

Missouri Section.

Washington University School of Medicine, April 13, 1932.

6152

Responses of Axons to Brief Shocks.

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In a previous paper¹ a range of latencies was postulated in the response of nerve fibers to short induction shocks. Using a 5-panel amplifier in conjunction with the von Ardenne cathode ray oscillograph, permitting the photographic recording of input potential changes significant to one microvolt and of time to 0.01σ , we are now able to secure by an inertialess method records of the potential changes in nerve resulting from the activity of a single fiber.

The monophasic axon spike varies in amplitude from 10 to 300 microvolts, depending largely on the mass of inactive shunting tissue. In the α range the rising phase at 16°C . varies in different experiments from 0.3 to 0.7σ . The falling phase may be as short as 1.0σ . The β spike seems to have comparable magnitudes, although statistically they may be a trifle longer. Spikes of B fibers in a gray ramus had a crest time, at 16°C ., of 1.4σ . Shapes and time functions of the axon spikes vary considerably in different experiments. The most important modifying factors seem to be the condition of the reacting fiber, the depth of tissue between it and the lead electrode, branches or adherent material between leads, potentials from remote active fibers, extraneous disturbances, the diphasic artifact, and the type of fiber most favorably placed in relation to the stimulating electrode.

The usual axon spike shows a short inception phase, most marked in nerves with sheaths, which we believe represents in part the potential change led through inactive tissue, ahead of the arrival of the excitatory process over the lead. Extremely small nerves may give axon spikes which show a vanishingly small period of incep-

¹ Erlanger, J., and Blair, E. A., *Am. J. Physiol.*, 1931, **99**, 129.

tion; the rise then begins linearly, the crest is sharp, and the visible decline ends abruptly. We believe that these curvilinear, triangular spikes are the least deformed of any we have recorded.

Quick shocks (duration less than 0.04σ) which appear to be uniform when subjected to physical and physiological tests, may be adjusted so that only an occasional response of a single axon occurs, indicating that extirpated fibers are subject to spontaneous changes in irritability. The interval between the delivery of the shock and the arrival of the spike at the lead also varies spontaneously. In a typical experiment at 16°C ., employing uniform shocks producing only occasional single axon responses, shock-spike intervals varied spontaneously over a range of 0.4σ . Increase in strength tended to decrease the spontaneous range and shorten the average shock-spike interval. Change of strength from just threshold to 3 times that value brought this spike still earlier so that the extreme range of its latency amounted to more than 0.7σ .

Submaximal spikes recorded at the site of stimulation have been assumed in the past to represent the time functions of undispersed axon spikes. In a typical experiment at 16°C . a composite α spike recorded at the site of stimulation had an overall time to maximum of 0.94σ . The time to maximum of the most irritable component α spike was nearly 0.4σ . Since fibers of much lower irritability than any involved above have spikes which are little longer than those of α , this difference cannot be attributed to the presence of significantly longer axon spikes; it must be assigned to fibers responding with latencies ranging in this case from less than 0.2σ up to 0.5σ or more.

A conducted action potential involving few units is of irregular height and shape. The most irritable fiber responds consistently with an almost uniform short latent period, and its spike is usually the first to arrive at the lead; some of the slower, but threshold, fibers respond only occasionally with long, variable latent periods. Although the shock-spike time is fairly constant, the pictures are constantly varying. The regular configuration of spike responses previously published is due to the smoothness of the sum of the component axon potentials despite the entrance of units after the crest is reached and despite a certain amount of play of the fibers responding.