

# Manipulation by the Crab Claw Is Dependent Upon Chordotonal Organ Afference

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**ABSTRACT** In crabs, the propus-dactylus (PD) chordotonal organ consists of about 80 bipolar sensory neurons whose dendrites are inserted into an elastic strand that spans the distalmost joint of chelae (claws) and walking legs. Movement of the dactyl to a closed position elongates the strand, while opening the dactyl shortens the strand. In response, the sensory neurons signal movements and positions. Is the crab dependent upon afference from the PD organ for voluntary control of the dactylus of the chelae? We quantified the manipulations of a standard food item by Dungeness crabs *Cancer magister* with intact chelipeds. Next, crabs were fed after the distal end of the elastic strand of the PD organ was detached (dPD) from the dactylus of both chelae or following a sham operation. All crabs fed avidly, but, in contrast to preoperative and sham crabs, statistical analysis revealed that dactyl-dependent manipulation (gripping, scraping, grasping, pulling, carrying, and cutting) by dPD crabs significantly decreased; crabs rarely used the dactyl following detachment of the elastic strand. Manipulations not dactyl-dependent that involved the chelipeds and walking legs to aid feeding (cradling, stabilizing, and guiding) significantly increased. Physiological recordings indicate that the position-sensitive neurons of the PD organ fire tonically following detachment, but the firing rate is greater than that characteristic for the dactyl open position. Results support the hypothesis that feedback from the PD organ is required for the initiation and execution of precise contractions of the opener and closer muscles during directed movements of the dactyl. *J. Exp. Zool.* 279:579-586, 1997. © 1997 Wiley-Liss, Inc.

Chordotonal organs (CO) are proprioceptors that provide feedback regarding joint movement and position in arthropod limbs. Those of Decapoda Crustacea have been subjects of considerable anatomical and electrophysiological study. Each organ consists of either an elastic strand or sheet in which are imbedded sensory neuron endings (Whitewar, '62). The organs have been named with the initials of the joint they monitor. For instance, the organ spanning the propus-dactylus joint is referred to as the PD organ (Burke, '53). The electrophysiological responses of CO neurons fall into two general categories: large units that fire phasically during movements and small units that fire tonically to maintained positions of joints (Wiersma and Boettiger, '59; Wiersma, '59). Output by CO has been shown to mediate resistance (Bush, '62, '65; Evoy and Cohen, '69; Spirito et al., '72), assistance (Vedel, '80, '82; DiCaprio and Clarac, '81), and intersegmental reflexes (Vedel et al., '75; Bush et al., '78; Clarac et al., '78).

The role that CO in walking legs play during locomotion in crabs has been examined. Immo-

bilization of the propus-dactylus (PD) or merus-carpus (MC) joint in *Carcinus maenas*, *Cancer magister*, and *Cardisoma guanhumi* leads to slight changes in the walking pattern (Clarac and Coulmance, '71; Evoy and Cohen, '71; Barnes et al., '72). Only slight postural changes were observed in the operated leg of *C. magister* when MC1, MC2, or myochordotonal organs (MCO) were selectively removed (Cohen, '65). If several MCO are extirpated, there is a generalized loss of muscle tone in operated and unoperated legs; however, walking is still coordinated but slower (Fourtner and Evoy, '73). CO, in addition to providing reflex information about the joints, may have a general excitability effect on the segmental movement control center; in their absence, there is a decline in motoneuron output and movement (Spirito et al., '73).

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In contrast to walking legs, chelipeds are used in a directed manner for combat and courtship and to manipulate food items. The contribution of CO to the control of the merus of chelipeds has been examined in crayfish. Notvest and Page ('86) examined claw extension in tethered *Procambarus clarkii* following inactivation of MC1, MC2, and the MCO. Their electromyogram results show that CO provide excitation to the thoracic motor centers or positive feedback that assists intended movements. In an effort to determine the importance of CO in the control of cheliped flexion, Field ('76) interfered with feedback from the PD and carpus-propus (CP1 and CP2) organs by immobilizing the respective joints or by severing the CP1 and CP2 nerves in the cheliped of hermit crabs (*Pagurus ochotensis*). He concluded from electromyogram studies that, having more than just a reflex role, CO feedback provides input to programmed motor activity.

