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# SHORTENING OF NERVE FIBERS ASSOCIATED WITH PROPAGATED NERVE IMPULSE

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*Summary* Conduction of the action potential along a crab nerve is accompanied by a 5-10 nm decrease in the length of the nerve. The tension developed during this shortening is 15-20 μg.

Several previous experiments suggested that electric excitation of the nerve fiber generated a rapid mechanical change in the fiber (1, 2, 3). Because of difficulties and uncertainties involved in measurements of minute and fast movement of a nerve, however, the existence of such a mechanical response of the nerve has not been accepted in the literature of neurophysiology (4, 5). Quite recently, we noted that a piezo-ceramic bender from Gulton Industries, Inc. is superbly suited for detecting small changes in tension and pressure. Using this mechanoelectric transducer, we could demonstrate a small increase in the swelling pressure of nerve fibers during the action potential (in preparation).

In the present paper, we describe an experiment in which a Gulton bender was used for demonstrating that a propagated nerve impulse is actually accompanied by a small, transient increase in mechanical tension. Furthermore, by using a lever connected to a nerve, we could observe, during nerve excitation, a small reduction in the length of the nerve. Several aspects of our finding agree with those previously described by Lettvin et al. (2).

Claw nerves of the blue crab, <u>Collinectes sapidus</u>, were used in most of the present experiments. After desheathing, an approximately 35-mm long nerve was introduced into a plastic chamber filled with seawater in a manner

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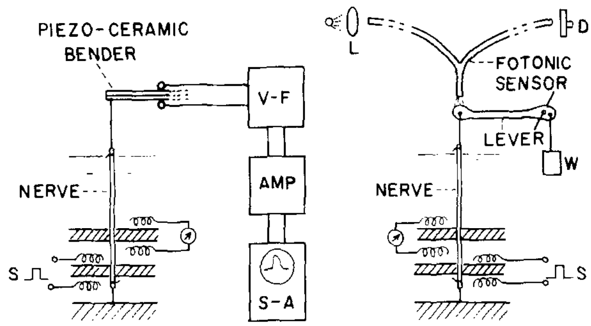


*Fig. 1* Left: Diagram of the experimental setup used for detecting small changes in the tension developed by a nerve following electric stimulation. S stands for a source of current pulses, V-F a voltage-follower, AMP an amplifier and S-A a signal averager.
Right: Diagram of the setup used for detecting small changes in the length of the nerve associated with a propagated action potential. L represents a light source and a lens, D a photo-detector connected to a signal averager through an amplifier.

illustrated schematically in Fig. 1. The nerve was passed through small holes in two partitions located near the bottom of the chamber. Each partition was about 3.5 mm thick, and the separation between the two partitions was about 5 mm. After inserting the nerve, the holes were sealed with vaseline. A pair of large silver electrodes placed across the lower partition were used for exciting the nerve with isolated current pulses of 3-9 mA in intensity and 0.2 msec in duration. The action potentials were recorded with a second pair of silver electrodes placed across the upper partition in the chamber.

For tension measurements, a piezo-ceramic bender of R050 type, generously generously supplied by Gulton Industries, Inc., New Jersey, was used in conjunction with a voltage-follower (AD515, Analog Devices). The voltage generated by hanging a weight at the tip of the bender was roughly 1 mV per 1 mg. The tip of a 4-mm long bender was tied to the upper end of the nerve with a thin thread. Initially, the nerve was stretched until a tension of about 200 mg was observed. The output of the voltage-follower was amplified by a factor of 1,000 and was then led to a signal averager (Model SW 71B, Nicolet Instrument Corp.). Electric stimuli were repeated at a frequency of about 5 shocks/sec, and the mechanical responses induced were recorded after averaging over usually 256 trials. By driving the bender with a calibrated condenser microphone, we found that the frequency of the bender extends up to approximately 10,000 Hz.

The lever used for displacement measurements was made of a thin (0.5 mm) aluminum plate (5 mm x 27 mm). In order to apply a small tension (of about 100 mg) to the nerve, a small weight was hung near the axis of rotation of the lever (see Fig. 1, right). The movement of the lever was measured by using a Fotonic sensor (Mechanical Technology, Inc.). This device consists of two bundles of optic fibers mixed at one end. One of the bundles was used for transmitting light from a 100 W quartz-iodine lamp (Osram) to the sensing end; the other bundle was employed for carrying the light reflected by the lever to a photo-diode (Pin-10, United Detector Corp.). The output of the photo-diode was amplified and was led to the signal averager. Initially, the intensity of the detected light was determined as a function of the distance between the lever and the sensor. Finally, the nerve was stimulated with brief electric shocks which were strong enough to excite all the fibers in the nerve, and the mechanical responses evoked were recorded after averaging over 512 trials.

Record A in Fig. 2 is an example of the records obtained with the piezo-ceramic bender. The upward deflection in the figure represents a rise of the tension exerted by the nerve to the bender. The lower trace

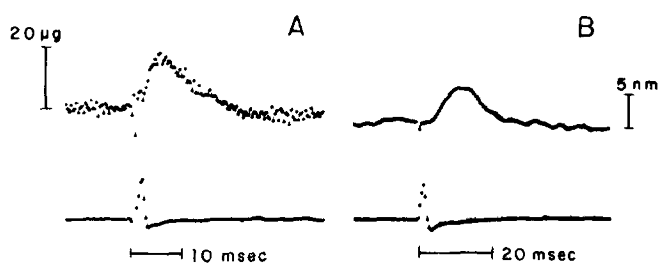


*Fig. 2* A: A signal-averager record showing a transient increase in tension developed by a crab nerve following electric stimulation (upper trace) and action potential (lower trace).
B: A record showing a small shortening of a crab nerve induced by electric stimulation (upper trace) and action potential (lower trace). 21-23°C.

in the figure shows the action potential recorded across the upper partition in the chamber. As expected from the relative positions of the recording electrodes and the bender, the recorded action potential was brief in duration and the mechanical response started at the peak of the action potential. The peak value of the tension developed ranged between 15 and 20 μg. The falling phase of the mechanical response was determined, under these experimental conditions, by the temporal dispersion of the action potentials traveling along individual nerve fibers. [An electron-microscopic study indicated that the fiber diameter in the crab nerve used varies between 2 and about 20 μm.]

Record B shows an example of the records obtained with the lever method for recording the movement. The observed movement was found to represent a shortening of the nerve associated with conduction of a nerve impulse. With an approximately 35-mm long nerve, the peak value of the shortening observed by this method ranged between 5 and 10 nm. The movement of the lever produced by electric stimulation of the nerve is evidently an isotonic counterpart of the tension developed by the nerve. The observed displacement response rises more slowly than the tension system developed during the action potential. Obviously, the slowness of the mechanical response observed with the lever is due to the inertia of the recording system.

It is not easy to compare our results with those of Lettvin et al. (2), because of significant differences in the experimental conditions. The tension we observed was more than one order of magnitude smaller than theirs and the duration of our response was roughly 40 times as long as theirs. In spite of these large differences in the results, the possibility cannot be precluded that Lettvin et al. actually observed signs of mechanical responses superposed on the thermal and/or electrophoretic effects of the strong stimulating current. Our investigation of the effects of a strong electric current on mechanical properties of the nerve fiber is now in progress.

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