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ON THE MINUTE ANATOMY OF THE NEURO-MUSCULAR SPINDLES OF THE CAT, AND ON THEIR PHYSIOLOGICAL SIGNIFICANCE. By ANGELO RUFFINI, *Lecturer on Histology, Royal University of Siena.* (Plates II. III.)

I WAS led to renew enquiry into the structure of the muscle-spindle by a discussion between myself and Prof. Kerschner, of Brünn, which arose when I returned to the subject after publishing a preliminary Note describing the endings of the nerve-fibres in the spindle[1]. I had, however, no wish to pursue further a polemical controversy after the appearance of the paper by Sherrington[2], who in treating of the subject accorded me priority of demonstration and exact description of the nerve-endings in the spindles.

The description of the nerve-ending in my first work, although correct so far as it went, was not entirely complete. I am glad now to furnish a complete account of the nerve-endings, adding various details to those previously given[3].

It is unnecessary to recount here in full the history of the study of the neuromuscular spindles. This has been done by others, and down to the year 1889 is easy of access to all in the last edition of Kölliker's *Gewebelehre.* Yet I must mention a few points that impart clearness to my description.

A. H. Hassall (1851) was first to report the presence in adult muscles of slender muscle-fibres, the function of which he believed to be the successive reproduction of new ones. Hassall's description and interpretation, although brief, show clearly he had before him "muscle-spindles[4]." Rollett (1856) noted in adult muscles certain fibres morphologically unlike the rest; but he furnished no exact description. To Weissmann (1861) certainly belongs

[1] Ruffini. *Rendic. d. R. Accad. dei Lincei. Cl. sc. fis. e. nat.* I. Ser. 5. 1892.

[2] Sherrington. This *Journal,* XVII. 1894.

[3] Ruffini. *Monit. Zool. Ital.* vii. Marzo, 1896.

[4] I borrow this criticism from Trinchese, *Mem. d. R. Accad. d. Sc. dell' Istituto di Bologna,* Sc. IV. X. 1890.

the credit of first clearly and accurately figuring and describing the so-to-say grosser characters of the muscle-spindle. For that reason I with Kölliker wish to associate his name with the bundle of muscle-fibres found inside the spindle—the "Weissmann-bundle." Between 1862 and 1864 besides Peremeschko's works, which shed no fresh light on the problem, appeared valuable observations by Kölliker and Kühne. These supplied many details of structure and were illustrated by accurate figures: in them the structures received for the first time special names, Kölliker calling them "muscle-buds," Kühne "muscle-spindles." After these papers none further appeared on the subject for fifteen years. Then between 1878 and 1883 appeared notices of the spindles in monographs by Ranvier, Kraske, Roth, Golgi, Krause, Millbacher, and Bremer. These notices besides contributing various fresh facts served to call general attention to the existence in embryonic and adult muscle of special structures whose nature and function were matter of conjecture and dispute. Roth, dissenting from the names introduced by Kölliker and Kühne, preferred to speak of the structures as "neuromuscular bundles." From 1885 to 1892 such a series of papers appeared that I should transgress the limits set me were I to deal with all details discovered and the various hypotheses advanced. It must suffice to recount the names of Mays, Mayer, Fränkel, Eisenlohr, Klebs, Kerschner, Felix, Eichhorst, A. Cattaneo, Babinski, Trinchese, Franqué, Dogiel, Santesson, Pilliet, Bloc and Marinesco, and Christomanos.

The most valuable work of this period was that of Cattaneo, Mays, Kerschner and Dogiel, and after their contributions the main desideratum left from the point of view of structure was exact knowledge of the mode of ending of the nerve-fibres that reach the spindle. That part of the anatomy remained still obscure.

Finally, from 1892 to the present day there have appeared, besides Thanhoffer's monograph, the researches of myself, of Kerschner and of Sherrington. It was only that year that the mode of nerve-ending in the spindle received, as Sherrington has pointed out, a great impetus from my work: this will be clear to anyone who will compare my own with the preceding descriptions. The interpretation of the function of these organs is intimately dependent on the knowledge of the structure of the nerve-ending. This is clear from the marked reticence as to functional interpretation rightly displayed by the investigators who busied themselves with the structures but did not decipher the nerve-ending. They contented themselves with calling them embryological, pathological, or "special" organs. Ranvier had, in fact, gone as far toward interpretation as any in calling attention to the likeness between their concentric lamellar capsule and that of a Pacinian corpuscle. At the latter end of 1888 Kerschner argued that they were sensory. It must be admitted by any temperate and dispassionate critic that this hypothesis was then premature and an *a priori* view without adequate anatomical fact for it. I was forced to enter on this question elsewhere[1] and will not now repeat the grounds for my critique; there seems to me neither place nor further necessity. To the various interpretations given of the spindle other than the sense-organ view it is now no longer necessary to refer.

Of the numerous names given to these special structures I have cited only a few. None of those proposed seem to me to fully satisfy the requirements exacted by the history or morphology of the tissue. General usage sanctions Kühne's name, "muscle-spindle." To change it for a new one seems to me hardly worth while. Yet it does seem to me necessary to prefix to the adjective *muscular* the further epithet *neuro*, thus in part adopting the suggestion of Roth. I therefore speak of *neuromuscular spindles*. The prefix *neuro* is required because as shown below the nerve-endings constitute the most interesting features of the whole specialised structure. I must preface my description of the nerve-endings in the neuromuscular spindles of the cat by a review of the structural characters of the spindles in mammals as a whole.

