

THE ROLE OF THE MUSCLE RECEPTOR ORGAN IN THE CONTROL OF ABDOMINAL EXTENSION IN THE CRAYFISH *CHERAX DESTRUCTOR*

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Summary

A platform was lowered from beneath suspended crayfish, *Cherax destructor*, to evoke slow abdominal extension. The movements were filmed and the length between segments plotted as a function of time. Unlike abdominal flexion, which starts posteriorly and progresses anteriorly, extension occurs at all joints simultaneously. Although the duration of extension varied from trial to trial for an individual, the movement was organised in a stereotyped manner: the abdomen achieved a consistent position for any given *proportion* of the time for complete extension. We examined the role of the abdominal muscle receptor organs (MROs) in extension by cutting the nerves of selected MROs to abolish their input. The extension movement was measured before and after nerve section for

animals with either unloaded or loaded abdomens. Removal of MRO input had no significant effect on extension of the unloaded abdomen. In animals with a loaded abdomen, the extension at joints spanned by sectioned MROs was slowed, whereas that at joints with intact MROs was not. The findings are consistent with the hypothesis that the MRO is an error detector in a servo-loop controlling abdominal position. The results provide the first demonstration that this load-compensating reflex loop operates during naturally evoked extension of the abdomen under constant load.

Key words: stretch receptor, load compensation, abdominal posture, crayfish, *Cherax destructor*.

Introduction

Control of body position involves spatial and temporal coordination of the movements of individual body parts. This requires complex integration in multisegmented animals, where forces may act across several joints. Regulation of abdominal position is necessary for escape, locomotion, defence and reproduction in crayfish. The abdominal muscle receptor organs (MROs), first described in lobsters by Alexandrowicz (1951), provide sensory input to the abdominal control system, but their role is still not fully understood.

Each abdominal hemisegment contains a tonic and a phasic MRO located dorsal to, and in parallel with, the superficial extensor muscles. A single MRO consists of a thin receptor muscle (RM) and a sensory neurone (SR). The SR has its dendrites embedded in the mid-section of the RM, which spans the articulation between abdominal segments. An increase in RM tension, arising either from passive stretch or from active contraction of the RM, deforms the dendrites and excites the SR (Wiersma *et al.* 1953). Neither the phasic MRO nor the phasic musculature is active during the postural movements examined in this study (Kennedy and Takeda, 1965*a,b*; Kennedy *et al.* 1966) and neither will be considered further here.

The superficial muscles control abdominal posture by acting across each of the five intersegmental joints. The antagonistic

superficial extensor muscles (SEMs) and superficial flexor muscles (SFM) determine the angle of each joint. The SEM and SFM groups are each innervated by a set of six motor neurones in each hemisegment. Each set contains five excitatory motor neurones and one peripheral inhibitor numbered in order of increasing fibre diameter (Kennedy and Takeda, 1965*b*; Fields *et al.* 1967). The SEMs attach to the anterior edge of the next posterior segment to draw it forward and produce extension. The superficial extensor motor neurones (SEMNs) that innervate the SEM of a particular segment run with the MRO fibres in the dorsal branch of the second root and enter the next anterior segmental ganglion (Hughes and Wiersma, 1960; Fields *et al.* 1967).

The tonic MRO is involved in an intrasegmental reflex in which SR discharge reflexly excites a single excitatory motor neurone (SEMn no. 2) that innervates over 90% of the SEM fibres in its own segment (Fields and Kennedy, 1965; Fields, 1966). Thus, if external forces flex the joint bridged by the RM, the SR responds, the afferent activity excites SEMn no. 2 and the SEM contracts until the RM unloads; unloading the RM turns off the feedback loop. The MRO is the length-detecting element in this resistance reflex that provides a basis for load compensation (Fields, 1966; Fields *et al.* 1967; Sokolove, 1973). SEMn no. 4, a motor neurone shared by the RM and

SEM, is responsible for adjusting the tension of the RM (Fields and Kennedy, 1965).

