ZOOLOGY

ON THE TOPOGRAPHICAL ANATOMY OF THE NERVOUS SYSTEM OF THE MESOTHORACIC LEG OF THE AMERICAN COCKROACH (*PERIPLANETA AMERICANA*). I

BY

E. D. NIJENHUIS [1]) AND D. DRESDEN

(From the Laboratory for Research on Biocides, National Council for Agricultural Research T.N.O., Vondellaan 6, Utrecht)

(Communicated by Prof. CHR. P. RAVEN at the meeting of November 27, 1954)

INTRODUCTION

Already for a long time the reflex mechanism of the insect leg has been investigated by physiologists. An outstanding object used in these studies has been the relatively low specialized leg of the cockroach.

Future studies, however, will be hampered by the lack of a detailed physiological analysis of the various elements such as muscles, nerves and sense organs. This field of research has been successfully endeavoured by PRINGLE and WILSON (1952) and their results may serve as an example of how to describe the elements quantitatively.

In order to gain further progress along this line a complete knowledge of the anatomy of the organs involved is indispensible. The anatomical data are to reveal information on two different subjects:

1. There must be obtained an overall picture of the sense organs and sensory nerves, and of the corresponding muscles, motor nerves and skeletal elements (joints), involved in well-defined reflexes.

2. The number of motor units and axons involved in the reflexes should be analysed as far as possible.

In a next paper this second point will be discussed. The anatomy of the motor mechanism of the roach leg has been investigated quite satisfactorily. The innervation of the muscles and the topography of the nerves, however, have been the object of relatively few investigations. Rather detailed data on the motor innervation have been reported by PRINGLE (1939) and a description of the femoral and tibial nerves in *Phyllodromia* has been offered by DEBAISIEUX (1938). As yet, a more or less complete picture is still lacking.

It is the aim of this paper to describe both the topography of the nervous system of the leg, and the innervation of the muscles and also to compare the results with those obtained in other insects.

[1]) Present address: Zoological Laboratory, University of Utrecht.

Material and methods

The mesothoracic leg was used throughout this study. Attempts failed to obtain a vital staining of the nerves. A treatment with alcohol 96 % (as already employed by Holste 1910) revealed very satisfactory results. By careful dissection under a binocular microscope it was possible even to trace the finest branches of the nerves. They could easily be distinguished from other tissues.

The results obtained by this method were compared and checked with a complete set of serial sections of the mesothoracic segment, available from previous investigations (Nijenhuis and Dresden 1952).

Topography of the peripheral nerves

Only four pairs out of the total of seven pairs of mesothoracic nerves are involved in the locomotor mechanism of the legs, viz. the nerves 3, 4, 5, and 6 (Pringle 1939). Each of the two nerves 3 and 6 branch into two main stems (3A, 3B and 6A, 6B respectively). These stems should be regarded as nerves of the same order as the other main nerves. In the following description, therefore, six nerves will be mentioned, viz. 3A, 3B, 4, 5, 6A and 6B.

The branches of these nerves will be designated as follows: rami of the first order (r) will be labelled with a number; the more distally they rise from the main trunk the higher this number is. In the same way second order rami will be indicated with small letters. Third order rami, if any, will be indicated with greek types. The authors are well aware of the fact that this way of designating the branches of a nerve is far from being an ideal one. As a result of it, for example, it could happen that two rami will be described as rami of a different order although they are quite equivalent with regard to their end-organs.

The only way to avoid this inconvenience seems to be to name all these nerves and their branches. Many complicated names would be needed in this case and it appeared to the authors, therefore, that the method used here presents a more desirable solution, however defective it may be.

In the following descriptions the nerves will be dealt with in the same sequence in which they are found when dissecting the roach from the ventral side.

A. Nerve 3B (fig. 1)

The trunkal part of this nerve runs very superficially, closely following the ventral body wall. Also the coxal part lays very close to the skin: it is only covered with the strongly flattened muscles 138 and 139c [1]). When dissecting from the ventral side, therefore, a complete picture of this nerve will never be obtained. This is the reason why fig. 1 presents

[1]) The numbering of the muscles, as proposed by Carbonell (1947), has been adopted here.

a dorsal view whereas all the other nerves are represented in ventral views.

Shortly before 3B leaves the coxa it runs more centrally. In the trochanter it fuses with the crural nerve (5). The axons of 3B which fuse with 5 supply nothing but the muscles 141 (reductor femoris) and 142 (extensor tibia).

