

FUNCTION OF A MUSCLE WHOSE APODEME TRAVELS THROUGH A JOINT MOVED BY OTHER MUSCLES: WHY THE RETRACTOR UNGUIS MUSCLE IN STICK INSECTS IS TRIPARTITE AND HAS NO ANTAGONIST

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Accepted 28 January 1991

Summary

The course of the common apodeme of the tripartite retractor unguis muscle is described for the stick insects *Carausius morosus* and *Acrophylla wulfingii*. This apodeme travels through the femoro-tibial joint well outside the axis of rotation of the joint, but movements of the femoro-tibial joint do not affect the position of the tarsal claws, which are moved by the retractor unguis muscle. The independence of tarsal position upon tibial position is not produced by a neural compensation mechanism but by a sophisticated morphological arrangement combined with specialized physiological properties. These mechanisms consist of two parts. (1) Moderate claw flexions are mainly produced by the smaller tibial parts of the muscle and their influence on claw position is not affected by tibial position, because they lie distal to the femoro-tibial joint. (2) The retractor unguis muscle works against strong elastic structures and the claw assumes the position where the elastic force is counterbalanced by the muscle force. The maximum muscle force of the strong femoral part of the muscle is nearly independent of muscle length. Therefore, the force it transfers to the elastic structures is also nearly independent of tibial position.

Introduction

In moving limbs there is an evolutionary tendency to place muscles in as proximal a position as possible because the moment of inertia of a given muscle mass increases with increasing distal positioning of the muscle. The same problem is obvious in robotics. In some cases this has led to the situation where the apodeme of a particular muscle (here called the investigated muscle) travels through a joint that is moved by other muscles (here called joint muscles). In most cases the apodeme of the investigated muscle does not go through the axis of rotation of the joint. This means that the movement of the joint by the joint muscles influences the position of the part of the limb governed by the investigated

Key words: stick insect, *Carausius morosus*, *Acrophylla wulfingii*, retractor unguis muscle, mutual influence of muscle action, muscle mechanics.

muscle, provided there is no compensatory effect on the investigated muscle. However, except for some examples where this effect is used for a special task (e.g. in passerine birds sitting on a stick), movement of the joint does not normally influence the position of the part of the limb governed by the investigated muscle. Therefore, one should expect to find compensatory effects on the investigated muscle. This is not, however, a necessary conclusion. We will present evidence that a sophisticated morphological arrangement and/or specialized physiological properties can do the same job. Apparently evolution follows a tendency that is also known from technical experience: if a certain problem can be solved either mechanically or by an information process, the mechanical solution seems to be the more advantageous.

We used the middle leg and hind leg retractor unguis muscle of the stick insects *Acrophylla wulfingii* Redtenbacher and *Carausius morosus* Brunner (for an anatomical description of the muscle in *Carausius*, see Godden, 1969; Walther, 1969, 1980; for a summary of stick insect anatomy, see Bässler, 1983). This muscle flexes the claw. It has no muscle as an antagonist, instead elastic structures function as antagonists (Walther, 1969). It consists of three parts that share a common apodeme; retractor unguis I (RUI) in the proximal part of the femur is the largest part of the muscle, retractor unguis II (RU II) is situated in the proximal part of the tibia and the tiny retractor unguis III (RU III) is situated in the distal part of the tibia. The retractor unguis apodeme travels between RUI and RU II through the femoro-tibial joint (moved by the extensor and flexor tibiae muscles) and distal to RU III through the tibio-tarsal joint (moved by the levator and depressor tarsi muscles).

Materials and methods

The experiments were performed using adult female stick insects of the species *Carausius morosus* (body length approximately 7 cm) and *Acrophylla wulfingii* (body length 18–22 cm) from the colonies at Kaiserslautern University.

Anatomy

The anatomical results were obtained using the following methods. (1) Reconstructions from serial transverse sections of *Carausius* middle or hind legs cut at 10 μm and stained either with Haematoxylin–Eosin or with Mallory's triple stain. (2) Whole mounts of legs of *Acrophylla* instars of different stages cleared with 10% KOH and embedded in Eukitt. (3) Direct preparations of middle and hind legs of adult female *Acrophylla* opened either from the posterior side or from the dorsal side. No differences between these preparations (except for the size) could be found. The results are therefore presented together.

