A NEUROPHYSIOLOGICAL ANALYSIS OF AGGRESSIVE BEHAVIOUR IN CARCINUS MAENAS

by

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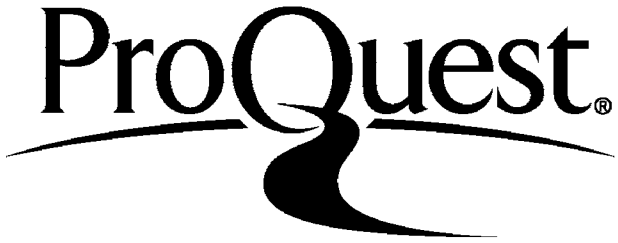


ABSTRACT

Agonistic activities, that is behaviours associated with aggression and defence were studied in Carcinus maenas. Two particular agonistic interactions which employ the chelipeds were chosen for detailed analysis; the fast strike and threat display behaviours.

The fast strike involves rapid flexion of the chelipeds and is completed within 30 to 60 ms. The limb is propelled forwards and downwards from the first two cheliped joints. Calculation of the energy required for a strike revealed that it is necessary for the muscles of the coxa - basi-ischium complex to develop energy before the strike is performed. It is found that this energy is produced by antagonistic muscles contracting together before the strike, allowing isometric tension development.

The moments of the coxa promotor and remotor muscles about the thorax-coxa joint give rise to a bistable articulation in which the coxa may be rapidly remoted or promoted in a "flip-flop" situation. Three of the basi-ischium muscles, the Anterior levator, Anterior and Posterior depressors, have an unusual geometry which gives them more than one function. The contributions of the coxal and basi-ischium muscles during the strike is discussed and a method by which the strike is performed, is suggested.

A strike only occurs from a threat display position in which the chelipeds are extended and levated. The threat behaviour was examined to determine the muscle activity which precedes the strike. Characteristic patterns of motor activity correspond to different postures of threat display. Manipulating various stimulus parameters presented to the crab showed that threat displays are most readily released by the rapid approach of large objects.

Neural activity recorded from the circumoesophageal connective nerves revealed that the presentation of stimuli representing rapidly approaching objects accompanies high frequency bursts of large spikes. This activity also corresponded to high frequency motor activity in the cheliped muscles which accompanies the adoption of extreme threat display positions.

CONTENTS

LIST OF ILLUSTRATIVE MATERIAL

ABBREVIATIONS USED IN THESIS

LIMB JOINTS

(from the proximal to the distal limb segments.)

T-Cx	;	thorax-coxa joint
Cx-BI	;	coxa-basi-ischium joint
BI-M	;	Basi-ischium-merus joint
M-C	;	merus-carpus joint
C-P	;	carpus-propus joint
P-D	;	propus-dactylus joint

MUSCLES

CxP	;	coxa promotor muscle
CxR	;	coxa remotor muscle
BI Al	;	BI Anterior levator muscle
BI Pl	;	BI Posterior levator muscle
BI Ad	;	BI Anterior depressor muscle
BI Pd	;	BI Posterior depressor muscle
Pd1	;	BI Posterior depressor muscle group 1
Pd2	;	BI Posterior depressor muscle group 2
PdH3	;	BI Posterior depressor heel muscle group 3
PdH4	;	BI Posterior depressor heel muscle group 4
PdH5	;	BI Posterior depressor heel muscle group 5
PdH6	;	BI Posterior depressor heel muscle group 6

MISCELLANEOUS

ejp	;	excitatory junctional potential
EMG	;	Electromyogram
M.r.f.	;	muscle response frequency
ms	;	millisecond
mV	;	millivolt
s	;	second

CHAPTER ONE

GENERAL INTRODUCTION

Behaviour includes all processes by which an animal senses its environment and the internal state of its body, and responds to changes which it perceives. Behaviours may be simple, when they are termed reflexes, such as the tail flip reflex of the crayfish (Wiersma, 1952) or may be complex, incorporating many reflexes, such as crab locomotion (review by Barnes, 1975).

Ethology is an approach to the study of animal behaviour. This term is used when biological methods are applied for the description, measurement and interpretation of behaviour in intact animals in nature or under conditions which approximate that of nature. Ethologists believe that behaviour is determined by inherited capabilities as well as experience gained by the individual in relation to its environment (Manning, 1972). There are, however, some behaviours which appear to be isolated from individual experience. They are believed to be composed of more or less stereotyped motor responses and are termed Fixed Action Patterns (Hinde, 1970). Ethologists believe that these patterns represent the end product of a neuromuscular complex which begins at the sense organ with the discrimination of a specific stimulus, which is termed the releaser. The discrimination of this stimulus acts upon a releasing mechanism in the central nervous system which, when adequately stimulated initiates the combination of motor responses which comprise the Fixed Action Pattern.

Reese (1964) described four goals of ethological investigations. Firstly, such studies should describe and classify the behaviour; secondly the underlying physiological mechanisms of the behaviour should be discovered; thirdly the development of the behaviour both in the individual during its ontogeny and in the species over the course of evolution should be understood; fourthly the ecological significance of the survival value of the behaviour to the species should be studied. All four goals can be examined from behavioural viewpoints while the first and second goals are usually studied using physiological techniques.

The study of neural mechanisms which govern behaviour was termed neuroethology (Hoyle, 1970). Hoyle categorised several behaviours from a neurophysiological point of view on the basis of a hierarchy of complexity of movements. The simplest behaviour would result from single contraction of a single muscle. Other levels of behaviour

include co-ordinated non-repeated movements, cyclically repeated sequences of co-ordinated movements, simple rhythmic movements, complex cycles of movement and learning.

The behaviours which Hoyle classified as complex cycles of movement include the Fixed Action Patterns, or instinctive behaviours. They are characterised by consisting of rigidly stereotyped patterns of movement which are almost identical in all individuals of a species, and can often be evoked most readily by simple stimuli. These behaviours include actions of escape, defence and aggression. The actions of aggression and defence are collectively termed agonistic behaviours. Within the Crustacea the agonistic behaviour of semi-terrestrial brachyuran crabs has been widely studied; including the Grapsidae (Bovbjerg, 1960), the Ocypodidae (Crane, 1957), together with many others reviewed by Reese (1964), Schöne (1968) and Wright (1968). However, the majority of these investigations have been studied from a behavioural point of view without emphasis on underlying physiological mechanisms.

Some types of agonistic behaviour have been modified through evolution into ritualised displays, which serve both to intimidate a rival and to reduce actual fighting to a minimum. Ritualisation is defined as the evolutionary development of communicative movements or postures from actions which originally served other purposes (Hazlett, 1973). Animals which engage in frequent hard physical combat will be at a disadvantage compared to those which are able to gain the needed environmental resources without physical damage from conspecifics. In most situations the loser in a ritualised fight has a better chance of reproduction than the loser in an unritualised fight, particularly if the combatants have potential weapons such as very large chelipeds. Prolonged fighting is extremely rare under natural conditions in crustaceans, as the weaker of the two combatants usually breaks away and escapes before any serious damage is done (Hazlett, 1973).

The use of specific postures, or displays, during agonistic interactions is common in many animals (Marler and Hamilton, 1968), including brachyuran crabs (Beer, 1959; Cameron, 1966; Crane, 1966; Schöne, 1968; Wright, 1968). Wright (1968) stated that at least three criteria must be met before a movement or posture can be termed a display. Firstly the movement must only be used in communication and not in other activities, such as feeding. Secondly, the occurrence of the posture in time and space must be such that it could usually be sensed by another animal and thus perform a communicatory function.

Thirdly, the movement must be more than an unmodified incomplete movement which replicates a directly functional motor pattern.

Certain features are common to all visual displays by brachyuran crabs. The body is raised high above the substratum, with the anterior part of the carapace higher than the posterior part. The merus of each walking leg is usually held horizontally and at right angles to the carpus and propus segments. These positions of display make the crab more obvious to the human eye and therefore, it is likely that they are more conspicuous to other crabs and exposed to predators. There must be some compensatory advantage of the display.

Wright (1968) studied the displays of more than 30 species of brachyuran crabs and proposed a series of names for the visual displays to facilitate comparative studies. The system was descriptive of the specific postures which serve to differentiate the displays. The displays were classed into two main groups based on the position of the chelipeds during the display. Each of these two groups include different subtypes which Wright believed represent intensities of aggression. The first group of displays was termed the Lateral Merus Display in which the merus of the cheliped is extended laterally, with the distal end of the merus raised and extended and the whole cheliped held horizontally. This is an extremely common display in brachyuran crabs and is shown by Carcinus, Portunus, Cancer, Hemigrapsus and Gecarcinus for example (review by Wright, 1968). The second group of displays was termed the Chela Forward Display in which the merus is extended anterio-dorsally so that the cheliped is held vertical with the tips of the claws hanging down. The merus is held at 45° from the horizontal as seen from the side. This is a less tense display and the chelipeds appear to dangle loosely from the merus-carpus and carpus-propus joints. This display is also shown by a variety of crabs, including Goniopsis pulchra, Ocypode and Grapsus (review by Wright, 1968).

The visual displays may be used for territorial purposes and courtship, or for agonistic interactions. They may be considered as a primitive form of language by which simple information from the displaying animal can be passed on to others. It is rather difficult to measure what information is conveyed by a displaying animal to another which receives the display. Some of the transmitted information may be tested by presenting models to animals and observing the resultant display.

Experiments using models to investigate crustacean displays have been performed several times in, for example, hermit crabs (Hazlett, 1966), spider crabs (Hazlett, 1972), Uca pugilator (Salmon and Stout, 1962), Carcinus maenas (Jensen, 1974) and the Blue Crab (Jachowski, 1974). These experiments showed that animals react to certain stimuli associated with a given display. For example, Salmon and Stout (1962) used clay models with attached chelipeds to demonstrate that Uca pugilator can recognise the sex of a model by virtue of the presence or absence of the large cheliped. Hazlett (1972) found that models which are presented in agonistic positions are effective visual stimuli in causing agonistic responses from the spider crab Microphyrs bicornutus. Jachowski (1974) demonstrated that reactions of the Blue Crab Callinectes sapidus, to dried models, consist of the same motor actions that they use when displaying to each other. Use of the models showed that the agonistic responses differed with the speed of approach of the stimulus, stimulus orientation, cheliped position of the model and the distance at which the model was presented. The crabs responded more often when the models were presented rapidly, frontally or with extended chelipeds, than when they were approached slowly, laterally or with folded chelipeds.

The term aggressive display, describes a situation in which an animal approaches another when one, or both of them are in an attitude of attack, with chelipeds raised, for example. Defensive displays are seen when an animal actively defends itself or retreats from the attacker. Schöne (1968) differentiated between agonistic activities with or without physical contact between opponents. The former was termed "fighting", and the latter "threat displays".

Schöne (1968) studied the agonistic displays of brachyuran crabs and found that aquatic species tended to use extended chelipeds for threat displays, the Lateral Merus Display of Wright (1968), and often terminate an interaction with fighting. He termed these, "wild fights" since the behaviour involves an irregular exchange of blows with the chelipeds. In some species of crab these blows take the form of fast strike actions in which the chelipeds are rapidly flexed anteriorly and medially from an extended cheliped position. This particular behaviour has been observed in Carcinus maenas (Bethe, 1897), Lambrus pugilator (Schäfer, 1958), Ocypode arenaria (Cowles, 1908) and the Blue Crab Callinectes sapidus (Jachowski, 1974). In Callinectes, Jachowski, (1974) reported that the crabs frequently

lunge forward at the same time as a strike is performed. The claws are initially held open, but snap shut at the end of a strike. The force of the blow may cause injury to the opponents. In these, and other, "wild fights" there appears to be a mutual measuring of physical strength and there is often the possibility of injury. "Wild fights" are commonly shown in the Dromiidae, Canceridae, Portunidae, Xanthiadae and Majidae.

In the more terrestrial species of brachyuran crabs, cheliped extension is less common and these animals used flexed, shield-like cheliped displays, the Chela Forward Display of Wright (1968). Wild fights are rarely observed, instead the crabs tend to formalise agonistic patterns. Threat and fighting follow fixed sequences. In Grapsus, for example the opponents touch only with the chelipeds and push against each other (Schöne, 1968).

Behaviour can be studied from an ethological aspect or from a physiological aspect. When the details of the behaviour and the circumstances under which the action may be expressed have been determined by observation then physiological studies of the action may be performed to determine the functional properties of the nerves and muscles through which the behaviour is expressed. However as stated by Delcomyn (1976), both these approaches have limitations. Behavioural studies can only imply which neural mechanisms are involved with a particular behaviour while physiological studies are often performed on highly dissected preparations which will behave quite unnaturally. A combination of both approaches is a better method of investigating animal behaviour, although this has its problems as well. Hinde (1970) suggested that describing a behaviour physiologically is often difficult. He wrote: "The analysis of behaviour can be aided by physiological data. The student who aims to pursue his analysis from the behavioural level to the physiological one is exposed to a special danger. Concepts useful at one stage in the analysis may be misleading at another". He gives examples that the terms of drive, urge and tendancy are useful at the behavioural level of analysis but are a handicap at the physiological level.

Despite these problems physiological studies have been performed on crustacean behaviour. These include simple activities such as eye movements (Burrows and Horridge, 1968) and more complex behaviours such as locomotion (Atwood and Walcott, 1965; Clarac and Coulmance, 1971; Barnes, 1975). Various agonistic behaviours

have also been studied at the physiological level (Bethe, 1897; Wiersma, 1952; Glantz, 1969; Burrows, 1969; Ritzmann, 1974).

One of the earliest physiological studies of crustacean behaviour was performed at the end of the last century by Bethe (1897 a,b) on Carcinus maenas. His papers described experiments on simple and complex reflexes concerned with the eye, antennae and statocysts, postural activities such as the righting reflex, walking and swimming, together with the more complicated and integrated postures associated with agonistic displays. These displays include the threat response, "Aufbäumreflex", tonic immobility, "Starrkrampreflex", the egg protection reflex, "Eierschutzreflex" and defence and escape "Verteidigungreflex".

Bethe initially described these actions from a behavioural point of view (Bethe, 1897a). For example, the Aufbäumreflex, the rearing behaviour, is displayed when the crab perceives a visual or mechanical stimulus. The responding crab rears up symmetrically, so that the body axis is at an angle of 45^{o} from the substratum. The walking legs are stretched out in such a way that the animal assumes a stable posture while the chelipeds are extended and raised. If the stimulation is persistent, the strike behaviour may follow, in which the crab rapidly strikes at the stimulus from an extended cheliped position denoting threat.

As well as these descriptive studies, Bethe also performed a series of physiological investigations in which he cut various parts of the nervous system and observed the behavioural result (Bethe, 1897b). For example, when the circumoesophageal connectives were cut before the thoracic ganglion, threat responses were still displayed although the crab assumed a different posture. Visual stimulation caused the crab to rear but the chelipeds were only slightly raised and remained flexed. The last pair of walking legs were not positioned far enough behind the body to produce the stable threat posture. Consequently when the crabs reared they often overbalanced. When Bethe cut only one connective, stimulation caused the crab to rear asymmetrically, and the ipsilateral side of the body was raised less than the intact, contralateral side. The probability of a threat response was greatly increased when the cerebral ganglion was split anterio-posteriorly. After this operation, Bethe reported that it was sufficient simply to approach the crab slowly and from a distance, to

evoke a complete threat response and repeated lunging strikes. The crabs became so aggressive that Bethe found it difficult to pick up the crabs, and he had to use a wooden stick to turn the crabs over before he could hold them safely. The effects of other operations are reviewed by Schöne (1961).

More recent physiological analysis of agonistic behaviours include the predatory strike behaviour of Squilla (Burrows, 1969), the escape response of Ocypode (Burrows and Hoyle, 1973), the snapping defence behaviour of Alphaeus (Ritzmann, 1974) and the defence reflex of the crayfish (Glantz, 1974 a,b,c).

Many agonistic behaviours of crustaceans involve extremely rapid movements and the physiological basis of such actions is often far from simple. The predatory strike behaviour of Squilla is an exceptionally fast movement. The strike consists of a rapid unfolding of the dactylus, propus and carpus about the merus of the raptorial second thoracic limb. Contact with the prey is made within 4 to 8 ms. It was calculated that the energy requirement for the strike could not be developed in the time occupied by a single muscle twitch, suggesting that energy must be developed and stored before the strike is performed (Burrows, 1969). By use of electrophysiological techniques and mechanical models, Burrows showed that the strike is produced by the co-contraction of the carpus extensor and flexor muscles of the raptorial limb. Contraction of the flexor muscles operates a click-joint in which a sclerite is pulled over a stop on the ventral wall of the merus. This locks the limb in a folded position and allows the extensor muscle to contract isometrically and therefore develop tetanic tension levels before the strike. When the flexors relax, the lock is disengaged and stored energy in the extensor muscles is released explosively.

Ritzmann (1973, 1974) studied the agonistic cheliped snapping behaviour of two Alpheidae shrimps. He found that the behaviour is produced by different means in the two animals. In Alphaeus californiensis, the action is produced by skeletal specialisations to the inner surface of the propus and dactylus of the snapping cheliped, which operates to lock the dactylus open and allows the dactylus closer muscle to contract isometrically. When the lock is disengaged, the force developed in the closer muscle is released and the claw snaps shut. In A. heterochelis a completely different mechanism is used to hold the claw open while the closer develops tension. When the claw is

fully open the insertion of the dactylus closer apodeme is positioned above the articulation between the dactylus and propus. This arrangement means that, in this position, contraction of the closer muscle cannot close the claw, and will therefore contract isometrically. As in A. californiensis, when the lock is disengaged, the tension developed in the muscle is suddenly released.

Crustacean agonistic behaviours have been studied at the neural level as well as the muscular level. For example, Glantz (1974 a,b,c), studied the stimulus parameters which elicit the defence reflex of the crayfish, and also the interneurones which participate in the coding of a given stimulus. Glantz (1974, a) found that when the crayfish is presented with a rapidly approaching target, the elicited defence behaviour demonstrated the properties of habituation, spontaneous recovery, dishabituation and stimulus generalisation. Subsequent experiments (Glantz, 1974, b) indicated that the motion detector units of the optic nerve respond in similar ways to the muscular responses recorded from the cheliped levatory muscles which are involved in the behaviour, Glantz suggested that the motion detectors provide a significant component of the visual afferent pathway of the defence reflex. He proposed that the reflex is elicited by a criterion number of motion detector spikes and that the stimulus velocity is coded by the mean discharge rate of these spikes (Glantz, 1974 c).

Another agonistic behaviour of the crayfish, the escape tail-flick reflex, has also been investigated. This is a particularly interesting behaviour since it can be produced by stimulation of a single nerve cell (Bowerman and Larimer, 1974). Many instances have been demonstrated in which the stimulation of single nerve cells elicit complex sequences of movement (reviewed by Larimer, 1976). These cells are termed "Command fibres" (Wiersma and Ikeda, 1964) and now include any premotor interneurone, stimulation of which provides a definite motor output. The behaviours caused by command fibre stimulation range in complexity from simple control of heartbeat in crayfish (Field and Larimer, 1975) to co-ordinated agonistic behaviours of the crayfish (Wiersma, 1952). Although the crayfish escape reflex can be produced by stimulation of a single command fibre (Bowerman and Larimer, 1974) some behaviours such as crayfish uropod movements, need the participation of several simultaneous commands to be completed (Larimer and Kennedy, 1969). However, since most command

systems can be released by simple patterns of stimulation to the command fibres, command pathways are thought to be permissive rather than instructive (DeLong, 1971).

Command fibres are often giant axons. For example the medial and lateral giant fibres in the crayfish abdominal nerve cord, serve as command fibres for the escape responses (Larimer et.al, 1971). However in some command systems the controlling fibres may be small in diameter. For example, the tonic abdominal extensor and flexor muscles of the crayfish, are controlled by a system of at least 18 small command fibres which cause extension, flexion and inhibition of muscle output (Larimer and Eggleston, 1971).

Although several studies in crustaceans have contributed substantial evidence that command fibre action is responsible for triggering behaviour there is a lack of recordings from such fibres in unrestrained preparations. When the behaviours are complex, obtaining direct evidence of underlying command activity is even more difficult. The approach often used is to compare a motor programme produced by interneurone stimulation with that of a freely behaving animal (Larimer and Eggleston, 1971; Kovac, 1974). Intracellular recording techniques are usually used to study the command fibre activity while EMG's and cinematography are usually used to examine the voluntary motor output.

Fraser (1974 a) studied five giant interneurones in the connective nerves of Carcinus maenas but was unable to establish the roles of the fibres in overt behaviour by electrical stimulation or by examination of nervous output in freely walking animals. However he was able to determine several responses of the fibres when selected stimuli, such as light and touch, were applied to the crab. He also performed several free-walking preparations while recording, extracellularly, from the connectives. In general, it was found that all giant fibre responses were more readily evoked in unrestrained crabs. The agonistic behaviour of threat could occur without any conspicuous giant fibre activity although the tracking response during threat, is accompanied by giant fibre activity. He concluded that although the giant fibres do not command the basic threat behaviour, they may be indirectly involved in the command pathway of this behaviour.

A second series of experiments on five directional statocyst giant fibres revealed that certain interneurones in the connectives of Carcinus could carry rotational information from the statocysts to the motor centres in the thorax (Fraser, 1974 b). These fibres

may be command elements in the threat and swimming behaviours. For example, when a crab rears, the anterior part of the body is raised. This would provide a strong input to a giant fibre termed cell A, which controls the position of the last pair of walking legs and consequently controls the stability of the threat posture.

Thus a variety of techniques has been employed to study the behaviour of crustaceans. These include simple observations of the action in freely moving animals and also complex physiological investigations involving dissected preparations. In only a few instances have complex behaviours been examined from both behavioural and physiological aspects. Several of these cases involve agonistic behaviours such as the strike of Squilla (Burrows, 1969), the rapid escape response of Ocypode (Burrows and Hoyle, 1973), the defensive snapping behaviour of Alphaeus (Ritzmann, 1974) and the defence reflex of the crayfish (Glantz, 1974).

In this thesis the agonistic behaviour of Carcinus maenas was examined using neurophysiological techniques. The behavioural acts were initially described using cinematography, a preliminary survey which is essential for any further work. It was found that, like other brachyuran crabs, Carcinus displays a variety of agonistic responses. Two agonistic interactions were chosen for detailed analysis; these were the threat display behaviour and the fast strike. It was found that the strike is an extremely rapid movement, and full flexion of the chelipeds take only 30 ms. This indicated that there may be special mechanisms which produce the strike and possibly involve the use of energy storage as in Squilla, or joint modifications as in Alphaeus heterochelis.

A strike behaviour is only performed from an extended cheliped position denoting threat. Therefore, the threat display behaviour was examined to determine the neuromuscular events that precede the strike. Both the strike and threat behaviours involve identical movements in all responsive crabs, which indicated that there may be discrete neural programmes controlling the performances of these actions. In an attempt to determine the presence or involvement of command fibres or other controlling neural elements, a series of experiments with free walking preparations was performed.

The results are presented in seven main sections:

1. The agonistic behaviours of Carcinus maenas are described and the threat and fast strike behaviour are examined in detail.
2. The energy requirement for a fast strike is calculated and it is found that energy storage is required to produce the fast strike.
3. The anatomy, neuromuscular responses and mechanical properties of the coxal and BI muscles of the cheliped are examined and suggestions are made concerning their possible involvement in a fast strike.
4. Electromyographic recordings are made from each muscle in the cheliped during a fast strike and the method of operation of this behaviour is discussed.
5. The stimulus parameters which affect the threat displays are examined using electromyographic recording techniques.
6. Extracellular recordings are made from the circumoesophogeal connective nerves and the characteristic patterns of neural activity which accompany the threat displays are examined.
7. Simultaneous recordings are made from the connectives and main cheliped muscles in free walking preparations during the performance of various agonistic behaviours.

CHAPTER TWO

THE AGONISTIC BEHAVIOUR PATTERNS OF CARCINUS MAENAS

INTRODUCTION

Agonistic activities include behavioural patterns of attack and escape and serve a communicatory function to control social interactions. Aggressive behaviour is displayed when two animals approach each other with one or both of them in a posture of attack. In many brachyuran crabs aggression is shown by raising and extending the chelipeds. The visual effect not only alters the shape but also the size of the crab. Defensive behaviour is signalled by lowering and flexing the chelipeds which makes the crab appear smaller. Schöne (1968) classified the aggressive behaviour patterns of crabs into two categories. The first occurs when physical contact is made between opponents; this is fighting behaviour. The second, when no contact is made, is the threat display. The latter is more stylised and follows certain rules and patterns.

The agonistic behaviour of Crustacea has been widely studied. Several species have been examined in great detail. These include the fiddler crabs of the genus Uca (Crane, 1957), a variety of species of hermit crabs (Hazlett and Bossert, 1965) and grapsid crabs (Beer, 1959; Schöne and Schöne, 1963; Wright, 1968). It is generally agreed by these authors that semi-terrestrial brachyurans primarily utilise visual and tactile signals as a means of communicating with other crabs and predators. Salmon (1965) studied the importance of acoustic signals in the fiddler crabs, but use of such behaviour is believed to be very limited in crustaceans (Hazlett, 1972).

Aquatic brachyurans have less ritualised patterns of agonistic behaviour and may rely more on tactile signals (Hazlett, 1972). Encounters between opponents often leads to physical interactions with an exchange of blows, or "wild fights" (Schöne, 1968), during which the crabs may injure each other.

The most common visual signal in semi-terrestrial brachyurans is the Lateral Merus Display, LMD (Wright, 1968) or Aufbäumreflex (Bethe, 1897). This involves a rapid movement of the chelipeds laterally and vertically, often accompanied by postural changes. In Carcinus maenas, for instance, the pereiopods are raised and the anterior part of the body is lifted from the substratum. In Mictyris longicarpus (Cameron, 1966) and some spider crabs (Schöne, 1968), this display is coupled with lateral extension of all the pereipods.

Wright (1968) divided the LMD into various subtypes. These were classified according to whether the chelipeds are extended laterally to their maximum, half flexed so that they point anteriorly or flexed so that they point medially. He named these displays High-intensity, Mid-intensity and Low-intensity LMD's. Wright suggested that each category reflects three different degrees of response of the crab, from a highly motivated state to a low state of aggressiveness.

A less common display in brachyuran crabs is termed the Chela Forward Display (Wright, 1968). In this the merus of each cheliped is extended antero-dorsally so that the limbs are held vertically with the dactyls pointing downwards. The merus of each cheliped is held at 45° from the horizontal when viewed from the side. The chelipeds, in fact, appear to dangle loosely from the merus-carpus joint in sharp contrast to the rigidity of the High-intensity LMD.

Wright suggested that the LMD is a more primitive display. As visual signals became increasingly important with the acquisition of a more terrestrial habit, the cheliped displays became more specialised. For example, some species of crab, including Lambrus pugilator (Schäfer, 1954), have developed contrasting colours on the chelipeds. Other terrestrial crabs have developed a more stylised and ritualised movement of the chelipeds, such as the cheliped waving action of Uca (Crane, 1957; 1966) and the reversed LMD of Cardisoma (Schöne, 1968).

Some species of grapsid and ocypodid crabs use the chelipeds in sexual displays. A male Pachygrapsus, for example, adopts a LMD when approaching the female (Bovbjerg, 1960). He pushes against the female with the chelipeds flexed; the pair then move, cheliped to cheliped, in a synchronous dancing motion. Helice, Uca, Ocypode and Hemiplax also display similar patterns (Schöne, 1968).

Wright (1968) suggested that the Chela Forward Display was developed as a specialised courtship pattern to contrast with other agonistic displays. As more elaborate social systems evolved, this display may then have been adopted for territorial defence as a less aggressive display. Eventually it may have succeeded the LMD as the main threat behaviour. However, whatever the display adopted, the effect in each case is to alter the shape of the crab and to increase the apparent visual size. At the same time the potential weapons, such as the claws and sharply pointed dactyls, are displayed. This would make the crab more noticeable and less attractive to an aggressor.

The use of tactile stimuli for communicatory signals is less common in brachyurans (Hazlett, 1972). When they do occur they are divisible into two categories, vibratory and non-vibratory. The former describes signals which are equivalent to acoustic signals received by animals which have sound receiving organs. An example is described by Hazlett (1966) in the hermit crab Coenobita, which produces sounds by stridulations. Non-vibratory signals include the shell tapping behaviour of some hermit crabs (Hazlett, 1966), and the cheliped tapping behaviour of Uca (Crane, 1967). Shell tapping in Pagurus bernhardus and some other hermit crabs has a dramatic result (Hazlett, 1970). The defending crab may give up its gastropod shell to the attacker without any bodily contact being necessary. The tapping patterns have been shown to be characteristic for each species. In Uca, if tapping with the chelipeds does not achieve the desired result, that is the submission of the receiver, then the aggressor uses force to throw the defendant backwards (Crane, 1967). Unlike the startling visual threat displays, tactile stimuli are generally confined to inter-specific encounters.

Visual signals, unlike tactile signals, can be viewed and received over long distances, especially when the display is as vivid as the High-intensity LMD. A positive selection pressure for developing such displays has arisen with adaptation to life on land (Schöne, 1968).

Chemical stimuli have not been shown to be used for threat displays in crustaceans. They can be used in sexual behaviour, although even this is rare, much more so than in insects. For example, female Pagurus bernhardus hermit crabs can produce a male stimulating chemical (Hazlett, 1970), as can the female swimming crab, Portunus sanguinolentus (Ryan, 1966)

Animal behaviour may be investigated by observing animals in their natural situations, noting the patterns which occur and their frequency. Behaviour may also be studied by experimental manipulation, by presentation of a series of models and recording the animals reactions. This method has been employed by Hazlett (1972) on the spider crab Microphrys, Jachowski (1974) on the Blue crab Callinectes, Salmon and Stout (1962) on Uca and Jensen (1974) on Carcinus maenas.

Jensen (1974) studied the threat display in Carcinus, using models made from both dried crabs and grey plastic plates. The plates

were cut into V shapes, which were presented both the normal way up and inversely and cigar like shapes which were presented both horizontally and vertically. He concluded that the threat display was less frequently released by models with a V shape, that is those which [redacted] appear to be like threatening crabs. To these and other models with a large horizontal axis, the crabs most frequently responded with an escape reaction. The models of submissive crabs and inverted V shapes released the most threat displays. Thus escape and threat behaviour are opposing reactions to opposite stimuli. Comparison of models with or without "chelipeds" showed that the crabs do not display to any particular morphological character of the cheliped but to the overall shape of the object. Also the crabs did not distinguish between the dried crab models and the plastic plates. Therefore it appears that no particular morphological character acts as a sign stimulus, but rather the crab assimilates the general form and orientation of a threatening object and responds accordingly.

The agonistic displays of certain crustaceans have been used for detailed physiological studies. The best documented is the defence and escape reflexes of the crayfish, first studied by Wiersma (1938). When specific interneurones are stimulated, the crayfish shows well defined motor activity. Medial and lateral giant axons, for example, generate the escape tail-flick reflex. Similarly, stimulation of other interneurones in the nerve cord generate the defence reflex of cheliped extension (Wiersma, 1952). Fibres such as these are termed "command fibres" since their stimulation can release partial or complete behaviour patterns which are reproducible from individual to individual.

The neural triggers to the agonistic behaviours of crayfish have also been searched for. Wiersma (1970) reported that the defence reflex receives substantial input from the space constant motion detectors in the optic nerve. Glantz (1974) studied the role of the optic nerve more closely. He found that the motion detector units of the optic nerve were activated early in the pathway of the defence reflex behaviour.

Another agonistic activity of crustaceans which has been examined is the strike behaviour of mantid shrimps. This is a particularly interesting behaviour since it involves an extremely rapid movement. The mantid shrimps Squilla and Hemisquilla, are

active predators. The second thoracic limbs are large and raptorial and are rapidly unfolded in a strike movement which may be aggressive or defensive. The physiological basis of this agonistic behaviour has been studied by Burrows (Burrows, 1969; Burrows and Hoyle, 1973), who found a skeletal click mechanism in the limb controlled by co-contraction of two antagonistic muscles. The operation of a stop allows the limb extensor muscle to contract isometrically before the limb moves. When the stop is removed, by flexor muscle relaxation, tension which has been built up in the extensors can be released, suddenly and explosively, within 8 ms.

The work presented here is a preliminary survey of the types of agonistic behaviour in Carcinus maenas. Certain of these behavioural patterns were then selected for further and more detailed analysis in an attempt to define their physiological basis.

MATERIAL AND METHODS

Carcinus maenas was obtained from the University Marine Biological Station, Millport, Scotland. A range of sizes of both sexes was used for the study of the general behaviour. Detailed work on the threat display and strike action was performed on male crabs of 60 to 80 mm carapace width. The crabs were maintained in tanks of circulating sea water at 10°C.

For observation of general behaviour, the crabs were placed in tanks, alone or with other crabs, in the laboratory. Some of the behavioural sequences were photographed using a Beaulieu R16 ciné camera.

Detailed analysis of the threat and strike behaviour was carried out by suspending the crabs in a glass tank full of sea water. A mirror was fixed at 45° at the back of the tank (Fig. 1). Small, lightweight plastic screws (Radiospares, London) were stuck onto the dorsal carapace with a fast action epoxy resin glue (Devcon 5-minute Epoxy resin). A metal rod with a centrally tapped thread in one end could then be screwed onto the plastic holder. The crab was suspended above the tank by supporting the rod in a clamp. The camera was positioned in front of the tank and could be adjusted to allow focussing upon the whole animal, the undersurface of the animal by virtue of the mirrored reflection, or onto specific joints. Film speeds of 8 to 32 f.p.s. were used for analysis of the strike behaviour. The films were examined frame by frame from the negatives using an enlarger.

Although high intensity illumination was not necessary for

filming, the experimental procedure had the effect of reducing the probability of the natural strikes to fast approaching stimuli. It was often found necessary to agitate the crab mechanically to induce a strike action.

RESULTS

SECTION ONE.

GENERAL DESCRIPTION OF THE TYPES OF AGONISTIC BEHAVIOUR

Carcinus maenas displays several types of agonistic behaviour which are directed towards other crabs or to appropriate stimuli. Since the behaviours under study did not appear to vary greatly whatever stimulus was presented, it was found sufficient to use a fast approaching hand as a general alarm stimulus.

A. Threat Displays

In common with many other brachyurans, *Carcinus* performs a vivid and definite threat display. When adequately stimulated the crab rears up, holding the anterior-posterior body axis at 45° to the substratum, with the pereiopods extended. The first pair of walking legs are directed forwards and spread obliquely, being extended laterally from the thorax-coxa to the merus-carpus joints and flexed medially from the carpus-propus joint (Plates 1 to 4). The second pair of walking legs are extended laterally, with the merus held at right angles to the anterior-posterior axis. The distal limb segments point forwards. The third pair of walking legs are also held laterally but the distal segments point backwards. All the segments of the fourth pair are extended backwards. This lowers the posterior part of the body while forming a stable and rigid stance, which is necessary because the chelipeds would otherwise overbalance the body as they are rapidly raised and extended. This display is the equivalent of the LMD (Wright 1968) and Aufbäumreflex (Bethe, 1897). In this present study the action described above will be termed the 'threat display' behaviour.

