ON THE FUNCTION
OF THE MOTOR END-PLATES
IN SKELETAL MUSCLES

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It has been shown by TSCHIRJEW and by HENRIQUES & LINDHARD, that the "current of action" in the skeletal muscle cannot be due to a propagated electric change. Most recently WEBER (Nauheim) in experiments not yet published, using a quite different arrangement, arrived at the same point of view.

TSCHIRJEW obtained "currents of action" of the usual type when the electrodes were placed exactly in the direction transversely to the muscular fibres, and HENRIQUES & LINDHARD have shown experimentally that the distance between the turning points of the disphasic curve, obtained by means of the string-galvanometer, is independent of the distance between the electrodes. The one electrode being placed over the active muscles, the other may be placed elsewhere on some arbitrary indifferent point without any change in the resulting curve; moreover, the disphasic current of action passes away almost entirely within the latent period of the muscle. The current of action must, therefore, be due to some local electric change. Evidence has been brought forward by HENRIQUES & LINDHARD which seems to indicate that the process in question takes place in the motor end-plates of the muscle. Thus, when the motor-plates are blocked by curare, the current of action disappears; it also disappears if the muscle is fatigued by stimulating the nerve. On the contrary, the

current of action persists unaltered in the asphyxiated muscle, rapidly brought into a state of extreme fatigue. Further, Henriques & Lindhard have succeeded in obtaining strong contraction of a directly stimulated muscle without any current of action, when care was taken to avoid "leading over" of the exciting current. Now it might be possible that the electric reponse of the muscle was nothing but currents in the intramuscular nerve-branches, but Henriques & Lindhard found repeatedly that the curve obtained when leading off from the muscle was of quite another order of magnitude than was the curve obtained from the nerve in the same preparation; the amplitude of the nerve-current being far less than that of the electric changes in the muscle. It is worth noting also, that the muscle can be stimulated directly by an electric current only when this is much stronger than the current neces-sary for stimulation through the nerve. It is most probable, therefore, that electricity is produced in the muscle, and, according to the above, that the production takes place in the motor-plates. It is further probable that the electro-motive force established in the plates may serve some physiological purpose, and we are thus led to reconsider the old theory that the function of the motor end-plate is to produce electricity which is in turn the adequate physiological stimulus to the contractile substance of the muscle. This theory (the "Entladungshypothese" of du Bois-Reymond), which seems to have been put forward first by A. v. Humboldt (1819) and revived independently half a century later by W. Krause (1863), was vigorously op-posed, especially by E. du Bois-Reymond, with the result that it disappeared from the discussion of physiologists before the end of the past century.

The theory concerned was originally based upon ana-
logies between the element in the electric organ of some
fishes and the muscular fibre with its motor end-plate. It
was adopted by W. KRAUSE who, because he was of the
opinion that the situation of the end-plate was "epilemmal",
could imagine no other possibility for interaction between
nerve and muscle. The opposition of DU BOIS-REYMOND
aimed at several points. He pointed out that the analogies
referred to were untenable for morphological as well as for
physiological reasons and, moreover, he regarded the theory
as superfluous, because it was shown clearly by KÜHNE
and by many other investigators, that the motor end-plates
are situated inside and not outside the sarcolemma. —
We will consider first the structure of the organs con-
cerned.

The motor end-plate (*Lamina nervorum terminalis
motoria*, W. KRAUSE 1863) is in mammals, reptiles, and at
least in some fishes as also in birds confined to a rather
narrow area on the muscular fibre. The size of the plate
seems to depend upon the thickness of the muscular fibre
but is independent of the size of the animal; it is on the
whole remarkably constant. In man the motor end-plate
has a diameter of 40—60 μ. In amphibia, on the other
hand, it forms a wide-spread ramification, and, while in
most cases there is only one end-plate in the mammalian
muscular fibre (for exceptions see AGDUHR), it is a com-
mon feature to find two or more in the muscular fibre of
the frog. To the special form of the motor end-plate in
the frog (Stangengeweih of KÜHNE) the term "end-brush"
has been applied; as however the function of the organ
in spite of differences in shape must be supposed to be
the same in all animals, it is most convenient to make

use of the same term for all. The motor end-plate is covered by the sarcolemma or perhaps by several membranes fused together (Telolemma of Kühne) viz., the sheath of Henle, the sarcolemma and the sheath of Schwann. When reaching the muscular fibre the nerve is deprived of its medullary sheath, and beneath the covering membranes we find the ramification of the axis cylinder (Nervengeweih of Kühne), the form and structure of which has been a subject of discussion among histologists throughout decennia. According to the more recent investigations of Boeke we must assume, that the axis-cylinder first divides into coarse bundles of neuro-fibrils forming the arborescent figure especially known from the preparations of Kühne; the branches then subdivide further into fine and thin fibril-bundles which ultimately as single fibrils forms small loops and rings. The nerve-ending is embedded in a granular protoplasmic mass containing large clear oval nuclei, readily to be distinguished from the nuclei of the sarcolemma, and presenting one or two distinct nucleoli. This structure is termed by Schäfer the "bed" or "sole" (Sohlenplatte of Kühne). The sole often causes a prominence of the telolemma and an excavation in the contractile substance of the muscular fibre; there is no lining membrane between the sole and the muscular substance proper, but by means of degeneration experiments it has been shown that the two substances are independent of each other. Only in amphibia is the sole indistinct, yet we find in the peculiar bayonet-shaped nerve-endings in frogs muscles scattered oval or somewhat pear-shaped granulated nuclei (Endknospen of Kühne) which undoubtedly may be regarded as homologous with the nuclei of the sole of the end-plate proper; this opinion is held by Krause who

points out that the end-plate in the
frog has often a single nucleus only.