Movement of the retractor unguis apodeme in isolated legs

The femur of an *Acrophylla* leg was fixed to a plate of plastic foam using dental adhesive (Scutan, Espe), posterior side up. The plane of movement of the tibia

was horizontal. A small window was cut into the femur approximately at its middle and the retractor unguis apodeme was held in a clamp which could be moved by a micromanipulator. The manipulator was moved by hand and the position of the clamp was read directly from the micromanipulator. Clamp position zero was defined from tarsal position and differed in different experiments (see Results section).

Force measurements

The forces produced by muscles or elastic structures were measured by a force transducer (Shinkoh UL) connected to a balanced bridge (Hellige TF 19) and a pen recorder. The force transducer could be moved by a micromanipulator.

Movement of the femoro-tibial joint

The animal (*Acrophylla*) was fixed on a cork plate with the body vertical and the head pointing upwards. The femur of the left hind leg was fixed in a horizontal position by Scutan with the anterior side pointing upwards and the plane of tibial movement being horizontal. The femoro-tibial joint, the tibio-tarsal joint and the tarsus were free to move. A small window was cut in the distal one-third of the fixed femur, the receptor apodeme of the femoral chordotonal organ was fixed to a clamp and then cut distal to the clamp (for the anatomy of the femoral chordotonal organ and its apodeme see Bässler, 1983, his Fig. 6.7). The clamp could be moved by a pen motor driven by a ramp generator. Details of this stimulation procedure are given in Bässler and Pflüger (1979). The mean stretch of the chordotonal organ corresponded to a femoro-tibial joint angle of 90°. The receptor apodeme was moved rampwise by 400 μm in both directions starting from the mean position. An amplitude of 400 μm corresponds to approximately 45° of joint movement. The leg movement was recorded by a video-system (Sony) and evaluated frame by frame.

Results

General anatomy

The following description is based on a reconstruction of the *Carausius* leg from serial sections and on preparations of *Acrophylla* legs (Fig. 1). Except for the larger size of *Acrophylla* the results were identical. The quantitative measurements are given only for *Acrophylla* because the physiological experiments were performed exclusively on this species.

In middle legs and hind legs, RUI is situated at the proximal end of the femur, slightly ventral to the midline. It consists of two separate bundles of muscle fibres that are separately attached to the retractor unguis apodeme (Godden, 1969; Walther, 1980). The retractor unguis apodeme travels through most of the femur close to the midline and towards the posterior side close to the two main tracheae (a larger main trachea on the anterior side and a smaller one on the posterior side). Some small tracheae leave the large main trachea on its ventral side and travel towards the body wall underneath the retractor unguis apodeme, where they join

