It remains to be ascertained whether signs
of other differences may be found.

It is reasonable to suppose that the potential in the late waves must be
derived from the third pile of fibers and from the unmyelinated fibers.
If these fibers have the same axon action potential form as the large fibers
it is easy to calculate the potential area they could yield; and this area
SOMATIC NERVE FIBERS OF SLOW CONDUCTION

can then be compared with the one experimentally observed. Unfortunately a technical difficulty lies in the way of accurate determination of the areas of the late waves in comparison with the A wave. The shock artefact, which is large on account of the strong stimuli, the retention of potential from the A wave, and the greater tendency toward diphasicity introduce an uncertainty as to the position of the base line, which cannot be accurately corrected; and this uncertainty introduces considerable error into the measurements of the area of waves of low potential and long duration. Therefore, in transferring the waves to a linear coordinate system prior to the measurement of the areas we have not taken the trouble of carrying over the exact form but have merely employed triangles drawn in their proper time and amplitude relations. The values we have obtained are included in table 3. It is not surprising under the circumstances that

<table>
<thead>
<tr>
<th></th>
<th>A</th>
<th>B</th>
<th>C</th>
<th>( \frac{B}{A} ) per cent</th>
<th>( \frac{C}{A} ) per cent</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Bullfrog sciatic of figures 1, 3 and 9</td>
<td>1,266</td>
<td>093</td>
<td>2,700</td>
<td>54.8 - 40.0</td>
<td>213.0</td>
</tr>
<tr>
<td>2. Bullfrog sciatic 11/20/28; approximate</td>
<td>1,178</td>
<td>350++</td>
<td>315</td>
<td>29.7</td>
<td>26.7</td>
</tr>
<tr>
<td>3. Bullfrog skin nerve of figures 4 and 5</td>
<td>454</td>
<td>105</td>
<td>732</td>
<td>23.1</td>
<td>12.3</td>
</tr>
<tr>
<td>4. Dog saphenous (11/24/28)</td>
<td>1,240</td>
<td>227</td>
<td>215</td>
<td>18.3</td>
<td>17.3</td>
</tr>
<tr>
<td>5. Dog saphenous of figures 6, 7 and 8</td>
<td>710</td>
<td>160</td>
<td>789+++</td>
<td>22.5</td>
<td>111.0</td>
</tr>
</tbody>
</table>

they vary irregularly among themselves; they can only be considered as approximations.

The area of the B elevation in figures 6 and 8 is 22.5 per cent of A. The area of all the fibers in the nerve measuring 6.25\( \mu \) and less is 20 per cent of those larger than this. There is thus sufficient area to account for B; but there is then very little left over for C, which may also occur, at least in part, in myelinated fibers, as will be indicated in a later part of the paper. In the frog skin nerve the area of the entire pile of small myelinated fibers, which includes the fibers measuring 4.25\( \mu \) and less, is 14.9 per cent of the area of the fibers measuring 4.75\( \mu \) and more. The B wave in figures 4 and 5 has an area 23 per cent of the A wave, therefore the small myelinated fibers would not supply the B wave alone. The same is true in the sciatic. The B wave in figures 1 and 9, after deducting the largest possible error due to the uncertainty of the position of the base line, is 40 per cent of the area of A, while the fibers below 7.25\( \mu \) have an area only 18 per cent of those above.
The result of the foregoing attempt to reconstruct the action potential of the B and C waves from the histological picture, using the constants of the A wave, is to show that it is impossible. Therefore the constants, which have been determined for the axon potentials of the A wave fibers, cannot apply to the potentials developing in the majority of the fibers in the last pile.

Sources of the A, B and C fibers. Somatic nerves acquire fibers by way of the dorsal and ventral roots and the gray rami communicantes, and the next step in the investigation consisted, therefore, in ascertaining which of the elevations of the action potential occur in these structures and which of them pass on into the somatic nerves.

Spinal roots: Bullfrog. Previous work on the bullfrog (Erlanger, Bishop and Gasser, 1926) has shown that the dorsal roots contribute to peripheral nerves an A elevation consisting of alpha, beta and gamma waves and the ventral roots an A elevation consisting of alpha. Stronger stimulation and higher amplification now reveal in the action potentials of the roots elevations traveling much more slowly than A.

Excised dorsal roots. Strong stimulation of the roots examined (6th to 9th inclusive) elicits an elevation in the action potential (see fig. 10, a, b, and c) that travels at rates usually ranging between 0.4 and 0.5 m.p.s., rarely as slowly as 0.3 m.p.s. or as rapidly as 0.6 m.p.s. (at room temperature, usually 23 to 24°C). To obtain these elevations in maximum amplitude the secondary coil must be set at 4 to 6 cm.; and the threshold usually is in the vicinity of 7 to 8 cm. Obviously as regards conduction rate and irritability these waves belong in the category of the C elevation of mixed nerve. The C action potentials appear in many configurations even at the short distances of conduction to which the observations are limited, usually 6 to 12 mm. (see fig. 10, b and c). Usually the elevations are rather long drawn out, and often are compounded of 2 or 3 waves; more usually they are plateau shaped. The action potentials of the roots of a pair may be strikingly alike in appearance. Calculation in a few cases in which C was well developed indicates that it may have as much as 15 to 30 per cent the area of A. Owing to the rapid deterioration of the elevations that results from the strong stimuli needed to elicit them, and to the very much greater diphasicity of C, these results necessarily are extremely inaccurate; but, if anything, C suffers more than A in the comparison because the record of A is made before the nerve is strongly stimulated for C.

