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REVIEW OF
"LOCALISATION MOTRICE ET KINESTHÉSIQUE"

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LOCALISATION MOTRICE ET KINESTHÉSIQUE (Les noyaux masticateur et
mésencéphalique du trijumeau chez le lapin). Par Edouard Willems,
Assistant à l'Institut d'Anatomie de l'Université libre de Bruxelles
(Institut Warocqué). Extrait de la Revue "Le Névraxe," Vol.
XII, 1911, pp. 9-224.

In this study Willems is concerned with the structure and functions
of the nucleus radialis descendens (noyau mésencéphalique) and the nu-
cleus motorius (noyau masticateur) of the nervus trigeminus, as these
appear in the rabbit. By way of introduction he gives an excellent out-
line of the literature touching these nuclei. His findings are briefly as
follows:

The nucleus radialis descendens of one side contains 1,578 vesicular
cells (p. 108) arranged in a column lying at the junction of the dorsal and
ventral plates (fig. 4, p. 40). This column extends caudad from the level
of the thalamus in the fetus—or the caudal edge of the colliculi superiores
in the adult—to the level of the nucleus motorius. In their general ap-
pearance these cell bodies are similar to those in the spinal ganglia.

The nucleus motorius is composed of an oval mass of 2,942 cells—
2,642 large and 300 small (p. 108)—which have the typical characters of
efferent neurones of the first order. This nucleus is situated in meten-
cephalon at the level of the emergence of the portio minor of the nervus
trigeminus. The total number of cell bodies in both nuclei (of one side)
is therefore 4,520.

The portio minor of the nervus trigeminus contains 4,859 medullated
fibers (the average of four determinations on fully grown animals).
This total may be further analyzed into 3,014 fibers of large diameter and
1,845 of small diameter (Table IV, page 147).

From the relation between the number of cells in the two nuclei com-
bined (= 4,520) and the number of medullated fibers (= 4,859) in the
portio minor, Willems concludes that all the fibers from both nuclei unite
in this division of the nervus trigeminus, there being no other source from
which these fibers could come. He has observed further the splitting
(i. e., division into two or more) of the fibers arising from the cells of
the nucleus radialis descendens before these enter the portio minor and
this phenomenon, so far as it goes, would help to explain the excess in
the number of fibers observed.

It is further possible that the number of small cells credited to the
nucleus motorius has been underestimated—which would also help to
reduce the disparity in the two enumerations—although as the numbers
show, this disparity amounts to an excess of only 339 fibers, or about 7
per cent. of the total number of cells.

The portio minor of the nervus trigeminus supplies in the rabbit nine
trigeminal muscles (p. 24).

The masseter, pterygoideus internus, sphenoidalis (distinguished and
described for the rabbit by the author) pterygoideus externus, digastricus

(anterior belly), temporalis, mylo-hyoideus, tensor palati and tensor tympani.

All the muscles in the domain of the nervus trigeminus are in the last analysis derived from the adductor or elevator of the mandibular arch of fishes (p. 31).

Excepting the digastric muscle—which receives about 200 fibers from the trigemino-facial plexus (p. 172)—all the muscles named above receive their entire innervation from the portio minor.

The evidence for this statement is based on the distribution of the portio minor as shown by dissection and on the chromolysis in the two nuclei following excision of the muscles or extraction of the nerves supplying them.

In the nucleus motorius a study of those cell groups which undergo chromolytic changes after operation makes possible a very complete reconstruction of the entire nucleus. Its different portions can thus be assigned to given muscles.

On the other hand, for causes not yet known, the chromolytic reaction can be obtained simultaneously in only about one half the cells which constitute the nucleus radialis descendens (i. e., in 815 out of 1,578 cells). Moreover, the cells which do react are not characteristically grouped for the several muscles.

Why the "axone reaction" does not appear in all of the cells of this nucleus is not at the moment clear. Nevertheless it is important to note that it does appear very evidently in more than half of the cells constituting the nucleus. It is therefore proper to emphasize the fact that there is conclusive evidence that fibers from *both* nuclei are distributed to several of the muscles, notably the masseter, sphenoidal, temporal and tensor tympani, while on the other hand there is some evidence—though less satisfactory—that the innervation of the remaining five muscles is also from *both* nuclei. It follows that certainly the four muscles above named—and probably all nine—receive a double nerve supply.

