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Dynamic responses of series force receptors innervating the opener muscle apodeme in the blue crab, *Callinectes sapidus*

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Abstract Receptors monitoring muscle force innervate the opener muscle apodeme in the walking legs of the blue crab, *Callinectes sapidus*. Biocytin backfills reveal 9–15 bipolar neurons with somata as large as 60 μm positioned at the distal end of the apodeme. Sensory endings insert into the apodeme and are in series with the opener muscle. The axons of these neurons form the opener apodeme sensory nerve that merges with the most distal branch of the opener motor nerve. Recordings reveal that the receptors are not spontaneously active nor do they respond to passive muscle stretch. Isometric muscle contraction evoked by stimulating the opener excitor motor neuron is the adequate stimulus for receptor firing. Most significant is the finding that during contraction, over a wide range of forces, the firing rate of individual receptors closely parallels the rate of change of isometric force. The peak instantaneous frequency typically occurs at the force derivative maximum, but not at maximum force development. Thus, receptors of the opener apodeme sensory nerve more closely monitor changes in isometric force rather than the total force achieved.

Key words Opener muscle · Force receptor · Tension receptor · Golgi tendon organ · Motor unit

Abbreviations *OASN* opener apodeme sensory nerve · *OE* opener excitor

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Introduction

Investigators of vertebrate Golgi tendon organs have examined the responses of individual afferents to contractile force of single motor units and muscle fiber twitch (Houk and Henneman 1967; Fukami 1981). In contrast, individual force receptors in decapod crustacean muscles have not been amenable to quantitative analysis.

In studies of the responses of apodeme receptors monitoring force, afferents in crab flexor (Macmillan and Dando 1972; Clarac and Dando 1973; Parsons 1982), closer (Hartman 1985) and bender (Cooper and Hartman 1994) muscles, contractions were evoked by stimulating entire motor nerves. Qualitative analysis of closer and flexor apodeme sensory responses suggests that these receptors respond to both the rise in force and the total force developed (Parsons 1982; Hartman 1985). However, in these experiments, investigators had poor control over motor unit recruitment; they activated an unknown number and combination of excitatory and inhibitory motorneurons to produce contractions evoking sensory activity. Interpretation of receptor responses from flexor (Parsons 1982) and bender (Cooper and Hartman 1994) muscle preparations is further complicated by the fact that it was not known which sensory units being recorded are in series and which are in parallel with muscle fibers.

To determine what aspects of motor unit isometric force (dynamic, static, or both) individual crustacean apodeme afferents monitor, we selected for study the opener muscle and its discrete sensory nerve in a brachyuran crab. All units composing the opener apodeme sensory nerve (OASN) are in series with the opener muscle. The opener muscle is innervated by three motor neurons: the opener excitor (OE), specific inhibitor and common inhibitor (Wiersma and Ripley 1952; Wiens and Rathmayer 1985). We stimulated the OE to evoke isometric contraction and examined the responses of individual apodeme units to single motor unit forces. In this

paper we report that individual series apodeme neurons of the OASN are primarily sensitive to the rate of change of contractile force, rather than total force achieved.

Materials and methods

Preparation

Blue crab, *Callinectes sapidus*, specimens were obtained from a commercial supplier in Crisfield, Maryland. They were maintained in laboratory aquaria containing artificial sea water (Instant Ocean; 1.019–1.024 ppt, 13–15 °C), fed squid periodically and were used within 3 weeks of capture.

Male crabs whose carapace measured 12.5–14.0 cm were caused to autotomize the second right walking leg. The tip of a hypodermic needle on a syringe containing saline solution at 10–11 °C was introduced into the cut tip of the dactyl and hemolymph was flushed from the excised limb. The *C. sapidus* saline solution of Blundon (1989) was buffered with TRIS to a pH of 7.6 at 10–11 °C. To expose the propus opener motor nerve and OASN, a longitudinal cut was made on both sides of the propus exoskeleton between the propus opener and closer muscles. The closer muscle was removed. A length of OASN was dissected free and severed at its junction with the most distal branch of the opener motor nerve (Fig. 1A). The sensory nerve was isolated without injuring the motor nerve.

