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# Observations on the Leg Receptors of *Ciniflo* (Araneida: Dictynidae)

## III. Proprioceptors

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**Summary.** The anterior and posterior proprioceptors at the tibio-metatarsal joint of the cribellate spider *Ciniflo* have been studied physiologically by recording from the individual receptor nerves in response to manipulation of the metatarsus. In the anterior organ ($TM_{ant}$) two flexion sensitive movement units, an extension sensitive position unit and a flexion sensitive position unit were identified (Figs. 2 and 3). In the posterior organ ($TM_{post}$) there are more units present, with representatives of the above categories and also some indication of an extension sensitive movement unit (Fig. 6). The results are compared with those of the corresponding receptors in crustaceans.

## Introduction

Amongst chelicerates, joint proprioceptors have been described in the legs of scorpions (Rao, 1964; Rao and Murthy, 1966; Laverack, 1966; Bowerman, 1976), spiders (Parry, 1960; Rathmayer, 1967; Rathmayer and Koopman, 1970) and *Limulus* (Pringle, 1956; Hayes and Barber, 1967) and in the pedipalps of scorpions (Bowerman and Larimer, 1973) and spiders (Rathmayer and Koopman, 1970). Nevertheless, our knowledge of the structure and function of these receptors in the above group is extremely limited when compared with that available for the crustaceans and insects (see, e.g., Clarac, 1976; Mill, 1976; Moulins, 1976; Wright, 1976).

In a structural study Parry (1960) showed that there was a second 'small' leg nerve in the spider *Tegenaria atrica,* which contained the axons from about 8 sensory cells associated with a joint receptor at the femoro-patella joint. In a more recent survey of the legs and pedipalps of the tarantula, *Dugesiella hentzi,* Rathmayer and Koopman (1970) found that each joint has at least two joint proprioceptors. In the legs each receptor consists of 4–15 sensory

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cells embedded in a connective tissue strand; there being a total of 135 neurons distributed between the 18 receptors distal to the coxa. The receptor described by Parry corresponds with the $R_{10}$ organ of Rathmayer and Koopman. Physiological work on these receptors in spiders seems to be confined to a study by Rathmayer (1967) on the receptors at the patella-femur joint in the tarantula (*Dugesiella* (= *Eurypelma*) *hentzi*; while scorpion joint receptors have been investigated by Rao (1964), Rao and Murthy (1966), Laverack (1966), Bowerman and Larimer (1973) and Bowerman (1976) and *Limulus* joint receptors by Pringle (1956) and Hayes and Barber (1967). In most cases recordings have been obtained from leg nerves which also innervate other sensory structures.

This paper presents a short study which deals primarily with the physiology of the anterior tibio-metatarsal joint receptor ($TM_{ant}$) in the walking legs of the cribellate spider *Ciniflo*; although some information is given on the posterior receptor at this joint ($TM_{post}$). These receptors correspond respectively with the $R_{15}$ and $R_{16}$ receptors of Rathmayer and Koopman (1970). Recordings have been obtained from the individual receptor nerves.

## Materials and Methods

The first and second walking legs of large specimens of *Ciniflo* were used. A leg was detached and placed on its side and a 5 mm length of 001 insect pin passed through the metatarsus 1.5–2.0 mm from the T-M joint. The leg was then anchored with staples, ventral side up, to a piece of balsa wood in the bottom of a perspex dish, leaving the T-M joint just beyond the edge of the wood (Fig. 1a, b). As soon as the leg was in position, the perspex dish was flooded with fresh spider Ringer (Rathmayer, 1965), and a continuous flow of this was maintained at a temperature of 15°C.

The ventral side of the patellar cuticle was removed, exposing the main leg nerve, and the remaining piece of patella was pinned down. Using a needle, a row of fine holes was pierced in the cuticle of the tibia along the exact centre of the ventral surface. With gentle teasing the cuticle could be split along this row and pulled away from the underlying connective tissue and muscle, and this joint was then also pinned to the balsa wood (Fig. 1b). This prevented damage to the nerves of the proprioceptors which lie just to either side of the centre line. Once the cuticle had been displaced the connective tissue, if present, was removed, revealing two small nerves leaving the main leg nerve and running to the anterior and posterior tibio-metatarsal chordotonal organs respectively. The nerves were cut as close to the main leg nerve as possible and teased away from the muscle they lie against. The cut ends were sucked into the micropipette of a suction electrode (Fig. 1b).

