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Responses of bender apodeme tension receptors in the Dungeness crab, *Cancer magister*

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Receptors monitoring tension are located on the apodemes of the bender (productor propoditis) muscle of walking legs and chelipeds of the Dungeness crab, *Cancer magister*. The bipolar neurons form a nerve, the bender apodeme sensory nerve (BASN), which joins the CP1 chordotonal organ nerve proximally. BASN units exhibit spontaneous activity at rest, and fire bursts of action potentials to rapid passive reduction of the carpopodite–propodite joint. Isometric contraction of the bender muscle results in BASN output that is directly related to force. Afferent activity ceases upon quick release of isometric tension, when tension drops to zero, and the unloaded muscle contracts isotonically.

Key words: Tension receptor; Proprioceptor; Bender muscle; Chordotonal organ; *Cancer magister*.

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Introduction

Receptors signaling joint movement and position, and muscle tension and length, are well known for vertebrate joints and appendages. The counterparts of such receptors have been described in the limbs and joints of arthropods, particularly crabs (Macmillan, 1976). Macmillan and Dando (1972) discovered that the apodemes of the powerful flexor and extensor muscles of the meropodite in the brachyuran crab *Cancer magister* are innervated by sensory cells reponsive to isometric tension development as well as to isotonic contraction against increasing loads. Eagles and Laverack (1987) examined the functional relationships between individual tension units, specific motor units, and tension in the flexor of the merus. They reported that for the flexor apodeme sensory units in *Cancer pagurus*, the frequency of firing of individual afferents did not appear to be a function of the rate or level of tension achieved, but, instead, depended on which excitatory motor neuron they stimulated.

Further investigation of the walking legs of *C. magister*, provided preliminary anatomical evidence that the other muscles also had tension receptors associated with their apodemes (Macmillan and Dando, 1972; Macmillan, 1976). Hartman (1985) provided anatomical and physiological evidence of tension receptors on the closer muscle apodemes in *Callinectes sapidus*. He showed that these receptors responded to forces of less than a gram. More recently,

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Tryba and Hartman (1993) reported similar low-threshold sensitivity for apodeme receptors monitoring tension development by the relatively feeble opener muscle in *C. sapidus*. In the latter experiments, in which the opener muscle was treated as a single motor unit, they report that the instantaneous firing frequency of individual tension units clearly increases with the rate and force of tension development.

Parsons (1980) showed that tension receptors of the flexor exhibit general arthropod mechanoreceptor anatomical features including a cell body, connecting sensillum, and sheathed sensory processes. However, the distal portion of the sensory ending is peculiarly convoluted as it passes through the hypodermis before terminating in the endocuticle (Parsons, 1980). Hartman (1985) and Tryba and Hartman (1993) showed that the tension receptors on the closer and opener muscle apodemes have similar anatomical features.

In this communication, we report the presence of receptors on the bender (productor propoditis) muscle apodeme at the carpopodite–propodite joint in *C. magister*. Our experiments indicate that while the receptors are responsive to passive length changes of the bender muscle, they meet the physiological criteria described for tension receptors (Hartman, 1985). Interestingly, the tension nerve joins the nearby CP1 chordotonal organ nerve before merging with the motor nerve to the bender muscle. We propose that, except for the opener muscle, tension nerves are associated with the chordotonal organ attached to each apodeme and merge with the motor nerve that innevervates each muscle.

Materials and Methods

Specimens of the Dungeness crab, *Cancer magister* measuring 10–12 cm across the carapace were caught in the boat basin area of Charleston, OR. They were either shipped to our laboratory where they were maintained in 80-gallon aquaria containing artificial seawater, or used for experimentation while we were in residence at the Oregon Institute of Marine Biology, Charleston, OR. The animals were fed squid periodically and used in experiments within 2 weeks of capture. The claws were used for experimentation because the tension and motor nerves are more accessible than those in walking legs.