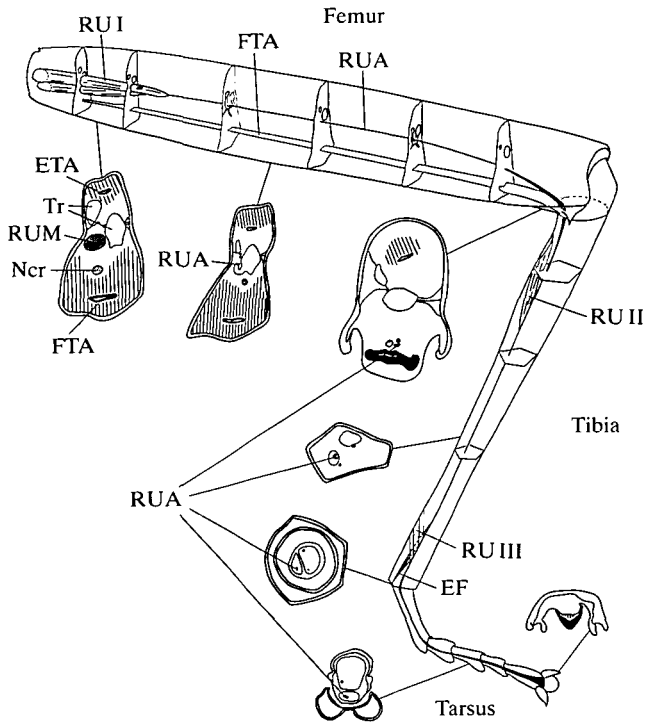


Fig. 1. The retractor unguis muscle and its apodeme in a stick insect hind leg seen from the posterior side. Gross anatomy from *Acrophylla wulfingii*, transverse sections from *Carausius morosus*. The transverse sections in the overview show the three-dimensional nature of the reconstruction. In the cross sections, the areas of flexor and extensor tibiae muscles are hatched. RUI, RUII, RU III, parts of the retractor unguis muscle (RUM). RUA, apodeme of the retractor unguis muscle; ETA, extensor tibiae apodeme; FTA, flexor tibiae apodeme; Tr, trachea; Ncr, nervus cruris; EF, elastic fibres. Femur length of *Acrophylla*, 3.7 cm; of *Carausius*, 1.4 cm.

the smaller main trachea. Side branches from these anastomoses supply the flexor tibiae muscle. The anastomoses between the two main tracheae stabilize the position of the retractor unguis apodeme. In the foreleg, the RUI muscle is situated more ventrally, owing to the deep indentation at the base of the prothoracic femur, but even in this leg, the apodeme approaches the midline of the femur, guided by the tracheal side branches (Godden, 1969).

As the retractor unguis apodeme approaches the femoro-tibial joint it becomes more ventrally situated. In the vicinity of the joint, it is flattened dorso-ventrally, as in all other joints. Inside the joint it lies just dorsal to the apodeme of the flexor tibiae muscle. The retractor unguis apodeme passes through the femoro-tibial joint greatly ventral to the axis of rotation of the joint. The exact axis of rotation of the femoro-tibial joint cannot be determined in a dissected preparation, because the socket of the joint cannot be seen in detail without destroying it. The distance between the axis of rotation and the retractor unguis apodeme can therefore only

be estimated. This distance ranges from 1.2 to 1.4 mm for *Acrophylla* middle legs and hind legs. An indirect measurement of this distance, which confirms this estimation, is presented below.

The retractor unguis apodeme continues through the whole tibia in a position somewhat ventral to the midline. The RUII muscle is attached to it near the proximal end of the tibia and the RUIII muscle near the distal end. Within the tibia, the retractor unguis apodeme is surrounded by a sheath of tissue, especially near the joints, which seems to guide it. The tibio-tarsal joint is also penetrated somewhat ventral to the middle. Inside the tarsus the retractor unguis apodeme travels on the ventral side, again guided by a sheath of tissue.

It is obvious that the distance between the axis of rotation of a joint and the retractor unguis apodeme is relatively large in the femoro-tibial joint and considerably smaller in the tibio-tarsal joint. Therefore, we concentrated further investigations on the femoro-tibial joint.

Dependence of tarsus position on retractor unguis apodeme position

In one series of experiments three isolated hind legs of *Acrophylla* were used. The legs were removed from the animal just before the experiments and the tibio-tarsal joint was immobilized in the 180° position using Scutan. (The tibio-tarsal joint can be moved by separate muscles within a wide range.) The retractor unguis apodeme was clamped in the middle of the femur, cut proximal to the clamp and then moved in steps. Retractor unguis apodeme position zero was defined as the position in which the tarsus is fully extended (approx. 190°). The retractor unguis apodeme was first moved towards the proximal end of the femur (until the tarsus was fully flexed) and then moved back again to zero. For each position of the retractor unguis apodeme the tarsal angle was measured. It was defined as the ventral angle between the longitudinal axis of the most proximal tarsal segment (and, in the fixed tibio-tarsal joint, also that of the tibia) and the longitudinal axis of the most distal tarsal segment. The measurements were taken at femur-tibia angles (angle between the longitudinal axes of femur and tibia) of 70°, 90° and 140°.

The measurements were identical for all femur-tibia angles, provided that the retractor unguis apodeme was positioned at zero by adjusting the clamp position according to the definition given above (position zero corresponds to a fully extended tarsus). Fig. 2 shows the results for one leg. The results for the other legs were nearly identical.