FOETTINGER suggests that the
nerve-endings proper are to be
found in the isotropic substance
of the muscular fibre, and BOEKE
concludes from his preparations
that the ultimate nerve-endings
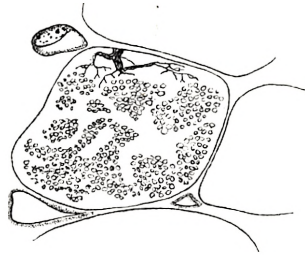must be sought in the contractile
substance of the fibre, forming still

Fig. 1. Cross-section of a mus-
cular fibre from bat (×1800).
The nerve-endings are not seen
to penetrate between the myo-
fibrils. After BOEKE.

finer loops and rings in the sarcoplasma beneath the sole
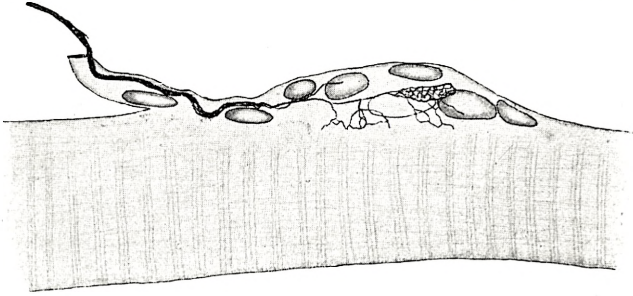than those seen in the sole itself. Yet neither in the only

Fig. 2. Profile-build of a muscular fibre with its motor end-plate
from a young mouse (×1800). The nerve-endings do not penetrate
between the myofibrils. After BOEKE.

cross-section figured by BOEKE as a paradigma (Fig. 1)
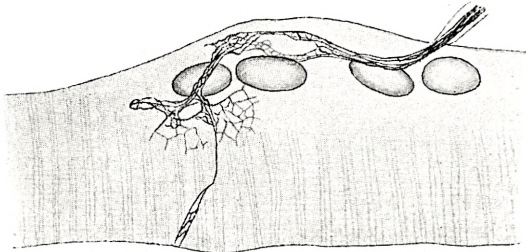nor in a real profile-figure (Fig. 2) are nerve-endings visible

Fig. 3. Oblique projection of a motor-plate on a muscular fibre
of bat (×1800). After BOEKE.

among the muscular fibrils, and the shadows seen in the
oblique optical sections (e. g. Fig. 3) may certainly be ex-
plained otherwise. Several observers have attributed other
structural elements to the motor-plates. Thus Ciaccio has
found the punctation of Boll which seems to be due to
minor rodlike structures, arranged perpendicularly to the
surface of the sole, especally below the nerve-endings
but not connected with the nerves, and this statement is
in the main confirmed by Ranvier. Also Kühne has
described similar structures, "fringes", which follow the
distribution of the "Nervengeweih" but, according to Kühne,
must be regarded as pertaining to the telolemma. As such
structures play an important part in the description of the
electric organs of fishes, they must be mentioned also in
this place, though their physiological rôle is by no means
evident.

Regarding the development of the motor end-plates
Boeke has made a great number of observations. The
motor nerve grows into the embryonic muscle-plate before
the individual fibres have been differentiated, but only at
a comparatively late embryonic state is the first trace of
the end-plate observed. At this time the nerve forms a
network, the stronger branches of which run across the
muscular fibres; the cross-striation of the fibres is visible,
and the nuclei begin to leave their originally central
position; the sarcolemma on the other hand is developed
afterwards. When running across a number of muscular
fibres the nerve presents as many minor thickenings from
which small fibrillar nets and loops are developed (Fig. 4),
gradually retiring from the stem and at last presenting
themselves as formed at the end of fine collateral twigs
(Fig. 5). In the corresponding place on the embryonic

muscle fibre we find a simul-
taneous accumulation of gran-
ular protoplasm and of muscle-
nuclei which are transformed
into the oval nuclei of the
sole, and thus the motor end-
plate is ready (Fig. 6). After

Fig. 4. First stage of the developing
motor-plates in the Talpa-tongue.
After BOEKE.

section of the nerve and degeneration of the nerve-endings
new ones are formed in a quite similar manner; as a rule
the old sole persists, and it seems to exercise some chemo-
tactic effect on the nerve-
branches from which the new
collaterals are given off. Thus
the motor end-plate consists
of two parts, a nervous one,
developed from the motor ner-
ves, and a non-nervous or mus-
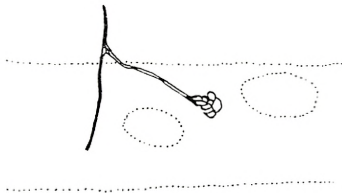cular part, developed from the

Fig. 5. More advanced stage. Talpa-
tongue. After BOEKE.

embryonic muscular fibre. It is necessary to keep this fact
in mind.