In order to find the CP1 organ and its associated tension nerve, yet leave the bender muscle and motor nerve uninjured for stimulation, the following dissection was carried out. The animal was induced to autotomize the limb by slowly cutting across the merus with stout scissors. The distal half of the propodite was removed. A patch of cuticle on the ventromedial side of the carpus was removed from an area where no muscle fibers were attached. The patch of cuticle and underlying pigment layer were lifted away and the stretcher muscle was removed. The preparation was then pinned, lateral side down, to a Petri dish that was lined with Sylgard.

After retracting the proximal part of the main leg nerve away from the preparation, the main leg nerve in the distal region of the carpopodite was pinned away from the bender apodeme. In this way, the carpopodite–propodite (CP1) chordotonal organ strand and its nerve bundle could be seen to be attached to the connective tissue around the distal third of the apodeme. By following the path of the CP1 nerve proximally, a smaller nerve could be seen branching from it. This nerve, the bender apodeme sensory nerve (BASN), ran along the apodeme toward the base of the CP1 elastic strand attachment. By teasing the BASN away from the CP1 nerve bundle in a proximal direction, the tension nerve could be seen to merge with the bender motor nerve. At this junction, the BASN was severed; about 2 cm of motor nerve was separated from the proximal end of the main leg nerve for stimulation (Fig. 1).

In order to improve the viability of preparations, *C. magister* serum, rather than artificial saline, was used as a bathing medium. Whole blood was obtained by cardiac puncture from living, commercially caught crabs at the Point St George Fisheries of Port Orford, OR. Blood pooled from many crabs was cooled in an ice-bath. The clot that formed was discarded, and the resulting serum was filtered through a coarse filter, and stored in bottles or vials at −80°C until needed. The serum was periodically changed during the dissection

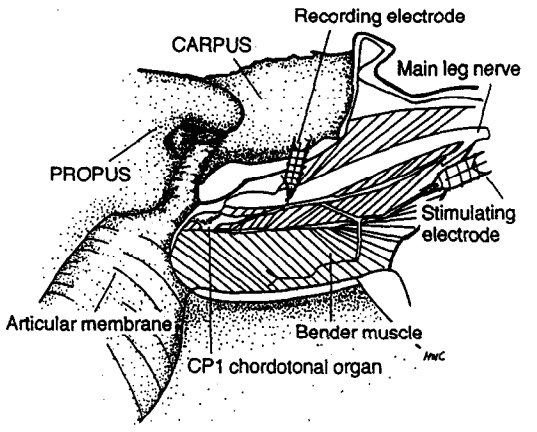

Fig. 1. Experimental arrangement for stimulating the motor nerve to the bender muscle and recording action potentials from the bender apodeme sensory nerve (BASN) of the right cheliped of *Cancer magister*. The stretcher muscle has been removed and the bender is viewed from the medial aspect. The carpus was fastened firmly to the recording dish but the propus could be moved and pinned at various positions to obtain production (+37°), extension (0°), and reduction (−37°) of the joint.

and at about 30-min intervals during the recording session. The preparation dish was fastened to a constant-temperature heat-sink which maintained its contents at 12–15°C.

For recording, the cut end of the BASN was drawn into a glass suction electrode having a tip diameter of about 20 μm (Hartman and Boettiger, 1967). A generous length of nerve was left outside the electrode so that it would remain flaccid and not be pulled from the electrode when the muscle contracted. The cut end of the bender motor nerve was drawn into another suction electrode having a tip diameter in the range of 40–50 μm. Stimulation was delivered to the nerve by a Grass S8 stimulator with a stimulus isolation unit interposed. Data were stored on VHS tape using an A. R. Vetter Co. (Model 420-D) data recorder. Following the experiment, data were analyzed using a MacADIOS 411 data acquisition system and a Macintosh microcomputer. Instantaneous frequency of the summed responses of the BASN was calculated and displayed for bin widths of 125 or 250 msec.