Opener muscle contraction was evoked by stimulating the stretcher motor nerve that contains the shared stretcher-opener excitor and the common inhibitor motorneurons. The stretcher motor nerve was exposed by cutting open the carpus exoskeleton and removing the bender muscle. A large distal stretcher motor nerve branch was cut and drawn into a stimulating suction electrode (Fig. 1A). This allowed stimulation of the OE and the common inhibitor without stimulating the opener specific inhibitor. The opener muscle preparation behaves as one motor unit.

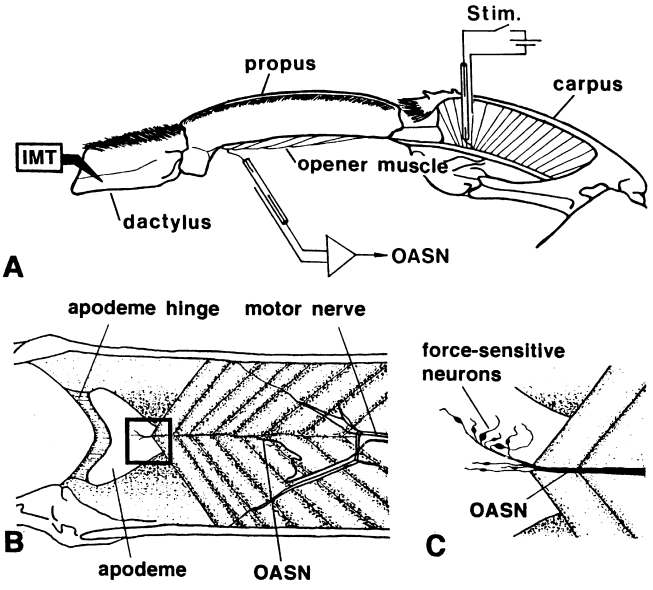

Fig. 1 A Illustration of the experimental set-up for stimulating the opener exciter (*OE*) in the walking leg of the blue crab *Callinectes sapidus* orthodromically via antidromic stimulation (*Stim.*) of the stretcher motor nerve in the carpus. Forceps mounted on an isometric transducer (*IMT*), and clamped to the dactyl, provided opener muscle force recordings. The opener apodeme sensory nerve (*OASN*) was drawn into a glass suction electrode for extracellular recordings. **B** Drawing that shows the distal portion of the opener muscle as viewed from the ventral side. The distal-most bifurcation of the opener motor nerve is shown for reference. **C** Camera lucida illustration showing the dendrites of nine bipolar receptor cells inserting into the apodeme distal to the muscle fibers; their axons merge to form the OASN

A range of isometric forces was achieved by evoking contraction at various in situ muscle lengths. The opener muscle is stretched when the dactyl is at 90° (closed) and flaccid when the dactyl is at 0° (open). Opener muscle lengths at dactyl positions of 0°, 30°, 60° and 90° were measured. The dactyl was then cut free from its condyles. The propus and carpus were firmly fastened to a Sylgard (Dow Corning) lined preparation dish with stainless steel staples. The saline-filled dish containing the preparation was fastened to a heat sink that maintained the contents at 10–11 °C. The dactyl was cut away except for a piece distal to the propus-dactylus articulation (Fig. 1). That dactyl piece was fastened to fine forceps attached to a force transducer (World Precision Instruments, Model Fort 250) that was mounted on a micromanipulator (Fig. 1A). This arrangement allowed measurement of opener muscle force during isometric contraction at the muscle lengths examined.

Stimulation and recording

OASN activity was recorded and the OE stimulated with glass suction electrodes (Fig. 1A). The OASN was arranged in the recording electrode so that it remained flaccid during opener muscle contractions. Action potentials from the OASN were amplified with an A. C. preamplifier and then fed into an Analog Digital Instruments MacLab/4 system (hardware and software) and an oscilloscope. Data were stored on a Macintosh SE/30 computer for later analysis. Stimulus pulse trains (250 or 500 ms) were delivered to the motor nerve every 30 s for five trials at each experimental frequency (80 and 100 Hz) with a delay of 1 min between each experimental frequency investigated. The OE was stimulated at fixed frequencies within the range reported for the OE during walking in *Carcinus maenas* (Zill et al. 1985) to evoke opener contraction. Force transducer output was amplified (WPI Transbridge, TBM4) and fed into the MacLab/4 in order to record muscle forces.