Fields *et al.* (1967) proposed two ways in which abdominal extension could be achieved. First, central drive for extension could recruit SEMN no. 4 to activate the RM and SEM together. In the absence of a load, extension would proceed with both the RM and SEM contracting at the same rate and the SR would remain silent. If, however, the extending abdomen encountered resistance, RM tension would develop faster than the SEM could unload it and the SR would discharge. Second, the central drive could activate motor neurones only innervating the SEM. In this case, the RM would not contract with the SEM, the MRO reflex loop would be bypassed, and a load would cause a slower extension. Activation of unshared SEMNs could only result in a centrally determined increment of SEM tension, whereas use of the shared SEMN no. 4 could provide length control (Fields *et al.* 1967).

Sokolove (1973) provided evidence that the MRO servo-loop operates during some voluntary extensions by monitoring MRO activity and recording an increased rate of discharge when the abdomen contacted a rigid stop. Page (1978), however, found evidence for load compensation during 'command-fibre'-evoked extensions that did not involve MRO activation. He suggested that another unknown load-compensating system must also operate in some circumstances.

In this study, we examined some spatial and temporal parameters of naturally evoked postural extensions of the unloaded and loaded abdomen. We then used this information to examine the effect of selective removal of MRO afferent activity for evidence that the load-compensating SR-SEMN no. 2 reflex is operating during these extensions.

Materials and methods

Specimens of the Australian smooth freshwater crayfish *Cherax destructor* (Clark) were obtained from commercial suppliers in western Victoria and maintained in shallow indoor aquaria at a temperature of 15–17 °C. They were subjected to a normal dark/light cycle (12h:12h L:D) and fed weekly with dry pellet prawn food. Intermoult crayfish of both sexes, with all appendages intact and with a cephalothorax length of 4.5–5.5 cm, were selected for the experiments.

The experimental preparation

Three days before an animal was first filmed, a plastic nut was attached to the posterior dorsal thoracic carapace with Araldite 5 min epoxy adhesive. The abdomen was moved to a fully extended position and a small drop of epoxy resin was placed in the centre of each abdominal segment for later use as a marker of segment position. The antennae were shortened to 3 cm to prevent them from contacting the walls of the recording tank. To load the abdomen, a 1.3 g lead weight was attached to the epoxy marker on the fifth abdominal segment (A5) of each animal 1 day before an experiment. This applied a load across the A4–A5 articulation and more anterior joints.

Abdominal extension

Extension movements were filmed in the early afternoon using natural daylight from nearby windows. The animal was suspended in a water-filled glass tank (45 cm×20 cm×25 cm) on a threaded Perspex rod that screwed into the plastic nut mounted on the thorax. This resulted in a body fixed in space, with the abdomen and all appendages free to move. The crayfish was positioned so that the appendages could not contact the walls of the tank, as this may inhibit abdominal extension (Page, 1981). The aquarium water, at the room temperature (17–19 °C), was kept well aerated. A movable platform was raised beneath the walking legs and the animal was allowed to settle for 2 min. This normally caused flexion of the abdomen, but if full flexion was not achieved in that time, the telson was touched lightly with a probe until the animal adopted its fully flexed posture.

Loss of contact with the substratum evokes a series of movements including abdominal extension (Larimer and Eggleston, 1971; Sokolove, 1973; Page, 1975*b*; Williams and Larimer, 1981). In these experiments, this was achieved by lowering the platform (a platform-drop). Only extensions that began with the abdomen in a stationary, fully flexed posture and proceeded smoothly to the fully extended posture maintained for a minimum of 1 s were analysed.

To prevent habituation to the mechanical stimulus, a dim light was shone briefly into the eyes of the animal at some time between every second or third platform-drop, and no more than six reflex responses were recorded on any one day for a particular animal. This procedure was followed over 2–3 days to obtain six smooth pre-treatment abdominal extensions per animal. Each animal then underwent one of three treatments. *Denervated* animals were those in which the dorsal nerves were sectioned on both sides of A4 to eliminate MRO input. *Sham* animals underwent the same operational procedure, but the dorsal nerves were not sectioned. *Control* animals were handled but not operated upon. All animals were given 3 days to recuperate before being refilmed during a further 2–3 days to obtain six smooth post-treatment abdominal extensions per animal. Each treatment was applied to five animals with an unloaded abdomen and to five animals with a load upon A5.