The tension neurons of the bender apodeme were revealed by staining the preparations for several hours in a 0.05% solution of Methylene Blue in HEPES buffered *C. magister* saline (Macmillan and Dando, 1972) at pH 7.4. The anatomy of the tension receptors was also determined by placing the cut end of the BASN in a petroleum jelly well, and backfilling the nerve with 300 mM $CoCl_2$ for 24 hr at 4°C. Backfilling was followed by several washes in saline, ammonium sulfide precipitation, fixation in Carnoy's, dehydration in an ascending alcohol series, and clearing in methyl salicylate. Drawings of the receptor cells and the preparations were made with the aid of a camera lucida fitted to a Wild M5 dissecting microscope.

Results

Anatomy of bender tension receptors in the claw

Both cobalt chloride backfills and Methylene Blue staining reveal a fine nerve, the bender apodeme sensory nerve (BASN), originating from several large bipolar neurons on the lateral face of the bender apodeme. The BASN exits midway along the ventral edge of the apodeme adjacent to the CP1 strand attachment and joins the CP1 nerve proximally before merging with the bender motor nerve (Fig. 2). Cobalt chloride backfilling revealed three tension neurons innervating the ventrolateral side and 5–7 associated with the medial side of the bender apodeme. The somata of these neurons are about 20 μm in diameter. Their

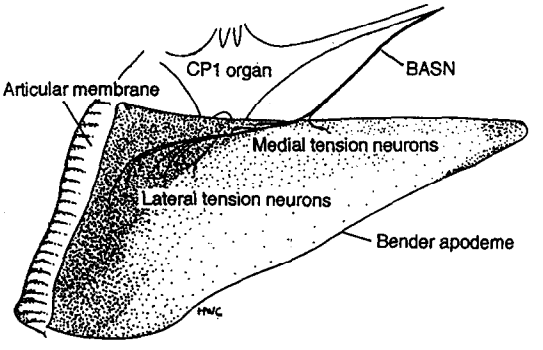

Fig. 2. A camera lucida drawing that illustrates the bender apodeme, the CP1 organ, and anatomy of tension neurons of the bender apodeme sensory nerve (BASN) of the right cheliped of *Cancer magister*. The sensory cells, revealed by cobalt chloride backfilling, are arranged along the apodeme in medial and lateral populations.

axons merge to form the BASN before joining the CP1 nerve. There are probably some additional tension neurons buried distally along the apodeme of the bender muscle that were not revealed by our staining procedures. Figure 2 shows the arrangement of the tension cells along the apodeme in a cobalt backfill preparation; this anatomy is typical of the five successful backfill cheliped preparations examined.

Responses of BASN to passive joint movements

The carpopodite–propodite joint of the chelipeds in *C. magister* can move over a range of about 65° (+37° fully producted to −37° fully reducted) as a result of contraction of the bender and stretcher muscles, respectively. The bender muscle is relaxed and flaccid at +37°, but fully stretched at −37°. To determine if the units of the BASN respond to passive stretch of the bender muscle, the propus was moved over the 65° range from +37° to −37° then returned to +37° while recording from the BASN. Before the movement was initiated, little spontaneous activity in the BASN was observed (Fig. 3). However, summed activity from several units increased markedly to a peak instantaneous frequency of about 125 Hz during the course of slowly (10°/sec) moving the propus to −37°, and declined to nearly 0 Hz as the joint was returned to +37° over the same time course. More rapid (20°/sec) passive movement of the joint to −37° evoked a higher rate of firing

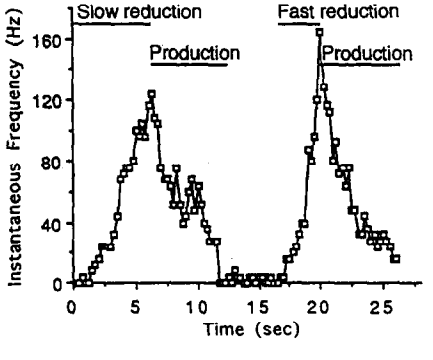

Fig. 3. Instantaneous frequency of discharges by the BASN to rapid, passive reduction and production of the propus. Instantaneous frequency in this and following figures was averaged for bin widths of 250 msec except as noted. Note the higher frequency burst of action potentials evoked by fast reduction.