Data analysis

Stored data was analyzed using the MacLab/4 Scope v3.26 software system cursor measurement and zoom features; this allowed accurate measurements of action potential interpulse intervals. The data was sampled at 4 kHz for digitization which truncated the size of the extracellularly recorded action potentials. Spike superimposition prevented discerning action potentials from all the individual units when recording from the entire nerve. Therefore, quantitative analysis was performed using data from OASN fascicles comprised of clearly distinguishable units. For graphical presentation, the first derivative (df/dt) of the force trace was smoothed, via the Savitzski-Golay method, i.e., moving boxcar average (Press et al. 1992); the number of points to each side of the sample point averaged with it was 20 for force records at 90°, and 15 for 60° and 30° force traces.

Anatomy

The OASN units were stained by backfilling the OASN with Sigma biocytin (4% in saline for 12 h at 10 °C) in second right walking legs of 14.0- to 15.2-cm animals. The biocytin-avidin backfilling technique has been described in Schmidt et al. (1992). Drawings of the stained preparation were made with the aid of a microscope and an attached camera lucida apparatus.

Results

Anatomy of the opener apodeme sensory neurons

The OASN is located distally on the ventral keel of the opener apodeme; proximally, it merges with the distal-

most branch of the opener motor nerve (Fig. 1B, C). Backfills of six preparations with biocytin revealed that the OASN contains 9–15 bipolar sensory neurons, the largest somata being 50–60 μm in diameter. The somata are located on the ventral surface of the distal opener apodeme. Each sensory ending inserts distal to the muscle fibers and toward the apodeme hinge; the neurons are in series with the opener muscle (Fig. 1B, C).

Responses of the OASN to passive movements of the dactyl

When the dactyl was positioned by means of the manipulator-mounted forceps at the 0° (muscle flaccid), 30°, 60° and 90° (muscle stretched) joint angles, no spontaneous activity was observed at any resting joint position (data not shown). To determine if passive stretch of the opener muscle evokes activity from OASN units, the dactyl and attached opener muscle was moved at various rates from 0° to 90° by manually changing the micromanipulator/transducer position. During that time, no action potentials were recorded from OASN units (data not shown). Therefore, the OASN units are not spontaneously active nor are they responsive to passive muscle stretch or relaxation.

Responses of OASN units to isometric contraction

To determine the responses of the OASN units during a wide range of developed forces, the transducer was adjusted so that the muscle length corresponded to joint angles of 0°, 30°, 60°, or 90°. As seen in the sample records from an OASN fascicle (Fig. 2), when the OE was stimulated at 100 Hz for 250 ms, three neurons within the fascicle responded to isometric contraction beginning at the very low force (> 10 mN) generated at 0°. Their latency shortened and output increased when

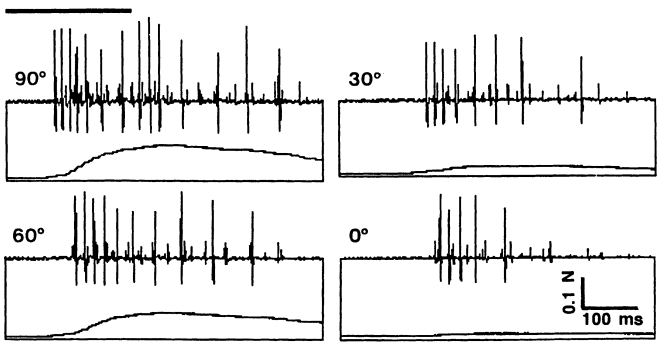

Fig. 2 Sample extracellular records of action potentials from OASN units firing in response to isometric force development. In each case the lower trace is the force record while the upper trace is the extracellular OASN record. The in situ muscle length was maintained at either the 90°, 60°, 30°, or 0° dactyl positions (as labelled) and in each case the OE was stimulated at 100 Hz for a 250 ms duration (Stimulus bar = 250 ms)

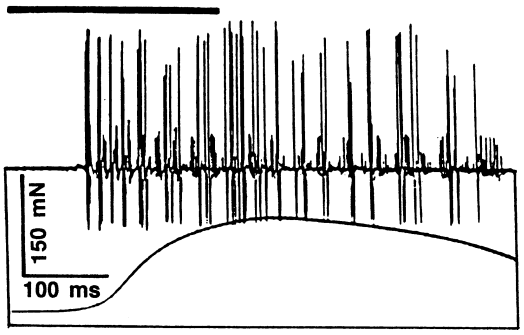

Fig. 3 Five superimposed force and OASN records in response to isometric contraction to illustrate the consistency of both force development and early afferent responses. The in situ muscle length was maintained at the 90° joint angle and the OE was stimulated at 100 Hz for a 250-ms duration (Stimulus bar = 250 ms)

the muscle was lengthened (30°, 60°, 90°) and greater force was produced upon contraction (Fig. 2).

