

The Structure of the PACINIAN CORPUSCLES CONSIDERED with REFERENCE to the HOMOLOGIES of the SEVERAL PARTS COMPOSING THEM. By EDWARD SCHÄFER, Assistant-Professor of Physiology in University College, London. (With Plates VIII and IX).

STUDIED generally, a Pacinian corpuscle may be looked upon as consisting of three parts—the central fibre, the core, and the capsular enclosure. I propose in the first place to note down the result of observations upon the structural appearances presented by each of these parts, as ordinarily met with, without entering into the consideration of the variations which present themselves more than may seem necessary for the elucidation of the structure; and then to discuss briefly the homologies which the component parts of the Pacinian corpuscle severally bear to the parts which compose the entering nerve, at the same time indicating the manner in which the structures of the one appear to become continued into those of the other.

The observations were in all cases made upon the Pacinian corpuscles from the cat's mesentery; these having been selected on account of the facility with which they are obtainable in the fresh condition, combined with the fact that, according to the unanimous testimony of observers, their structure differs in no essential particular from that of the corpuscles met with on the nerves of various parts of the human body.

The Central Fibre.

As first shown by Grandry, this presents a distinct appearance of fibrillation, the fibrils, as a rule, crossing one another very obliquely (see Plate VIII, fig. 2, *ef*); thus rendering it difficult or impossible to trace each separate fibril throughout its whole length. The central fibre is uniform in size except towards its extremity, where most commonly it becomes enlarged; but sometimes there is no distinct swelling, the fibre being merely marked at its sides with minute denticulations or projections, from which, in preparations stained with chloride of gold, fine fibrils occasionally appear to proceed outwards. (In one instance the central fibre terminated abruptly after traversing only two thirds of the length of the core, by a rounded extremity, uniform in diameter with the rest of the fibre.) The terminal enlargement, when present, varies much both in size and shape, in some cases having a simple rounded outline, in others an irregular shape, with

acuminate processes. Its substance either appears granular, or more homogeneous, and refracting the light strongly; in the first case the fibrils composing the central fibre may often be seen to spread out into the substance of the enlargement; in the second this last is probably covered with a thin layer of white substance similar to that composing the medullary sheath of the nerves, and the arrangement of the fibrils is thus obscured. The terminal enlargement as well as the remainder of the central fibre becomes deeply stained by chloride of gold, much more deeply than the substance composing the surrounding core, but even in very successfully stained preparations I have hitherto failed to discover a fine network of nervous fibrils around the extremity, as described by A. Budge. If the terminal enlargement is of considerable size it may contain a clear, round nucleus, with nucleolus, generally obscured by the granular substance of the enlargement. A nucleus is not, however of frequent occurrence, as Jacobowitsch and Ciaccio have described.

It is not at all uncommon to find the central fibre accompanied for a short distance within the core by the white substance of the medullary sheath (B, fig. 3); this has been noticed by various observers, as well as the fact that the white substance may reappear here and there, especially at a bend in the core; I have besides in more than one instance noticed the medullated fibre passing quite through one Pacinian (generally a smaller one) to terminate in another, without loss, or even diminution in thickness, of its medullary sheath (A, fig. 3). Axel Key and Retzius also describe the fibre as occasionally retaining the medullary sheath as far as the terminal enlargement. Ordinarily there is no medullary or white substance surrounding the fibre in its course; this fact is readily determined by the action of osmic acid, which speedily blackens the fatty substances which mainly compose the medullary sheath of the nerves.

Sometimes, when the central fibre bifurcates, one of the branches may retain a medullary sheath and the other be continued as a pale fibre.

With regard to the presence or absence of a membranous structure corresponding to the primitive sheath (Schwann's sheath) of the nerves, it will be sufficient here to state that no indication of such a structure could be detected immediately investing the central fibre, either when viewed longitudinally or in transverse section, nor any nuclei in the immediate neighbourhood of the fibre which might belong to such a sheath.

In its behaviour to staining fluids the central fibre of the

Pacinian corpuscle precisely resembles the axis-cylinder of a nerve.

The Core.

The substance composing the core is commonly described as being alike throughout; but in many corpuscles, if not in all, an outer nucleated part, of variable extent, may be distinguished from the almost homogeneous, non-nucleated substance which immediately surrounds the central fibre. On careful focussing, and under a high power of the microscope, the inner part presents an appearance of indistinct longitudinal striation, which in a transverse section appears irregularly concentric (see Plate VIII, fig. 2 A); the outer appears composed of protoplasmic cells, like connective-tissue corpuscles, each with a clear oval nucleus; next to the inner part are a few flattened nuclei seen in section as mere lines.

