

duration pulses must be taken seriously in the light of the findings of Skoglund and others (2,3) that peripheral afferent fibers show repetitive responses to rectangular and to linearly increasing currents at intensity levels which are not far in excess of the rheobase. It is not clear whether the likelihood of repetitive firing is equally great for both pulse forms. Neither is it clear whether the probability of repetitive firing is different for fibers of different structural characteristics.

The results of the present study justify the assumption of a one-to-one relationship between stimulus to and response of single pyramidal fibers within the limits of the stimulus parameters used in the previous investigation. Unfortunately, the evidence presented can be applied only to fibers conducting at velocities in excess of 35 meters per second. These are in all likelihood those fibers which have diameters above the median value. Thus we must remain in ignorance about the behavior of the great number of smaller fibers which are found in the medullary pyramid.

Summary. 1. Responses of single pyramidal

fibers to stimulation with rectangular electrical pulses of varying parameters have been studied in the cat and the macaque. 2. Those fibers conducting at velocities in excess of 35 m.p.s. do not respond repetitively to pulses of less than 4.0 msec. in duration. Some fibers have shown off-responses to pulses in excess of this duration. 3. All fibers studied have followed repetitive stimulation up to frequencies of 500 per second without response deficit.

1. Brookhart, J. M., *Res. Publ. Assn. Nerv. Ment. Dis.*, 1950, v30, 157.
2. Skoglund, C. R., *Acta Physiol. Scandinav.*, 1942, v4 (Suppl. 12), 1.
3. von Euler, C., and Skoglund, C. R., *Acta Physiol. Scandinav.*, 1947, v14, (Suppl. 47), 1.
4. Brookhart, J. M., Moruzzi, G., and Snider, R. S., *J. Neurophysiol.*, 1950, v13, 465.
5. Lloyd, D. P. C., *J. Neurophysiol.*, 1941, v4, 525.
6. Brookhart, J. M., and Morris, R. E., Jr., *J. Neurophysiol.*, 1948, v11, 387.
7. Lloyd, D. P. C., and McIntyre, A. K., *J. Neurophysiol.*, 1950, v4, 39.

Received January 27, 1953. P.S.E.B.M., 1953, v82.

Electron Micrographs of Motor End-Plates.*† (20112)

H. W. BEAMS AND T. C. EVANS.

From the Department of Zoology and Radiation Research Laboratory, State University of Iowa, Iowa City, Ia.

The purpose of this paper is to report some preliminary observations on the motor end-plates as seen in electron micrographs. The present concept concerning the nerve muscle relationship at this point is that there is no direct connection between them. Impulses are thought to be transmitted from nerve to muscle at this site by a humoral substance, inorganic ionic changes, or by the action of end-plate potentials(1). However, the possibility

of some more or less direct morphological relationship existing between nerve and muscle at this juncture, such as the "periterminal net" of Boeke(2), while discredited, has never been disproved(3).

Material and methods. The material for this study consists of the motor end-plates of the intercostal muscles of the rat. The gold chloride method used for the demonstration of the end-plates was that described by Warren(4). Further treatment of the tissue for electron microscope study consisted of bleaching the gold impregnated pieces of muscle and associated end-plates in a solution of 0.5% potassium cyanide in 50% ethanol. This process was watched under the dissecting microscope so that it could be stopped at the

* Grants to the Radiation Research Laboratory from the Iowa Division of the American Cancer Society have made possible the purchase and maintenance of the electron microscope.

† We are indebted to Drs. C. D. Janney and A. W. Sedar of the State University of Iowa, for aid in the operation of the electron microscope.