The force developed and receptor output were remarkably consistent upon repetitive OE stimulation. In Fig. 3 the sensory recordings of five consecutive trials (100 Hz for 250 ms at 90°) are overlaid and the force traces superimposed. As may be seen, the responses of OASN units were nearly identical during the rise in force development; they were more variable at the plateau of contraction and relaxation even though the force records are identical (Fig. 3).

The large- and medium-sized OASN units from this experiment were selected for further analysis to determine which aspects of the isometric contraction they monitor (dynamic, static, or both). One additional smaller unit from this preparation was also analyzed; however, as its response properties were very similar to those units shown, the data are not presented here (Tryba and Hartman 1993). The OE was stimulated at 100 or 80 Hz for 250 ms and the resultant isometric force and receptor responses were recorded ($n = 5$ trials at each stimulus frequency). The data set illustrated is from one preparation but is typical of the kinds of responses obtained from four complete experimental preparations and numerous other preliminary experiments. Typically, the firing frequency other OASN units rose rapidly during the rise in muscle force development and quickly declined before the plateau and during relaxation. As expected, the shortest isometric latency, most rapid rate of force development (peak df/dt) and maximum force were achieved following OE stimulation at 100 Hz with the muscle fully elongated (130 ± 0.8 mN at 90°) (Fig. 4A, filled box).

If the firing by the large unit is plotted for five repetitions of the 100-Hz OE stimulus regime, it may be seen that the peak instantaneous frequency of the largest unit occurred at about 82 Hz within 140 ms. As the rate of force development slowed, this unit's instantaneous response rapidly declined to approximately 28 Hz (at about 200 ms) then rose erratically to about 70 Hz (at 317 ms) and quickly decreased to about 12 Hz during