The chela portion of the chelipeds of the brachyuran crab *C. magister* consists of a robust propus containing a relatively weak opener muscle and a powerful closer muscle. The PD organ is the only CO monitoring movements and positions of the dactyl of the chela. During opening movements of the dactyl, the elastic strand of the PD organ shortens (relaxes), evoking activity in large relaxation-sensitive movement sensory neurons; closing movements lengthen (stretch) the strand, causing smaller, elongation-sensitive movement neurons to respond. Maintained dactyl positions are signalled by small, nonadapting, position-sensitive neurons (Hartman and Boettiger, '67; Boettiger and Hartman, '68). The importance of this afference to the coordinated manipulative ability of chelae is unknown. In this communication, we report that the central nervous system of the crab is dependent upon kinesthetic information from the PD organ for voluntary control of the cheliped dactyl during feeding. Detachment of the distal end of the elastic strand from the dactyl significantly reduces dactyl-dependent behaviors in unrestrained crabs.

## MATERIALS AND METHODS

Juvenile Dungeness crabs *Cancer magister* in the seventh to ninth instar were collected from Padilla Bay, Washington, and were maintained in holding tanks with running seawater at 13°C at the Shannon Point Marine Center. The chelipeds and walking legs were inspected, and only crabs with pristine appendages were selected for feeding experiments. Each crab was placed separately

in a 9.5 L glass aquarium containing beach sand about 15 mm deep; the tanks were partitioned so that the animal faced the video camera used to record feeding. Running seawater to the aquaria was filtered through a fine screen to eliminate potential food items in order to keep the crabs hungry.

In our experiments, each crab was daily fed a single blue mussel *Mytilus edulis* ranging in size from 25–40 mm and from which one valve had been removed. Feeding behavior was recorded for three consecutive days with either a Sony CCD-SP7 or a CCD-TR7 video camera. On the fourth day, each crab received one of two surgeries, either the detachment of the PD organ from the dactyl of both chelae or a sham surgery on both chelae. A depression on the lateral face of the dactyl marks the distal attachment of the PD organ strand (Fig. 1). A triangular patch of cuticle measuring about 3 mm on each edge that encompassed the attachment point was cut and lifted away. In order to ensure the release of the strand, we cut the integument beneath the attachment point using fine-tipped iridectomy scissors. The hole in the cuticle was patched with 3M Sylux Plus Dental Restorative material; curing was accomplished with the aid of a high intensity fiber optic lamp. The sham surgery was identical except that the site of dissection was an area just dorsal to the PD organ attachment so as not to disturb the elastic strand. These surgeries were relatively super-

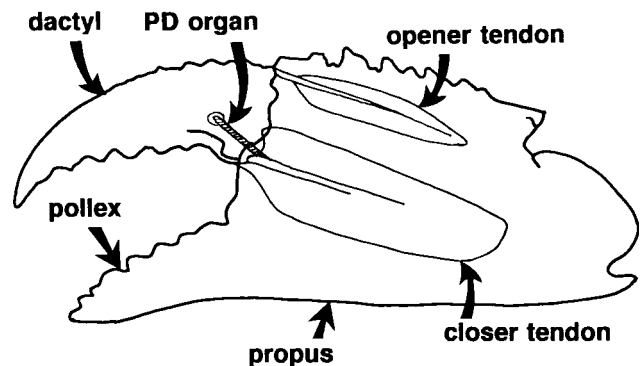


Fig. 1. A view into a chela of *Cancer magister* showing the positions of the closer and opener apodemes in the propus and their attachments to the dactyl. The elastic strand of the PD organ is shown connected to a point on the shelf of the closer apodeme at one end and to a depression on the cuticle of the dactyl at the other. Contraction of the closer muscle closes the dactyl and lengthens the elastic strand; contraction of the opener muscle opens the dactyl and shortens the elastic strand. The elastic strand can be detached from the dactyl by cutting away a patch of cuticle over the depression.

ficial and did not disturb the underlying dactyl nerve and resulted in little loss of blood. Had we chosen to sever the PD organ nerve in chelipeds, it would have not been possible without major trauma, including the destruction of many muscle and nerve fibers, great blood loss, and cutting the nerve monitoring closer muscle force.