The mammalian neuromuscular spindle requires a description quite apart from the neuromuscular spindles studied in amphibia and reptiles. The following general critique is based on the most interesting work of Sherrington, on Kölliker's summary, and on my own researches.

We have in the neuromuscular spindles of mammals to consider (1) their general form, (2) their topography, (3) their number, (4) the capsule and its relationships, (5) the lymphatic space, (6) the bundle of striped muscle-fibres (bundle of Weissmann), (7) the nerve-fibres and their endings.

(1) *Form.* The neuromuscular spindle is not invariably fusiform, although approximately so in the vast majority of cases. In my gold preparations the proximal end is very often the larger. Along the organ occur one or more fusiform dilatations which as will be shown coincide with regions of nerve-ending. Frequently a spindle is compound, that is, consists of two or rarely three simple spindles conjoined (Sherrington). The entire length is given by Kölliker at 7—4 mm. by Sherrington at 8—3·5 mm. The diameter at entrance of the nerve-fibres varies according to Kölliker between 72 μ and 9 μ, and

[1] *Anat. Anzeig.* 1893.

the greatest width of a spindle varies according to Sherrington between 80 μ and 200 μ.

(2) *Topography.* A. Cattaneo and Kölliker advance the rule that the region of the muscle which contains spindles is the near neighbourhood of the tendon. Sherrington found them numerous also in the fleshy mass of muscles and close to aponeuroses and intra-muscular septa, in the latter case sometimes inclined at an angle with the general trend of the muscle-structure. I have myself also found them in these situations and in the fleshy mass of the muscle, especially near to nerve-branches, as Kerschner and Kölliker have also correctly observed.

(3) *Number.* As for their number in the different muscles of the body we still know but little. Kölliker states on the basis of his own observations on a child of four that each belly of the omohyoid contains at least fifteen. Sherrington believes them relatively more numerous in the small muscles of the foot and hand than in the large muscles of the leg. He found many of them, however, close to the aponeurosis of the *vastus internus cruris.* I can add nothing further of my own knowledge on these points. I am pretty sure, however, that in a number of muscles the neuromuscular spindles are more numerous than the musculo-tendinous organs of Golgi. The ocular muscles are an exception, for in them Sherrington did not find a single spindle, although it is a well ascertained fact that they possess musculo-tendinous organs. It is an old statement, recorded by the majority of those who have studied spindles, that they appear more numerous in embryonic infant muscles than in adult. This it was which contributed with other circumstances to lead to an erroneous view of the meaning and function of the structures. To me it appears a statement altogether without foundation. The number of spindles in embryonic muscles is not absolutely greater than in adult, but it is true they form relatively more conspicuous fractions of the muscles because the parts outside the spindles are then relatively small. Similarly the tendon organs of Golgi are relatively more conspicuous in embryonic tendons than in adult.

(4) *Capsule and its relations to other elements.* Each spindle is enveloped in a capsule sheath made of concentric lamellæ, varying in number with the spindle and animal species. The lamellæ completely resemble those of a Pacinian body. They are composed of dense fibrillate connective tissue; but we do not know if the fibrils are disposed in two strata, an outer longitudinal and inner circular, as

in the lamellæ of the Pacinian organ. The lamellæ are lined on either face with a layer of endothelium, and the spaces between the lamellæ contain fluid, probably lymph.

But while the structural characters of the capsule itself are now known with tolerable precision, little has yet been ascertained regarding its arrangement around the organ and along the length of the organ. Sherrington, who has furnished us with a number of valuable facts about the structure of the capsules, says on this point little more than that the fibrous tissue of the capsule at the distal apex of the spindle adheres closely to the tendon bundles of the spindle itself. Kerschner only says that at each pole of the spindle the capsule thins away owing to disappearance of its lamellæ and adheres more closely to the muscle-bundle.

My own preparations show clearly that the disposition of the capsule may differ in different parts of the spindle. I cannot absolutely deny that the proximal end at its extremest distance from the nerve termination is provided with a capsular investment, but I can say that I have never succeeded in finding it. The muscle-fibres are there always well apart from one another, and not closely bound together as in the rest of the spindle. This leads me to believe that the capsule there is either altogether wanting or is reduced to a single lamella that is very easily torn in the manipulation of preparing the specimen. The capsule begins to manifest itself with full distinctness where the nerve-fibres apply themselves to the spindle. From that place its layers gradually increase in number, to reach a maximum of 6—8 in that region which corresponds with the portion of the nerve-ending that I shall describe and call the "primary ending." Thence the capsular lamellæ gradually decline in number, and end by meeting and adhering to the tendinous portion of the spindle (Fig. 1).

The capsule of the spindle is surrounded by the *perimysium internum*, which divides it from the surrounding muscular fibres. In this perimysium course the numerous blood vessels already noted by Cattaneo, Kerschner and Kölliker. One of these vessels usually runs along the outer part of the capsule, and from it proceed capillary blood vessels which take a more or less spiral direction within it (Sherrington). A fact not yet noticed so far as I know is the existence of elastic fibres on the capsule of the spindle. I have found them both in man and in the cat. These elastic fibres are abundant, but I cannot say with certainty whether they lie on or between the lamellæ or enter as an intrinsic part into the actual substance of the lamellæ, as Tartuferi[1] demonstrated is the case with the elastic fibres of the capsular lamellæ of the Pacinian organ. From their distribution and appearance I incline less to the last than to the two former possibilities; but there may also be intrinsic elastic fibres in the lamellæ that would for demonstration require some special method such as that devised by Tartuferi.