Sham and denervated animals were anaesthetised in crushed ice for 20 min and the dorsal region of A4 exposed for surgery. The operating instruments were sterilised in absolute ethanol. In each hemisegment, the location of the MRO pair was estimated under the dissecting microscope using external markers, and a 1 mm diameter hole was drilled into the cuticle using a dental drill. The underlying hypodermis was pierced and a fine probe was used to locate the MRO pair. It was often necessary to remove a small amount of connective tissue at this stage. The surgery on sham animals concluded here. For *denervated* animals, the tonic and phasic RMs were raised with a fine hook and the dorsal nerve sectioned close to the RMs, care being necessary to avoid cutting nearby SEMNs that branch from the dorsal nerve to the SEM.

The hole was temporarily sealed with soft dental wax and the surrounding cuticle was dried with absorbent wedges. A

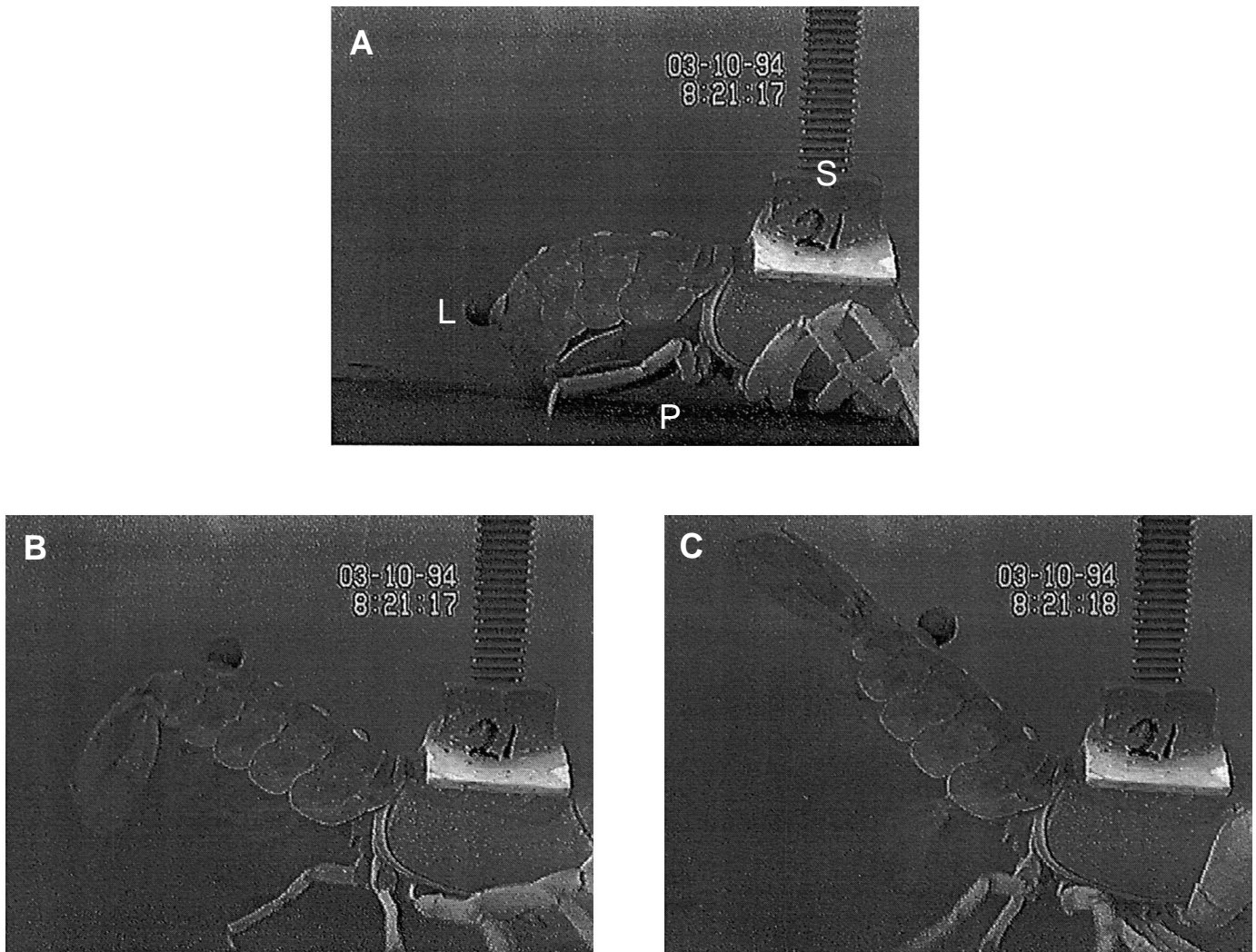


Fig. 1. Video images of a postural extension of the abdomen in response to a platform-drop for a crayfish *Cherax destructor* (animal no. 21). (A) Fully flexed position at 0% extension time. L, load on A5; P, platform raised beneath the animal; S, suspension system holding the animal in the water column. (B) Intermediate position at 50% extension time. (C) Fully extended position at 100% extension time.

more permanent seal was made by heating a small drop of beeswax with a temperature-controlled heat probe and using it to cover the plugged hole and surrounding cuticle. The animal was returned slowly to room temperature. The outcome of each operation was verified by *post mortem* dissection at the completion of filming, and results from animals that failed to meet the surgical objective were discarded. Thirty-four animals were used to obtain the 30 successful replications required.

Data recording and analysis

Evoked abdominal extensions were filmed through the glass sides of the experimental tank with a Sony Hi8 video camera recorder. The camera was maintained perpendicular to, and a set distance from, the long axis of the animal, and the focal length of the lens remained constant throughout the experiments. The recordings were transferred onto S-VHS cassettes with a Panasonic S-VHS time lapse recorder and viewed with a Sony Trinitron colour video monitor.

The total time for each abdominal extension was measured using a field-by-field tape advance button, where each field advance represented 20 ms (50 fields s^{-1}). Extension was defined as first detectable movement from the fully flexed position until the abdomen became stationary again in the fully extended position (Fig. 1).