Inspection of fig. 1 will show that the numbering of the rami 7 and 8

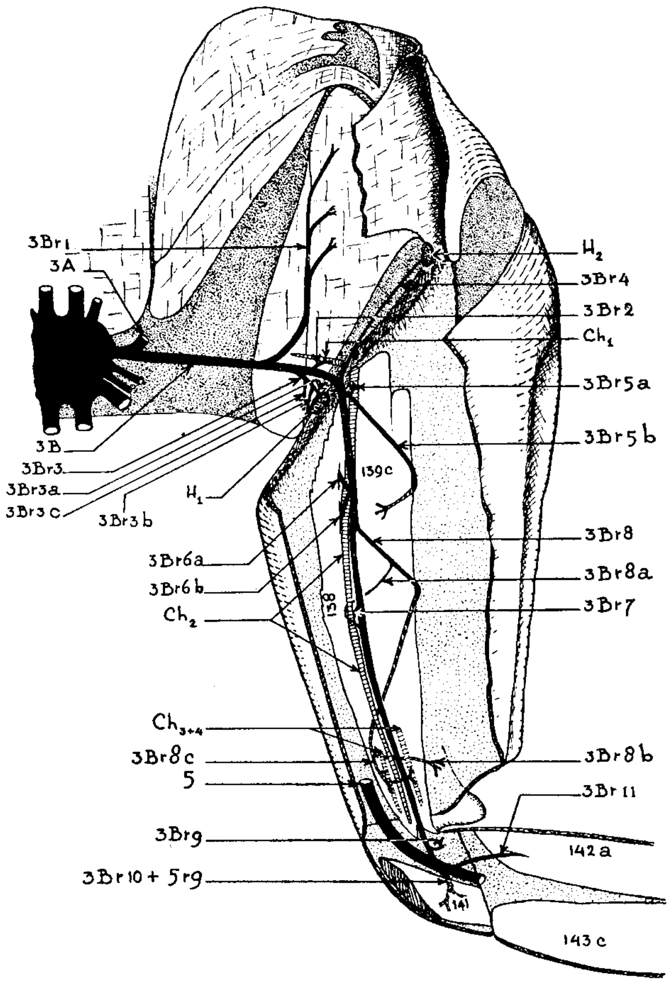

Fig. 1. Nerve 3B, dorsal view. Explanation: H_1, H_2: the inner and outer coxal hair plate respectively. Ch_1, Ch_2, Ch_3, Ch_4: the coxo-trunkal, proximal coxal and the two distal coxal chordotonal organs. Muscles are indicated according to CARBONELL

(r7 and r8) appears unlogical. Unfortunately these branches were designated (NIJENHUIS and DRESDEN 1952) in an animal in which their sequence happened to be the opposite of the normal situation. In order to avoid confusion, however, it is suggested to accept this unlogical designation.

The curious course of r8a is worth mentioning. After it has split off from r8 it runs back towards the main nerve. Sometimes they attach to each other, giving the impression of a real fusion, but usually they do not. The r8a then loops around the chordotonal organ and eventually fuses with the main nerve. From a fibre analysis it became very likely that the axons of r9 are the same as those of r8a. They serve the sensory supply of the lateral trochanteral wall.

The nerve 3B appears to be an important sensory nerve, supplying not only praecoxal sense organs but the more important ones in the coxa as well: two hair-plates and four coxal chordotonal organs. Over and above this it supplies the sensory innervation of the anterior coxal wall. Only four of its branches contain motor fibres, r6 and r7 (supplying levator muscles of the trochanter: 138 and 139c), r10 (fuses with a branch of nerve 5 and supplies the reductor femoris: 141) and r11 (innervates the extensor of the tibia: 142).

B. Nerve 3A (fig. 2)

This nerve, which represents the more cranial trunk of number 3, has its ramifications restricted to the field of the coxal adductors and promotors. Special mentioning deserves r1b, which leaves this field and runs to the cranio-medial tip of the pleural arm. In its course it bends around