There is no definite and constant elevation in the dorsal root cor-

---

7 We are numbering the roots as in our previous publication, though we have since learned that what is regarded in other animals as the first spinal root is atrophic in the frog. From the developmental standpoint, therefore, the numbers by which we designated frog roots are too small by one.
SOMATIC NERVE FIBERS OF SLOW CONDUCTION

responding in rate of conduction and irritability with the B elevation of mixed nerve.

Fig. 10. Dorsal root action potentials of the bullfrog. \( \times 2/3 \).

a, 7th root (4/20/29). 3 panels but shunted slightly to bring A within range of film. 33,000\( \omega \). Conduction distance 0.65 cm. Stimulus maximum for C. C rate 0.4 m.p.s.

b, Same as a, but with unshunted 4-panel amplification, i.e., more than 18 times a. Single transit.

c, 9th root (4/20/29). 4 panels, 72,500\( \omega \). Conducting distance 1.2 cm. Stimulus maximum for C. Rate of C 0.47 m.p.s. Single transit.

d, 9th root (4/10/29) stimulated, lead from trunk central to rami. Three single transits of spot on one film. 4 panels, 95,000\( \omega \). Conduction distance 1.31 cm. Stimulus maximum for C. C rate 0.4 m.p.s. The base line is badly deformed by the shock artefact. The time marks apply to the middle deflection.

e and f, 7th trunk (7/11/29) stimulated, lead from dorsal root. 4 panels, 233,700\( \omega \), 1/2 mf. 28.5\( ^\circ \)C. Single transits by the newest technique.

In e the stimulus was applied distal to attachment of rami. Conduction distance 4.0 \( \pm \) cm. Stimulus maximum for C. Rates, \( C_1 = 0.74 \), \( C_2 = 0.45 \) m.p.s.

In f the stimulus was applied central to attachment of rami. Conduction distance 2.0 \( \pm \) cm. Stimulus maximum for C. Rates, \( C_1 = 0.62 \), \( C_2 = 0.39 \) m.p.s. Ratio of areas of \( C_1 \) in f and g is 1:1.5.
The dorsal root C wave in the trunk. Records have been made of the action potentials traveling in either direction through preparations consisting of the dorsal root and the nerve trunk formed by its union with the ventral root. These preparations either have been removed from the body clear of all other tissues as in previous studies (Erlanger, Bishop and Gasser, 1926) or, more usually, they have been removed along with the tissues of the back through which the roots pass on their way from the vertebral canal to the subperitoneum. Excepting the small dorsal branch and the rami communicantes, the preparations are branchless. Observations have been confined to the 7th, 8th and 9th roots.

The records (see fig. 10, d, e, f) show that the dorsal root C elevation travels the whole length of the preparation in either direction and without any material changes in the form other than those attributable to the changing phase relations of the action potentials traveling at different rates in the contributing axons. The areas of the action potentials recorded in the root and started by stimulation of the trunk, first, peripherally of, and then, centrally to the junction point with the rami communicantes cannot be measured with sufficient accuracy (see fig. 10, e and f) to be of any material assistance in reaching a decision as to whether or not any of the C fibers of the dorsal root leave via the rami. It is only possible to say, on the basis of such measurements, that if any fibers at all leave, the maximum cannot exceed a third. Direct evidence that few if any of the dorsal root fibers leave the trunk by way of the white ramus has been obtained by stimulating the 7th dorsal root while leading from the 7th rami. In such experiments no perceptible deflection has been obtained in the case of preparations known to be sensitive, the posterior roots having subsequently yielded good C elevations in direct leads.

The A action potential, it has been shown (Erlanger, Bishop and Gasser, 1926), suffers a delay of about 0.14 $\sigma$ in passing through the posterior root ganglion. The C fibers conduct so slowly that a lag of this magnitude would be imperceptible; as a matter of fact our data throw no light whatsoever upon this question.

Inferences from the histology of the dorsal roots. Previous studies have shown that the configuration of the main parts of what we now designate the A elevation can be accounted for by the potentials in ordinary myelinated axons. The dorsal roots contain, in addition, a few small finely myelinated fibers and unmyelinated fibers. Whether these form a sufficient fraction of the total area to supply the observed relative area (up to $\frac{1}{3}$ of A) of the C action potential does not appear likely, though it remains for future work to settle this question.

Excised ventral roots. The results obtained in the case of the ventral

* The word trunk, unqualified, will be used to designate this part of the peripheral nerve.
roots varies with the root. Considering first the isolated roots, strong stimulation of the 6th or 7th roots invariably elicits, in addition to the A elevation, a wave traveling at rates ranging usually between 0.7 and 0.9

Fig. 11. Ventral root action potentials of the bullfrog. × 1/5.

a, 7th root (5/3/29). 4 panels, but greatly shunted to bring record within range of film, 4,000°. Conduction distance 1.1 cm. Stimulus maximum for A. Conduction rate 37.0 m.p.s.

b, same as a except that line is slower (24,000°), and stimulus maximum for C. Single transit.

c, same as b except that line is still slower (29,000°), C is further forward where the time intervals are longer, and the shunt is removed. Zero of time is at the beginning of C. Single transit.