The position of the abdomen at different stages of the extension time was recorded by placing a clear acetate sheet on the monitor screen and drawing on it the position of the epoxy markers on each abdominal segment. The length between markers on adjacent segments, a function of the degree of extension/flexion at that joint, was entered into a computer using a standardised digitising tablet. This method of analysis avoided the need for complex positional analysis over several joints and for calculating absolute angles between segments.

The range of each abdominal extension was measured by constructing a line from the posterior dorsal edge of the thorax

to the dorsal surface of the A5–A6 joint at both 0% and 100% of the extension time, and measuring the angle between these two lines. The extension range (degrees) and time (s) were combined to give the mean angular velocity of the extension ($^{\circ}\text{s}^{-1}$).

Results

Response to the platform-drop

When resting on the platform, *Cherax destructor* had its abdomen fully flexed, swimmerets stationary and all four pairs of legs in contact with the platform. The first three pairs of legs were always directed anteriorly, and the fourth posterior pair to the rear. Each animal responded to the platform-drop by extending all abdominal segments. Swimmeret beating and leg waving also accompanied the abdominal extension. This behaviour is similar to that described for the crayfish *Procambarus clarkii* following a loss of contact with the substratum (Larimer and Eggleston, 1971; Sokolove, 1973; Page, 1975b; Williams and Larimer, 1981), although the abdomen of *P. clarkii* rarely achieved full flexion prior to the extension. A small extension at the thoraco-abdominal joint consistently preceded the abdominal extension in some animals, causing the fully flexed abdomen to lift slightly before extending. Goodall *et al.* (1990) recorded a similar response for the Norway lobster *Nephrops norvegicus* immediately before abdominal extensions evoked by acoustic stimuli.

Analysis of the length between adjacent segmental markers in *C. destructor* revealed that in contrast to abdominal flexion, which begins in the most posterior segment and proceeds anteriorly (Page and Sokolove, 1972), extension occurred between all segments simultaneously throughout the entire movement (Fig. 2). The rate of shortening between segments was greater early in the extension movement and decreased at the more extended end of the range. The mean (\pm S.E.M.) angular velocity of the extension of the unloaded abdomen in *C. destructor* was $84.0 \pm 3.8^{\circ}\text{s}^{-1}$ (60 trials in 10 animals). This was significantly greater than the mean angular velocity of extension in the crayfish *Orconectes rusticus* and *O. virilis*

($16 \pm 0.5^{\circ}\text{s}^{-1}$) and *P. clarkii* ($40 \pm 4.9^{\circ}\text{s}^{-1}$) in response to an uplift stimuli (Page, 1975b). The mean (\pm S.E.M.) extension range in *C. destructor* of $89.0 \pm 2.0^{\circ}$ (60 trials in 10 animals) was also greater than those described in all three species by Page (1975b).