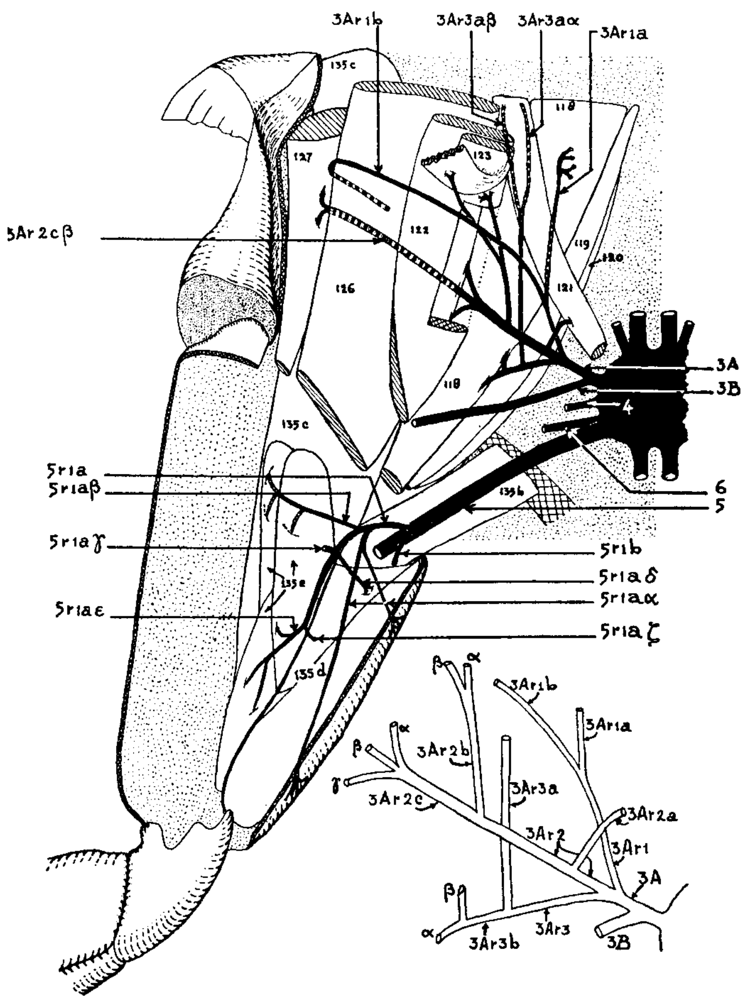

Fig. 2. Nerve 3A and part of the coxal branches of nerve 5. Ventral view

the muscles 126 and 135c. Dorsally of the pleural arm this branch fuses to form a plexus with 6Ar4. This plexus supplies the muscles 114, 115 and 116 (fig. 5). However, it was impossible to determine what part of this motor innervation should be accounted to either of the two components.

A remarkable course shows r2cβ as it traverses the flat muscle 126 to reach muscle 127 which is innervated by it.

Nerve 3A appears to have largely a motor function, a sensory function only being ascertained with respect to r1a which supplies the lateral margin of the basisternum.

We were unable to determine the character of r3aα and r3aβ. They are situated at the dorsal side of muscle 121, and it is likely that r3aα enters the most cranial part of this muscle, thus supplying it together with r2a. The other branch is supposed to innervate the tip of episternum 1. The following muscles are innervated by nerve 3A:

The adductors (118, 119, 120 and 122, 123, 124) and promotors (126, 127), the trunkal muscle 121 and one or more of the trunkal muscles 114, 115 and 116.

C. Nerve 4 (fig. 3)

The domain supplied by this small nerve is found dorsally from that of nerve 3A and it is bounded in between the superficial layer of ventral adductors and promotors of the coxa and the area of the sternal and

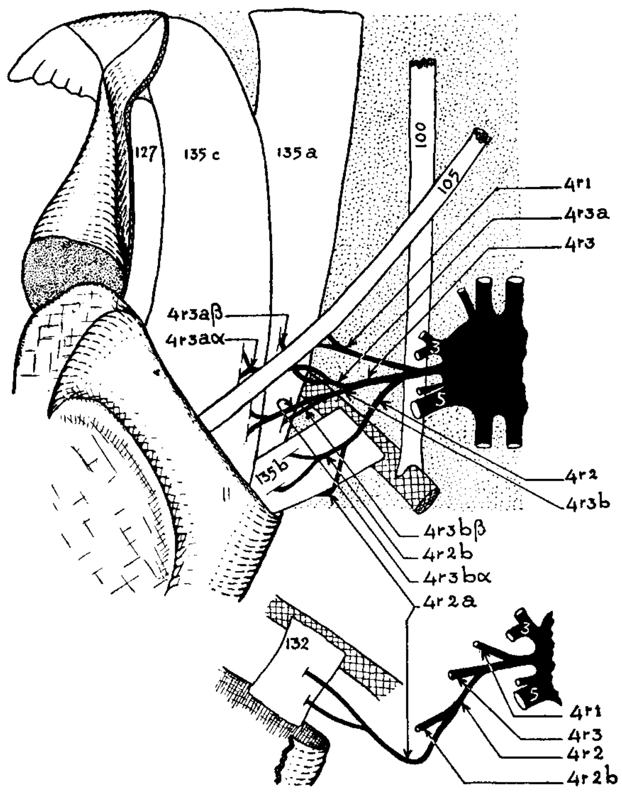

Fig. 3. Nerve 4, ventral view

pleural arm. This nerve has only a motor function. It innervates those depressors of the trochanter which do not originate in the coxa, viz.