(5) *The lymphatic space.* Between the inner face of the capsule and the outside of the Weissmann-bundle exists a space which Golgi and then Sherrington have declared to be lymphatic. That it is really a lymph space is indeed placed beyond doubt by Sherrington's success in injecting it by injecting the lymphatics of the limb. According to Sherrington the space may measure from 5μ—15μ across toward the ends of the spindle, and up to 40μ—50μ in the middle region between the poles. In this space are discoverable proteid precipitates and some lymphocytes, never blood-corpuscles. The space is spanned by tenuous membranes and filaments, on which are endothelial cells. Outward the membranes and filaments join the inmost lamella of the capsule, inward the connective sheath of the Weissmann-bundle (Sherrington). To this space Sherrington gave the name "periaxial space"; to me a preferable term would seem "perifascicular space."

(6) *The bundle of striped muscle-fibres* (*Weissmann's-bundle*) The centre of the neuromuscular spindle is occupied by a bundle of striped muscle-fibres which in honour of its first describer it is only just to designate Weissmann's-bundle. This bundle is composed of 3—4 fibres in the rabbit, 3—10 in man (Kölliker), 2—12 in the cat and monkey (Sherrington). In a compound spindle as many as twenty fibres may be observed but are never existent as a single bundle (Sherrington). The diameter of these fibres is less than that of ordinary muscle-fibres. The parent fibres in the spindles of the rabbit measure 38μ—53μ, and the daughter fibres 19μ—22μ (Kölliker). In the cat and monkey they average between 6μ and 28μ (Sherrington). Their striation is very marked. In cross-section they present an appearance somewhat similar to the cardiac fibres of Purkinje or the myoblasts of Schaffer (Sherrington). In general they are furnished with sarcolemma, but on some of the fibres sarcolemma cannot be demonstrated (Sherrington). Nuclei are more abundant in their sarcolemma than in that of ordinary muscle-fibres.

[1] Tartuferi. *Bulletino delle Sc. Med. di Bologna*, Ser. VII. Vol. iv.

The substance of these muscular fibres is provided along its whole length with numerous nuclei, many of which lie in a bed of granular protoplasm (Golgi). In these nuclei Sherrington never found karyokinetic figures, a point which militates against their being as once urged centres of muscular growth. It seems that the fibres of the bundle lie simply apposed without intervention of connective tissue (Kölliker), and that the bundle is ensheathed in a delicate layer of connective tissue described by Sherrington and called by him the "axial sheath."

Of the two ends of the Weissmann-bundle one is muscular. This may be called the proximal end. The other is tendinous and may be called the distal end. In the muscular or proximal end lie the so-called *parent* muscular fibres, which by lengthwise subdivision make *daughter* fibres. One parent fibre can split into as many as three *daughter* fibres. The parent fibres are of much greater diameter than the individual daughter fibres, and in cross-section present various polygonal figures, while the daughter fibres are generally circular (Sherrington). The muscle-fibres proceed, gradually diminishing in breadth as they approach the tendinous or distal end of the spindle. Not all the fibres become tendinous at the same point, and hence the length of their tendon filaments separately varies. Sherrington has observed some 500μ to 600μ in length. These tendons of the spindles end ultimately by being lost either in the fibrous tissue of aponeuroses or of intramuscular septa or of the proper tendon of the muscle as a whole. It often happens, as A. Cattaneo first showed, that the tendon of a spindle joins or merges into a tendon bundle containing a Golgi organ. This happens especially often with spindles that lie in vicinity of the muscle-tendon.

From what has been said it will be clear that the Weissmann-bundle need not itself be fusiform. Wide above in the muscular end of the spindle it gradually diminishes in width and becomes very slender at the tendinous end; but each bundle has on its course more than one fusiform expansion, an expansion which is however of only moderate dimension. The Weissmann-bundle presents a circular rather than an angular cross-section. Its diameter in the median part varies from 32μ to 90μ. One often finds the bundle placed eccentrically in the circular space of the capsule, but this is due to asymmetry in the capsule itself, which at one side will come close to and at another lie far from the Weissmann-bundle. In longitudinal section the Weissmann-bundle is always found to extend in a right line (Sherrington).

(7) *The nerve-fibres and their endings.* I shall in this section confine my description entirely to the spindles of the adult and new-born cat. I shall refrain from treating of other animals, because on the one hand my series of preparations from other animals is still an incomplete one, and on the other it seems well before attempting comparison between spindles in different groups of animals to obtain a fairly complete view of the type of structure in one living species. The task of description and explanation is much lightened thereby.

In my first communication on this theme I wrote at a time (1892) when no one had observed exactly how the nerve-fibres behave inside the neuromuscular spindles—in spite of Kerschner's later assertions to the contrary. Prior to the publication of my communication the only authors who had given, I will not say a description but a partial sketch of the terminal apparatus of the spindle were Kölliker and Kerschner. The latter sought to distinguish a sensori-motor termination in the spindle; the former recognised no such distinction but confined himself to speaking of a mode of termination remotely corresponding to that claimed by Kerschner as sensory. All they say is that amyelinate fibres spirally ensheath the Weissmann muscle-fibres and here and there show free ends. In 1893 Kerschner went further and defined more precisely certain anatomical data, but that was a year after the appearance of my own work. With this necessary prelude I pass to an exposition, as clear and brief as I can make it, of my own observations.