Willems is of the opinion that the fibers in the portio minor of one side are all from homolateral cells.

The central connections of the two nuclei are not of the same type. The cells of the nucleus motorius have characteristic motor connections, while those forming the nucleus radialis descendens do not have motor connections, but on the contrary are largely associated with secondary sensory pathways. The distinction is sharp.

The histological differences between the two nuclei are also notable. In the nucleus radialis descendens the vesicular cells—consisting of a large and a small form—give rise to but few minor dendrites. One main dendrite, however, leaves the cell to pass in the direction of the bundle of fibers coming from the nucleus motorius.

These outgrowths sometimes split and generally exhibit a rapid decrease in diameter as they pass away from the cell body—the so-called "conical diminution."

Moreover, these outgrowths arise without any initial constriction such as is characteristic of the axone, but, on the other hand, always give rise to one or more small branches which do have the initial constriction and general appearance of axones. Many of these latter pass to the cells of the nucleus motorius and there terminate about them.

In contrast to this arrangement, the cells of the nucleus motorius have typical dendrites and axis cylinder processes, which latter form a well-defined root bundle that passes out in the portio minor.

Aside from the axones, coming from the nucleus radialis descendens, there end around the cell bodies and dendrites of the neurones forming the nucleus motorius a mass of terminals derived from a number of other sources.

Many of the foregoing observations evidently suggest that the nucleus radialis descendens is sensory in function.

If that were the case, then we might expect that its fibers in the portio minor and to the several muscles would be present in about the same proportion as the sensory fibers in the muscular nerves of other mammals.

If the number of fibers from each nucleus corresponds with the number of cells in each, then about 35 per cent. of the fibers would come from the nucleus radialis descendens. This is just above the lower limit for the number of sensory fibers in the muscular nerves (cat) as given by Sherrington ('94-'95) (p. 138).

On the other hand, the axone reaction shows that the masseter, sphenoidal and temporal muscles are connected with 1,199 cells in the nucleus motorius and 800 cells in the nucleus radialis descendens. Thus the latter are about 40 per cent. of the total number. Therefore about 40 per cent. of the fibers in these cases might be regarded as coming from the nucleus radialis descendens.

It appears then that there is nothing in the numerical relations of the fibers from the two nuclei which opposes the idea that those from the nucleus radialis descendens are sensory in function.

From his findings, of which the foregoing is but a bare outline, Willems makes the following argument:

1. With the partial exception of the digastric, above noted, the muscles in the domain of the nervus trigeminus receive all their fibers from the nucleus radialis descendens and the nucleus motorius.

2. There is no instance known where the motor fibers going to a muscle arise from two separate nuclei diverse in structure and connections.

3. These two nuclei are plainly diverse in structure and connections.

4. The nucleus motorius is admittedly motor in function. The function of the nucleus radialis descendens has heretofore been in doubt. Willems concludes that it is sensory, mediating muscular sensibility.

In more detail the reasons for this conclusion are the following:

The cells of the nucleus radialis descendens are histologically similar to spinal ganglion cells. The axones, arising from the main outgrowth (dendrite), which forms the peripheral fiber, pass in large measure to the cells of the nucleus motorius and end about them.

The main outgrowths enter the portio minor and are distributed with the fibers from the nucleus motorius to the several muscles. Their proportional representation is that of the sensory fibers in a muscular nerve. The central connections of the cells of the nucleus motorius are with motor tracts. The central connections of the cells of the nucleus radialis descendens are mainly with the nucleus motorius, but also with some secondary sensory pathways.

As the sensibility of muscles is mediated by afferent nerves, it seems most probable that the nucleus radialis descendens is a sensory nucleus mediating muscular sensibility. These neurones are then afferent neurones of the first order, homologous with the neurones forming the ganglia of the cerebral or spinal nerves. The group is however unique in mammals in that it forms a nucleus having a single sensory function and also in

that it is permanently included in the wall of the neural tube. These conclusions are well founded and the paper constitutes a contribution of first-class importance to our knowledge of the mammalian nervous system.