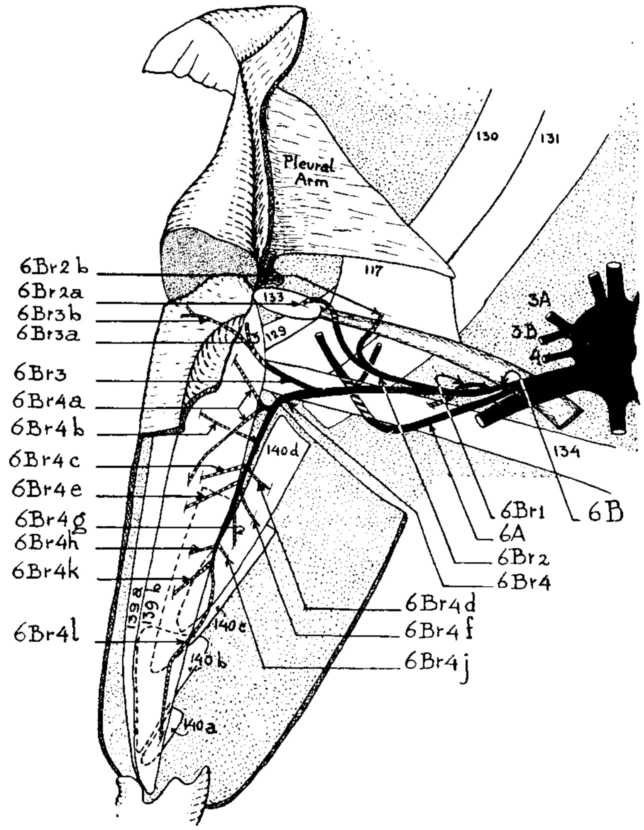

Fig. 4. Nerve 6B, ventral view

135a, 135b and 135c. Besides it supplies the small anterior rotator (105) and the small remotor of the coxa (132).

D. Nerve 5

Number 5 is the most important nerve of the leg. It has no branches in the thorax and only a few are found in the coxa. However, from beyond the trochanter, where the remaining motor axons of nerve 3B are taken up (fig. 1), it is the only nerve supplying the leg. Almost everywhere along its course the main trunk lies centrally in the leg.

The coxal, trochanteral, femoral and tibial branches of this nerve deserve a more detailed description.

1. *Coxal branches of nerve 5 (fig. 2 and 5)*

The proximal twig (r1aα) of r1a is a small sensory nerve which usually bifurcates near its origin. In a number of cases, however, this bifurcation does not occur and more distally a second twig separates itself from r1a.

This variability does not apply to the sensory areas innervated by these small twigs.

In the distal part of the coxa r3 can be found. Along a short distance it is united with the remaining, distal fibres of 6Br4 (fig. 5). From a histo-

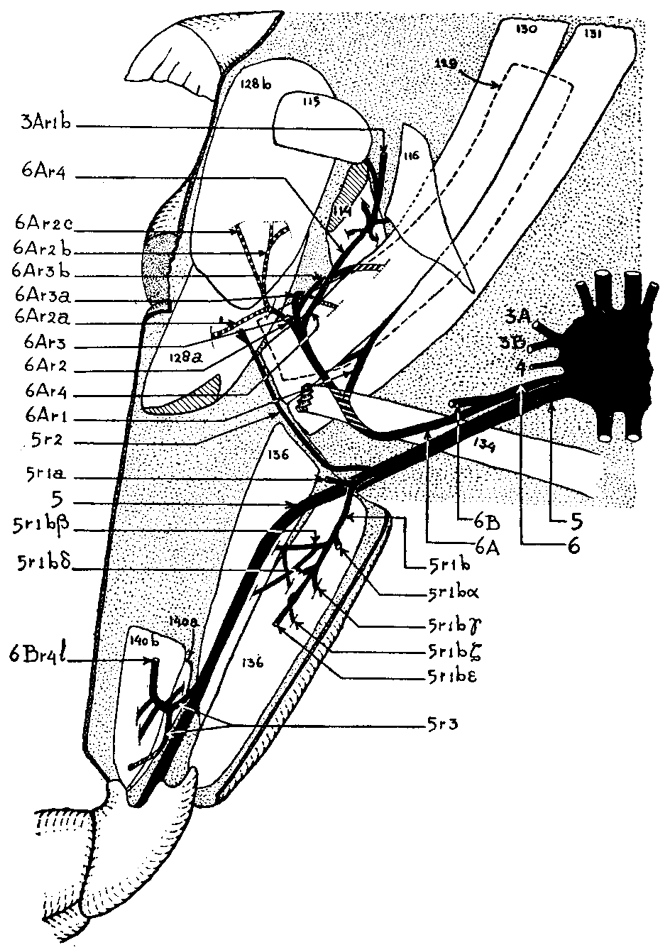

Fig. 5. Nerve 6A and part of the coxal branches of nerve 5. Ventral view

logical fibre analysis it could be ascertained that no exchange of fibres takes place in this plexus, each branch containing the same axons at either side of it.

The part played by nerve 5 in the sensory innervation of the coxa is but small: the median wall of the coxa is supplied by r1aα, the posterior wall of the meron by r2 and the posterior wall of the coxo-trochanteral joint by r3. The only coxal muscles innervated by 5 are those depressor muscles of the leg, which have their origin in the coxa (viz. 135d, 135e, 136 and 137).