Organisation of the abdominal extension

Analysis of extension in *C. destructor* showed that each animal achieved a fully extended position that was consistent from trial to trial, as was found for *P. clarkii* (Williams and Larimer, 1981). Each animal also adopted its own characteristic fully flexed position prior to each extension. However, the extension times varied from trial to trial (Fig. 3A). Despite this, the extensions of each animal were temporally stereotyped. They were organised such that the length between segments at a given proportion of the extension time was consistent from trial to trial (Fig. 3B). Thus, each animal had its own stereotyped and symmetrical extension response where the abdominal position achieved was a function of the extension time.

To minimise variation when comparing extensions from different animals, the intersegmental lengths were standardised against full flexion. For each extension, the percentage change in length between segments after $Z\%$ extension time was calculated as $(x-y/x)100$, where x is the distance (in mm) between segments at 0% extension time (full flexion) and y is the distance (in mm) between segments at $Z\%$ extension time. For the experiments assessing the effects of the various treatments on abdominal extension, we examined the change in intersegmental length after 50% extension time. The data were analysed using a Student's t -test set at 5% significance.

Effect of sham operation

Before examining the effects of removing MRO afferent input, it was first necessary to determine whether the general effects of surgery affected abdominal extension. A Student's t -test between control ($N=5$) and sham ($N=5$) groups of animals showed no significant difference in the change in length

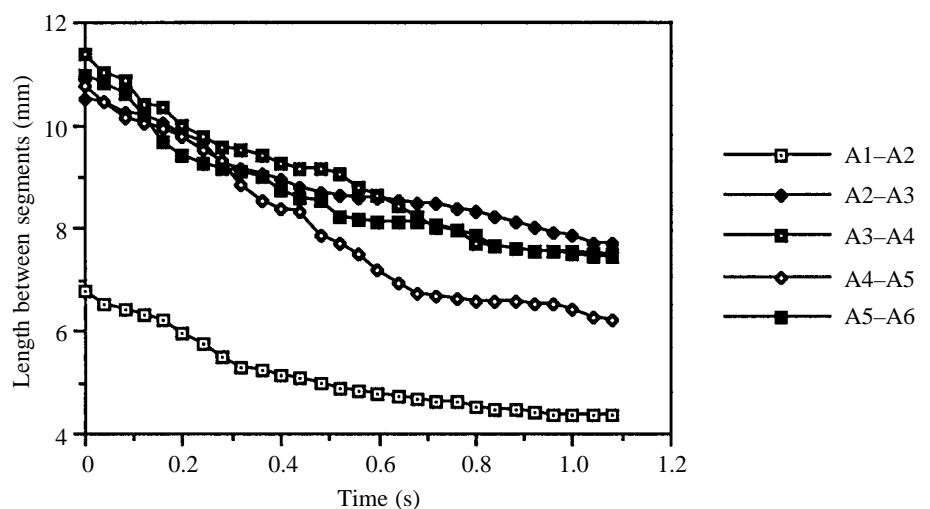
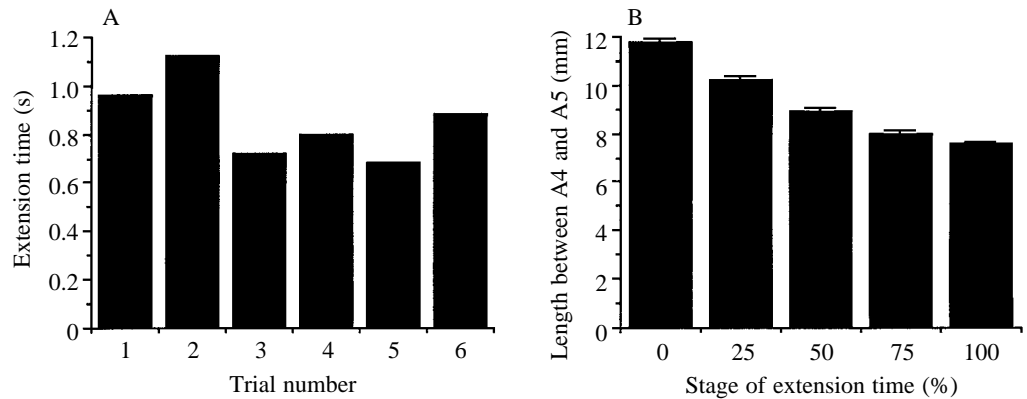


Fig. 2. The length between adjacent segment markers during a single postural extension of the abdomen in a crayfish *Cherax destructor* (animal no.7).