Following the surgeries, the animals were returned to their respective tanks and fed as before for an additional three consecutive days. Upon completion of the feeding bouts, all detached PD (dPD) and selected sham-operated (sPD) crabs were induced to autotomize the chelipeds by cutting across the merus. Each claw of dPD crabs was dissected and the PD organ inspected to determine if the operation to release the strand had been successful or, in the case of the sham surgeries, if the operation had avoided the PD organ attachment. To find the PD organ, we cut a large window in the dorsal region of the propus, severed the apodeme of the opener muscle and removed the opener muscle. A smaller window was cut into dorsal region of the dactyl that included the medial condyle. The lateral condyle was left intact, and the distal attachment of the elastic strand was not disturbed. To assist locating and observing the PD organ, we immersed the exposed propus in seawater after staining it with several drops of methylene blue stock solution (0.5%) applied topically.

In order to define and categorize feeding behaviors, videotape records were played back on the Sony CCD-SP7 camcorder at 20.0% real time or a Panasonic AG-2400 VCR at 17.7% real time. Preoperative (control) behaviors were defined, tabulated, and quantified as the number of feeding acts per 5 min time interval. Videotape records of postoperative sham and dPD crabs were tabulated and quantified in the same way. Preoperative, sham-operated, and crabs with detached PD organ strands fed avidly and usually completed individual feeding bouts within the 5 min period.

The experiment was designed as a randomized complete block blocked by the crab. Analysis of variance (ANOVA) was used to analyze the data to determine if there were significant differences between the incidence of preoperative and postoperative behavioral acts. The level of significance,  $\alpha$ , was set at 0.05 prior to any data collection. The behaviors for both the left and right chelipeds were counted and then combined for the analysis since data from each cheliped is a subsample of the experimental unit, the whole crab. The data are modeled by the equation  $X_{ijl} = \mu + t_i + p_j + e_{ij}$

+  $E_{ijl}$ , where  $\mu$  is the overall mean,  $t_i$  is the surgery effect (dPD or sPD),  $p_j$  is the between-crab effect,  $e_{ij}$  is random variance, and  $E_{ijl}$  is variance within each crab. By comparison of the preoperational behaviors with the postoperational behaviors, each animal served as its own control. A total of 15 crabs were used in the final analysis: eight that received the PD detachment surgery and seven that received the sham surgery.

It is not possible to record chronically PD organ nerve activity before and after detachment of the elastic strand in claws of behaving crabs. Instead, recordings were made from the nerve following the removal of chelae. Chelae were dissected according to the procedure described earlier but without the assistance of staining. A long length of the PD nerve was isolated from the main leg nerve and drawn into a glass suction electrode for recording. PD nerve recordings were made while the dactyl of the chela was positioned with a probe to produce normal positions and following detachment of the strand. Amplified signals were led off to an Apple SE/30 computer using MacLab hardware and software (Hartman and Cooper, '94).

## RESULTS

Following analysis of the videotape records of preoperative crabs, we were able to define and categorize ten distinct behavioral acts common to crabs feeding on blue mussels. The behavioral acts were easily grouped into two categories: those that rely upon the dactyl to execute and those that do not (Table 1). Dactyl-dependent behaviors involve fine manipulation and dexterity and include gripping, scraping, grasping, pulling, carrying, and cutting food. Of these behaviors, cutting is the rarest. Also observed were more coarse behaviors that included cradling, stabilizing, chiseling, and guiding. These dactyl-independent acts required either the use of the pollex, supporting food against the mouthparts with the chelipeds, or support and manipulation of food using the first and second walking legs (Table 1).

A typical feeding sequence involving the chelae consisted of a crab first using one chela to grip the mussel valve and then holding the meat in front of the mouth. The dactyl of the other chela was then used as the instrument to scrape the meat loose. Following this, chiseling was often used instead of scraping. The chela used for chiseling and scraping was then used to grasp the meat that had been loosened, to pull it free from the valve, and to carry it to the mouth. When the

TABLE 1. Repertoire of behavioral acts of a *Dungeness* crab *Cancer magister* when it feeds upon a blue mussel *Mytilus edulis* that has had one valve removed