d, 7th root (7/11/29). 4 panels, 180,000 1/2 mf. 28°C. Trunk stimulated (stimulus maximum for C) distal to rami, lead from root. Conduction distance 3.8 cm. Shock and A elevation merged. Single transit.

e, same as d except that trunk is stimulated central to rami. Conduction distance 1.8 cm. C rate 0.72 m.p.s. Single transit.

f, same as d except that root is stimulated, conduction distance is 0.6 cm., and line is faster (50,000°). C rate 0.83 m.p.s. Note that there is a C wave in e and f, but not in d. Single transit on duplitized film.

g, 7th root (7/15/29) stimulated (at maximum for C, 5.4 cm.), lead from rami. 233,700°, 1/2 mf. 30.4°C. Conduction distance 2.0 cm. C rate 0.28 m.p.s. In the same preparation there was no deflection when the dorsal root was stimulated. Single transit.
m.p.s. (see fig. 11, a, b, and c). Occasionally the rate is as high as 1.0 or as low as 0.6 m.p.s. Evidently this is a somewhat faster moving elevation than the posterior root C. To obtain it in maximum amplitude the coil has to be down to about 5 or 6 cm. Irritability and conduction rate seem to put this wave in the C category. Upon the whole the ventral root C wave is simpler in form than the posterior root C. Usually it seems to be made up of two parts, a high first wave $C_1$ and a lower second wave $C_2$ (see fig. 11, c). Relative to $A$, it is the highest of all the $C$ elevations, sometimes attaining a thirteenth the amplitude of $A$. Its area may be 36 per cent that of $A$.

Over twelve preparations of the 8th ventral root have been examined. All had magnificent $A$ elevations, and, with but one exception, no other elevations. The exception had a very small $C$ wave.

In the case of the 9th ventral root, of twelve preparations examined, all with good $A$ elevations, nine exhibited an elevation traveling at rates ranging usually between 1.0 and 0.7 m.p.s., but these were very much lower in amplitude than the $C$ waves of the 6th and 7th roots; three had not a trace of any wave other than $A$.

There is no elevation in the motor roots having the characteristics of $B$.

The ventral root $C$ beyond the root. The motor $C$ elevation passes in either direction between the root and the trunk, but in a majority of the cases the whole of it leaves the trunk by the rami communicantes. Thus of six of the 7th roots studied the entire elevation left the trunk in four; in two preparations, both from the same animal, a very small wave, started by stimulation of the ventral root and traveling 0.6 m.p.s., was recorded in the trunk beyond the rami. In no other root-trunk preparations has a ventral root $C$ wave been found passing the point of emergence of the rami. The number of observations, however, has not been large enough to justify a definite statement at this time regarding any but the 7th preparation.

The result usually obtained in the 7th root-trunk preparation is as follows: upon stimulation of the preparation in successive trials from below upwards while leading from the root, the $C$ elevation first appears in the record when the stimulating electrode touches the point of origin of the rami communicantes, as may be seen in figure 11, d, e and f. Direct proof that the $C$ fibers leave by the rami can be obtained by recording in the rami the action potential started by stimulation of the trunk close to its origin; a very fine double $C$ wave results. Or, if the motor root (7th) is stimulated with shocks gradually increasing in strength and a lead is taken from the corresponding ramus nothing presents in the record excepting the shock artefact until the coil approaches 10, when an elevation traveling at the rate of about 0.3 and 0.6 m.p.s. (two preparations) appears; it attains maximum height at a coil separation of 4 to 5 cm. (see fig. 11, g). The $C$ elevation is propagated, if anything, more slowly in the trunk and ramus than in the root.
The path taken by the motor C elevation and the peculiarity of its distribution between the several roots indicates clearly that it is formed by preganglionic fibers of the sympathetic system (see Langley and Orbeli, 1910).

Inferences from the histology of the white rami and motor roots. The white ramus of the frog is known to be composed mainly of fine myelinated fibers. A teased 7th white ramus of the bullfrog we have found to be made up almost exclusively of thin-sheathed myelinated fibers measuring for the most part 4μ in diameter, but ranging up as high as 7μ even. This picture has been confirmed by osmic acid preparations.

Past work indicates that the potentials of the ordinary myelinated fibers make up the A elevation of the anterior root. If the A and C elevations are produced by distinctive fibers it seemed that it should be possible to recognize the two fiber types by a histological comparison of the 7th and 8th motor roots since the 7th has a well-developed C elevation and the 8th none. Accordingly osmic acid preparations were made of roots whose action potentials had been recorded. The histological differences were not nearly as striking as we expected to find them. Both of the roots contain very fine myelinated fibers, the 8th a few, the 7th considerably more, but obviously not enough to make the white ramus. The 7th contains also some undifferentiated ground substance, possibly unmyelinated fibers, but again probably not enough, if they become myelinated, to make up the white ramus. Since usually all, or practically all, of the motor root C passes into the ramus, since it passes with equal facility in either direction, since the dorsal root contributes no appreciable potential to the white ramus, and since the ventral root C wave is propagated at about the same rate in root, trunk and ramus (slower, if anything, in the trunk and ramus), the histological observations, as far as they go, seem to indicate, 1, that myelinated fibers as large in diameter as 4μ or more can conduct at a C (0.7 m.p.s.) rate, and, 2, that with the apparent alteration in the histology of the C fibers from that of root fibers, whatever it may be, to that of the fibers of the white rami there is little, if any, alteration in the rate at which the impulse is conducted.

