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## RESTING TENSION AND POSTURE IN ARTHROPODS

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This study was prompted by reports of resting tension in muscles of various arthropods (Machin & Pringle, 1959; Hoyle, 1968; Burns & Usherwood, 1978; Hoyle, 1978; Hawkins & Bruner, 1979) and our observation that when the legs of the cockroach and crab are severed from the thorax, the joints appear to assume rather fixed angles. Recently Chesler & Fournier (1981) have shown that significant resting tension exists in one of the femoral extensors of the cockroach (muscle 177d) (Carbonell, 1947). The purpose of this study was to determine if resting tension is characteristic of all the limb muscles and if it could account for the fixed angle of the joint. We present evidence in this report that resting tension in the leg muscles of the cockroach, *Periplaneta americana*, and the crab, *Carcinus maenas*, is responsible for maintaining a relatively fixed angle in the joints of the limbs. These data, along with other evidence, provide a good argument for a system in which posture is partially maintained in these arthropods by resting tension which appears to be passive in nature. The maintenance of posture by this passive mechanism could result in an energetic savings in a quiescent arthropod.

All experiments were performed on amputated legs which were pinned firmly to a Sylgard base in a dish filled with oxygenated saline (Chesler & Fournier, 1981). Tension recordings in the cockroach were made by gripping the cut tendon with the welded ends of a pair of No. 5 forceps rigidly attached to an RCA 5734 transducer tube. The transducer was mounted on a Narishige (M3) micromanipulator and the length of the muscle was determined directly from the vernier as the muscle was shortened from its maximum physiological length. The initial tension, produced after stretching the muscle to its maximum physiological length, was allowed to decay to a steady-state value (approximately 15 min) before measurements were made. All tension measurements made after muscle shortening were also steady-state values.

Fig. 1 illustrates the length-tension relationships of resting tension in the meta-thoracic femoral extensor muscles 177d and 178 of *P. americana*. Muscle 177d not only develops far more resting tension at maximum physiological length than 178, but it also develops tension over its entire physiological range. 177d had a mean resting tension of  $2.6 \pm 0.4$  g ( $n = 11$ ) at maximum physiological length while muscle 178 had a mean resting tension of  $0.11 \pm 0.04$  g ( $n = 4$ ). The difference in these values is particularly striking since muscle 178 is about 13 times more massive than 177d (wet mass 3.8 mg and 0.3 mg respectively). Ultrastructural studies (Fournier, 1978) show

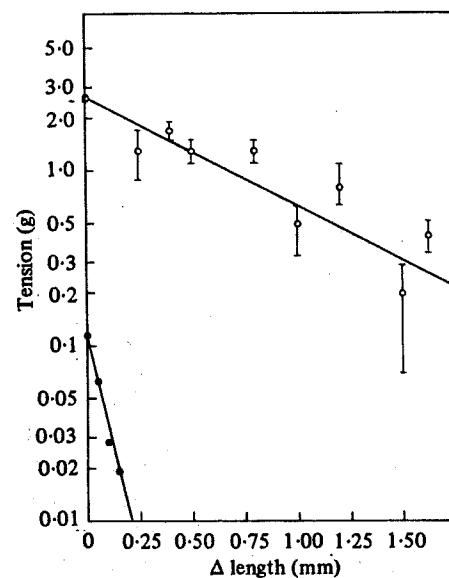


Fig. 1. Length *v.* log-tension relationships for the metathoracic femoral extensor muscles 178 (●) and 177d (○) of the cockroach *P. americana*. The mean tension values for each length are given with error bars of  $\pm 1$  s.e. for 177d. Similar bars for muscle 178 have been omitted for clarity.  $\Delta$  length = 0 represents maximum physiological length (full femoral flexion) and  $\Delta$  length = 1.60 mm represents minimum physiological length for both muscles. Regression lines were calculated from each set of data with correlation coefficients of 0.65 ( $n = 49$ ) for 177d and 0.93 ( $n = 19$ ) for 178.

that muscle 177d has fibres with long ( $7.5 \mu\text{m}$ ) sarcomeres and numerous mitochondria while 178 has relatively short ( $3.7 \mu\text{m}$ ) sarcomeres and few mitochondria. Another femoral extensor (177d') (Becht, 1959) which is ultrastructurally and biochemically intermediate ( $4.2 \mu\text{m}$  sarcomere length, numerous mitochondria) has a low mean resting tension of  $0.10 \pm 0.02$  g ( $n = 4$ ).