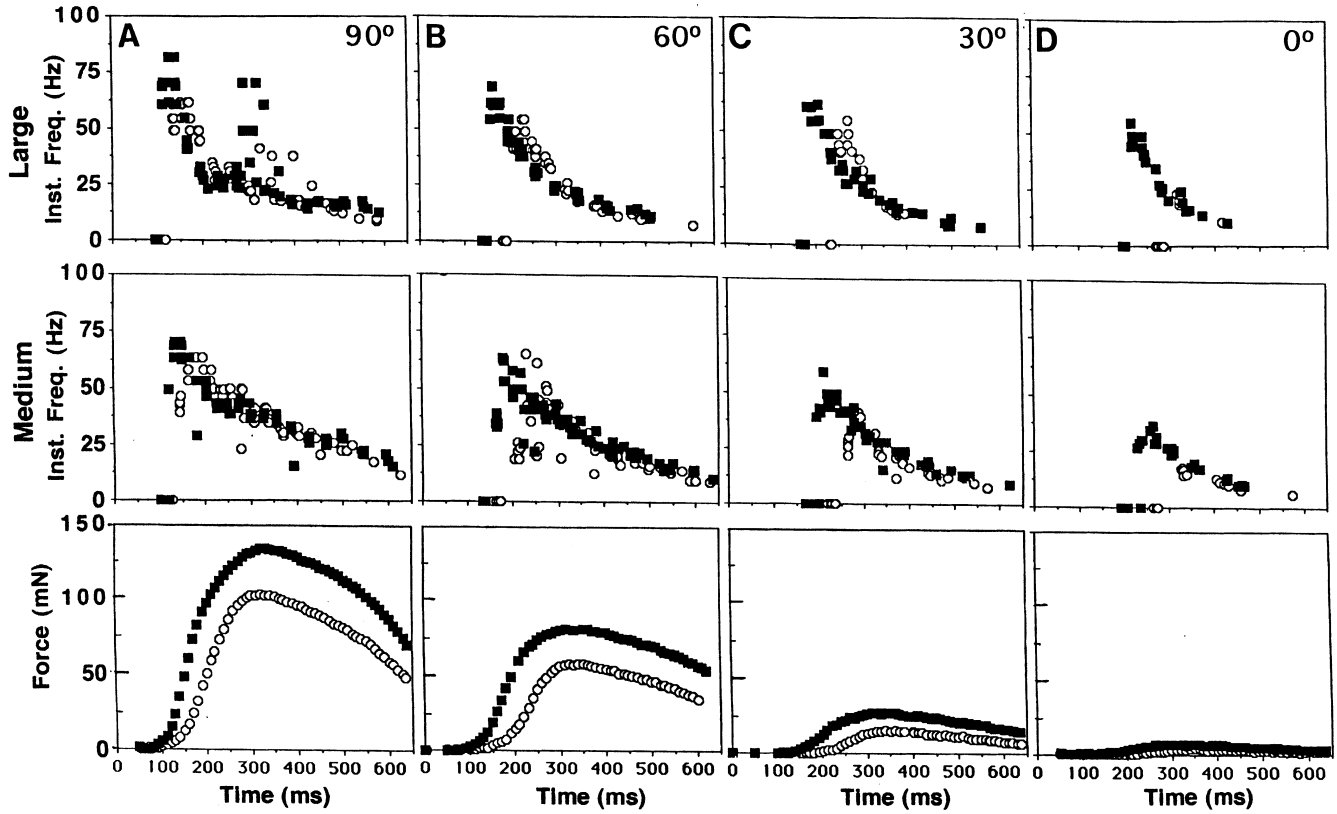

Fig. 4A–D Instantaneous frequency plot of the responses of two OASN units (large and medium size) from a preparation when the OE was stimulated at 100 Hz (*filled box*) or 80 Hz (*open circle*) for 250 ms (n = 5 trials overlaid). The dactyl was maintained at the 90° (**A**), 60° (**B**), 30° (**C**) or 0° (**D**) positions. The isometric force trace is aligned with the instantaneous frequency plot (n = 5 trials overlaid) with respect to the time base. Note that the peak instantaneous frequency for each unit occurs early in the development of force; the firing rate is declining before maximum force is achieved

relaxation (Fig. 4A, top instantaneous frequency plot row). The erratic increase in frequency of the large unit (at approximately 317 ms) following the peak instantaneous frequency was observed in two of the five trials. Similar, but more consistent responses were observed for the medium-sized OASN unit, whose peak instantaneous frequency was about 70 Hz within 135 ms; the firing rate declined to approximately 37 Hz by 325 ms followed by further diminution to 15 Hz as the muscle relaxed (Fig. 4A, bottom instantaneous frequency plot row).

When the initial muscle length was shortened (i.e., to that at 60°, 30°, or 0° joint positions), OE stimulation at 100 Hz resulted in a longer isometric latency, slower rate of force development and lower maximal force (i.e., 78 ± 1.4 mN at 60°; 25 ± 0.8 mN at 30°; 8 ± 0.1 mN at 0°). As can be seen in Fig. 4B, the instantaneous frequency of the large afferent peaked at 69 Hz within 174 ms when the muscle contracted at 60°; this frequency rapidly declined to about 24 Hz at 300 ms and further decreased to 12 Hz during relaxation. The medium-sized OASN unit had a similar firing pattern when isometric force developed at that muscle length (60°). The peak instantaneous frequency (64 Hz) can be observed at 180 ms, declined to 35 Hz at 320 ms, and during relaxation firing declined from 33 to > 15 Hz (Fig. 4B).

Following OE stimulation at 100 Hz with the muscle length fixed at the 30° or 0° joint positions, the two OASN unit's peak firing rate occurred during the rise in force; their frequencies rapidly declined as force development slowed, peaked and underwent further diminution during muscle relaxation (Fig. 4C, D). The latency of OASN units' increased and their firing frequencies were low during isometric contraction at 0° (versus 30°) when the force development rate was very low (Fig. 4C, D).

At the muscle lengths indicated above, stimulation of the OE at 80 Hz (versus 100 Hz) evoked isometric contraction that had a longer latency and achieved a lower rate of force development and final force. In response, both the large and medium OASN units had a longer latency and lower instantaneous frequency (Fig. 4A–D, open circles). Additionally, as the muscle fibers were maintained at more flaccid positions and the OE stimulated at 80 Hz, the latency increased and the instantaneous frequency declined for both units (Fig. 4A–D). Following opener contraction evoked by 80 Hz stimulation, at 90°, 60°, 30°, or 0°, the large and medium afferents again responded with the peak firing rate occurring during the rise in opener force; the frequency rapidly declined before the muscle force reached its maximum and settled to a somewhat tonic firing frequency as the muscle relaxed (Fig. 4A–D).