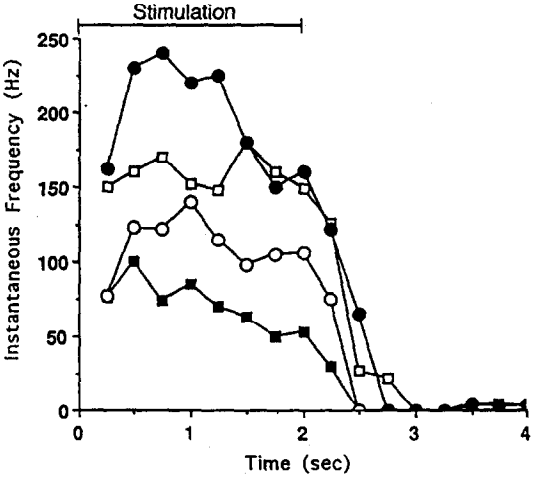

Fig. 4. Instantaneous frequency of discharges by the BASN to isometric contractions of the bender muscle as a result of stimulating the bender motor nerve at various frequencies. The propus was fully reducted and pinned to the preparation dish so as to stretch the muscle fibers before stimulation at 20 Hz (■), 40 Hz (○), 60 Hz (□), and 100 Hz (●) for 2 sec.

(*c.* 160 Hz) from the BASN (Fig. 3). If the joint is maintained at −37° (not shown), the neural activity slowly declines to its basal activity over several seconds. This pattern of activity to passive joint movement was observed in the several preparations examined.

Responses of the BASN to isometric contraction

The force of muscle contraction increases when excitatory motor neurons are stimulated at increasing frequency. One would expect sensory neurons responsive to tension to monitor this increase in force. With the propus fastened so that the bender muscle is stretched (approximating −37°), the bender motor nerve was stimulated for 2 sec at frequencies of 20, 40, 60 and 100/sec to produce successively greater contractile forces. These contractions of the muscle evoked responses by sensory units in the BASN that paralleled the force developed by the muscle. As may be seen in Fig. 4, when the motor nerve is stimulated at 20/sec, the firing by BASN units rose to a peak instantaneous frequency of about 100 Hz in the first 0.5 sec but declined steadily to 50 Hz, even though stimulation continued for an additional 1.5 sec. Raising the rate of stimulation to 40/sec produced

greater muscle contractile force and a peak instantaneous frequency of about 125 Hz by the BASN units. The rate of firing declined slowly thereafter to about 110 Hz by the end of stimulation. When the stimulus frequency was elevated to 60/sec the output by the BASN units peaked at about 160 Hz within 0.5 sec of stimulus delivery; that discharge rate continued for the period of stimulation. Upon stimulation at 100/sec, the instantaneous frequency of BASN units rose quickly to about 230 Hz, but dropped to about 160 Hz by the end of stimulation. As the bender muscle relaxed following cessation of stimulation, the instantaneous frequency of firing by BASN units dropped to zero. The several preparations examined all showed the same general responses. That is, with an increase in the stimulus frequency, the isometric latency of contraction shortened, resulting in an earlier output and higher frequency of firing by BASN units. Also, following the completion of stimulation, BASN units continued to fire for at least an additional 0.5 sec after the stimulus ended. The post-stimulus sensory response increased in duration with an increase in muscle relaxation period, following higher frequency stimuli. One second after the termination of the stimulus, the tension nerve activity usually returned to the basal level preceding stimulation.