Relative irritabilities of dorsal and ventral root C fibers in the frog. By stimulating the 7th trunk central to its rami and leading from the dorsal and ventral roots separately it becomes possible to determine accurately the relative irritabilities of the dorsal and ventral root C fibers. Repeated alternation of the readings between the two roots compensates any error that might arise on account of the necessary succession of the observations. Readings in one preparation, three from each of the roots, gave thresholds of 10, 10, 10 in the ventral root and 8.5, 8.5, 8.5 cm. in the dorsal root. The calibration curve of the induction coil indicates that shocks at 8.5 are about twice as high as shocks at 10 cm. It will be recalled that
the motor C wave travels faster by about 80 per cent than the sensory C wave; the relative irritabilities of these two sets of fibers agree fairly well, therefore, with their relative conductivities.

*Mammalian roots.* A study similar to that made in the bullfrog has been carried out on the spinal roots of the cat; action potentials have been recorded in excised dorsal and ventral roots of the 7th lumbar and 1st sacral segments, usually at body temperature; also in the tibial branch of the sciatic nerve either in situ, and then with cut ends exposed to room temperature, or excised with a root attached and at body temperature, the stimuli in all cases being applied to one or the other of the roots above mentioned. There were certain technical difficulties more or less peculiar to this set of experiments. 1. The strong induction shocks needed stimulated not only at the cathode but often also at the anode (Heinbecker, 1928); often, too, the responses were repetitive; and when these things happen the resulting pictures were very difficult to interpret. 2. The repeated strong stimulation needed in such instances to make possible the interpretation of the picture soon damaged the preparation. 3. When the preparation was left in situ the strong shocks often spread to, and stimulate, muscle. To avoid the possibility of mistaking escaping muscle action potentials for nerve action potentials only those observations were regarded as acceptable during the course of which the muscles did not obviously contract. A brief account of the results of this series of experiments will suffice.

In the excised dorsal roots the usual A elevation has again been demonstrated (Erlanger, Bishop and Gasser, 1926) and, in addition, an elevation having the conduction rate and relative irritability of C of warm-blooded somatic nerve. Our best record of such a wave is seen in figure 12, a; it was obtained from a root at 25.5°C., stimulated maximally for C (coil at 5.4 cm.). The coil positions for the thresholds of the A and C elevations were 27.7 and 7.7 cm., respectively. The amplitude of the A elevation was not recorded; but on the basis of the amplification factor it can be asserted that it exceeded that of C at the least eighteen times. The conduction rate of the first C elevation was 0.71 m.p.s., of the second 0.25 m.p.s. In the root at body temperature the rates of the first C wave have usually ranged between 1.8 and 1 m.p.s. We have never seen in these roots any wave consistently occupying the position of B.

When the root is stimulated and the lead taken from the tibial nerve, slow moving waves are recorded, but, as might be expected, they are low in amplitude. At very short distances of conduction, even, and in the roots themselves, C is apt to be low; it is not surprising, therefore, that only low C elevations have been recorded at the longer distances of conduction and at the much greater dilutions of the responding C fibers by unaffected fibers that obtain when the root is stimulated and the lead taken from the
SOMATIC NERVE FIBERS OF SLOW CONDUCTION

peripheral nerve. Two records are reproduced, one, figure 12, b, from an in situ preparation, the other, figure 12, c, from a preparation mounted in the moist chamber. Both show a low but definite double elevation the first wave of which travels at the rate of 1.8 m.p.s. in one and 0.85 m.p.s.

in the other, the second elevation (in c) at the rate of 0.35 m.p.s. It should be pointed out that when first seen on the face of the oscillograph these C waves were considerably higher in amplitude; by the time the records were made they had suffered as a result of the preliminary stimulation. The

Fig. 12. Dorsal root action potential in the cat. Natural size.

a, 1st sacral (4/26/29) at 25.5°C. 4 panels, 25,000 ø. Conduction distance 0.7 cm. Stimulus maximum for C, 5.9 cm. A merged with shock escape. Rates, C1 0.71, C2 0.25 m.p.s. Single transit.

b, two deflections from an in situ 1st sacral root-tibial preparation (4/13/29). 4 panels, 139,000 ø. Body temperature. Root stimulated, lead from tibial. Conduction distance 10 cm. approximately. Stimulus maximum for C, 2.9 cm. C rate 1.8 m.p.s. The line is deformed by the shock artefact. Single transits.

c, isolated 1st sacral root-tibial preparation (5/8/29) at 36°C. 4 panels, 69,000 ø. Conduction distance 3.15 cm. Stimulus maximum for C. Rates, C1 0.85, C2 0.35 m.p.s.; A (in another record) 52 m.p.s. The thresholds were A 29.2, C 5.6 cm. Single transit.
thresholds of A and C in preparation c were 29.2 and 5.6 cm., and the conduction rate of A 52.2 m.p.s.

Nothing resembling a B wave has been seen in these dorsal root preparations.

