

The Small Leg-nerve of Spiders and a Probable Mechanoreceptor

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SUMMARY

Besides the main leg-nerve there is, in spiders, a 'small leg-nerve' which is mainly sensory. About 8 of the fibres arise from neurones which form a ganglion at the femur-patella joint and appear anatomically to be joint mechanoreceptors, but if so must supplement the lyriform organs. Cutting the small leg-nerve has no effect on the walking pattern nor on the detection of prey, which almost certainly depends on mechanoreception. The small leg-nerve contains one motor fibre which innervates the claw elevator. This muscle has a double innervation, a second fibre running in the main leg-nerve. There are interesting parallels between the small leg-nerve in spiders and *Limulus*.

INTRODUCTION

PRINGLE (1956) has recently thrown light on proprioception in chelicerates. In *Limulus* (Pringle, 1956), where 'slit' sense-organs of the campaniform type are lacking, movement at the leg-joints produces tonic and phasic responses in the 'small leg-nerve'. Pringle associates these responses with the large and small multipolar ganglion cells which occur at the joints (Stuart, 1953, reproduced in Pringle, 1956). The small leg-nerve arises from the ventral nerve-ring independently of the main leg-nerve and runs throughout the leg supplying the joints, a small area of cuticle in the tibia, and three muscles (flexor trochantaris, flexor femoris, and claw opener). In a scorpion and amblypygid Pringle (1955) showed that the slit organs (lyriform organs) characteristic of most arachnids are sensitive to strain in the cuticle like the campaniform sensillae of insects; but he also obtained a distinct large fibre response to rapid forced movement of the joints which could not be elicited by pressure on the cuticle but which appeared in response to probing at the joint membranes where there was some evidence of a sensory structure. When Dr. Pringle drew my attention to this, I found a corresponding sense organ at the femur-patella joint of the spider's leg, supplied by a small leg-nerve like the one occurring in *Limulus*. As this nerve runs close to the dorsal surface of the femur it can be cut with little damage to the leg, and operated spiders rapidly recover. It has not, however, been possible to establish the functions of either the sensory or the motor elements of the small leg-nerve by this means.

ANATOMY

Methods

Most of this work has been done on the common British house spider *Tegenaria atrica* (Koch), whose leg articulation and musculature have recently

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been described (Parry, 1957). The course of the small leg-nerve was traced by dissection under a binocular microscope, verified and amplified by serial sections which provided the micro-anatomical details. The brittleness and impermeability of the cuticle are an obstacle to good sectioning, so the following details are given of a procedure which gave adequate results. The spider is anaesthetized with carbon dioxide and the required part on the leg isolated by proximal and distal cuts. If a joint is to be examined in other than the fully flexed position it must be held at the required angle by drawing the piece of leg

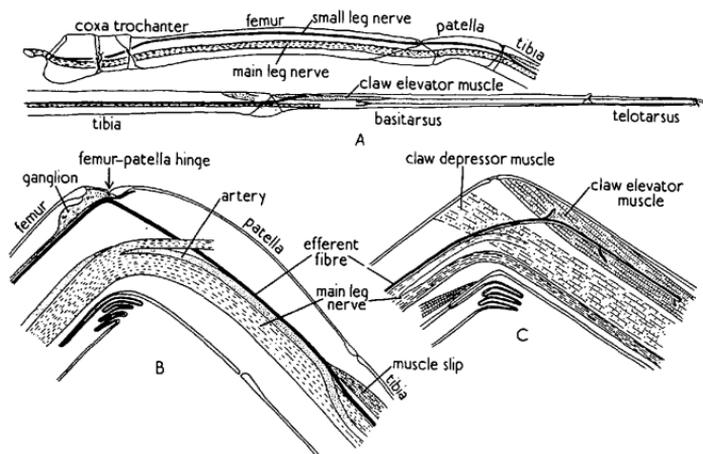


FIG. 1. A, *Tegenaria atrica*; leg showing the course of the small leg-nerve (indicated by the thick black line). B, median vertical section through the patella region showing the ganglion below the femur-patella hinge and the single efferent fibre (thick black line) with the muscle-slip attached to it. C, median vertical section through the tibia-basitarsus joint, showing the innervation of the claw-elevator muscle by the efferent fibre of the small leg-nerve and one fibre from the main leg-nerve.

carefully into narrow glass tubing before fixation. Five hours in Carnoy's mixture produces adequate fixation and is followed by two baths of 95% alcohol (12 h each), one bath of methyl benzoate (12 h), one bath of 1% celloidin in methyl benzoate (24 h), one bath of benzene, and three baths (40 min each) of 56° C paraffin wax in a vacuum embedding oven. Whenever possible, recently moulted spiders are chosen. The sections were stained with Mallory's triple stain or Heidenhain's iron haematoxylin.