The threat display has several degrees of intensity. From a fully resting position a crab may move straight into an extreme threat display in which both chelipeds are extended laterally to their extreme at all joints and extended 180° from each other (Plate 4). This is a quick movement and takes less than 500 ms to achieve. Since the crab raises itself as it spreads its chelipeds, the visual impression is of an object increasing rapidly in size and diameter. The display is orientated towards the stimulus. This display is termed Full Threat and is taken to indicate the maximum intensity of threat behaviour

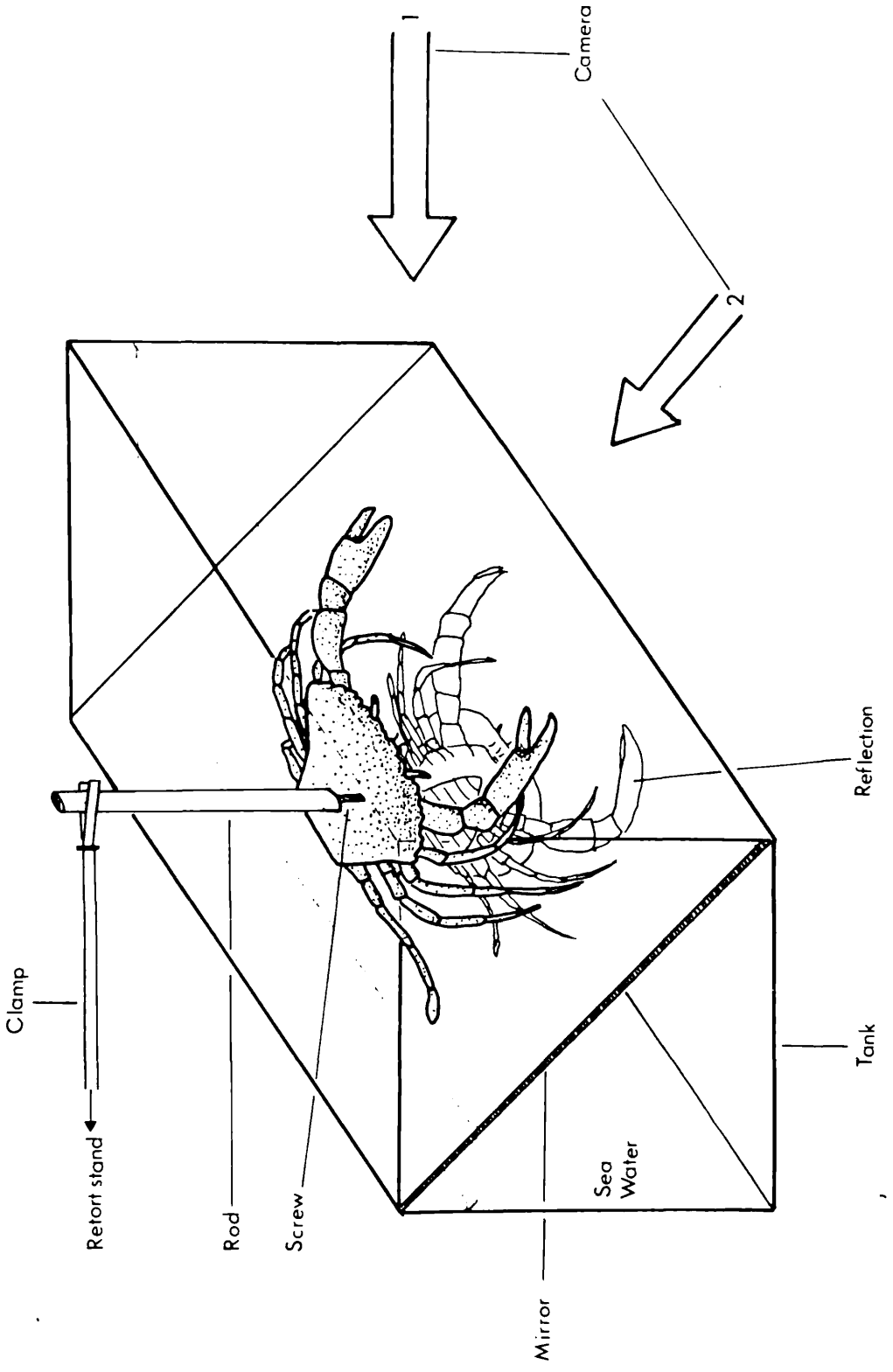
FIGURE 1

APPARATUS FOR EXAMINING THE AGONISTIC BEHAVIOUR

Small plastic screws were stuck onto the dorsal carapace of the crab with a quick action epoxy resin glue. A metal rod with a centrally threaded hole was attached to the screw. This enabled the crab to be suspended by holding the rod in a metal clamp and retort stand.

The crab was suspended in a glass tank full of cooled sea water. A mirror was placed at an angle of 45° diagonally across the tank. A ciné camera was positioned in front of the tank. By adjusting the camera height and focus, the movements of the crab could be filmed directly from the front or from below using the reflection in the mirror. Two representative positions for the camera are indicated on the figure. Position 1 would allow specific joints to be filmed and position 2 would allow the mirror reflection to be filmed.

CHAPTER 2 FIGURE 1



from the crab. If a stimulus which is presented from behind the crab is detected, the animal will often threaten while quickly flipping over backwards, using the last pair of pereiopods, to face the stimulus. It does not turn round in a circle to orientate itself.

A second form of threat display is shown when the chelipeds are slightly less levated and extended (Plate 3). Although this is a difference of only a few degrees, about 5 to 10°, it is quite distinct. Crabs can switch from this to a Full Threat posture and then back again, which only takes a few ms (Plate 9.). This second display is termed Three-Quarter Threat display.

In the next category of threat display, the chelipeds are neither as extended nor raised as high. They are directed more medially from the carpus-propus joint. The pereiopods similarly assume less extreme positions. This posture is termed Half-Threat display (Plate 2).

A fourth form of threat display is exhibited in which the chelipeds are still slightly raised from the substratum but are tucked in towards the mouth from the merus-carpus joint (Plate 1). The two dactyls may almost touch each other, shielding the front of the crab, in the most extreme form of this fourth display. The whole display posture is termed Shallow Threat display.

The crab can move rapidly from rest to Full Threat without necessarily adopting the intervening threat displays. Three-Quarters Threat can be maintained for several minutes if stimulation is continued. When stimulation stops the crab will move slowly into the less intense forms of threat but if restimulated, will rapidly resume the Full Threat posture.

Throughout Three-Quarters Threat the limbs of the crab are held rigid. If the stimulus is moved slightly a visible quivering can be observed in all the legs. If the stimulus is moved slowly to either the right or left the crab can respond in one of two ways. It may either move slowly in the same direction as the stimulus, so that it is always facing it, or the crab may keep its legs still while moving the body, tracking the stimulus and leaning towards the side of stimulation. The claw nearest the stimulus may drop slightly while the other is lifted. This behaviour was termed Unsymmetrisches Aufbäumen by Bethe (1897).

PLATES 1 to 4

THE THREAT DISPLAYS: 1

These four photographs show the four different postures of threat display shown in an unrestrained crab.

PLATE 1. SHALLOW THREAT.

In this display, the body of the crab is lowered and the claws, which are closed, rest on the substratum. The chelipeds are directed anteriorly.

PLATE 2. HALF THREAT.

In this display posture, the crab slightly lifts its whole body from the substratum and the chelipeds are raised and directed medially from the distal joints.

PLATE 3. THREE-QUARTERS THREAT.

In this third display, the chelipeds are almost fully levated and extended at all joints so that they are directed laterally. The body is raised such that the anterior is higher than the posterior.

PLATE 4. FULL THREAT

In this fourth display position, the chelipeds are held fully levated and extended laterally to their extreme at all joints with the claws maximally open. The body axis assumes an angle of 45° from the substratum with the anterior much higher than the posterior. The display is orientated towards the stimulus. In all four displays, the walking legs are stretched out from the body, forming a stable posture.

PLATES 1 TO 4

1

2

3

4

PLATES 5 to 8

THE THREAT DISPLAYS: 2

These four photographs show the four threat display postures shown in the experimental situation in which the crab is suspended from the dorsal carapace.

PLATE 5. SHALLOW THREAT

In this display, the chelipeds are flexed towards the mouth from the merus-carpus joint. The walking legs hang loosely from the thorax-coxa and coxa-BI joints and are directed medially from the distal joints.

PLATE 6. HALF THREAT

In this second display the chelipeds are directed medially from the merus-carpus joint such that the claws point anteriorly. The walking legs are extended slightly from the merus-carpus joint.

PLATE 7. THREE-QUARTERS THREAT

In this display the claws are directed more laterally as the merus-carpus joint of the cheliped is extended. The walking legs are almost fully levated and extended at all joints.

PLATE 8. FULL THREAT

In this fourth display position the chelipeds are extended from all the joints and are raised so that the merus almost touches the ventral carapace. All the walking legs are extended and levated.

Comparison of these four plates with plates 1 to 4 show that the positions of the chelipeds assumed by a suspended crab during threat displays do not differ greatly from the positions shown in unrestrained crabs. The main difference lies in the positions of the walking legs which are extended more in the Shallow and Half Threat display positions of unrestrained crabs.

PLATES 5 TO 8

5

6

7

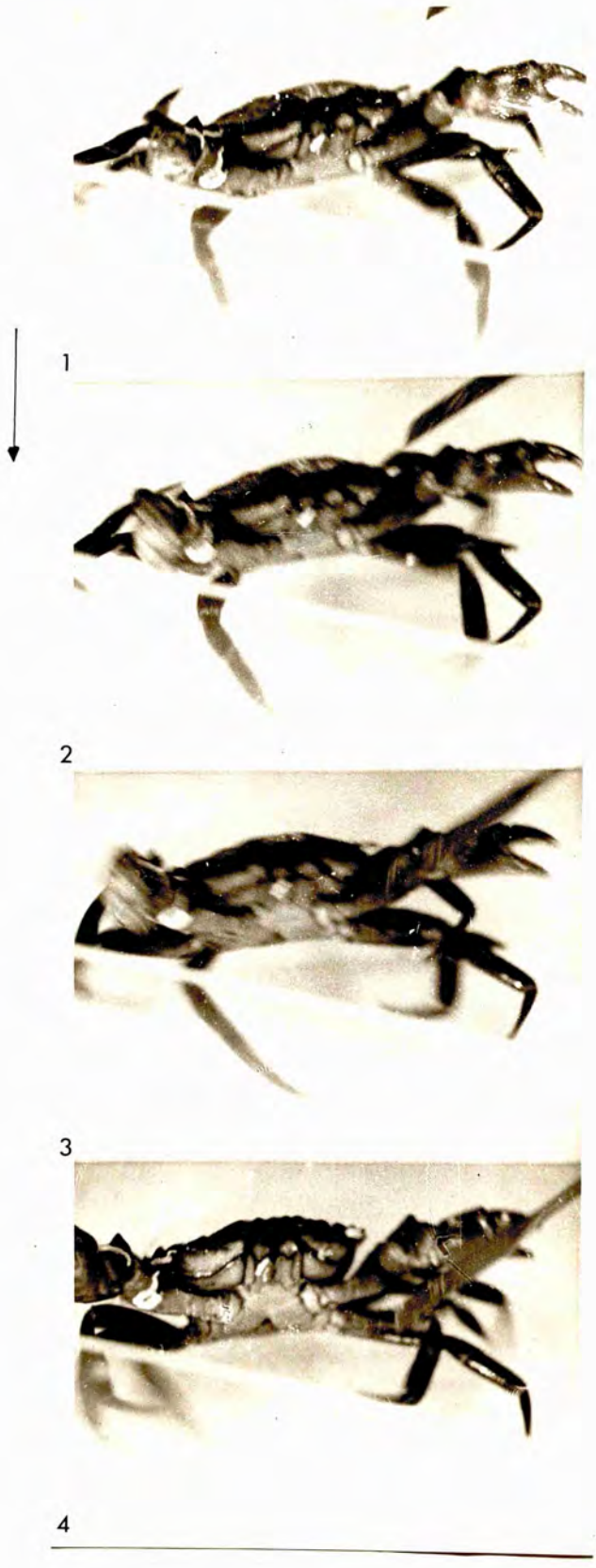
8

PLATE 9. MOVEMENT FROM THREE-QUARTERS TO FULL THREAT DISPLAYS

This is a continuous sequence of four frames with 40 ms between each and demonstrates the rapidity of cheliped movement from Three-Quarters to Full Threat display, and also shows the difference between the two postures.

In Frame 1 the crab shows a typical Three-Quarters Threat display, with the chelipeds almost fully levated and extended laterally. The anterior part of the body is raised higher than the posterior. The presentation of a stimulus, a metal rod, in Frame 2 caused the crab to move rapidly into a Full Threat display; the movement was completed by Frame 4. It can be seen that a Full Threat display involves an increase in extension and levation of the chelipeds and the anterior part of the body is raised even higher so that the body axis assumes an angle of 45° from the substratum.

PLATE 9



1

2

3

4

Threat is most readily displayed by male crabs, especially those with a carapace width of between 50 and 80 mm. Large crabs often only display when stimulation is persistent. Females and smaller crabs tend to use other agonistic patterns, such as escape.

In the experimental procedure, where the crab was suspended, all intensities of threat were still shown. The only difference was the position of the walking legs which were extended more horizontally in Full Threat and became progressively more flexed as the intensity of threat decreased (Plates 5 to 8). Apart from this there was no indication that the pattern and sequence of threat behaviour differs in any way between the normal and experimental situation.

During threat displays Carcinus emits a constant strong current of water from above the maxillae which is directed towards the stimulus. Water emission has also been observed in the Blue crab (Jachowski, 1974), Potomon (Erpenbeck and Attevagt, 1966) and Grapsus (Kramer, 1967). It is unlikely to have any chemical function as water taken from around such a crab was not found to influence the aggressiveness of other crabs.

B. The fast strike behaviour

When a crab is in Three-Quarters Threat positions and stimulation is continued, small twitches of the cheliped directed from the coxal and basi-ischium, BI, joints can be seen. These twitches are directed inwards and downwards. The arm is then flicked back and levated again. The twitches take only 5 to 20 ms. In the more alert crabs this precedes a second agonistic behaviour, the fast strike, in which the chelipeds are suddenly flexed forwards and downwards from the threat position. The claws, which are usually open at the beginning of a strike movement, are closed by the time the arms have moved to the midline of the body (Plate 10).

When the tips of the dactyls have approached the midline of the body, the chelipeds are re-extended to threat positions almost as quickly as they were flexed. The rapid promotion takes only 30 to 60 ms to achieve while re-extension is slightly more variable and may last for 30 to 90 ms. Occasionally a strike is performed with only one cheliped. When this happens unrestrained crabs often topple over when the cheliped passes the midline of the body and upsets the rigid threat posture. In a typical strike

behaviour the chelipeds do not usually clash together. This is largely because the two most proximal joints are re-extended before the distal joints.

Strike actions do not begin from any other posture except threat, particularly the Full and Three-Quarters display. They are also characterised by the presence of small, discrete flexing-extending twitches prior to the rapid flexion of the chelipeds. Since these twitches precede the strike they are termed pre-strike twitches and their most flexed position is termed the pre-strike position. The chelipeds can assume four alternative postures from the pre-strike position. One alternative is re-extension to Three-Quarters and Full Threat displays, a second is the rapid flexion and depression of a fast strike, a third is a slower flexion and depression of a slow strike behaviour and a fourth is a very slow depression into a resting posture.

C. The slow strike behaviour

A slow strike is similar to the above behaviour but takes over twice as long, 150 to 250 ms. The action often ends with the chelipeds clutching the stimulating object and holding it for a short time. The object may be brought towards the mouth or dropped, and a threat posture resumed.

D. Pushing behaviour

From a Shallow Threat display a crab may perform another agonistic behaviour in which the chelipeds are held in front of the mouth like a shield. If stimulation is continued one or both chelipeds may be repeatedly extended forwards and backwards from the carpus-propus joint in a pushing action. The claws are usually held closed. The pushing actions last between 500 ms and 1s, and have little force behind them. Water emission is also displayed during this behaviour.

E. The Starrkramp-reflex.

Bethe (1897) described this behaviour, which occurs most commonly when a crab is picked up. It involves a tense stretching of all the limbs and has the effect of making the crab larger and difficult to hold. It would probably deter many predators from swallowing the crab.

F. Egg-protection reflex.

This behaviour, termed Eierschutzreflex (Bethe, 1897), occurs when most females and younger crabs are picked up. They do not attack or threaten but curl up in this egg protection posture. The

PLATE 10 THE FAST STRIKE BEHAVIOUR

This is a continuous sequence of 12 frames with 40 ms between each and shows the fast strike behaviour in an unrestrained crab. The crab to the right of the photographs, the attacking crab, directs its strike behaviour to the crab on the left which remains in a threat display position throughout.

Frame 1 Both crabs assume a Three-Quarters Threat display in which the chelipeds are held levated and extended laterally with the claws open. The attacking crab shows how the walking legs are positioned so that the body assumes a rigid stance. All the walking legs are extended laterally from the proximal joints but the first pair point anteriorly from the merus-carpus joint, the third pair are directed laterally and the fourth pair are directed posteriorly. (The second limb had been autotomised).

Frame 2 The attacking crab moves from the threat display position and the chelipeds begin to flex.

Frame 3 This shows the pre-strike position of the attacking crab in which the chelipeds are depressed slightly and are directed more medially while the claws begin to close.

Frame 4. The fast strike begins; the chelipeds are suddenly and rapidly flexed forwards and downwards.

Frame 5 Flexion is complete when the tips of the dactyli near the midline of the body; the claws are closed at the end of the strike but do not clash together.

Frame 6 Immediately after the strike the chelipeds are re-extended and re-levated. Extension initially begins from the thorax-coxa and coxa-BI joints.

Frame 7 The distal cheliped joints begin to extend while the proximal joints are almost fully re-levated and re-extended.

Frame 8 The claws are open as the cheliped re-assumes positions of threat.

Frames 9 to 12 The attacking crab re-adopts the Three-Quarters Threat display with the chelipeds raised and extended.

PLATE 10

PLATE 11 THE SLOW STRIKE BEHAVIOUR

This is a continuous sequence of 16 frames with 40 ms between each and shows the slow strike behaviour in an unrestrained crab.

Frames 1 to 3 The crab assumes a Three-Quarters Threat display position with the chelipeds almost fully levated and extended from all the joints.

Frame 4 The chelipeds are slightly flexed and begin to be directed medially in this first stage of the slow strike.

Frame 5 The slow strike continues as the chelipeds continue to flex from the thorax-coxa and merus-carpus joints.

Frame 6 The claws are brought together.

Frame 7 The slow strike is complete and the crab begins to lower the anterior part of its body towards the substratum.

Frames 8 to 10 The crab remains in a lowered position with the chelipeds flexed and the claws together.

Frame 11 The crab begins to readopt threat display postures and slowly raises its body.

Frames 12 to 15 The chelipeds are slowly re-extended.

Frame 16 The crab assumes a Half Threat display position.

PLATE 11

chelipeds are maximally flexed at all joints and tucked under the mouth with the dactyls directed towards the abdomen. The walking legs are similarly depressed and fully flexed at all joints, which directs the dactyls into the abdomen. This would have the effect of completely covering and protecting any eggs the female may have. Any further approach to the abdomen is accompanied by quick piercing movements from the sharp dactyls of the walking legs. The name of this behaviour is not accurate since it can occur in some males and in females without eggs.

G. Defence behaviour

Unresponsive or fatigued crabs may assume a crouching position in which the front of the body is lowered onto the substratum while the chelipeds are tucked in front of the mouth. The pereiopods are similarly tucked beneath the body. The crab may crawl backwards towards a wall or corner with the posterior end of the body raised. This has the effect of withdrawing any potential weapons, such as the claws and sharp dactyls, the opposite effect to a Full Threat display.

H. Escape and retreat behaviour

A threatening crab can suddenly switch its behaviour from a rigidly standing threat posture to a sideways or retreating escape movement. The chelipeds are still held in the threat position and the front of the crab is directed towards the stimulus as the crab escapes. This behaviour was termed Fluchtreflex by Bethe (1897).

SECTION TWO.

THE FAST STRIKE BEHAVIOUR

As previously described the strike behaviour begins from extended positions of all the cheliped joints. This particular agonistic behaviour was chosen for a more detailed study since it was observed that it involves extremely fast movements and may, therefore, utilise energy storage mechanisms like Squilla or specialisations to the muscles involved in the movement. The position of each cheliped joint and segment during the strike was examined in detail in order to determine the sequence of joint movement and angular velocities achieved. The joint angles were measured directly from the negatives of the ciné films rather than applying movement transducers to the limb. This meant that not only could the joint excursions be measured more precisely, but also the cheliped was not loaded with transducers which may otherwise slow the strike.

Furthermore, the movements of all the joints could be measured during a single strike. A simultaneous analysis of the excursions of all the joints would be difficult to achieve if transducers had to be applied to all the limb segments at one time, and would almost certainly have impeded limb movement.

A representative fast strike is shown in Plate 12. The angular excursions and angular velocities of the four main joints, the thorax-coxa (T-Cx), coxa-basi-ischium (Cx-BI), merus-carpus (M-C) and carpus-propus (C-P) are shown in figures 5 and 6. The rotational movement of the coxa and BI segments is shown in Figure 7.

A. The thorax-coxa joint; (T-Cx)

The T-Cx joint moves in an anterior-posterior plane, remoting and promoting the cheliped. The coxa segment moves through 60° from full remotion to full promotion (Fig.2). During the Full Threat display this joint is more or less rigidly held at an angle of 5 to 15° promotion (Plate 12, Frames 1 to 4). Promotory movements at this joint, from 15 to 20° promotion, precede the fast strike. These are the pre-strike twitches.

At the beginning of a strike this joint is suddenly flexed to between 22 and 30° promotion, the pre-strike position (Plate 12, Frame 7). When this position is exceeded the actual strike can be said to have begun. It lasts for 30 to 60 ms, during which time the joint is rapidly promoted to within a few degrees of full promotion (Fig. 5; Plate 12, Frame 9). It is then re-extended before the other joints have reached their maximum strike positions (Plate 12, Frame 10). This re-extension movement is termed the recovery action and is almost as rapid as the strike although peak recovery velocities are not achieved until 60 ms after full promotion.

When the coxa has returned to the threat position, the joint often exhibits a feature termed "bounce". This is where small flexing and extending movements are seen before the more rigid position of the threat displays are resumed.

B. The coxa-BI joint (Cx-BI)

The Cx-BI joint moves in a dorso-ventral plane, levating and depressing the cheliped. The BI segment can move through an arc of 65° from full levation to full depression (Fig. 3). During Full Threat the BI is levated to within 5° of full levation (Plate 12, Frames 1 to 4). This joint also displays pre-strike twitches which cause the BI and merus to oscillate through 10 to 15°. These twitches

are closely linked to those of the coxa; flexion of the coxa coupling with depression of the BI.

Like the coxa, the BI has an angle beyond which a strike inevitably occurs, the pre-strike position. This angle is reached when the joint is depressed between 15 and 20° from full levation and is achieved at the same time as the coxa reaches its pre-strike position (Fig. 5).

Once the coxa has begun to promote, the BI begins to depress (Plate 12, Frames 8 and 9), although the attainment of peak angular velocity lags behind the coxa by 30 to 40 ms (Fig. 6). Similarly it reaches the point of maximum depression, between 45 and 55°, 30 to 40 ms after full promotion of the coxa (Fig. 5). The BI is never fully depressed during a strike. Recovery movements are almost symmetrical with the strike angles.

Again, before rigid threat positions are resumed, bouncing or small depressory-levatory movements, can be seen. These are often linked with the bouncing seen in the coxa so that when the coxa twitches forwards the BI is often depressed and when the coxa oscillates backwards the BI is often levated.

C. The BI-merus joint

The BI-merus joint can only move through 5° and its movement could not be measured from the film. The merus can be visualised as an extension of the BI limb segment, contributing little to the strike movement.

D. The merus-carpus joint; (M-C).

The M-C joint moves in a medial plane, flexing and extending the carpus and distal cheliped segments through an excursion of 85° (Fig. 4A). The joint is held between 10 and 15° flexion during Full Threat postures (Plate 12, Frames 1 to 4). There does not appear to be such a rigidly controlled angle beyond which strike always occurs. Instead the pre-strike position may occur when this joint is held at any position between 12 and 25° flexion, but rarely at the most extreme extensions displayed for Full Threat. Thus a strike is preceded by a small flexion from Full and Three-Quarters Threat positions (Plate 12, Frames 6 and 7).

After the coxa has begun promotion the M-C joint is rapidly flexed (Fig. 5). However unlike the more proximal joints, it suddenly changes in direction of movement and is slightly re-extended.

PLATE 12 THE FAST STRIKE

This is a continuous sequence of 16 frames with 31.25 ms between each and shows the fast strike behaviour in a crab which was suspended from the dorsal carapace. The photographs show a ventral view obtained by focussing the ciné camera on the mirrored reflection of the crab. The lines on the cheliped were drawn with Liquid Tippex to heighten definition of movement.

Frames 1 to 4. The crab assumes a Full Threat display with all the cheliped joints fully extended.

Frame 5 The rigid posture of threat is suddenly disturbed as the crab prepares for a strike behaviour.

Frame 6 The chelipeds are slightly flexed towards the pre-strike position.

Frame 7 The pre-strike position is assumed in which the T-Cx and M-C joints are partially flexed so that the claw is directed forwards.

Frame 8 The fast strike begins as the chelipeds are propelled downwards and medially from the Cx-BI and T-Cx joints respectively.

Frame 9 The fast strike is complete as the T-Cx joint is almost fully promoted and the claws reach the midline of the body.

Frame 10 Re-extension of the cheliped, the recovery action, occurs immediately after promotion of the T-Cx joint is complete. Re-extension begins from the T-Cx joint.

Frame 11 Recovery from strike continues with re-extension from the distal cheliped joints.

Frame 12 The T-Cx and Cx-BI joints are almost fully extended and levated, while the distal joints continue to extend.

Frames 13 and 14 The recovery action is completed as the distal joints are re-extended.

Frames 15 and 16 The crab adopts a Three-Quarters Threat display position.

PLATE 12

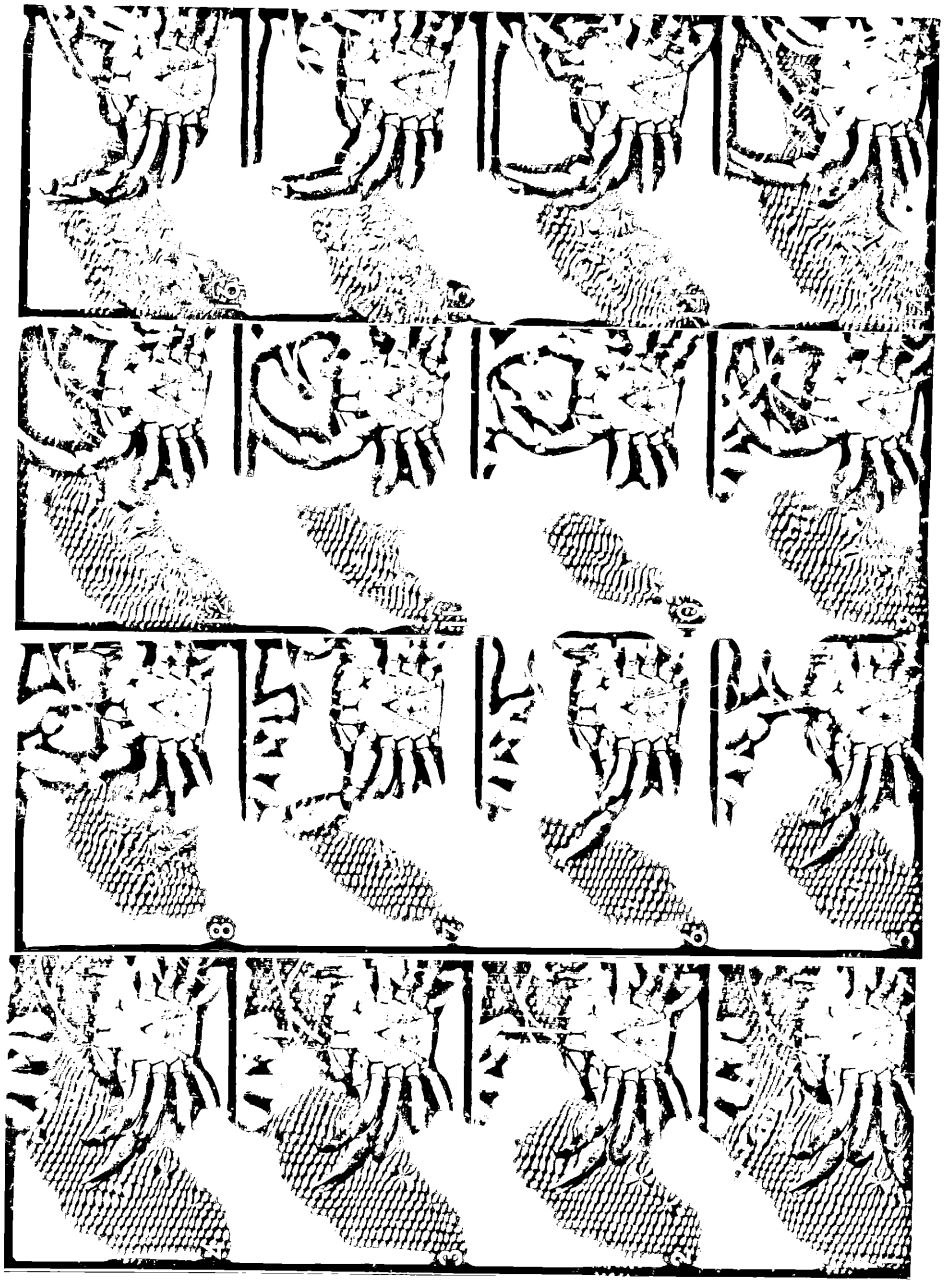


FIGURE 2

MOVEMENT OF THE THORAX-COXA JOINT: T-Cx

This diagram illustrates how the movement of the T-Cx joint was measured from the films. BI, Basi-ischium; pp, Cx-BI posterior pivot; vp, T-Cx ventral pivot. The crab is viewed ventrally.

A vertical line was drawn anteriorly from the abdomen, line aa. Line bb was drawn through the ventral pivot of the T-Cx joint to cross aa at 90°. Line c was extended from bb to cross the Cx-BI posterior pivot. The angle of the joint at this position was called 0° promotion (Diagram i). The angle subtended between lines bb and bc during movement of the segment was measured from full remotion to full promotion, an excursion of 60°. Diagram ii illustrates the joint position when the coxa is fully promoted, at 60° promotion.

CHAPTER 2 FIGURE 2

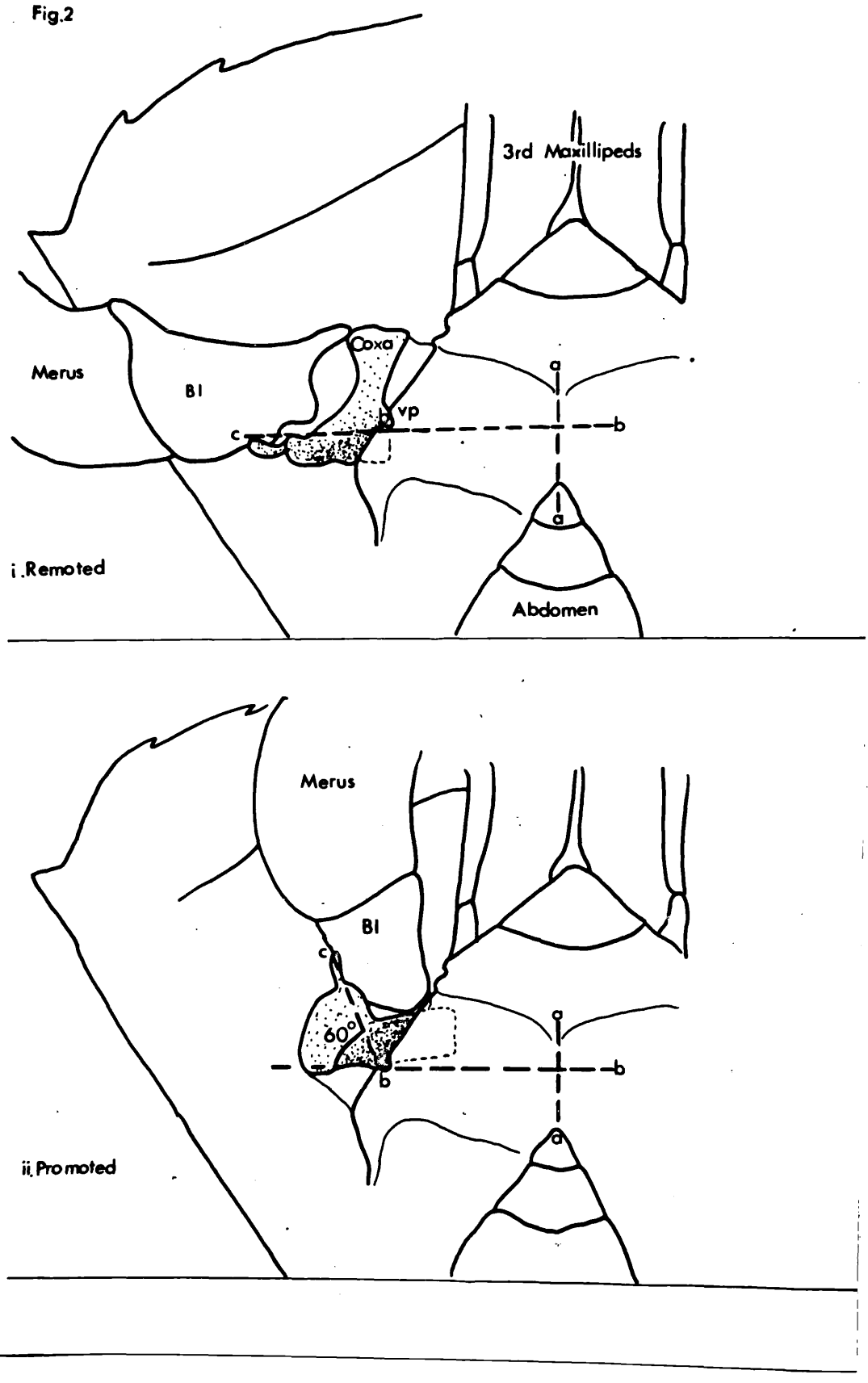


FIGURE 3

MOVEMENT OF THE COXA-BI JOINT: Cx-BI

These diagrams illustrate how the movement of the Cx-BI joint was measured from the films. ap, Cx-BI anterior pivot; BI, Basi-ischium; CxPt, coxa promotor muscle tendon insertion; vp, T-Cx ventral pivot. The crab is viewed anteriorly in Figures i and ii and ventrally in figures iii and iv.

Diagrams i and ii. These diagrams illustrate the full movement of the BI segment from full levation (i) to full depression (ii). Line dd was drawn from the tip of the BI to the ventral most edge of the coxa promotor muscle tendon head, which inserts on the coxal rim. Line ee was drawn at right angles to dd across the central surface of the coxa when the BI segment was fully levated (Diagram i). This line was almost parallel to a furrow which runs across this surface. The angle subtended between lines dd and ee was called 0^{o} depression. As the BI depresses the angle subtended between the two lines decreases. The Cx-BI joint moves through an arc of 65^{o}.

Diagrams iii and iv. It was not possible to measure the Cx-BI joint movement directly from the films because the propus completely obscures the Cx-BI joint during a strike. To overcome this a ventral view was used by positioning the camera to focus on the reflection in the mirror. The ventral distance between the anterior pivot of the Cx-BI joint and the BI tip (Line Lmax on Fig.iii) was measured in a series of crabs of the sizes used in these experiments. The BI was moved through the full excursion from levation to depression (from Lmax to Lmin on Diagram iv). This decreasing ventral distance, L, was measured for each degree of depression and enabled the production of a conversion graph of BI ventral length against the angle of Cx-BI joint depression measured from the crab, (Diagrams i and ii). Before each experiment the ventral length of the BI at maximum levation, equivalent to Full Threat positions, was measured and noted for each crab. This ventral distance at Full Threat was also measured from the enlarged negatives and gave a factor for converting all the measured, enlarged values to the real values. For example, if the real value was 2 cm and the enlarged value 8 cm, all the enlarged lengths must be multiplied by 0.25 to give the actual lengths. These lengths could then be simply read off the calibration graph to convert them into degrees depression.