In a second series of experiments on two middle legs and two hind legs, a similar procedure was used. The retractor unguis apodeme was clamped at a femur-tibia angle of 90° and the clamp position was held constant while the femur-tibia angle was varied. The initial tarsal angle was then decreased by moving the clamp proximally and the measurements were repeated. The smaller the initial tarsal angle, the smaller was the maximum possible femur-tibia angle. Fig. 3 shows the results. An extension of the femoro-tibial joint resulted in a decrease in tarsal

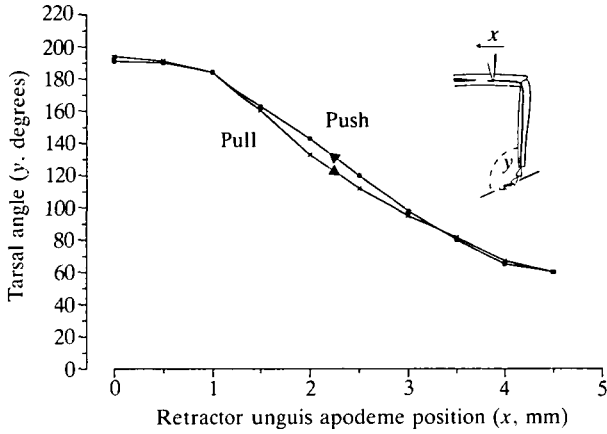


Fig. 2. Tarsal angle (the angle between the longitudinal axis of the tibia and the longitudinal axis of the most distal tarsal segment) in relation to retractor unguis apodeme position (position zero corresponds to a tarsal angle of 190°). The tibio-tarsal joint was fixed at 180°.

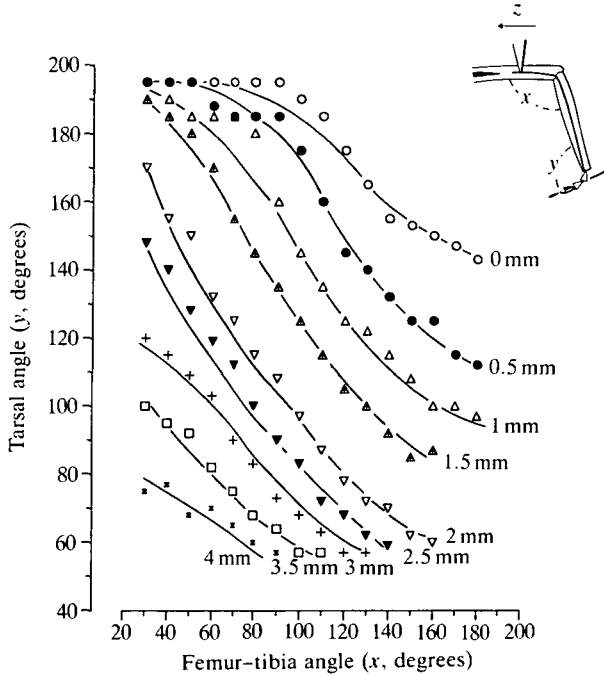


Fig. 3. Tarsal angle in relation to femur-tibia angle. The retractor unguis apodeme position was fixed. In this figure the zero position of the retractor unguis apodeme is defined as the position in which the tarsus is fully extended at a femur-tibia angle of 90°. The values are given for different, fixed retractor unguis apodeme positions. The tibio-tarsal joint was fixed at 180°.

angle. This again demonstrates that the retractor unguis apodeme travels significantly ventral to the axis of rotation of the femoro-tibial joint.

To test whether the immobilization of the tibio-tarsal joint influenced the results, two control experiments were performed. In the first, the retractor unguis apodeme was moved in the usual way in three isolated hind legs with fixed femoro-tibial joints but free tibio-tarsal joints. Initially, as the proximal movement of the retractor unguis apodeme was increased only the tarsus was flexed and the tibia-tarsus angle remained constant at its initial position of approximately 200° . The tibia-tarsus angle only decreased for approximately 20° after the tarsus had been fully flexed. Thus, the movement of the retractor unguis apodeme does not significantly influence the tibia-tarsus angle within the physiological range of retractor unguis apodeme movement. In the second control experiment, the tibia-tarsus angle of three other hind legs was altered while the retractor unguis apodeme was held in a fixed position (femur-tibia angle 90°). The tibia-tarsus angle had no effect on tarsal bending. This confirms that the retractor unguis apodeme crosses the tibio-tarsal joint quite close to its centre.