Because 177d and 178 belong to a complex set of muscles operating the coxa-trochanter-femur joint and because certain femoral extensors originate in the thorax, the effect of resting tension on joint position is difficult to assess. The femur-tibia (FT) joint was more amenable for study because extension and flexion of the tibia is brought about by the action of only two antagonistic muscles. Angles of the FT joint were measured by cutting the legs from the thorax and measuring the position of the unrestrained appendages with a protractor. The mean value of the FT joint in the cockroach was  $72 \pm 6^\circ$  ( $n = 11$ ); total angular range  $137^\circ$ . When these muscles were stretched to their maximum physiological length, the extensor and flexor tibiae had mean resting tensions of  $3.9 \pm 0.3$  g ( $n = 11$ ) and  $4.3 \pm 0.7$  g ( $n = 10$ ) respectively. These muscles, like 177d, develop measurable tension over their entire physiological range (Fig. 2a).

The point where the antagonistic muscles exert equal tension was determined graphically. This point corresponds to an angle of  $78^\circ$ , which is within one standard deviation of the measured FT joint angle.

In the shore crab, *C. meanas*, we measured the angle of the meropodite-carpodite

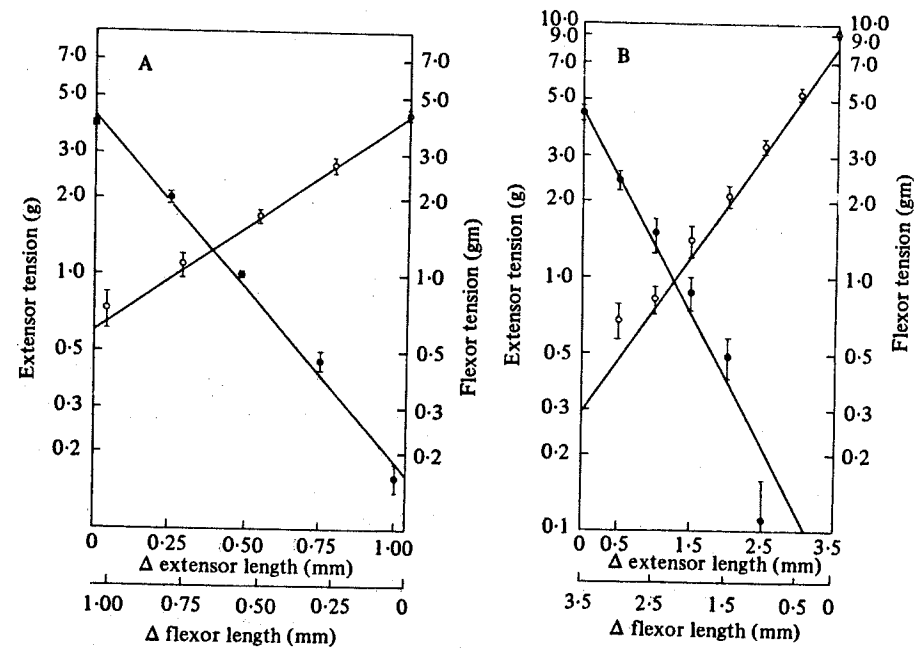


Fig. 2. Length v. log-tension relationships in the extensor and flexor tibiae of *P. americana* (A) and the MC extensor and flexor of *C. maenas* (B). In both plots, extensor data are represented by filled circles and flexor data by open circles. The mean values for each muscle length are given with error bars of  $\pm$  s.e. (A)  $\Delta$  length = 0 represents maximum physiological length and  $\Delta$  length = 1.04 mm represents minimum physiological length for both muscles. Regression lines were calculated from each set of data with correlation coefficients of 0.92 ( $n = 60$ ) for the extensor and 0.74 ( $n = 59$ ) for the flexor. The point of equal tension occurs at a joint angle of  $78^\circ$ . (B)  $\Delta$  length = 0 and  $\Delta$  length = 3.5 mm represent maximum and minimum physiological length respectively for both muscles. The calculated regression line for the extensor had a correlation coefficient of 0.87 ( $n = 43$ ) while the regression line for the flexor had a correlation coefficient of 0.92 ( $n = 66$ ). The point of equal tension occurs at a joint angle of  $80^\circ$ . In both (A) and (B), the joint angle for a given muscle length was determined using the formula  $\theta_j = \Delta l_{\text{ext}} (\theta_i / l_i) + \theta_f$ , where  $\theta_j$  = joint angle,  $\Delta l_{\text{ext}}$  =  $\Delta$  length (extensor),  $\theta_i$  = total angular range of the joint,  $l_i$  = physiological length range of the muscle,  $\theta_f$  = mean maximum flexed angle ((A)  $27^\circ$ , (B)  $30^\circ$ ).