Table 1 Peak isometric force derivative (peak df/dt) and the time of occurrence (at time) for the large and medium OASN units following stimulation of the OE at 100 Hz for 250 ms. The in situ muscle length was held at the 90°, 60°, or 30° joint positions. The peak instantaneous frequency of firing for each cell occurs at the same time or within a few ms of the time of peak df/dt

Joint angle (degrees)	Peak df/dt ($mN \cdot ms^{-1}$) at time (ms)	Large cell peak inst. freq. (Hz) at time (ms)	Medium cell peak inst. freq. (Hz) at time (ms)
90°	1333 at 143	82 at 139	69 at 133
60°	852 at 179	61 at 176	53 at 181
30°	353 at 207	61 at 207	44 at 219

The peak firing rate of OASN units did not occur during maximum isometric force development, regardless of joint position or frequency of OE stimulation (Fig. 4A–D). Rather, it occurred at the same time the opener muscle contracted at the highest rate of change of isometric force (peak df/dt). This relationship is more evident if the rate of change of force (first derivative of force, df/dt) and instantaneous frequency of the large- and medium-sized units are plotted at muscle lengths corresponding to the various joint angles (Fig. 5A–F; Tables 1, 2). Note that while these data are shown for one trial at each joint angle, at each position and motor neuron stimulation frequency, the same relationship was observed in the other four trials (data not shown). Furthermore, the instantaneous frequency of both units paralleled the force derivative (Fig. 5A–F). As one might expect and as may be seen in Fig. 5A–F the lower threshold (medium) unit typically fired at slightly higher instantaneous frequency than the larger unit during relaxation.

During contraction at the 30° and 0° dactyl positions, where the rate of change of force development was relatively low, the peak instantaneous frequency of the relatively high threshold (large and medium) units was not observed to occur at the peak df/dt. For example, at the 30° joint position following 80 Hz OE stimulation, the peak instantaneous frequency of the medium sized unit (in contrast to the large unit) occurred 32 ms after the peak df/dt (Fig. 5F, Table 2). Furthermore, at this position the medium unit fired at a lower instantaneous frequency than that of the large unit during relaxation when OE was stimulated at 80 Hz (Fig. 5F). At the 0° joint position following stimulation of the OE, the df/dt was relatively low and not much force developed (Fig. 5D). The peak instantaneous frequency of the OASN units did not occur at the same time as the maximum df/dt at the 0° joint position (data not shown).

Table 2 Peak isometric force derivative (peak df/dt) and the time of occurrence (at time) for the large and medium OASN units following stimulation of the OE at 80 Hz for 250 ms. The in situ muscle length was held at the 90°, 60°, or 30° joint positions. The peak instantaneous frequency of firing of each cell occurs at the same time or within ms of the time of peak df/dt

Joint angle (degrees)	Peak df/dt ($mN \cdot ms^{-1}$) at time (ms)	Large cell peak inst. freq. (Hz) at time (ms)	Medium cell peak inst. freq. (Hz) at time (ms)
90°	951 at 180	62 at 170	64 at 180
60°	647 at 227	54 at 227	66 at 228
30°	323 at 256	41 at 256	41 at 288

Discussion

In contrast to the bender (Cooper and Hartman 1994) and flexor apodeme sensory nerves (Parsons 1982) which contain sensory units that are in series and in parallel with muscle fibers, units of the opener (see Results) and closer apodeme sensory nerves are in series (Hartman 1985). In parallel Golgi tendon organ and apodeme afferents are likely to fire upon rapid passive stretch of the muscle. Additionally, the sensitivity of in-parallel receptors may decrease during contraction; this arrangement is thought to result in a decrement in force produced within the receptive field of these units. Because all of the OASN force receptors are in series, little, if any, unloading of the receptors is likely to occur.

Until now, it has been generally supposed that apodeme sensory nerves monitor peak muscle force. The most significant finding in our quantitative study of OASN units is that the output of these series receptors closely parallels the first derivative of muscle force (Fig. 5). That is, they are particularly sensitive to the rate of change of force development. Furthermore, the firing rate of OASN units is declining during peak muscle force, and declines further during relatively sustained forces and relaxation. None of the OASN units ever fired tonically (Figs. 4, 5) nor did their peak instantaneous frequencies occur during maintained isometric contraction. These data suggest that series apodeme receptors do not provide accurate feedback regarding peak force.