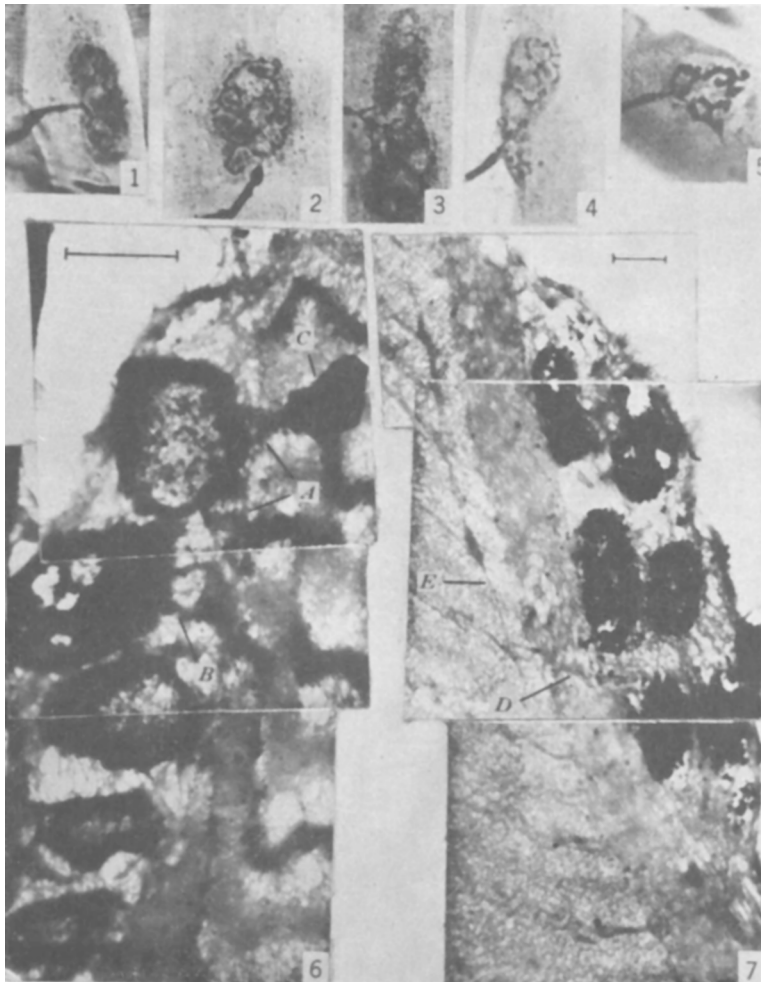


FIG. 1, 2, 3, 4, and 5. Whole mounts of motor end-plates showing the variation in size and distribution of the nerve endings within the sole-plate sarcoplasm. Small granules may be seen (Fig. 1-2) in the sole-plate sarcoplasm between the branching nerve endings.

FIG. 6. Electron micrograph of section through motor end-plate. An apparently close relationship of the Z membranes of the muscle and the nerve endings is seen at A and B. The dark irregular mass at C is thought to be an artifact (excessive gold deposit). Cross sections of neurofibrils appear in the upper cross section of nerve ending.

FIG. 7. This section shows a layer of sarcolemma between the end-plate and muscle fiber. Here some of the Z membranes may be seen to penetrate the overlying sarcolemma layer and extend well within the sole-plate sarcoplasm (D and below). The object at E is unidentified. It may represent the space between two adjacent myofibrils.

proper stage of differentiation by placing the pieces in 70% ethanol. Further preparation of the tissue was made according to the method of Beams, *et al.*(5). The scale on the electron micrographs equals 1 μ .

Results. Fig. 1, 2, 3, 4, and 5 are whole mounts of motor end-plates that were included to show the type of preparation that was used for electron microscope study. Detailed

studies on this type of preparation have been made by many and will not be further discussed here(3).

At the bottom right of Fig. 7 the sarcolemma seems to split, sending a relatively thin layer over the surface and enclosing the end-plate; the inner layer continues between the end organ and the contractile portion of the muscle. The gold impregnated cross sections

of the nerve endings are seen within the fibrous appearing sole-plate sarcoplasm. Because of the density of the impregnated nerve endings, nothing can be observed of their detailed structure. The interesting part of this figure is that the Z membranes of the muscle seem to penetrate the overlying layer of sarcolemma and to end in the sole-plate sarcoplasm. At D this condition can best be seen; but it is also evident in the Z membranes extending below the one at D. The longitudinally oriented line at E is unidentified unless it represents the space between two adjacent myofibrils.

An even more striking illustration of the penetration of the Z membranes into the sole-plate sarcoplasm is shown in Fig. 6, A and B. Although the gold impregnated Z membranes are somewhat distorted, they nevertheless can be clearly followed into the sole-plate, where they are observed to come in close association, if not in direct contact with, the nerve endings. This condition is the same as that in Fig. 7 except that here the Z membranes stand out more sharply because of being more deeply impregnated with gold. Much the same sort of general structure of the end-plate exists in Fig. 6 as in Fig. 7, except that the sarcolemma is not so evident. The body at C, Fig. 6 is thought to be an artifact due to excessive gold deposit.

In the upper cross section of the nerve ending in Fig. 6 can be seen dark irregularly arranged granular-like structures that may be only gold deposits; however, the smaller, more numerous, and less dense elements present are probably neurofibrils. The structure of the peripheral elements of the nerve endings is masked by the gold.

Discussion. Histological illustrations of the motor end-plate show it to be in direct contact with the contractile portion of the muscle(2). However, this does not always seem to be the case since sometimes a layer of sarcolemma may be seen to lie between

them. The work herein reported seems to demonstrate in the motor end-plate a closer association of the Z membranes of the muscle fiber with the nerve endings than is generally thought. The only previously described type of morphological structure within the end-plate with which this condition can be compared is the "periterminal net" of Boeke(2). However, we do not think a direct morphological connection exists between the Z membranes of the muscle and the nerve endings, but rather that the relationship here between the two is comparable to that which exists at a synapse. It is conceivable that nerve impulse transmission would be facilitated more under the morphological conditions herein described for motor end-plate, whether it be by neuro-humoral substance, or by end-plate potentials, than it would be if the impulse had to pass, however the method, for relatively long distances through the sole-plate sarcoplasm to reach the underlying muscle.

Summary. The Z membranes of the underlying muscle fiber appear to penetrate the end-plate and extend for some distance into the sole-plate sarcoplasm. Here they were observed to be in close association, if not in direct contact with, the nerve elements. Such an arrangement represents a closer association of the nerve and contractile muscle elements at the motor end-plate than is generally thought to be present.

1. Gasser, H. S., Erlanger, J., Bronk, D. W., Lorente de Nó, R., and Forbes, A., *Symposium on the synapse*, 1939, C. C. Thomas, Publisher, Springfield, Ill.
2. Boeke, J., *Cytology and cellular pathology of the nervous system*, 1932, Ed. by W. Penfield, P. B. Hoeber, Inc., N. Y.
3. Hinsey, J., *Physiol. Revs.*, 1934, v14, 514.
4. Warren, O., *Turtlox News*, 1944, v22, 169.
5. Beams, H. W., van Breemen, V. L., Newfang, D. M., and Evans, T. C., *J. Comp. Neur.*, 1952, v96, 249.

Received January 30, 1953. P.S.E.B.M., 1953, v82.