It has been shown by BOEKE that very slender non-
medullated nerve-fibres end in the muscular fibres either
connected with or indepen-
dent of the medullated motor
nerves; the endings of these
nerves seem to be in small
end-plates of a structure quite
similar to the usual motor
plates.

Perusal of the literature

Fig. 6. Still more advanced stage
from bat (× 2600). After BOEKE.

concerned shows that the electric organs of fishes
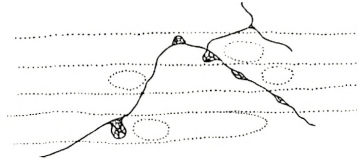vary in shape and origin, thus in *Malapterurus electricus*

the electric organ belongs to the skin and may be developed from plain muscles or most probably from glands (embryos of this animal have not yet been found), but in *Gymnotus electricus*, in the *Torpedo*-group, in *Mormyrus*, and in a number of species belonging to the genus *Raia* the organ is, according to Babuchin, developed from cross-striped muscles.

With regard to the strength of the shock produced the electric fishes have been arranged in two groups, the strong-electric viz. *Malapterurus, Gymnotus* and *Torpedo*, and the weak-electric viz. *Raia, Mormyrus* and some other fishes. To the last-named group the term "pseudoelectric" has been applied by E. du Bois-Reymond, as the electric nature of the peculiar organ found in these animals was at that time doubtful. Krause regarded these organs as transitional forms between the electric organs proper and the motor-plates; yet the real electric nature of the organ of the skate has been proved by Burdon-Sanderson & Gotch, and Ewart has shown, that the structure as well as the development of the tail-organ in *Raia* is essentially the same as found by Babuchin in the strong-electric *Torpedo*. It has been a matter of discussion, whether the weak-electric organ is in a state of progressive or of regressive development. Iwanzoff holds that it is a rudiment, but Ewart gives very good reasons for the opinion that it is really in a progressive development.

The electric organ of the fishes is built up of a number of plates (Electroplax of Ballowitz) of different shape and dimensions, each covered by a thin structureless membrane (Electrolemma of Ballowitz) and surrounded by gelatinous tissue, the whole enclosed in a sort of chamber of connective tissue developed from the peri- or endo-

mysium and forming rows or columns according to the structure of the original muscles (Fig. 7). — In the description of the various electric organs I follow the more recent observers.

In *Torpedo* the very thin plates are developed from parts of the muscles of the jaw and gills and form perpendicular columns; the vessels and nerves enter the
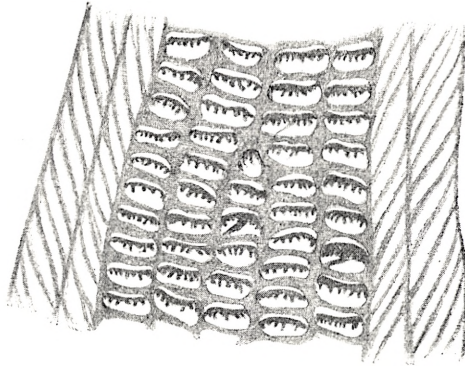

Fig. 7. Longitudinal vertical section through the electric organ and its investing muscular cones from a skate 90 cm. in length (×15). After EWART.

compartment containing the plate from the ventral side. The nerves subdivide, losing their medullary sheath, in a great number of fine branches ending in some manner or other on or in the superficial layer of a large protoplasmic mass, the non-nervous part of the electric plate.
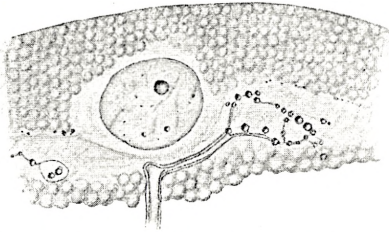

Fig. 8. Oblique section through the electric plate of *Fimbriotorpedo ocellata* (× 3000). After FRITSCH.

In this mass two layers may be distinguished, a ventral granular layer, presenting the punctation of BOLL or, in section, the palisade-structure ("electric rods" of BALLOWITZ); it is continued dorsally in a more homogeneous layer containing a number of large round or oval nuclei with one or two distinct nucleoli (Fig. 8). According to the mode of preparation the nuclei may be surrounded by a bright halo or by fine granular protoplasm. The nuclei are so

large, that they often cause bulging of the electrolemma. Ballowitz describes a very fine spongy network consisting of granulated threads as filling up the protoplasmic plate.