In the fully reducted position (at $-37°$), the bender muscle fibers are fully stretched and as the joint is producted, the bender muscle becomes increasingly flaccid. Therefore, tension units should respond maximally to contractions when the joint is at $-37°$ and minimally to contractions when the joint position is at $+37°$. In order to achieve a range of *in situ* muscle rest lengths, and therefore differing tensions, the CP joint was pinned in turn at $+37°$, $0°$ (joint extended), and $-37°$ and the bender motor nerve stimulated for 2/sec at 40/sec. As may be seen in Fig. 5, with the joint fixed at $+37°$, stimulation resulted in a long period of isometric latency which evoked a slow build-up of impulses from the BASN; the responses after initially rising to 60 Hz, fell quickly to about 25 Hz after 1 sec where they remained until the stimulation was concluded. Upon stimulation with the joint fixed at $0°$, the discharge frequency by the BASN rose more quickly to about 75 Hz and remained at that level until contraction ceased. Maximum firing by the tension nerve was achieved with the joint at $-37°$. Upon stimulation with the joint fully reducted, the firing rate reached a peak of about 175 Hz in less than 0.5 sec, then fell into a frequency range from 100 to 150 Hz for the duration of contraction. It should be noted that the rate of spontaneous firing by the BASN increased as the muscle was stretched prior to stimulation, but in each case, the firing rate fell to the basal level following stimulation (Fig. 5).

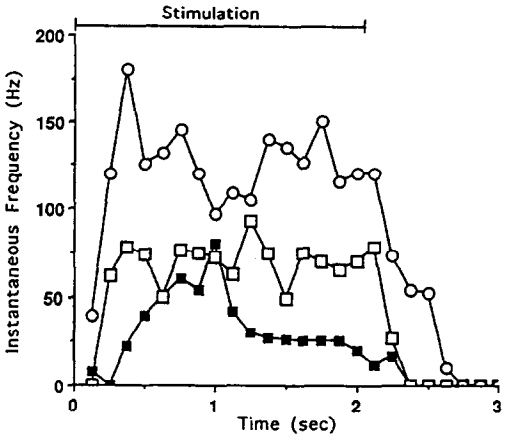

Fig. 5. BASN discharges to isometric contractions when the bender muscle is positioned at various *in situ* muscle lengths before stimulation. The propus was fastened, fully reducted, at $-37°$ (○) so as to stretch the bender muscle, or extended to $0°$ (□), or completely producted at $+37°$ (■) so as to make flaccid the bender muscle. Stimulation was for 2 sec at 40/sec. Bin width was 125 msec.

Responses by the BASN to "quick release" from isometric contraction

The "quick release" experiment was applied to the bender muscle preparation and the responses of the BASN recorded. If a muscle contracting isometrically has one end suddenly released so that the muscle contracts isotonically against no load, the force quickly drops to zero. The frequency of firing by tension receptors, being series elements, should abruptly decrease during the release phase until isometric contraction begins again at the new muscle length (Hartman, 1985). With the propus segment pinned in the fully reducted position ($-37°$) so as to fully stretch the bender muscle

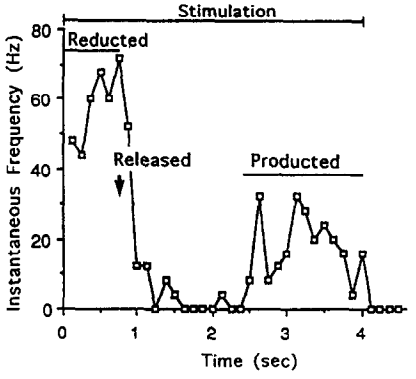

Fig. 6. BASN responses during quick release from isometric contraction. With the propus pinned at the fully reducted position so as to stretch the bender muscle, the bender motor nerve was stimulated at 60 Hz for 4 sec. After 750 msec stimulation, the propus pin was released (quick release) causing the bender muscle to contract isotonically until the propus reached the fully producted position. At this time (*c.* 2.5 sec), the bender began to contract again isometrically, but produced less force at this muscle length.

fibers, the motor nerve to the bender was stimulated at 60/sec for a period of 4/sec. After a 750 msec period of stimulation, the pin restraining the propus was released, allowing the bender muscle to contract isotonically.