The peak firing rate of OASN units occurred at the same time or within a few milliseconds of the maximum force velocity (Fig. 5, Tables 1, 2), but not at the peak muscle force (Figs. 3–5). These results were consistently observed when the OE was stimulated at 100 Hz or 80 Hz and the muscle length was at 90°, 60°, or 30° joint positions (Fig. 5, Tables 1, 2). The low threshold and dynamic sensitivity of OASN units is further evidenced by their short latencies (Fig. 4). Similarly, reexamination of closer apodeme (Hartman 1985) and flexor apodeme (Parsons 1982) sensory nerve records indicates that their units also display considerable dynamic sensitivity during both isotonic and isometric contractions of the muscle regardless of the motor unit(s) recruiting them. Parsons (1982) noted that the rise of isometric force appeared to be a primary determinant of flexor apodeme sensory nerve output; qualitatively, the output increased when the flexor developed force at faster rates. In contrast, upon contraction at a slower rate of force development, the same flexor apodeme units did not respond (or responded poorly) even when the same final force was achieved. Likewise, for OASN units, at very low

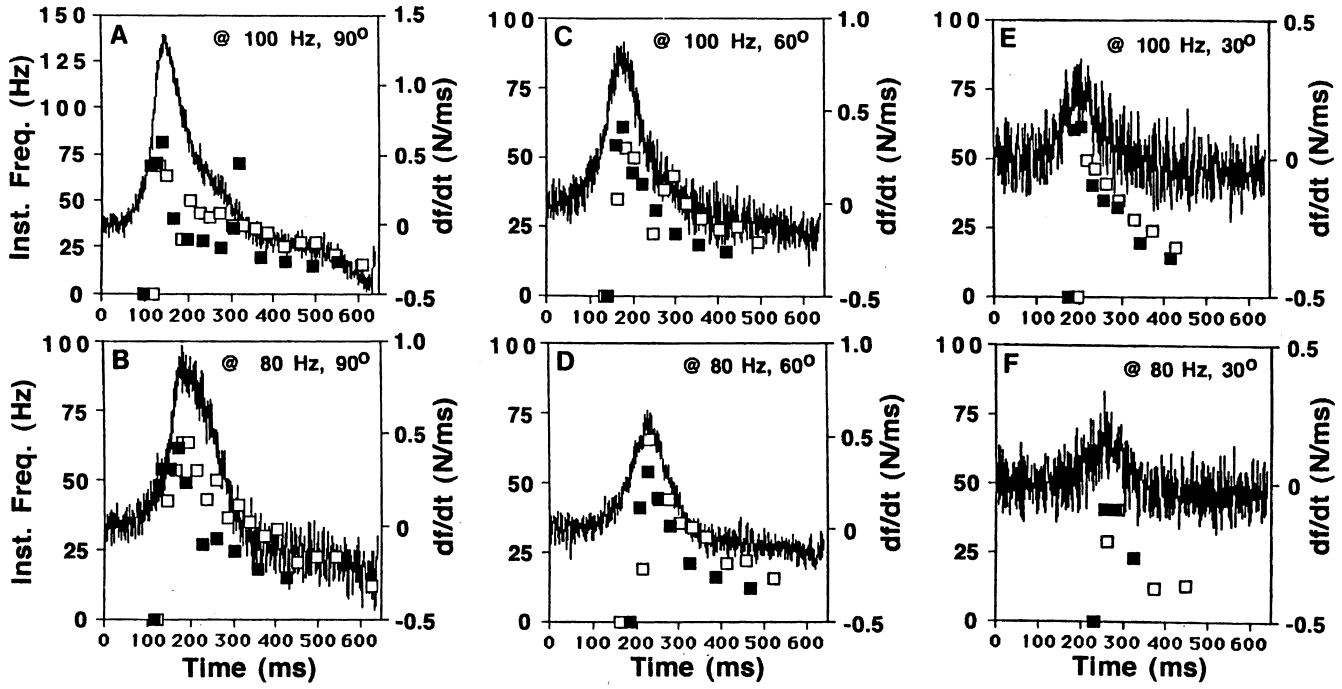

Fig. 5A–F Instantaneous frequency plot of large (*filled box*) and medium sized (*open box*) OASN units and the isometric first force derivative (d*f*/d*t*). The in situ muscle length was maintained at the (**A, B**) 90°; (**C,** D) 60°; (**E, F**) 30° joint positions. The OE was stimulated for 250 ms at either 100 Hz (**A, C, E**) or 80 Hz (**B, D, F**) (n = 1 trial). Note the scale changes for d*f*/d*t* in **A, B–D, E** and **F**; also note the instantaneous frequency scale in **A** is changed for subsequent figures. The peak instantaneous frequency of firing of both units is seen to parallel the force derivative

