Physiology. — *"On the segmental skin-innervation by the sympathetic nervous system in vertebrates, based on experimental researches about the innervation of the pigment-cells in flat fishes and of the pilo-motor muscles in cats."* By Dr. G. VAN RIJNBERK. (Communicated by Prof. C. WINKLER.)

(Communicated in the meeting of October 26, 1907.)

We possess numerous, though dispersed, data, obtained either by means of experiments on animals or founded on clinical observations, tending all to confirm the opinion, that in vertebrates and in man, the efferent nervefibres, intended for the skin, which are conducted by the grey connecting branches from the lateral column of the N. sympathicus towards the mixed spinal nerves, are distributed within the area of the skin that is supplied with afferent fibres by the spinal nerve. As moreover, in general, save slight deviations, the efferent sympathetic fibres of the grey connecting branches have their origin in the ganglia of the column in which these branches apparently originate, we may assume that the zones of the skin, innervated by the ganglia of the sympathetic column are nearly identical in their distribution with the zones of the skin, supplied by the different corresponding spinal ganglia. Less numerous are the data about the relative extent of the sympathetic and spinal zones of the skin, but indirect indications apparently support the view that the zones of the skin innervated by the spinal ganglia are more extensive than the zones of the different corresponding sympathetic ganglia. With this reservation however we apparently may hold it very probable, that the innervation of the skin both by the sympathetic and by the spinal ganglia is taking place according to the self-same morphological scheme. Hitherto nevertheless no direct proofs have been given by demonstrating on the self-same object the relative distribution and extent of these innervation-areas. It has been my purpose to do this now by means of a few simple experiments.

A. *The sympathetic innervation of the pigment-cells and the spinal innervation for sensibility of the skin in flat fishes.*

Since the elaborate researches of G. POUCHET [1]) we know that in several species of fishes the phenomenon of the variability of colouring

[1]) G. POUCHET. Des changements de coloration sous l'influence des nerfs. — Journal de l'anatomie et de la physiologie. Tome 12 p. 1—90, and p. 113—165, Parijs 1876.

in the skin is directly influenced by the sympathetic nervous system. If in a turbot the connecting branches of some spinal nerves or these nerves themselves, in that upward turned half of the body containing the eyes, are cut through, there appears on the skin a more or less sharply defined dark zone. POUCHET considered this phenomenon to be caused by a paralysis of the pigment-cells in consequence of the section of the nerves, and he called the dark zones appearing after section, "paralytic" zones. He made however no further researches as to the significance of these zones, when considered as innervation-areas of sympathetic ganglia, and since, to my knowledge, nobody has taken up again these yet so extremely interesting researches. I have done so at the present time, and added unto this a comparative investigation about the sensible innervation of the skin.

For objects I got numerous specimens of Solea (impar, vulgaris, monochir) and Rhomboidichthys (mancus seu podas). This latter species in particular, and likewise Solea impar, have furnished me with excellent results, and the more detailed demonstration is principally based on experiments made on these animals. The operative part of these experiments was very simple. By a longitudinal incision, cleaving skin and muscles, and passing along the lateral line of the organ of sense in the ventral portion of the skin of the caudal part of the pigmented half of the body bearing the eyes, the origins of a few haemal vertebral spinous processes were laid bare and the

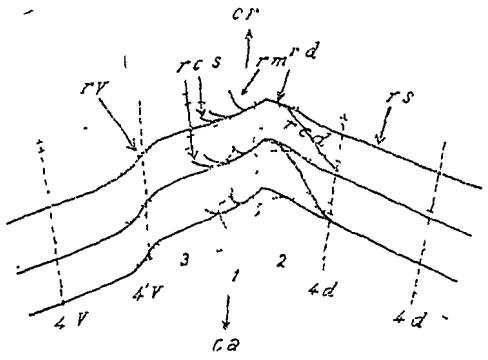

Fig. 1.