Category	Behavior	Description
Dactyl-dependent	Grip	Holding the valve between the dactyl and pollex (chela)
	Scrape	Using the dactyl to loosen meat from the valve
	Grasp	Holding meat between the dactyl and pollex
	Pull	Grasped meat is pulled from the valve
	Carry	Chela brings meat that is pulled from valve to the mouth
	Cut	Chela severs strands of meat held in the mouth free from the valve
Dactyl-independent	Cradle	One or both chelipeds hold the meat to the mouth by wrapping around the valve
	Stabilize	One or both first and sometimes second walking legs support or manipulate the valve
	Chisel	Pollex used as a wedge to loosen meat from the valve
	Guide	Chela used to push meat that is not grasped towards mouth

crab could no longer effectively remove meat from the valve using that chela, it would switch so that the chela formerly used to grip the valve was used to manipulate the meat and to carry it to the mouth, and the other chela was used to grip the valve. Crabs appeared to use either chela with equivalent facility. The sequence of dactyl-dependent acts involved precision and were intended movements.

Counts of the number of occurrences of each behavioral act from a typical animal before and after detachment of the distal end of the elastic strand of the PD organ from the dactyl are shown in Figure 2. As may be seen, over the 3 day test period prior to the dPD surgery, dactyl-dependent acts for the crab were far more common than the

dactyl-independent acts. Following the bilateral detachment of the elastic strand from the dactyls, dactyl-dependent behaviors during the 3 day post-operative feeding period were rare. Instead, the crab fed itself by increasing the number of dactyl-independent acts, particularly cradling, stabilizing, and guiding. The graph also reveals that prior to the surgery the crab showed little evidence of handedness in food manipulation; the left and right chelae are employed about equally (Fig. 2). The claws of *Cancer* species show no evidence of dimorphism as do, for example, the claws of blue crabs and American lobsters.

Data comparing the incidence of feeding acts before and following the sham surgery for a typical crab are shown in Figure 3. The number of dactyl-dependent behaviors during the preoperative period far outnumbered the dactyl-independent acts. This crab did not use the technique

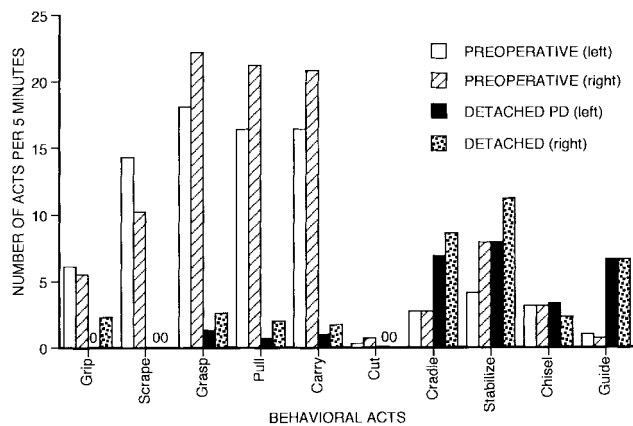


Fig. 2. A comparison of the incidence of behavioral acts in a representative crab for 3 days before and for 3 days following the detachment of the elastic strand of the PD organ from the dactyl. The preoperative animal relies heavily upon dactyl-dependent acts (grip, scrape, grasp, pull, carry, and cut) to feed. There is no evidence of handedness; the crab uses each chela with equal facility. Following detachment, there is a decline in the number of dactyl-dependent acts and an increase in the dactyl-independent acts of cradle, stabilize, and guide.

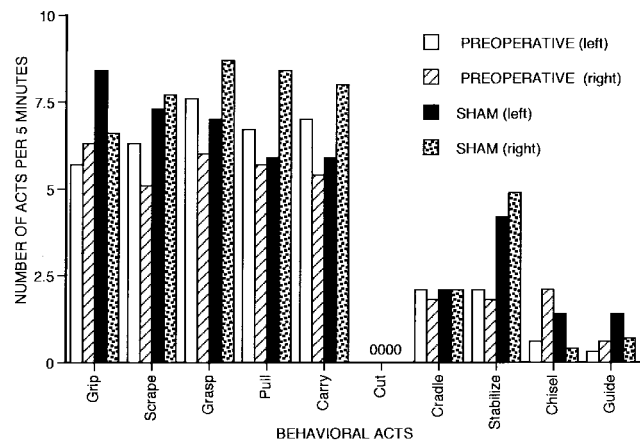


Fig. 3. A comparison of the incidence of behavioral acts in a representative crab for 3 days before and 3 days following a sham surgery on the dactyl. There is little change except for a slight increase in the number of dactyl-dependent acts and an increase in stabilizing behavior following the sham surgery. There is no evidence of handedness.