Inferences from histology. Mammalian dorsal roots have been found by Ranson (1914) to contain more than twice as many unmyelinated fibers as myelinated. He has found, furthermore, that all of the former, as well as a few fine myelinated fibers, pass from the dorsal roots into Lissauer's tract. The obvious inference is that the C waves we have observed in mammalian dorsal roots are formed by the action potentials of these fibers. Whether the fine myelinated fibers are present in sufficient number to produce a legible deflection we do not know. If they are, the absence of any slow moving wave other than C may be taken to indicate that these fine myelinated fibers and the unmyelinated fibers both conduct at the C rate.

CONTRIBUTION OF THE GRAY RAMI TO MIXED NERVE. In the bullfrog it is a simple matter, since the parts involved are covered only by peritoneum, to make a preparation consisting of one of the trunks of the lumbosacral plexus, formed by the union of any one of the contributing pairs of spinal roots, with its rami communicantes attached. The lead in these experiments is from the distal end of the preparation from a point somewhat central to its union with the other sciatic components, and the stimuli are applied to the sympathetic chain, often with one ganglion intervening, and to the trunk central to the rami. By including one ganglion a sufficient length of gray ramus is obtained to obviate danger of spread of the stimuli through the short rami to the trunk.

The results obtained have been perfectly definite and can best be presented by citing just one of the experiments (see fig. 13). The record (a) resulting from stimulation of the trunk (the 9th in this case) maximally is made up of an A elevation traveling 54 m.p.s. and a double C elevation, the two parts of which travel 0.78 and 0.45 m.p.s., respectively, rates that are typical of C components. These elevations appear on the screen as their characteristic thresholds are reached. B is conspicuously absent, as may be seen by comparing this record (a) with the next record (b).

When the rami are stimulated maximally the record (b) consists of two elevations which by their conduction rates, namely, 3.11 and 0.51 m.p.s., (and their thresholds) are definitely identified with B and C. Then the trunk and the rami are laid across the electrode and together stimulated maximally. The record obtained (c) obviously is a combination of records a and b of this series, and has the appearance of a typical mixed nerve action potential; it is made up of an A elevation traveling at the rate of 50.0 m.p.s., a B elevation traveling 2.10 m.p.s. and a double C elevation with components traveling 0.66 and 0.40 m.p.s. The discrepancies in
Fig. 13. Records of the gray ramus contribution to mixed nerve in the bullfrog (4/12/29). Preparation consists of the excised 9th trunk with rami attached. The lead in a, b, and c is from the trunk peripheral to rami. 4 panels. All single transits. The records are written on a line deformed by the shock escape. Natural size.

a, stimulus applied to the trunk central to rami. 60,000Ω. Conduction distance 2.8 cm. Stimulus maximum for C, 4.4 cm. The record shows two elevations, namely A traveling at an A range of rate, not determinable in this record, and two C elevations, C1 traveling 0.73 and C2 0.44 m.p.s.

b, rami stimulated. 50,000Ω. Conduction distance 2.25 cm. The record shows two elevations, B traveling 3.11 m.p.s. and C (probably C2) traveling 0.5 m.p.s.

c, rami and trunk stimulated simultaneously on one stimulator. Two single transits. The record shows an A elevation, rate not determinable here, a B elevation traveling 2.88 m.p.s. and two C elevations, the first, indistinct, moving 0.75 and 0.43 m.p.s., otherwise the same as b.
the conduction rates are not beyond the limit of error considering the shortness of the nerve and the differences in the strength of the stimuli.

It should be pointed out that the conduction rates of the B elevations, but not of the C elevations, in this series of experiments, have been slower than those of the B elevation as measured directly in the sciatic nerve, though but little if any slower than B in the bullfrog's skin nerve. Whether

Fig. 14. Records of the gray ramus contribution to mixed nerve in warm-blooded animals. All single transits. Natural size.

a, excised gray ramus preparation of the cat (4/24/29). The gray ramus is stimulated and the lead is from the lumbosacral trunk to which it runs. 4 panels, 24,000\(\omega\). 36.5°C. Conduction distance 1.2 cm. Stimulus maximum for C. The only elevation is C, traveling at the rate of 0.98 m.p.s.

b, record from a gray-ramus-femoral-nerve preparation of the dog, in situ (5/15/29). 4 panels, 12,000\(\omega\). Rectal temp., 34.5°C. Conduction distance 8.3 cm. Stimulus maximum for B. B conduction rate 11.9 m.p.s. On duplitzed film.

c, same as b, but stimulus maximum for C, and line slower, (162,000\(\omega\)). B rate 9.3 m.p.s., C rate 1.62 m.p.s.

the intervening ganglion on the path of the sympathetic fibers here is responsible for this difference is not the province of this paper to ascertain.

Confirmation of the entrance of B by way of the gray ramus can easily be obtained from a preparation consisting only of the trunk by stimulating on either side of its junction point with the rami, while leading peripherally; a B wave appears in the record only when the electrodes are at or peripheral to the ramus junction.

Similar experiments to those just described have been carried out in the
cat and dog. Gray ramus-nerve preparations have been examined both after excision, but at body temperature, and in situ. The excised preparation consists of a segment of nerve trunk 1 to 2 cm. long, cut high enough up in the intervertebral canal to include the rami, and its communicating branches from the sympathetic chain, themselves usually over 1 cm. The stimulus is applied to the ramus and the lead is from the nerve trunk. The in situ preparations were made according to the method of Langley (1891). In the anesthetized animal a good exposure is made of the abdominal sympathetic chain. The appropriate part of the chain is divided into segments by transection immediately below each ganglion. The preparation is arranged for stimulation centrifugally, the femoral nerve is cut above the origin of the saphenous nerve, and its freed central end placed upon the leads. The two ends of the preparation, therefore, are at room temperature, the rest at a low body temperature. The exposed nerve is kept moist by frequent applications of Ringer’s solution to it, and, by trial stimulations, the gray ramus is found that gives the highest action potential in the nerve.