The suction electrode consisted of a piece of $^1/_4''$ diameter perspex tube connecting two lengths of polyethylene tubing. The end of one piece of tubing was connected to a syringe, while a glass micropipette (internal diameter about 30 μm) was inserted into the free end of the other piece. A length of platinum wire entered the perspex tube through an airtight hole (sealed with Araldite) and passed down the micropipette. The assembly was mounted on an aluminium supporting rod held in a micromanipulator. Nerve potentials were amplified and recorded using conventional techniques.

To move the metatarsus about the tarso-metatarsal (T-M) joint, a wire guide attached to a micromanipulator was used. By moving the guide at an angle of 45° to the horizontal, and allowing the pin in the metatarsus to run freely in the guide, the T-M joint could be bent quickly and easily through 110° (Fig. 1c). Mechanical stops were attached to the micromanipulator to prevent over-extension or over-flexion of the joint. The movement of the guide was monitored by a displacement transducer (Intersonde, DR68) attached to the micromanipulator. The output from the transducer was displayed on the second channel of the oscilloscope. It should be noted that the transducer monitors the motions of the wire guide and that a ramp stimulus applied to the guide results in a partially sinusoidal movement of the metatarsus. Thus the monitor trace gives only an approximate indication of movement about the T-M joint.

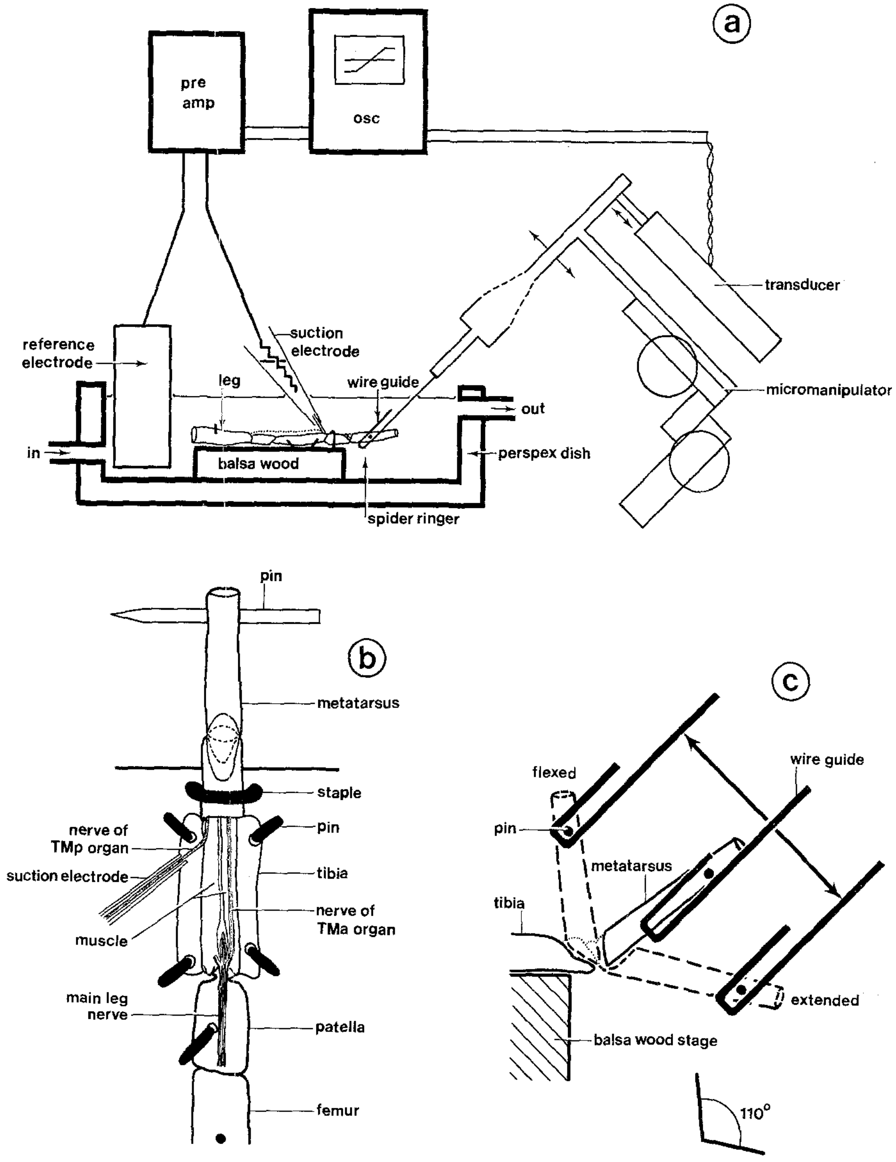

**Fig. 1. a** Diagram of the apparatus used for stimulating and recording from proprioceptors. **b** A right leg pinned ventral side up, dissected, and ready for recording. **c** Diagram to show the movement of the wire guide (large arrows) and the range of movement produced in the metatarsus (broken lines)

## Results

### *Anterior Tibio-Metatarsal (TM) Organ*

Four units have been identified in the anterior organ ($TM_{ant}$) and this agrees with the structural evidence of Rathmayer (1969). What is considered to be the usual situation is illustrated in Figure 2 which shows two tonic and two

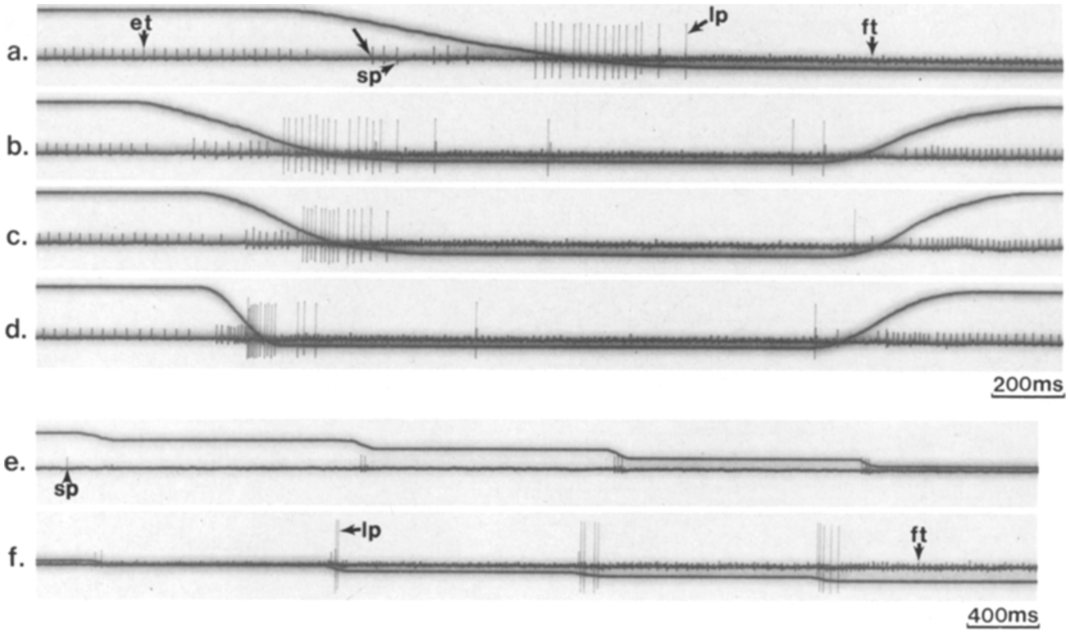

**Fig. 2. a–d** The response of the $\text{TM}_{\text{ant}}$ organ to flexion of the T-M joint at four different velocities. Four units are present: *et*, extension sensitive tonic unit; *sp*, small flexion sensitive phasic unit; *lp*, large flexion sensitive phasic unit; and *ft*, flexion sensitive tonic unit. Note that the flexion sensitive tonic unit starts firing (arrow) at the same position as the small phasic unit. **e–f** Flexion with a 'staircase' stimulus. The ranges of the small phasic, large phasic and flexion sensitive tonic units can be seen to be quite discrete. Down on monitor trace = flexed