In *Gymnotus*, the most powerful of the electric fishes, the electric organ is in the main developed from the ventral muscles of the long and strong tail; the very thick plates are situated perpendicularly, presenting a posterior and an anterior surface; the vess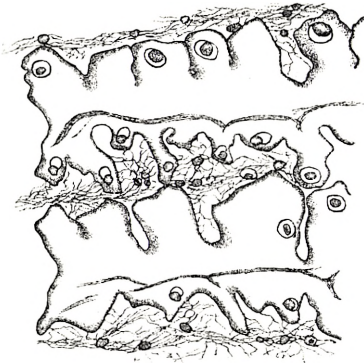els and nerves enter the compartment from behind. The posterior surface of the plate is occupied by shorter and longer papillæ, to which the nerve twigs are attached, losing their medullary sheath; none-medullated fibres cannot be traced further. Long and close papillæ beset the anterior surface of the plate, filling up almost the whole of the anterior lodge of the compartment containing the

Fig. 9. Sagittal section through the ends of two electroplaxes of *Gymnotus*. Alcohol preparation. The *Pacinian* line is seen. After Ballowitz.

plate (Fig. 9). Palisade structure is conspicuous on both sides, and the large oval nuclei are likewise distributed in both superficial layers as well as in the papillæ; according to Ballowitz the whole mass of the plate is interwoven with the fine network mentioned above. Between the nuclear layers the middle of the plate or disc is apparently homogeneous, but, when acted upon by certain reagents, the disc is liable to cleave in two parts; yet the cleft only appears in the middle of the disc and does not reach the edges; it is always situated nearer the back than the front

of the plate. This cleft (*Pacinian* line of SACHS) is looked upon as a phenomenon of shrinking, though it is not easy to see, how shrinking should cause a regular cleavage of the disc, always of the same form and position, if the mass was homogenous. It might seem, as if the cleft corresponds to the intermediate layer of the weak-electric organ of *Raia* and *Mormyrus*.

The electric discs of *Malapterurus*, though not developed from skeletal muscles, present essentially the same structure as already described. The discs are nearly circular and arranged

Fig. 10. *a*. A group of electric discs of *Malapterurus*; natural size.
b. Front view of a single disc; highly magnified. After BALLOWITZ.

perpendicularly with a posterior and an anterior surface (Fig. 10 *a* and *b*). In front the plate is almost even except in the middle, where we find a deep and rather narrow depression or hole surrounded by a wall. On the back we find a central cave from the bottom of which a long conical stalk projects backward; the basis of the stalk forms the wall and the deep
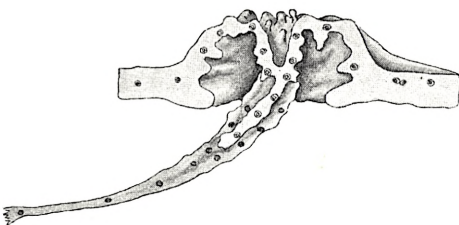
Fig. 11. Section through the central part of a disc of *Malapterurus*. The stalk is seen to be continuous with the anterior layer of the disc. After BALLOWITZ
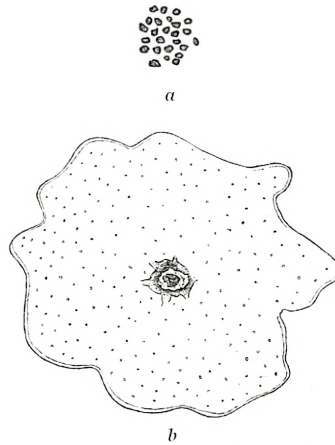
depression on the front of the plate; the end of the stalk has an intumescence to which the nerve is connected, losing its medullary sheath (Fig. 11). Apart from

Fig. 12. *a*. A muscular fibre from a *Raia radiata*. The motor plate and the nerves in connection with it have been considerably enlarged.

the complicated structures described the disc is thick in the centre and thin at the edge. Large oval nuclei are arranged in the main parallel to the anterior surface, only a few are found at the posterior; the thin end of the stalk as a rule contains 3 nuclei. Both sides of the disc show palisade structure, yet, according to Ballowitz, the rods in front and in the stalk appear different from those of the posterior aspect of the plate; also the fine network in the protoplasm has been found by Ballowitz. The disc may show the Pacinian line when treated with alcohol and other reagents.

The electric organs are as a rule innervated from the same sources as are the muscles from which they are developed; only in the case of *Malapterurus* do we find a quite different arrangement, the whole electric organ being innervated from a single enormous nerve-cell, the very thick axis-cylinder of which ramifies in the skin and is distributed to the discs.

Also a number of weak-electric fishes have been thoroughly investigated, and from the beautiful observations of Ewart we have got a very clear idea of the development of these organs. In the genus *Raia* the electric organ is developed from the lateral muscular column of

Fig. 12 *b*. A muscular fibre from the same animal which has reached the club stage. The anterior end is slightly concave and completely covered by the motor plate. The striation in the fibre is identical with that of the adjacent muscles.

the tail. The conversion of the muscular fibre into an electric element takes place at a different stage of development in the different species, at an early stage, if the conversion is complete, as in *R. batis*, at a late stage, if, as in *R. radiata*, it is only incomplete. In the embryonic fibre some of the central nuclei, from which ordinarily the nuclei of the sarcolemma are formed, appear at one end of the fibre, where a mass of granulated protoplasm accumulates simultaneously, thus forming the nuclei of the sole of the motor end-plate (Fig. 12 *a*); then the fibre becomes club shaped (Fig. 12 *b*), as the end-plate as well as the contractile substance beneath it increases in mass, while the other end of the fibre remains unaltered; at last the club is transformed into a shallow "cup" (Fig. 12 *c*). At this stage the development is stopped in *R. radiata* (Fig. 12 *d*). We may suppose that in this case the electromotive force is only very weak and that, on the other hand, the muscular fibre is still able to contract. As development proceeds in the other species observed, the cross-striped substance gradually disappears, while the motor end-plate highly increases in size and becomes more and more flattened or cup-shaped, assuming successively the form of the perma-
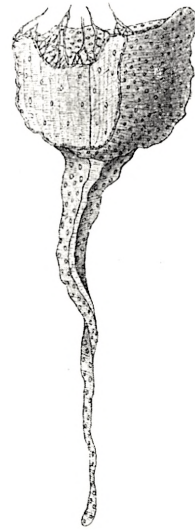