All of the preparations successfully made (nine) have given good C waves (see fig. 14, a and c); four, in addition, all femoral nerve preparations, have disclosed a wave, with its threshold definitely in the B range, traveling at rates that have varied between 17.9 and 8.4 m.p.s. (see fig. 14, b and c). In the experiment in which the conduction rate was 8.4 m.p.s. (dog) the rate of the B wave in the saphenous nerve of the same animal under exactly the same conditions was found to be 8.5 m.p.s. The B wave in the gray ramus has had in all cases the characteristic brevity of warm-blooded B, to which reference will be made in the discussion. Four of the gray ramus preparations displaying a C but not a B wave were of the sciatic plexus: for some unknown reason we have as yet failed to ascertain the path by which B fibers find their way into the sciatic nerve in warm-blooded animals. Whatever the meaning of this experience may be, our experiments have disclosed no other source of B fibers than the gray rami.

Discussion. On fundamental differences between A, B and C fibers. The first question that suggests itself here has to do with the possibility of recognizing by their morphology the fibers whose action potentials make up the A, the B and the C elevations. In a preliminary report based upon a parallel investigation of fibers in the involuntary nervous system conducted by Heinbecker in this laboratory (1929) the conclusion was reached that “unmyelinated fibers can be identified,” among other ways, “by a conduction rate slower than that of the ordinary myelinated fibers of peripheral nerves. . . . . ” In a subsequent preliminary report based on the study of nerves of the involuntary nervous system and various other nerves Heinbecker and Bishop (1929) are lead to infer that the B elevation corresponds to the thinly myelinated, the C elevation to the
unmyelinated axons in islands composed of these fibers. Now, it turns out that there is one set of observations made in the present investigation that seems to be incompatible with this view, namely, those concerned with the C elevation in the ventral roots of the bullfrog. This elevation passes into, and seems to account completely for, the white ramus action potential. The white ramus fibers are thinly myelinated ranging in diameter between 2 and 7μ, the 3–4μ fibers predominating; yet they conduct at or very close to the C rate and have nearly, if not quite, the irritability of C fibers. An observation also of significance in this connection is the apparent lack in the roots of a sufficient number of these small myelinated fibers to make up the white ramus, coupled with the fact that in the root and the white ramus the propagation rates of C are substantially alike. Evidently, here are fairly large, though thinly myelinated, fibers that have the conductivity and irritability of C fibers; and in the root the continuations of these fibers, apparently altered in histology, conduct at the same rate as the fibers in the white ramus. In view of these findings it seems best for the present not to attempt a classification of the B and C types of fibers on a histological basis.

It has been shown above that of the action potential area of mixed nerve there is not enough left, after deducting the area of the A potential, to provide all of the B area. Other sources of potential that remain to be called on are the unmyelinated fibers and perhaps the smaller myelinated fibers, if the area of the potentials of the individual fibers of this variety is larger than that of the A variety. Heinbecker (1929) presents evidence indicating that fibers of slow conduction have relatively long lasting action potentials; if, in addition, it could be shown that the amplitude of their potentials is not correspondingly lower the small myelinated fibers might suffice to supply the full amount of the energy that is liberated with the B wave, and in this respect the view would still be tenable that B of somatic nerves derives its potential from small myelinated fibers and C from unmyelinated fibers. But now that small myelinated fibers have been found that have the conductivity and irritability of C fibers, the need of exercising caution in assigning potential waves to types of fibers becomes very obvious. Moreover, in certain animals, the dog's saphenous, for example, we have been unable to distinguish any considerable group of fibers that can be regarded as thinly myelinated, yet the action potential of this nerve exhibits an exceptionally well developed B wave.

Another consideration that may have some significance in this connection is the contention of neurologists, generally, that one and the same nerve fiber may in part of its course be myelinated, in another unmyelinated. This seems to be particularly true of postganglionic fibers (see Ranson and Billingsley, 1918); but motor fibers, even, may lose their sheaths, some distance, for instance, from their terminations (Garven, 1925). It would
be surprising if, merely through loss or acquisition of myelin, fibers could be so changed in their reactions as to pass from one of the groups, A, B or C, into another. It seems much more reasonable to suppose, in view of our findings, that the striking differences in conductivity and irritability of the three fiber groups are due to some fundamental difference in the composition of the fibers, related, perhaps, in some way to the systems to which the fibers belong. The B fibers, for instance, evidently are postganglionic. However, there are, presumably, other postganglionic fibers; for mixed nerve acquires quite a large C component by way of the gray rami. The A group is made up of voluntary motor fibers and of sensory fibers, probably those belonging to the epiergic group. The C fibers of the dorsal roots would then be left to care for protopathic sensation, a possibility that has been considered by Ranson and Von Hess (1915) in relation to the unmyelinated fibers of the posterior roots. These illustrations are certainly suggestive of the possibility that there is a difference in the materials composing the fibers of each of the groups that accounts for the differences in their reactivities.