I have used throughout the gold chloride method. I am convinced from long trial that from this of all existing methods one can expect the clearest—indeed surprisingly clear—results.

The nerve-endings are not of quite similar kind or abundance in all neuromuscular spindles in the cat. Hence apart from mere convenience of description or desire to schematise one must distinguish three types of spindles:

1st type. Spindles with complex terminations.
2nd „ Spindles with intermediate terminations.
3rd „ Spindles with simple terminations.

In general there can be distinguished in the cat three distinct kinds of nerve-ending—*the primary ending, the secondary ending,* and *the plate-ending.*

The primary ending. This is that of which Kerschner and Kölliker speak, and of it I furnished a description and figure in 1892. It offers a singular appearance not seen in any other known nerve-ending. In some spindles its elegance and regularity are simply surprising (Fig. 1 and Fig. 3). Its nerve-fibre just before joining the spindle almost always splits into two or more secondary divisions, which do not part but course together in one bundle and plunge into one and the same spindle. Each of these secondary divisions in turn subdivides into tertiary. This subdivision usually occurs in close proximity to the Weissmann-bundle well within the capsule of the spindle. Each branch, secondary or tertiary, constituting an ultimate branch of the nerve-fibre just before actually meeting a muscle-fibre loses the myelin sheath and presents a marked constriction or node.

Here I must briefly digress, in reference to this node. It is now some years since the point engaged my attention[1]. In the varieties of nerve-endings that I have studied generally and specially I have found each nerve-fibre prior to the terminal expansion exhibit a remarkable node. I can affirm that this is a fact universal in the modes of ending of nerve-fibres at present known (motor-plates, Golgi organs, Golgi-Mazzoni organs, Pacinian corpuscles, Meissner organs, the organs described by myself in the deep cutaneous connective tissue, the neuromuscular spindles, &c.). It is at this node that the nerve-fibre loses its myelin sheath, becomes "pale," and as a "pale" fibre proceeds to form the nerve-ending proper. This ultimate node in my judgment requires a special name since it makes the boundary between the terminal and preterminal portion of the nerve-fibre, and because at it the nerve-fibre lays aside the myelin sheath. I therefore call it the *preterminal* node. The morphological characters of this constriction will be described later.

After losing its myelin sheath at the preterminal node the nerve-fibre applies itself to one of the muscle-fibres of the Weissmann-bundle and ends on it. Beyond the preterminal node this pale nerve-fibre is quite small and round, but after a short further course becomes flat and broad so as to present perfectly the form of a riband. This riband wraps right round the muscular fibre. The muscle-fibre can be clasped in either of two ways. Most often the clasp is just like that of a tendril and is spiral; the turns lie very close together at the middle of the nerve-ending, and gradually open more and more apart in a direction away from the middle to finish in a free end, which often is enlarged at one of the two extremities of the nerve-ending. Less frequently the pale fibre runs along the outer surface of the muscular fibre forming a delicate band, which however remains equal neither in thickness nor width but is narrow and broader from point to point

[1] Ruffini. *Monit. Zool. Ital.* VII. 5.

along its course. From one of the margins of this band but not at equal intervals start riband-like fibres like that which composes the spiral form of ending. These fibres run right round the muscle-fibre transversely and finish by meeting again at the opposite end of the band-fibre from which they spring. (Fig. 5 *a*.)

It is clear that the difference between these two modes of ending of the pale fibre consists in the former presenting a perfect spiral without appreciable morphological modification of the amyelinate fibre itself, which in its whole length preserves unaltered its flat wide riband shape. In the latter mode of ending there are a succession of rings, continuity between which is effected by a longitudinal band that unlike the rings and spiral is but rarely of perfect riband form.

But there exist forms intermediate between these two endings and the two forms themselves can occasionally be found on the same fibre. I judged it well therefore to speak of the two together under the single term—annulo-spiral ending. Bearing in mind the riband shape of the fibre it seems better still to speak of the annulo-spiral riband ending. As many muscle-fibres as lie in the spindle at the region of this ending are supplied with annulo-spiral ribands. Hence this ending catches the eye owing to its great depth of tint and is recognised at a glance even under low magnification.

Not every *primary ending* is so elegantly regular as the above description states. In some the pure spiral or ring form occurs only here or there, the greater part showing *S* or *C* forms intercalated among forked, hooked or comma-shapes. In these the width of the naked nerve-fibre is hardly ever so great as in the characteristic riband. Hence the less regular primary endings appear less tinted and less voluminous than the ordinary regular type. That in these organs the primary endings are not all of exactly identical form need not occasion surprise, for a corresponding degree of variety is met in all other species of nerve-ending. It is difficult to find two individual end-organs of the same species perfectly alike in detail of nerve-ending. It obviously therefore behoves the observer to note the limits of morphological variation of each kind of organ.

At the extremities of each primary ending, that is following it toward the poles of the spindle, are generally to be found the extremities of the naked axis cylinder; I say "generally" because in the middle of the "ending" can also be seen here and there a free ending branch of the nerve-fibril. At the extremities of the primary ending the spiral gives place to short fibres set in various directions and possessing expanded ends. The annulate endings spread similarly. At the extremities therefore of a primary ending a larger or smaller number of rounded clavate or leaf-like figures constantly occur. It is not however strictly correct to say as stated in my first paper and afterwards by Kerschner that part of the primary ending is a "flowered-ending." Later and more diligent search has shown me that the "flowered-ending" is a distinct and separate ending, occurring near but independent altogether from the primary ending. The flowered-ending will be described below. Neuromuscular spindles of the 7—12 days' kitten show primary terminations beautifully. The amyelinate fibres have not then however acquired the flatness and width, although their arrangement and course is similar to the adult form.