Osmic acid (as shown by Michelson), chloride of gold, hæmatoxylin, and most of the ordinary staining fluids, colour the whole core much as they colour protoplasm.

The Capsular Envelope.

The structure of this can only be properly elucidated by the study of sections and by teased preparations. Examined in the ordinary way, fresh, in an indifferent fluid, the core of the Pacinian corpuscle appears, as is well known, surrounded by and enclosed in a number of concentric membranous "capsules," which, since Hoyer showed that treatment with nitrate of silver brings to view epithelioid markings upon them, have since been commonly regarded as composed each of a single layer of flattened cells with a certain amount of connective-tissue fibres, both white and elastic, on one or both surfaces. The so-called capsules, also, appear separated from one another by a clear fluid, less in amount both close to the core and near the exterior of the corpuscle, so that at these parts the capsules appear closer together than in the intermediate region.

But a new¹ view of the structure has recently been brought forward by Axel Key and Retzius, according to whom the supposed simple capsules each consist of *two* layers of flattened cells, placed, as it were, back to back; and they draw attention to the fact, which had been previously pointed out by Ciaccio, that the intercapsular spaces are not merely filled with an albuminous fluid, but are, to a greater or less extent in different parts, pervaded by fibres both white and

¹ A somewhat similar view seems to have occurred to Henle and Kölliker, and to have been rejected by them.

elastic, which are more abundant in the immediate neighbourhood of the cells, forming, here, in fact, definite layers, but some of which pass obliquely across the interspaces and connect these layers. The observations here to be recorded as to the structure of the capsular envelope are for the most part confirmatory of those of Key and Retzius.

The fibres which lie between the so-called capsules may be seen even by the ordinary method of examination, but since their general direction is transverse to the long axis of the corpuscle they appear mostly as fine dots or granules in the fluid (fig. 2), being seen in optical section; by the employment of the fine adjustment, however, it may be determined that the dotted appearance seen is in reality due to the presence of fibres.

In thin sections of Pacinians which have been prepared with chloride of gold the layers of the capsular envelope, at least the outermost ones, are readily separable, as shown in Pl. IX, fig. 4, *a a'*. In such preparations the albuminous fluid between the so-called capsules is coagulated, and the membranes which bound it are thereby more firmly united, so that when an attempt is made to separate the layers the separation takes place at the line of the capsules, that is, between the two layers of cells of which each so-called capsule is composed. So that we are able to peel off from the capsular envelope layers or tunics which are covered on either surface by a stratum of epithelioid cells, the space between these strata being occupied by fibres and an albuminous fluid, or, in other words, the coats of the Pacinian corpuscle are in reality hollow, and composed of the following structures, viz. a layer of thin flattened cells bounding them externally; a space containing a clear fluid with a greater or less number of fine fibres, the latter being chiefly collected near the cells, but some extending obliquely across the interspace; and a layer of flattened cells bounding the space internally.

What have hitherto been called the capsules of the Pacinian corpuscle are not isolable without rupture of the fibres which stretch across the interspaces, and each capsule must therefore be regarded as belonging half to one tunic of the corpuscle and half to another. Sometimes, indeed, as has long been known, a cleft containing fluid may here and there be seen between the two halves, these being slightly separated from one another. It will therefore be better, in future, altogether to discard the term "capsules" and to speak only of the "coats" or "tunics" of the corpuscle, meaning thereby the hollow layers, bounded by flattened cells, above described; to apply the term capsules to these compound

tunics, as Key and Retzius propose, would be productive of endless confusion, the term having been so long used in a different sense.

By far the readiest mode of demonstrating the fibrous structure of the coats of the Pacinian is to immerse the latter in dilute solution of chromic acid ($\frac{1}{6}$ per cent.) for some days, and then either to make thin sections of the corpuscle with a razor, or carefully to break it up with needles upon a glass slide. If the latter method be employed it will be found that the tunics of which the capsular envelope is composed very readily tear in a direction transverse to the axis of the corpuscle, and small shreds are obtainable which exhibit the general structure of the tunics and the arrangement of the fibres within them in the clearest possible manner. This is shown in surface view in fig. 6, Plate IX, and in profile in fig. 5; the details of the structure will be best understood by referring to the description of the Plates.

Continuity of the Structures composing the Entering Nerve with those of the Corpuscle.