2. *Trochanteral branches of nerve 5 (fig. 6)*

Approximately the whole sensory innervation of the trochanter is provided by trochanteral branches of nerve 5 (trochanteral hair plate, campaniform sensilla and the sensilla scattered over the skin). The only exception is the lateral articular membrane which is supplied by 3Br9.

The axons of r9 leave 5 at exactly the same spot where those of 3Br10 do so, thus giving rise to one single nerve, innervating muscle 141. Hence

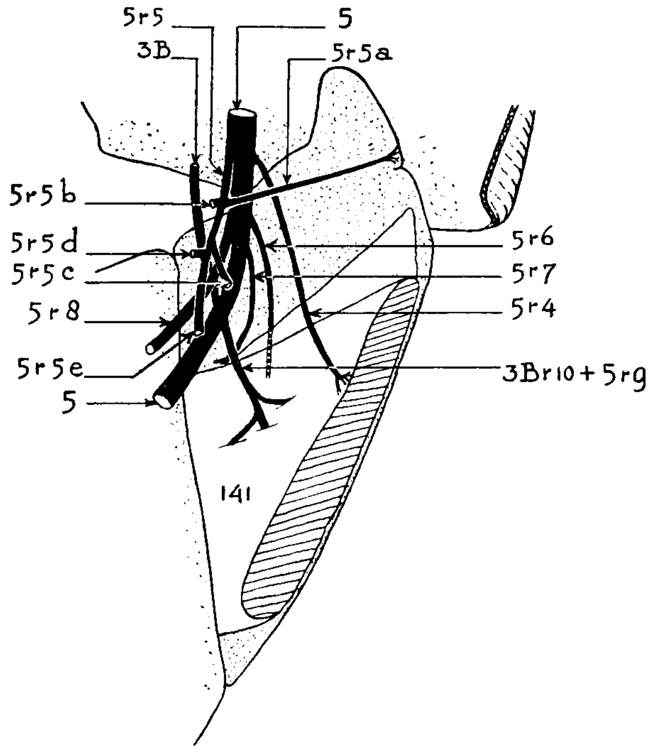

Fig. 6. Trochanteral branches of nerve 5. Anterior view

this muscle is supplied by fibres originally confined to two different main nerves; it is, so far, the only muscle in which such a situation could be ascertained.

3. *The femoral and tibial branches of nerve* 5 *(fig. 7)*

Just before nerve 5 leaves the trochanter the important sensory branch r8 arises from it (fig. 7). This branch presents itself as a big ligulate nerve, attached to the latero-anterior wall of the main femoral trachea. Some of its secondary branches supply the important femoral and tibial scolo-paria. Others provide the sensory innervation of the anterior femoral wall; in their course they traverse the muscles 142a and 143b.

Beyond the subgenual organ the main branch r8 is found running distally along the anterior wall of the tibia. Its smaller twigs probably supply the sensilla scattered over the anterior tibial wall. At any rate they do not supply the group of campaniform sensilla at the base of the tibia, which do not receive any innervation from r8.

The trunk of nerve 5, running along the median wall of the main femoral trachea, has only two sensory branches in the femur, viz. r11 (campaniform sensilla at the posterior side of the base of the femur) and r12 (innervation of the posterior femoral wall).

The femoral motor branches of 5 are very short and numerous. They supply the large group of tibial flexor muscles (143) and the praetarsal flexor muscle (146a).

At the base of the tibia nerve 5 is found in the median haemolymphal

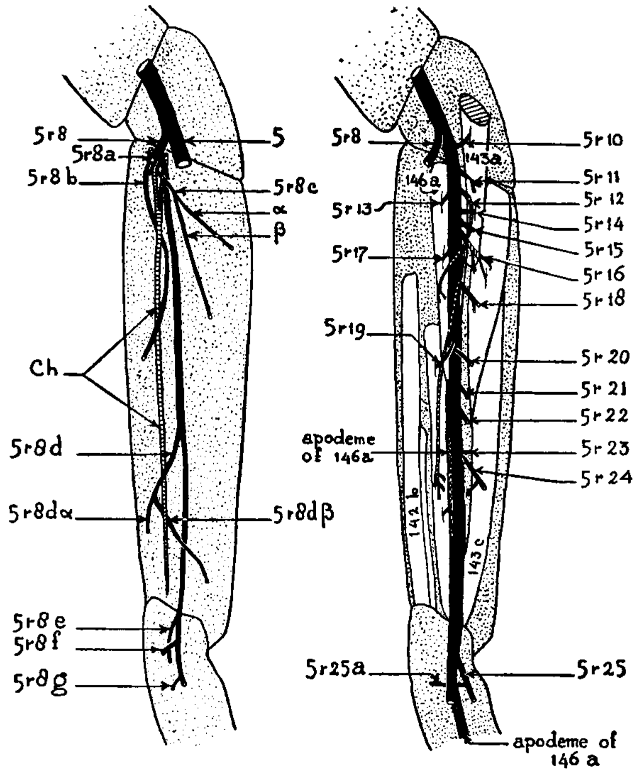

Fig. 7. Femoral branches of nerve 5. Anterior view. Ch: femoral chordotonal organ

cavity in which the muscles are situated. Running distally along the medio-posterior wall of the tibia, r25 innervates the area of the posterior tibial wall as well as the small basal group of campaniform sensilla.