termed cutting. The sham surgery had little effect on feeding behavior. The dactyl-dependent behaviors showed a slight increase in number; the number of dactyl-independent acts was about the same as during postoperative feeding except for an increase in stabilizing behavior. Also, whether preoperative or sham surgery data are considered, this crab showed little evidence of handedness. None of the preoperative or sham-operated crabs ( $n = 15$ ) showed any evidence of handedness (data not shown).

The summary data for preoperative crabs that later had the dPD surgery resulting in the bilateral detachment of the elastic strand of the PD organ from the dactyl of the chelae ( $n = 8$ ) are shown in Figure 4A. As is evident, dactyl-dependent behavioral acts were much more frequent than dactyl-independent acts in the preoperative crabs. In particular, animals repeatedly used the dactyl to grip, scrape, grasp, pull, and carry the food; cutting acts rarely occurred. The most commonly employed dactyl-independent behavior was

the use of the first and second walking legs to stabilize the food during feeding; the other dactyl-independent behaviors were only occasionally used during preoperative feeding. Following bilateral detachment of the elastic strands, there was a dramatic and significant decline in the initiation of all behavioral acts that are dactyl-dependent (Fig. 4A). Indeed, use of the dactyl was rare. Compensating for the decline in dactyl use was a significant increase in the dactyl-independent behaviors of cradling, stabilizing, and guiding. The incidence of chiseling declined; however, the difference was not significant. Dissection and methylene blue staining revealed that bilateral detachment of the PD organ had been successfully accomplished in all crabs and that the elastic strand had shrunk back into the propus.

Summary data of crabs that received sham surgeries ( $n = 7$ ) are illustrated in Figure 4B. Dactyl-dependent behavioral acts were seen to be far more common than dactyl-independent behavioral acts during both preoperative and postoperative