As may be seen in Fig. 6, isometric contraction with the joint reducted elicited a burst of action potentials from the BASN which rose to the 48–73 Hz range. Upon release of the propus, the instantaneous frequency of firing by the BASN dropped quickly to 0 Hz as the propus moved toward the producted position. When the propus reached the completely producted position, approximately 1.5 sec after release, the bender muscle again contracted isometrically; as expected, the reduced tension developed at this shorter muscle length caused the BASN units to fire at a much lower instantaneous frequency, about 25–30 Hz. Sensory activity dropped to zero when stimulation of the motor nerve and contraction ceased (Fig. 6).

Discussion

Anatomical features and physiological experiments indicate that the BASN monitors tension developed by the bender muscle. In *C. magister*, 10–12 bipolar tension neurons are located at the distal to middle region of the bender apodeme; their axons form a discrete nerve, the BASN, which proximally joins the nerve of the adjacent CP1 chordotonal organ (Fig. 2). More proximally, the BASN merges with the productor motor nerve. The association of tension nerves with chordotonal organs was first observed in *C. magister* by Macmillan and Dando (1972) for the flexor apodeme sensory nerve (FASN) and the extensor apodeme sensory nerve (EASN) which join the MC1 and MC2 organs respectively. Similarly, the CASN exits the closer apodeme near the junction of the elastic strand and the apodeme, runs parallel with the PD organ nerve, before merging with the closer motor nerve (Hartman, 1985). Our observations and those of Macmillan and Dando (1972) indicate the reductor muscle also has a tension nerve; the reductor apodeme sensory nerve (RASN) joins the nearby CP2 chordotonal organ. The opener apodeme sensory nerve (OASN) which clearly monitors tension is exceptional; it immediately joins the opener motor nerve and is not associated with a chordotonal organ (Tryba and Hartman, 1993). The propus–dactylus joint, unlike the carpus–propus and merus–carpus joints, has but one chordotonal organ, the PD organ; the PD organ elastic strand is attached to the closer apodeme (Whitear, 1962).

The sensory neurons which are associated with the bender muscle and its apodeme in *C. magister* meet the physiological criteria described for tension receptors (Hartman, 1985). The instantaneous frequency of firing by the BASN rises when the nerve to the bender muscle is stimulated at increased frequency (Fig. 4). Likewise, motor nerve stimulation, with the muscle fixed at increasing *in situ* muscle lengths, also increases the output by the BASN tension units (Fig. 5). Sensory responses to isometric contraction at different joint angles were similar to activity reported for the FASN in the walking legs of *C. maenas* (Parsons, 1982) and *C. magister* (Macmillan and Dando, 1972), the CASN and OASN in *C. sapidus* (Hartman, 1985; Tryba and Hartman, 1993), the tension nerve associated with the tailspine flexor muscles of the horseshoe crab, *Limulus polyphemus*

(Eagles and Hartman, 1975), and tension receptors monitoring the anterior flexor muscle in the legs of *L. polyphemus* (Gregg and Eagles, 1984). In these cases, increasing the muscle fiber length resulted in increased activity during stimulation. This is to be expected since the more flaccid the fibers at the onset of stimulation, the less the ability of the muscle fibers to apply force to the tension receptors. In our experiments, the carpopodite–propodite joint was held in three positions. The most relaxed position for the muscle fibers is at $+37°$. Stimulation under isometric conditions produced the lowest sensory activity as compared to the other two positions. The mid position of 0°, resulted in stretching the fibers before the onset of stimulation and produced an increased firing rate by the tension nerve. When the muscle fibers were fully stretched by holding the joint at $-37°$, the onset of neural activity was reduced and the firing rate was the greatest when compared to the other joint positions (Fig. 5). These responses are in keeping with other observations seen in crustaceans, as well as in the vertebrates (Spiro and Sonnenblick, 1964; Gordon *et al.*, 1966). Spiro and Sonnenblick (1964) found that total tension developed by a muscle is the sum of the resting tension and the active tension as sarcomere length is increased.