CHAPTER 2 FIGURE 3

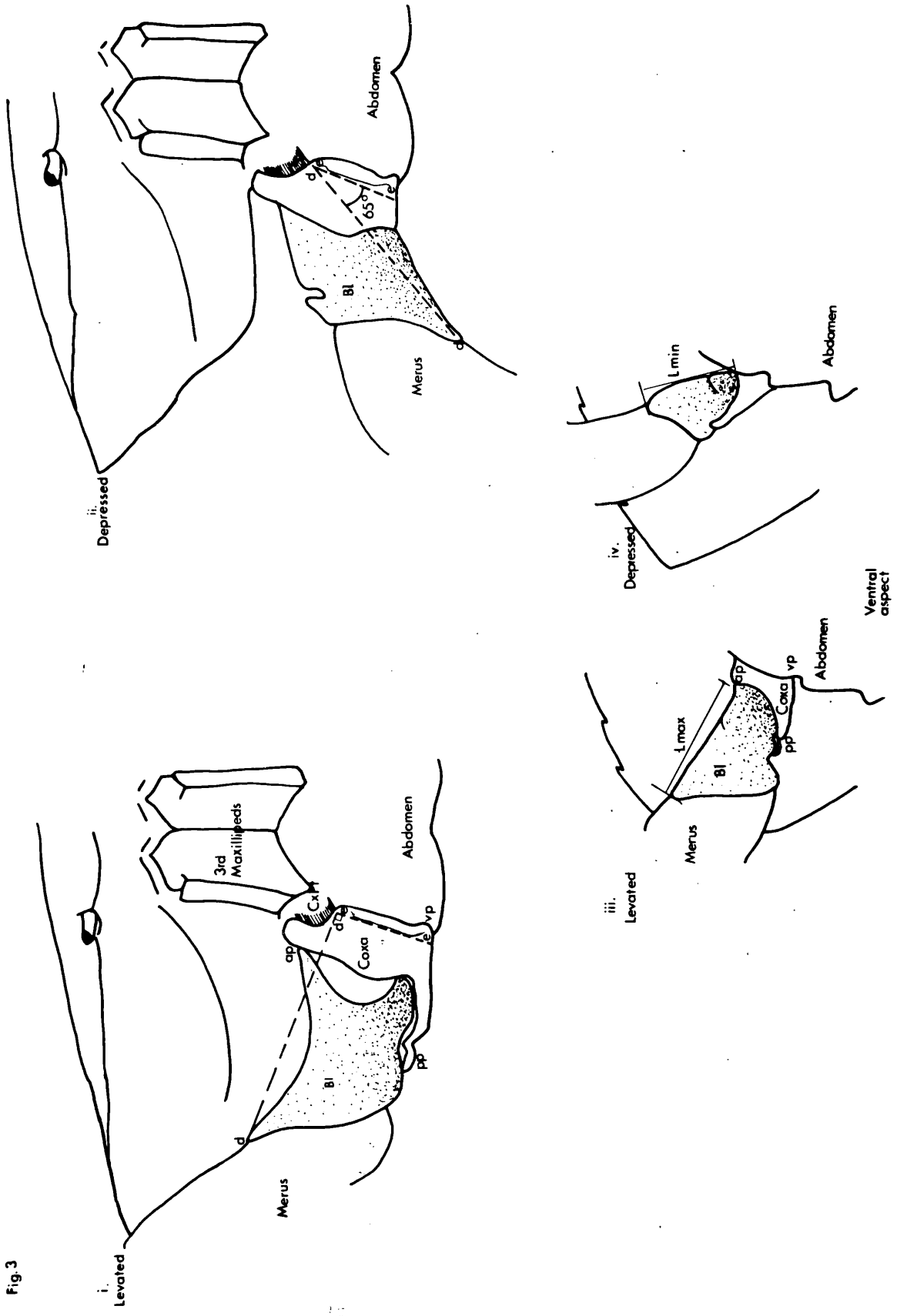


Fig.3

FIGURE 4

MEASUREMENTS OF THE MOVEMENTS ABOUT

THE DISTAL JOINTS OF THE CHELIPED

Shaded segments, segments which are measured; C, carpus segment; D, dactylus segment; M, merus segment, P, propus segment.

A. MERUS-CARPUS JOINT: M-C

In order to measure the movement about the M-C joint, line a was drawn just beneath the M-C and C-P pivots when the carpus was fully extended. Line b was extended from this along the merus. This was called 0^{o} flexion of the M-C joint. As the carpus rotated the angle between these lines was measured as the degree of flexion, that is from 0^{o} full extension to 85^{o} full flexion.

B. CARPUS-PROPUS JOINT: C-P

In order to measure the movement about the C-P joint, line d was drawn between the tip of the propus and the C-P joint. An angle between this and line a, above, was measured as the angle of flexion about the C-P joint. Thus the propus moves from 0^{o} full extension to almost 80^{o} full flexion.

C. PROPUS-DACTYLUS JOINT: P-D

In order to measure the movement about the P-D joint, line e was drawn vertically at right angles to the P-D pivot. Line f was drawn from the dactylus tip to cross line e at an angle of 90^{o}. This was measured as 0^{o} or fully closed. As the dactylus opened, this angle enlarged to 60^{o}, fully open.

CHAPTER 2 FIGURE 4

Fig.4

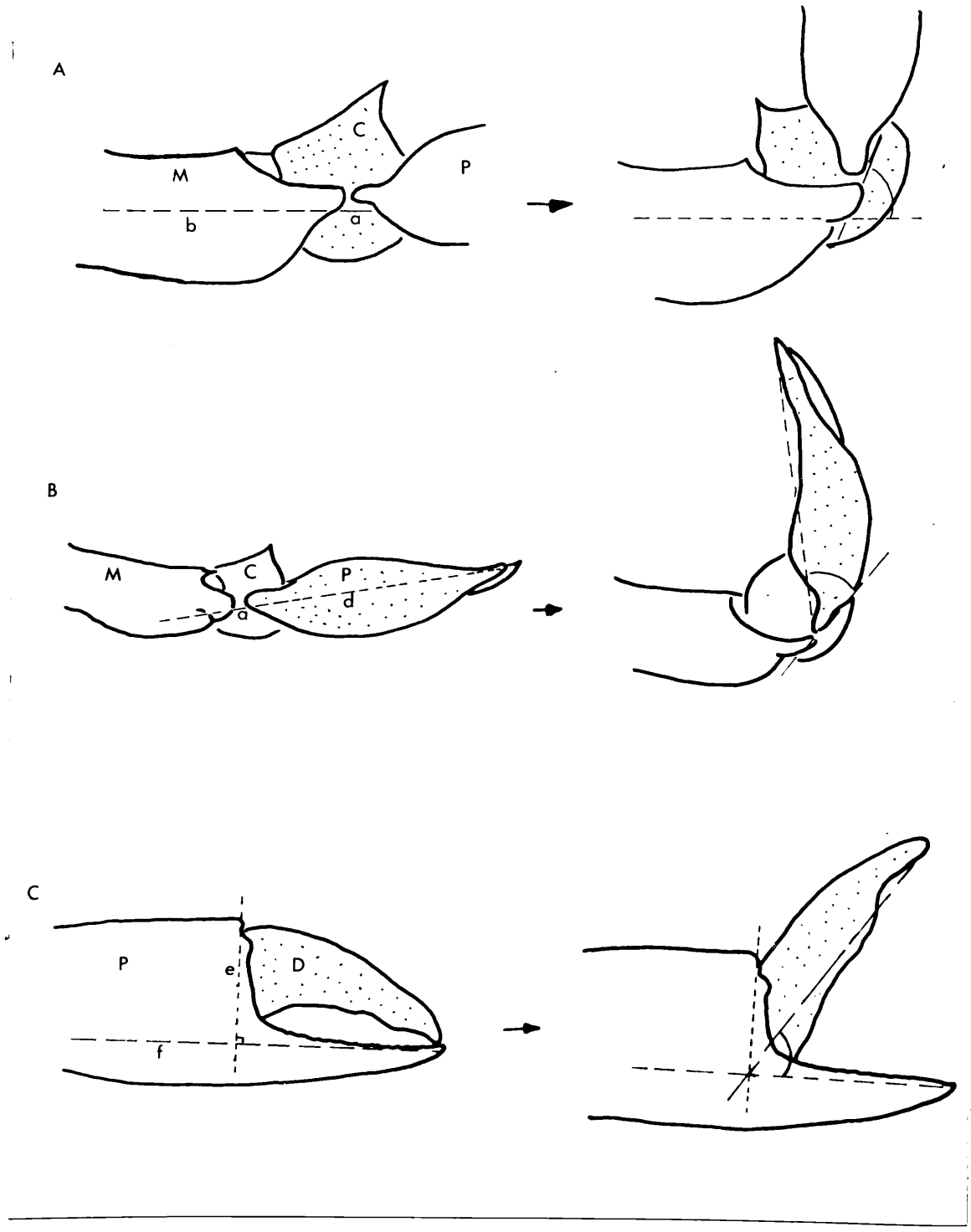


FIGURE 5

THE CHELIPED JOINT MOVEMENTS DURING
A FAST STRIKE

The dotted lines represent the time from the beginning to the end of a strike. The ordinate represents joint position in degrees and the abscissa represents the time, in ms, of each joint position with respect to the end of the strike. The positions and times were obtained from the films. The graphs demonstrate that the T-Cx is the first joint to achieve greatest flexion and begins to re-extend before the BI has finished its depression movement. During the strike the M-C and C-P joints display a small reversal in direction before resuming the rapid flexion. These twitches are closely linked in the two joints.

Pre-strike activity is indicated to the left of the dotted lines. The feature of pre-strike twitches, small depressory-promotory movements are demonstrated. The recovery from strike movements are indicated to the right of the dotted lines. This is the period when the cheliped is re-extended. After recovery, "bouncing", small oscillatory twitches, in the T-Cx and Cx-BI joints can be seen.

The threat display is not as rigidly maintained after the strike as compared to before the strike. Instead all the joints tend to oscillate slightly.

CHAPTER 2 FIGURE 5

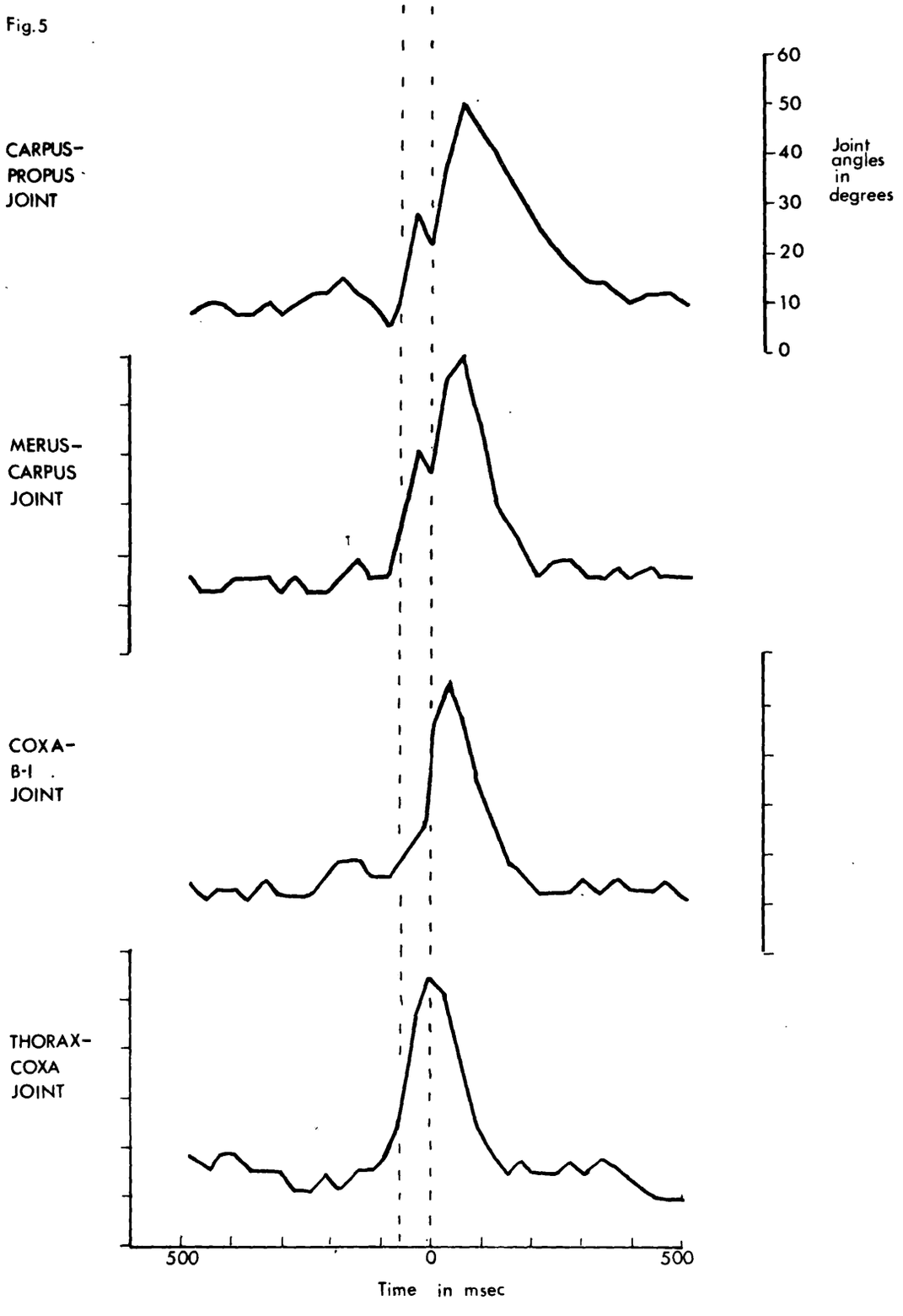


FIGURE 6

THE ANGULAR VELOCITIES OF THE CHELIPED JOINTS DURING A FAST STRIKE

A. The continuous line represents the angular velocity of the T-Cx joint during the strike movement indicated in Fig. 5, plotted against time. The discontinuous line represents the angular velocity of the Cx-BI joint during the fast strike indicated in Fig. 5. Angular velocities above $0^{o}/s$ indicate positive strike velocities, that is movements made in the direction of strike. Values below the zero line indicate negative strike velocities, that is movements in the direction of threat and recovery.

B. The continuous line represents the angular velocity of the M-C joint, and the discontinuous line represents the angular velocity of the C-P joint. The ordinate and abscissa are as above. The strike action occurs within the two arrowed lines. These graphs demonstrate that the T-Cx joint achieves its maximum angular velocity before the other three cheliped joints. The angular velocity of the M-C and C-P joints are similar in time course and values during the strike and recovery, but are less similar during the preceding threat displays. This would suggest that there is a strict control linking the excursion of these two joints during the strike and recovery with a more flexible control in threat positions. The angular velocities of the T-Cx and Cx-BI are also closely linked but are separated by 30 ms throughout the strike and recovery movements.

CHAPTER 2 FIGURE 6

Fig. 6

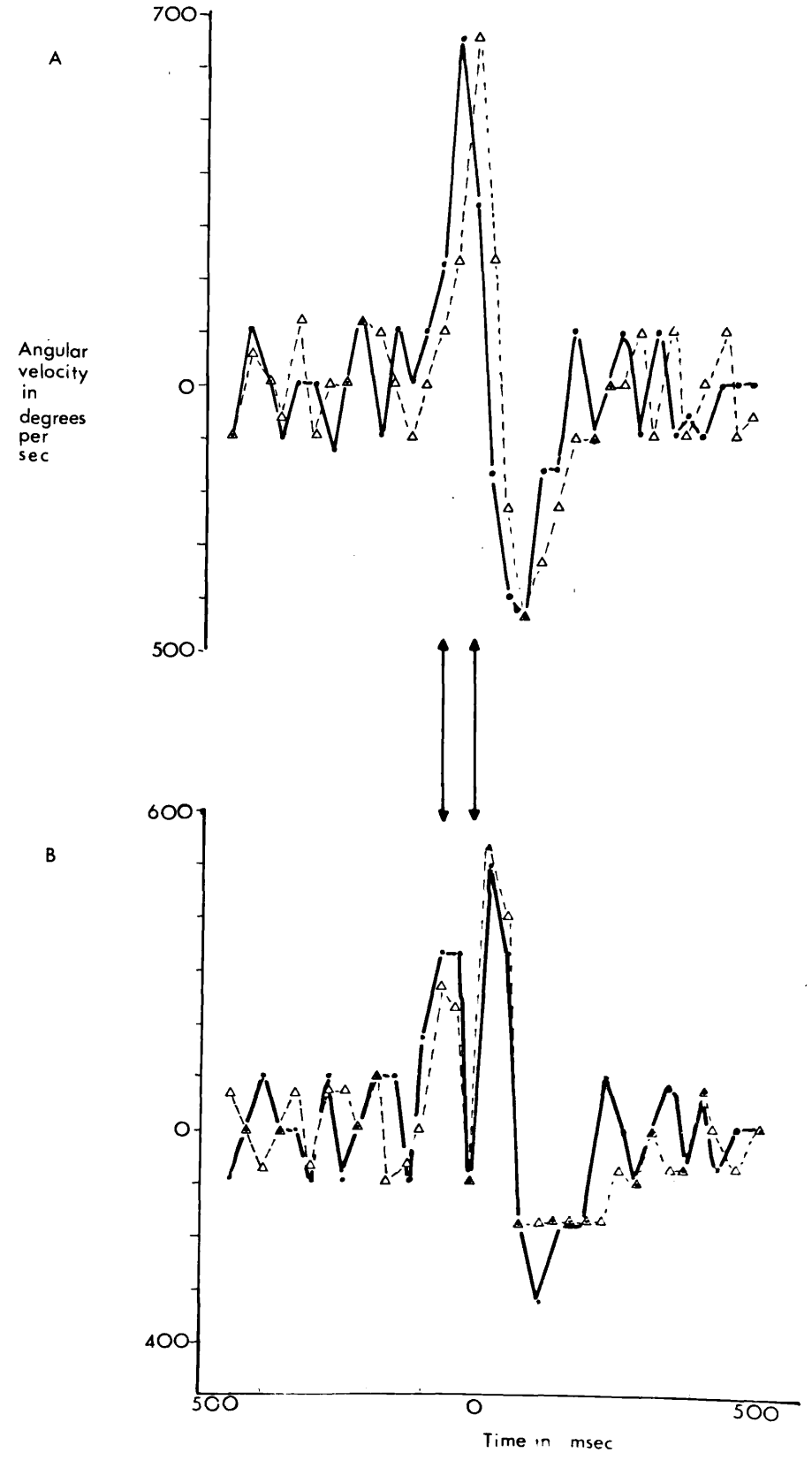


FIGURE 7

THE RADIAL EXCURSION OF THE T-CX AND CX-BI JOINTS DURING A FAST STRIKE

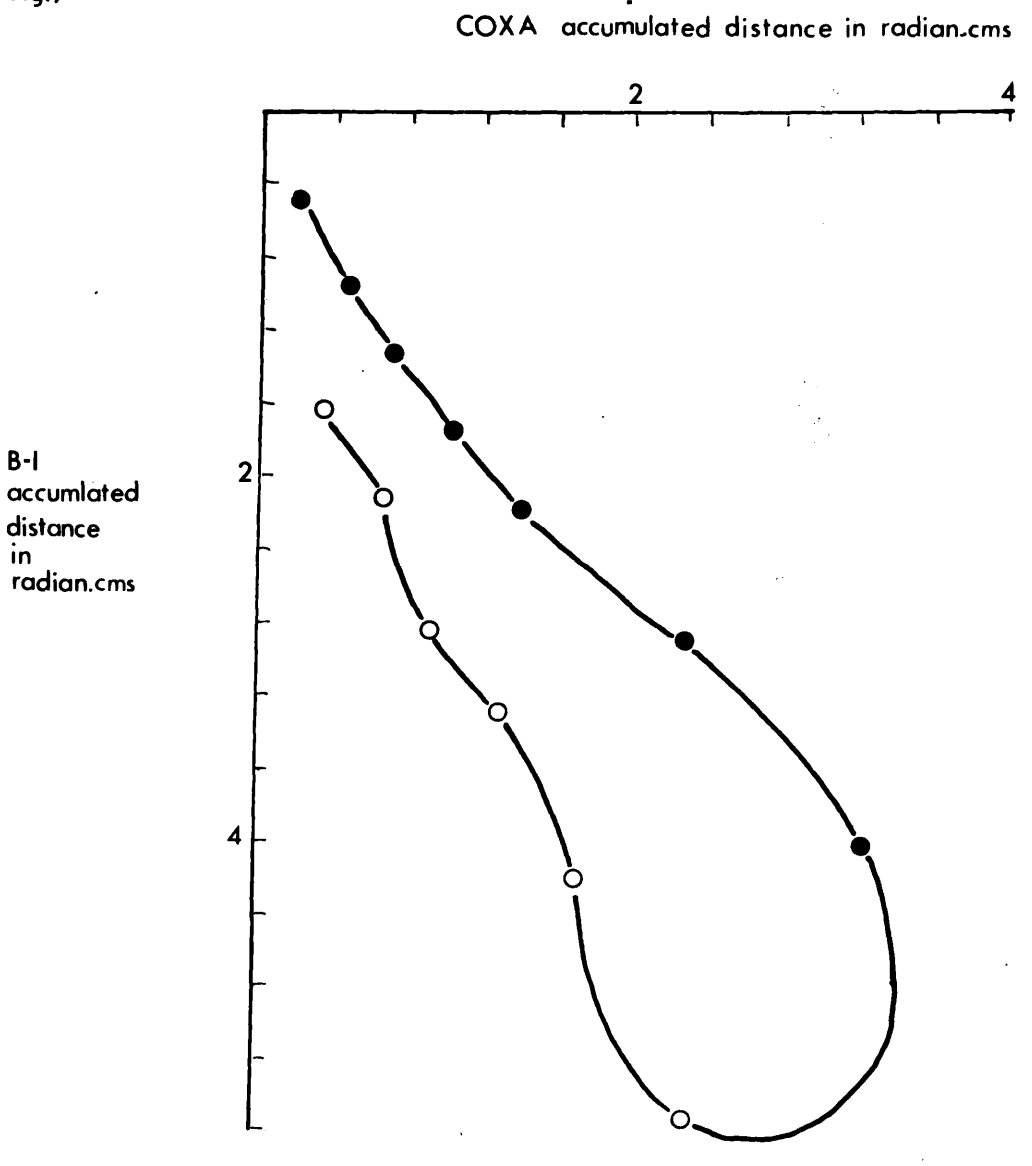
The angles subtended by the coxa and BI about their respective joints during the fast strike indicated in Fig. 5 were converted into radians. These values were then multiplied by the lengths of the coxa and BI, 1.0 cm and 1.5 cm respectively. This allows the movement to be plotted as accumulated distance in radian cms. The promotion of the coxa is indicated on the abscissa and the depression of the BI is indicated on the ordinate. Closed circles represent the accumulated distances in the direction of the strike, and open circles represent the distance in the direction of strike recovery.

The graph demonstrates that the excursion of the BI and coxa during a fast strike is not elipsoidal but has a "hump" between the end of the strike movement and the beginning of cheliped re-extension. This is caused by continued BI depression while the coxa begins to re-extend.

The graphs also show that the combined joint excursion taken during the strike, does not follow the same line as that taken during strike recovery.

CHAPTER 2 FIGURE 7

Fig.7



After 30 ms it is again rapidly flexed, finishing at 50 to 60° flexion. This re-extending twitch has the effect of momentarily widening the distance between the two approaching chelipeds. It is possible that this action also prevents the two chelipeds from clashing together at the end of a strike.

Maximum flexion of the M-C joint is reached 60 to 100 ms after the coxa has begun the recovery movement. Re-extension of the carpus is rapid and the threat positions are resumed within 100 to 200 ms.

E. The carpus-propus joint; (C-P)

The C-P joint moves in a medial-lateral plane, flexing and extending the claw of the cheliped in an excursion of 80° (Fig 4B). The propus is almost fully extended in the Full Threat display. The C-P joint does not have a definite pre-strike angle although again a strike rarely begins when this joint is fully extended, but rather when it is flexed to between 5 and 20° (Plate 12, Frame 7).

The values for the angular excursions and velocities of the C-P joint closely follow those of the more proximal M-C joint (Figs. 5 and 6). The strike movement is also interrupted by a brief and sudden re-extension which occurs at the same time or just after that of the M-C joint. Recovery from strike is not as rapid as flexion, and lasts from 200 to 300 ms.

F. The propus-dactylus joint; (P-D)

The dactylus can be opened and closed about the propus-carpus joint in an excursion of 60° (Fig. 4C). During threat displays the claw of the cheliped is held open at an angle of between 25 and 45° extension. The dactylus closes during the strike movement of the cheliped and is partially or completely closed by the end of the strike, when the two dactyl tips are closest together. During re-extension of the cheliped the claws re-open slowly or rapidly. The whole action of the P-D joint during a strike is relatively labile in comparison to the other cheliped joints.

SECTION THREE

COMPARISON OF THE FAST AND SLOW STRIKE BEHAVIOURS

As previously described a slow strike is similar to a fast strike but has a longer time course, between 150 and 250 ms

as opposed to the 30 to 60 ms duration of a fast strike. Detailed analysis of the movement with cinematographic techniques revealed that the joint movements also differ in slow and fast strikes. A representative slow strike is shown on Plate 13. The angular excursions and velocities of the cheliped joints during a slow strike are shown on Figures 8 and 9.

In a slow strike the distal joints of the chelipeds, the M-C and C-P, are slowsly flexed before the T-Cx joint (Plate 11, Frame 5). There is not a critical angle beyond which the coxa is suddenly promoted. The positions of maximum flexion or depression are generally less than those of the strike although occasionally the distal joints may continue flexion during the re-extension stage of the T-Cx joint.

SECTION FOUR.

CALCULATION OF FORCES INVOLVED IN A FAST STRIKE

Figures 5 and 6 indicate that the power to propel the cheliped forwards and downwards during a fast strike must be derived from the T-Cx and Cx-BI joints because these joints propel all the other segments of the limb anteriorly and medially. It has been demonstrated that the fast strike is an extremely rapid movement and high angular velocities are delivered to the cheliped. Therefore it is possible that the muscles involved may need to develop and store energy before the limb is promoted. Thus the forces that the coxal and BI muscles must produce to accelerate the limb were calculated in order to determine the energy involved in a fast strike. This was achieved by use of the equation to calculate the kinetic energy of a rotating body (Alexander, 1968). Rotational kinetic energy, Ek, is given by equation 1 below:

$$Ek = \tfrac{1}{2}Iw^2 \qquad (1)$$

were I is the moment of inertia of a body about its axis of rotation and W is the angular velocity in radians/s. The rotational kinetic energy is measured in ergs.

The crab, which was filmed for the strike movements indicated in Fig. 5, was used to calculate the moment of inertia of the cheliped. The cheliped which was filmed, was sawn into 1 cm strips from the T-Cx joint to the tip of the dactylus. Each strip was weighed separately. The moment of inertia is given by equation 2 below (Alexander, 1968);

$$I = \sum (mr^2) \qquad (2)$$

PLATE 13 THE SLOW STRIKE

This is a continuous sequence of 15 frames with 40 ms between each and shows the slow strike behaviour in a crab which was suspended from the dorsal carapace. The photographs show a ventral view obtained by focussing the ciné camera on the mirrored reflection of the crab.

Frame 1 The crab assumes a Three-Quarters Threat display position with the cheliped almost fully extended at the T-Cx joint but slightly flexed from the M-C joint.

Frames 2 and 3 The presentation of a stimulus, a plastic rod, accompanies the beginning of flexion from the joints of the cheliped which precedes the slow strike.

Frame 4 The T-Cx joint is flexed so that the claws are directed anteriorly. Comparison of this stage with the pre-strike position shown in Plate 12, Frame 7 shows how the claws are directed more medially before a slow strike than before a fast strike.

Frame 5 The slow strike begins and the cheliped begins to flex from the M-C and C-P joints.

Frame 6 The slow strike continues as the cheliped is promoted and depressed from the T-Cx and Cx-BI joints respectively.

Frame 7 Flexion of the cheliped continues.

Frame 8 The slow strike is complete.

Frames 9 and 10 Instead of immediate re-extension shown in the fast strike (Plate 12, Frames 9 and 10), the arm remains flexed and depressed for some time before gradually re-extending.

Frame 11 The cheliped is slowly re-extended and re-levated from the T-Cx and Cx-BI joints respectively.

Frame 12 The distal cheliped joints begin to re-extend.

Frames 13 and 14 The cheliped continues to re-extend slowly.

Frame 15 A Half Threat display posture is adopted with the cheliped flexed at the M-C joint so that the claws are directed forwards.

PLATE 13

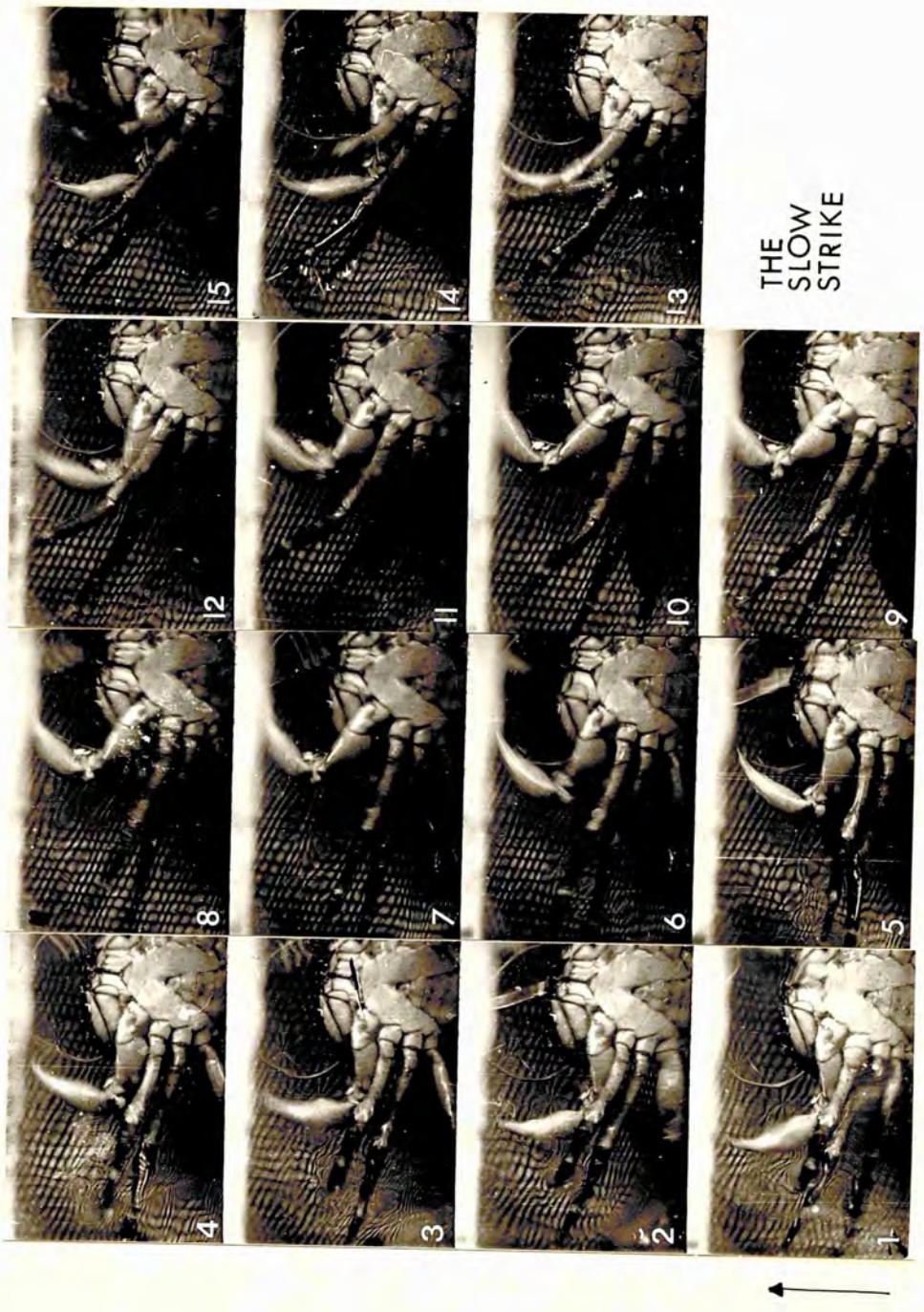


FIGURE 8

THE CHELIPED JOINT MOVEMENTS DURING A SLOW STRIKE

The vertical dotted lines represent the time from the beginning to the end of a slow strike. The ordinate represents joint position in degrees and the abscissa represents the time, in ms, of each joint position with respect to the end of the slow strike. The positions and times were obtained from the films. The dotted line on the graph of T-Cx joint position represents the excursion of this joint during a typical fast strike. Comparison of all these graphs with Fig. 5 clearly shows that the slow strike is a slower, more deliberate movement with a pause at the end of flexion during which the claw often grasps the stimulating object. The whole action lasts over three times as long as the fast strike, that is 250 ms as compared to 30 to 60 ms for a fast strike. Flexion and re-extension movements are almost symmetrical in their angular excursions and time course. Unlike the fast strike there are no pre-strike twitches or "bounce" features.

CHAPTER 2 FIGURE 8

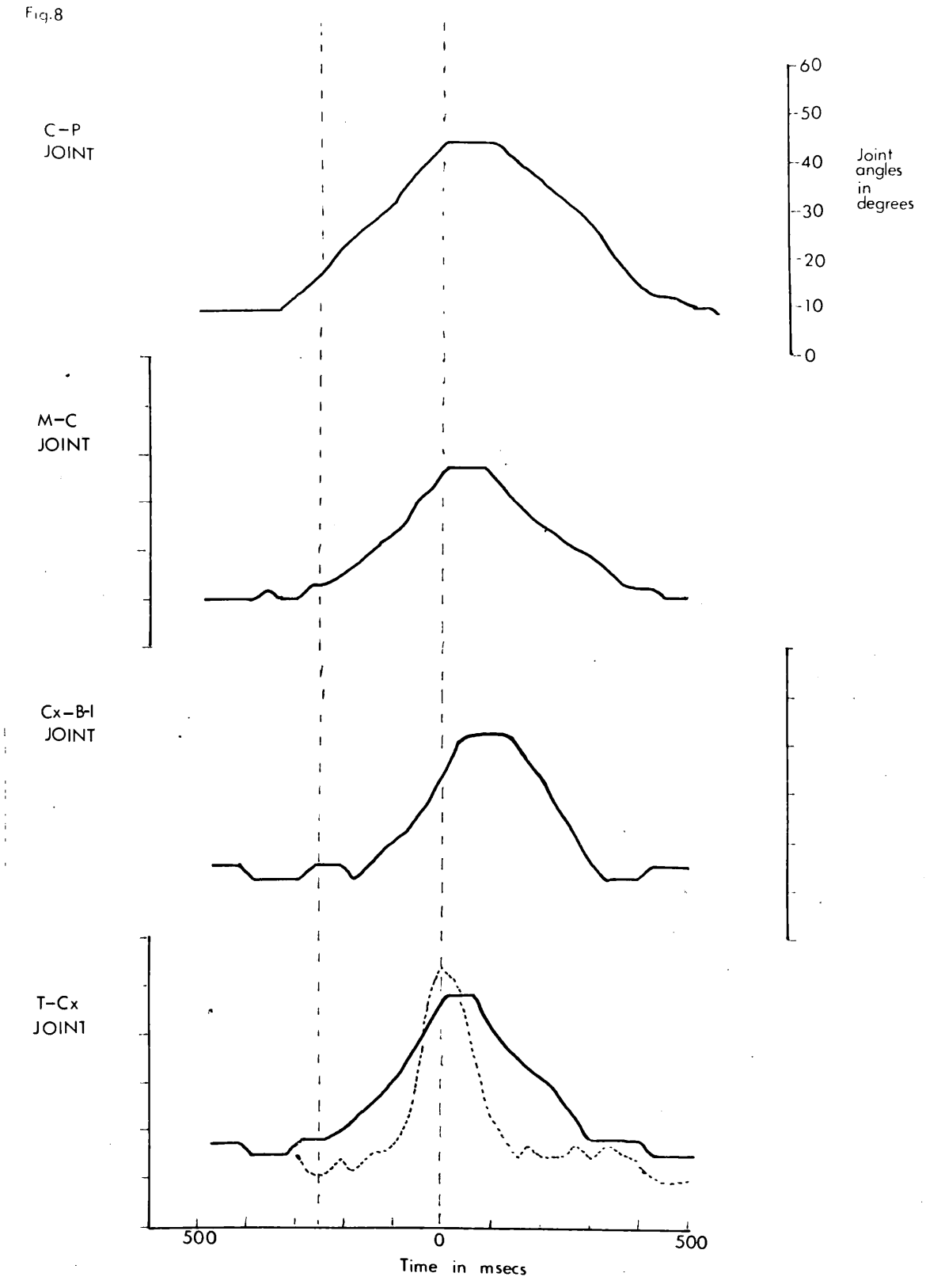
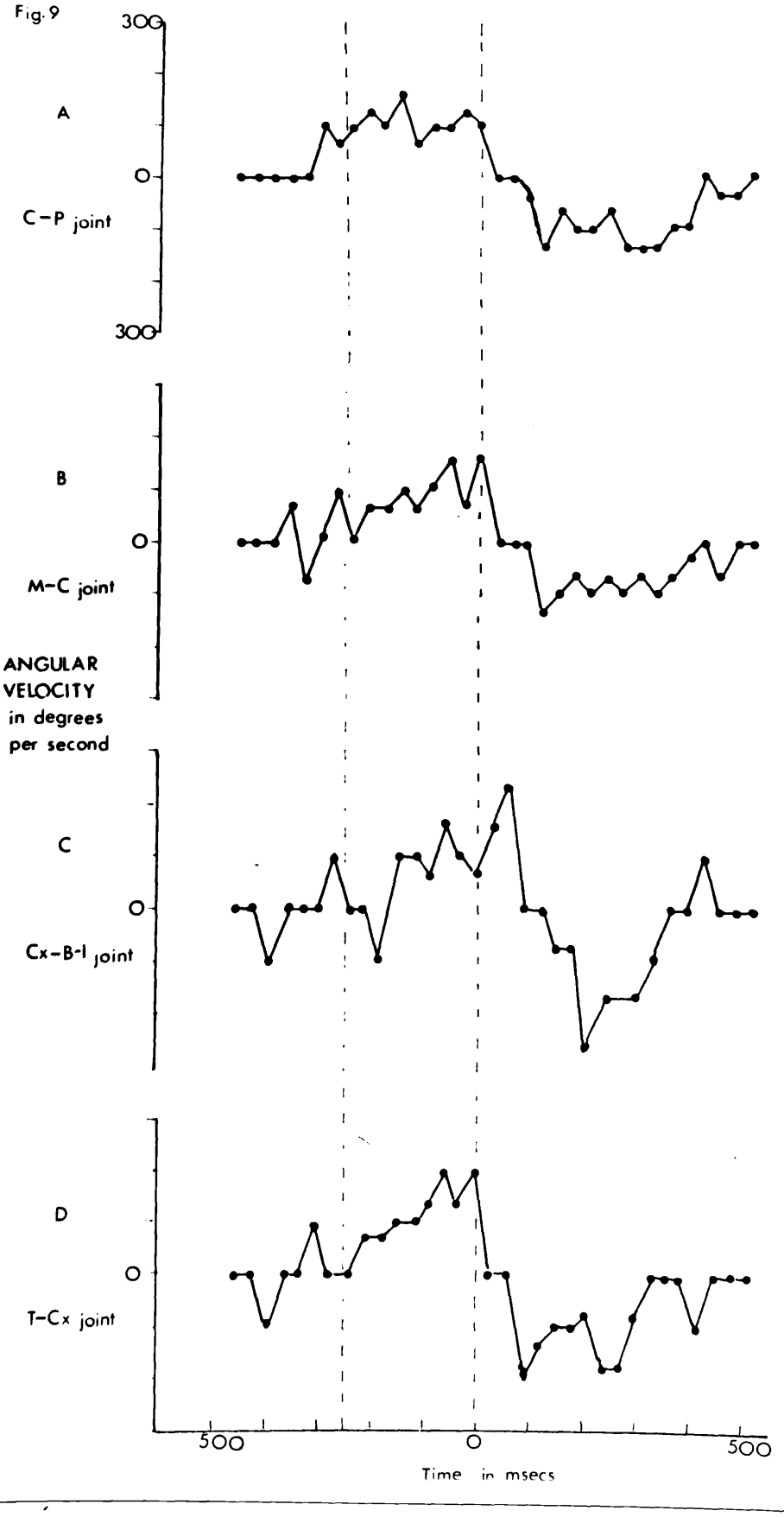


FIGURE 9

The four graphs represent the angular velocities of the cheliped joints which are achieved during the slow strike indicated on Fig. 8. The ordinate and abscissa is the same as Fig. 6. Graph A represents angular velocity of the C-P joint, Graph B represents the angular velocities of the M-C joint, Graph C represents the angular velocities of the Cx-BI joint and Graph D represents the angular velocities of the T-Cx joint. The dotted lines represent the time from the beginning to the end of the slow strike. These graphs demonstrate that, unlike the situation in the fast strike, there are no sudden peaks of angular velocities, but instead there are slow rises in positive and negative strike velocities. All the maximum velocities which are achieved in a slow strike are less than the peak fast strike velocities.