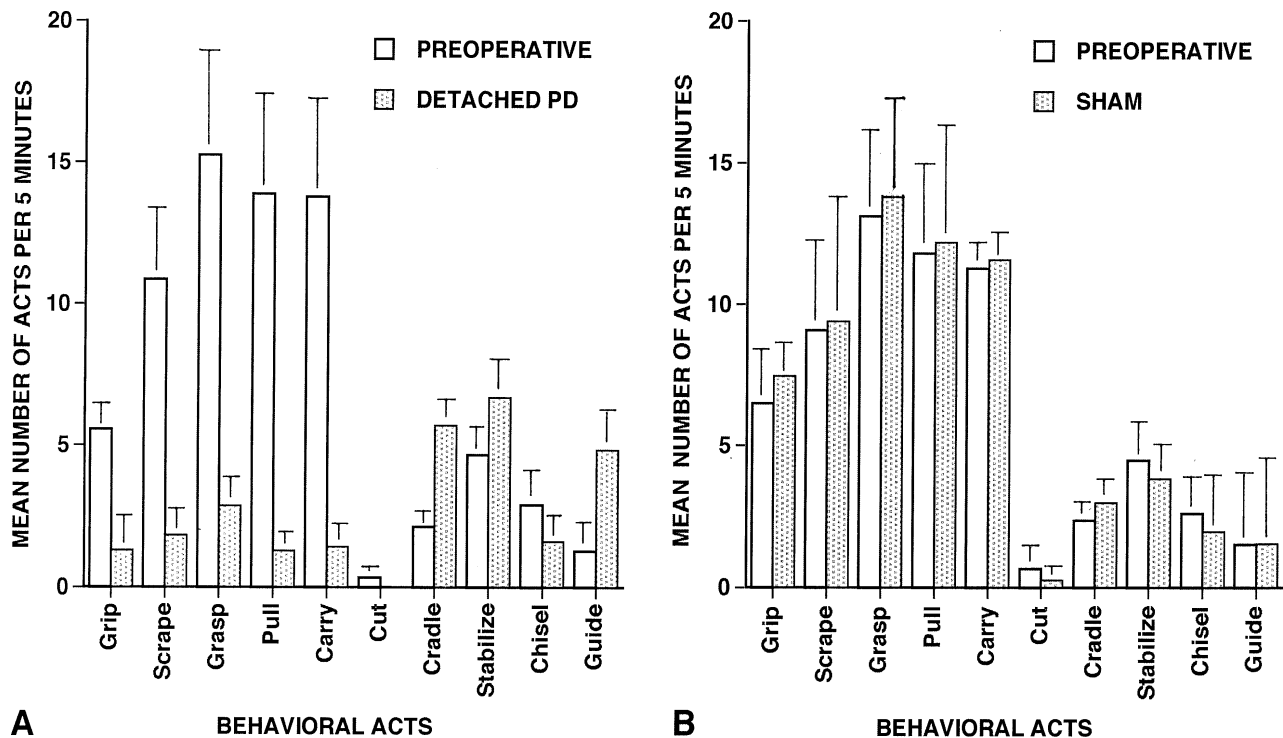


Fig. 4. Summary comparing the means of feeding behavioral acts for all crabs for 3 days before and 3 days following detachment of the elastic strand from the dactyl (A) or sham surgery (B). The acts by both the left and right chelipeds were counted and then combined for statistical analysis since data from each cheliped is a subsample of the behavior of the whole crab. Error bars indicate 95% confidence intervals. A:

There is a significant decline in means for all dactyl-dependent acts following detachment of the elastic strand from the dactyl accompanied by a significant increase in the means for the dactyl-independent acts of cradle, stabilize, and guide.  $N = 8$ . B: There is no significant change in the means of any dactyl-dependent or dactyl-independent behavioral acts resulting from sham surgery.  $N = 7$ .

feeding. Indeed, there is no significant difference in the incidence of behavioral feeding acts between control and sham-operated animals (Fig. 4B). Dissection combined with staining of selected sham-operated crabs showed that the sham surgery had not detached the elastic strand or injured any of the PD organs in any way.

What signals issue from the PD organ nerve when the PD organ is intact and following release of the strand, as would be the case when the elastic strand is detached from the dactyl? As seen in Figure 5A, the middle open position of the dactyl was signalled by the tonic firing of small- to medium-sized neurons. If the dactyl is held fully open, the strand is at its shortest physiological length, and firing frequency of the small- and medium-sized units increased (Fig. 5B). When the strand is detached from the dactyl, it becomes completely flaccid. This was accompanied by high frequency firing of several small neurons (Fig. 5C). The firing by these units persisted with only a slight decline in frequency over the next 45 min of observation.

### DISCUSSION

While all preoperative, sham-operated, and dPD crabs fed avidly, bilateral detachment of the elastic strand of the PD organ from the dactyl of the chelae had a profound effect on the initiation and maintenance of fine, manipulative, dactyl-dependent feeding behaviors. There was a significant decline in the number of all dactyl-dependent acts. Indeed, dPD crabs rarely used the dactyl (Figs. 2, 4A). Accompanying the quantitative decline in the initiation of fine manipulations was an observable loss of dexterity and maintenance of acts if a crab attempted to use a dactyl. For example, if gripping was attempted, the mussel valve appeared not to be gripped firmly because the dactyl was not completely closed. With the reduction in the incidence and effectiveness of gripping and the

dactyl-dependent acts that ordinarily followed, a significant increase occurred in use of the dactyl-independent behaviors of cradling, stabilizing, and guiding. These acts which employ the chelipeds and walking legs provided an alternative and effective means of bringing food to the mouth, where the maxillae and maxillipeds accomplished removal of food from the valve.