Fig. 12 *d*. Completely developed "cup" from an adult *R. radiata*. The thick wall of the shallow cup is composed of muscular substance, still distinctly striated, with a few scattered nuclei. The outer layer is thin (thickened sarcolemma); the long "tail" is compressed and irregularly striated. After EWART.

Fig. 12 c. A still more advanced stage (cup-stage).

nent electric plate characteristic of the species concerned. (Fig. 13 a—c).

The fully developed electric element in *R. batis* (Fig. 14) consists, according to Ewart, of 3 layers: The electric layer, the fibrillar layer, and the alveolar layer. The electric layer which must be regarded as the highly enlarged end-plate may again be subdivided into two layers, a superficial granular and a deeper nucleated layer; in the first-named we find the nerve-endings. The nerve entering the chamber, developed from the connective tissue surrounding the original embryonic muscular fibre, loses its medullary sheath and divides dichotomously into numerous branches ultimately forming minor loops in the granular layer (cfr. Fig. 15). The deeper ayer contains numerous large oval nuclei each surrounded by a halo of bright protoplasm. The fibrous layer is formed by a striated

Fig. 13 a. Longitudinal horizontal section through the tail of an embryo of *Raia batis* showing the muscular fibres developing into clubs. The muscular striation still persists, even at the expanded portions.

Fig. 13 b. Club from a slightly older embryo. The development of the different layers has begun. The "tail" is still muscular.

Fig. 13 c. Still more advanced stage. The three layers in the developing electric plate are distinctly seen.

The stages figured in Figg. 13 b and c were both present in the same animal. After Ewart.

substance developed from the muscular substance proper;
in the fully developed organ of *R. batis* it contains no
nuclei, while in other species scattered nuclei are found.
The wave-like or meandrine striation does not possess any
relation to the original cross-striation of the muscular fibre;
other investigations have shown, at least, that no aniso-
tropic substance is present. Of the lower portion of the
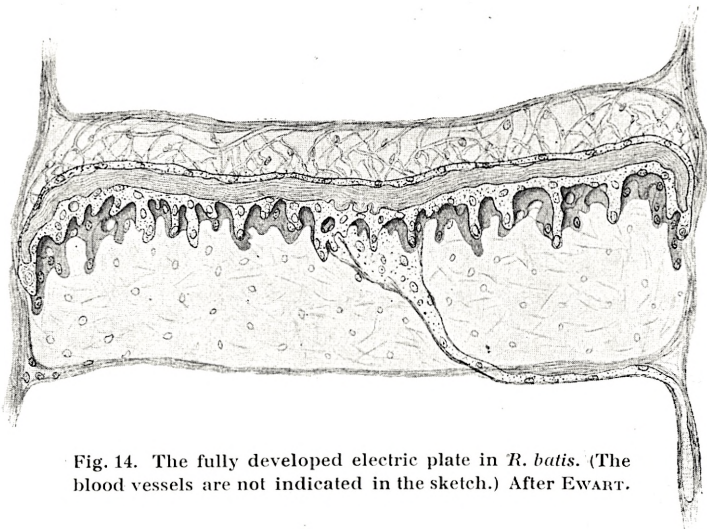embryonic fibre only a slender tapering appendix remains,

Fig. 14. The fully developed electric plate in *R. batis*. (The
blood vessels are not indicated in the sketch.) After EWART.

here and there presenting a trace of cross-striation; it pro-
jects backwards, perforating the alveolar layer, into the
gelatinous matter filling the posterior lodge of the com-
partment. In *R. radiata*, the most primitive form, the stri-
ated layer consists of slightly altered cross-striped muscular
substance (Fig. 12 *d*) containing numerous muscle-nuclei.
The alveolar layer which, like the electric layer, develops
from the elements ordinarily forming the sarcolemma, and
which around the borders of the striated layer is in direct
continuity with the first-named, is in *R. radiata* an almost

unaltered sarcolemma, while in its most differentiated shape
in *R. batis* it forms a spongy network from which numer-
ous prolongations project backwards into the gelatinous
tissue; this thick layer contains numerous large oval nuclei
surrounded by clear protoplasm, not to be distinguished
from those in the electric layer. Thus the arrangement is
quite similar to that found in the thick discs of *Gymnotus*
only that, instead of the *Pacinian* line in the *Gymnotus*-
plate, we find in *R. batis* the thick striated layer as the last
remnant of muscular substance. — The vessels and nerve
of the plate enter the septum between two compartments;
then the vessels bend forward to the alveolar layer of the
preceding plate while the nerve bends backward to the
electric layer of the plate next behind.