(MC) joint in amputated legs. Tension recordings in the extensor and flexor were made by attaching the tendon to a Grass tension transducer by means of a hooked pin tied to a thread.

Tension was recorded in the extensor and flexor over the entire physiological length. Resting tension in the extensor and flexor at maximum physiological length was  $4.4 \pm 0.8$  g ( $n = 8$ ) and  $9.1 \pm 1.1$  g ( $n = 10$ ) respectively. The angular range of the MC joint was found to be  $140^\circ$  while the measured angle of the unrestrained joint had a mean value of  $82 \pm 10^\circ$  ( $n = 33$ ). Fig. 2(b) graphically illustrates the point of equal tension, which corresponds to an angle of  $80^\circ$ . This angle is within one standard deviation of the measured angle.

To determine if an active process may be involved in the maintenance of resting tension, tension measurements were made while varying the potassium ion concentration of the saline. If the resting membrane potential in normal saline was above the

excitation-contraction threshold, salines with low  $K^+$  concentrations should eliminate or significantly reduce resting tension. In both the extensor and flexor tibiae of the cockroach and the MC extensor and flexor of the crab, resting tension was not altered significantly in low potassium (1.0 mM- $K^+$ ) saline. When low-potassium salines were exchanged with normal saline (10 mM- $K^+$ , cockroach; 12 mM- $K^+$ , crab) no increase in tension was observed. These findings are consistent with data from other arthropod muscles in which the threshold for potassium contracture was at least 20 mM- $K^+$  or greater (Huddart, 1969; Huddart & Abram, 1969). However, muscle 177d differed in that tension was reduced from  $2.6 \pm 0.4$  g to  $1.5 \pm 0.8$  g ( $n = 6$ ) in low- $K^+$  solutions. Nevertheless, resting tension was never reduced by more than 50% of its value measured in normal saline.

From the data presented in Fig. 2, we suggest that resting tension in the antagonist muscles maintains the joint at a fixed angle. This conclusion is based on the correspondence between the measured angle and the angle derived graphically from the length-tension plots. In addition, the tension exerted by the antagonistic muscles at the point of equal tension is 1.2 and 1.0 g for the cockroach and crab respectively. At these points, the value of the passive tension developed by each muscle at a single joint in a single leg is approximately equal to the weight of the animal (0.9 g, cockroach; 1.5 g crab - in sea water). These data suggest that passive tension may play a significant role in posture. If we assume that the total weight of the animal is applied to a single muscle (extensor), the exponential increase in tension resulting from the applied load would result in a relatively small angular change of the joint (23°, cockroach; 30°, crab). Therefore, the stiffness of the muscles in the joints of all the legs might be sufficient to support a resting arthropod. A more rigorous analysis of all supporting limbs and joint angles would be required to prove this hypothesis.

The low-potassium experiments indicate that resting tension is not due to a voltage-sensitive excitation-contraction process. This suggests that resting tension is the result of the passive properties of the muscle fibres and/or the connective tissue sheath surrounding the muscles. This passive tension may thus explain the rather paradoxical observations in cockroaches (C. R. Fortner, unpublished results) and crabs (F. Clarac, personal communication) that these animals can maintain postural positions in the absence of muscle electrical activity (EMG). A lack of EMGs during maintained resting tension has also been noted in the leg of the scorpion (R. F. Bowerman, personal communication). From our data and these observations, we conclude that non-neural resting tension can be used to maintain joint position in arthropods and provide an energetically favourable means of maintaining posture.

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no def. ! Really ?

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