We conclude that meaningful feedback from the PD organ is required for the initiation and execution of purposeful precise contractions of the opener and closer muscles controlling the dactyl. With the PD organ detached, the elastic strand shrinks to a length that is shorter than when the claw is held open. Detachment results in the complete loss of the phasic input signalling movement, direction of movement, and velocity of movement (Boettiger and Hartman, '67) because the elastic strand no longer lengthens and shortens upon joint movement to actuate the receptor cells. There is also loss of meaningful tonic input providing accurate assessment of static joint position (Hartman and Boettiger, '67). Our physiological experiments indicate that there is a high frequency steady stream of tonic input from the position neurons after detachment; however, that excitation does not result in volitional use of the dactyl. The significant reduction in the number of intended movements of dPD cheliped in all likelihood reflects a decline in motor activity to the opener and closer muscles. Nonetheless, dPD crabs were able to accomplish feeding by a shift in the motor program which included greater use of nondactyl portions of the chelipeds and the walking legs. No change was seen in the feeding behavior of crabs receiving the sham surgery. This is significant because motor activity to the meropodite extensor muscle was reduced upon inactivation of individual chordotonal organs (MC1, MC2, and MCO) but also after sham surgeries in crayfish claws (Notvest and Page, '86).

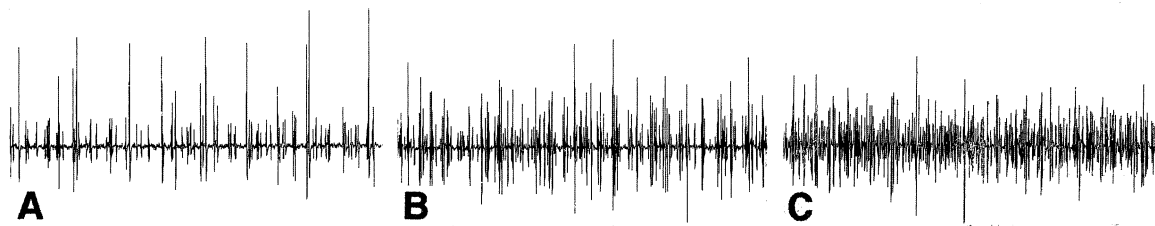


Fig. 5. Recording from the PD organ nerve of a chela when the dactyl is partially open (A) or fully open (B) and when the elastic strand is detached (C). Tonic firing by small- and medium-sized position fibers is at low frequency in A and

increases in B. Detaching the strand results in very high frequency of firing by small units (C); the firing rate declined very little over the next 45 min. Each record is a 1 sec duration sample.

Afference from other receptors in the chelae remained undisturbed in these experiments. These receptors include the funnel canal organs in the dactyl which monitor cuticular deformations and receptors of the propus which monitor forces exerted by the closer and opener muscles (Hartman, '85; Tryba and Hartman, '97). The axons of the closer apodeme sensory nerve (CASN) merge with the PD organ at the attachment of the elastic strand to the apodeme (Hartman, '85). Had we elected to extirpate the PD organ or cut its nerve rather than detach its elastic strand from the dactyl, the force-sensing afferents on the closer muscle apodeme would have also been destroyed as well. In brachyurans, nerves from receptors monitoring the force of the adjacent muscle merge with the MC1 and MC2, PD, and CP1 and CP2 chordotonal organs (Macmillan and Dando, '72; Hartman, '85; Cooper and Hartman, '94). There is evidence that force-monitoring receptors are an integral part of the MC1 and MC2 chordotonal organs in anomurans and macrurans as well (Macmillan et al., '81, '82). Thus, extirpation of chordotonal organs or cutting their nerves in those animals also eliminates input from apodeme force-sensitive receptors and confounds interpretation. While the force-sensitive receptors of the opener and closer were intact in our experiments, it is evident that their input does not compensate for loss of PD organ feedback. This provides further evidence that the modalities are separate functionally (Tryba and Hartman, '97).

It appears from a variety of studies that walking is centrally patterned and that input from chordotonal organs, especially those at the extremities, plays but a minor role in the coordination of locomotion (Clarac and Coulmance, '71; Evoy and Cohen, '71; Barnes et al., '72). On the other hand, there is convincing evidence that, in walking legs, force-sensitive mechanoreceptors (funnel canal organs) at the tip of the dactyls provide significant input adapting patterning of motor neuron activity and determining leg coordination (Zill et al., '85; Libersat et al., '87a,b). In contrast to the minor coordinating role played by the PD organs in walking legs, it is evident from our study that PD organ afference is required if chelae are to be used to initiate and maintain feeding behavior. This raises the hypothesis that, in contrast to walking legs, directed chelae behaviors are uncoupled from central pattern generator rhythmic commands; they are more likely to be governed by descending influences and reflexes or a completely dif-

ferent central pattern generator network than the walking legs.

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