Observations indicate that it is mainly motor nerves that arise from the tibial trunk of 5, just as is the case in the femur.

E. Nerve 6B (fig. 4)

The prae-coxal part of the area innervated by 6B adjoins that of nerve 4 cranio-dorsally. Here the small adductors of the coxa (133 and 134) and also muscle 117 (connecting the sternal arm with the pleural arm) are innervated.

Ventrally of muscle 134 the trunk of 6B runs to the lateral side of the coxa. After it has split off the small sensory branch r3 (supplying the anterior and posterior wall of the meron) its remainder, r4, bends sharply distally and enters the coxa. Here it innervates those levator muscles of the trochanter (139a, 139b and 140) which have their origin at the meron and the posterior wall of the coxa.

F. Nerve 6A (fig. 5)

This nerve innervates muscles, dorsally of the pleural and sternal arm. The group of remotor muscles (129, 130, 131) is not innervated by one common branch, but the muscle 129 receives a separate branch.

It could not be determined whether one or more of the muscles 114, 115 and 116 are innervated by 6A. This was due do the existence of a plexus between 6Ar4 and 3Ar1b, as has been pointed out before.

Finally it should be mentioned that the big coxal posterior rotator muscle 128 belongs to the innervation area of 6A.

(To be continued)

ON THE TOPOGRAPHICAL ANATOMY OF THE NERVOUS SYSTEM OF THE MESOTHORACIC LEG OF THE AMERICAN COCKROACH (*PERIPLANETA AMERICANA*). II

BY

E. D. NIJENHUIS AND D. DRESDEN

(From the Laboratory for Research on Biocides, National Council for Agricultural Research T.N.O., Vondellaan 6, Utrecht)

(Communicated by Prof. CHR. P. RAVEN at the meeting of November 27, 1954)

INNERVATION OF THE LEG OF THE COCKROACH AS COMPARED WITH THAT OF OTHER INSECTS

The situation in the mesothoracic leg of the cockroach may be summarized as follows:

1. With the exception of a small contribution delivered by nerve 6B, almost the whole sensory supply of the leg is provided by the nerves 3B and 5.

2. More nerves are involved in the motor innervation of the leg. The innervation of the muscles moving the coxa is provided by 4 main nerves, viz.:

3A: promotors and adductors.
4 : anterior rotators and small remotors.
6A: posterior rotators and remotors.
6B: small adductors.

The muscles of the remaining articulations are innervated as follows:

3B: levator of the trochanter, reductor of the femur, extensors of the tibia.
4 : truncal depressors of the trochanter.
5 : coxal depressors of the trochanter, reductor of the femur, flexors of the tibia, flexors and extensors of the tarsus and flexors of the praetarsus.
6B: levators of the trochanter.

The main branches of the nerves 4 and 6B arise in the praecoxal region and the branches supplying the trochanteral muscles have their ramifications into these muscles near the edge of the coxa. Thus, distally from the praecoxa only two main nerves are to be found in the leg, namely 3B and 5. (Distally in the coxa they unite to form a plexus).

According to data of PRINGLE (1939) and also on account of our own observations it may well be assumed that in the other legs the course of the nerves will be very similar to that found in the mesothoracic leg.

Also in other species of insects the mutual differences between the innervation of the three pairs of legs seem to be only slight (HOLSTE 1910).

More or less exhaustive descriptions of the innervation of an insect-leg are very scarce. Besides the classical work of HOLSTE (1910) on *Dytiscus*, the only more recent publication we know of is that by RICHARD (1950) on *Calotermes*. According to HOLSTE the nerves involved in the innervation of the leg in *Dytiscus* are:

n. coxalis anterior
n. coxalis posterior
n. coxalis inferior
n. extensor trochanteris
n. ischiadicus.

It is possible to compare these nerves with those found in the roach. In doing so a striking resemblance can be observed.

Thus, according to its situation as well as to its end organs, n. coxalis anterior may be compared with 3A. It innervates the flexores coxae, which correspond topographically to the promotors and adductors in the roach. A branch running dorsally innervates the m. levator elytri. It may be compared with 3Ar1b.

Much resemblance to nerve 6 is shown by n. coxalis posterior, which bifurcates near the ganglion in the same way as does number 6; the two main branches also correspond functionally to 6A and 6B. (The first branch innervates, among other things, the m. depressor elytri; hence it may be compared with 6Ar4. The second one supplies flexors of the trochanter).

