

nerves the relationship between fiber size and conduction rate (Gasser & Erlanger<sup>4</sup>) fails to hold as between one main group of axons and the next. There is a sharp break in character between the first and second groups in the properties discussed above, and much less difference in certain respects between the small myelinated and unmyelinated fibers. The first group of axons conducts through the superior sympathetic ganglion of the turtle in either direction, the second irreversibly, indicating a motor fiber synapsing in this system. Part of the third group axons, at least, also synapse here and are motor and part go through probably having synapsed in other ganglia more centrally. Some at least of the post-ganglionic fibers synapsing with the second group pre-ganglionic are also second group fibers. If the second group axons are the thinly myelinated ones, post-ganglionic myelinated fibers are therefore present. There are many more of these fibers post-ganglionically than pre-ganglionically.

It is anticipated that such thinly myelinated axons associated with unmyelinated will contribute to B and C elevations in other nerves where present, and the investigation of their properties is being extended to test this possibility.

The potential analysis of the sympathetic nerves has been undertaken by Heinbecker, the study of the differentiation between types of axons in various nerves is a joint research of Bishop and Heinbecker.

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### The Action Potential in Fibers of Slow Conduction in Spinal Roots and Somatic Nerves.

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The group of waves, *alpha*, *beta*, *gamma* and *delta*, hitherto described as constituting the conducted action potential of mixed somatic nerve<sup>1, 2</sup> are confluent and are produced by groups of fibers conducting at rates ranging in round numbers, in the bullfrog, green

<sup>4</sup> Gasser, H. S., and Erlanger, J., *Am. J. Physiol.*, 1927, lxxx, 522.

<sup>1</sup> Gasser, H. S., and Erlanger, J., *Am. J. Physiol.*, 1922, lxii, 496.

<sup>2</sup> Erlanger, J., Gasser, H. S., and Bishop, G. H., *Am. J. Physiol.*, 1924, lxx, 624.

frog (at room temperature) and dog (at body temperature), between 40 and 10, 35 and 8 and 80 and 30 m.p.s., respectively. Together they form what may be called the *A* elevation. When the record obtained from these nerves by the cathode ray oscillograph is continued through 200 to 300  $\sigma$ , instead of stopping after 10-15 $\sigma$  as has been usual hitherto, and higher amplification, 100,000 instead of 8,000, is used, 2 additional and discrete elevations, which, like *A*, may be compound, appear in succession as the stimulation is raised to strengths far beyond those previously employed by us. The second, or elevation *B* travels at the rate of about 5 to 2 m.p.s. in mixed nerves of the bullfrog and green frog and 17 (20 in one case) to 11 m.p.s. in the dog, the rates in the contributing fibers ranging down to about 2 to 1 m.p.s. in the frog and to about 8 m.p.s. in the dog. The third or *C* elevation is conducted at the rate of 0.7 to 0.5 in the frog and 1.5 to 0.8 m.p.s. in the dog, the rates in the slowest fibers ranging down to about 0.3 m.p.s. in the frog and to 0.5 m.p.s. in the dog. The 3 elevations, *A*, *B* and *C*, are propagated at such diverse rates that in less than 1 cm. of conduction they become quite clear one of the other, in this respect differing strikingly from the *alpha-beta-gamma* waves of *A* which are confluent at all distances of conduction. The heights of induction shocks threshold for *A*, *B* and *C* in the bullfrog, directly measured by the oscillograph, roughly are, to cite a single instance, 3, 7(+) and 38 volts, respectively; for maximum action potentials *B* and *C* in this case required shocks reaching 38 and 80 volts. This is mentioned merely to indicate how much stronger the stimuli must be to elicit *B* and *C* than those ordinarily used to elicit the action potentials hitherto recorded by us. *A*, *B* and *C* elevations are present also in the action potentials of skin nerves of the bullfrog and of the dog. In some muscle nerves *B* may be absent or insignificant (phrenic of the dog), in others variable (dog) or well developed (frog).

In the bullfrog, of the 3 possible sources of the waves of mixed nerve, all of the anterior roots examined contribute *A* elevations, while some contribute fast travelling *C* waves (about 0.8 m.p.s.); posterior roots supply *alpha*, *beta* and *gamma* (and possibly *delta*) waves to the *A* elevation, and *C* waves slower than those from the anterior root (rate about 0.5 m.p.s.); and finally grey rami contribute *B* and also *C* processes, the latter first recognized, in the sympathetic nerve of the turtle, by Heinbecker. It would seem, therefore, that there are anterior root, posterior root and sympathetic *C* waves in somatic nerves. The posterior root *C* elevations, like the *A* eleva-

tion,<sup>3</sup> are conducted, as nearly as can be determined, at the same rate in either direction through the root ganglion; thus far no evidence has been obtained indicating that the fibers concerned make a synaptic junction there. The rate of conduction of a given *C* process seems to be the same in the root as it is in the nerve trunk.

In the cat, posterior roots (7th lumbar and 1st sacral) contribute to somatic nerves *A* and *C* waves, *C*, as well as *A* being regularly present in root preparations; the corresponding anterior roots supply an *A* wave; and the lower grey rami send in a *C* wave and *B*.

It has been shown<sup>4</sup> that to a first approximation the fibers forming the *A* elevation conduct at rates that are proportional to their diameters. If the *B* and *C* fibers obeyed the same rule, their sizes, in the bullfrog, for example, would range in the case of *B* between 2.5 and 0.5 $\mu$  and in the case of *C* between 0.35 and 0.12 $\mu$ . But somatic nerves contain no group of myelinated fibers ranging between the limits demanded by *B*; and myelinated fibers small enough in diameter to conduct at the *C* rate do not exist. The wave in the saphenous nerve of the dog, which answers the present description of *B*, originally was labelled *delta*.<sup>5</sup> Because its rate was slower than could be accounted for on the basis of the fiber-size rule it was believed to be formed by the action potentials of unmyelinated fibers. There are reasons for believing that this elevation and the corresponding elevation in other mammalian somatic action potentials is homologous with the *B* elevation of cold-blooded nerve, namely, its position in the action potential picture, its source, and its failure to obey the fiber-size rule. It travels, however, at a relatively faster rate than the *B* of cold-blooded nerve. The *C* fibers contributed by the sympathetic system probably are unmyelinated.<sup>6</sup> And presumably the *C* elevation in the posterior roots is formed by the action potentials of the unmyelinated fibers (and finely medullated fibers) described by Ranson<sup>7</sup> as passing into the Zone of Lissauer in the cat. The nature of the fibers forming the *C* elevation seen in certain of the anterior roots of the frog is undetermined. The obvious failure of *B* and *C* to obey the fiber-size rule that holds for the *A* system forces the conclusion that the rule can hold only in the case of fibers belonging to one and the same system.

<sup>3</sup> Erlanger, J., Bishop, G. H., and Gasser, H. S., *Am. J. Physiol.*, 1926, lxxviii, 574.

<sup>4</sup> Gasser, H. S., and Erlanger, J., *Am. J. Physiol.*, 1927, lxxx, 522.

<sup>5</sup> Erlanger, J., *Am. J. Physiol.*, 1927, lxxxii, 644.

<sup>6</sup> Heinbecker, P., *Proc. Soc. Exp. Biol. and Med.*, 1929, xxvi, 349.

<sup>7</sup> Ranson, S., *J. Comp. Neurol.*, 1914, xxiv, 531.