CHAPTER 2 FIGURE 9



where m is the mass of each segment in grams, and r is the distance in cm from the centre of each segment to the axis of rotation, that is, the T-Cx joint (Fig. 10). The moment of inertia was calculated to be 511.0784 $g.cm^2$.

Since the rotational energy for the strike movement is calculated about both the T-Cx and Cx-BI joints, the maximum angular velocity for a strike is not simply 660°/s, the peak velocities of both joints (Fig. 6), but a resultant of these two velocities, that is 940°/s (Fig. 10b). The rotational kinetic energy will therefore be;

$$Ek = \tfrac{1}{2}Iw^2$$

$$I = 511.0784\ g.cm^2.$$

$$w = 940 \div 57.3 \text{ radians/s}$$

$$= 16.405 \text{ radians/s.}$$

$$w^2 = 269.12 \text{ radians/s.}$$

$$\text{Therefore } Ek = \tfrac{1}{2} \times 511.0784 \times 269.12$$

Therefore the rotational energy of the limb = 0.688×10^5 ergs.

There are three major muscles which could be involved in the strike movement, flexing and depressing the limb from the T-Cx and Cx-BI joints. These are the coxa promotor, the BI Anterior depressor and the BI Posterior depressor muscles. The mean weights of these muscles were measured from 10 crabs of a similar size to the crab used for equation 1.

The mean weights were:

Coxa promotor muscle	0.613 gm
BI Anterior depressor muscle	0.602 gm
BI Posterior depressor muscle	0.455 gm
Total	1.670 gm

Insect flight muscle can produce energy at a rate of 3 to 9×10^5 ergs/gm. muscle/s. (Weis-Fogh, 1956; Machine and Pringle, 1959). The three coxal-BI muscles weigh 1.67 gm, and therefore, at the mean rate of this energy production, 6×10^5 ergs/gm. muscle/s, the muscles could produce:

$$(6 \times 10^5 \text{ ergs}) \times 1.67 \text{ gm/s}$$

$$= 10.02 \times 10^5 \text{ ergs/s}$$

which is equivalent to 0.01002×10^5 ergs/ms.

FIGURE 10

A. MOMENT OF INERTIA OF THE CHELIPED

In order to obtain a quantitative estimate of the energy released during a strike, the moment of inertia of the cheliped was calculated in a method described by Alexander (1968).

Each line on the figure represents a distance of 1 cm from the T-Cx pivot. The cheliped was cut into strips along these lines and each part weighed, value M. To derive the moment of inertia these weights were individually multiplied by the square of the radius between the centre of each strip and the T-Cx joint. The values were then summed to fulfil the equation;

$$I = \sum (mr^2)$$

From right to left these values were;

	m(gms)	r(cms)	$r^2(cm^2)$	$mr^2(g.cm^2)$
A	1.1078	0.5	0.25	0.2769
B	0.6795	1.5	2.25	1.5289
C	0.9369	2.5	6.25	5.8556
D	1.4312	3.5	12.25	17.5322
E	1.4891	4.5	20.25	30.1543
F	2.5253	5.5	30.25	76.3903
G	1.8597	6.5	42.25	78.5723
H	2.1951	7.5	56.25	123.4744
I	1.2884	8.5	72.25	93.0869
J	0.5646	9.5	90.25	50.9552
K	0.3016	10.5	110.25	33.2514
				511.0784

The resulting moment of inertia was 511.0784 $g.cm^2$

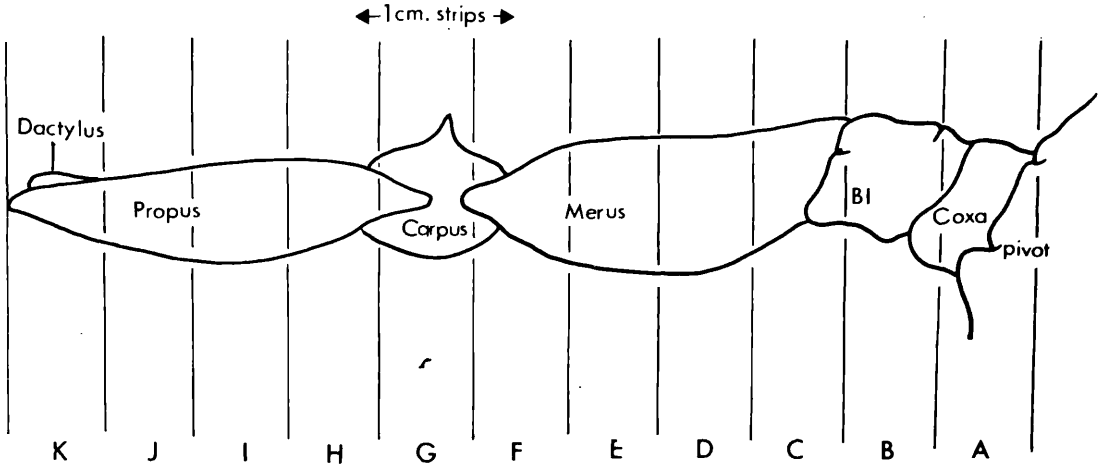
B. CALCULATION OF THE MAXIMUM STRIKE ANGULAR VELOCITY

The maximum angular velocity achieved by the cheliped during a strike was not simply the maximum velocity of the T-Cx and Cx-BI joints, that is 660°/s, (Fig.6), but a combination of these two. This was calculated in the following manner. The horizontal line on figure 10B represents the maximum strike angular velocity of the T-Cx joint, 660°/s, and the vertical line represents the maximum strike angular velocity of the Cx-BI joint, 660°/s. The resultant of these two lines gives the maximum angular velocity of the whole promotory depressory strike movement given by these two joints to the rest of the cheliped. Therefore, the maximum strike velocity is 940°/s. The scale represents 100°/s.

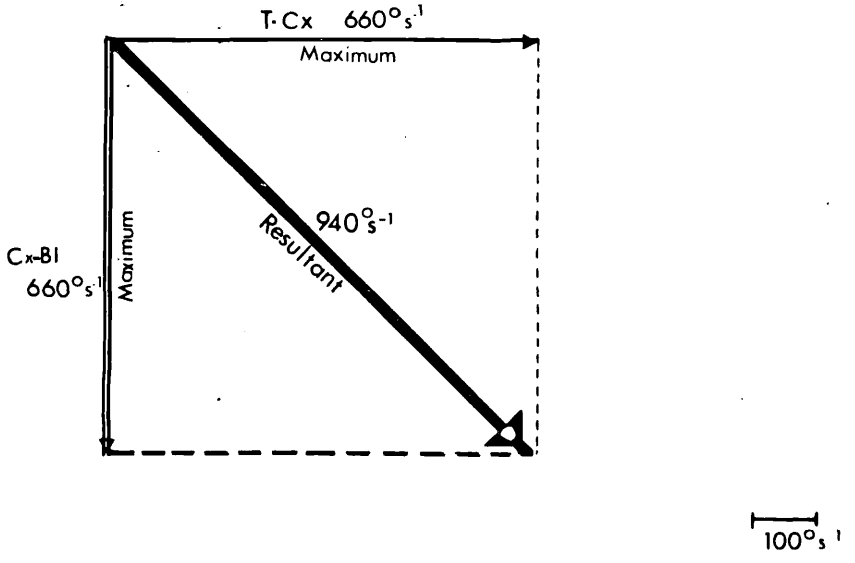
CHAPTER 2 FIGURE 10

Fig.10

A Moment of inertia.



B. Angular velocities



The maximum time for the completion of rapid coxal promotion in a fast strike is 60 ms, the minimum time is 30 ms. Therefore:

1. The three muscles could produce $.01002 \times 10^5$ ergs in 1 ms.
2. In 30 ms the muscles could produce $(.01002 \times 10^5 \text{ ergs}) \times 30$
   $= .3006 \times 10^5$ ergs.
3. In 60 ms the muscles could produce $(.01002 \times 10^5 \text{ ergs}) \times 60$
   $= .6012 \times 10^5$ ergs.

Both energy values are insufficient to produce the amount of energy necessary for a strike, since the known energy requirement has been calculated to be $.688 \times 10^5$ ergs from equation 1. Instead the muscles would need almost 69 ms to produce this known requirement.

That is; $(.01002 \times 10^5 \text{ ergs}) \times 69 = .69138 \times 10^5$ ergs.

This time requirement is almost 10 ms longer than the maximum time for a strike, and almost 40 ms longer than the minimum time for a strike.

A skeletal muscle of a toad which is fully stretched by a load, has a rate of energy production of 8×10^4 ergs/gm. muscle/s (Hill 1949). If this rate of energy production is used for the three coxal-BI muscles then they could produce;

$$(8 \times 10^4 \text{ ergs}) \times 1.67 \text{ gm/s}$$
$$= 13.36 \times 10^4 \text{ ergs/s}$$
$$= 1.336 \times 10^5 \text{ ergs/s}.$$

Therefore:

1. The three muscles could produce $.001336 \times 10^5$ ergs in 1 ms
2. In 30 ms the muscles could produce $(0.001336 \times 10^5 \text{ ergs}) \times 30$
   $= .04008 \times 10^5$ ergs.
3. In 60 ms the muscles could produce $(0.001336 \times 10^5 \text{ ergs}) \times 60$
   $= .08016 \times 10^5$ ergs.

These values are far below the necessary energy requirement of $.688 \times 10^5$ ergs. In fact these muscles would require over 500 ms to produce this requirement.

That is; $(.001336 \times 10^5 \text{ ergs}) \times 500 = .668 \times 10^5$ ergs.

Tension values for single muscle fibres of crayfish are given by Zachar and Zacharová (1966): 8.2 kg/cm^2 as compared to 4 kg/cm^2 for the frog.

Therefore it can be seen that these muscles must store energy to achieve the fast strike within the appropriate time. Burrows (1969) stated that the latent period for the initiation of a muscle contraction in a single barnacle muscle fibre is 5 ms. The time taken to reach peak tetanic tension is a further 100 ms. When muscle latency periods are taken into consideration, it is even more apparent that energy storage is necessary which is released during the strike.

The recovery from strike is almost as rapid (Fig. 5) and is completed within 30 to 90 ms. In this movement the maximum resultant angular velocity is 600^{0}/s. The rotational kinetic energy for strike recovery will therefore be:

$$Ek = \tfrac{1}{2}Iw^2$$

$$I = 511.0784 \text{ g.cm}^2$$

$$w = 600 \div 57.3 \text{ radians/s}$$

$$= 10.471 \text{ radians/s}$$

$$w^2 = 109.641 \text{ radians/s}$$

$$\text{Therefore} \quad Ek = \tfrac{1}{2} \times 511.0784 \times 109.641$$

Therefore the rotational energy of the limb = $.280 \times 10^5$ ergs.

There are two large and two small muscles which could be involved in strike recovery, re-extending and re-levating the limb from the T-Cx and Cx-BI joints. These are the large Dorsal and small Ventral coxa remotor muscles together with the large BI Anterior and small BI Posterior levator muscles. The mean weights of these muscles in ten crabs were:

Dorsal coxa remotor muscle,	0.444 gm
Ventral coxa remotor muscle,	0.017 gm
BI Anterior levator muscle,	0.242 gm
BI Posterior levator muscle,	0.066 gm
Total	0.769 gm

Using the mean insect flight muscle values given above, that is 6×10^5 ergs/gm. muscle/s, these four muscles could produce;

$$(6 \times 10^5 \text{ ergs}) \times 0.769 \text{ gm/s}$$

$$= 4.614 \times 10^5 \text{ ergs/s}$$

which is equivalent to 0.004614×10^5 ergs/ms. Therefore;

1. These four muscles could produce $.004614 \times 10^5$ ergs in 1 ms
2. In 30 ms the muscles could produce $(.004614 \times 10^5 \text{ ergs}) \times 30$
   $= .1384 \times 10^5$ ergs
3. In 90 ms the muscles could produce $(.004614 \times 10^5 \text{ ergs}) \times 90$
   $= .4153 \times 10^5$ ergs.

The known energy requirement for strike recovery is $.280 \times 10^5$ ergs and so although this amount could be produced in the maximum strike recovery time it could not be produced in the minimum recovery time. When the latency periods are considered again it appears that this movement also requires the prior development of energy.

DISCUSSION

It is apparent that the display patterns studied here fit the three criteria given by Wright (1968) presented in the General Introduction. The threat displays, for example, could not be directly functional in feeding, they occur temporally and spatially in such a way that they would be detected by another animal and are not incomplete movements from a directly functional motor pattern.

The degree of aggression of Carcinus maenas appears to be communicated by body posture. An aggressive crab will always extend its chelipeds while levating the body. This gives the visual impression of greatly increasing body size and shape. A defensive crab displays the reverse features and tucks the chelipeds into the body away from any aggressor. These displays are common among other crustaceans such as Ocypode (Hughes, 1966), Uca, (Crane 1966), hermit crabs (Hazlett and Bossert, 1965), the spider crab Microphyrs (Hazlett, 1972), together with many other examples reported by Reese (1964), Schöne (1968) and Wright (1968).

Since the agonistic displays are clearly defined they doubtless serve to minimize the necessity for actual physical contact between crabs or predators. This may be one reason why, in Carcinus, the strike movement does not always follow a threat display. Apart from the large amount of energy required to generate a fast strike, a fully threatening large crab may suffice to deter the majority of predators or other intruders.

The observed agonistic behavioural patterns seen in Carcinus are certainly not unique. For example many species of crabs threaten with outstretched chelipeds and submit with a flattened posture (Jachowski, 1974; Sinclair, 1977). However, Carcinus performs the threat display quickly and readily. The strike action is less widespread in crustaceans and is largely confined to the Portunidae and Canceridae although similar behaviour is shown by the crab Lambrus pugilator (Schäfer, 1954). Schäfer reported that Lambrus often strikes at predatory sea birds when the crab is exposed on the beach.

The energy production rates calculated for the fast strike movement indicate that there must be energy development and storage before the strike and possibly for the recovery action. Energy storage in muscles usually occurs during a period of isometric contraction when muscles can build up tension by contraction against an antagonistic load. This is the situation in the locust (Bennet-Clark and Lucey, 1967) and Squilla (Burrows, 1969). This may be the case for the strike since this movement is preceded by a period of pre-strike, during which the limb displays little movement but is obviously not the case for the recovery movement because re-extension of the cheliped follows immediately after the strike. Since this is not the case for recovery movements there may be some modification to the coxa and BI complex by which the fast re-extension is achieved.

The strike of Squilla (Burrows, 1969) is caused by a rapid unfolding of the distal joints of the raptorial second thoracic limb. This is a predatory movement during which prey may be speared on the end of the dactylus, caught between the propus and dactylus or hit by the closed propus-dactylus joint.

The strike velocities achieved by Squilla are much faster than those of Carcinus. The prey are hit 4 to 8 ms after the movement has begun. After only 2 ms, the whole distal part of the arm moves at $10{,}000^{\circ}/s$. This requires an angular acceleration of $6{,}660{,}000^{\circ}/sec^2$. Burrows calculated that the strike would require 1.25×10^5 ergs in 1.5 ms, and that over 40 ms would be required for the limb extensor muscles to produce this energy.

Burrows used electromyographic techniques to show that the strike is produced by co-contraction of two antagonistic flexor and extensor muscles of the carpus. The propulsive forcefor the strike is derived from the extensor muscles of the carpus. These

are capable of building up tension before the strike by virtue of skeletal modifications. A "click" mechanism is found between the merus and carpus, and comprises a small sclerite which can be pulled over a stop on the ventral wall of the merus when the small lateral flexor muscle contracts. A second sclerite is operated by a second muscle, the medial flexor. When both sclerites are engaged, the limb is locked and extension cannot occur. This allows the large extensor muscles to develop tension before limb movement, and will contract isometrically. When the small flexor muscles relax, the sclerite stops are unlocked and the tension developed in the extensor muscles is explosively released allowing the limb to be propelled forwards in a strike.

A different type of mechanical stop is shown in the locust. In this animal the stop is achieved by the co-contraction of the extensor and flexor tibiae muscles. The fast tibial extension is brought about by the contraction of the large extensor tibiae muscles of the hind legs. When the tibia is flexed the flexor muscle has a greater mechanical advantage over the extensor (Heitler, 1974). A second mechanism is also operated when the tibia is fully flexed during the period before a jump. The tibia can actually be locked in the flexed position by virtue of a lump, Heitler's lump, located in the femur. (Heitler, 1974). When the flexor relaxes, the lock is disengaged and the tibia extends with the full force of the energy built up in the extensor muscles.

Energy storage takes a different form in the jump of the flea Spilopysyllus, (Bennett-Clark and Lucey, 1967). To cause a jump, an energy requirement of 2.25 ergs is needed in 0.75 to 1.0 ms. This is not possible by direct mechanical action. It was found that, in this animal, energy is not stored by the muscles but in a resilin pad located between the notum and pleuron. The metathoracic femur is depressed for 100 ms before a leap. It was suggested that this gives the femur depressor tendon over-centre properties with respect to the trochanter-femur joint. Energy can now be stored in the resilin pad if the muscle continues to contract. It is then released by contraction of another muscle, termed 63a which pulls the depressor tendon away from the over-centre position. This allows the femur to depress rapidly and so enables the animal to jump.

Rothschild (1975) studied the jump of the flea Xenopsylla cheopis and suggested that the jump occurs in a series of events (Rothschild et al., 1975). Firstly the flea crouches down, arching the back and contracting the body. The femur is then raised by contraction of the trochanter levator muscle. This engages trochanteral hooks into sockets. The distal part of the muscle apodeme is held between the hooks, and the proximal part is wedged into a socket in the upper edge of the coxa, which preloads the apodeme. Contraction of the ventral longitudinal muscles of the thorax engages several hooks and catches which stiffens the thorax and presses the coxa against the abdominal sternum. Contraction of the epipleural muscles compresses the resilin pad. When the levator and longitudinal muscles relax, the lock on femoral descent is removed. The jump is then initiated by a rapid twitch of the trochanter depressor muscle. As the twitch tension rises the hooks are disengaged and the elastic energy stored in the resilin pad is released.

The description of the agonistic behaviour patterns of Carcinus forms the foundation for study on the physiological basis of behaviour. The choice of any specific behaviour for such a study is important. The behaviour should be simple yet adaptable and should be reliably and easily evoked. For this study the threat display and strike behaviours of Carcinus were chosen for such an examination. The threat display is shown by all responsive crabs and may lead to a strike movement if the crab receives appropriate stimulation.

It has been shown the strike behaviour of Carcinus requires that energy must be developed before the strike can be performed. It is also suggested that there is likely to be a modification of the coxal and BI joints by which rapid recovery movements are performed. To determine how the strike and recovery are achieved, the following series of experiments were undertaken;

1. The anatomy of the coxa and BI regions of the chelipeds was examined in detail to determine whether there are any skeletal stop mechanisms.
2. The physiological characteristics of these muscles were examined using intracellular recording techniques.
3. The moments about the joints of these muscles were calculated and the geometry of the joints investigated.

4. The strike behaviour was examined using extracellular electromyographic techniques to determine the physiological basis of the strike and threat behaviour in Carcinus maenas.

CHAPTER 3

ANATOMY AND NEUROMUSCULAR PHYSIOLOGY OF THE COXAL-BI COMPLEX IN THE CHELIPED OF CARCINUS.

INTRODUCTION

Evolution of the crustacean motor system is connected with the evolution of articulated limbs and a highly developed cross-striated musculature adapted to the performance of fast and complex movements. The muscle fibres are multinuclear and gathered into separate muscle bundles. The fibres are generally attached at one end to the hypodermis and by the other end to an apodeme or tendon.

Arthropod muscles are multiterminally and polyneurally innervated. The former term describes a situation when one axon forms a dense network of branches at many points on the surface of the muscle fibre (Fatt and Katz, 1953). Polyneural innervation describes a condition in which an individual muscle fibre may be innervated by two or more axons (Wiersma and Ripley, 1952). Historically the investigation of crustacean nerve-muscle preparations dates back to the 1880's with studies by Richet and Biedermann. Richet (1882) studied facilitation in the crayfish claw muscles and noticed that single stimuli are sometimes ineffective while repetition may cause contraction. Biedermann (1887) obtained evidence for the existence of peripheral inhibitory axons in the claw nerve-muscle system of Astacus.

Crustacean muscles and neuromuscular systems display a wide variety of responses to stimulation. Not only do the muscles of different species show marked diversity in fine structure, contraction and electrical responses (Atwood, 1965), but even within a single muscle the electrical responses recorded from individual fibres may vary greatly from fibre to fibre (Atwood and Dorai Raj, 1964). In different fibres, responses to depolarization of the membrane range from all or nothing spikes in some crab leg fibres for example (Atwood, 1965), to large and small graded responses in most crustacean fibres (Fatt and Katz, 1953; Atwood, Hoyle and Smyth, 1965), to absence of graded responsiveness (Atwood, 1963). All ranges of electrical response may be displayed in one muscle. For example in Chionectes tanneri, depolarization of selected fibres produces graded responses, decreased responsiveness and muscle spikes (Atwood, 1965).

When compared to vertebrates, crustaceans use fewer motorneurones to control their muscles which limits the number of motor units available for recruitment during muscle contractions. However they have developed a greater range of muscle responses and wider diversity of neuromuscular junctions and muscle fibre components to counter this.

Membrane depolarization is associated with tension such that muscle fibres possess a critical point beyond which further depolarization produces contraction (Atwood, Hoyle and Smyth, 1965). Atwood (1963) showed that the tension of a muscle fibre is related to the product of the time and amount of depolarization above the threshold at which the muscle fibres begin to contract. There is a wide range of tension responses in different crustacean muscle fibres. For example, the deep abdominal extensor muscle of the crayfish contract maximally within 10 to 20 ms, while the superficial abdominal muscles develop tension slowly over several seconds (Abbott and Parnas, 1965).

Crustacean motor units can produce a continually variable muscle tension in a single muscle fibre unlike the majority of vertebrates, in which values between twitch and tetanic levels are less variable. This grading of tension may be further enhanced by the presence of peripheral inhibition which may completely counteract the effect of excitatory motor axons (Wiersma, 1961) or alter the speed of contraction of a particular motor unit (Bush, 1962; Wilson and Davis, 1965).

The fibres also show an ultrastructural difference particularly with respect to the length of muscle sarcomeres and in quantity of sarcoplasmic reticulum. Electronmicrographs show clearly outlined myofibrils with sarcomeres separated by sarcoplasmic reticulum layers. The myofibrils may be grouped into bundles or irregularly arranged. Three types of fibre are distinguished (Atwood 1963, 1967; Hoyle, 1969). These are termed phasic or "Fast" muscle fibres which have short sarcomeres of 2 to 4 μm, a well developed sarcoplasmic reticulum and small regularly arranged myofibrils. They develop tension, and relax, quickly. The time constant of the mechanical response is 5 to 20 ms. Membrane responses consist of large excitatory junctional potentials, ejp's. The second type of fibre is termed tonic or "slow". These contract and relax slowly. Their time constant is 50 to 800 ms. They possess long sarcomeres of 12 μm,

a minimum amount of sarcoplasmic reticulum and bundles of large myofibrils. Their membrane response consist of small ejp's which facilitate and summate. The third fibre type is termed mixed. These have intermediate membrane responses between the other two and their sarcomeres are less extreme in length.

In the abdominal muscles of the crayfish, phasic and tonic fibres are clearly differentiated (Parnas and Atwood, 1966). The deep abdominal extensor muscle consists entirely of rapidly contracting muscular elements of the phasic fibre type and possess short sarcomeres. Adjacent fibres may show electrotonic interactions. The superficial extensor muscles contain tonic fibres with long sarcomeres and only contract slowly. The deep abdominal extensors are adapted for phasic twitch contractions while the superficial extensors are adapted for tonic contractions.

Various crustacean species have developed specialized motor units for specialized functions. Many are adapted for fast speeds. The remotor muscle of the second antenna of Homarus, for example, is functionally divided into two parts (Mendelson, 1969). One produces slow powerful contractions and is used for postural control. The other produces very brief twitches and can achieve frequencies over 100/s without fusion. This second part is responsible for producing the buzzing sound Homarus makes when disturbed. High contraction velocities are also shown in the closer muscle of the shrimp (Wiersma, 1961), in which a single impulse is sufficient to cause a twitch which closes the claw. In the homologous muscle of the other thoracic legs such twitches are much weaker and may even be absent.

The axons which innervate muscle fibres can also be classed into different categories. As in the muscle fibres, these categories are termed phasic and tonic depending upon the characteristics of the axon (Wiersma 1961). Phasic axons are usually large in diameter and cause large ejp's which fatigue rapidly upon repetition, a process termed defacilitation. They are used for causing rapid movements and generating sudden increases of tension in the muscle. Tonic axons are generally smaller in diameter and fire in longer bursts. They fatigue less rapidly and generate small ejp's.

The presence of inhibitory axons in crustaceans was initially demonstrated by Biedermann (1887) in the crayfish claw muscles. Hoffmann (1914) found that stimulation of a thin nerve to the

dactylus opener and closer muscles of the crayfish and lobster, resulted in opener excitation and closer inhibition. Stimulation of a thicker nerve to these muscles produced opener inhibition and closer excitation. Inhibitory axons are generally used to control the effect of excitatory tonic potentials and may be used in a variety of ways to regulate the muscle response. For example they can regulate the development of muscle tension caused by the excitatory potentials (Werman et al., 1961) or they may be used to inhibit one excitatory unit while leaving another unaffected (Wiersma, 1961).

Inhibition may also occur at the presynaptic level. An example of this feature is found in the dactylus opener muscle of Carcinus (Bush, 1962), in which there are two inhibitory axons. One of these axons has its effect pre-synaptically and the other post-synaptically. Inhibitory axons are largely confined to muscles which have varied movements such as those in the walking legs and not those concerned with regular orderly movements, such as the stomach (Wiersma, 1941; Bush, 1962; Atwood 1965, 1967; Atwood and Bittner, 1964).

Thus crustacean muscles, although relatively sparse in the number of motor units that they possess, are exceptionally adaptable in response due to several features of these motor units. These include inhibition, both pre- and post-synaptic, long and short term facilitation of ejp's, depression of synaptic responses, overlapping of innervation fields, alteration of nerve impulse pattern and frequency and the grading of muscle tension.

Because of the small number of efferent axons it has been possible to detect the number, function and course of leg axons in different crustacean species. The known motor patterns for the thoracic leg muscles of the Reptantia are all identical. Seven muscles are present which move the three distal joints. This is shown in figure 6a, taken from Wiersma (1961).

The musculature and innervation of the proximal limb segments in decapod crustaceans has been less widely studied. Cochran (1935) described the anatomy of the whole leg in the Blue crab Callinectes sapidus but apart from this, studies of the proximal muscles have been largely confined to investigations into specific problems and features such as autotomy (McVean, 1973, 1974), and proprioception (Bush, 1962, 1963, 1965) for example. In crustaceans autotomy occurs at a breakage plane in the BI segment and so a

knowledge of some of the anatomy of this region was found to be necessary in order to understand this phenomenon (McVean 1973, 1974; Moffett, 1975; McVean and Findlay, 1976). However the structure of the proximal joints of the cheliped, the limb used for the strike behaviour, has been studied even less. It has been shown that the fast strike behaviour of Carcinus requires energy storage. This energy must be developed by the coxal and BI muscles as their action determines the acceleration given to the rest of the cheliped. The speeds achieved in the re-extending recovery movement requires either energy storage or some form of mechanical or muscle modification. Therefore a detailed study of the structure and properties of the coxal-BI complex of the cheliped was a pre-requisite if the control of the fast strike was to be analysed.

MATERIAL AND METHODS

Large male specimens of Carcinus maenas were obtained from the University Marine Station at Millport, Scotland. They were maintained in circulating tanks of sea water at 12°C.

ANATOMY. The anatomy of the coxal and BI muscles was examined using freshly killed specimens which were subsequently dissected using a binocular microscope. The gross innervation of these muscles was determined using methylene blue. The mechanical effects of the muscles was determined by manipulating the limb segments through their excursions of movements and observing the changes in length of the various muscles.

NEUROPHYSIOLOGICAL RECORDINGS. In order to record the neuromuscular responses of the coxal and BI muscles, the walking legs of the freshly killed crabs were removed and the carapace was lifted by cutting along the ecdysial line. The stomach, gills and mouth appendages were also removed. This exposed the thoracic muscles of the coxa and BI segments. Further removal of muscle tissues and endophragmal skeleton allowed the individual muscles to be reached. The preparation could be secured and orientated in the required position. Movement of the coxa and BI segments was restricted by positioning small pins on either side of these segments. The preparation was viable for 1 to 2 hours when maintained in cold sea water or ringer.

The nerves were stimulated using paired hook electrodes which

were constructed from electrolytically sharpened tungsten wire. The stimulating electrodes were attached to a double channel stimulator (S.R.I. Croydon, Surrey) which was connected to a S.R.I. variable cycle timer. The timer enabled the stimuli to be delivered in bursts.

Muscle junctional potentials were recorded intracellularly with glass microelectrodes of 5 to 15 M ohm resistance, filled with 3M KCl. The electrodes were connected to a high impedance amplifier (H. 1 Probe 8124 CFP. Searle Instruments, Harlow) which was attached to one beam of a Tetronix 502A oscilloscope. Photographs were taken directly from the oscilloscope, using a Telford oscilloscope camera.

Muscle tension was monitored by grasping the tendon of the muscle between a pair of fine forceps. The forceps were attached to the wand of a tension transducer (Type DI George Washington, Sheerness) mounted in a micromanipulator.

RESULTS

SECTION ONE

ANATOMY OF THE COXAL AND BI MUSCLES

The coxa articulates with the thorax by two pivots, a dorsal one which articulates with the anterio-ventral corner of the epimeron of the 4th thoracic somite, and a ventral pivot which articulates with the posterio-lateral corner of the sternum of the somite. Movement of the coxa is forwards and backwards horizontally in an excursion of 60°. The BI articulates anterio-dorsally and posterio-ventrally with the coxa. It can be moved up and down in an excursion of 65° (Figs. 2 and 3, Chapter 2).

There are two main coxal muscles, the coxa promotor, CxP, and the Dorsal coxa remotor, CxR. There is also a small Ventral coxa remotor muscle. The BI is controlled by three main muscles, the Anterior levator, Al, the Anterior depressor, Ad and the Posterior depressor, Pd. There are also two smaller muscles, the Posterior levators, Pl, and the lesser Posterior depressor. This is summarized in table 1. The muscles will be described in the sequence that they are revealed during dissection.

1. The coxa promotor muscle; CxP (Fig.1)

The CxP lies in the 4th thoracic sternal muscle chamber (Fig. 1). It is divisible into three parts. Division 1 forms the largest bulk of the muscle and arises from the anterior face of the 4th thoracic endosternite. It lies almost parallel to division 2 and is separated from it by a centrally running tendon. Division 2 arises

from the posterior face of the 4th thoracic endosternite. Division 3 consists of a thin, long strip of muscle arising from the inner side of the 3rd endopleurite.

The muscle passes downwards and forwards from its origin and inserts onto a large wedge shaped tendon. The wide tendon is attached to the anterior and dorsal side of the coxa. The muscle is grossly innervated by a thick nerve which branches from the main leg nerve trunk. The CxP nerve divides into two main branches, one which innervates muscle division 3 and a larger one which innervates all the parts of divisions 1 and 2.

2. The BI Anterior depressor muscle; Ad (Figures 1 and 2)

The Ad lies in the ventral part of the 4th sternal muscle chamber. It arises from the inner wall of the 4th thoracic sternite, following a posterio-lateral upward course to insert onto a broad but thin tendon. The tendon head attaches to the ventral rim of the BI close to the anterior Cx-BI pivot.

The Ad is largely innervated by two short nerves which branch from the main leg nerve as it spans the length of the muscle. The smaller of these two branches innervates the proximal end of the Ad. The other branch lies in the mid line of the muscle and divides into two, one division runs proximally and the other runs distally.

Several thick cuticular nerves overlie the Ad. These traverse the muscle and run into the yellowhypodermis which covers the whole of the inner surface of the carapace.

3. The BI Anterior levator muscle; Al (Fig. 2)

The Al may be divided into two parts. Each inserts onto one wing of a bifurcated tendon. Part 1 of the muscle extends into the 4th thoracic pleural chamber and inserts onto the anterior wall of this chamber. Part 2 originates below the CxP and lies almost parallel to the leg nerve trunk. It originates on the ventral medial surface of the posterior wall of the 4th thoracic sternal wall. The apodeme is inserted onto a flexible tendon head which attaches to the dorsal rim of the BI close to the anterior Cx-BI pivot.

The leg nerve gives off a thick nerve which passes over the Al. This nerve then branches several times to innervate the two parts of the muscle.

4. The BI Posterior levator muscle; Pl

This is a small muscle group confined to, and originating within, the coxa. It is subdivided into three sections. The two

FIGURE 1

Ad, BI Anterior depressor muscle, B-I, Basi-ischium; Cx-BI post pivot, coxa-BI joint posterior pivot; CxP, coxa promotor muscle; D, dorsal; L, lateral; M, medial; T-Cx, thorax-coxa joint; Th, thoracic; V, ventral. In this diagram the coxa of the cheliped was promoted and the BI depressed.