Scheme of course and distribution of the main trunks of the spinal nerves in the caudal portion of the Pleuronectidi (taken from a preparation of Rhombus laevis), 1, body of vertebra, 2, neutral spinous process, 3, haemal spinous process, 4'*d*, 4"*d*, 4'*v*, 4"*v*, first and second longitudinal septum of the dorsal and ventral muscles, — *cr*, *ca*, cranial and caudal boundaries of the preparation. — *r.d.*, *r.m.*, *r.v.*, ramus dorsalis, medius and ventralis of the spinal nerves — *r.c.d.*, *r.s.*, ramus communicans and ramus spinosus of the dorsal nerve-trunks. — *r.c s.*, left sympathetic connecting branch.

ventral branches of the spinal nerves were sought. In most cases these were caught up and torn off together with the connecting branches of the N. sympathicus.

In all cases the visible consequence of these operations consisted constantly in the appearance on the skin of a more or less sharply defined dark field, i. e. darker than the surrounding skin. Distribution and extent of these dark fields were dependent on the place in the segmental arrangement of the sectioned nerves and on their number. The shape of these fields was always identical, being that of a band, beginning in the dorsal marginal fin, going somewhat obliquely cranialward to the lateral line of the organ of sense, and thence somewhat obliquely caudalward towards the ventral marginal fin, wherein it terminated. Thus much for the shape and the general distribution of these zones. As regards their extent, the following may be stated. After destroying the connecting branch of one single spinal nerve I never observed any plainly visible change in the colouring of the skin. After destroying the connecting branches of two consecutive nerves, usually a narrow, not very dark zone was observed, that might be not easily defined. Only when three consecutive branches were destroyed, there appeared a plainly visible, sharply defined dark zone.

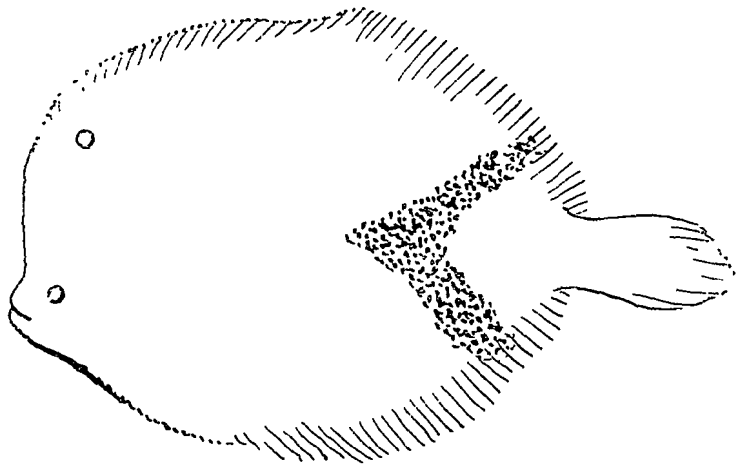

Fig. 2. [1])
Rhomboidichthys mancus, dark zone appearing after cutting through three spinal nerves and the sympathetic connecting branches.

If more than three branches were destroyed, there was found a dark zone, identical as to shape and position, only broader. If after a first section of viz. three branches, still another couple of branches,

[1]) This figure and fig. 3, 4, 6, 7, 8, 9 are reproductions of photographies counterdrawn in outline.

lying next to these first ones either cranially or caudally, were destroyed, the originally observed dark zone was afterwards constantly found uniformly broadened, either the cranial boundary being removed cranialward or the caudal boundary being removed caudalward, according to the case. By these means a series of indications was furnished, tending to prove that the skin-areas supplied with pigmento-motor fibres by each connecting branch or by the ganglia of the sympathetic column, are themselves likewise uninterrupted, zone-shaped fields. Still further data on this subject were obtained in the following manner.

