

Citation:

J. Boeke & Groot, G.J. de, Physiological regeneration of neurofibrillar endnets (tactile discs) in the organ of Eimer in the mole, in:

KNAW, Proceedings, 10 II, 1907-1908, Amsterdam, 1908, pp. 452-459

Zoology. — "*Physiological regeneration of neurofibrillar endnets (tactile discs) in the organ of Eimer in the mole.* By Dr. J. BOEKE and Dr. G. J. DE GROOT. (Communicated by Prof. G. C. J. VOSMAER).

(Communicated in the Meeting of November 30, 1907).

In recent years several authors (RANVIER, VON LENHOSSEK inter alia) have called attention to the fact, that there where intraepithelial nerves in mucous membranes or in the epidermis are found penetrating even between the superficial layers of epithelium cells covering the sensory surface (so for example in the peribulbar nerve-endings between the taste-buds in the papillae of the tongue, etc.), we have to draw the conclusion, that at the same time as the superficial cells degenerate and are cast off, the sensory nerves with their knob-like end-swings or end-loops of the neurofibrillae must undergo a perpetual change and growth. But then these are always the fine ramifications and endings of the nerves, which branch between the deeper layers of epithelium cells. Real neurofibrillar endnets like those which are formed round the base of the tactile cells of MERKEL, are always found in the deeper layers of the epidermis, where they lie protected by the other epithelium cells. These tactile cells nowhere degenerate so quickly as it is the case with the superficial cells of the upper layer of the epithelium, and need not be replaced by other cells coming from the deeper strata. There is no need of a quick regeneration of the neurofibrillar endnets (and the tactile cells).

But suppose we had a tissue, where in the uppermost strata of a stratified epithelium, in which the superficial cells quickly degenerate and are cast off, we find real tactile cells with distinct neurofibrillar endnets, which therefore must degenerate at the same time as the surrounding cells, how would the process of regeneration of the neurofibrillae take place there?

In the course of investigations carried on in the histological laboratory at Leiden we found a favourable object to study this question in the sensory organs in the snout of the earth-mole (*Talpa europaea*).

Here we find an extremely sensitive tissue (the organ of EIMER) the elements of which are only protected by a very thin horny layer, and which by reason of its lying at the tip of the snout must, on account of the well-known habits of the animal, continuously form new horny cells for the protecting horny layer above, because otherwise the functional cells would very soon come to lie at the surface and be liable to be injured.

The structure of the peculiar organ first described by EIMER (1870) and the innervation of it, have been studied in the course of this year (1907) by two authors¹⁾ by means of the recent improved methods of staining the neurofibrillae. Both give about the same description but arrive at different conclusions.

As is well known, the organ of EIMER consists of thickenings of the epidermis, formed by columns of epithelial cells in the shape of an hourglass, which form small round prominences on the surface of the snout, and which, because the columns of cells are longer than the thickness of the epidermis at the place where they are found, project with their base into the corium, and form here a bulging out of the epithelium, generally described as "buffer-shaped". Each of the columns is made up of several strata of more or less flattened epithelial cells, which at the base of the column do not reach from one side to the other, but are wedged-shaped and overlapping each other with the thinned-out ends. Nearer the surface the cells gradually become flattened and larger, until only two cells lying at the same niveau, fill out the entire cross-section of the sensory column (fig. 1, 5). There the column ends as it reaches the horny layer. The cells of the column are, according to BOTEZAT, true spiny cells like the other cells of the epidermis (fig. 3).

In the axis of the column a thick nerve fibre, the axial fibre, runs through the whole length of it, penetrating into the epithelium at its base. Sometimes there are two or three axial fibres. Around the column of cells a set of 18 or 19 thin, unbranched nerve fibres, closely set, somewhat zigzag, run upwards between the outer ends of the cells of the column and the adjoining epidermis-cells, until they reach the horny layer. These are called rand-fibres to distinguish them from the axial fibre. At the base of the column between the epidermis-cells a small number of tactile cells of MERKEL are found, and underneath the epidermis in the corium one or two small Pacinian corpuscles.