The small leg-nerve

Fig. 1, A shows the course of this nerve by a line of exaggerated thickness. It branches from the main leg-nerve in the coxa, passes close to the single coxa-trochanter articulation and to the anterior trochanter-femur articulation, then runs mid-dorsally along the length of the femur to a small ganglion

below the femur-patella hinge-line. Only a single axon runs beyond this point: it runs freely in the patella, lies in contact with the main leg-nerve (from which it can be freed by dissection) in the tibia, and terminates on the claw elevator muscle in the proximal region of the basitarsus. At the level of the patella-tibia articulation the fibre is closely associated with a slip of the basitarsal depressor muscle. This unusual feature is described in detail below.

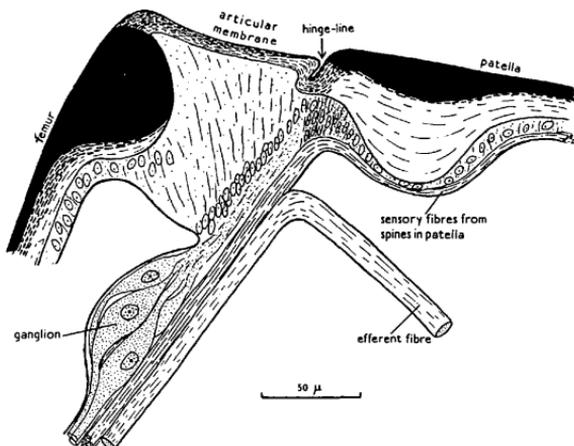


FIG. 2. *Tegenaria atrica*; median vertical section through the femur-patella hinge, showing details of the small leg-nerve and its ganglion.

The femur-patella ganglion (figs. 1, B; 2)

The patella moves on the femur about a transverse dorsal hinge-line, the two articulations being at the two ends of the hinge. The small leg-nerve runs to the mid-point of the hinge and, as stated above, only a single fibre proceeds farther down the leg. One group of small fibres penetrates the basal membrane of the patella: it has not been possible to trace these in detail, but a few fibres have been followed to sense cells at the bases of spines. The remaining fibres run to a group of 8 neurones which form a small ganglion just below and proximal to the hinge. The dendrites from these neurones can be followed running at the base of the tall epithelium which lies below the hinge, and they appear to terminate close to the cuticle at the point where most bending actually occurs.

The muscle-slip (figs. 1, A; 3)

The single fibre of the small leg-nerve which continues beyond the femur-patella hinge runs through the patella just dorsal to the main leg-nerve and the artery. At the level of the patella-tibia joint it is attached to a small group of muscle-fibres which run distally to join the more anterior of the two

basitarsal flexor muscles (muscle 23, fig. 1, in Parry, 1957), most of whose fibres originate at the proximal end of the tibia. Fig. 2, A-D illustrates the relationship between the nerve-fibre and the muscle-slip. Fig. 3, A is a transverse section of the nerve-fibre in the patella just before reaching the muscle. Fig. 3, B shows the muscle-fibres arising on the nerve-fibre sheath. In fig. 3, C they have reached their full diameter but are still enclosed in the nerve-fibre sheath. In fig. 3, D the muscle-fibres are joining the basitarsal flexor muscle, whose fibres, it will be noted, are 3 or 4 times the diameter of those making up the muscle-slip. There is no indication that the nerve-fibre innervates the muscle-slip.

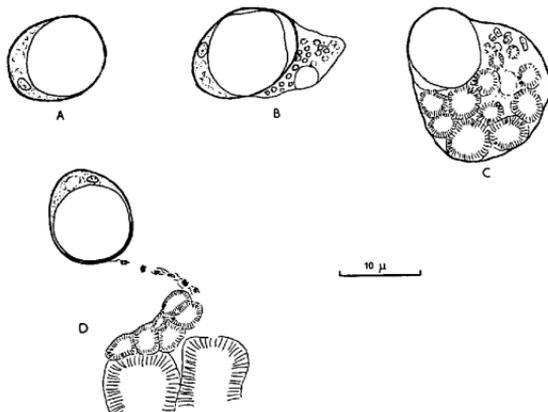


FIG. 3. *Tegenaria atrica*; A-D, successive transverse sections through the small leg-nerve (efferent fibre) at the level of the patella-tibia joint, showing the origin of the muscle-slip.