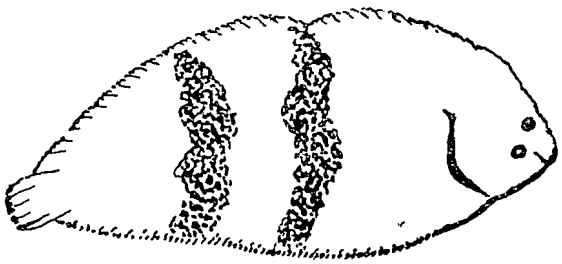

Fig. 3.
Solea impar. Isolation of four spinal nerves between four nerves cut through cranially and four other ones cut through caudally of them.

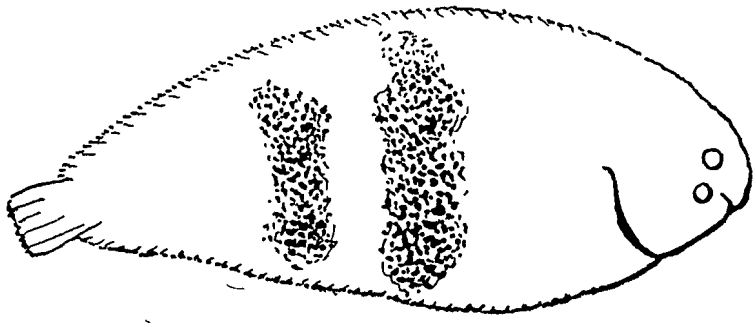

Fig. 4.
Another solea, on which a similar operation had been made.

If a few, viz. four connecting branches were destroyed, and again also four other ones cranially or caudally from these, leaving intact e. g. four branches between the two, two dark zones appeared of about equal breadth, enclosing between them a somewhat broader zone of lighter colouring, corresponding to the uninjured branches. (Fig. 3 and 4). By means of similar experiments the supposition that the ganglia of the sympathetic column innervate zone-shaped skin-areas becomes nearly a certainty. Some results too were obtained as to the extent of these areas. Comparative calculations, as shown before, starting from measurements of the darker and lighter zones, made with as much accuracy as was possible, have shown that the cranial-

caudalward breadth of a skin-area innervated by a ganglion of the sympathetic column, having an average length of 20 cm. may be approximated at 7 mm., and that the areas overlap one another somewhat more than half.

The foregoing having been duly stated, a comparison between the scheme of the spinal and that of the sympathetic innervation of the skin lay very near indeed. Once the ventral (and dorsal) branches of a couple of spinal nerves having been cut through together with the sympathetic connecting branches, it is easy enough to define the extent and the distribution of the insensible zone of the skin resulting from this operation, and to establish a comparison between these and those of the dark zone. In order to facilitate this definition, I augmented the irritability for reflex actions in the animals by intoxicating them with a small quantity of a solution of the sulphuric salt of strychnia in sea-water (1 : 10.000). After this a slight scratching of the skin by means of a pin's point was sufficient to produce a plainly visible general reaction, making it possible to define the boundaries between the sensible and insensible areas with great precision. I found the results of a series of experiments to be nearly invariable, so that I may communicate them here with sufficient certainty.

Generally then the anaesthetic areas and the dark zones, observed after the section of spinal nerves and their corresponding sympathetic connecting branches are found to accord completely as regards their extent, distribution and arrangement. Consequently the pigmento-motor sympathetic fibres, originating in a certain ganglion of the N.sympathicus and its connecting branch, are distributed precisely within that area of the skin that is supplied with sensory fibres by the corresponding spinal ganglion. Both schemes therefore cover one another completely, and the above given particulars about the innervation of the pigment-cells, holds good likewise for the sensory innervation of the skin. Thus the central innervation of the skin in Pleuronectidae is divided into a series of segmental areas, which considered in their functional significance, may be distinguished in sensory and pigmento-motor skin segments, but according completely as regards their distribution and extent.