This diagram shows the positions of the coxa promotor and BI Anterior depressor muscles. The CxP is divisible into 3 parts. Division 1 lies in the anterior side of the 4th thoracic endosternite while division 2 lies in the posterior side of this endosternite. The 3rd endopleurite was removed to display division 3 of the CxP which arises from the inner surface of the endopleurite wall. Before removal, this endopleurite would overlie the proximal end of the CxP. The whole muscle is innervated by a thick nerve which branches from the main leg nerve trunk. The CxP nerve divides into two, one part innervating division 3 of the muscle and the other part innervating divisions 1 and 2.

The BI Anterior depressor muscle lies on the ventral part of the 4th sternal muscle chamber and follows a posterio-lateral course to insert on the ventral rim of the BI.

CHAPTER 3 FIGURE 1

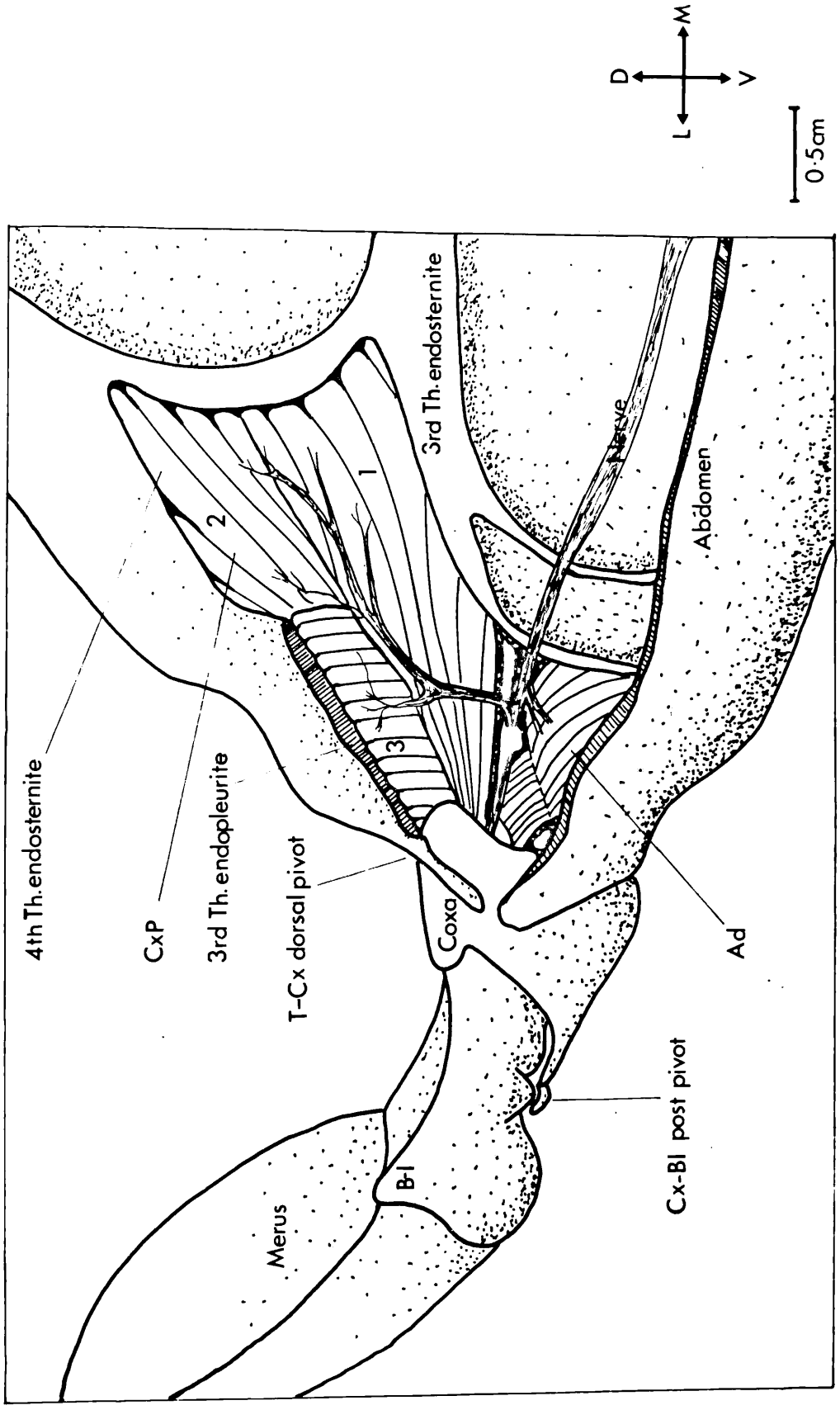


Fig.1

large sections are termed Posterior levators 1 and 2 (McVean and Findlay, 1976). They originate onto the dorsal surface of the coxa and insert separately onto two small tendons. PPL_1 (McVean and Findlay, 1976) inserts onto the arthrodial membrane on the dorsal surface of the BI rim. PPL_2 inserts onto a dorsal projection of the Anterior levator tendon head. The third section is termed the Rotatory Posterior levator, RPL (McVean and Findlay, 1976) and also originates on the dorsal surface of the coxa and inserts onto a tendon which rotates against the tendon head of the Anterior levator muscle.

5. The BI Posterior depressor muscle; Pd (Figs 3 and 4)

The Pd is a complex muscle with one large section and several smaller parts. The main section, termed Pd1, lies between the Dorsal coxa remotor and the Anterior levator muscles in the outer and anterior part of the 4th pleural muscle chamber. It originates on the anterior wall of this chamber and then passes downwards to insert onto a long tendon blade (Fig.3). This long blade is attached flexibly to a broad heel shaped tendon head which inserts onto the ventral rim of the BI close to, and slightly overlapping, the insertion of the Anterior depressor muscle.

Another section of the muscle, termed Pd2, inserts along the proximal end of the long tendon blade. Pd2 is a strip of muscle which originates laterally onto the most ventral and anterior portion of the 4th pleural chamber. The insertion of the muscle is restricted to the main tendon blade.

There are four small but distinct muscles which attach onto the heel of the tendon. One of these originates in the thoracic chamber while the others are confined to the coxa. The former is termed the Posterior depressor heel muscle 3, PdH3, and originates from the ventral anterior wall of the 4th sternal muscle chamber. It is a long strip like muscle which overlies the anteriorly facing surface of the heel, and inserts onto the most ventral part of the heel. Beneath PdH3 is a wider band of muscle fibres comprising PdH4 which also inserts onto the anterior-ventral face of the heel. However PdH4 originates on the ventral surface of the coxa and not in the thorax.

The two remaining Posterior depressor heel muscles insert onto the dorso-posterior surface of the heel (Fig.4). PdH5 is a thin muscle comprised of long parallel fibres which originate

FIGURE 2

Legend as before with the addition of Al, BI anterior levator muscle; C.N, cuticular nerves. In this diagram the coxa of the cheliped was remoted and the BI levated. The CxP was removed. This diagram shows the large bulbous form of the BI Anterior depressor muscle and the bifurcating nature of the BI Anterior levator muscle. The Ad is innervated by 2 nerves which branch from the main leg nerve. One branch innervates the mid and distal regions of the muscle while the other innervates the proximal regions. Several thick cuticular nerves, which run to the hypodermis, overlie the Ad.

The Al is divisible into 2 parts. Part 1 extends into the 4th pleural muscle chamber and part 2 originates below the CxP in the 4th sternal muscle chamber. Both parts of the muscle are innervated by several small nerves which branch from the main leg nerve.

CHAPTER 3 FIGURE 2

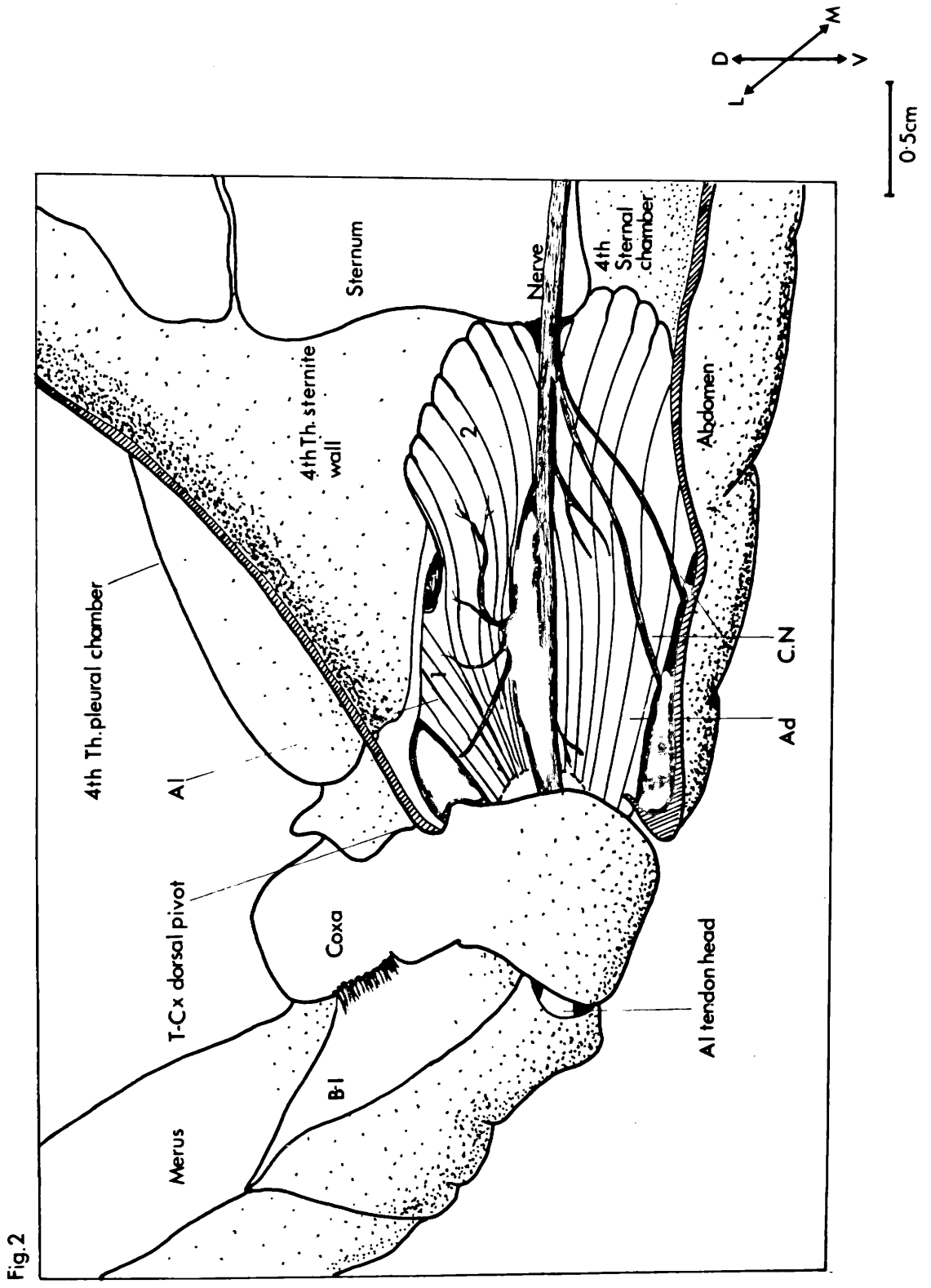


Fig.2

from the dorsal rim of the coxa, close to the dorsal T-Cx pivot. It overlies a smaller, thinner muscle, PdH6, which originates more ventrally on the dorsal coxal rim (Fig. 4).

The main Posterior depressor nerve gives off several small branches to these muscles. One branch runs to PdH3 and PdH4 in front of the heel, another branch runs over the heel to innervate PdH5 and PdH6 and a third branch runs parallel to the main tendon blade. This third branch bifurcates and innervates both sides of Pd1 and also Pd2.

6. The Lesser BI Posterior depressor muscle (Fig. 5a)

This is a small muscle which may be divided into two sections. Both are tapered and are broader at the origin. The muscle is confined to the coxa and originates on the posterio-ventral rim beneath PdH5 and PdH6. Both parts of the lesser Posterior depressor muscle converge onto a small tendon which attaches onto the BI rim, posteriorly to the Pd heel.

7. The Dorsal coxa remotor muscle; CxR (Fig. 4)

The CxR is a broad pinnate muscle which runs parallel to Pd1 in the outer and posterior region of the 4th pleural chamber. It originates along the anterior and posterior walls of this chamber, beneath Pd1. It takes a forward and downward course to insert onto a long narrow tendon which attaches to the posterior side of the coxal rim.

The CxR is innervated by a thick nerve which loops over and behind the Posterior depressor tendon blade. The main part of the nerve runs along the midline of the muscle and branches to the sides. One of the more proximal branches supplies a discrete ventro-medial area of the muscle.

8. The Ventral coxa remotor muscle (Fig. 5b)

This is a small fan shaped muscle which originates along the rim of the apodemal foramen between the 4th and 5th thoracic segments. It attaches to a small, thin tendon which inserts next to the Dorsal coxa remotor tendon, on the posterier side of the coxal rim.

SECTION TWO

NEUROMUSCULAR PHYSIOLOGY

The innervation of the five main coxal and BI muscles is

FIGURE 3

Legend as before with the addition of; A, anterior; dp, T-Cx dorsal pivot; P, posterior; Pd Posterior depressor muscle sections; PdH, Posterior depressor heel muscle sections.
In this diagram the coxa of the cheliped was remoted and the BI levated. The Ad and Al were removed. The 4th pleural muscle chamber was opened and part of the coxa cut away to display the origins of the Pd muscle groups. The dotted lines represent the part of the heel which is covered by PdH3 and PdH4.
This diagram illustrates the origins and insertions of the subdivisions of the BI Posterior depressor muscle. The Pd is divisible into 6 parts. The largest part, Pd1, has its origin in the 4th pleural muscle chamber and inserts onto a long tendon blade. Pd2 inserts onto the proximal end of the tendon and originates in the most ventral part of the 4th pleural muscle chamber.
The tendon is flexibly attached to the Pd tendon head, a firm heel shaped structure. 4 other Pd muscles insert onto the heel, two insert onto the anterior face, PdH3 and PdH4, while two insert onto the posterior face, PdH5 and PdH6. PdH3 originates in the 4th thoracic sternal chamber while the other 3 heel muscles all originate in the coxa. PdH4 comprises a wide band of muscle fibres which insert along the coxal rim, either side of the T-Cx ventral pivot. Both PdH5 and PdH6 originate along the coxal rim by the T-Cx dorsal pivot although PdH5 overlies the smaller PdH6. These two muscle groups are comprised of thin, longitudinally running parallel fibres.

CHAPTER3 FIGURE 3

Fig.3

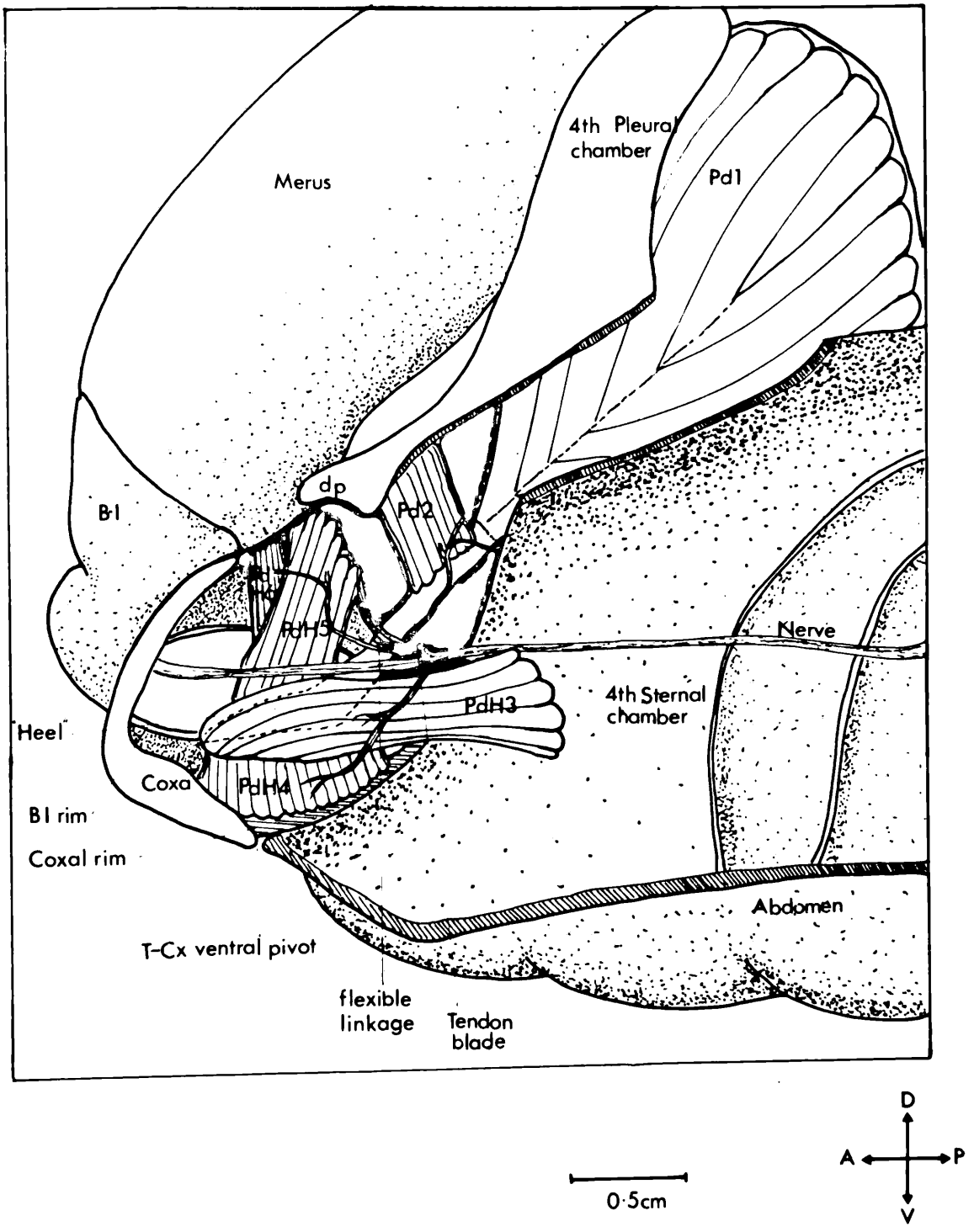


FIGURE 4

Legend as before with the addition of CxR, coxa remotor muscle. In this diagram the coxa of the cheliped was remoted and the BI levated. The Pd was removed from the heel shaped tendon head. The 4th pleural muscle chamber was opened to display the origins of the 2 coxal remotor muscles.

This diagram demonstrates the positions of the 2 coxal remotor muscles and the origins and insertions of PdH5 and PdH6.

The Dorsal coxa remotor is a large pinnate muscle which originates along the anterior and posterior walls of the 4th pleural chamber, below Pd1. It runs forward and downward to insert onto a long tendon which attaches to the posterior side of the coxal rim. The thick CxR nerve runs longitudinally, and branches repeatedly, over the muscle.

The Ventral coxa remotor is a smaller muscle which inserts ventrally to the Dorsal CxR, on the coxal rim.

CHAPTER 3 FIGURE 4

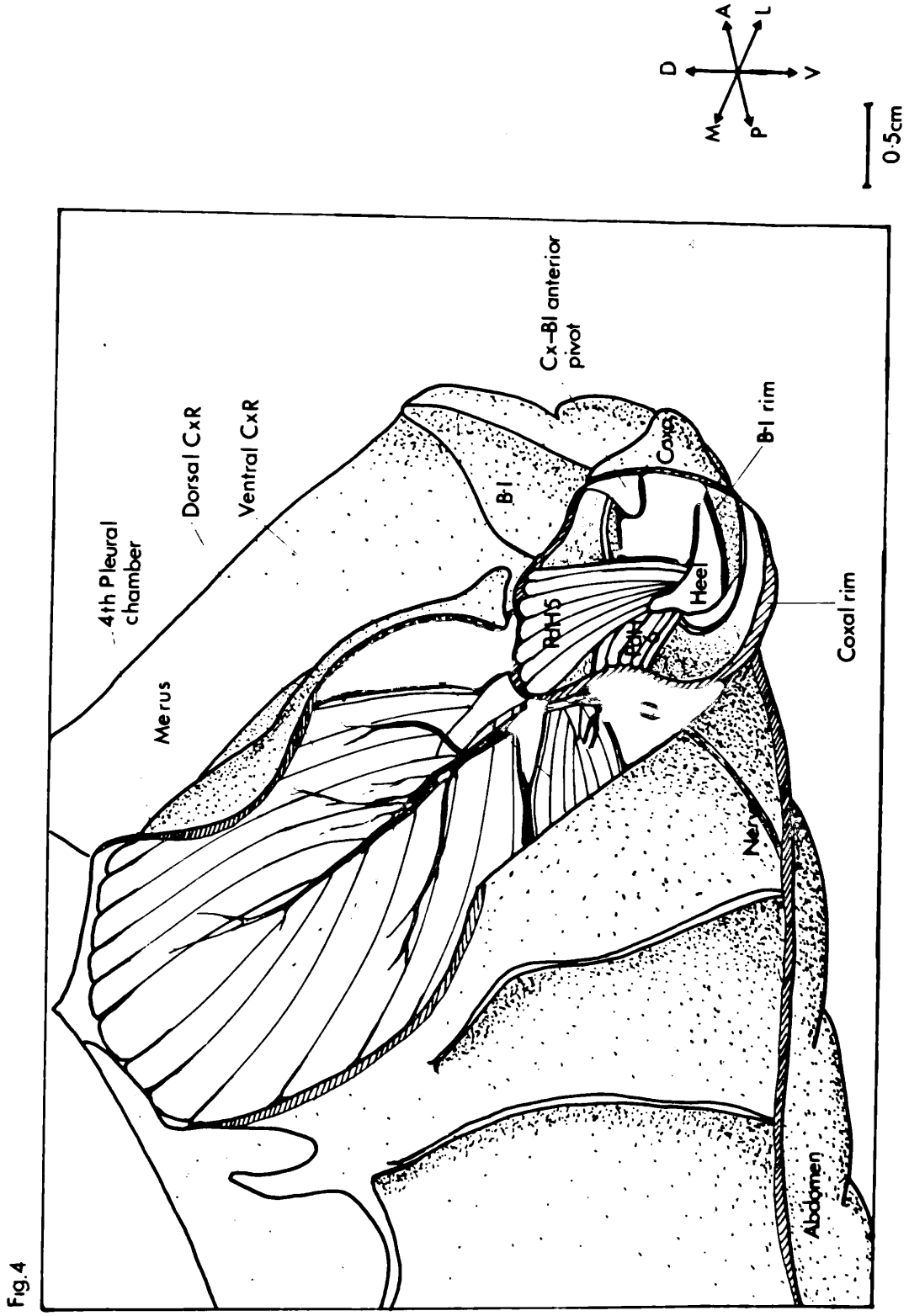


Fig.4

FIGURE 5a

Legend as before with the addition of; alt, Anterior levator tendon head; ap, Cx-BI anterior pivot, Pdt, Posterior depressor tendon head. In this diagram the coxa of the cheliped was remoted and the BI was levated.

This diagram illustrates the positions of the BI Lesser Posterior depressor muscle which can be seen after removal of all the sections of the main Posterior depressor muscle and the small Posterior levator muscles. The Lesser Posterior depressor is a small muscle which may be divided into 2 parts. Both parts converge onto a small tendon which attaches to the BI rim close to the Pd heel insertion.

This diagram also illustrates the insertions of the 2 coxal remotor muscles, the large Dorsal and smaller Ventral coxa remotors.

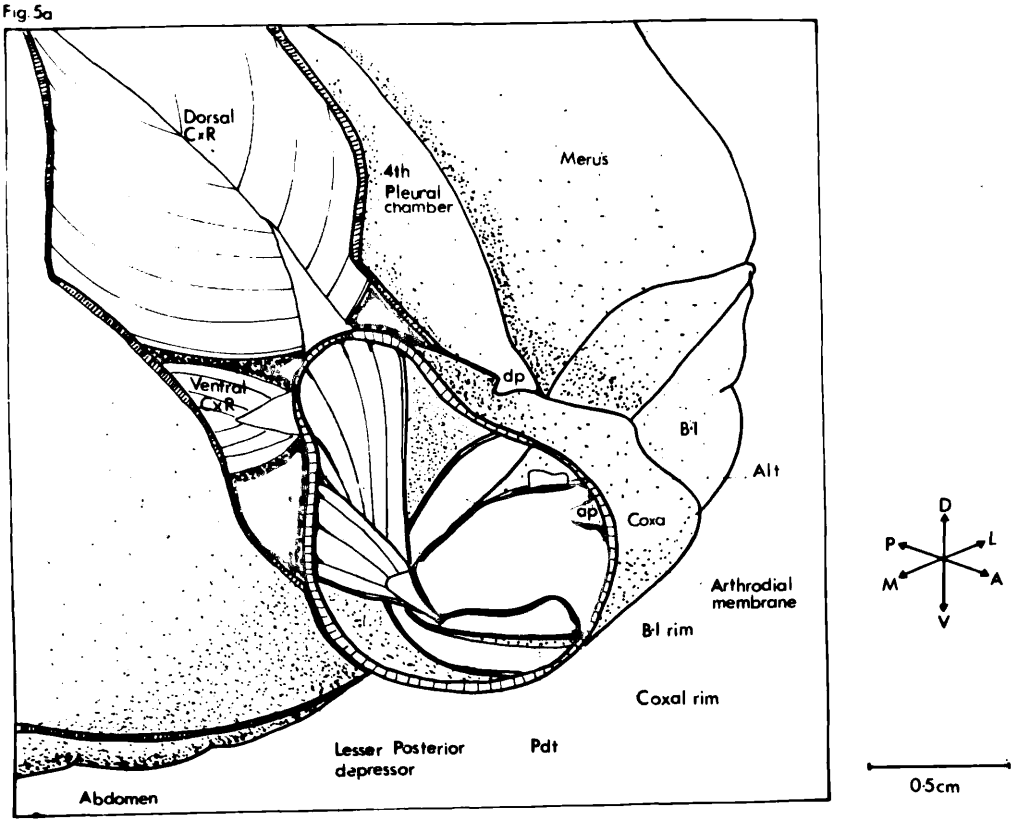
FIGURE 5b

Legend as before. In this diagram the coxa of the cheliped was semi-promoted and the BI semi-levated.

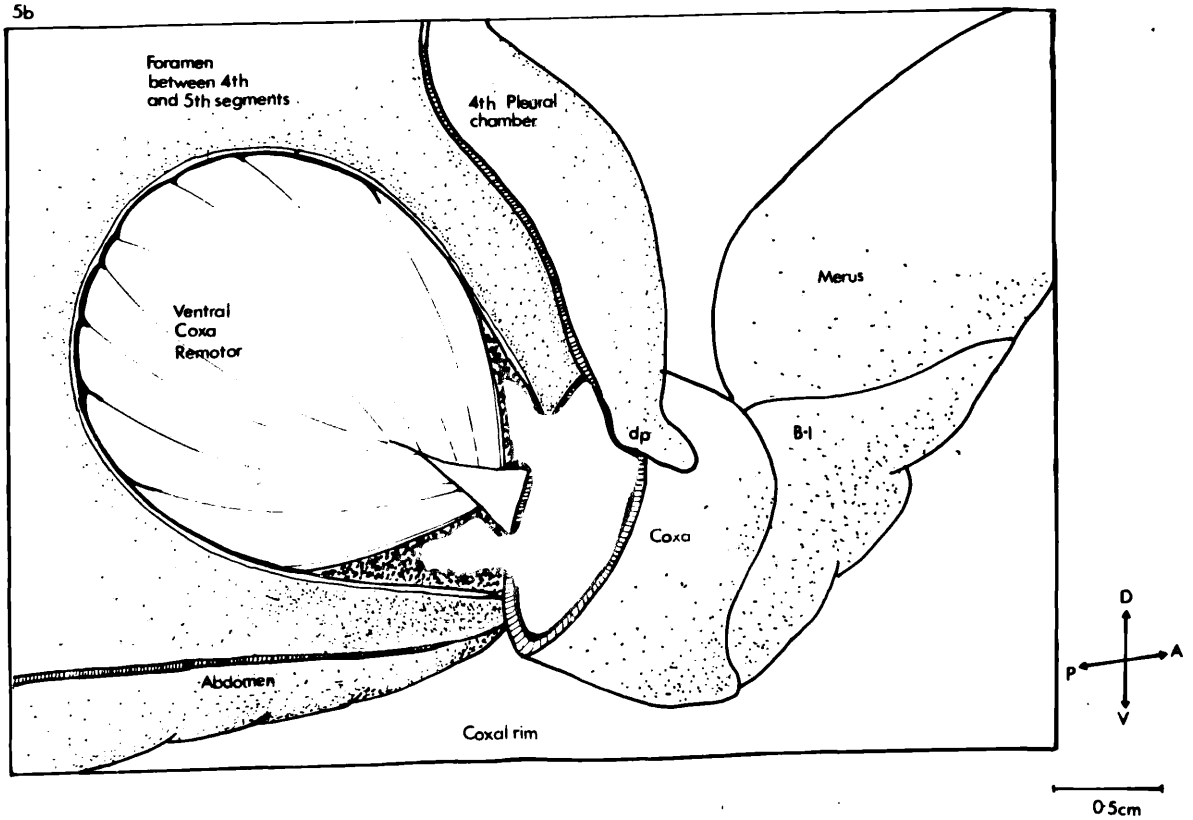
The Dorsal coxa remotor muscle was removed to demonstrate the fanlike nature of the small Ventral coxa remotor muscle. This muscle originates around the perimeter of the apodemal foramen between segments 4 and 5 of the thorax.

CHAPTER 3 FIGURE 5

Fig. 5a



5b



indicated on figure 6b, and table 2.

1. THE DORSAL COXA REMOTOR MUSCLE (Figs. 7, 8 and 9)

The CxR responded to stimulation of the coxa remotor nerve with ejp's of 4 discrete sizes indicating the presence of at least 4 motor axons. There were three tonic motor units and one phasic motor unit.

Tonic Unit One. (Fig. 7 a to c) When axon 1 was stimulated, small ejp's, 1 mV, were produced which lasted for 10 ms. Muscle tension was only developed at stimulation rates above 30 Hz and was very slight (Fig. 7c).

Tonic Unit Two (Fig 7, d to g) Stimulation of axon 2 produced larger ejp's, 3 mV, which displayed a similar pattern of facilitation to that caused by axon 1. Muscle tension was developed at stimulation rates of 20 Hz and above (Fig. 7g).

Tonic Unit Three (Fig. 8) Stimulation of axon 3 produced larger ejp's, 6 mV, which lasted for 20 ms. Upon repeated stimulation, the ejp's facilitated considerably more so than in the other muscles. Occasionally this facilitation lead to the production of a graded spike response in the muscle fibres (Fig. 8d).

Muscle tension responses were larger when axon 3 was stimulated. Tension developed slowly with stimulation, but then rose rapidly to a peak, 500 ms after the beginning of stimulation (Fig. 8e). Under maximal stimulation rates the decay from peak tetanic tension to zero was extremely rapid (Fig. 8g).

Phasic Unit One (Fig. 9) Axon 4 has a distinct innervation area. The nerve branches from the main CxR nerve at the proximal end of the muscle and mainly supplies the proximal and medial muscle fibres. This has the mechanical effect of pulling the whole muscle more medially when stimulated, which increases the mechanical advantage of the muscle. The muscle fibres responded with large ejp's, 12 mV, which lasted for 60 ms. They did not facilitate and readily generated graded spike responses. The number of these responses increased as the rate of stimulation was increased (Fig. 9d) and their size was 20 to 30 mV.

When a single stimulus was applied, twitches in the innervated muscle sections were visible. At 10 Hz the twitches summated into a smooth rise in muscle tension (Fig. 9e). At even greater rates the graded spike responses caused sudden large and irregular increases in tension (Fig. 9f to i).

TABLE 1.

MUSCLE	SECTION	ORIGIN	INSERTION	ACTION
Coxa Promotor	1	Anterior face of 4th thoracic endosternite.	All insert onto a broad wedge shaped tendon which attaches to the anterio-dorsal coxal rim.	Promotion of the coxa.
	2	Posterior face of 4th thoracic endosternite.		
	3	Inner surface of 3rd endopleurite.		
Dorsal coxa remotor (CxR)		Anterior and posterior walls of 4th pleural chamber.	Onto a long tendon blade attached to the posterior side of the coxal rim.	Remotion of the coxa.
Ventral coxa remotor		Along the rim of the foramen dividing the 4th and 5th thoracic segments.	Onto a small tendon next to the CxR.	Remotion of the coxa.
BI Anterior levator (Al)	1	Anterior wall of 4th pleural chamber.	Separately onto 2 wings of a bifurcated tendon which attaches flexibly to dorsal rim of the BI.	Levation of the BI.
	2	Posterio-ventral surface of 4th sternal chamber.		
BI Posterior levator (Pl)	PPL1	Dorsal surface of coxa.	Tendon attached to arthrodial membrane.	Levation of the BI.
	PPL2	Dorsal surface of coxa.	Dorsal projection of Al tendon head.	Levation and autotomy.

TABLE 1 (CONT)

MUSCLE	SECTION	ORIGIN	INSERTION	ACTION
	RPL	Dorsal surface of coxa.	Tendon close to Al tendon head.	Special use in autotomy.
BI Anterior Depressor (Ad)		Inner wall of 4th thoracic sternum.	Thin broad tendon attached to ventral rim of the BI.	Depression of the BI
BI Posterior Depressor (Pd)	1	Anterior wall of 4th pleural chamber.	Onto a long tendon which is attached flexibly to a heel shaped tendon head.	Depression of the BI.
	2	Laterally on the ventral part of 4th pleural chamber.	Onto the proximal part of the long tendon blade.	Depression of the BI? Alteration of position of tendon and heel.
	3	Ventral anterior wall of 4th sternal chamber.	Anterior face of tendon heel.	
	4	Ventral rim of coxa.	Anterior face of tendon heel.	
	5	Dorsal rim of coxa.	Posterior face of tendon heel.	
	6	Dorsal rim of coxa.	Posterior face of tendon heel.	

TABLE 1 (CONT)

MUSCLE	SECTION	ORIGIN	INSERTION	ACTION
Lesser BI Posterior depressor	1	Posterior-ventral rim of the coxa.	Small tendon attached to the ventral rim of coxa.	Depression of the BI.
	2	Posterior-ventral rim of the coxa.	Small tendon attached to the ventral rim of coxa.	

FIGURE 6.

THE INNERVATION PATTERNS OF THE CHELIPED MUSCLES OF CARCINUS MAENAS

a. From Wiersma (1961).
This diagram illustrates the innervation of the 3 distal cheliped segments. Inhibitory nerves are represented by discontinuous lines. Excitatory nerves are represented by continuous lines.

DO = Dactylus opener muscle.
DC = Dactylus closer muscle.
PE = Propus extensor muscle.
PF = Propus flexor muscle.
CE = Carpus extensor muscle.
CF = Carpus flexor muscle.
A = Carpus accessory flexor muscle.

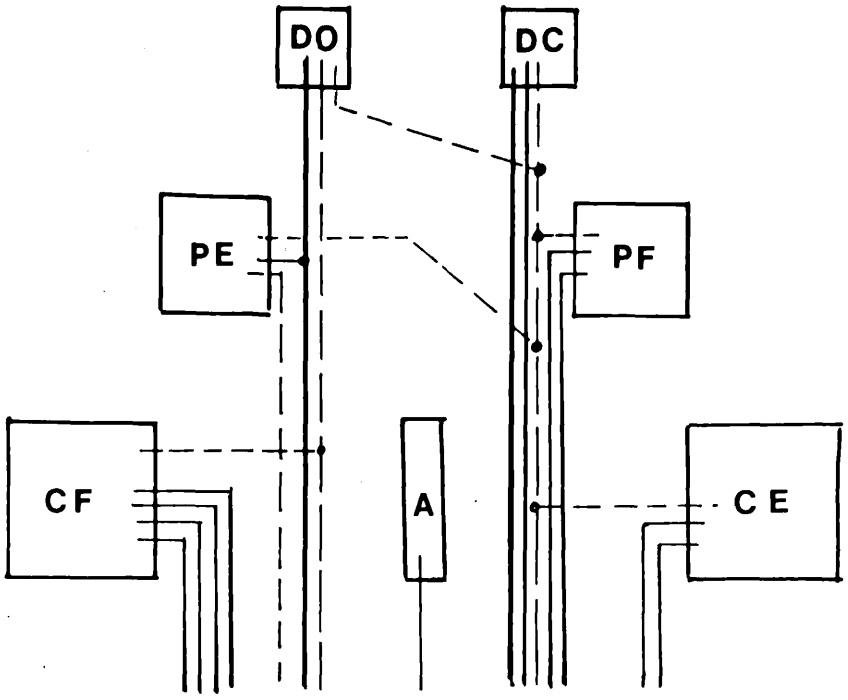
b. Personal observation.
This diagram illustrates the motorneurones of the main coxa and BI muscles identified in the experiments.