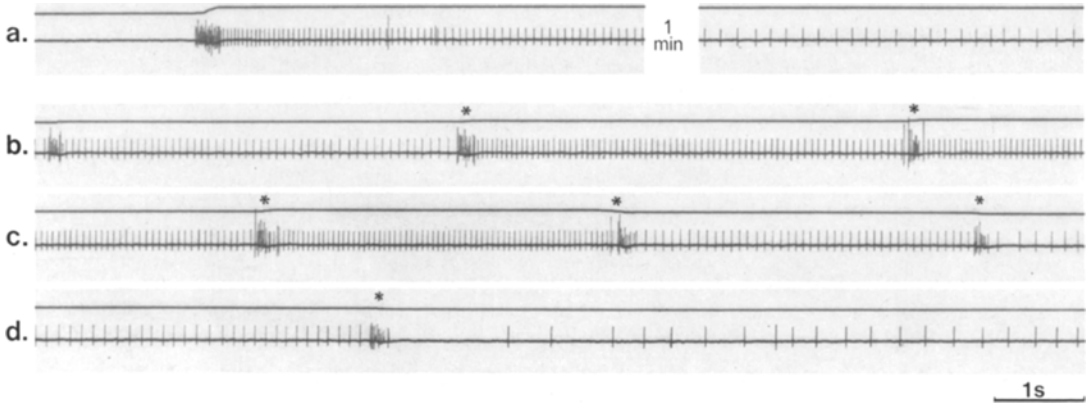

**Fig. 3. a** Adaptation of the extension sensitive tonic unit over 1 min. The gap of 1 min indicates the period during which the recording camera was switched off. **b–d** Showing a hysteresis effect in the extension sensitive tonic unit. The movements of the joint occur at the asterisks (*). The first four movements (including the first at the beginning of trace **b**) are slight extensions, the last three are slight flexions. Up on monitor trace = extended

phasic units. Both the phasic units are unidirectional, responding to flexion. One tonic unit is sensitive to extended positions and the other (smaller) tonic unit responds in the flexed position.

*Phasic Units*. In the preparation shown in Figure 2, the two phasic units are active over different ranges, but the ranges are velocity sensitive. Thus, during a flexion of 1 s duration, their ranges did not overlap (Fig. 2a) but, as the velocity of flexion increased, both units started to fire at a more extended position and hence over a wider range of movement. When the duration of flexion was reduced to about 200 ms (Fig. 2d) the ranges of the two units became adjacent to each other. It is considered that the single spikes at the beginning of the extension in Figure 2b–d are the result of a slight judder in the wire guide, which is not acting at right angles to the metatarsal pin in this position.

The effect of bending the leg in small ramps produces similar range fractionation (Fig. 2e, f). In other preparations overlap of the ranges was observed.

The situation with regard to the phasic units was not always as precise as this, although out of 18 preparations from which recordings were obtained, 13 showed two phasic units both of which were unidirectional flexion units in 8 of these. In 4 cases, one of the units was flexion sensitive and the other bidirectionally sensitive, while in 1 case there was one flexion sensitive and one extension sensitive unit. Of the remaining 5 preparations only one phasic unit was seen in 4 cases (in 3 of these it was flexion sensitive, in the other extension sensitive) while the fifth preparation had at least 3 phasic units. Possibly, in this last preparation, another nerve was sucked into the micropipette along with the anterior TM proprioceptor nerve (there are other very small nerves in this region). Thus 11 preparations were certainly compatible with the idea of two phasic flexion units.

*Tonic Units*. Of the two units shown in Figure 2a–d, one fires exclusively in the extended position, the other exclusively in the flexed position. Both of these units show the phenomenon of hysteresis, in that their range about the two extreme positions is, in the short term at least, dependent on the immediately previous direction of movement. Thus the extension sensitive unit starts to fire at about the half-way point during extension, yet stops firing as soon as flexion commences. Furthermore, the maximum impulse frequency of the extended position unit is reached before complete extension is achieved. Conversely, the flexion sensitive unit begins firing during flexion soon after flexion starts (about 1/5th flexed), but appears to stop firing during extension at a slightly more flexed position.