B. The sympathetic innervation of the pilo-motor muscles and the spinal sensory innervation of the skin in cats.

The well-known researches of LANGLEY (1893) [1]) have shown that

[1]) J. N. LANGLEY. — Preliminary account of the arrangement of the sympathetic nervous system, based chiefly on observations upon pilomotor nerves. Proceedings

the sympathetic nerve-fibres, intended for the pilo-motor muscles of the skin of the trunk in cats, originate in the series of ganglia of the column of the N. sympathicus, that they are conducted along the grey connecting branches towards the relative corresponding spinal nerves, thence following the primary dorsal nerve-trunks and the (dorsal) skin branches of these, to terminate in the pilo-motor muscles of the dorsal portion of the skin. Besides he has demonstrated that by far the greater number of the nerve-fibres, originating in the sympathetic ganglion, the "pilo-motor" nerves as he called them were conducted along the selfsame grey connecting branch towards the one spinal nerve segmentally corresponding with it, and that along the dorsal skin-branch or branches of this nerve, they jointly reach the skin, where they are distributed within one uninterrupted area, that may be sharply defined. He found further more, that these skin-areas, supplied with pilo-motor nerve-fibres by the series of sympathetic ganglia form a regular series, arranged on both sides of the mid-dorsal line of the body. As regards the relation between the innervation of the skin by fibres for the pilo-motor muscles from the sympathetic ganglia, and the innervation by sensory fibres from the spinal ganglia, he confined himself to comparing the arrangement of the pilo-motor skin-areas innervated by the sympathetic ganglia with the results of the researches made by TÜRCK and SHERRINGTON about the spinal innervation in the dog and the monkey. Direct comparisons between the sensory and the pilo-motor innervation of the skin were not made by him. These have been made recently by me.

The way in which to do this was clearly indicated. At present, especially after the anatomical studies of BOLK on man, we may take it for granted, that there does not occur an interchange of nerve-fibres destined for the skin between the spinal nerves in the trunk-area in mammalia. Consequently the serially arranged skin-branches of the dorsal portion of the body represent separately the different spinal and sympathetic nerve-fibres intended for the dorsal portion of the skin of the trunk from the spinal nerves and sympathetic connecting branches in which they originate. In order therefore to obtain a knowledge of the innervation of the dorsal skin-portion relatively by the spinal and by the sympathetic ganglia, it is sufficient to define separately and then to compare the different areas of dis-

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of the R. Society of London, vol. 52, n°. 320, p. 547—556 Februari 1893. London. J. N. LANGLEY. The arrangement of the sympathetic nervous system based chiefly upon pilomotor nerves. Journal of Physiology (Foster) vol. 15 n°. 3 p. 176—244. 1893. Cambridge.

tribution of the pilo-motor and of the sensory fibres having their course in the dorsal nerve-branches of the skin. This may be done in a very simple way.

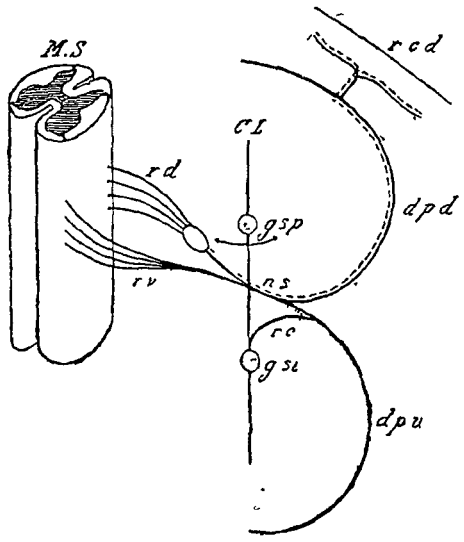

Fig. 5.

Scheme of the course of the (post ganglionic) pilomotor- and of the sensory nerve-fibres toward the skin of the trunk-area in cats.