Schlichter found in *Mormyrus oxyrrhyncus* a structure
of the electric plate similar to that in *R. batis*. He describes
the electric plate as consisting of an intermediate layer and
two cortical layers fusing along the edge of the first. The
cortical layers correspond to the electric and the alveolar
layer of Ewart with the exception that, in *Mormyrus,* the
vessels along with the nerve enter the compartment of the
plate from the posterior aspect. The caudal cortical layer
presents numerous papillæ to which the nerve-endings are
attached often by spiral tours; here the nerve-twigs lose
their medullary sheaths and cannot be traced further.
In the cortical layers we find the large oval nuclei known
from the *Raia*-plate, and in addition the author, as a pupil
of Ballowitz, describes the palisade-structure and the
fine protoplasmic network. The intermediate layer con-
tains more or less altered cross-striped muscular substance
which, as already stated by Babuchin, seems to originate

from several, or at least more than one, embryonic mus-
cular fibre.

According to the above, it must be regarded as certain
that the motor end-plate and the electroplax are homo-
logous or rather identical organs, as already pointed out
by a number of investigators and especially by those
dealing with the development of the organs concerned
(BABUCHIN, EWART). The prominent Russian observer BA-
BUCHIN writes (1870): ". . . dass die elektrischen Organe
eigentlich Muskeln sind, aus denen nur die Muskelsub-
stanz entfernt ist, und umgekehrt: die Muskeln sind elek-
trischen Organe, in welchen unter allen elektrischen Platten
Muskelfasern eingeschoben sind."—"Die elektrischen Platten
und die motorischen Endplatten sind in morphologischer
Hinsicht identisch."

Accepting this point of view, we must regard it as
probable that electricity is produced also in the motor
end-plates. Then the next question to be solved is, in
which of the structural elements concerned the electricity-
production may be supposed to take place. In this respect
it has undoubtedly been a source of confusion that the
term end-plate has been employed to denote the nerve-
endings, (Nervengeweih), as well as the whole structure
described above. Nevertheless it is obvious that all previous
authors have laid special stress on the nerve-endings, the
ultimate distribution of the axis-cylinder, as the essential
structure. This view is held also by BURDON-SANDERSON &
GOTCH, who state that each electric plate in *Raia batis*
develops an electromotive force of .02 Daniell, while *M.
sartorius* in the frog, in which the number of nerve-endings
is of the same order of magnitude, when stimulated through
the nerve, develops .026 Daniell. On the other hand, the

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protoplasmic mass forming the sole of the end-plate and the non-nervous part of the electroplax in fishes has been regarded as a negligible or noxious structure.

RANVIER believes that in *Torpedo* the dorsal homogeneous layer in all the plates in a column are directly connected with each other and represent the positive pole of a battery, the negative pole of which is formed by the nerve-endings and the electric rods ("cils electrique"). The function of the intermediate layer, i. e. the protoplasmic layer with the large nuclei, may be that of the glass in a LEYDEN jar. E. DU BOIS-REYMOND points out the fact that the motor-plate consists of two parts: the end-plate proper and the sole, but from an electric point of view the sole must be regarded as inexpedient ("zweckwidrig"), representing a resistance between the end-plate proper and the contractile substance. He admits, however, that in fishes the electric discharges take place in the electric plate which he erroneously regards as homologous to the contractile substance, and that the discharge is proportional to the thickness of the plate. BURDON-SANDERSON & GOTCH regard the electroplax as "a supporting structure" only, and are of the opinion that the alveolar layer (in *Raia batis*), owing to its large surface, may perhaps facilitate the nutrition of the whole plate. Even when the plate morphologically is situated in the place of a muscular fibre, it belongs histologically to the nervous system and not to the muscle.

This whole reasoning leads to the theory put forward by RANVIER, that the electricity is produced in the nerve-cell or cells from which the electric organ is innervated, and then distributed through the nerves to the elements of the organ. E. DU BOIS-REYMOND, however, describes this theory as "völlig sinnlos" and, considering the fact that in

Malapterurus a single pair of scarcely visible cells, according to the theory, should produce an electric charge which, when distributed to the skin, might give a shock of 200—300 Volts, it would seem, that the characterisation of DU BOIS-REYMOND is rather pertinent. On the other hand, the assumption that the electricity is produced in the end-plate proper, i. e. the nerve-endings, is not much better. The great variability in shape of this structure, the fact that each animal has its own mode of distribution of the nerve-endings, make this theory improbable a priori, but the decisive objection to the theory is, that the peripheral nerves with their axis-cylinders and nerve-fibrils are conducting and not energy-producing organs. The division of the nerve cannot cause the energy of the unknown process started in the nerve-cell to increase; we must suppose, on the contrary, that the increased cross-section of the axis-cylinder caused by the ultimate divisions of the nerve must diminish the energy conducted by each fibril. Besides the nerve-endings BALLOWITZ regards two structural elements as especially important viz. the "rods", and the fine network with the oval nuclei, towards which the rods are directed. The electric rods of BALLOWITZ are found in most, perhaps in all, electric fishes, but the development of these structures does not run parallel to the electromotive force of the electric organ, thus the palisade-structure is most pronounced by far in the weak-electric, only moderately developed "cup" of *Raia circularis* (Fig. 15), and it is admitted by BALLOWITZ that the rods are connected with the electrolemma and not with the nerve-endings. The rods are most probably identical with the brush-like structures, "fringes", described by KÜHNE in connection with the telolemma of the motor end-plate, and KÜHNE supposes