Figure 3b–d shows the effect of four small stepwise extensions followed by three flexions of similar magnitude (in the extended part of the position range) on the extension sensitive position unit. After each small extension, the impulse frequency increases then adapts during the maintained position. During each small flexion movement, the impulse frequency drops markedly and then recovers gradually. However, for any particular leg position, the impulse frequency is always higher when the joint has been extended, rather than

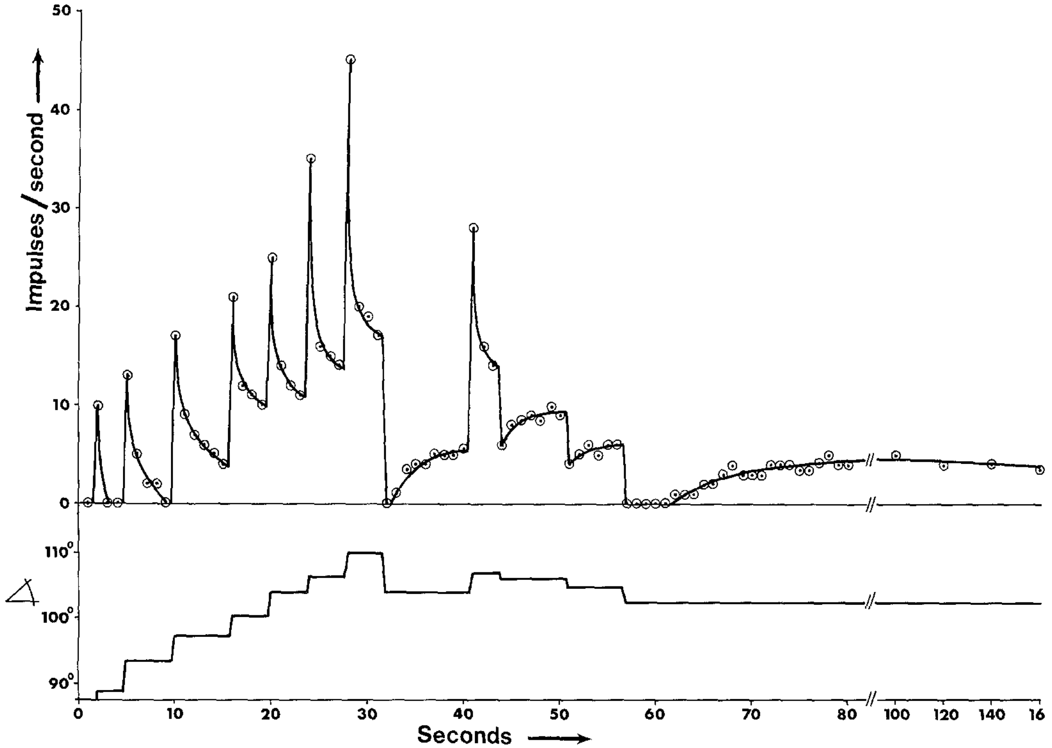

**Fig. 4.** A graph of impulse frequency of the extension sensitive tonic unit from TM$_{ant}$ against time during a series of stepped extension and flexion movements. The approximate angle of the joint is given in degrees below the graph (110° = fully extended, 0° = fully flexed). The 5th and 8th positions are at the same leg angle; as are the 6th and 10th positions. Note that the initial frequency after an extension movement (5th position) is much higher than after the flexion movement to the same joint angle (8th position). The same is true for the 6th and 10th positions. This is an example of hysteresis. However, if the curves for the individual positions are extrapolated for about 30 s on the horizontal axis (see Fig. 5), the adapted levels at the two positions would be much more similar

when it has been flexed, to reach that position. The hysteresis effect is shown graphically in Figure 4.

The extension sensitive unit (and probably also the flexion sensitive unit) shows, in addition to the short term hysteresis effect, long-term adaptation of the firing rate after movement ceases (Figs. 3a, 5). Thus the extension sensitive unit illustrated in Figure 5 adapts rapidly during the first 10 s, but thereafter the rate of adaptation falls off markedly. However, this unit still showed some signs of adaptation even after 3 min and it is difficult to understand the physiological significance of this.

Part of the observed hysteresis effect clearly results from the long term adaptation of these units, since successive extensions spaced only about 10 s apart produce a summation effect; conversely with successive relaxations. In addition the excitatory phasic component elicited by extensions shows some indication of being larger in more extended parts of the range; but more controlled extension steps need to be applied before this can be confirmed.