The retractor unguis muscle has no antagonist. Extension of the tarsus is apparently produced by elastic forces built up during tarsal flexion. In Fig. 2 there is no detectable hysteresis. Apparently the structures responsible for the elastic forces can totally override the friction inside the system. Two structures could be candidates for these elastic elements: the tarsal joints themselves and the elastic fibres situated between the retractor unguis apodeme and the ventral cuticle at the distal end of the tibia (see Fig. 1 and Walther, 1969). To distinguish between these two possibilities, the following two series of experiments were performed.

The retractor unguis apodeme in the femur was moved, as previously described, in three hind legs with the femur-tibia angle held at 90° and with the tibio-tarsal joint free. The tibia was opened at the centre, and the movement of the retractor unguis apodeme there was measured (Fig. 4A). Again, there is no hysteresis.

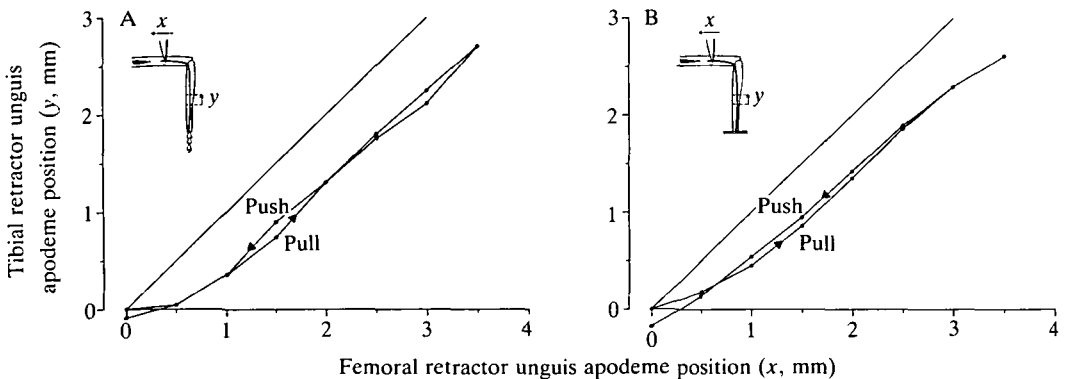


Fig. 4. Tibial retractor unguis apodeme position in relation to femoral retractor unguis apodeme position. The 45° slope is also drawn. (A) Intact leg; (B) tarsus amputated.

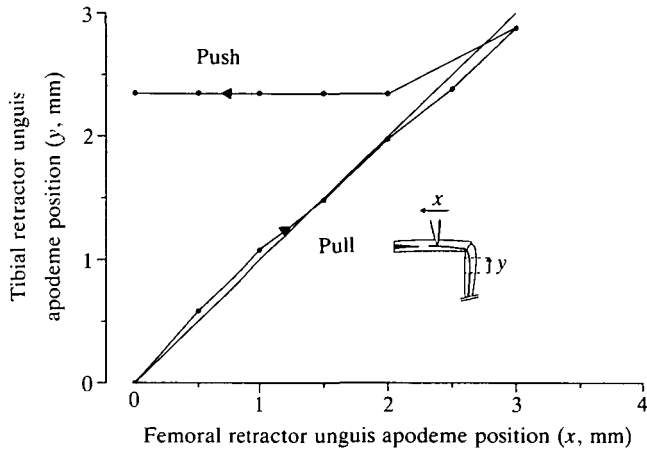


Fig. 5. Tibial retractor unguis apodeme position in relation to femoral retractor unguis apodeme position. The 45° slope is also drawn. The tarsus was amputated and the elastic fibres in the tibia were destroyed.

After removal of the tarsus at the tibio-tarsal joint (which cuts the distal apodeme attachment) the curve was unchanged, showing that the elastic fibres inside the tibia are sufficient to move the retractor unguis apodeme back without hysteresis (Fig. 4B).