that they may play some rôle in the nutrition of the plate, facilitating the absorption of the nutritive material; at all events, there is no reason to believe that they are "electric". As for the intracellular network, it is not an independent structure, but, if it really exists, it must be a part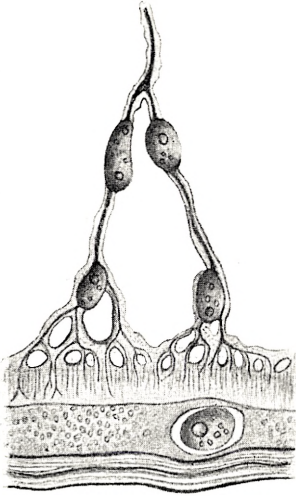 of the cell, and BALLOWITZ has no other reason to ascribe electric properties to this structure than its very existence. If we consider the non-nervous part of the organs concerned, we find always a protoplasmic mass containing several nuclei of a characteristic shape. For this structure BALLOWITZ has introduced the term "Electroplax", analogous to "Myeloplax", to denote a multinucleated giant-cell, though in certain cases the author, like BABUCHIN, regards the nuclei as belonging to individual cells. According to the development of the plate as described by EWART, we must hold, however, that the first-named assumption is the only tenable one. FRITSCH has paid attention to the giant-

Fig. 15. Structure of the electric layer in *Raia circularis* showing nerve with nuclei on the sheath, palisade structure and one of the large nuclei of the nucleated lamina. Also two lamellæ of the striated substance is seen. After EWART.

cell, because it is found in all electric plates in spite of differences in shape and structure, but he does not pursue the question further. BABUCHIN, like all other observers, regards the nerve-endings as the most important part of the plate and the sole or protoplasmic mass as an appendix; nevertheless he points out that the less the non-nervous part of the electric plate is developed, the weaker is the

electric shock produced by the organ. In *Torpedo*, the weakest of the strong-electric fishes, the non-nervous part of the plate is less in mass, while in the powerful organ of *Gymnotus* it is most voluminous. Also in *Malapterurus*, where we find a comparatively large protoplasmic mass and few nerve-endings, the electric shock is strong. BABU-CHIN also calls attention to the fact that small individuals, though they possess the whole number of plates character-istic of the species, give a much weaker shock than do the large ones, and thus the strength of the shock must depend in part on the mass and not only on the number of the plates; and the mass in turn depends on the development of the non-nervous part of the plate. According to these considerations as well as to the above criticism of the nerve theories, the only possible explanation of the facts known seems to be to regard the non-nervous part of the electric plate and the sole of the motor end-plate as multi-nucleated giant-cells having the function of producing electricity.

From a morphological point of view an objection to the hypothesis can be derived only from the peculiar "plates" found in amphibia. It must be justifiable, however, to re-gard the "Endknospen" as scattered parts of a sole. Cer-tainly, the intrafibrillar network of BOEKE, if it existed, would oppose the theory, but its existence is highly im-probable; intrafibral nerve twigs must, if we are to believe in them, be figured in a more "materialised" shape, than are the shadows figured by BOEKE. And it is very difficult to understand why a nerve should have connection with a com-plex structure like the motor end-plate just before its real terminal distribution in the muscular fibre. What purpose would be served by a nervous network in the sole itself,

if we had a second network just beneath the sole? Also
if we consider the structure of the muscular fibre such a
network would be incomprehensible. The muscular fibre
is built up by a number of sarcostyles imbedded in sarco-
plasma, each consisting of very numerous "sarcous ele-
ments", the contractile elements proper; we cannot imagine,
that the termination of the nerve-fibrils a little nearer to
a very limited number of these elements would be of any
advantage to the organism.

Apart from morphological reasons E. DU BOIS-REYMOND
opposes the "Entladungshypothese" also on purely physio-
logical grounds, though he admits, that the electric phen-
omena accompanying innervation and contraction are
most probably of the same nature as is the shock of the
electric fishes. He emphasises that, electricity being devel-
oped in the motor-plate or in the analogous electroplax, the
latent period of the shock, when evoked indirectly (through
the nerve), plus the latent period of a directly stimulated
muscle, should be equal to the latent period of the in-
directly stimulated muscle. Now MAREY has shown that the
latent peroid of the indirectly excited organ of *Torpedo* is as
long as is the latent period of an indirectly excited muscle.
Further, BERNSTEIN has shown that the "negative contrac-
tion-wave" of the muscle has no measurable latent period
at all. This objection does not hold, however, for several
reasons. DU BOIS-REYMOND himself is aware that MAREY
did not work on fresh, unfatigued material which is es-
sential, especially when the latent period is to be deter-
mined, nor is it permissible to compare time-relations from
experiments on the organ of *Torpedo* with those obtained
from frogs muscle. Moreover the statement of BERNSTEIN
must be understood quite otherwise than as does DU BOIS-

REYMOND; the "negative contraction-wave" is just the elec-
tric shock of the motor-plates in the muscle.