EIMER already described small varicosities or knoblike swellings of the nerve-fibres in the upper part of the columns. The nerve-fibres run more or less zigzag between the cells. EIMER himself and after him HUSS (1898) thought that these knoblike varicosities were lying intracellular, the nerve-fibres running between the cells. The varicosities are therefore attached laterally to the nerve-fibres.

¹⁾ EUGEN BOTEZAT. *Anat. Anzeiger*, 30 Bd. 1907.

M. BIELSCHOWSKY. *Anat. Anzeiger*, 31 Bd. 1907.

In this year (1907) BIELSCHOWSKY¹⁾ has investigated the nerves of the organ of EIMER by means of his method of staining the neurofibrillae, and although he does not give much that is new, as he says himself in his paper, his study is interesting because with that by BOTEZAT it is the only one, in which the new staining methods for the nervous system are used for this organ. We may quote here what he says about the course and the peculiarities of the nerve-fibres, because this makes clear his opinion better than a long description. The course of both the axial fibre and the randfibres he assumes to be entirely intercellular: "irgend ein näherer Konnex der Fasern zu den Epithelzellen findet nicht statt; ihr Verlauf ist ein rein intercellulärer. Im Bereiche der äusseren Schicht weisen sie in scheinbar regelmässigen Abständen die bekannten punktförmigen Varikositäten auf. Die Varikositäten sind offenbar nur auf Zerfallsvorgänge zurückzuführen. Dafür spricht der Umstand, dass sie immer erst in der Verhornungszône des Epithels deutlich hervortreten. Aehnliche Beobachtungen kann man auch am Schweinerüssel and anderen rüsselförmigen Säugerschnauzen machen". (l.c. p. 189).

In his last paper, published some months before the paper by BIELSCHOWSKY appeared (April 1907), BOTEZAT²⁾ who in his paper of 1903 pronounced the same opinion as EIMER and HUSS, viz. that the knoblike thickenings of the nerve fibres penetrate into the cells of the column of EIMER, adopts the view that they are epicellular, after a study of the nerves coloured with methylene blue and after the method of RAMON Y CAJAL. "Der Beweis hierfür lässt sich am besten dadurch erbringen, dass man die Terminalknöpfchen fast genau zwischen den Zellen des Organs liegen sieht." BOTEZAT states that the varicosities possess a netlike structure. Because they are excessively small, the extreme sensibility of the snout must be due to the very large number of the terminal knobs ("tactile discs") and not to their great perceptibility. A column of EIMER consists of about 15 layers of cells, and in each layer about 20 of these tactile knobs are to be found. The total number therefore is in each organ of EIMER 300, and for the entire snout more than 100000³⁾. According

1) M. BIELSCHOWSKY, Ueber sensible Nervenendigungen in der Haut zweier Insectivoren (*Talpa europaea* und *Centetes ecaudatus*). Anat. Anzeiger. Bd. 31, p. 187—194, 1907.

2) EUGEN BOTEZAT. Ueber die epidermoidalen Tastapparate in der Schnauze des Maulwurfs etc. Archiv für Mikroskopische Anatomie. Bd. 61. p. 730—764. 1903.

3) EUGEN BOTEZAT. Die fibrilläre Struktur von Nervenendapparaten in Hautgebilden. Anat. Anzeiger. Bd. 30. p. 321—344. 1907.

to BIELSCHOWSKY the total number is $\pm 150,000$, together with more than 5000 end-bulbs and numerous cells of MERKEL.

Although he does not ascribe to the varicosities a high degree of perceptibility, BOTEZAT assumes all of them (both of the axial fibre and of the rand-fibres) to be tactile discs, in accordance with most authors. A difference in structure between the different tactile discs or knobs he mentions without paying much attention to it.

Now the facts seem to us to point to a different conclusion.