The termination of the efferent fibre

Beyond the point of origin of the muscle-slip, the small leg-nerve, composed of its single fibre, proceeds along the dorsal surface of the main leg-nerve from which it can be freed by dissection as far as the approach to the tibia-basitarsal joint. Here (fig. 1, c) it leaves the main leg-nerve in company with one other fibre. The two fibres are for a short distance loosely attached to the nerve supplying the claw depressor muscles and then proceed to the median claw elevator muscle (muscle 27, fig. 1, in Parry, 1957), to which they send repeated branches. They appear to branch simultaneously.

FUNCTION

Method. An attempt was made to establish the function of the elements of the small leg-nerve by destroying it and comparing the behaviour of operated spiders and normal ones. The nerve can be cut in the femur where it runs close to the dorsal surface between the paired patella flexor muscles. The

spider is covered with an inverted Perspex box which fits closely to the sides of the body, allowing the legs to protrude. Carbon dioxide is passed through the box. The chosen leg is clamped with light pressure at the base of the femur to prevent loss of blood and a flap of cuticle is cut near the distal end. This is folded back and the small leg-nerve destroyed with a hooked needle.

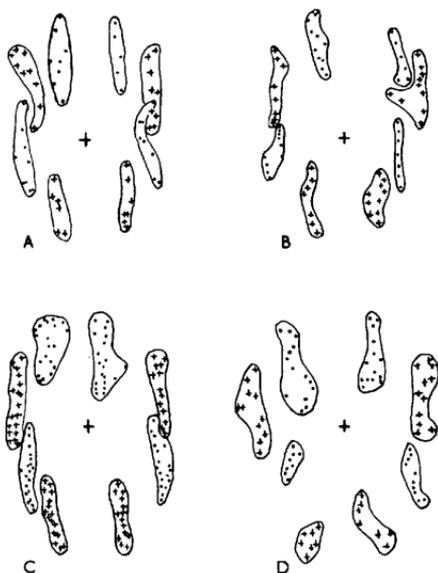


FIG. 4. *Tegenaria atrica*. Walking patterns of normal spiders (A, B); and of spiders in which the small leg-nerve of the first left leg has been cut (C, D).

The flap is then replaced and sealed with paraffin wax. Sometimes the operated leg is used as soon as the spider recovers from the anaesthetic, while at other times it is held stiffly for some hours—probably when the clamp has been too tight.

Three aspects of behaviour were examined, namely, claw retraction, walking, and prey detection. As the results were all negative the experiments will be described briefly.

Claw retraction. The spider is held down by means of the box mentioned above, no anaesthetic being used, and the legs touched with a needle so that the claws are set in motion. The activity of three claws on operated legs (two different spiders) appeared normal.

Walking. During the course of this work many spiders with one or more small leg-nerves cut were watched as they walked, both on a flat surface and on their webs, and no abnormality could be detected. To confirm this

impression spiders with one operated leg were filmed while walking and the 'stepping pattern' of their legs compared. The 'stepping pattern' is a diagram showing the position of each foot (relative to the body) in successive frames of the film during a few cycles of movement. Typical patterns are shown in fig. 4: A and B were taken before, and C and D after the front left leg-nerve had been cut, and it can be seen that the operation had no significant effect.

Detection of prey in the web. Spiders kept in crystallizing bowls of 9-in. diameter build webs across the bowl. A strip of blotting paper round the inside circumference, near the top, helps the spider to get a footing and usually determines the plane of the web. The spider constructs a retreat on the edge from which it will usually emerge immediately a small cockroach is dropped anywhere on the web, and run straight to the prey. This response will take place in darkness and there is little doubt that it depends on a mechanical sense of considerable delicacy.

To test the role of the small leg-nerve in this response, the nerve was cut in each leg, usually over several days. A cockroach was then dropped on the web every day or so, and the response recorded. A negative response in such an experiment does not, of course, necessarily mean that the prey is not detected: normal spiders do not invariably respond. But a *positive* response from an operated spider indicates that prey detection is not dependent upon any element of the small leg-nerve. That this is the case is indicated by the following results.