For the establishment of these conclusions, quantitative tests have been largely used, and in this connection the author expresses appreciation of the quantitative work on the nervous system which has been published during the last fifteen years by American authors in the *Journal of Comparative Neurology and Psychology*. Since all of the author's applications of the quantitative tests did not bear directly on the main argument, some were not mentioned in the foregoing outline, but before closing this review we wish to comment on several of these, since they are important for our notions of the general architecture of the nervous system.

We shall discuss three points only:

(a) The splitting of fibers in their peripheral course.

(b) The classification of fibers in the portio minor, according to diameter.

(c) The relation between the weight of a muscle and (1) the number or (2) the diameter of the fibers passing to it.

(a) The fact that fibers split or divide in their course has been long known but the large proportion of splitting fibers has been appreciated only recently, and even yet the fact has not received due consideration in the text-books. For example, Dunn ('99, '02) showed that in the nerves to the frog's leg, splitting occurred in 10 per cent. of the fibers going to the thigh and 22 per cent. of those going to the shank. Dunn ('09) further showed in the case of a frog in which the legs were supplied by the sensory fibers alone, that practically the same amount of splitting occurred: namely, 10 per cent. in the thigh and 28 per cent. in the shank. Thus among the fibers going to the leg of the frog, *both the sensory and motor* split in considerable numbers.

From the physiological standpoint, the idea of splitting motor fibers meets no great obstacle, but the splitting of sensory fibers runs counter to the established doctrine of "local signs" in its usual form, and is therefore less readily accepted, although it may be noted that it seems to offer an anatomical basis for at least some cases of "referred pain."

In the study of the portio minor, Willems, dealing with both sensory and motor fibers together, finds that the combined branches of the portio minor contain 5,564 fibers as contrasted with 4,859 fibers in the trunk at the point of emergence. Thus there is an increase of 703 fibers or 14.4 per cent. (Table IV, p. 147) due to splitting.

At the same time he observed within the metencephalon, as previously stated, a splitting of the fibers arising from the cells of the nucleus radialis descendens, thus contributing a new observation on the splitting of sensory fibers.

(b) In examining the cross-section of the portio minor, Willems finds fibers of both large and small diameter, and raises the questions of their grouping and significance.

Touching the grouping, it is desirable to form an opinion as to whether these fibers fall into two groups, the large and the small, or form a graded series from large to small (p. 139).

Boughton ('06) maintained in the case of the purely motor oculomotor nerve (of the rat and cat) the division into two groups, and the data of Sherrington ('94-'95) are susceptible of a like interpretation, although not so interpreted by Sherrington himself.

Willems found in the portio minor of the adult (see Table IV, p. 147, mean of last four records from mature animals) an average of 3,013 large and 1,845 small fibers, the small fibers being therefore 38 per cent. of the total.

On the other hand, he found in the case of the rabbit ten days old, an average of 2,493 large fibers and 773 small—the small fibers thus representing 23 per cent. of the total number. Since in the adult the cells of the nucleus radialis descendens are about 35 per cent. of the sum of the cells in the two nuclei combined, and since the sensory constituent of a mixed nerve is usually credited with the great majority of the small fibers, Willems concludes that the small fibers form a recognizable group—that they come mainly from the nucleus radialis descendens, and that their small diameter is additional proof of their sensory function. The relative number of small fibers appears to increase after birth, because, according to Willems, medullation takes place in them as a class at a later date than in the motor fibers. This argument is not convincing.

Boughton's observations were made on a purely motor nerve—the oculomotor—the sections being taken only shortly distad of the point of emergence. In this nerve there is a tendency for the fibers to appear in two groups—distinguished by their average diameters.