M S. = medulla spinalis. — *r.d*-*r.v* = dorsal and ventral root. — *N.S.* = mixed spinal nerve. — *d p.d.*-*d p.v.* = dorsal and ventral trunk of the spinal nerve.. — *r.e d.* = dorsal ramus cutaneus. — *C.L.* = lateral column of the N. Sympathicus. — *g.sp.*-*g.sl.* = ganglion spinale, sympathic ganglion. — *r.c.* = grey connecting branch — — — — define the course of the spinal sensible fibres .... that of the pilomotor fibres.

I obtained this scheme by defining first by means of SHERRINGTON's method of isolation the surface of the sensible area innervated by a certain skin-branch and next by the stimulus of an induced current applied to the same branch, causing the surface of the skin-area, innervated by the pilomotor fibres from this branch, to become visible. In order to do so, the hair on the trunk of the cats I made use of, were first cut uniformly by means of a so-called tondeuse to a length of about half a c.M. Afterwards, under narcotics and with aseptic precautions (as far as possible, the skin not being shorn) a longitudinal incision was made in the skin along the mid-dorsal line, and the skin was folded back to both sides. The connective tissue having been prepared the series of dorsal skin-nerves was in most cases pretty plainly distinguishable, and it was very easy to choose a definite branch for isolating and to section the three branches lying next to this one both cranialward and caudalward, either after

having loosened them from the adjacent blood-vessels that mostly follow the same course, or else together with the bloodvessels between a double ligature. The skin was then skitched and the animal was allowed a few days quiet. After this the sensible and the insensible areas to be found in the skin were defined and their boundaries carefully indicated by means of coloured demarcation-lines. Finally the animal was again brought under narcosis, the incision in the skin was reopened and the isolated nerves were laid bare and stimulated. The area-field, on which the hair was rising, was demarcated by another colour.

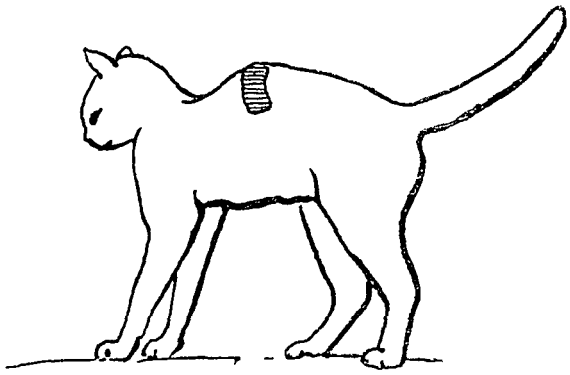

Fig. 6.
Pilomotor area of the 7th thoracal nerve

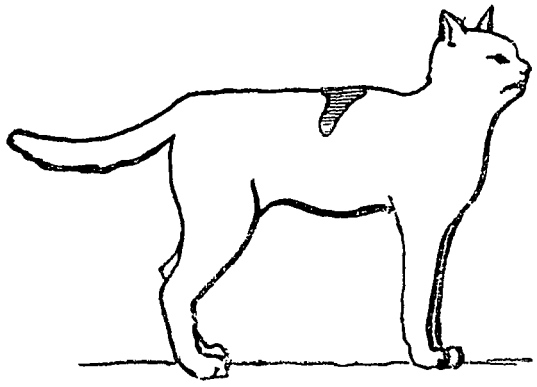

Fig. 7.
Pilomotor area of the 8th thoracal nerve in the same cat.

As regards the pilomoter nerves I can be short, as I have hardly anything to add to the very accurate communications of LANGLEY on this subject. Like him I found in my experiments that the areas in which during the irritation of different skin-branches and on different animals the hair rose, showed rather important

differences, both as to their extent, shape and boundaries and as to the intensity of the phenomenon itself. Usually the field, in which the hair rose, was nearly rectangular, and save for a slight deviation caudal-ward, it was lying vertically on the mid-dorsal line. In the most successful experiments the pilo-motor areas extended nearly unto the dorsal axilla-inguinal line over a dorso-ventral surface of almost 60 m.M. The cranio-caudal breadth amounted on the average to 26 m.M. For an instance of the proportions of the pilomotor areas in an exceptionally favourable case I refer to the photographs represented in fig. 6 and 7.