The quick release experiment is a particularly useful one for determining if a receptor is monitoring tension. Muscle force rises during isometric contraction, falls to zero upon release of one tendon end, and slowly increases again at the new length as muscle slack is taken up (Hill, 1970). Being series elements, the output by tension units should follow the pattern of firing at high frequency initially, followed by an abrupt silencing of output upon quick release, then a slow increase in frequency at the shorter muscle length. The experiment clearly eliminates receptors monitoring muscle length (parallel elements) and movement and position receptors (chordotonal organs) from consideration because they will fire during the release phase. This criterion has only been applied to tension receptors monitoring tension of the anterior flexor muscle in *Limulus* legs (Gregg and Eagles, 1984), the CASN of *C. sapidus* (Hartman, 1985), and now the BASN of *C. magister* (Fig. 6).

Rapid, passive reduction of the propus, which stretches the bender muscle, evokes a dynamic response from the BASN (Fig. 3). Sensory activity then declines over a slow time course if the joint is held at the reducted position. The same pattern of responses was reported for the FASN to passive movements of the flexor (Macmillan and Dando, 1972; Parsons, 1982). As Parsons (1982) described, a slow passive movement lengthens the muscle fibers without exerting as much force on the apodeme as a rapid movement. In vertebrates and in *Limulus*, even though the tension units are in series with the immediately adjacent muscle fibers, many tension units are in parallel with other muscle fibers (Zelena and Soukup, 1983; Eagles and Hartman, 1976). Those units in parallel are probably the tension sensory neurons that fire upon rapid, passive stretching of the muscles. This is likely to be the case for tension neurons in the bender, extensor, and flexor muscles. There is a different arrangement of tension neurons and muscle fibers on the closer and opener muscle apodemes. In both muscles, the dendrites of the tension neurons insert into a distal shelf on the apodeme where few muscle fibers are attached. The vast majority of fibers are proximal to the dendrite insertions; the tension units are in series with the muscle. As a result, the tension receptors monitoring the opener and closer muscles, the OASN and CASN, respectively, do not respond to passive muscle stretch (Hartman, 1985; Tryba and Hartman, 1993). Golgi tendon organs in vertebrates also respond to very rapid passive muscle stretching; however, as with crustacean tension receptors, the units have a much lower threshold to forces developed as a result of muscle contraction (Jansen and Rudjord, 1964).

Although not yet examined in any systematic manner on a single species, data are beginning to accumulate on the number of tension neurons found on the apodemes of the various limb muscles. In the walking legs, the propus–dactylus joint is mainly supportive during walking. The dactyl is moved by the opener and closer muscles. Tryba and Hartman (1993) reported that there are about 10–12 tension neurons associated with the opener muscle of

C. sapidus while Hartman (1985) working with the same species found 25–35 neurons on its stronger antagonist, the closer muscle. Anatomical findings reported in this communication, indicate that 10–12 tension units comprise the BASN; the bender is not a strong muscle. The merus houses two particularly strong muscles, the flexor and extensor. Cross-sections of the FASN in *C. maenas* indicate the presence of about 18 large to medium sized axons and numerous smaller axons innervating the flexor apodeme (Parsons, 1980). These limited data would seem to suggest that stronger muscles have more tension receptors on their apodemes. Alternatively, there may be a relationship between the number of tension units and the number and types of motor units making up a muscle. We suspect that each muscle apodeme has a modest number of tension units tuned simply to the various rates and the range of forces developed.

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