In another series of experiments using three hind legs, the dependence of retractor unguis apodeme position in the tibia on its movement in the femur was measured in the intact isolated leg. The elastic fibres in the tibia were then destroyed: the curve did not change markedly. This indicates that the elasticity of the tarsus was also sufficient to move the retractor unguis apodeme back (see also Walther, 1969). When, in addition, the tarsus was also removed, the retractor unguis apodeme did not return to its initial position in the tibia (Fig. 5).

The distance between the axis of rotation of the femoro-tibial joint and the retractor unguis apodeme

The distance between the axis of rotation of the femoro-tibial joint and the retractor unguis apodeme can be calculated in the following way from the data shown in Figs 2 and 3. It is assumed that this distance is constant for all femur-tibia angles (but see below). Suppose that a certain tarsal angle (e.g. 150°) is maintained at a femur-tibia angle of 30° (the smallest possible femur-tibia angle) and with a certain retractor unguis apodeme position (initial position, in our example: 2.5 mm). If the femur-tibia angle is then brought to 180°, the tarsus flexes. One has now to look for the retractor unguis apodeme position that produces a tarsal angle of 150° with a femur-tibia position of 180° (in our example: 0 mm). The difference between this retractor unguis apodeme position and the initial position is slightly less than twice the distance between the axis of rotation of

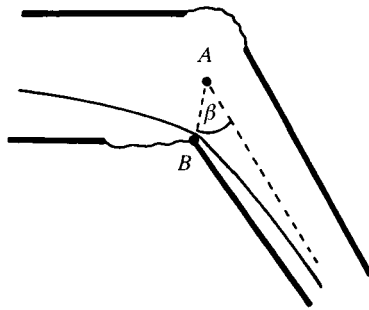


Fig. 6. Position of the retractor unguis apodeme in the region of the femoro-tibial joint. *A*, axis of rotation of the femoro-tibial joint; *B*, point where the retractor unguis apodeme enters the tibia. See text for a definition of β .

the femoro-tibial joint and the retractor unguis apodeme (if the tibial movement had been 180° , it would have been exactly twice this distance).

According to these calculations, the distance between the axis of rotation of the femoro-tibial joint (*A* in Fig. 6) and the point where the retractor unguis apodeme enters the tibia (*B* in Fig. 6) is 1.2–1.3 mm. This value was used to calculate the movement of the retractor unguis apodeme in the tibia when the apodeme was clamped within the femur and the femoro-tibial joint was moved. From anatomical measurements, it was assumed that the angle β between *BA* and the longitudinal axis of the tibia is 20° (Fig. 6). Within the limits of measurement, the calculation fits the data for femur–tibia angles of between 30° and 150° . When the femur–tibia angle approaches 180° , the calculated values differ from the measured values to some extent, indicating that the distance between the retractor unguis apodeme and the axis of rotation of the femur–tibia joint becomes smaller.

Forces produced by RUI, RUII and elastic structures

The experiments described in this section were performed with *Acrophylla* legs connected to the animal. In one series of experiments using four middle legs the forces produced by RUI and RUII were measured separately by force transducers attached to the apodeme. The retractor unguis apodeme was cut between the two muscles. The animals were touched on the abdomen from time to time to produce active movements.

In most cases the forces of RUI and RUII increased at the same time. Very rarely only RUI contracted. After a period of activity, the force of RUI dropped to the initial value in all cases, but the force of RUII often fell below the original value at first, and then slowly climbed to the initial value (Fig. 7), which was reached after 10–60 s. Apparently, the RUI muscle did not actively produce force in the inactive animal, but, in many cases, the RUII muscle did. The maximum forces produced were 21–27 mN for RUI and 9–21 mN for RUII (with RUII forces measured relative to the value for the inactive animal).