CxR = Coxa remotor muscle.
CxP = Coxa promotor muscle.
BI Al = BI Anterior levator muscle.
BI Ad = BI Anterior depressor muscle.
BI Pd = BI Posterior depressor muscle.

Thick lines represent phasic axons, thin lines represent tonic axons.

Fig.6

a.



b.

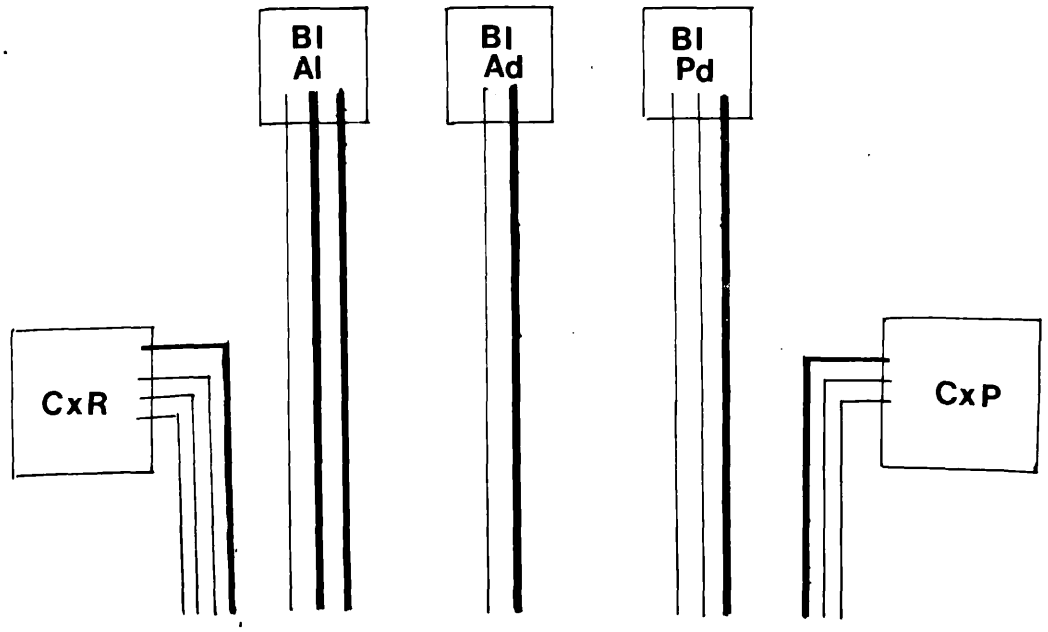


FIGURE 7.

THE COXA REMOTOR MUSCLE, CxR.

This series of recordings illustrates the neuromuscular responses of the CxR to stimulation of two tonic axons.

a,b,c,d: Lower traces; stimulus markers.
Upper traces; intracellular recordings from a typical muscle fibre.

c,f,g: Upper traces; tension monitored from the whole muscle.
Lower traces; ejp responses.

Scale:	Vertical	Horizontal
a,d.	5mV	20 ms
b,e.	5mV	250 ms
c.	20 mV and 1 gm	250 ms
f.	10 mV and 1 gm	250 ms
g.	5 mV and 1 gm	250 ms

a. This trace shows the excitatory junctional potentials, ejp's, in response to a single stimulus delivered to axon 1.

b. These traces demonstrate the facilitation of the ejp's when axon 1 was stimulated at 10, 30 and 40 Hz for 500 ms.

c. These traces show the tension developed in the whole muscle as a response to stimulation of axon 1 at 30, 40 and 50 Hz for 500 ms.

d. This trace shows the larger ejp responses to a single stimulus delivered to axon 2.

e. Stimulation of axon 2 produced a pattern of facilitation which is similar to that produced by axon 1. The axon was stimulated at 10, 20, 30, 40 and 50 Hz for 500 ms.

f. These traces demonstrate the small amount of tension developed in the muscle when axon 2 was stimulated at 10, 30 and 50 Hz for 500 ms.

g. The axon was stimulated at 50 and 100 Hz for 1 s.

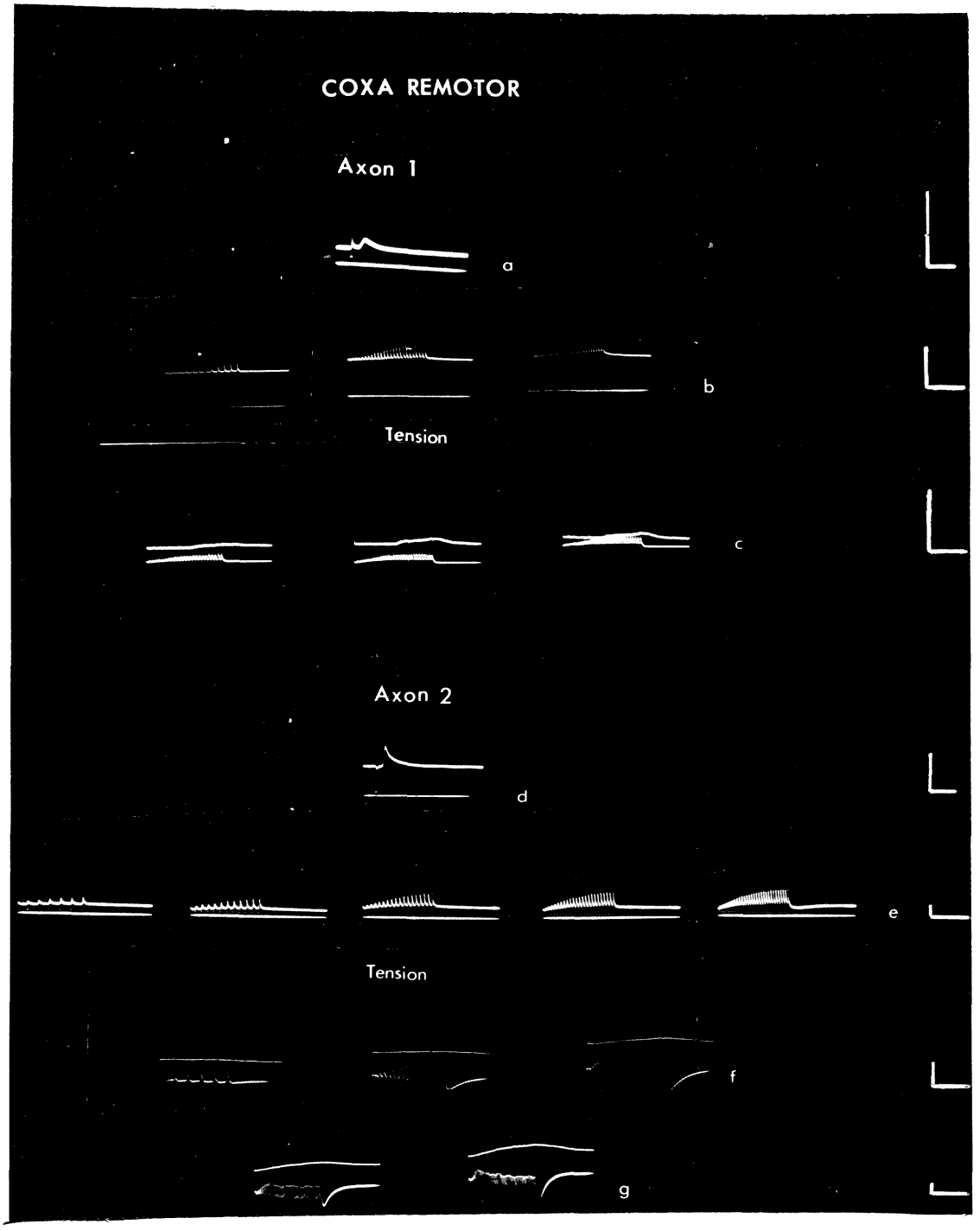

COXA REMOTOR
Axon 1
a
b
Tension
c
Axon 2
d
e
Tension
f
g

FIGURE 8

This series of recordings illustrates the CxR response to stimulation of tonic axon 3.

a to d; Upper traces; ejp responses.
Lower traces; stimulus markers.

e to g; Upper traces; muscle tension responses.
Lower traces; ejp responses.

Scale:	Vertical	Horizontal
a,b.	5 mV	20 ms
c,d.	10 mV	250 ms
e.	20 mV and 1 gm	250 ms
f.	10 mV and 0.5 gm, 1 gm, 2 gm.	250 ms
g.	10 mV and 1 gm.	250 ms

a. This trace shows the superimposed responses when single stimuli are delivered to axons 1,2 and 3.

b. The size of an ejp in response to a single stimulus delivered to axon 3.

c. Axon 3 was stimulated at 10,20,30,40 and 50 Hz for 500 ms. The considerable degree of facilitation can be seen.

d. In a different muscle fibre graded spikes were displayed when the axon was stimulated at 40 and 50 Hz.

e. The axon was stimulated at 40 and 50 Hz for 500 ms. The slow rise time for tension development can be seen.

f. These traces demonstrate the effects of the graded spike responses. The axon was stimulated at 50 Hz in all the records but the gain on the tension monitor was progressively reduced. All show step like rises in tension due to these secondary spike responses.

g. This trace demonstrates the rapid decay of muscle tension when the axon was stimulated at 50 Hz for 1 s.

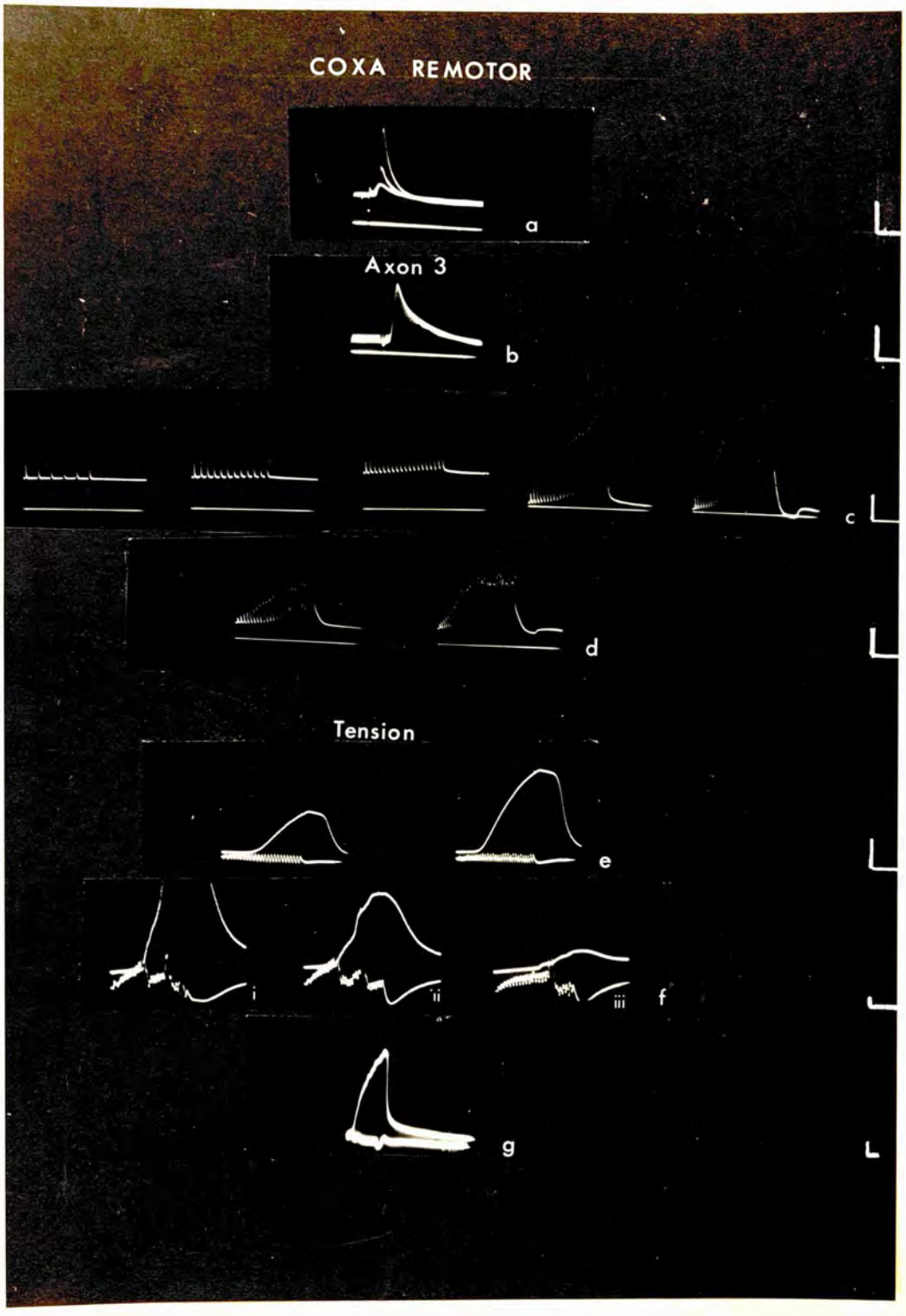

COXA REMOTOR
a
Axon 3
b
c
d
Tension
e
i
ii
iii
f
g

FIGURE 9

This series of recordings illustrates the CxR response to stimulation of its phasic axon.

a to d; Upper traces; ejp responses.
Lower traces; stimulus markers.

e to i; Upper traces; muscle tension responses.
Lower traces; ejp responses (stimulus marker in trace e).

Scale:

	Vertical	Horizontal
a,b.	10 mV	20 ms
c,d.	10 mV	250 ms
e.	1 gm	250 ms
f.	20 mV and 4 gm.	250 ms
g,h.	10 mV and 4 gm.	250 ms
i.	5 mV and 4 gm.	250 ms

a. This trace demonstrates the relative sizes of the ejp's produced by a single stimulus delivered to axons 2,3 and 4 individually.

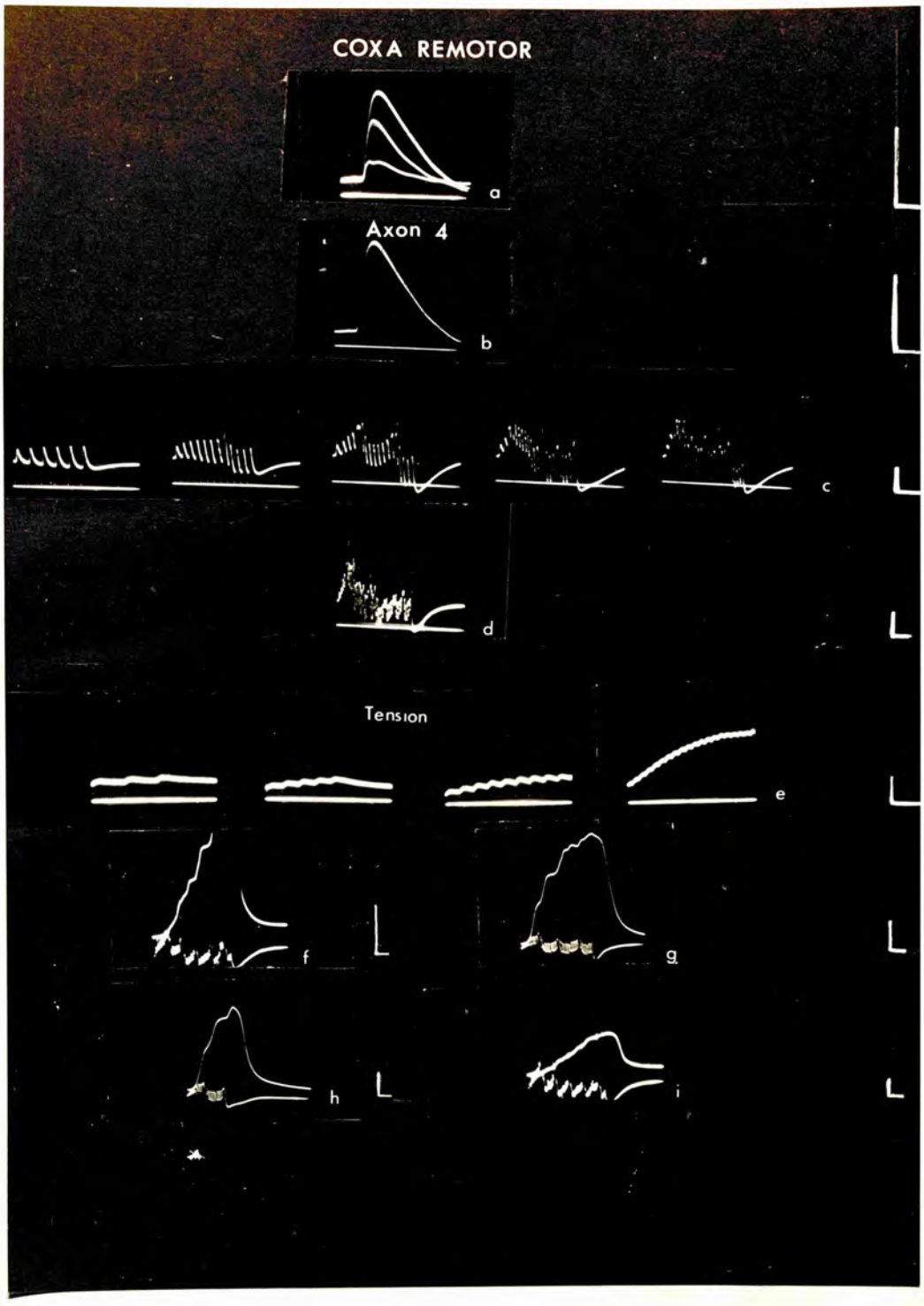
b. This trace demonstrates the large size of an ejp produced by a single stimulus delivered to the phasic axon, axon 4.

c. These recordings demonstrate the feature of secondary spike responses which are readily evoked in the muscle fibres when this axon is stimulated. The stimulation rates were 10,20, 30, 40, and 50 Hz for 500 ms.

d. The axon was stimulated at 50 Hz for 1 s to demonstrate the increasing number of spike responses which occurred when this axon was stimulated at these rates.

e. Twitch responses were demonstrated in the muscle when axon 4 was stimulated at 2,4,5 and 10 Hz.

f to i. These traces show the step like rises in the development of muscle tension due to the graded spike responses of the muscle fibres. The axon was stimulated at 50 Hz for 1 s in f, g and i and 500 ms in h. The gain of the tension monitor was progressively reduced.


COXA REMOTOR
a
Axon 4
b
c
d
Tension
e
f
g
h
i

2. THE COXA PROMOTOR MUSCLE (Figs 10,11 and 12).

The CxP responded to stimulation of the coxa promotor nerve with ejp's of 3 different sizes indicating the presence of at least 3 motor axons. Two produced tonic muscle responses and one produced phasic muscle responses. All 3 motor units were uniformly distributed over the muscle.

Tonic Unit One (Fig 10) Stimulation of axon 1 generated small ejp's, 1 mV, which lasted for 10 ms. The ejp's facilitated considerably with repeated stimulation, (Fig. 10c). The tension rise in the muscle was barely perceptible at rates of stimulation below 50 Hz and even at these frequencies the delay in rise time was 500 ms (Fig. 10e).

Tonic Unit Two (Fig 11) When axon 2 was stimulated the ejp's were larger, 5 mv, and did not show such marked facilitation (Fig. 11a). Some of the fibres displayed secondary spike responses at high stimulation frequencies although the number of these responses rarely exceeded 4 in a 500 ms burst of stimulation (Fig. 11b).

Muscle tension was developed at stimulation frequences above 10 Hz and increased to a tetanic peak at 50 Hz (Fig. 11e). When stimulation was stopped the peak tension was maintained for 250 ms before decay began (Fig. 11e).

Phasic Unit One (Fig.12) Stimulation of axon 3 generated large ejp's 12 mv, which readily produced spike responses to repeated stimulation (Fig. 12c). The sizes of these secondary spikes was 40 to 50 mv.

Single ejp's caused small twitches in the muscle which fused into a steady tension rise when stimulation was increased above 10 Hz, (Fig. 12 d,e). Unlike the CxR muscle, the graded spike responses were not associated with marked increases in muscle tension. Decay from peak tension levels was slow, taking over 600 ms (Fig.12g).

3. THE BI ANTERIOR LEVATOR MUSCLE (Figs 13 and 14).

The Al is innervated by at least 3 axons, one which produces tonic muscle responses and two which produce phasic muscle response. The area of innervation is uniform.

Tonic Unit One (Figs 13 and 14) The ejp's generated by stimulation of axon 1, were small, 1 mV, but facilitated considerably with

FIGURE 10

THE COXA PROMOTOR MUSCLE, CxP.

This series of recordings illustrates the neuromuscular responses of the CxP to stimulation of tonic axon 1.

a,b,c: Upper traces; intracellular recordings from a typical muscle fibre.
Lower traces; stimulus markers.

d,e: Upper traces; tension monitored from the whole muscle.
Lower traces; ejp responses.

Scale:	Vertical	Horizontal.
a,b.	5 mV	20 ms
c.	5 mV	250 ms
d.	5 mV and 1.25 gm	250 ms
e.	5 mV and 1 gm	250 ms

a. This trace demonstrates the relative sizes of the ejp responses produced by single stimuli delivered to axons 1,2 and 3 individually.

b. A single ejp response produced by a single stimulus delivered to axon 1.

c. The axon was stimulated at 10,20 and 30 Hz for 500 ms.

d. These records demonstrate the barely perceptible rise in muscle tension when axon 1 was stimulated at 10 and 20 Hz for 500 ms.

e. When axon 1 was stimulated at 50 Hz for 1 s the muscle displays a slow rise in tension.

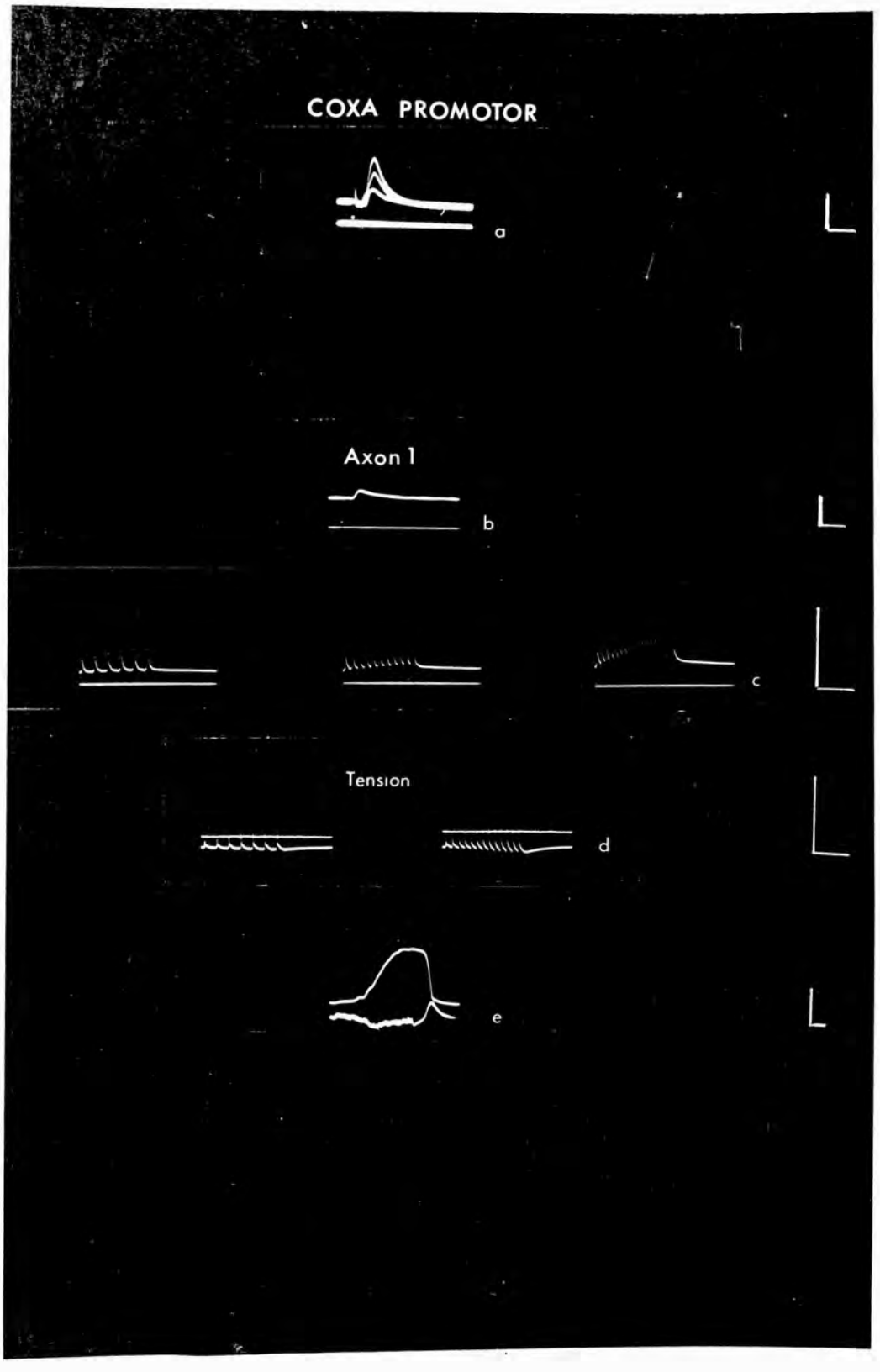

COXA PROMOTOR
a
Axon 1
b
c
Tension
d
e

FIGURE 11

This series of recordings illustrates the CxP responses to stimulation of tonic axon 2.

a,b: Upper traces; ejp responses.
Lower traces; stimulus markers.

c to e; Upper traces; muscle tension responses.
Lower traces; ejp responses.

Scale:	Vertical	Horizontal
	a,b. 10 mV	250 ms
	c to e. 10 mV and 4 gm	250 ms

a. Axon 2 was stimulated at 10,20,30 and 40 Hz for 500 ms.

b. The axon was stimulated at 10,20,30,40 and 50 Hz for 500 ms. These two series of recordings show that some fibres do not develop secondary spike responses (line a) while others generate spike responses at stimulation frequencies of 30 Hz and above (line b).

c. This trace demonstrates the muscle tension response when axon 2 was stimulated at 10 Hz for 500 ms.

d. When the axon was stimulated at 20 and 30 Hz for 500 ms the tension developed in the muscle was greater.

e. The traces demonstrate the delay in tension reduction from peak tetanic levels. The stimulation rates were 30, 40, and 50 Hz for 500 ms.

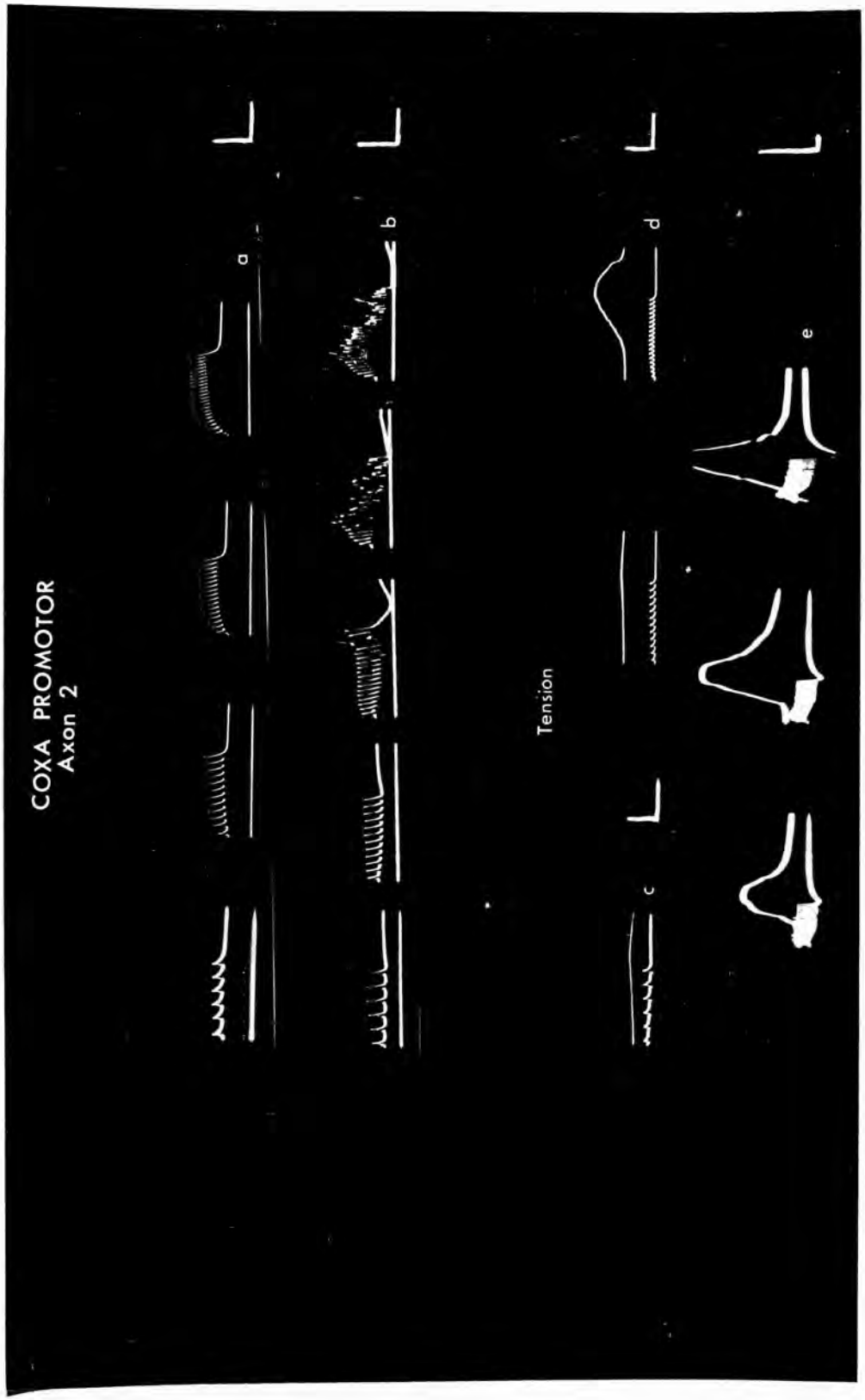

COXA PROMOTOR
Axon 2
Tension
a
b
c
d
e

FIGURE 12

This series of recordings illustrates the CxP responses to stimulation of the phasic axon, axon 3.

a to c; Upper traces; ejp responses.
Lower traces; stimulus markers

d to g; Upper traces; muscle tension responses.
Lower traces; stimulus markers.

Scale;	Vertical	Horizontal
a,b,c.	10 mV	250 ms
d.	20 mV and 1 gm	250 ms
e.	20 mV and 2 gm	250 ms
f,g.	10 mV and 2 gm	250 ms

a. The axon was stimulated at 10,20 and 30 Hz for 500 ms.

b. The generation of graded spikes was demonstrated when the phasic axon was stimulated at 40 and 50 Hz for 500 ms (reduced gain).

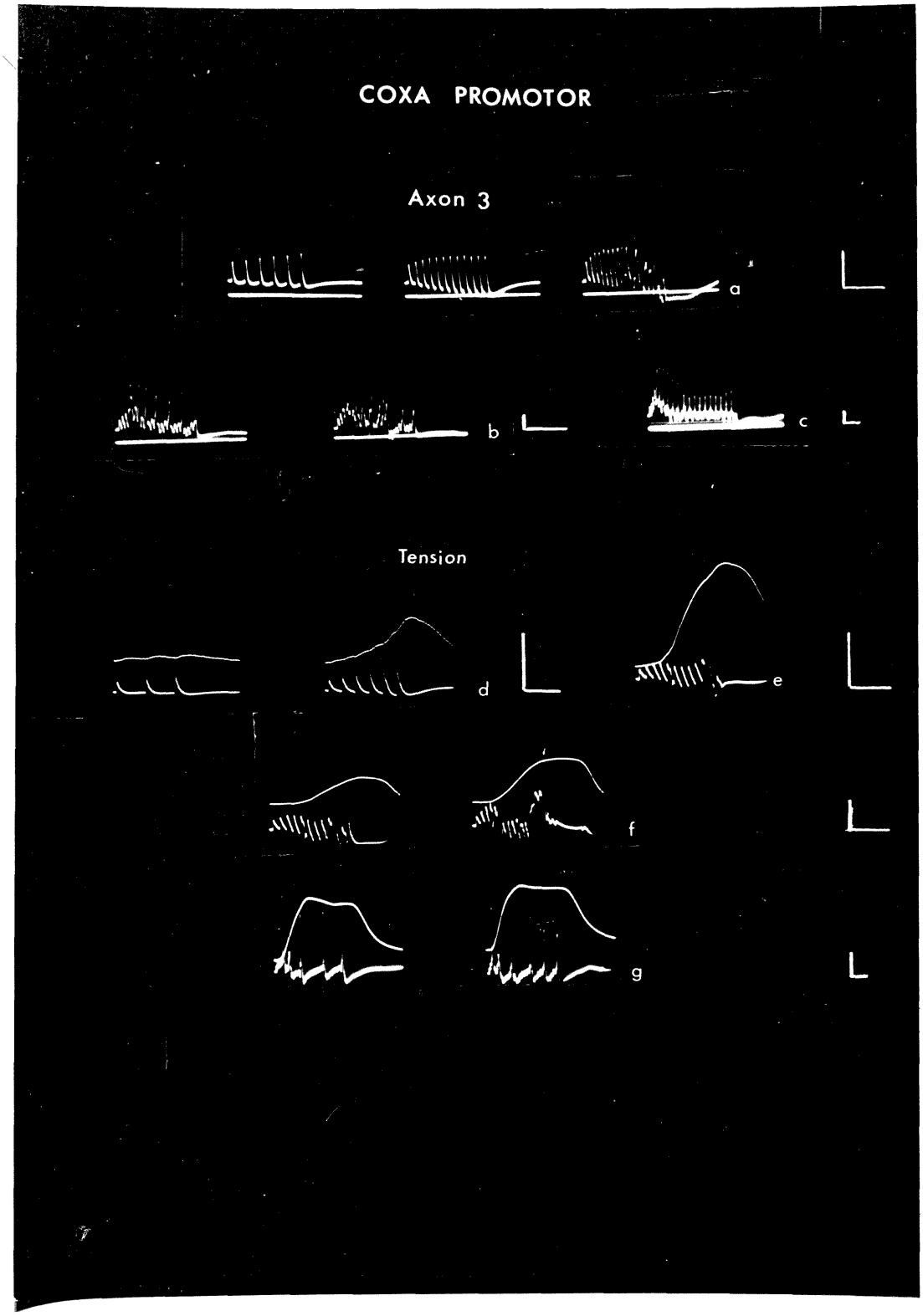
c. This trace shows the numerous graded spike responses which are produced when this axon was stimulated at 50 Hz for 1 s.

d. The axon was stimulated at 5 and 10 Hz for 500 ms. The twitch responses of the whole muscle are demonstrated.

e. The muscle twitches fused when the axon was stimulated at 20 Hz for 500 ms.

f. Stimulation of axon 3 at 20 and 30 Hz for 500 ms produced a smooth rise in muscle tension. This is dissimilar to the irregular rise in CxR muscle tension when its phasic axon was stimulated.

g. When the axon was stimulated at 30 Hz for 1 s there was a slow rise to peak muscle tension. Peak tensions were maintained for a few hundred ms after stimulation had ceased before the beginning of a slow decay rate.


COXA PROMOTOR
Axon 3
a
b
c
Tension
d
e
f
g

repeated stimulation delivered to the axon (Fig.13d). Muscle tension responses were not substantial although when stimulation was stopped there was a delay of 200 ms before the tension began to decay (Fig. 14d).

Phasic Unit One (Figs 13 and 14) When axon 2 was stimulated, larger ejp's, 5 mV, were generated. The second ejp in a series was always smaller than the first but subsequent potentials facilitated (Fig. 13e). Each ejp caused a small twitch in the muscle which fused into a slow but smooth rise in tension at stimulation frequencies of 30 Hz and above (Fig. 14e,f,g).

Tension decay was slow and did not begin until 200 ms after the end of stimulation. (Fig.14g).

Phasic Unit Two (Figs 13 and 14) When axon 3 was stimulated, large muscle spikes, 25 to 30 mV, were produced (Fig.13a). Defacilitation of the spikes was demonstrated which is unlike the responses produced by stimulation of axon 2 (Fig. 13f).