The opinion of BIELSCHOWSKY, that the varicosities of the nerve-fibres are due to "Zerfallsvorgänge", seems to us to be erroneous. In the first place these varicosities do not appear first in the horny zone. On the contrary, as soon as the cells are transformed into horny cells, the fibres and their varicosities degenerate, and the first varicosities appear seven to eight layers of cells lower down. In the second place the varicosities are much too regular and are distributed with a far too great regularity to be the mark of degeneration, and are always present in nearly the same number. In the third place their structure does not point at all to "Zerfallsvorgänge."

But in his description BOTEZAT too does not seem to have hit the point. He does not give an explanation of the difference in structure of the varicosities and of their mode of attachment to the nerve-fibres, and of the fact that they are only to be found in the peripheral part of the nerve-fibres and not in the basal half.

When we treat a small piece of the snout of the mole, after fixation in formaline, according to the method of BIELSCHOWSKY—POLLACK, and study a correctly differentiated preparation in thin (6μ) longitudinal sections (that is a longitudinal section of the nerve-fibres and of the column of cells, the section being made at right angles to the surface of the epidermis of the snout), the following details will be seen: the structure and form of the varicosities ("Terminalknöpfchen, Seitenknöpfchen") are not the same in the course of the nerve-fibres. When we follow a rand-fibre from the base of a column of EIMER to the top, the first swellings appear at a distance of 10 to 12 cell-layers from the top (fig. 1, 5). The swellings are here only loosely built small nets, lying in the course of the nerve-fibres, nothing but a local slackening of the bundle of neurofibrillae in the fibres, the fibrillae probably forming a few anastomoses. From this point upwards we see these networks appearing with great regularity in the course of the nerve-fibres where the fibre passes another cell of the column, and each time the reticular structure becomes finer and more distinct (fig. 1, 3).

In the upper four to five rows of cells a change in the form and

arrangement of the networks becomes visible. The small swellings of the nerve-fibre no more lie in the course of the nerve-fibres, but more and more pass to the side of it (fig. 1, 3) and at last they lie entirely beside the nerve-fibre, being connected with it by means of a very small and short stalk (fig. 1, 2, 3). The swellings of the rand-fibres always pass to that side of the fibre lying close against the cells of the column of EIMER, and so project centripetally (fig. 1, 6). So when we look at a rand-fibre from the outside of the column, as in fig. 5, we see nothing or only very little of this change of place of the varicosities, and only when we play up and down with the micrometer-screw of the microscope, we are able to make out that the peripheral rows of varicosities lie in reality underneath the fibres.

So in the first place we see a very regularly occurring change of place of the varicosities, as the fibre approaches the surface of the epithelium. When we only take the place of the fibre we are examining in the section into account, this change is always found to take place with perfect regularity.

In the second place the following change may be seen: the nerve-fibres of the organ of EIMER (both the rand-fibres and the axial fibres) run between the cells of the epithelium. The first swellings or varicosities, the small loose nets lying in the course of the fibres, of course also appear between the cells. But as soon as these varicosities get larger and change their places, so that they come to lie besides the fibres, they push their way *into* the substance of the cells of the sensory column and not between these cells. They become *intracellular*. In the preparations stained after the method of BIELSCHOWSKY the cells and their margins and nuclei are so clear and distinct, that when we only take care to examine thin sections (5—6 μ), this fact may be stated with perfect clearness. Fig. 1, 2 and 3 give a good idea of it; when we examine longitudinal sections of the rand-fibres, the section passing through the axis of the sensory column, we see as it were the varicosities or knobs push their way into the protoplasm of the cells. In cross-sections now and then we come across places, one of which is figured in fig. 4. The tactile knob growing into the flat epithelial cell, pushes its way into the protoplasm apparently with some force so that the flattened nucleus is curved in by it. Similar drawings are given by HUSS.