In a second series of experiments, using three hind legs, the femur was again

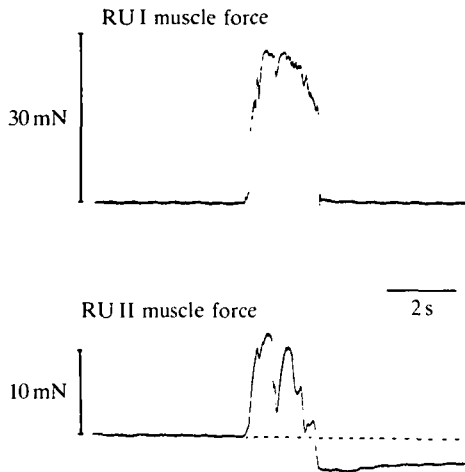


Fig. 7. Typical recordings of force development of muscles RUI and RUII. The time is too short to see that the force of RUII recovers to its initial value.

opened from the posterior side within the distal half and the retractor unguis apodeme was cut. At first, the part of the apodeme leading to the RUI muscle was clamped. The clamp was fixed to a force transducer which could be moved by a micromanipulator. The force produced by the muscle was measured for different positions of the clamp in the inactive animal as well as after the animal had been activated by squeezing its abdomen. Minimum muscle length corresponded to a totally relaxed tarsus at a femur–tibia angle of 30° . Fig. 8 shows the dependence of the forces produced by the muscle in the inactive animal upon the position of the retractor unguis apodeme and also the maximum forces produced by RUI in the active animal. In both cases, forces show little increase with increasing muscle length. It remains an open question whether this is due to an unusually flat load–displacement plot for this muscle or to a neural compensatory mechanism caused by unknown sense organs.

The force transducer was then attached to the end of the retractor unguis apodeme that travelled distally. The forces produced by the elastic structures in the tibia and tarsus were measured at different positions of the retractor unguis apodeme in the femur. The results are also shown in Fig. 8. The forces are considerably higher than the muscle forces and depend to a high degree on retractor unguis apodeme position. Similar results have been obtained for *Carausius* (Walther, 1969).

Tarsal angle during real or fictive movements of the femoro-tibial joint

In these experiments, carried out on four hind legs, the femoral chordotonal organ was stimulated and movements of the tibia and tarsus were recorded. Stimulating the femoral chordotonal organ with ramps of different velocities at an amplitude of $400 \mu\text{m}$ in the open-loop system caused movements of the femoro-

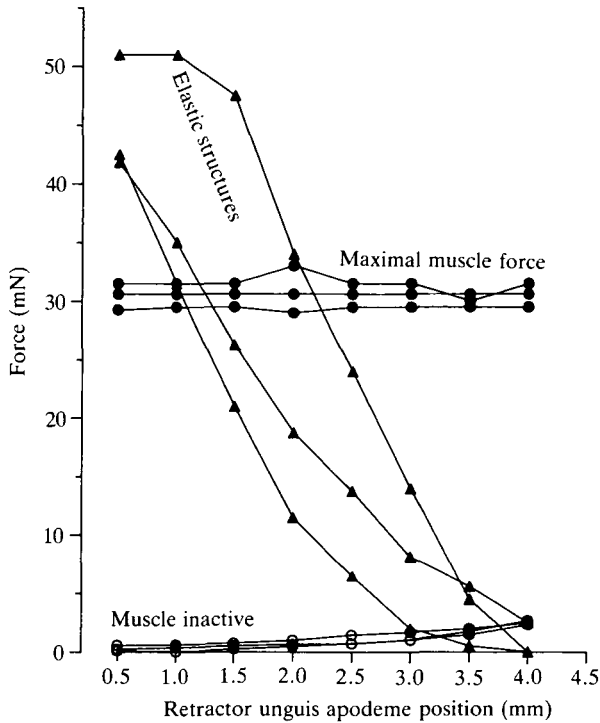


Fig. 8. Forces produced by the elastic structures (▲) (tarsal joints and tibial elastic fibres), the inactive RUI muscle (○) (only static forces) and the maximal force produced by the RUI muscle in the active animal (●) in relation to the position of the retractor unguis apodeme. Position zero of the retractor unguis corresponds to its position with a totally relaxed tarsus, at a femur–tibia angle of 30° . The values for three hind legs are given separately.

tibial joint of $70\text{--}85^\circ$. During 114 such movements no significant change in tibia–tarsus angle and in tarsus position could be detected (accuracy of measurement for the latter 5°). In all the tested legs the tarsus was kept slightly flexed (tarsal angles between 130° and 100°) and these angles did not change. After some time the apodemes of the extensor and flexor tibiae muscles were cut close to the joint, leaving the retractor unguis apodeme intact. No significant change in tibia–tarsus angle and tarsal position could be measured during 46 ramp stimuli to the femoral chordotonal organ. Again, the tarsus was kept slightly flexed during the experiments.