Fig. 3. (A) The extension times of six trials in a crayfish *Cherax destructor* (animal no. 18). (B) Mean length between A4 and A5 (mm) at various percentage stages of the extension time (obtained from the same six extensions shown in A for animal no. 18). The bar above each column is +1 S.E.M. Note the low error in length between segments at given proportions of the extension time.



between A4 and A5 after 50% extension time, for animals with either unloaded ($P=0.322$) or loaded ($P=0.798$) abdomens.

Effect of removing MRO input

For animals with an unloaded abdomen, the effect of sectioning the dorsal nerves in A4 on the extension at the A4–A5 joint is illustrated in Fig. 4A. A Student's *t*-test between sham ($N=5$) and denervated ($N=5$) animals with an unloaded abdomen showed no significant difference in the change in length between A4 and A5 after 50% extension time following removal of MRO input ($P=0.832$).

For animals with a fixed load upon A5, the effect of sectioning the dorsal nerves in A4 on the extension at the A4–A5 joint is shown in Fig. 4B. A Student's *t*-test between sham ($N=5$) and denervated ($N=5$) animals with a loaded abdomen showed that the change in length between A4 and A5 after 50% extension time was significantly lower after sectioning the dorsal nerves in A4 ($P=0.004$). The reduced extension at the loaded A4–A5 joint indicates that the SEM controlling the A4–A5 joint contracted at a slower rate in the absence of MRO input. We propose that this lag results from the removal of the load-compensating SR–SEM no. 2 reflex.

Intersegmental effects

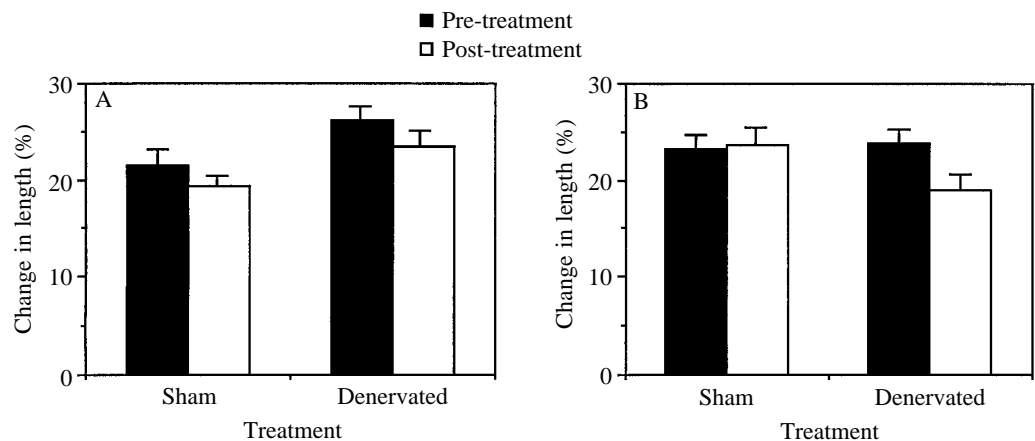
To test whether removal of MRO input in A4 altered the extension at joints other than A4–A5, we also analysed extension at the A3–A4 and A5–A6 joints. We found no

significant differences in extension at either of these joints following removal of MRO input in A4, for animals with either unloaded (A3–A4, $P=0.970$; A5–A6, $P=0.898$) or loaded (A3–A4, $P=0.492$; A5–A6, $P=0.100$) abdomens.