Each twitch contraction caused by stimulation of the axon, was relatively large and clearly visible in the muscle although their time course was slow, over 20 ms (Fig.14a,b,h). Even when stimuli were delivered at rates of 5 Hz, this decay was slow enough to cause a marked step like rise in tension (Fig. 14 i,j). The twitches fused into a smooth rise in muscle tension at stimulation frequencies of 20 Hz and above (Fig. 14 k, l). When the axon was stimulated at high frequencies the muscle tension rose steeply but did not begin to decay until 200 ms after the end of stimulation (Fig. 14m).

4. THE BI ANTERIOR DEPRESSOR MUSCLE (Figs.15 and 16)

The Ad is innervated by at least 2 motor axons. Stimulation of one of these axons produces tonic muscle responses while stimulation to the other produces phasic muscle responses. The tonic innervation is uniform over the muscle while the innervation field of the phasic axon is largely concentrated in the mid region of the muscle.

Tonic Unit One (Fig. 15 a and b) Stimulation of axon 1 generated small ejp's, 3 mV, which did not facilitate to any extent (Fig. 15b). The muscle responded with a steady rise in tension to stimulation of this axon. Peak tetanic tensions were only reached after axon 1 had been stimulated for 750 ms at maximal frequencies. The decay rate of tension was also slow.

FIGURE 13

THE ANTERIOR LEVATOR MUSCLE. A1

This series of recordings illustrates the neuromuscular responses of the A1 to stimulation of the one tonic axon and two phasic axons.

Upper traces; intracellular recordings from a typical muscle fibre.

Lower traces; stimulus markers.

Scale;	Vertical	Horizontal
	a to c; 10 mV	20 ms
	d to f; 10 mV	250 ms

a,b,c; These traces demonstrate the relative sizes of the 3 ejp responses when single stimuli were delivered to axons 1,2 and 3 individually. Axon 1 produces tonic muscle responses and axons 2 and 3 produce phasic muscle responses.

d. This trace illustrates the facilitation of ejp's when axon 1 was stimulated at rates of 10,20,30,40 and 50 Hz for 500 ms.

e. These traces demonstrate that when axon 2 was stimulated, the second ejp produced in a burst of stimulation is always smaller than the first, while succeeding potentials facilitate. The axon was stimulated at 10,20 and 30 Hz for 500 ms.

f. These traces also demonstrate that the first ejp is larger when axon 3 was stimulated, although succeeding potentials did not facilitate. The stimulation rate was 10, 20, 30 and 40 Hz for 500 ms.

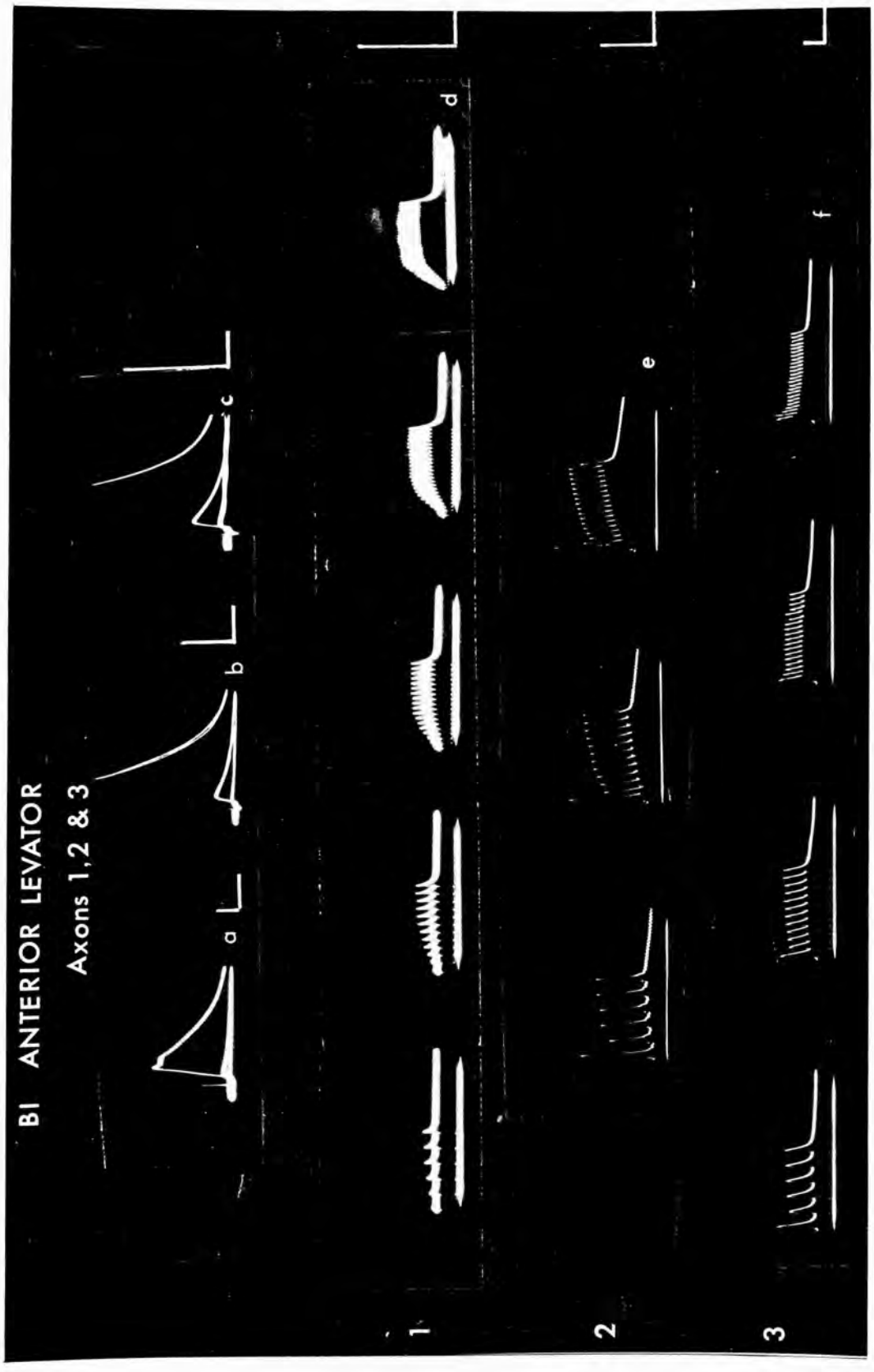

B1 ANTERIOR LEVATOR
Axons 1,2 & 3
a
b
c
d
e
f
1
2
3

FIGURE 14

This series of recordings illustrate the tension responses of the A1.

Upper traces; tension responses monitored from the whole muscle.

Lower traces; ejp responses.

Scale;	Vertical	Horizontal
a,b,e,h.	10 mV and 2 gm	20 ms
c,d.	10 mV and 2 gm	250 ms
f,g.	20 mV and 2 gm	500 ms
i to m.	20 mV and 4 gm	500 ms

a,b. These records demonstrate the muscle tension response produced by single ejp's when axon 1,2 and 3 were stimulated individually. In trace a the responses are superimposed and the time is half that of the recordings in trace b.

c. These traces illustrate the muscle tension responses when the 3 axons were individually stimulated at a frequency of 10 Hz.

d. These traces demonstrate the muscle response when axon 1 was stimulated at 10 and 20 Hz for 500 ms.

e. A single stimulus to axon 2 caused a small twitch in the muscle.

f. When the axon was stimulated at 10 Hz the twitches fused into a gradual rise in tension.

g. These traces illustrate the smooth rise in tension when axon 2 was stimulated at 40 and 50 Hz for 500 ms.

h. This record is comparable to trace e and was due to a single stimulus delivered to axon 3.

i,j. When axon 3 was stimulated at 5 Hz a step like rise in tension was displayed.

k,l. When the period of stimulation to axon 3 was increased to 1s and 500 ms at 10 Hz respectively, the rise in tension fused into a progressive and smooth increase.

m. These traces illustrate the long delay between the end of stimulation and the beginning of tension decay. Axon 3 was stimulated at 10, 30,40 and 50 Hz for 500 ms.

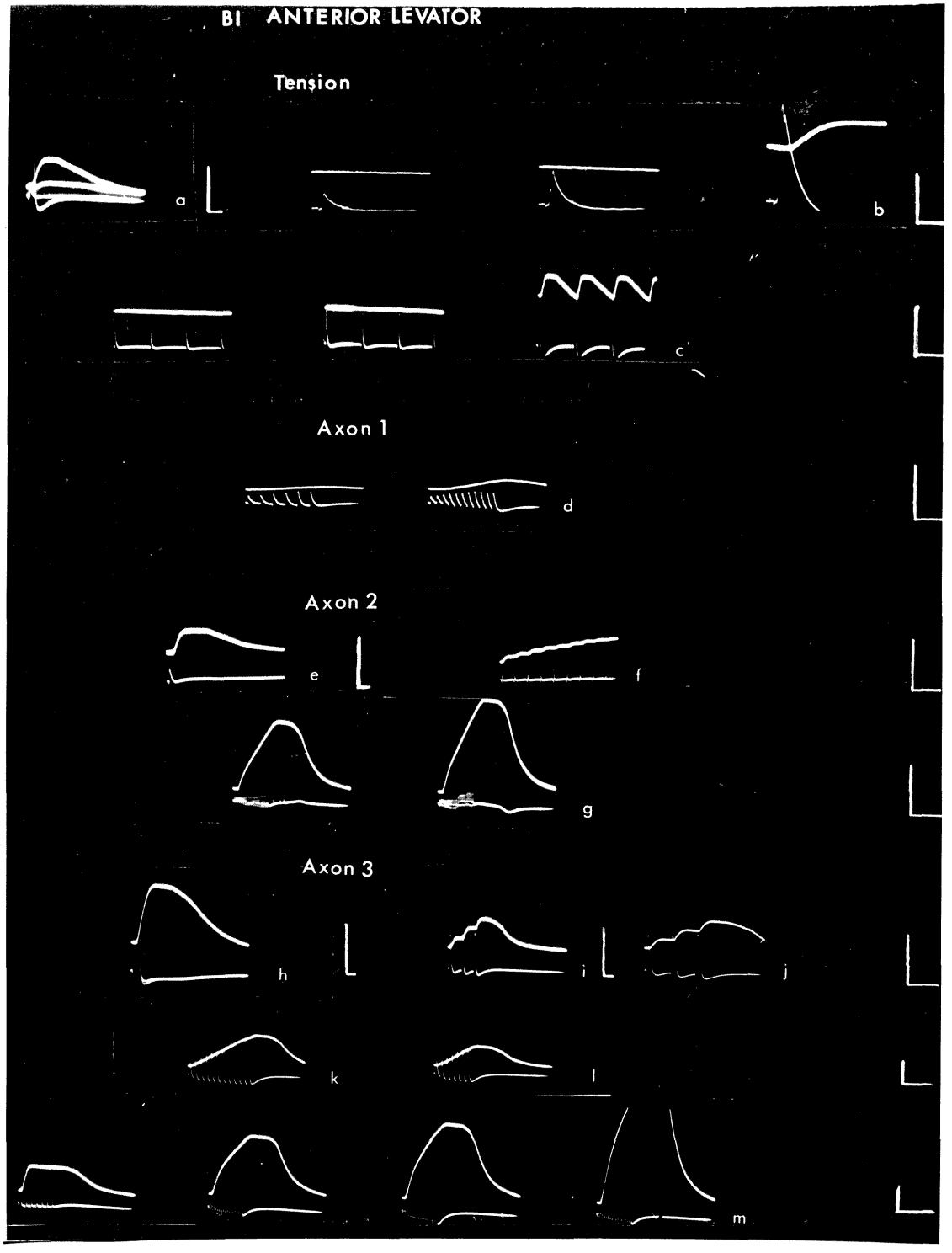

B1 ANTERIOR LEVATOR
Tension
a
b
c
Axon 1
d
Axon 2
e
f
g
Axon 3
h
i
j
k
l
m

FIGURE 15

THE BI ANTERIOR DEPRESSOR MUSCLE: Ad.

This series of recordings illustrates the neuromuscular responses of the Ad to stimulation of the tonic and phasic axons.

Upper traces; intracellular recordings from a typical muscle fibre.

Lower traces; stimulus markers.

Scale;	Vertical	Horizontal
	a,c. 10 mV	20 ms
	b,d,e,f,g. 10 mV	250 ms

a. Tonic axon 1 was stimulated to demonstrate the size of a single ejp response, which was 3 mV.

b. The axon was stimulated at 10,20,30 and 40 Hz for 500 ms. No secondary spike responses were generated.

c. Axon 2 was stimulated to demonstrate the larger phasic ejp response. The ejp responses ranged from 10 to 30 mV.

d. The axon was stimulated at 10,20,30,40 and 50 Hz for 500 ms. This illustrates the secondary spike responses which were evoked at stimulation frequencies of 30 Hz and above.

e. When axon 2 was stimulated at 50 Hz for 1 s a large number of secondary spike responses were produced.

f and g. These traces display the characteristics of post tetanic potentiation. Axon 2 was initially stimulated at 10 Hz. This rate was increased to 50 Hz for 250 ms in trace f and 500 ms in trace g. The rate of stimulation was then reduced back to 10 Hz. The feature of post tetanic potentiation is displayed. Following a high frequency burst of stimulation, succeeding stimulation generated facilitated ejp's.

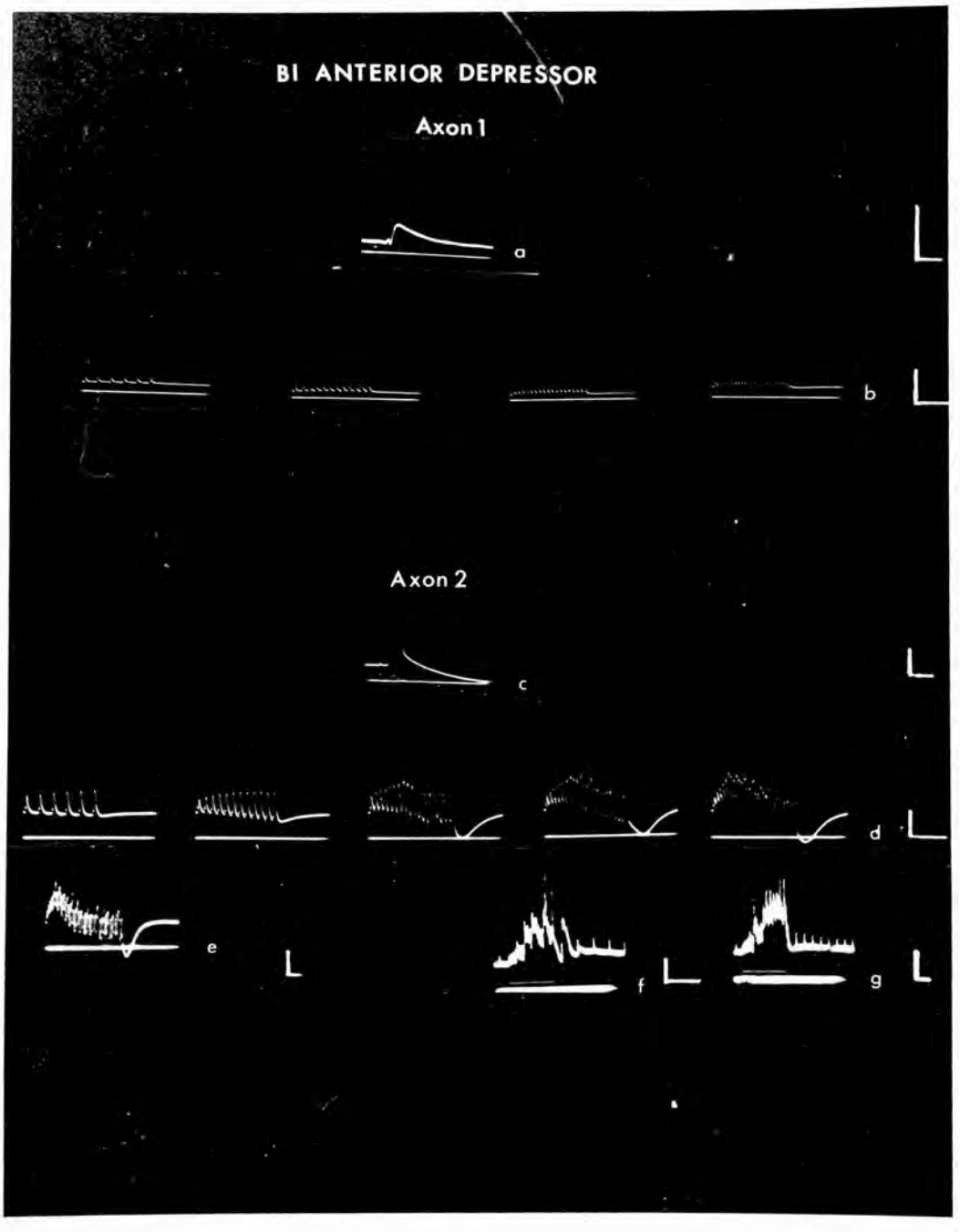

BI ANTERIOR DEPRESSOR
Axon 1
a
b
Axon 2
c
d
e
f
g

FIGURE 16

This series of recordings illustrates the Ad muscle tension responses to stimulation of the phasic axon.

Upper traces; tension responses monitored from the whole muscle.

Lower traces; ejp responses.

Scale;	Vertical	Horizontal
	a,b. 20 mV and 1 gm	250 ms
	c to f.20 mV and 1 gm	250 ms
	g to i.10 mV and 5 gm	250 ms

a and b. Twitches generated by stimulating the axon at 10 Hz are shown in these 2 traces.

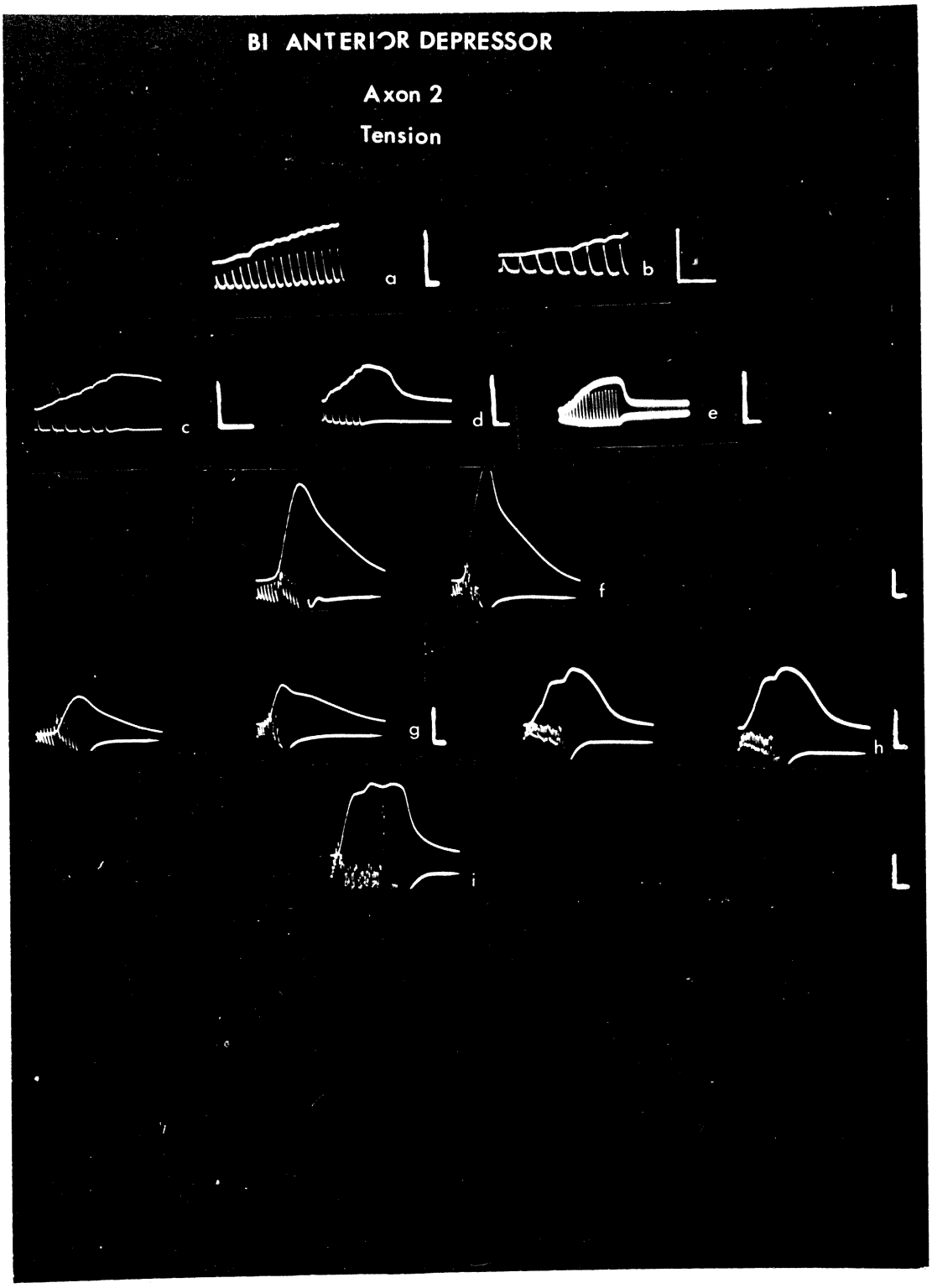
c,d and e. The phasic axon was stimulated at 10 Hz for 500 ms in c, 500 ms in d and 2 s in e.

f. Axon 2 was stimulated at 20 and 30 Hz for 500 ms. The slow tension decay rate is demonstrated.

g. These traces illustrate the above feature at a reduced gain.

h. The axon was stimulated at 50 Hz for 500 ms. Both traces show sudden increases in tension development due to graded spike responses in the muscle fibres.

i. Stimulation of axon 2 at 50 Hz for 1 s quickly produced a tetanic peak of tension which was reached after 300 ms. This was followed by irregular rises in tension due to the graded spike responses.


BI ANTERIOR DEPRESSOR
Axon 2
Tension
a
L
b
L
c
L
d
L
e
L
f
L
g
L
h
L
i
L

Phasic Unit One (Figs 15c to g and 16) Stimulation of axon 2 generated large ejp's which varied from 10 to 30 mV. Graded spike responses were readily produced at stimulation frequencies of 20 Hz and above (Fig. 15d). This unit displayed the characteristics of post-tetanic potentiation (Fig. 15f and g.).

Muscle twitches were displayed when axon 2 was stimulated at low frequencies. The twitches fused into a fast rise in tension at stimulation rates of 10 Hz and above (Fig.16 a to f). The rise time to peak tension levels, 150 to 200 ms, was much faster than the decay time to zero tension which could take over 1 s (Fig. 16 f,g).

5. THE BI POSTERIOR DEPRESSOR MUSCLE, Pd1 (Figs. 17,18 and 19).

The main division of the Posterior depressor muscle, Pd1 is innervated by at least 3 motor axons, two produced tonic responses in the muscle and one produced phasic muscle responses.

Tonic Unit One (Fig. 17) The muscle responded with small ejp's, 1 mV, when axon 1 was stimulated. The ejp's caused only slight development of muscle tension except at very high frequencies of stimulation (Fig.17c).

Tonic Unit Two (Fig. 18) Stimulation of axon 2 produced larger ejp's, 6 mV, which facilitated considerably with repeated stimulation to the axon, (Fig. 18 b). At high levels of stimulation, graded spike responses were generated although there was rarely more than one such response in a 500 ms period of high frequency stimulation.

Muscle tension was developed at rates of 20 Hz and above when axon 2 was stimulated (Fig. 18 c). The occasional spike response from different muscle fibres caused an irregular rise in tension at high rates of stimulation.

Phasic Unit One (Fig. 19) When axon 3 was stimulated large ejp's, 12 mV, were generated which lasted for 30 to 40 ms (Fig. 19 a). A graded spike response may be generated after only 100 ms of high frequency stimulation (Fig. 19c). If high stimulation rates were maintained the interval between successive spikes decreased (Fig. 19 d,e).

The muscle responded with small twitches which fused into a steadier and steep rise in tension at stimulation frequencies of 20 Hz and above (Fig. 19 g). The rise to peak tension levels was

FIGURE 17

THE POSTERIOR DEPRESSOR MUSCLE: Pd1

This series of recordings illustrates the neuromuscular responses of Pd1 to stimulation of tonic axon 1.

a,b; Upper traces; intracellular recordings from a typical muscle fibre.
Lower traces; stimulus markers.

c. Upper traces; tension responses recorded from the whole muscle.
Lower traces; ejp responses.

Scale;	Vertical	Horizontal
a.	2 mV	20 ms
b.	5 mV	250 ms
c.	10 mV and 1 gm	250 ms

a. This trace demonstrates the small ejp, 1 mV, produced by a single stimulus delivered to tonic axon 1.

b. These traces demonstrate the facilitation of the ejp's when the axon was stimulated at 10,20,30,40 and 50 Hz for 500 ms.

c. These traces show the slight rise in muscle tension when the axon was stimulated at 10,20 and 30 Hz for 500 ms.

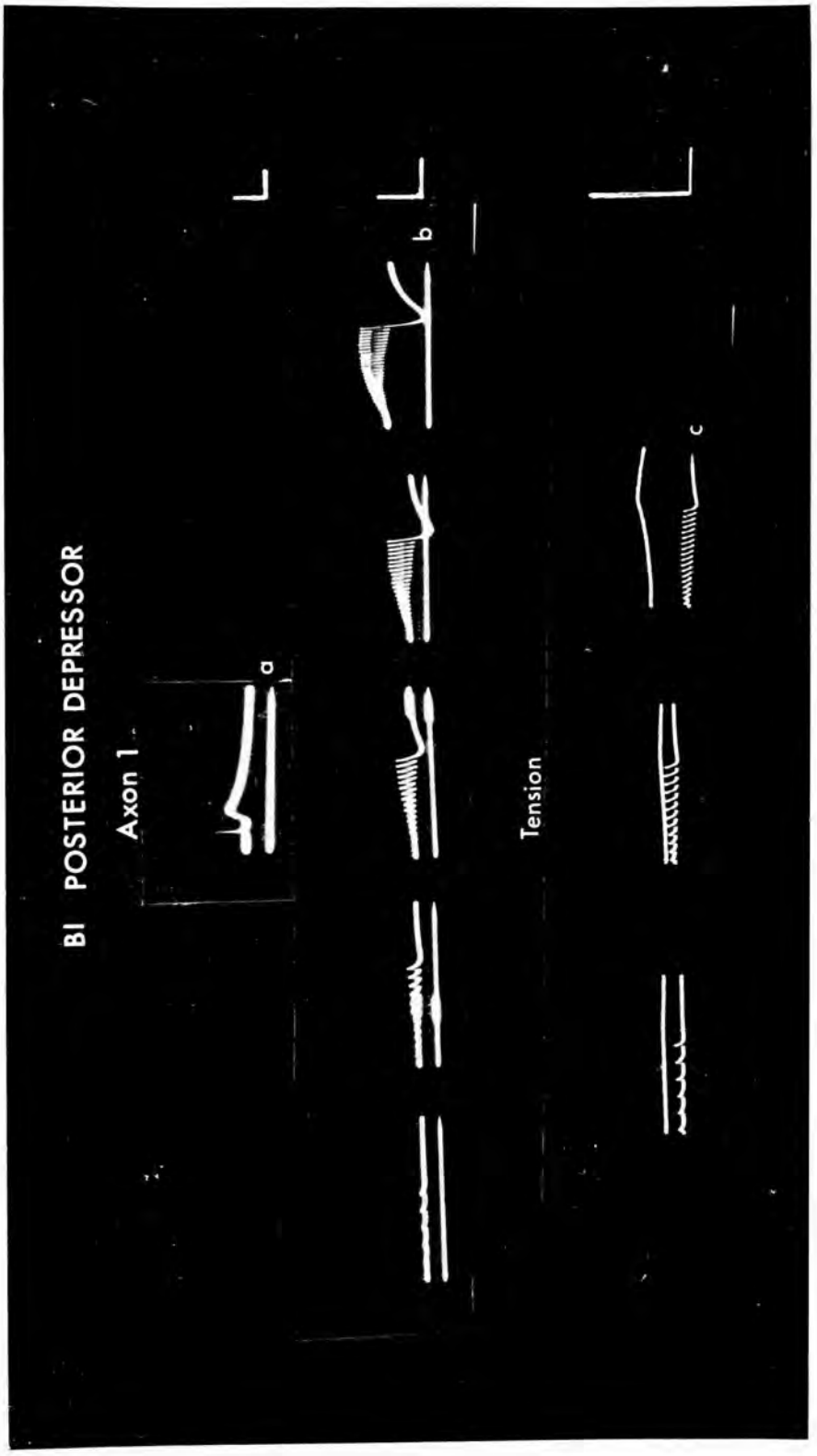

BI POSTERIOR DEPRESSOR
Axon 1
a
b
c
Tension

FIGURE 18

This series of recordings illustrates the neuromuscular responses of Pd1 to stimulation of tonic axon 2.

a,b; Upper traces; ejp responses
Lower traces; stimulus markers.

c to e; Upper traces; muscle tension responses.
Lower traces; ejp responses.

Scale;	Vertical	Horizontal
a.	5 mV	20 ms
b.	5 mV	20 ms
c.	10 mV and 1 gm	250 ms
d.	10 mV and 2 gm	250 ms
e.	10 mV and 4 gm	250 ms

a. This trace demonstrates the large ejp response produced by a single stimulus delivered to axon 2.

b. The axon was stimulated at 10,20,30 and 40 Hz for 500 ms.

c. The tension responses due to stimulation rates of 10,20 and 30 Hz for 500 ms is demonstrated. The muscle developed sudden and considerable tension at frequencies of 20 Hz and above.

d. The axon was stimulated at 30 and 50 Hz for 500 ms. The sharp increase in tension with increasing stimulation rate is demonstrated. Small irregular rises indicate the presence of graded spike responses elsewhere in the muscle.

e. When stimulated at 50 Hz for 2 s the muscle responded with an irregular but increasing development of tension.

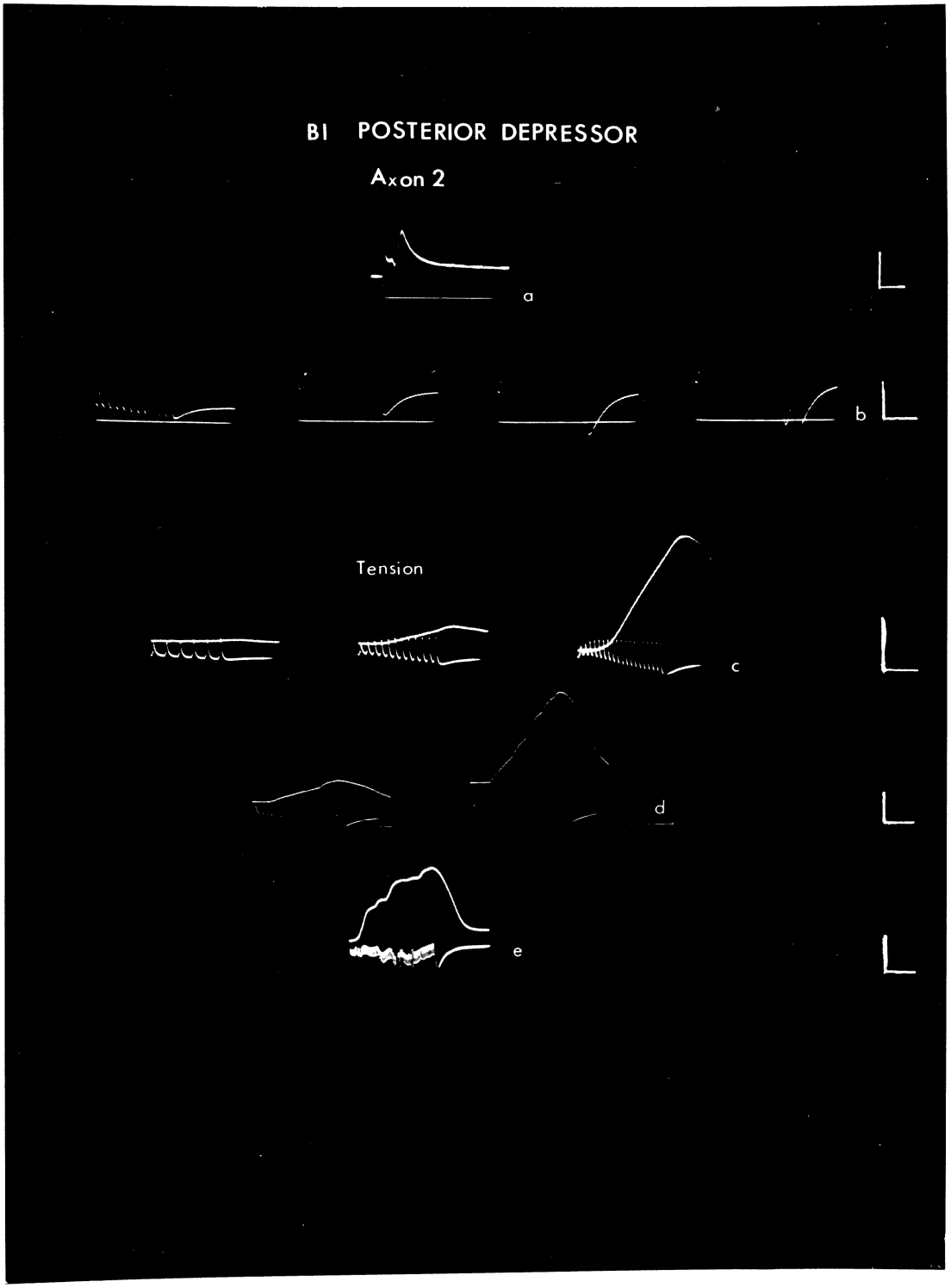

B1 POSTERIOR DEPRESSOR
Axon 2
a
b
Tension
c
d
e

FIGURE 19

This series of recordings illustrates the neuromuscular responses of Pd1 to stimulation of the phasic axon, axon 3.

a to e; Upper traces; ejp responses.
Lower traces; stimulus markers.

f to j; Upper traces; muscle tension responses.
Lower traces; ejp responses (stimulus marker in trace)

Scale:	Vertical	Horizontal
a.	10 mV	20 ms
b.	10 mV	250 ms
c.	10 mV	175 ms
d,e.	20 mV and 1 gm	250 ms
f,g.	20 mV and 5 gm	250 ms
h,i.	5 mV and 5 gm	250 ms
j.	5 gm	250 ms

a. This trace demonstrates the large size of an ejp response, 12 mV, produced by a single stimulus delivered to axon 3.

b. The axon was stimulated at 10,20,30,40 and 50 Hz for 500 ms. The graded muscle spike responses were readily generated. The time taken to produce these responses occured progressively earlier as the repetition rate was increased.

c and d. The axon was stimulated for 100,200,300,400 and 500 ms at 100 Hz. The traces demonstrate that at this frequency of stimulation a secondary spike response can be generated after only 100 ms.

e. When the axon was stimulated at 100 Hz for 1s, the fibres responded with an increasing number of secondary spikes.

f. The muscle responded with small twitches when the phasic axon was stimulated at 10 Hz.

g. The twitches fused into a steady rise in tension at stimulation frequencies of 20 and 30 Hz.

h and i. These traces illustrate the muscle tension response when the phasic axon was stimulated at 50 Hz for 500 ms and 1 s respectively. The graded spike responses in the muscle fibres produced extra twitches in the increasing tension. Rapid decay in tension from peak to zero levels are also demonstrated.

j. The axon was stimulated at 200 Hz for 1 s. This trace illustrates the fast decay rate from peak tension to zero.