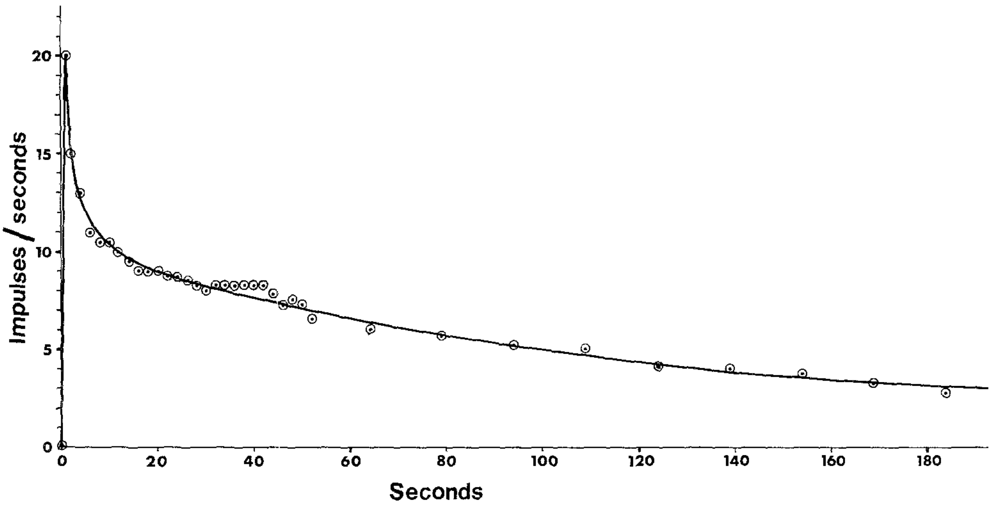

**Fig. 5.** A graph of impulse frequency against time during a maintained extension of the extension sensitive tonic unit from $\mathrm{TM}_{\mathrm{ant}}$. At time 0s, the joint was extended in 0.5s and maintained in this position. For the first 50s the impulse frequency was measured every 2s and thereafter every 15s

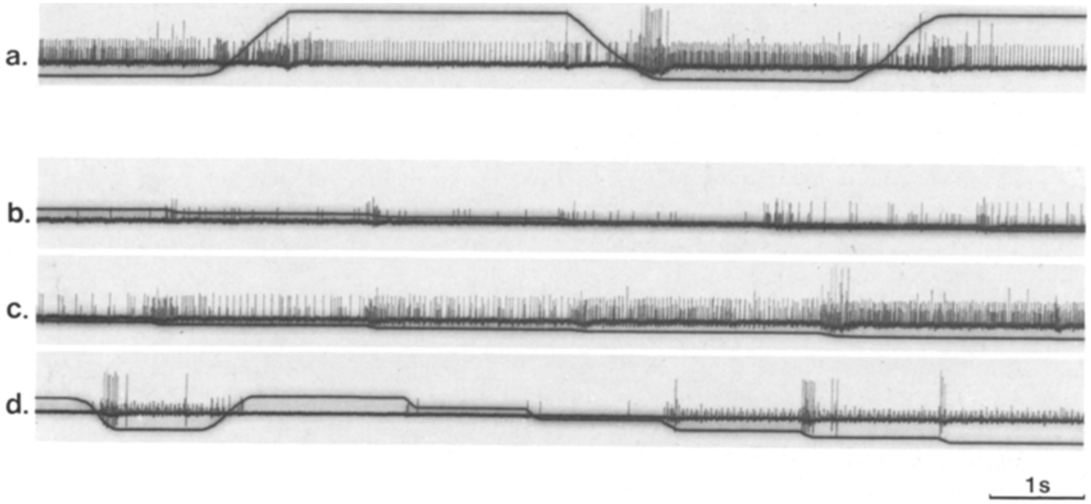

**Fig. 6. a** Response of $\mathrm{TM}_{\mathrm{post}}$ to full extension and flexion. Down on monitor trace = flexed. **b–c** Stepwise flexion of the same organ showing differential sensitivity of the two flexion sensitive tonic units. **d** Another preparation with a clearly defined flexion sensitive phasic unit in addition to three flexion sensitive tonic units. A second, smaller phasic unit is also present