Discussion

The anatomical observations and the experiments on legs removed from the animal show that the retractor unguis apodeme travels through the femur–tibia joint far away from its axis of rotation. Therefore, the distance between the origin of the RUI muscle and the tarsus depends on the position of the femoro-tibial

joint. The change in this distance during a 150° movement of the femoro-tibial joint is sufficient for a total flexion of the tarsus, provided that the RUI muscle is absolutely stiff.

When the femoral chordotonal organ signalled a movement of the femoro-tibial joint, the slightly flexed tarsal position was not altered. This occurred both when the joint could be moved by the extensor and flexor tibiae muscles and when the joint remained immobile because the muscle apodemes had been cut. This shows two things: (1) a movement of the femoro-tibial joint does not influence the tarsal position in the living animal; (2) since there was no influence of femoral chordotonal organ stimulation on tarsal position, either in the moving or in the immobile femoro-tibial joint, this effect could not have been caused by a neural compensatory mechanism. Instead, mechanical properties of the system must be responsible for the immobility of the tarsus during movements of the femoro-tibial joint.

From our experiments, two mechanisms can be proposed that compensate for the change in the distance between the origin of the RUI muscle and the tarsus during movements of the femoro-tibial joint. First, moderate flexion of the tarsus is produced mainly by RUII (and perhaps also by RUIII). RUI only comes into play when the animal becomes active. This is demonstrated by the force measurements reported in this article but was also confirmed by simultaneous electrophysiological records from all three parts of the retractor unguis muscle (G. Radnikow, unpublished results). The maximum force of RUII was found to be approximately 20 mN, which is sufficient to counterbalance the force of the elastic structures at moderate tarsus flexion (see Fig. 8). Since the retractor unguis apodeme passes through the tibio-tarsal joint close to its centre, and since the inactive RUI muscle does not produce noticeable force during its elongation, movements of other joints cannot influence a tarsal position that is only caused by RUII and RUIII muscles.

The mechanism described above explains the advantage of a divided RU muscle. The smaller RUII and RUIII muscles are situated distal to the femoro-tibial joint. They are large enough to flex the unloaded tarsus moderately but small enough not to produce a large moment of inertia. The larger (and heavier) RUI is situated as far to the proximal end of the femur as possible, so that it does not produce a large moment of inertia. It generates the large forces necessary for grasping the ground.

Second, the tarsal position is a function of the force that is transferred by the retractor unguis apodeme to the elastic structures. The tarsus flexes to the position in which the retractor unguis force is counterbalanced by the elastic force. Let us assume (contrary to reality) that the RUI muscle is exclusively responsible for the retractor unguis force. A change in femur-tibia angle would then change the length of the RUI muscle. However, Fig. 8 shows that the RUI force is, in contrast to that of many other muscles, not very dependent on muscle length. (The reason for this characteristic is unknown.) Therefore, a change in femur-tibia angle would only slightly alter RUI force. Since a marked change in muscle force

is necessary for a change in tarsal position (Fig. 8), a movement of the femoro-tibial joint should produce only small movements of the tarsus, even if the whole retractor unguis force is produced by RUI.

For the mechanism described above, there are two prerequisites: in the contracting muscle the force must be nearly independent of muscle length, i.e. the muscle should not be very stiff, and the muscle must work against a rather stiff elastic structure. These prerequisites cannot be fulfilled by a pair of antagonistic muscles for the following reasons. To produce flexion the flexor should contract but should not be stiff, i.e. should not increase force when passively elongated, and the inactive extensor should be stiff, i.e. should produce rather strong forces when passively elongated. For extension movements, the inactive flexor should be stiff and the active extensor not stiff. Muscles do not act in this way. This might provide an explanation of why it is advantageous for the retractor unguis muscle to have no antagonist but to work against elastic structures.

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