Kühne (1863) noted the remarkable breadth of the nerve-fibre entering the spindle. But among the nerve-fibres of the spindles only those which form the primary ending strike the observer as of largest size. These exceed in size the nerve-fibres of the Golgi tendon-organ (Fig. 1). Usually a single nerve-fibre gives the primary termination; but it is not rare to find instances in which that is formed by two fibres which can be followed back as independent fibres into a neighbouring nerve-trunk. When a spindle lies far removed from the nerve-trunk its nerve-fibres are quite long and join the spindle always at its proximal end and run parallel with it close upon it. On reaching the place of termination the nerve-fibres without change of direction pierce the capsule and end as above described.

When on the other hand the spindle is situate close to the nerve-trunk the nerve-fibre of its primary termination is quite short, and passes from the nerve-trunk toward the spindle diagonally to the latter's long axis, and almost always in a direction from the proximal toward the distal end of the spindle. Arrived at the region of the terminal expansion the fibre bends abruptly toward the spindle and joins it in a direction more or less at right angles to the long axis of the organ. Two fibres can contribute to form the termination, one entering one side of the spindle, the other the other. These fibres are invested with a thick sheath of Henle, which as has been already noticed by Kühne is continuous with the capsule of the spindle. Sherrington mentions an example in which one of these fibres measured 35μ from edge to edge of the sheath of Henle.

When these nerve-fibres pierce the spindle at right angles to its axis it is easy to see how the sheath of Henle when the nerve-fibre bends to meet the spindle begins to gradually widen like the mouth of a trumpet or funnel, to terminate insensibly by expanding over and fusing with the capsule of the spindle (Fig. 1). Here I may cite an old opinion of mine and a recent fact. In regard to the capsule of the terminal nerve-organs described by me in 1891 (a description unavoidably delayed in publication until 1893) I submitted on defensible anatomical grounds that the investing capsule was supplied by the Henle sheath of the nerve-fibres distributed to the organs. The self-same view I would also submit in regard to the capsule of the Golgi tendon-organ, so admirably demonstrated by A. Cattaneo, and in regard to all other capsulate end-organs, including the Pacinian corpuscles. Now I said above that the capsule of the neuromuscular spindle begins to be clearly manifest where the nerve-fibres meet the spindle. From this fact in view of the analogy between the manner of behaviour of the Henle sheath in the organ I described, in the tendon-organs, and in the spindles I cannot avoid the impression that the relation of the Henle sheath to the capsule is similar in all. I do not suggest that the nerve-fibre which provides the primary ending is the only one the Henle sheath of which forms the capsule; the sheaths of all the numerous nerve-fibres which go to the spindle may show the same relation to the capsule (hence perhaps the greater number of capsular lamellæ in the spindle than in the other two organs), but that has not as yet been actually demonstrated for the nerve-fibres other than of the primary ending.

The secondary ending. Beside the primary there exists in the spindle of the cat another ending distinct in morphological character and in the individuality of its nerve-fibres (Fig. 1). This has not been previously noticed, nor did I myself become thoroughly acquainted with the secondary ending until pursuing the present sustained research. The nerve-fibres of the secondary ending are never so large as those of the primary. They always enter the spindle at some distance from the entrance of the primary fibre. Hence the fibres for the two endings, although they may take a parallel course, hardly ever lie in the same nerve-branch. Sometimes the fibres of the two endings arise from altogether different nerve-trunks. The fibres for the secondary ending have a less thick Henle sheath, but the sheath behaves as does that of the primary nerve-fibre. The nerve-fibres usually divide into secondary branches only after having penetrated the spindle, and the secondary branches are never numerous.

It is noteworthy that together with these fibres for the secondary ending there often run one or two extremely minute myelinate fibres which enter the spindle but are in fact independent of the distribution of the nerve-fibres of the secondary ending.

The secondary ending is very different from the primary ending. Beyond the preterminal node the secondary branches quickly break up into a large number of varicose axis-cylinders, joined together by extremely delicate and short filaments. These varicose axis-cylinders are of diverse form, round, forked, triangular, leaflike, etc. and often resemble in arrangement a spray of flowers. In observing them I am often reminded of those organs first described by Golgi in muscular aponeuroses, and discovered by myself to be also in the subcutaneous tissue of the human finger pulp and called by me, Golgi-Mazzoni organs. As with the primary endings so here, the naked nerve-fibrils of the secondary ending are applied around and upon the muscle-fibres of the Weissmann-bundle but are hardly ever so heaped together as those of the primary ending. Just as somewhat aberrant forms occur among the primary endings so among the secondary are some which possess a typical feature recalling the less common *S* and *C* claspers of primary endings. One can say that exceptional forms of primary endings approach somewhat the secondary ending type, while exceptional forms of secondary ending distantly recall here and there the type of the primary ending. A practised eye never however has the slightest difficulty in distinguishing between the two forms, even when they are atypical.

The secondary ending lies almost always hard by the primary. That is why in my first communication I erroneously looked on this secondary ending as a side appendage of the primary. I had not then seen that it is another ending altogether distinct. I did however give morphological details concerning it, and called it the "flower-spray ending" (or "flowered ending"), a name which I propose to keep. This "flowered ending" is like the annulo-spiral well seen in the muscles of the week-old kitten.