### *Posterior Tibio-Metatarsal (TM) Organ*

Seven experiments were carried out on the posterior TM organ ($TM_{post}$). There are 2–4 phasic units; also a single extension sensitive tonic unit and 2 or 3 flexion sensitive tonic units giving a total of about 8 units (Fig. 6). The application of a staircase stimulus (Fig. 6b, c) shows that the smaller flexion sensitive tonic unit has a wider range than the larger one. Of the phasic units one at least is a unidirectional flexion sensitive unit (Fig. 6d) and there is probably also at least one extension sensitive phasic unit, a category which is not represented in $TM_{ant}$.

## Discussion

The present results indicate that, in *Ciniflo,* $TM_{ant}$ contains 4 sensory cells and $TM_{post}$ 5–8 sensory cells; while the number of cells described anatomically for the corresponding receptors in *Dugesiella* are 4 and 10–13 respectively (Rathmayer and Koopman, 1970). Indeed the greatest number of sensory cells described by Rathmayer and Koopman in a single joint receptor is 15. This contrasts markedly with the corresponding receptors in crustaceans, where a single joint receptor may contain up to 80 sensory cells (Mill and Lowe, 1973; Lowe et al., 1973). This difference may be associated with the development of lyriform organs at the joints in araneids.

The general characteristics of the proprioceptor cells in araneids are similar to those of crustacean joint chordotonal organs in that the potentials recorded from movement units are generally larger than those recorded from position units; a situation which, in the crustaceans at least, is reflected in the larger physical size of the movement cells. However, while the crustacean sensory cells are all bipolar with each dendrite ending in a ciliary derivative (Moulins, 1976) some at least of those in araneid joint receptors are multipolar (Rathmayer and Koopman, 1970).

In general in spiders, as well as in crustaceans and scorpions, the majority of phasic receptors are unidirectional (respond to only one direction of movement) and are velocity sensitive (Burke, 1954; Wiersma and Boettiger, 1959; Laverack, 1966; Rao and Murthy, 1966; Rathmayer, 1967; Mill and Lowe, 1972; Bowerman, 1976), and in crustaceans and spiders some degree of differential sensitivity is often observed (Mill and Lowe, 1972; Mill, 1976; this paper). There is certainly little evidence for bidirectional units in these groups, although such units cannot be ruled out entirely in spiders and scorpions. Essentially, the results obtained in the current study are in accord with those of Rathmayer (1967) for the patella-femur joint of *Dugesiella,* except that, at the tibio-metatarsal joint of *Ciniflo,* flexion sensitive units tend to dominate, whereas Rathmayer observed two extension units and one flexion unit. However, according to Hayes and Barber (1967) all the units described for *Limulus* joint receptors (excluding the TRO) are bidirectional.

The tonic receptors in crustaceans and arachnids usually have a distinct phasic component and fire maximally at one or other extreme of the movement range. They adapt slowly and hence, in the short term at least, a hysteresis effect occurs. In general, extended position sensitive cells show a higher firing frequency for a particular position if that position is achieved by extension rather than by flexion; the reverse situation occurring in flexed position sensitive cells (Wiersma, 1959; Laverack, 1966; Rao and Murthy, 1966; Mill and Lowe, 1972).

Differential sensitivity has been observed in the position units of both the posterior T-M organ and the F-P organ. As the flexed or extended position is approached, more position units are triggered. Thus, although the individual units fire over different ranges, considerable overlap occurs. The results of the current study differ from those of Rathmayer (1967) on the patella-femur joint of *Dugesiella* in that all of the tonic units which he recorded from were extension sensitive.

More work is certainly needed on these limb proprioceptors both in araneids and also in scorpions, especially since all of the previous physiological work has been on compound nerve preparations, under which circumstances it is generally only possible to ascribe sensory units to the joint and not to the specific receptor involved if there is more than one at the joint.

Finally, the fine structure of the araneid proprioceptors is, regrettably, not well established. Preliminary electron microscope observations (unpublished) support the light microscope work of Rathmayer and Koopman (1970) who state that they find no evidence of scolopales. The sensory cells are enclosed in a connective tissue sheath, while the dendrites terminate among the hypodermal cells of the articular membrane.

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