Further DU BOIS-REYMOND maintains that the lines in
the electric field evoked by a discharge in the motor end-
plate must run in the main transversely to the direction
of the muscular fibre concerned. If the hypothesis is right,
it must be claimed, therefore, that the muscular fibre is
stimulated as easily when the exciting current runs trans-
versely to the fibre, as when it is running along the fibre,
and further, that the fibre in question is not alone affected,
but, that neighbouring fibres are stimulated too. The first
deduction may be right but is not incompatible with the
hypothesis. It has been shown by SACHS that the stimul-
ating power of a current is independent of its direction
in relation to the muscular fibre. SACHS also found that
only the fibre stimulated really contracts, but he is aware
that this fact does not involve any decisive objection to
the theory concerned. The currents in question are only
weak, and the telolemma covering the end-plate as also
the sarcolemma of the neighbouring fibres may be regarded
as a sort of isolation for the individual fibre, while on
the other hand the end-plate is not isolated from the con-
tractile substance of the stimulated fibre itself.

The most serious objection to the theory is the one
brought forward by BURDON-SANDERSON & GOTCH as well
as by DU BOIS-REYMOND, that the electric organ in fishes
is not influenced by curare. GOTCH has found that the
muscles of *Torpedo* may be completely paralysed by curare
without any influence on the electric organ. Yet it must
be remembered that the muscles of the electric fishes
are also very resistant against curare, and it is probable
from the observations of SACHS on *Gymnotus* that even

the very strong electric organ of this animal may really be paralysed by very high doses of curare, but certainly not until the effect on the muscles is complete. Similar observations have been made by several authors, i. a. by Ranvier, on *Torpedo*. Certainly, very high doses are always required. Ranvier injected subcutaneously, on a *Torpedo* of 40 cm. length, 1 cc. of a saturated solution of curare. Sachs and also Ranvier have observed a state of increased excitability preceding the paralysis in curare-poisoning. It may be added that the curare employed by the authors has not been standardized, and that the diffusibility of this colloïd substance has not as yet been recorded.

E. du Bois-Reymond himself puts forward the hypothesis, that the electro-motive force of the electric organ is due to the summation of a great number of "nerve-currents" which, according to his opinion, are stronger than are the "muscle currents". Now the "nerve-current", according to the author, is due to the tension difference obtained when leading off from the surface and the cross-section of the nerve, and he imagines that the electric plate in some way or other may represent a "cross-section" of the nerve entering it. It is certainly unnessesary now-adays to discuss this theory.

In some other respects the physiological agreement between the electroplax and the motor end-plate is evident. Burdon-Sanderson & Gotch state that in *Raia batis* the direction of the organ-current is the same as found in the motor plate. In *R. batis* the current runs in the direction proximally distally, that is to say, it follows the rule of Pacini which claims that the current always runs from the side where the nerve enters the plate, to the other. The only known exception to this rule is represented by the

disc of *Malapterurus*. MAX SCHULTZE has pointed out, however, that even this exception is only apparent. As described above, the nerve of the organ of *Malapterurus* enters the compartment from behind and is attached to the peculiar stalk of the disc, but as stated also by BALLOWITZ the stalk resembles in structure the anterior and not the posterior layer of the disc which it only penetrates, and it is thus in accordance with the rule of PACINI that the current in *Malapterurus* runs from head to tail.

It may be noted also, that FUJI, in an extensive investigation of *Astrape japonica*, has shown that the behaviour of the fatigued electric organ of this fish very closely resembles that of a fatigued muscle.

According to our reasoning and to the facts brought forward in this paper it is most probable that the old "Entladungshypothese" is right; and it might be added, that a similar mechanism may possibly exist also on the afferent side of the nervous system. In a number of receptors nerve twigs ramify or end in spiral-tours among or around peculiar sensory cells which are easily excited by external stimuli. The excitation may give rise to "currents of action" indicating, presumably, that electric discharges take place in the sensory cells. The afferent nerves may be stimulated at any point of their course with the same result, as if the sensory organ itself were stimulated, but the stimulation of the nerve requires much more energy than does the stimulation of the sensory cell; thus the sensory cells, like the multinucleated cell constituting the motor end-plate, may be regarded as an energy-producing cell. We may imagine a reflex-action to proceed in the following manner: Some stimulus or other excites a nervous end-bulb in the skin, the cells in the end-bulb produce

electricity which in some way or other evokes a nervous impulse which travels along the afferent nerve. The impulse passes over through a synapsis to an efferent neurone and travels along the efferent nerve to a motor end-plate, where it releases an electric discharge which evokes contraction of a muscular fibre.

SUMMARY

An inquiry into the available literature shows that the motor end-plates in skeletal muscles and the electroplaxes in the electric organ of fishes are identical structures.

We must assume that the essential part of both these structures is a multinucleated giant-cell, the function of which is to produce electricity.

The old hypothesis, that the function of the motor end-plates is to produce electricity which serves as the adequate stimulus to the contractile substance of the muscular fibre, is most probably right. It is supported as well by morphological reasons as also by a number of facts brought forward in recent experiments on the electric phenomena in skeletal muscles.

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