The plate-ending. Kerschner in 1888 noted this kind of ending and called it the motor apparatus, but nowhere has he ever given of it either description or figure. It was only after publication of my first Note that it became clear that Kerschner alluded to the kind of ending figured in Fig. 3 *a* of my Note. Besides an objective description of this ending I must give a comparison between it and ordinary motor end-plates, not that from such a comparison a physiological function can be proved, but that from it a certain inference regarding function may be defensibly proposed.

The size of these plate-endings is most variable. Some are met with very much smaller than motor end-plates (Pl. III. a—γ), some about equal to them, and some very much larger than they; these last, the large ones, are the most common (cf. Pl. III.). From my own observations they appear to me unfurnished with granular supporting substance and with the Doyère eminence. The nerve-fibre which makes a plate-ending after it has laid aside its myelin sheath at the preterminal node breaks up into a few short, extremely delicate branched endings. These quickly begin to form what may be called coronets, by means of rounded varicose nerve-fibrils and very minute hooks set side by side. These coronets, which combine in various ways in the "plate," terminate by free ends which are obviously enlarged into bosses at the outer edge of the plate. By this arrangement arise a number of most delicate and elegant knobbed arborescences altogether different from the other two kinds of endings seen in the neuromuscular spindles. Rarely it can be seen that a pale fibre instead of an arborescence makes rather a web, in which however are constantly to be seen alternate widenings and narrowings of the naked nerve-fibre (Pl. III. a—κ).

If we compare now the structure of this nerve-ending with that of motor end-plates we see at once the great difference between them. The motor end-plates, usually smaller, vary very little in size. They are generally rounded, furnished with granular supporting material and with the Doyère eminence. The nerve-fibre after the preterminal node breaks up it is true into slender twigs, but these in forming the nervous-expansion never give the appearance of the coronet or the net but are short and thick, presenting here and there some irregular varicosities. The outer branches, often curved, give many or few side twigs that not unfrequently join one another, thus forming a network of extremely close mesh. The naked nerve-fibres of the motor plates also terminate with free but slightly widened ends (Pl. III. a—f).

The nerve-fibres going to furnish the plate endings are the smallest nerve-fibres as a rule of all those going to the spindle. They have a very closely fitting sheath of Henle and are really independent of the fibres which provide the other nerve-endings of the spindle. They do not always take a direct path to the spindle, especially when the latter lies far from the nerve-trunk. They then wind in various directions and run long distances before penetrating the spindle. These fibres can enter into the spindle either with the fibres of the primary endings, or with those of the secondary ending, or separately at a distance from either. In every case after having entered they also run constantly through a longer or shorter stage of winding and twisting before furnishing the terminal expansion. This is characteristic, as is also another fact that demands attention here. However exhaustively I have examined my preparations I have never once seen these fibres either before or after their entering the spindle divide into secondary branches. Each ending has a nerve-fibre to itself, which can be traced right back into the nerve-trunk from which it proceeds (Pl. II. Fig. 1, *pl. e.*).

Both the morphological characters of the nerve-fibres of these endings and their mode of behaviour differ therefore from those of motor end-plates.

In the spindles of a week-old kitten these endings can be seen perfectly clearly. They do not however then possess all the characters of the fully-formed endings of the adult cat, and in that respect they resemble the other forms of ending in the spindle.

This brings me to the end of the analysis I have made to the best of my power of all the kinds of nerve-endings contained in the neuro-muscular spindles. There remains the disposition of these endings within the spindles. The classification I gave above distinguished three types of spindle: 1st type, spindles with complex nerve-ending: 2nd type, spindles with intermediate nerve-ending: 3rd type, spindles with simple nerve-ending. It remains to be shown in what the difference between the three types consists.

I. *Neuromuscular spindles with complex nerve-ending.* In these, all three of the above-described forms of nerve-ending co-exist, and for that reason these are the spindles richest in nerve-fibres (Pl. II. Fig. 1). Apart from the organs of special sense (eye, ear, etc.) the body possesses no terminal organ that can compare with these in richness of nerve-fibres and of nerve-endings. These do not however occupy the whole length of the Weissmann-bundle, nor are they ever much separated one from the other except for the plate-endings. The last, as said above, lie often far removed from the situation of the primary and secondary endings. Of primary endings usually only one can be found in each spindle. Rarely there are two, and then these lie widely apart. The Weissmann-bundle in the region of this ending is often slightly fusiform. Of the flower-spray endings there are constantly a pair. These bear three different relations in respect to the primary ending: (α) one flowered ending lies on the proximal, another on the distal side of the primary ending, so that the primary is between them; (β) both flowered endings lie on the proximal side of the primary ending; (γ) both flowered endings lie on the distal side of the primary ending. Whichever disposition occurs the closeness with which the primary and secondary endings keep together is curiously clear. The relation between them appears to me always contiguity not continuity.

