THE FINE STRUCTURE OF THE ELECTRIC ORGAN OF THE ELECTRIC EEL AND TORPEDO RAY*

PRELIMINARY COMMUNICATION

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PLATE 76

Electric organs or tissues have been described in seven families of fish (Dahlgren, 1), but all of them have several features in common. The tissues occur as a series of more or less flattened plates or electroplaques, each of which consists of a nucleated cytoplasmic syncytial plate having a relatively large surface area. The plates are supplied with nerve endings on one surface only. On one or both surfaces of the electroplaques, tiny rodlets or *Stäbchen* have been frequently described.

Examination of the electric organs of *Electrophorus electricus* and *Torpedo occidentalis* with the electron microscope has confirmed these features, but has also revealed further interesting details. Fig. 1 is a photomicrograph at low magnification showing half a dozen electroplaques of *Electrophorus electricus* cut in cross-section, each suspended in an individual rectangular connective tissue compartment. Numerous papillae appear on both the anterior and posterior surfaces (the top and bottom respectively in the photograph) of each electroplaque. The surfaces of both anterior and posterior papillae bear minute rodlets which are not visible at this magnification. Fig. 2 is an electron micrograph of the anterior surface, similar to the area outlined by the upper rectangle in Fig. 1. The rodlets are now seen to consist of invaginations of the delicate plasma membrane of the electroplaque. These apparently tubular structures (*t*) measure 500 to 1000 A in diameter, and several micra in length. Groups of isolated vesicles (*v*) are seen frequently near the tubular invaginations.

The posterior surface of the electroplaque of the eel also displays tubular structures of similar character. This surface differs from the anterior one in the possession of a wealth of nerve endings. These terminate, as a rule, upon the papillae at close enough intervals to show a sectioned nerve on the average of every ten micra. One such ending is illustrated in Fig. 3 which represents an

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area similar to that contained in the lower rectangle in Fig. 1. The nerve ending is closely approximated to the electroplaque surface, although separated from it by an intermembranous space which is about 500 A in width. Under no circumstance has fusion of the cytoplasm of the nerve ending with that of the electroplaque been observed. Schwann cell cytoplasm is seen to form a sheath around the axon ending, except at the junction of the latter with the indented surface of the electroplaque. The termination of the Schwann cell is indicated by two arrows. An accumulation of vesicles (*v*) within the nerve terminal can be seen adjacent to the plasma membrane at the site of contact of the nerve ending with the electroplaque. These vesicles measure about 350 A in diameter and are similar to those found in the presynaptic member of synapses seen elsewhere in the nervous system (Palade and Palay, 2, and De Robertis and Bennett, 3). The arrow marked *x* in Fig. 3 points to a place which suggests the rupture of such a vesicle through the plasma membrane of the nerve terminal into the junctional space.

At first glance, the electric organ of *Torpedo occidentalis* seems completely different from that of the eel, but on closer inspection, the basic features which characterize electric tissue are discernible. Fig. 4 represents a photomicrograph of the electric organ of *Torpedo* oriented in the same way as the organ in the electric eel (Fig. 1). Papillae are absent in *Torpedo* so that the electroplaques (Fig. 4, *e*) are closely stacked as broad, parallel sheets with little intervening space. Fig. 5 presents an electron micrograph of the non-innervated dorsal surface of a *Torpedo* electroplaque equivalent to Fig. 2 of the eel. Again, the rodlets appear resolved as tubular invaginations which are a little narrower and are more branched than in the eel, whereas vesicles associated with the tubules are less obvious. Fig. 6 illustrates the ventral surface of the *Torpedo* electroplaque which has far fewer invaginations than the dorsal surface. A relatively large nerve ending is visible in the electron micrograph; it is applied closely to the electroplaque from which it is separated by an intermediate space of several hundred angstroms. A portion of a Schwann cell (*s*) surrounds the lower surface of the nerve termination. Numerous dense granules about 150 A in diameter are visible randomly distributed in the nerve ending, in addition to a number of vesicles (arrow, *v*) similar to those in Fig. 3.

Physiological evidence (Keynes and Martins-Ferreira, 4, and Altamirano *et al.*, 5) indicates that electric tissue is a highly specialized, unidirectional ion transfer mechanism capable of high peak capacity. The most conspicuous morphological specialization of electric tissue resides in the extensive system of tubular invaginations and associated vesicles. It is possible that these invaginations and vesicles may bear some functional relationship to the highly developed electrolyte transport of these tissues.

A full report of these studies is being prepared for future publication.

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EXPLANATION OF PLATE 76

FIG. 1. Photomicrograph of the electroplaques (*e*) of the electric eel. Helly's fixation, double embedded in nitrocellulose and paraffin, Mallory's stain. Upper and lower rectangles localize Figs. 2 and 3 respectively. Anterior aspect of the tissue faces the top. × 90.