During post-natal growth the relative number of the small fibers increases, but these small fibers never become large fibers. Thus all of the characters which Willems uses to distinguish the sensory from the motor fibers in the portio minor occur in a nerve containing motor fibers only. In this connection Willems criticises, as without foundation, Boughton's statement that the small fibers (in the oculomotor) are those which "come in after the period of most rapid growth." The criticism is too severe. Probably many of the small fibers are present as unmyelinated axones from an early period, but that some of the axones do grow in later is rendered probable from such observations as those of Ranson ('04) on the fibers which grow across the site of a lesion in the corpus callosum of the albino rat.

To sum up this matter it does not appear probable that Willems' general interpretation of diameter in relation to function in the case of the portio minor is correct, and it is also evident that the observations of Boughton cannot be used to support his conclusion.

(c) (1) Willems finds in general that the number of fibers per unit of muscle weight tends to increase as the muscle becomes lighter (= smaller). For the first seven muscles this increase is moderate, i. e., from 3.8 fibers per centigram of muscle in the heaviest muscle—the masseter—and 2.8 for the next heaviest—the pterygoideus internus—it increases regularly to 9 fibers in the mylohyoid, while in the case of the two remaining muscles, the tensor palati has 23 and the tensor tympani 333 fibers per unit of weight. This determination is unique, so that there are no observations with which it can be fairly compared.

Donaldson ('03) showed that the number of motor fibers passing to the muscles of the thigh and of the shank of the frog's leg are distributed to these divisions of the leg in proportion to the weight of the muscles. But as to the number of fibers to the individual muscles of known weight, we have as yet no data and hence the relations in this case do not bear on those found by Willems.

(c) (2) Touching the last point, on the relation between the diameter of the myelinated fibers and the muscles which they supply, the existing observations are as follows:

Schwalbe ('81) from a study of the diameters of the nerve fibers to the arm and leg of the frog, concluded that the fibers of largest diameter had the longest course. This says nothing, however, concerning the diameter of fibers and the weight of the muscles which they supply, except by implication.

Dunn ('99, '02), working on the frog, determined that among the fibers entering the frog's leg, those of largest diameter ended in the thigh, and among the remainder, those of largest diameter in turn ended in the shank. This showed that Schwalbe's inference was incorrect that as a matter of fact the larger fibers ran the shorter course, but again did not establish, except by implication, the relation of the diameter of the fibers to the individual muscles.

Herrick ('02), however, did associate the diameter of the nerve fibers with the degree of development of the end organs, concluding that the more functionally active end organs received the fibers of greater diameter.

Willems finds that the distribution of the fibers of different diameter to the muscles innervated by the *portio minor* does not fit with any of the preceding views, expressed or implied. With the observation of Donaldson ('03) which apply to segments of the leg, no direct comparison is really possible, nor can Herrick's criterion be applied, so that the failure of Willems's observations to fit with those just cited has no bearing on the correctness of the latter, but indicates merely the need of further work in order to make such comparisons possible.

Willems's data do not show anything regular in the distribution of fibers of large diameter, but they do show, with the exception of the tensor tympani, that in the remaining muscles the proportion of small fibers tends to increase as the weight of the muscles increases, though more slowly.

Willems's results in this field lead him to make some interesting suggestions on the possible relations between the diameter of nerve fibers and the secondary growth of muscles as indicated by the size of the muscle fibers—suggestions well worth further examination.

Two general matters remain to be mentioned. The paper before us unfortunately contains a considerable number of misprints of all kinds, but especially misprints of numbers. Fortunately there is no instance, however, where these misprints seriously modify the argument, yet one consequence is that some of the numbers given in this review are different from those printed in the original paper. A carefully prepared list of corrections, in addition to the "errata" sheet which accompanies the paper, would add greatly to the usefulness of these observations. *Graphique VI* seems to have been omitted (see p. 128).

It is interesting to note that the author feels his labors to have been increased and his results complicated by the fact that he was obliged to use rabbits of various and unknown breeds and of undetermined ages. Failure to get this last datum made it necessary for him ultimately to exclude three out of seven of his series of quantitative and numerical determinations as they had plainly been made on immature individuals.

It is hardly necessary to enlarge on this topic, but since work of the sort here reviewed is bound to be more frequent in the future, it is evident that, as a first step, standard strains of animals of known ages should be generally available for the purpose of such studies.

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