<i>Spider</i>	<i>Date of operation</i>	<i>Dates with response</i>	<i>Dates with no response</i>
A	17 Aug.: all legs and palps	18, 20, 21, 22, 23, 26, 28, 30 Aug.; 11 Sept.	24, 29 Aug.; 10 Sept.
B	8 Aug.: all legs	13, 14, 18, 21, 23, 24, 27 Aug.	20, 22, 29, 30, 31 Aug.; 1, 11, 12 Sept.
C	16 Aug.: all legs	18, 20, 22, 23, 24, 27, 30, 31 Aug.; 10 Sept.	21, 28, 29 Aug.
D	1 Oct.: all legs; 9 Oct. palps	6, 9, 10 Oct.	2, 3, 4 Oct.

The date of operation is that on which the last leg-nerve was cut. It is not known whether a 'small leg-nerve' occurs in the palps, but in two experiments these were removed.

Notes on subsequent examination of operated spiders

Spiders A, C, and D: all legs dissected and in each one the small leg-nerve was found broken or was missing in the femur.

Spider B: all legs sectioned and the efferent fibre in the patella either found to have the dark appearance characteristic of a cut nerve or else to be missing. The cut in the femur could not always be confirmed as the nerve sometimes extended to the confused region of the operation.

These results show that no elements of the small leg-nerve, nor any sensory terminations in the palps, are essential for the detection of prey in the web.

DISCUSSION

I have shown that the small leg-nerve in the spider is mainly sensory, containing about 8 axons from a ganglion situated below the femur-patella hinge and a number of axons from sensory hairs on the patella. The single motor axon innervates the claw retractor muscle which also receives another axon from the main leg-nerve. The following points call for comment.

(a) There is an interesting parallel between the presence of a small leg-nerve in spiders (and probably in scorpions—Pringle, private communication) and in *Limulus* (Patten & Redenbaugh, 1900; Pringle, 1956). In the latter, also, it is mainly sensory, supplying groups of multipolar nerve-cells at four of the joints and also a small area of sensory hairs on the tibia. Its motor axons innervate three muscles: the claw elevator (opener) and the flexors of the trochanter and femur.

(b) *Limulus* has no cuticular mechanoreceptors of the lyriform-campaniform type and Pringle (1956) has shown that the multipolar nerve-cells supplied by the small leg-nerve are proprioceptive in function. He suggests that the smaller cells, lying close to the joint membrane, are non-adapting position receptors; while the larger cells, lying some distance proximal to each joint, are phasic movement receptors. On analogy with *Limulus* it is tempting to suggest that the femur-patella ganglion in the spider leg is also proprioceptive, but if so it must in some way supplement the lyriform organs which are present at all the leg joints and which Pringle (1955) has shown to be mechanoreceptors. Of alternative functions the detection of prey seemed a likely possibility—it almost certainly depends on an extremely delicate mechanical sense—but this idea has not been borne out by the experiments described above. The problem should be quickly solved when it becomes possible to record electro-physiologically from spider nerves.

(c) There is, however, a further parallel between the *Limulus* and spider small leg-nerves which suggests that the latter may be concerned in some way with mechanoreception. In *Limulus* Pringle points out that the small leg-nerve is 'always rather accurately located between points at the femuro-tibial and trochantero-femoral joints which do not move relative to one another when the segments flex and extend; [while,] at the trochantero-femoral joint, a small, fine muscle with close striation . . . runs from trochanter to femur and is attached by connective tissue to the small nerve where this runs round the inner curve of the trochanter. It is hard to see that this muscle can have any function other than to hold the nerve in this region away from the cuticle of the trochanter at or very near to the position of zero stretch when this segment moves. Such an arrangement is well suited to provide a fixed reference line for sensory structures responding to movement through the pull of other connective tissue strands whose outer insertion is on moving parts.' In the spider the small leg-nerve passes very close to the coxa-trochanter

articulation, the anterior trochanter-femur articulation, and the femur-patella hinge line, so that movement at these joints will have little or no effect on the nerve. In the patella itself the nerve (now consisting of a single fibre) runs freely in the haemocoel to become loosely attached to the main leg-nerve in the tibia, and it is at the level of the patella-tibia joint that the small slip of muscle is attached to the nerve. This muscle could, like the muscle in *Limulus* described by Pringle, regulate tension in the nerve and at the femur-patella ganglion.

(d) The efferent innervation of the claw elevator appears to consist of two fibres only—one from the small leg-nerve and one from the main leg-nerve. A double innervation—by a fast and a slow fibre—is the common condition in insects, and Hoyle (1957) has recently shown that the claw-closer muscle in *Limulus* also receives a fast and slow fibre. If the spider's small leg-nerve carries the slow fibre to the claw elevator, this would probably explain why cutting the nerve had no apparent effect on the response of the claw to general stimulation.

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