It is not possible to indicate with precision what piece of the Weissmann-bundle the three endings commonly, so to say, frequent—in other words the position of their usual habitat along the length of the bundle. I imagine they tend to lie rather more toward the distal than the proximal end of the bundle. But I believe that in all probability the tract of the Weissmann-bundle in which these nerve-endings are found corresponds with that part of it which Sherrington calls the *equatorial region.* This region differs from the distal and proximal in some characters which it is well to state here. "The surface zone," writes Sherrington, "soon gets thickly encrusted with or almost completely occupied by a sheet of nuclei." "The nuclei are spherical or slightly oval, are clear, and measure about 6μ diameter. Cross-sections reveal beneath the nuclear sheet a thin tubular layer which is fibrillated. This tubular layer invests a central core of hyaline substance which runs rod-like along the axis of the intrafusal fibre in this region. The striation is obscured by the nuclei clothing the face of the attenuated fibre, but where seen in the adjoining regions the striation is very marked and coarser than in the ordinary muscle-fibres outside the spindle." I think there is little doubt that the layer of nuclei seen by Sherrington is a nucleated layer of material at the base of the nerve-ending; a character common to many other forms of nerve-ending. For this reason I propose to call this region *the terminal* or *equatorial region.*

The plate-endings are found placed as frequently at the proximal extremity (or proximal polar region of Sherrington) as in the distal (or distal polar region of that author). Their number varies. As many as ten or more can be found in each of those regions. Much scattered in position these plate-endings are sometimes far distant from the region of the other endings, and especially in the proximal polar region. In the distal polar region they may lie anywhere in the bundle so long as it has not become tendinous. Occasionally a plate-ending lies close to the region of the primary and secondary endings, but never really within that terminal or equatorial region.

II. *Neuromuscular spindles with intermediate nerve-ending.* The terminal (equatorial) region is here more simple than in the preceding.

In it is found but one primary ending and one secondary. The extent of the terminal region is therefore more restricted. The two endings lie in contiguity, the secondary being sometimes proximal, sometimes distal. The plate-endings answer the description given above, but appear less numerous.

III. *Neuromuscular spindles with simple nerve-ending.* In the terminal region of these but one nerve-ending exists, namely the primary ending. The terminal region is therefore even more restricted than in the immediately preceding type. The primary ending corresponds usually with that already stated to be only exceptionally found (Fig. 3). The plate-endings are as in the preceding types but much fewer in number.

Two facts appear clear from the above: (1) of the three kinds of nerve-endings the primary ending and the plate-ending are met with constantly in every type of neuromuscular spindle: (2) the secondary ending is the one which varies and may be absent altogether, whence the name I desire for it.

Among the three types of spindles besides difference in quantity and quality of nerve-endings there appears to me to exist also a difference in length and number of muscle-fibres in the Weissmann-bundle. In the third type of spindle these muscle-fibres are short and few. The three types of spindle are not all equally numerous in the muscles of the cat. Most frequent are those of the first type, least frequent those of the second.

Physiological Considerations.

The histological and experimental facts we now possess about the neuromuscular spindles permit no longer in my opinion of any doubt that they are sensorial. This was suspected by Kerschner in 1888, rendered more than probable by the results of my histological analysis in 1892, and finally indisputably proved by Sherrington's experiments in 1894. Of the two formerly established opinions one regarded the spindles as embryonic centres for the development of new muscle-fibres, the other as pathological products. These views we should now regard as of merely historical interest. Sherrington besides furnishing us with some valuable observations on the structure of the spindles has shown by experiment that the myelinate fibres of the spindle take their origin in the cells of the ganglia of the spinal nerve-roots. If to his results are added the new anatomical ones afforded by my observations it is clear we have a true basis for the new conception of the physiological meaning of the neuromuscular spindle. Granted, however, that the spindles are sense-organs what form or quality of sensation do they subserve? Sherrington relying on his experimental work maintains that they are especially adapted for stimuli of mechanical kind. I can neither oppose nor lend support to this opinion; to do so would be to go beyond the field of anatomical analysis where prudence bids me remain.

Before concluding this account I have still to answer a question which Sherrington put before himself and to which he admits he could not give a satisfactory reply. Is the Weissmann-bundle like the rest of the muscle directly connected with the motor nerve-fibres? In other words, are there motor nerve-endings in the Weissmann-bundle? That the motor nerve-fibres of the surrounding muscular tissue do not pass to and furnish motor end-plates to the bundle of Weissmann I can affirm in the most definite way without fear of controversion. Extremely often it happens that one can see muscular fibres round about the neuromuscular spindle which possess more or less abundant terminal arborisations of motor end-plates, but never have I observed a single fibre pass from a motor nerve-bundle to go and end in a Weissmann-bundle.

But that does not exclude the possibility that there may exist motor terminations proceeding from efferent fibres of isolated course, all the more as we saw there is that kind of nerve-ending which we called the "plate-ending." Can we therefore attribute to that kind of ending a motor function for the striped muscle-fibres of the Weissmann-bundle? I have too many doubts to answer that question in the affirmative. I have already shown the difference that separates the motor end-plates from these plate-endings of the spindle. On comparison of the two I have, taking my stand on histological analysis, to deny that these endings have a motor function. The structure of the plates in the spindle, the characters and procedure of their nerve-fibres, the striking quantity of them as compared with the fibres of motor end-plates, certain very significant embryological features (which have reference to the different epoch at which complete development is attained by the two kinds of ending) of which I cannot yet speak with too great confidence, induce me rather to believe in spite of the view taken by Kerschner that the plate-endings in the spindle are also sensorial in nature.

I trust that by persevering in my comparative researches and further in those embryological which I have already commenced I shall be able so much the sooner to say a final word also on this question.

PLATE II.