The entering nerve of the Pacinian corpuscle consists usually of a single medullated fibre enclosed in a prolongation of the neurilemma of the nerve-trunk from which it springs.¹

Enumerating the structures which compose the nerve-fibre and its special sheath from within out, there is, first, the axis-cylinder occupying the centre of the fibre; around this the medullary sheath or white substance of the nerve; immediately external to this a delicate layer of protoplasm with clear oval nuclei imbedded in it at definite intervals (the protoplasm is more abundant in the neighbourhood of the nuclei, and the layer is, moreover, much better marked in young nerves); this protoplasmic layer is enclosed by the

¹ By the term *neurilemma* has long been described and is commonly understood the special sheath, now ascertained to possess a laminated structure, which envelopes each funiculus or bundle of nerve-fibres, and a prolongation of which may often be traced accompanying even single fibres, as, for instance, in the case of those passing to the Pacinian corpuscles. Moreover, Ranvier, to whom we owe much of what is known concerning the structure of the funicular sheath, retains the use of the term. Owing, however, to its having been applied somewhat indiscriminately, and occasionally used to indicate the sheath of Schwann or primitive sheath of the nerve-fibre, many histologists altogether deprecate the employment of the term, and substitute for it that of *perineurium*. I shall in this article continue to employ the term "*neurilemma*," since it is in common use in this country, it being, however, clearly understood that the laminated funicular sheath alone of the nerve is thereby meant.

primitive sheath of the nerve or sheath of Schwann; whilst enveloping all are the numerous laminæ composing the neurilemma. There is, moreover, altogether within the latter, a certain amount of finely filamentous connective tissue, which has long been known and described (Sharpey), in which the nerve-fibre lies imbedded. According to Key and Retzius this fibrillar layer (which they name the "endoneurium") is bounded externally, next to the neurilemma, and perhaps also internally, next to the sheath of Schwann, by a delicate stratum of flattened cells.

They further show, and it is not difficult to confirm the observation, that the lamellæ which compose the neurilemma (perineurium) agree in structure with the coats of the Pacinian, each lamella consisting of an inner and outer bounding layer of flattened cells enclosing fibres between them, the only difference being that in the case of the neurilemma the interstitial fluid is either absent or inconsiderable in amount. Moreover, the number of layers is far greater in the capsular envelope of the Pacinians.

Tracing now the continuity of these various parts of the entering nerve with the parts of the Pacinian corpuscle, we find, in the first place, the axis-cylinder of the nerve becoming directly continuous with the central fibre of the corpuscle (fig. 2). The medullary sheath, on the other hand, terminates, under ordinary circumstances, as soon as the nerve enters the core; more rarely, as we have seen, it continues to surround the axis-cylinder in its passage through the core. It certainly does not expand to form the core, as has been sometimes supposed, for in the first place the core is not blackened by osmic acid; and in the second place, when the axial fibre retains its medullary sheath, this exhibits an entirely different appearance from the surrounding core, from which it is distinctly marked off. To take next the primitive sheath or sheath of Schwann. This is more or less closely applied to the medullary sheath of the nerve just before it reaches the core, but then (fig. 2, *p s*) appears to open out and to pass to the exterior of the core, running at first apparently between the outer and inner parts of the core, but at length becoming lost to view. So that the main part, at least, of the core, since it lies within the prolongation of the sheath of Schwann (so far as this can be traced) between it and the central fibre, corresponds with the delicate protoplasmic layer which lies between the sheath of Schwann and the medullary sheath of a nerve-fibre. The outermost portion of the core, on the other hand, is distinctly continuous with the fine connective tissue in which the

nerve-fibre lies embedded within the neurilemma; indeed, this tissue loses in great measure its fibrillated appearance as the nerve-fibre approaches the core, and exhibits a confusedly curdled aspect, which seems due to the presence of a number of nuclear bodies like those above described in the outer part of the core (see fig. 2).

The continuity of the outer layers of the Pacinian with the corresponding layers of the neurilemma may be readily observed even in the fresh condition; moreover, in silvered preparations the layers of flattened epithelioid cells which bound them are distinctly traceable spreading out from the stalk over the body of the corpuscle (Plate IX, fig. 1). In teased preparations also the whole of the entering nerve and its neurilemma may occasionally be plucked away, with those layers of the capsular envelope which are continuous with the neurilemma adhering to it. The more internally situated coats of the Pacinian seem, on the other hand, to be superadded;¹ near the stalk end of the corpuscle they commence abruptly, being attached to the innermost part of the neurilemma (Plate VIII, fig. 2); this is then prolonged around the core to form the innermost layer of the capsular envelope, sometimes even a little beyond the core, enclosing a prolongation of this; and the inner coats are again united with it at the further end, so that they form with the enclosed core a tolerably compact mass which it is easy to isolate.

The observations here recorded are in part founded upon preparations made by Mr. H. Price, student at University College.

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¹ According to K. and R. it is the *outer* layers that are superadded.