The n. coxalis inferior may correspond to nerve 3B. Distally in the coxa it fuses with the n. ischiadicus, just as is the case with 3B and 5 in the roach. The muscles and sense organs innervated by this nerve correspond nicely to those supplied by 3B. It is assumed by HOLSTE that the fibres of the n. coxalis inferior which have been fused with the n. ischiadicus reappear in the trochanter, supplying sense organs in its skin. So far this assumption has not been verified. Thus the possibility remains that a more or less complete resemblance will be found with the innervation by the corresponding axons of 3B in the roach.

Already its name, n. extensor trochanteris points to a correspondence between this nerve and nerve 4 in *Periplaneta*. In fact, both nerves innervate the trunkal depressors of the trochanter.

Finally, as can be concluded from the data given by HOLSTE, the n. ischiadicus is evidently comparable with nerve 5.

The fundamental correspondence between the anatomy of the nerves of a leg in *Dytiscus* and in *Periplaneta* may have been well established by this comparison.

A very close resemblance is found between the situation in *Periplaneta* and that in termites (RICHARD 1950). Only 2 nerve-trunks originate from the ganglion of a termite, viz.:

n. coxalis anterior and n. coxalis posterior.

These two nerve-trunks are, however, comparable with the main nerves of the roach. The n. coxalis anterior corresponds entirely to nerve 3. The n. coxalis posterior forms three main branches, each of which—according to their innervation area—may be compared with nerve 4, 5, or 6 respectively.

Although the number of nerves, arising from the ganglion may vary in different insects, this variation seems to be of little importance, since a constant number of corresponding main branches is present.

The course of the nerves restricted to the femur and tibia has been studied in many other insects. Some of these studies are valuable for our problem, others are not. FRIEDRICH (1929–1930), for example, developed some ideas concerning the structural plan of the insect leg. His ideas, however, appear to us to be unsatisfactorily sustained by facts. Very useful information has been presented by DEBAISIEUX (1935; 1938) in his investigations on the innervation of the femur and tibia in many groups of insects. It was found that in the femur usually two nerves appear, which have been formed by bifurcation of the main stem (nerve 5), viz.:

n. femoralis dorsalis, which supplies the femoral scoloparia and often also the subgenual organ. It therefore corresponds very well to r8 in *Periplaneta*.

n. femoralis ventralis, which is the femoral remainder of the main trunk itself (according to the terminology of SNODGRASS, which we have adopted, these two nerves should have been designated as n. femoralis lateralis and n. femoralis medialis respectively).

The n. femoralis ventralis bifurcates, usually at the base of the tibia, thus giving rise to two branches:

n. tibialis anterior, corresponding to the main trunk of nerve 5, and:
n. tibialis posterior, corresponding to 5r25 in the roach.

According to HOLSTE the n. femoralis dorsalis (his ramus e) in *Dytiscus* does not enter the tibia. Also in some other insects the subgenual organ is supplied by a branch of the n. femoralis ventralis or the n. tibialis anterior. Many forms intermediate between these two extreme possibilities have been found. In *Phyllodromia*, a species closely related to *Periplaneta*, the n. femoralis dorsalis and the n. femoralis ventralis are attached to each other; in *Apis* they fuse together, whereas in *Panorpa* the n. femoralis dorsalis emits a branch back into the n. femoralis ventralis.

From the available information it may be concluded that a fundamental uniformity exists of the structural plan of the periferal nervous system of the insect leg. Within the frame of this plan differences can be found between the species and often it is difficult to see how anatomical or functional differences of the thorax or of the leg can account for them.

Some of these differences will be mentioned here.

1. Although the characteristic number of 6 main nerves has been found throughout, the number of nerve trunks originating from the ganglion may vary (*Calotermes*).

Even within the same species individual differences occur: in *Periplaneta* we found that 3A and 3B may originate as one single nerve, branching at a distance of more than 1 mm from the ganglion, but in other individuals they may as well arise separately from the ganglion.

It follows that the number of nerve trunks originating from the ganglion does not present a characteristic property of the "structural plan".

2. It happens in a number of cases that two nerves are fused along a certain distance, their axons thus being enveloped by one common nerve sheath. The existence of these formations, however, is not constant. For example, the trochanteral plexus between nerve 3B and nerve 5 may be found in a number of species (*Blattoïdea*, *Dytiscus*) but in others it may be absent (termites). According to RICHARD in *Calotermes* the reductor femoris only receives axons from nerve 5, whereas in *Periplaneta* we found that this muscle is supplied by fibres from the nerves 3B and 5. In locusts the same plexus is found and here the extensor tibiae is supplied by fibres from 3B and 5 (HOYLE 1953).

It seems as if the formation of a plexus is correlated with some functional demand to supply a muscle with fibres from two different main nerves.

THE ROLE OF THE NERVES OF THE LEG IN THE LOCOMOTOR MECHANISM

An analysis of the walking movements in the cockroach has been given by HUGHES (1952a). According to this author the protraction phase of the meso- and metathoracic legs mainly consists of: promotion of the coxa and levation of the leg (as a result of flexion of the trochanter). The retraction phase, during which the propulsive force is given to the body, mainly results from remotion of the coxa and depression of the trochanter.