Discussion

Cherax destructor responds to the platform-drop with a stereotyped abdominal extension in which there is a symmetrical shortening between all segments throughout the entire extension. This contrasts with abdominal flexion, which begins in the most posterior segment and proceeds anteriorly (Page and Sokolove, 1972). Although our method of analysis would not be likely to detect any small sequential delay in activation between segments, it is clear that the command for extension differs from that for flexion in that it travels to all segments at about the same time, a conclusion supported by the results of Page *et al.* (1984), who recorded a similar SEM response latency in A1 and A5 following mero-carpal joint stimulation in *P. clarkii*. Our finding that naturally evoked extensions are proportionately stereotyped each time they occur indicates that they are centrally coordinated. This finding is consistent with the observation that voluntary extensions in *P. clarkii* are similar to those elicited by electrical stimulation of extension 'command fibres' (Larimer and Eggleston, 1971; Sokolove, 1973; Page, 1975a) and the absence of such command units in the circumoesophageal connectives of

Fig. 4. Histograms showing the mean change in length (%) between A4 and A5 after 50% extension time for animals with (A) unloaded abdomens and (B) loaded abdomens. Calculated for sham ($N=5$) and denervated ($N=5$) groups of animals before (filled columns) and after (open columns) treatment. The bar above each column is +1 S.E.M.



Orconectes virilis and *O. rusticus* is matched by the absence of complete abdominal extension movements (Page, 1975a,b). Our loading and denervation experiments show that the centrally generated extensions can be locally modulated by sensory inputs.

Page (1978) found that the addition of a load to 'command-fibre'-evoked extensions resulted in a general increase in firing of the SEMNs, often without any increase in SR discharge. The lack of SR discharge in response to a load in that case may be due to the type of extension 'command fibre' stimulated. Command fibres that excite only unshared SEMNs (Fields *et al.* 1967; Page, 1975a) may bypass the MRO reflex loop. Nevertheless, Page's (1978) finding is intriguing because Sokolove (1973) also recorded an increase in the activity of some of these neurones in response to load during naturally evoked extensions. This suggests that additional receptors may be involved in these behaviours. Possible candidates for this role are the cord stretch receptors (Grobstein, 1973a,b; Savati and Macmillan, 1993).

There are three ways in which extension can occur: by drive onto the receptor muscle to activate the local SR-SEMNs, by drive onto motor neurones shared by the receptor and the working muscles or by drive onto motor neurones exclusive to the working muscles. The first possibility is unlikely because there is, to date, no evidence that the receptor muscle receives exclusive motor innervation in any species, and some extensions occur without MRO activation at all. Our results show that load compensation is occurring, so that the second mechanism is certainly operating in the extensions we studied. Sokolove (1973) also reported occasional MRO discharges, presumably detecting deviations from the prescribed segmental position, during unimpeded, naturally evoked extensions in *P. clarkii*. The third possibility is not mutually exclusive to the second, and it is probable that motor neurones other than SEMN no. 4 are also activated during the extension in *C. destructor*. Sokolove (1973) found that activity in SEMN no. 4 is accompanied by motor output in all of the other excitatory SEMNs at different stages of extension in *P. clarkii*.

The finding that the removal of MRO input had no significant effect on the extension of the unloaded abdomen was not unexpected. Eckert (1961) and Sokolove (1973) suggested that activation of the MROs only occurred when isometric conditions were imposed, such as when the abdomen was prevented from extending at the centrally determined rate. Our findings support this hypothesis, as extensions at unloaded joints deprived of MRO input were indistinguishable from extensions when the MRO remained intact. Removing MRO input from segments of a loaded *C. destructor* abdomen caused a significant slowing of extension only between the segments bridged by that receptor, demonstrating a local load-compensating role for the MRO. Extensions at neighbouring joints were not altered. There is some evidence in *P. clarkii* that MRO activity evokes weak ipsilateral SEMN responses in the neighbouring anterior and posterior segments, but these intersegmental interactions may be due to mechanical coupling

between segments rather than to reflex connections (Fields and Kennedy, 1965; Fields, 1966; Nja and Walloe, 1975).

The results reported here could, perhaps, have been anticipated by the earlier work on both *P. clarkii* and *C. destructor*. Nevertheless, this is the first demonstration of the load-compensating role of the MRO servo-loop in naturally evoked abdominal extensions under constant load and it provides further information about the organisation of extension movements.

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