Another question is, whether these varicosities or tactile knobs lie in the protoplasm of the cell, become an integrating part of it. The facts seem to point to the contrary. On observing

the fibres and their tactile knobs closely under the highest power, we get the impression that even there where the knobs lie intracellularly, the neurofibrillae are still surrounded by a very thin layer of perifibrillar substance, taking a different stain from the protoplasm of the cell itself. But of course this layer of perifibrillar substance must be continuous with the surrounding protoplasm. The neurofibrillar network remains entirely independent, but a trophic connection of the perifibrillar substance and the protoplasm surely must be present. This seems to us to be beyond doubt, and we may venture to suggest, that only now the varicosities reach their full development, are real tactile discs; as long as they lie between the cells, the varicosities are only parts of the nerve-fibres where the neurofibrillae are getting looser and growing out, but only when they pass to the side of the fibres and grow into the cells, they become real tactile neurofibrillar end-nets. The rows of varicosities are merely stages of development of the tactile discs.

The end-knobs or terminal discs in the upper row of cells of the sensory column, which are already on the point of passing into the horny layer, are for the greater part already lying loose in the cells, the nerve-fibres themselves and the connecting stalks atrophying. So in fig. 5 the four knobs, represented by black spots in the upper row of cells, are entirely separated from the nerve-fibres below, and the same fact is to be seen in the fig. 1 and 3, where a part of the nerve-fibre (the stalk of the end-knob) was still stained. The argument, that this independence of the terminal knobs is due to the connecting stalks not being cut in the section examined, is annihilated by a close study of many sections. Thus we can state with perfect accuracy, that the connecting fibre really does not exist any more (at least, is not stained as the functional fibres are).

The axial fibre shows the same peculiarities as the rand-fibres, but the tactile nets are larger and more rounded; the axial fibre too runs between the cells until its end; even there where, in the upper part of the column, the entire cross-section is composed of two cells, the line between these cells runs just through the middle of the transverse plane (cf. Huss) and leaves a small room just in the axis of the column, occupied by the axial fibre (fig. 6). The tactile nets grow out from the fibre now at one side and then at the other, and grow into the cells of the sensory column just as it was described for the rand-fibres.

So we find the same peculiarities of structure in all the nerve-fibres and their tactile neurofibrillar networks. The same cause seems to us to underlie all these differentiations, which we may describe