Besides the propulsive forces directed about parallel to the body axis, transversal forces come into play. In the protracted position for example, the transversal component of the horizontal strut effect of the coxae will be maximal. This transversal force may well be compensated by an active adduction of the coxa. During the retraction phase this transversal force decreases and according to HUGHES the activity of the adduction muscles would thus decrease too.

However, we are inclined to assume that the latter become even more active during retraction. This assumption was made in connexion with the possibility that during the retraction the inertness of the body will be the cause of a passive abduction of the coxa (cf. DRESDEN and NIJENHUIS 1953).

From Table I it can be seen that there are only two nerves of which the axons serve antagonistic locomotor functions.

TABLE I

Component of motion	Nerves active during:	
	protraction	retraction
promotion — remotion of the coxa	3A	6A, 4
adduction — abduction of the coxa	(3A, 6B)	3A, 6B
levation — depression of the trochanter	6B, 3B	4, 5

In this connexion the situation in locusts is remarkable, where the extensors of the tibiae are the most important locomotor muscles. During the retraction phase the quick response of these muscles is not provided for by axons of 3B, as is the case in *Periplaneta*, but by axons of nerve 5 (HOYLE, 1953; EWER and RIPLEY, 1953). Thus nerve 5 seems to play an important part in the innervation of the muscles for retraction, even in more specialized insects where these muscles are not the same as in the more primitive forms.

This situation may be tentatively correlated with some localisation of the neurons for protraction and those for retraction in different regions of the ganglion. A suggestion of the same kind has been made by HUGHES (1952b) when he assumes that the neurons for flexion and those for extension may be located at different sites of the ganglion.

Speculating a little further along these lines it may be expected that the system of ascending giant fibres, of which it is known that they play a part in flight-reactions (ROEDER 1948; COOK 1951), will show to have their synapses in the regions of the dendrites of the retraction-neurons. If, as a result of specialisation, a species uses a new muscle in the retraction system, it is clear that this muscle should be innervated by a "retraction nerve".

Unfortunately it is, as yet, impossible to check these suggestions, which of course should be regarded as very tentative speculations.

A study of the neural interrelations inside the ganglion is needed before some progress along this line can be expected, and, so far, very scarce information on this field is available (cf. ZAWARZIN 1924).

SUMMARY

The subject of this study has been the nervous system of the mesothoracic leg of *Periplaneta americana*. Special attention was paid to the topography of the nerves. The following picture of the innervation has been obtained: most of the coxal sense organs are innervated by nerve 3B, and those in the more distal parts of the leg are supplied by nerve 5.

The muscles involved in the protraction of the leg are innervated by the nerves 3A, 3B and 6B. Those serving the retraction receive their

nervous supply from the nerves 4, 5 and 6A, and, as far as adduction of the coxa is concerned, also from 3A and 6B.

It has been noted that the peripheral nervous system of the cockroach has much in common with what is known of that of some other insects, and it was suggested, that in insects one structural plan may be underlying this system. Within this common structural plan a number of variations occur, and it is tentatively suggested that some of them be correlated with structural and functional properties of the thoracic ganglion.

REFERENCES

CARBONELL, C. S., Smith. Misc. Coll. **107**, no. 2 (1947).
COOK, P. M., Quart. J. micr. Sci. **92**, 297 (1951).
DEBAISIEUX, P., La Cellule **44**, 273 (1935).
———, ibid. **47**, 79 (1938).
DRESDEN, D. and E. D. NIJENHUIS, Proc. Kon. Ned. Akad. Wetensch. Ser. **C 56**, 39 (1953).
EWER, D. W. and S. H. RIPLEY, J. exp. Biol. **30**, 170 (1953).
FRIEDRICH, H., Z. wiss. Zool. **134**, 84 (1929).
———, ibid. **137**, 30 (1930).
HOLSTE, G., Z. wiss. Zool. **96**, 419 (1910).
HOYLE, G., Nature **172**, 165 (1953).
HUGHES, G. M., J. exp. Biol. **29**, 267 (1952a).
———, ibid. **29**, 387 (1952b).
NIJENHUIS, E. D. and D. DRESDEN, Proc. Kon. Ned. Akad. Wetensch. Ser. **C 55**, 300 (1952).
PRINGLE, J. W. S., J. exp. Biol. **16**, 220 (1939).
——— and V. J. WILSON, ibid. **29**, 220 (1952).
RICHARD, G., Ann. Sci. Nat. Zool., 11e série, **12**, 65 (1950).
ROEDER, K. D., J. exp. Zool. **108**, 243 (1948).
SNODGRASS, R. E., Principles of Insect Morphology (New York and London, 1935).
ZAWARZIN, A., Z. wiss. Zool. **122**, 323 (1924).