Fig. 1. Semi-schematic figure of a neuromuscular spindle of the first type, namely, with complex nerve-ending; adult cat.

c, capsule.

m.n.b., (motor nerve-bundle) nerve-bundle which goes to end exclusively in the motor end-plate in the muscle-fibres round about the neuromuscular spindle.

b. W., bundle of Weissmann.

pl.e., plate-ending.

n.tr., nerve-trunk.

pr.e., primary ending.

s.e., secondary ending.

Fig. 2. Primary ending of a neuromuscular spindle of the first type; Camera lucida, Koristka ocul. 4, objective 8* × 620.

Fig. 3. Primary ending in a neuromuscular spindle of the third type; adult cat. Drawn as above.

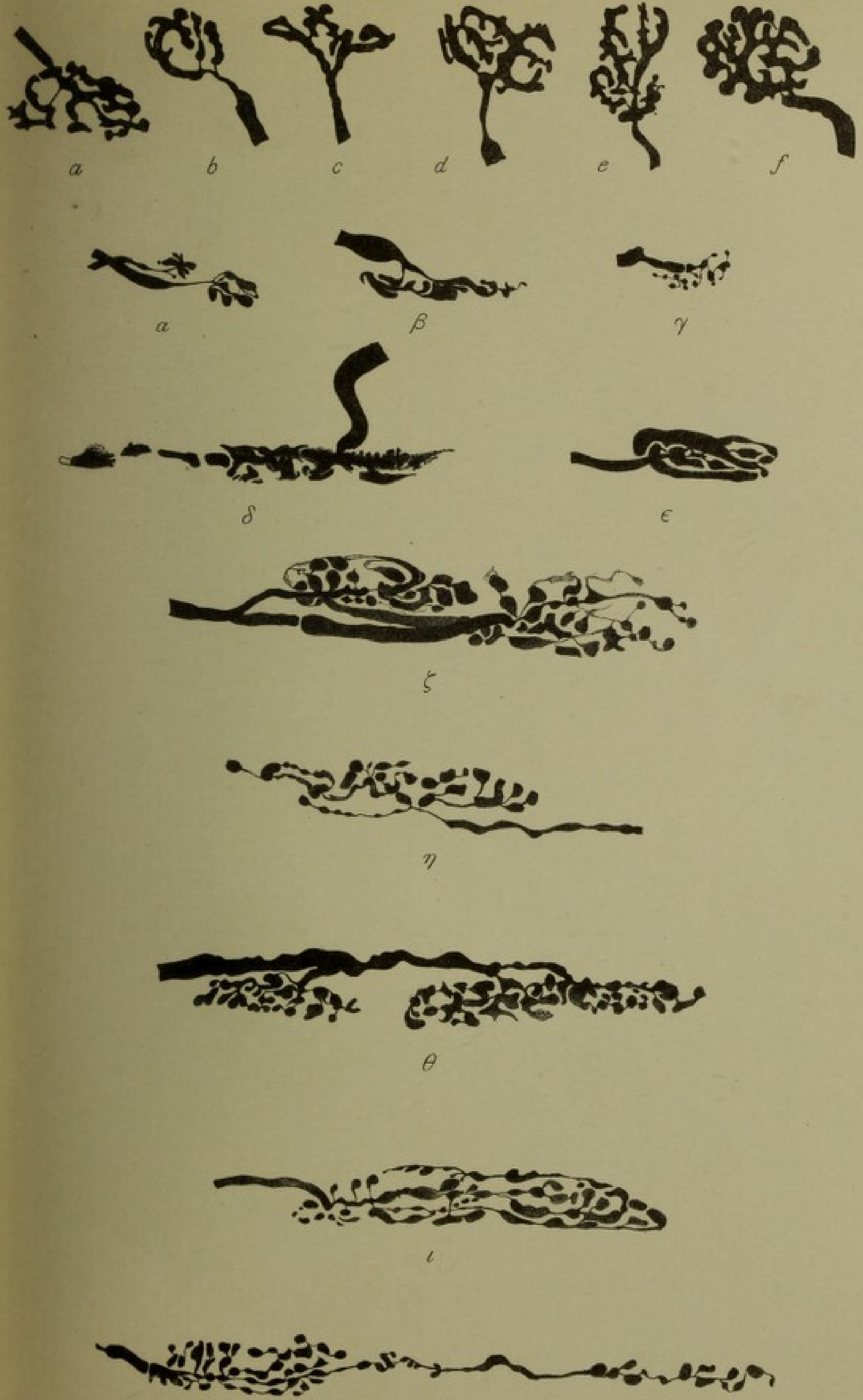
Fig. 4. Secondary ending in a neuromuscular spindle of the first type; adult cat. Drawn as above.

Fig. 5. (*a*, *b*) Short lengths of muscle-fibres from the Weissmann bundle, drawn in detached portions from a primary ending in a spindle of the first type, in order to show the ending-form of rings taking origin from the longitudinal band: this in *b* takes the exceptional appearance of a broad flat riband; adult cat. Drawn as above.

PLATE III.

Fig. *a*—*f*. Various forms of ordinary motor plates from the adult cat. These "plates" are figured from specimens taken from the same cat which furnished the preparations of the spindles represented in the preceding figures. Drawn as above.

Fig. α—κ. Various types of "plate-endings" from those smaller (α, β, γ) to those larger than the common motor end-plates. These endings also have been drawn from preparations obtained from the same cat as that from which the motor end-plates *a*—*f* were taken. The preparations for both were obtained with the very same chloride of gold reaction.



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