The isolated sensible areas usually presented a shape not greatly different from that of the pilomotor areas described above. Like these they were generally nearly rectangular, lying almost vertically on the mid-dorsal line, and they showed likewise a slight deviation caudal-ward, perhaps even somewhat more marked. Cranially and caudally they were bounded by the insensible areas; ventrally they passed without any distinct boundaries into the lateral part of the body, where sensibility was retained wholly intact. The cranio-caudal breadth of the sensible areas was on the average 30 m.M., their dorso-ventral extent of course was not to be defined; that of the insensible areas was on the average 60 m.M.

We may now pass on to a comparison between the sensible and the pilomotor skin-areas. On account of what I remarked before about the variability both as to shape and extent of these latter ones, it may be inferred already that the results of this comparison presented likewise great differences. On one important point however the results of all my experiments are in accord: the pilomotor skin-area was always to be found within the sensible area of the isolated nerve-branch. In this respect the principal problem I had put before me in all my experiments, may be considered to have been solved, at least for that portion of the skin of the trunk on which I made my experiments. As regards further the relative extent of the sensible and of the pilomotor skin-areas, and the exact situation of the latter within the former, I found, as remarked before, great differences. Sometimes the pilomotor field area had an extent nearly equal to that of the sensible field, both fields being consequently almost identical. In the majority of cases however the pilomotor skin-area was less extensive in all directions than the sensible area. The place, occupied by the pilomotor field within the sensible field differed greatly in different cases. Generally it was lying almost in the midst of it, as is shown in the cats, photographies of which are represented in fig. 8 and 9.

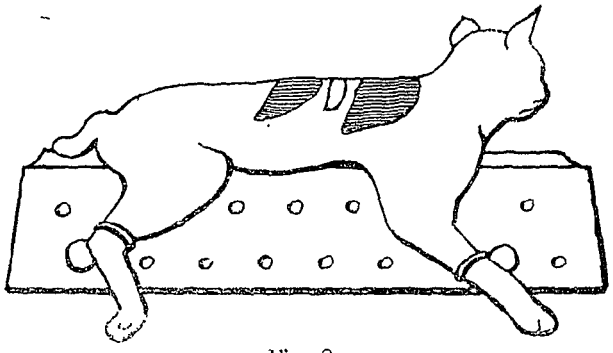

Fig. 8.
Situation of the pilomotor skin-area (white) within the sensible area nearly isolated by insensible areas (hatched transversally).

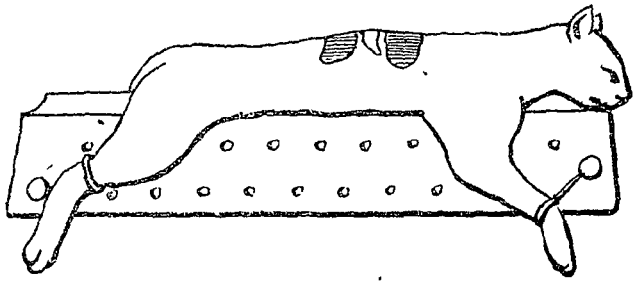

Fig. 9.
The same in another cat.

In another case however it lay nearer to the cranial or caudal boundary of the sensible area, I have not been able to state a definite rule in this respect.

Returning now to the principal problem aimed at by my researches, we find that from the above statements it has become evident that the pilomotor nerve-fibres and the sensory fibres having their course in the dorsal skin-branches of the skin of the trunk in cats, are distributed within areas of the skin that are in accordance as to situation and arrangement but not as regards their extent. Thence it follows that the sympathetic ganglia and the spinal ganglia innervate the skin after the same scheme, and although the relations in cats are less simple than those found in flat fishes, still I believe that here likewise the scheme of the pilomotor innervation of the skin by means of the marginal column of the sympathetic nervous system may be called a "segmental" scheme.