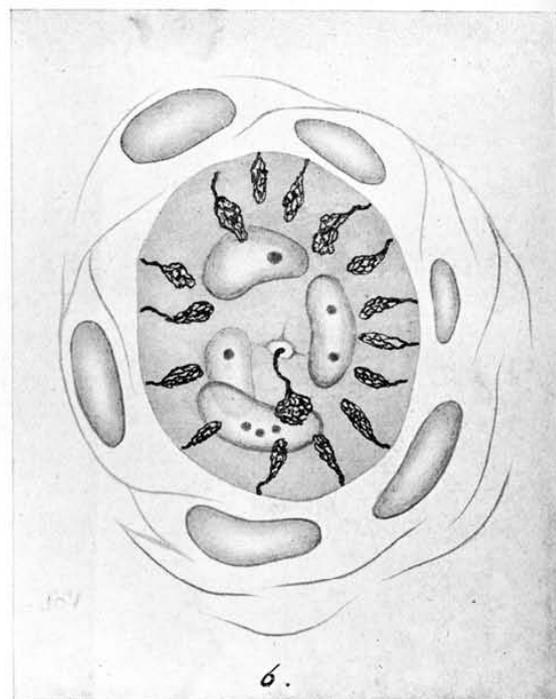
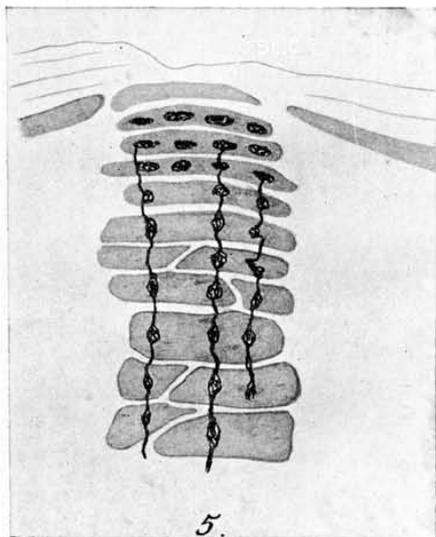
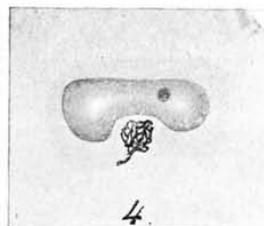
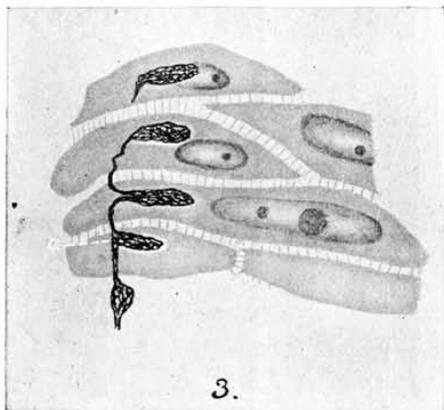
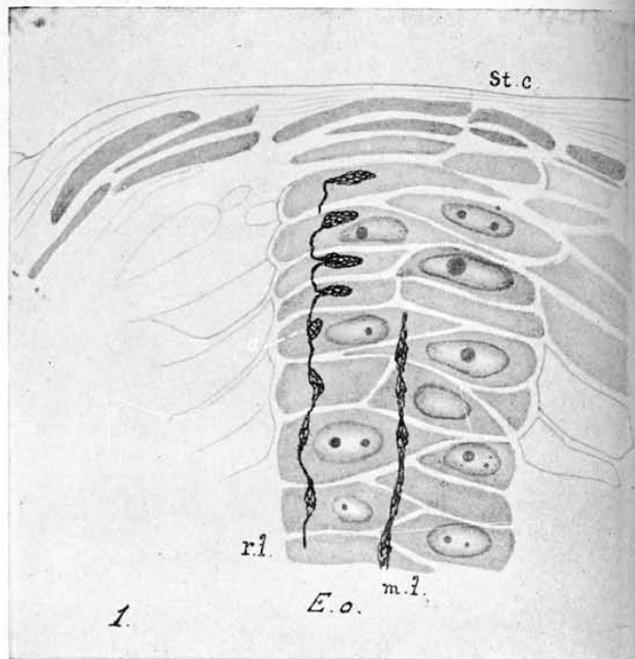
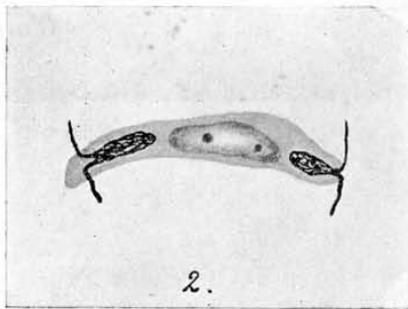
as a getting more and more differentiated and independent of the tactile discs (or varicosities) as we draw nearer to the surface of the sensory column.

When we see now, that the horny layer above the columns of the organ of EIMER is always thinner than in the adjacent parts of the epidermis (so for example in fig. 1, st. c.), as it was the case in all the preparations examined, and when we bear in mind, that these prominences on the surface of the snout of the mole are continually exposed to all sorts of mechanical insults, the question, put at the beginning of this paper, may be answered in the following manner:

The horny layer above the cells of the column of EIMER being very thin and composed of a few layers of cells, and the horny scales being lost very soon by desquamation, there must be a continual moving upwards of the cells of the deeper layers of the column of EIMER, to take the place of the thrown off cells. With these cells the nerve-fibres must grow upwards at the same rate. About in the middle of their course these nerve-fibres begin to form tactile discs. These corpuscles first appear as places in the course of the fibres where the neurofibrillar structure is looser; these first varicosities little by little pass out of the course of the fibre and grow into the cells of the column of EIMER, and so become real tactile discs. These tactile discs lying at the side of the nerve-fibres and remaining attached to them by a short stalk, are a direct argument for the growing upwards of the nerve-fibres together with the cells of the column. Otherwise the cells would take with them the tactile corpuscles and sever them from the fibres they belong to or draw out the stalks in an oblique direction. Of this no trace is to be found anywhere. It is very probable, that only when the varicosities grow out to small tactile discs and come to lie intracellularly, they acquire a heightened perceptive faculty. As they are continually travelling upwards to the surface, new varicosities are formed underneath in the course of the same nerve-fibre. As soon as the cells undergo the transformation into horny scales, the tactile discs and their connecting stalks and the nerve-fibres atrophy, the former remaining visible longer than the latter. Only the upper rows of tactile discs, of the form of the networks of fig. 2 and fig. 3, seem to be fully developed.

They are continually replaced by others, coming from below. The nerve-fibres of the column of EIMER chiefly grow at the base of the column and atrophy at its top.

Perhaps these views may be extended to other intraepithelial



J. Boeke a. n. del.

nerve-endings. It will be difficult to find an object of study as favourable as the organ of EIMER.

Leiden, Anatomical Cabinet.

DESCRIPTION OF THE FIGURES ON THE PLATE

All the figures are drawn from life from preparations made after the method of BIELSCHOWSKY-POLLACK, with a camera lucida of ABBE. Fig. 1 and 5 are enlarged 1200 times, the others 1600 times. Apochromate-oil-immersion. Sections 5 and 6 μ .

Fig. 1. Longitudinal section of the upper part of a column of EIMER of the earth-mole. A rand fibre (*rf*) and a part of an axial fibre (*mf*) are seen. The horny layer (*stc*) above the column of EIMER is distinctly thinner than at both sides of it.

Fig. 2. Longitudinal section of a flat cell of the upper part of a column of EIMER, with two tactile discs, growing into the same cell. The netlike structure and the curious drawing in of the connecting fibre, is clearly shown.

Fig. 3. Longitudinal section of the upper part of a column of EIMER, to show the developing of the tactile discs, and the final atrophy of the nerve-fibre.

Fig. 4. From a cross-section through the upper part of a column of EIMER. A nucleus curved in by a tactile disc

Fig. 5. Longitudinal section through the peripheral part of a column of EIMER. Three rand-fibres are shown. The tactile discs lie behind the nerve-fibres. The intracellular position of the tactile discs is clearly to be seen. The upper cell, in which lie four tactile discs, is being transformed into a horny cell. The nerve-fibres degenerate.

Fig. 6. Cross-section through the upper cells of a column of EIMER. In the section of 6 μ four cells were to be seen, lying two and two in the same niveau.

The tactile discs of the rand-fibres all grow centripetally into the cells, the axial fibre runs between the cells.

Astronomy. — " *β Lyrae as a double star.*" By J. STEIN, S. J. at Rome. (Communicated by Prof. H. G. VAN DE SANDE BAKHUYZEN).

1. As far as I know, Professor E. C. PICKERING was the first who, led by his spectroscopic investigations, suggested that β Lyrae might be a close double, the components of which describe circular orbits in a light-period¹).

This surmise was confirmed by BELOPOLSKY²) in 1892. He measured the displacement of the luminous *F*-line on some fourteen spectrographs. They were found to show a minimum (in absolute value) at the time of the minima and a maximum at the time of the maxima of

¹) Spectrum of β Lyrae. By Prof EDWARD C. PICKERING. A. N. 3051 (1891).

²) Les changements dans le spectre de β Lyrae. A. BÉLOPOLSKY. Memorie della Società degli Spettroscopisti Italiani. Vol. XXII, 1893.