The adoption of such a view would by no means preclude the possibility that structural differences also affect conduction and irritability. Within each of the groups the fibers differ among themselves rather widely in these respects. This gradation, in so far as A is concerned, has been shown to be referable to the diameters of the A fibers,—the larger the fiber the higher its conductivity and irritability (Gasser and Erlanger, 1927). And it may well be that diameter differences of the constituent fibers account for the range in conductivity and irritability within the other groups, B and C, also.

On the relation of A, B and C of cold-blooded nerve to A, B and C of warm-blooded nerve. In so far as concerns their origins, the evidence is quite clear that the A, B and C fibers of cold-blooded animals are the homologues of the A, B and C fibers of warm-blooded animals; the corresponding groups obviously are alike in respect to kind. Nevertheless it is possible to demonstrate in the case of one of the groups, namely, B, certain quantitative differences related to the class of animals, warm- or cold-blooded, to which the fibers belong.

We may consider first differences in conduction rate. Since conduction rate depends upon fiber diameter (among the large myelinated fibers, at least) and since the B and the C fibers have not yet been definitely identified, a comparison of the ratios of A rates, of B rates and C rates, warm-blooded to cold-blooded, can for the present have only a tentative value in this connection. Nevertheless, let us assume that the relative differences in diameters of the largest fibers in each of the groups, A, B and C, of warm- and cold-blooded animals are the same and that temperature affects all of the fibers alike. The justifiability of the latter assumption has already been demonstrated as regards A (Gasser and Erlanger, 1927):
and the fact, shown above, that at room temperature $C$ of warm-blooded nerve has about the same conduction rate as $C$ of cold-blooded nerve indicates the applicability of the rule to this process, also. Then, from average conduction rates numerical values can be derived expressing the conduction rates of the $A$ elevations, the $B$ elevations and the $C$ elevations in nerves of one class of animal relative to those in nerves of the other class. The number of observations in the dog (saphenous) and in the bullfrog (sciatic) is sufficient to make a comparison of this kind worth while. The values obtained in these animals are

\[
\begin{align*}
\text{Dog A} & \quad 82.8 \quad = \quad 1.97 \\
\text{Bullfrog A} & \quad 42.0 \\
\text{Dog B} & \quad 13.8 \quad = \quad 3.07 \\
\text{Bullfrog B} & \quad 4.53 \quad = \quad 3.07 \\
\text{Dog C} & \quad 0.97 \quad = \quad 1.6 \\
\text{Bullfrog C} & \quad 0.59 \\
\end{align*}
\]

The $A$ and the $C$ ratios, it is seen, do not vary so very widely from a mean of 1.80, a result which may be taken to indicate that the $A$ and the $C$ fibers of the dog and frog have comparable conduction rates. The very much larger ratio derived from the comparison of the $B$ conduction rates suggests either that the $B$ fibers of the two classes of animals differ more widely either in respect to size or in respect to some other structural factor affecting conduction rate, or in constitution than do the $A$ or $C$ fibers. The $B$ fibers of the dog, furthermore, seem to be somewhat more irritable relative to $A$ and $C$ than those of the bullfrog, though our data relative to this property are not sufficiently numerous to justify more than a tentative statement regarding it. Differences in constitution, if they obtain, might be regarded as a reason for suspecting that the $B$ fibers of the two classes of animals may not be comparable functionally. Opposed to any functional difference, however, is the fact that in both mammals and amphibia the $B$ wave gets into peripheral nerves apparently only by way of the gray rami.

The $B$ waves of cold- and warm-blooded nerve differ from each other in still another respect, namely, as regards their durations, both absolute, and relative to the durations of their companion $A$ and $C$ waves. The data for making these comparisons are derived from table 1, and include all of the observations on the sciatic of the bullfrog and the dog's saphenous that are sufficiently complete for the purpose. They are collected in Table 4. The comparison is facilitated by the fact that the average conduction distances turn out to be alike for the two nerves.

The table shows that if we multiply the average durations of the eleva-
tions in warm-blooded nerve by three, which in this case seems to be the factor necessary to care for the effect of the difference in temperature at which the two sets of observations were made, the \( A \) values and the \( C \) values derived agree remarkably closely among themselves. The \( B \) values, however, differ widely, \( B \) in the cold-blooded nerve being almost five times as long as \( B \) in the warm-blooded nerve.

The brevity of warm-blooded \( B \) signifies, and to this reference has already been made, that it is constructed of axon action potentials traveling at rates that range between relatively narrow limits. In addition, it means that the component action potentials must have a duration that is less