rates of opener muscle tension development, the peak instantaneous frequency did not occur at the peak d*f*/d*t* (Fig. 5; see medium cell at 30°/80 Hz OE stimulus, or both units at 0°/100 Hz or 80 Hz OE stimulus). It may be the case that the relatively high threshold OASN units examined do not accurately monitor these slow rates of change of force, but smaller, lower threshold units do. Alternatively, relatively low rates of force development (i.e., at 0°) are not accurately monitored by OASN units.

The OASN units responded by firing at a higher frequency in response to the greater isometric contraction produced following an increase in OE stimulation frequency. Similar results were reported for *C. maenas* and *C. magister* flexor apodeme sensory nerve (Parsons 1982; Macmillan and Dando 1972), *C. sapidus* closer apodeme sensory nerve (Hartman 1985), and *C. magister* bender apodeme sensory nerve (Cooper and Hartman 1994) units. Increasing the frequency of excitatory motor neuron stimulation results in enhanced frequency-dependent facilitation at neuromuscular junctions (Dudel and Kuffler 1961; Atwood and Bittner 1971). In our experiments, both isometric force development rate and peak force increased and the isometric latency decreased during 100 Hz OE stimulation compared to 80 Hz stimulation (Fig. 4) Accordingly, the latency of OASN units declined and they fired at a higher instantaneous frequency during the force rise following 100-Hz OE stimulation. This increase in frequency was followed by a rapid decline in the instantaneous frequency during maintained contraction and relaxation (Figs. 4, 5)

Stimulating the OE when the opener muscle was held at increasing initial in situ muscle length results in an increase in peak force, rate of force development, and decrease in isometric latency as described for a variety of crustacean (Hartman 1985; Cooper and Hartman 1994) and vertebrate neuromuscular preparations (Gordon et al. 1966). When initial muscle length was changed in a graded series from 0° to 90°, OE stimulation (i.e., frequency and duration constant) resulted in an increase in rate of force development, a higher plateau and a decrease in the isometric latency period (Figs. 2–4). For example, at 90° the shortest isometric latency, OASN latency and highest rate of force development was observed compared to that at any other joint angle tested (Figs. 3, 4A, B). Accordingly, the highest peak instantaneous frequency occurred at the peak of the force derivative at 90° (Fig. 5A, B).

Appreciable dynamic sensitivity of Golgi tendon organs has also been demonstrated. For example, isometric tetanic contractions of a motor unit evokes phasic responses from series Golgi units during the rise in force; their activity declines to a relatively tonic firing frequency during the plateau of force (Davies et al. 1995). Furthermore, the phasic response of these force receptors rises much more rapidly than the rate of tension increase (Alnaes 1967; Houk and Henneman 1967; Jami and Petit 1976; Jansen and Rudjord 1964; Stuart et al.

1972; Horcholle-Bossavit et al. 1990; Davies et al. 1995). The dynamic sensitivity of Golgi tendon organs is particularly evident following efferent stimulation at physiological rates, i.e., at frequencies that do not induce tetanus (Henneman and Mendell 1981; Hoffer et al. 1987; Horcholle-Bossavit et al. 1990). The responses of OASN tension receptors appear to be similar to those reported for Golgi tendon organs (Horcholle-Bossavit et al. 1990). The dynamic sensitivity of Golgi tendon organ and series apodeme receptors suggests that they are well suited to provide feedback concerning oscillations in muscle force during locomotion.

The series receptors of the opener and closer muscles in crab walking legs are doubtless active during loaded contractions (i.e., during stance). This information would seem vital to the central nervous system upon the initiation of walking (when overcoming inertial forces), to the maintenance of walking, and particularly useful when walking on inclined surfaces or uneven terrain.

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