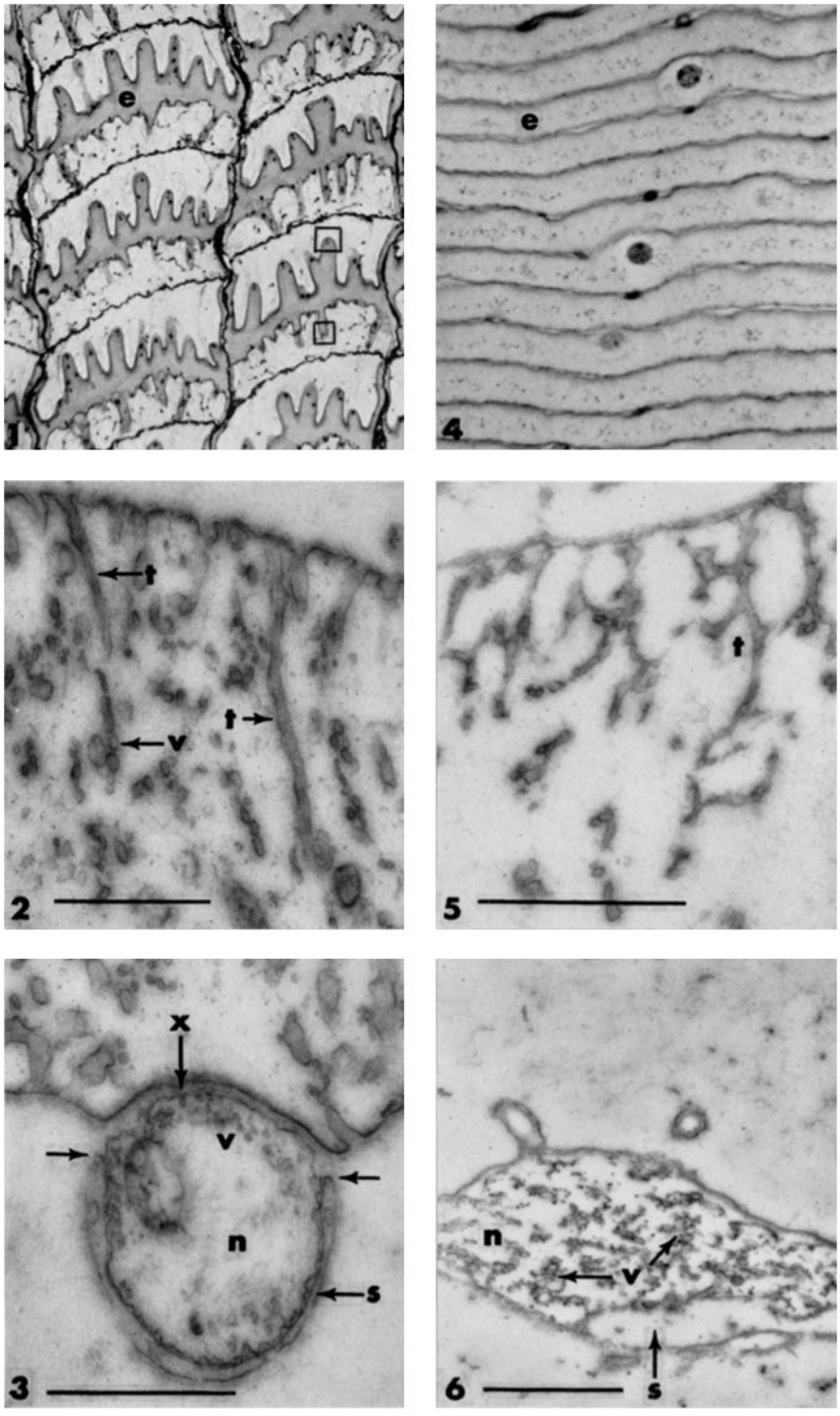
FIG. 2. Electron micrograph of the anterior surface of a single electroplaque on the eel, from a region similar to that enclosed by the upper rectangle, in Fig. 1. Tubular surface invaginations (arrows, *t*) and vesicles (arrow, *v*) are seen. The line in this and subsequent figures represents one micron. Eel tissues fixed in 1 per cent buffered OsO_4, embedded in *n*-butyl methacrylate.

FIG. 3. Electron micrograph of the posterior, innervated surface of one electroplaque of the eel, from a region similar to the lower rectangle in Fig. 1. The nerve ending (*n*) is covered by Schwann cell cytoplasm (*s*) which terminates at the arrows, leaving the nerve ending devoid of a Schwann sheath in the region of contact of the nerve ending and the electroplaque. The arrow (*x*) shows a vesicle apparently opening into the intermembranous space between the nerve terminal and the electroplaque.

FIG. 4. Photomicrograph of the electroplaques (*e*) of the *Torpedo*. Helly's fixation, double embedded in nitrocellulose and paraffin, Mallory's stain. Dorsal aspect of the tissue faces the top. × 200.

FIG. 5. Electron micrograph of the dorsal surface of an electroplaque of *Torpedo*, showing tubular invaginations (*t*). Orientation same as Fig. 4. *Torpedo* tissues fixed in 0.5 per cent OsO_4 plus veronal-acetate buffer and sea water, embedded in *n*-butyl methacrylate.

FIG. 6. Electron micrograph of the ventral, innervated surface of an electroplaque of *Torpedo*, showing a portion of a nerve ending (*n*) with vesicles (arrows, *v*), and many small, dense granules. Schwann sheath cytoplasm is present at *s*.



(Luft: Electric organ of electric eel and torpedo ray)