<table>
<thead>
<tr>
<th>TABLE 4</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>NUMBER</strong></td>
</tr>
<tr>
<td></td>
</tr>
<tr>
<td></td>
</tr>
<tr>
<td>Bullfrog sciatic</td>
</tr>
<tr>
<td>8</td>
</tr>
<tr>
<td>9</td>
</tr>
<tr>
<td>Average</td>
</tr>
<tr>
<td>Dog saphenous</td>
</tr>
<tr>
<td>12</td>
</tr>
<tr>
<td>14</td>
</tr>
<tr>
<td>16a</td>
</tr>
<tr>
<td>16b</td>
</tr>
<tr>
<td>17a</td>
</tr>
<tr>
<td>17b</td>
</tr>
<tr>
<td>18</td>
</tr>
<tr>
<td>Average</td>
</tr>
<tr>
<td>( \times 3 )</td>
</tr>
</tbody>
</table>

than 1.2 \( \sigma \), less, indeed, than the duration of the briefest of the \( B \) elevations, which is 0.9 \( \sigma \). Since the duration of the \( A \) axon action potential lies in the vicinity of 0.6 \( \sigma \) (Gasser and Erlanger, 1927), it follows that the action potentials of the \( A \) and the \( B \) axons of warm-blooded nerve are of the same order of magnitude. We have no data bearing on the duration of the action potential in the \( B \) fibers of cold-blooded nerve; we assume, however, merely on the basis of duration of the \( B \) elevation, that it is considerably longer than that of the corresponding \( A \) fibers. The \( B \) fibers of warm-blooded nerve, therefore, differ from those of cold-blooded nerve (1) in conducting relatively more rapidly (2) in being slightly more irritable relatively and (3) in having a relatively brief action potential.
SUMMARY

On the basis of conductivity and irritability it is possible to distinguish in all somatic nerves three groups of fibers, designated A, B and C. The A fibers are those that produce the familiar somatic nerve action potential in which the cathode ray oscillograph has disclosed alpha, beta and gamma waves; they include the large myelinated fibers down to about \( 5 \) m. The B and the C fibers include the myelinated fibers not contributing to A and unmyelinated fibers.

In round numbers the range of conduction rates of the fibers contributing to A in the dog and cat is 90 to 30 m.p.s., of the B fibers 20 to 10 m.p.s., of the C fibers 1.6 to 0.3 m.p.s.; in the bullfrog the ranges are, for A, 50 to 10 m.p.s., for B, 5.5 to 1.3 m.p.s., and, for C, 0.9 to 0.2 m.p.s. In the green frog the rates are all somewhat slower than in the bullfrog.

The differences in irritability of the three types of fibers are such that by gradually increasing the strength of stimulus (induction shocks) it is possible to elicit in succession, with intervening gaps, the A elevation of the action potential, the B elevation and the C elevation. With the inductorium used by us under a more or less constant set of conditions the coil separations in centimeters have been for the A threshold and maximum 30 and 20, for B, 18 and 10, and for C, 8 and 4. Taking the shock height at 30 cm. as 1 the approximate shock heights at the other coil positions just given are 2.1, 2.4 and 6.0, 15.7 and 203.0, respectively.
The A elevation always is compound, B occasionally so and C usually. In the sciatic of the bullfrog at the usual distances of conduction the amplitudes of the elevations relative to C (= 1) in round numbers typically are 5 and 100 for B and A, respectively; in the skin nerve of the bullfrog the relative heights may be 1, 3 and 40 and in the saphenous of the dog (a skin nerve) 1, 4 and 40 for C, B and A, respectively.

The B fibers of warm-blooded nerve have a somewhat higher reactivity relative to A and C than those of cold-blooded nerve. When allowance is made for difference in temperature the A fibers in both warm- and cold-blooded nerve conduct at about the same rate, likewise the C fibers, but the warm-blooded B fibers conduct considerably more rapidly than the cold-blooded B fibers. Similarly, the durations of the cold-blooded and warm-blooded A and C waves are each of the same order of magnitude; but the warm-blooded B elevation has about a fifth the duration of cold-blooded B. Its duration is such as to indicate that in warm-blooded nerve the duration of the axon action potential of B is of the same order of magnitude as that of A.

The A fibers enter somatic nerves via the spinal roots, B fibers via the gray rami and C fibers via the dorsal roots and the gray rami in both warm- and cold-blooded animals; but, seemingly, in warm-blooded animals not all of the gray rami transmit B fibers.

In the frog, the 6th, the 7th and the 9th (usually), but not the 8th (with rare exceptions), ventral roots, these being the only roots investigated, contain fibers which produce a C elevation traveling at the rate of 0.8 m.p.s.; these fibers leave the nerve by the white rami, though occasionally (observed twice in the 7th root) some of them pass on in the peripheral nerve. Since the fibers of the white rami are for the most part thinly myelinated and range around a diameter of about 4μ, it follows that such fibers, despite their relatively large size, can conduct at a C rate. Undoubtedly, unmyelinated fibers also conduct at the C rate; but it has not yet been precluded that they, also, may conduct at a B rate. For the present, therefore, it is manifestly impossible to define B and C fibers on a histological basis.

Figure 15 summarizes schematically the main findings of this research.

The expenses of this research have been defrayed in part by a grant from the Ella Sachs Plotz Foundation.

**BIBLIOGRAPHY**

Bishop. 1927. This Journal, lxxii, 492.
Bishop, Erlanger and Gasser. 1926. This Journal, lxxviii, 592.
Erlanger. 1927. This Journal, lxxii, 644.
Erlanger, Bishop and Gasser. 1926. This Journal, lxxviii, 574.
Erlanger, Gasser and Bishop. 1924. This Journal, lxx, 624.
Gasser. 1928a. This Journal, lxxxv, 372.
1928b. This Journal, lxxxv, 569.
Gasser and Erlanger. 1927. This Journal, lxxx, 522.
Heinbecker. 1928. This Journal, lxxxvi, 423.
Ranson and Von Hess. 1915. This Journal, xxxviii, 128.