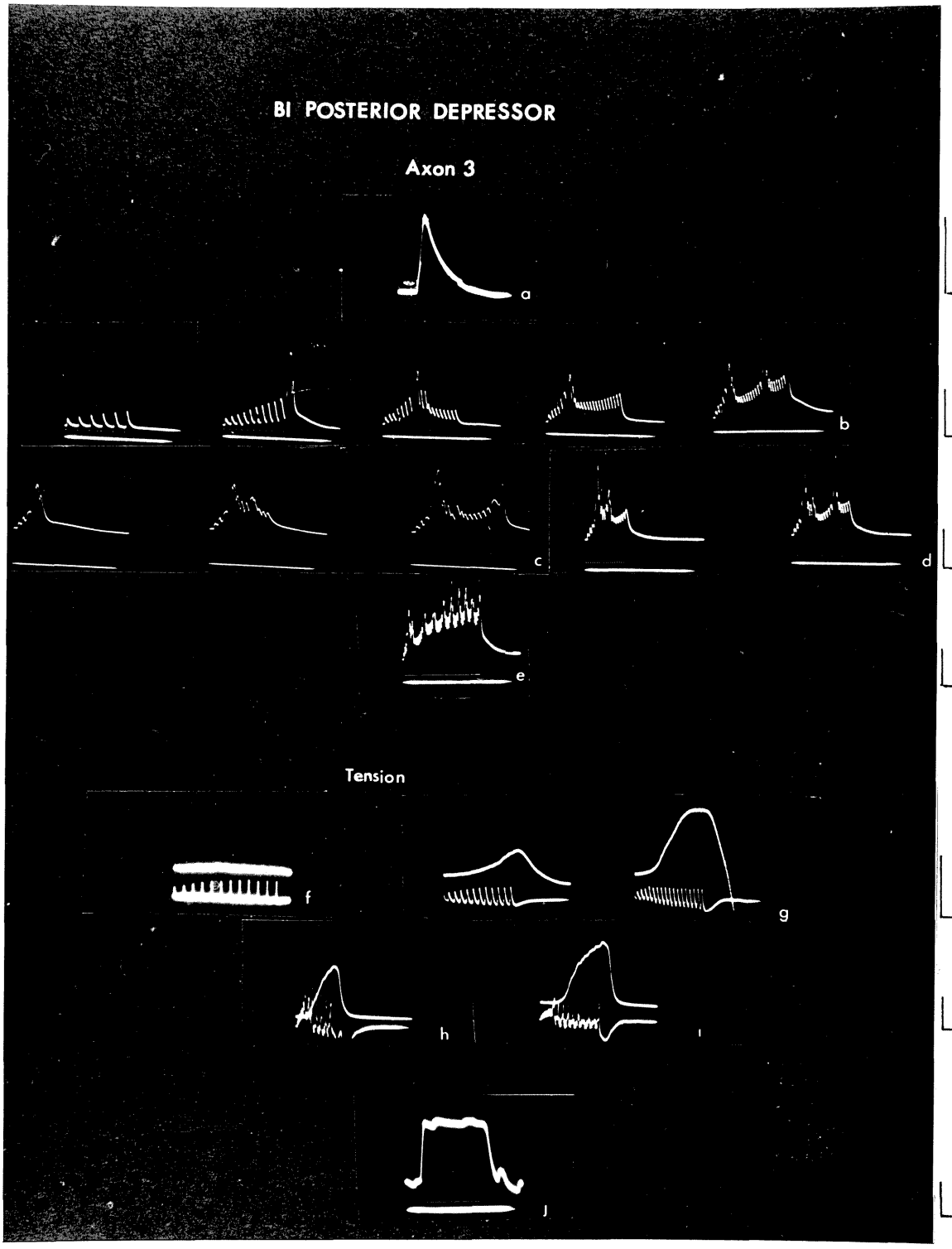

BI POSTERIOR DEPRESSOR
Axon 3
a
b
c
d
e
Tension
f
g
h
i
j

FIGURE 20

THE BI POSTERIOR DEPRESSOR MUSCLES: PdH3, PdH4, PdH5, PdH6.

This series of recordings illustrates the neuromuscular responses of the muscles attached to the heel shaped tendon of the Posterior depressor muscle. These are the anteriorly attached muscles PdH3 and PdH4 and the posteriorly attached muscles PdH5 and PdH6.

Upper traces; intracellular recordings from a typical muscle fibre.

Lower traces; ejp responses.

Scale;	Vertical	Horizontal
a,b,c,d,f.	2 mV	20 ms
c,e,g,h.	2 mV	250 ms

a. This trace demonstrates the relative sizes of the ejp's of the anteriorly attached Pd heel muscles, PdH3, and PdH4, produced by a single stimulus delivered to axons 1 and 2 individually.

b. This trace demonstrates the ejp response, 4 mV, produced by a single stimulus delivered to axon 1.

c. Axon 1 was stimulated at 10,20,30,40 and 50 Hz for 500 ms.

d. This trace demonstrates the ejp response, 6 mV, produced by a single stimulus delivered to axon 2.

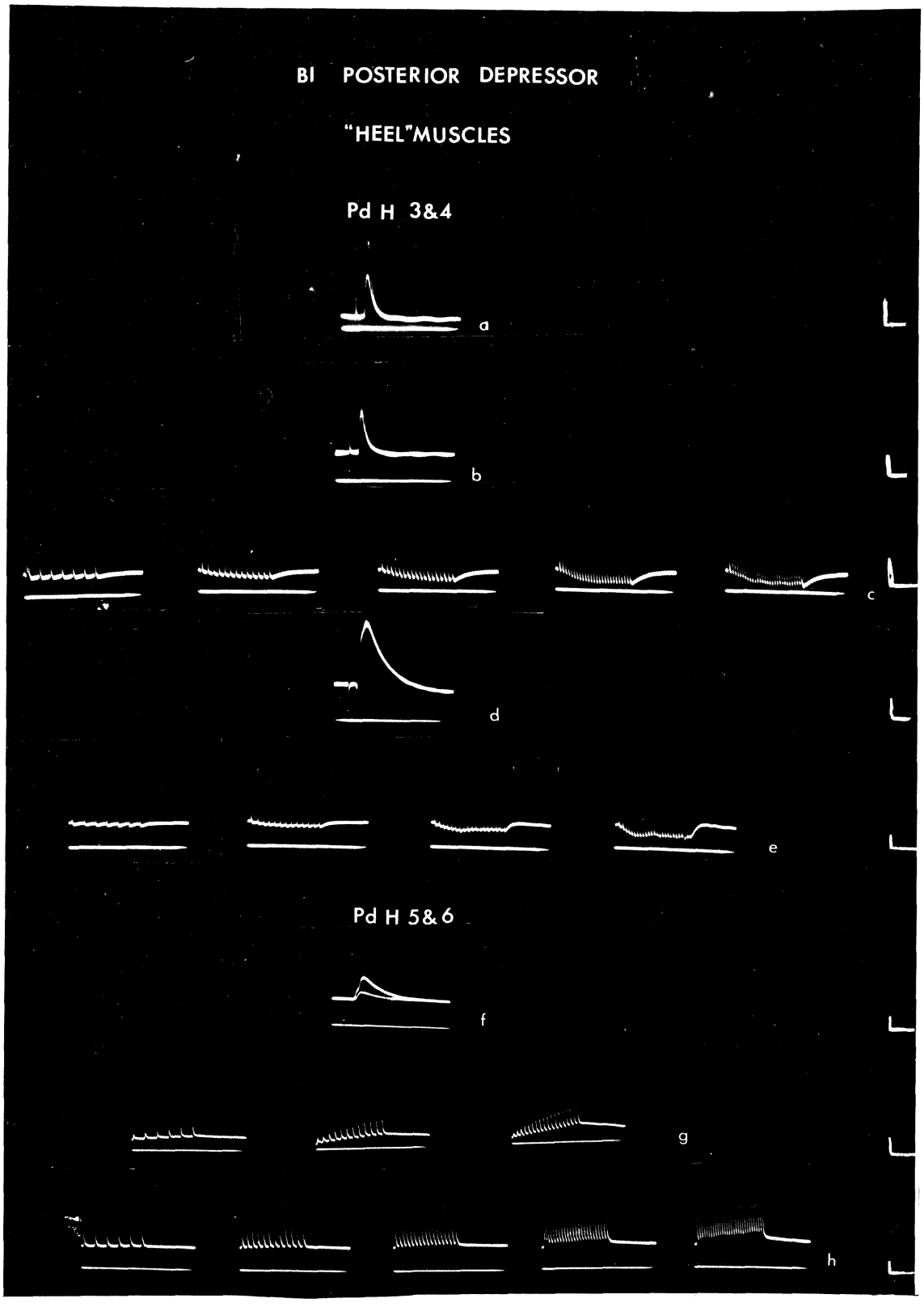
e. Axon 2 was stimulated at 10,20,30 and 40 Hz for 500 ms. These traces indicated that ejp's do not facilitate.

f. This trace indicates the relative sizes of the ejp's of the posteriorly attached Pd heel muscles, PdH5 and PdH6, produced by a single stimulus delivered to axons 1 and 2 individually.

g. Axon 1 was stimulated at 10,20,and 30 Hz for 500 ms. Thesetraces demonstrate the facilitation of the ejp's.

h. Axon 2 was stimulated at 10,20,30,40 and 50 Hz for 500 ms. These traces demonstrate that when this axon was stimulated the ejp's did not display such marked facilitation as that produced by axon 1.

CHAPTER 3 FIGURE 20



rapid, 350 ms, but the decay was even faster, 200 ms (Fig.19 i,j). Once peak tetanic tension was reached it could be maintained throughout stimulation and decayed almost instantly stimulation was stopped (Fig. 19 j). As demonstrated in other muscles, the graded spike responses increased the tension that had developed in the muscle. As more spikes were produced, greater levels of muscle tension were developed (Fig. 19 h,i).

6. THE BI POSTERIOR DEPRESSOR MUSCLES PdH3 and PdH4 (Fig.20a to e)

These muscles are innervated by at least 2 motor axons which produced tonic muscle responses. Stimulation of axon 1 produced small ejp's, 4 mV, while stimulation of axon 2 produced larger ejp's, 6 mV. Faciliation of ejp's was not demonstrated when either axon was stimulated.

7. THE BI POSTERIOR DEPRESSOR MUSCLES PdH5 and PdH6 (Fig.20f to i)

These muscles are also innervated by at least 2 motor axons which produced tonic muscle responses. Stimulation of axon 1 produced small ejp's, 2 mV, which facilitated with repeated stimulation (Fig. 20g). Axon 2 generated larger ejp's, 4 mV, which did not display such marked facilitation (Fig. 20i).

Since selective stimulation caused contraction of either the anterior or the posteriorly attached heel muscles, it is unlikely that they are commonly innervated.

DISCUSSION

Although no specialized skeletal structure or muscle types were found in the coxal and BI complex of the cheliped, a number of features were observed which may have a relevance when considering the method of operation of a fast strike. The most significant feature was the positions of the muscle origins and insertions. Some of the BI muscles are unusual in that they pass through the coxa and originate in the thorax. This will influence their mechanical action, and contraction of these muscles must not only move the BI segment but may also affect the position of the coxa.

Another significant muscular modification is the division of the Posterior depressor muscle into 1 large and 5 small muscle groups together with its possession of a flexible link between the main muscle and the tendon insertion. Contraction of the small subdivisions is likely to have little effect on depression of the BI. Indeed in this respect they would almost be superfluous as

TABLE TWO.

THE NEUROMUSCULAR RESPONSES OF THE 5 MAIN COXAL AND BI MUSCLES

MUSCLE	AXON	MOTOR UNIT RESPONSE	EJP	MUSCLE PROPERTIES	MUSCLE TENSION RESPONSE	
					CHARACTER	DECAY.
COXA REMOTOR	1	Tonic	1 mV		Slow rise	Slow
	2	Tonic	3 mV		Slow rise	Slow
	3	Tonic	6 mV	Few graded spike responses	Fast rise	Fast
	4	Phasic	12 mV	Graded spike responses	Twitches and fast rise	Very fast
COXA PROMOTOR	1	Tonic	1 mV		Slow rise	Slow
	2	Tonic	5 mV	Few graded spike responses	Slow rise	Slow
	3	Phasic	12 mV	Many graded spike responses	Twitches and slow rise	Slow
BI ANTERIOR LEVATOR	1	Tonic	1 mV		Slow rise	Slow
	2	Phasic	5 mV	1st ejp larger	Twitches and slow rise	Slow
	3	Phasic	30 mV	Muscle spikes	Twitches and slow rise	Slow
BI ANTERIOR DEPRESSOR	1	Tonic	3 mV		Slow rise	Slow
	2	Phasic	30 mV	Many graded spike responses	Twitches and fast rise	Very slow
BI POSTERIOR DEPRESSOR, Pd1	1	Tonic	1 mV		Slow rise	Slow
	2	Tonic	6 mV	Few graded spike responses	Slow rise	Slow
	3	Phasic	12 mV	Many graded spike responses	Twitches and fast rise	Very fast

there are two other large depressor muscles and a smaller one. It would seem more likely that they influence the mechanical action of Pd1. This view is supported by the alignment of the heel muscle fibres. Contraction of PdH3 and PdH4 would tilt the heel anteriorly, the reverse being caused by contraction of PdH5 and PdH6. The fibres of Pd2 are similarly ill-aligned for depression, being almost at right angles to the tendon blade. Contraction of these fibres would pull the tendon blade laterally. As the Posterior depressor muscle has such a complex form it is possible that it also has a more complex function than simply depression of the limb. Alterations in muscle tension of the minor divisions would alter the direction of force developed by the large Pd1 and possibly alter its mechanical action.

The fast strike cannot be due to neuromuscular specializations. There are no fast muscles equivalent to the antennal remotor of Homarus (Mendelson, 1969), for example. This would further indicate that energy storage is necessary before the strike is released. However the muscles show two modifications which may be used to produce a fast strike. Firstly all of the main muscles, except for the Al, can generate large secondary spike responses. This will have a considerable increase on the amount of tension developed by the muscles. Secondly all the main muscles receive at least one phasic axon which may be introduced to generate sudden twitch responses in the muscles and therefore also increase muscle tension levels.

The CxP has a slow tension rise time before peak values are reached. This would indicate that it must build up tension before a strike. The rapid promotion of the cheliped could not be caused solely by relaxation of the CxR, followed by contraction of the CxP because the time in which the strike occurs, 30 to 60 ms, is far too short. The CxP displays a latency to peak tension of 300 to 400 ms even at the highest rates of stimulation. Pd1 also has a slow tension rise when the tonic axons are stimulated which again indicates that the rapid depression of the limb could not be caused simply by relaxation of the Al and tonic contraction of the Pd. There must either be prior development of muscle tension and possibly also the recruitment of the phasic axon.

Examinations of the anatomy and physiology of the muscles have not provided any obvious explanation of how the fast strike is achieved. There are a number of muscular properties which when considered together with the geometry of this region, may explain how the rapid strike is performed. In the next section the interaction between muscles and joints of the coxal and BI complex is examined in detail.

CHAPTER 4

THE MECHANICS OF THE T-Cx and Cx-BI JOINTS OF THE CHELIPED

INTRODUCTION

The limbs of arthropods have been specialised in numerous ways to serve roles other than normal locomotion. Many of these roles involve rapid or forceful movements. This had led to alterations of the muscles and joints which control these limbs. An example of such a modification on a large scale is shown in pterygote insects in which the anterior and posterior tergo-coxal muscles function both in walking and in flight. These muscles act synergistically in flight, elevating the wings, but antagonistically in locomotion for protracting and retracting the limb (Wilson, 1962).

Modifications for fast movements or unusual roles are not limited to the insects. Such changes have occurred several times in crustaceans. An example of specialization of muscles for fast movements is shown in some swimming crabs. In Portunus sanguinolentus, the last pair of walking legs are modified into broad paddles and are used independently in slow to medium speed swimming but are synchronized in rapid escape swimming. In these limbs the muscle which produces the power strokes, the BI levator, is specialized physiologically to allow for these varations in speed (Hoyle and Burrows, 1973). There are three distinct groups of muscles comprising white, light pink and deep pink coloured fibres. Each group is separately innervated and have different physiological properties. The white fibres produce rapid twitch contractions and are used only in fast swimming and escape responses. The membrane responses of the deep pink fibres range from complete electrical inexcitation to graded electrogenesis. However, their contractions are slow and they are probably used for slow swimming and maintenance of limb position. The light pink fibres range in responses from ones which can produce twitches, to others which produce only graded responses and slower contractions. The light pink fibres provide the main thrust for swimming. By recruitment of different numbers of the four axons supplying the light pink fibres, a wide range of motor responses are available, and provide this group with the capability to be used in both swimming and escape. For example, during slow swimming only two axons are active but in rapid escape, four axons which innervate the light pink fibres, fire.

Rapid and repetitive movements are achieved without muscle specializations in the different gaits of Ocypode ceratophthalma. This crab reaches extremely high speeds of movement on land. It was found that a maximum speed of 2.1 m/s can be achieved (Burrows and Hoyle, 1973).

Analysis of electromyograms recorded during fast running indicated that the crabs cannot move in a normal push-pull movement, that is pushing with the trailing legs and pulling with the leading legs. Instead it was found that the crab travels along in a leaping movement which increases the effective length of the steps.

In some cases muscles serve dual functions. In Carcinus maenas, for example, the BI Anterior levator muscle levates the limb during locomotion and also provides the force for autotomy of the limb. This dual function is regulated by the Posterior levator muscles, of which there are two groups in each of the walking legs (McVean and Findlay, 1976). Contraction of one of these groups, termed PPL, is synergistic with the Anterior levator and aids levation. Contraction of the other group, RPL, switches the action of the Anterior levator into its second function. The force of the Anterior levator is now directed onto a cuticular plug which spans the limb breakage plane and causes autotomy (McVean and Findlay, 1976).

Thus by merit of their separate insertions on the BI, these two Posterior levator muscles have quite different functions, RPL aids in autotomy and PPL aids in limb levation. The position of PPL is further adapted. It inserts onto the arthrodial membrane overlying RPL. Contraction of PPL prevents the RPL from rotating and so discourages accidental autotomy.

Rapid and sudden movements may be achieved by specializations to the geometry of the joints or muscles involved. In the locust jump, specializations to both are used. The tibia and femur segments of the hind limbs of locusts have been elongated which improves the performance of a jump. The metathoracic extensor tibiae muscle is greatly increased in volume and altered in shape relative to the equivalent muscles in the pro- and mesothoracic legs. The muscle fibres are short and pinnate, a situation which enables a muscle to develop a large force along its tendon (Alexander, 1968). However this alone would not be sufficient to allow the locust to jump as far as it does without the concurrent skeletal modifications to the limb.

The geometry of the joint gives the small tibia flexor muscle a large mechanical advantage over the extensor when the tibia is fully flexed (Heitler, 1974). The mechanical advantage of the tibia flexor decreases rapidly as the joint extends. This means that any residual flexor tension does not slow the movement. In addition to this mechanical advantage ratio a second mechanism operates when the tibia is fully flexed. There is a femoral projection, Heitler's lump, which acts as a locking

device to hold the tibia flexed against the developing extensor muscle tension. As the tibia is flexed, the flexor tendon slides onto either side of the lump. This locks the tibia against the femur and considerable extensor tension can be developed without the tibia moving (Heitler, 1974).

Skeletal modifications which allow isometric tension development are used in the strike action of Squilla (Burrows, 1969). As previously described, the mantis shrimp, Squilla, has a greatly enlarged raptorial second thoracic limb which is used to spear prey. The physiological basis of this behaviour is described in Chapter 2. Further investigation into this behaviour showed that the neuromuscular physiology of the muscles involved were not specially adapted in any way for rapid movements (Burrows and Hoyle, 1972), indeed it was found that the muscles are not specialized for fast contractions as may be expected, but for slow contractions. The largest extensor muscle, for example, takes 700 ms to reach peak tetanic tension and 1 s to relax from this.

In the case of snapping shrimps a variety of modifications have been developed allowing rapid movements. These include skeletal modifications, alterations of geometry of joints and the adaptation of muscle insertions. Shrimps of the family Alpheidae have one cheliped which is greatly enlarged and can be closed with great force. Rapid closure of the large cheliped causes a jet of water to be expelled from a socket between the dactylus and propus. A loud snap occurs at the same time. This behaviour is used in aggression and defence.

In Alphaeus californiensis skeletal modifications have facilitated this behaviour. This shrimp has extremely well matched discs located on the dactylus and propus. These stick to each other by cohesive forces of the layer of water between the surfaces of the two discs. When the dactylus opener muscle contracts, the claw of snapping cheliped is cocked open (Ritzmann, 1973). A large amount of force can be developed in the dactylus closer, which is excited by a stream of high frequency nervous impulses. This excitation continues until the force holding the two discs together is overcome. When this point is reached the dactylus snaps shut and excitation to the closer ceases (Ritzmann, 1974).

In Alphaeus heterochelis the snapping behaviour is achieved by an entirely different means. In this shrimp the two discs are much smaller than those of A. californiensis. The discs can stick together but only a small force is needed to separate them. They certainly do not provide enough force to counter tension which may develop to in the closer. When A. heterochelis fully opens the dactylus, the insertion of the closer muscle apodeme is pulled up and lifted over the P-D pivot point, around

which the dactylus closes. Therefore contraction of the closer will not cause the dactylus to close. Instead closer contraction simply pulls the dactylus further against the propus. This means that the claw is effectively locked open. A small projection lies on the ventral part of this closer apodeme onto which a small strip of muscle inserts. When this small muscle contracts it pulls the apodeme down. Thus if it contracted after the main closer muscle has built up tension during the period of lock, it will release the apodeme by pulling it back below the pivot point, allowing the closer to release its tension. This causes the dactylus to snap shut.

In each of the above cases, modification to the muscles and joints have improved the performance of movements which the animal could otherwise not do so well. It has been shown that Carcinus rapidly propels its large chelipeds in a depressory-promotory strike behaviour which lasts 30 to 60 ms (Chapter 2). The calculation of energy required for the fast strike has indicated that there must be energy storage before the strike and possibly for cheliped re-extension. Detailed anatomical observations did not reveal the presence of any skeletal modification which could act as a click mechanism. However modifications of the muscle and tendon head was observed in the case of one BI muscle, the Posterior depressor, although it is thought unlikely that this alone could cause the rapid strike. Similarly neuromuscular investigations of the main coxal and BI muscles did not indicate any specializations of muscles which would allow especially fast contractions, although some do have physiological properties which may aid the strike performance. It is again thought unlikely that these modifications alone could produce the strike behaviour.

These considerations indicated that the fast strike must either be caused by a completely different mechanism to the types described above or must be caused by the action of several modifications. In this section the geometry of the joints and pivots of the two coxal and BI complex was studied in order to estimate their contributions in the performance of the fast strike behaviour.

MATERIALS AND METHODS

The five main coxal and BI muscles, namely the coxa remotor, coxa promotor, BI Anterior levator, BI Anterior depressor and BI Posterior depressor muscles were exposed in freshly killed crabs as previously described.

ONE - GEOMETRY OF THE JOINTS

Various parameters were measured as the segments were manipulated about their joints. These are shown on Figure 1 and include:

1. The distance between the tendon head and the axis of rotation for all five muscles, line p.
2. The distance from the origin to the insertion of the muscles at extreme positions of their possible excursion, value L. For the coxa these occur at full promotion and full remotion, while for the BI these occur at full levation and full depression. In the case of the BI muscles their lengths were measured at 4 extreme positions, that is levated promoted, levated remoted, depressed promoted and depressed remoted.
3. The angle subtended between the line of force exerted by the muscle, which in this case was equivalent to the line of the tendon axis and line p, was also measured at these extreme positions, value θ°.

Using these values, diagrams, drawn to scale, were constructed to represent the movement of the muscle insertions as the joints were rotated and the directions of force exerted about the joints. These diagrams allowed the mechanical advantage to be measured. This was calculated by dropping a perpendicular line between line M, representing the direction of force of the muscle, and the axis of rotation, R. The mechanical advantage is represented by value d. Line M is usually equivalent to the line of the tendon axis since most muscles act in a straight line along this axis. In other cases where the muscle origins are not symmetrical about the main tendon, line M would represent a resultant direction of the component parts.

TWO - MECHANICAL ACTIONS OF THE BI MUSCLES

The distance from the origin to the insertion of each of the 3 main BI muscles was measured at various positions. If they were observed to shorten it was assumed that contraction of the muscle would rotate the segment in an identical direction. For instance, if during passive depression of the BI, the Ad was observed to shorten, it was assumed that active contraction of this muscle would cause depression of the limb. As a means of confirming the actions of muscles, the muscles were carefully stripped from their tendons in some preparations. The tendons were then manipulated using fine forceps.

FIGURE 1

CALCULATION OF THE MOVEMENTS OF A MUSCLE ABOUT A JOINT

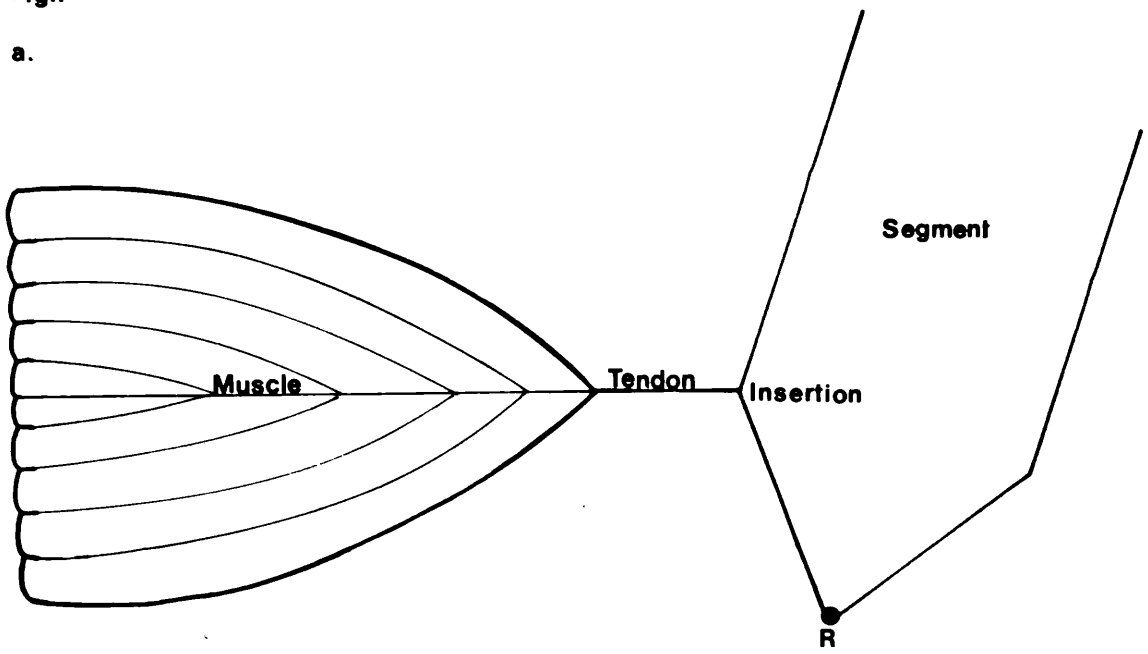
(a) In Fig. 1a, contraction of the muscle will rotate the segment to which it is attached about the pivot point R. This situation is illustrated in a more diagrammatic form in Figure 1b.

(b) The muscle is represented by line Y-X. R is the pivot of rotation. The constant value p, from X to R, is equivalent to a perpendicular line dropped from the muscle insertion to the axis of rotation. θ^{o} represents the angle subtended between the muscle tendon and p. In this situation the direction of force exerted by the muscle, M, is directly along the line of the tendon. Li represents the shortest length of the muscle, when the segment is at one extreme of movement, X_1. When the segment is rotated to the other extreme of movement X_2, the muscle lengthens to Lii, and θ decreases. Thick lines represent the situation at one extreme movement, thin lines represent the situation at the other extreme.

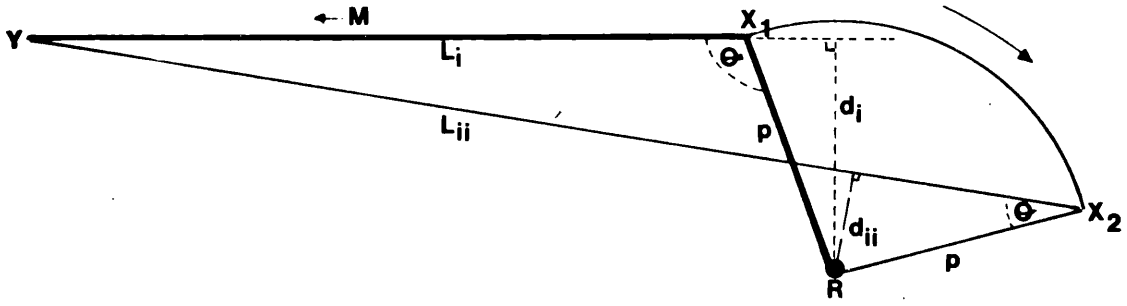
Calculation of the mechanical advantage of the muscle is achieved by dropping a perpendicular line from the axis of the tendon to the pivot point. This is value d. Values di and dii on the figure represent the mechanical advantage at the two extremes of joint position. It can be seen that in this case, the mechanical advantage is decreased when the muscle is at its longest length.

Fig.1

a.


Segment
Muscle
Tendon
Insertion
R

b.


M
Y
L_i
L_{ii}
X_1
θ
d_i
p
d_{ii}
θ
X_2
R
p

RESULTS

SECTION ONE. GEOMETRY OF THE JOINTS

A. The coxal muscles and the T-Cx joint

The mechanical advantage of each muscle can be related to the joint positions which are adopted during the strike behaviour. In this way antagonistic and synergistic muscles can be compared and suggestions made concerning the effects that their mechanical advantages would have on the performance of a fast strike.

The movement of the insertions of the CxP and CxR muscles are shown together in figure 2a and the mechanical advantage of the muscles during rotation of the limb is shown on figure 2b. The mechanical advantage of the CxR muscle increases over the first 15^{o} of promotion, which are angles equivalent to the joint positions adopted during the threat display. As the coxa is promoted from these positions, the mechanical advantage steadily decreases. The CxP has a small mechanical advantage during the limb positions adopted in threat but the advantage increases rapidly over the first 20^{o} of promotion to reach a maximum at 40^{o} promotion. The advantage changes little from this position to full promotion.

If the tension in the CxP is equal to that in the CxR, then the coxa is stable at two positions; one is when the joint is fully remoted and the other is when it is fully promoted. This is equivalent to the positions adopted in Full Threat displays and at the end of the strike. Figure 2b demonstrates that there is a point of equal mechanical advantage which is reached when the coxa is promoted to 28^{o}. This is a point of extreme instability as any sudden alteration in promotory or remotory mechanical advantage would swing the joint in the appropriate direction. This is comparable to an electrical "flip-flop" circuit and is termed a bistable condition. A flip-flop circuit is a basic digital memory unit which is obtained by cross coupling two electrical circuits. The output of each circuit is connected to the input of the other. The most important property of this feedback combination is that it can exist in one of two stable states. The circuit can be made to flip from one stable state to the other by application of a suitable trigger pulse. This is comparable to the situation in the T-Cx joint and is explained in figure 3.

The bistable condition in the T-Cx joint may be used in producing a fast strike. If the limb could be moved towards the point of instability when the muscles are already under tension, sudden injection of a small promotory force would flip the limb in a promotory direction and so cause the rapid strike. Figure 2b demonstrates that once the bistable position

FIGURE 2

a. MOVEMENT OF THE COXA REMOTOR AND PROMOTOR MUSCLE INSERTIONS ABOUT THE THORAX-COXA JOINT

The coxa remotor muscle, CxR, is represented by the two lines at the top of the diagram. The coxa promotor muscle, CxP, is represented by the two lines at the bottom of the diagram. The thick lines represent the situation when the T-Cx joint is fully remoted, thin lines represent the situation when the joint is fully promoted, an excursion of 60°. The movement of the muscle insertion is indicated by the arcs between 0 and 60°. Intermediate angles of 20° and 40° promotion are represented by dotted lines.

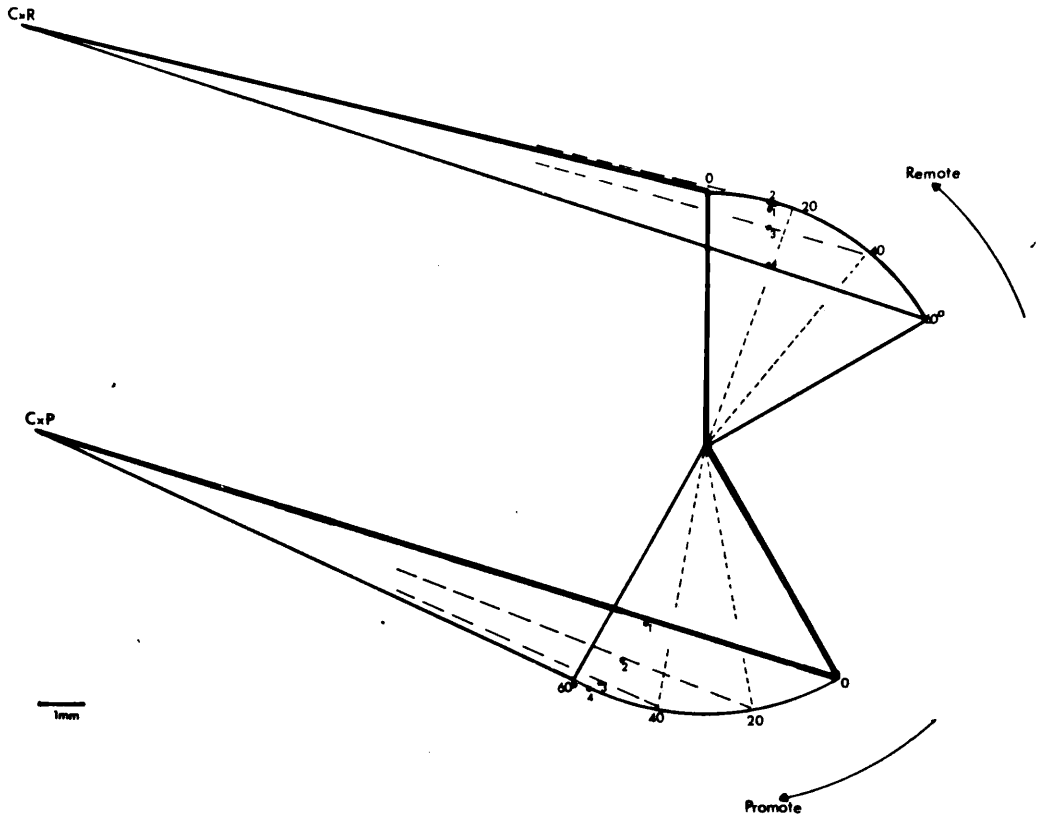
When the T-Cx joint is fully remoted, the CxR is at its shortest length and the CxP at its longest. The reverse situation applies when the joint is fully promoted. Four values of d, the mechanical advantage, are shown for each muscle at increasing angles of promotion; 0°, 20°, 40° and 60°. These are indicated by 1, 2, 3 and 4 respectively. These values were measured by extending a line from the muscle origins to the appropriate position on the locus and are indicated by the discontinuous lines. It can be seen that the mechanical advantage of the CxR increases during the first 20° of promotion and then decreases steadily. The mechanical advantage of the CxP increases throughout promotion, but more rapidly at the initial stages of movement.

b. THE MECHANICAL ADVANTAGE OF THE COXA REMOTOR AND PROMOTOR MUSCLE DURING PROMOTION OF THE T-Cx JOINT

The CxR is represented by the thin lines and crosses, the CxP is represented by the thick lines and closed circles. The vertical dotted lines represent the positions of the joint between threat to the beginning of pre-strike and pre-strike to the beginning of strike. There is an overlapping region between strike and pre-strike from which the crab can either perform a strike or can re-extend the chelipeds into threat positions. The graph illustrates the rapid increase in the mechanical advantage of the CxP during the first 30° of joint promotion. The CxR also shows an initial increase in mechanical advantage but decreases after 15° promotion. This is just after the positions adopted in threat have been exceeded.

CHAPTER 4 FIGURE 2

Fig. 2 a.



b.

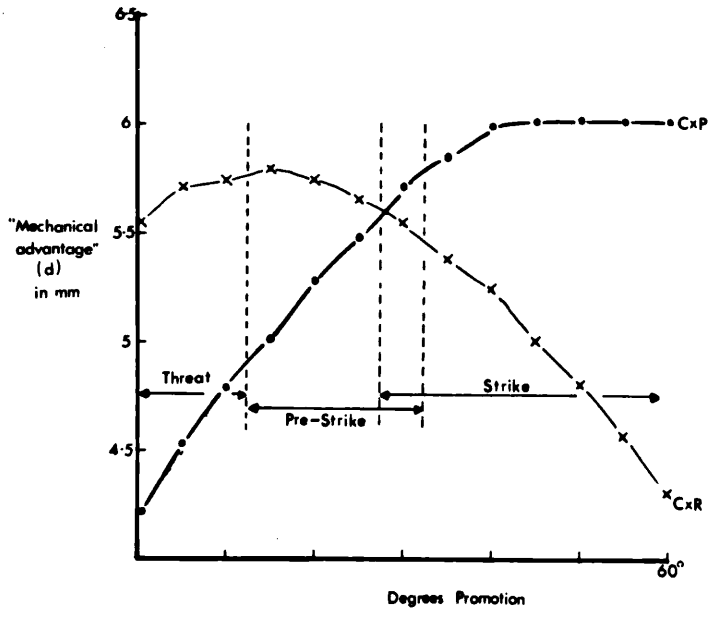


FIGURE 3

THE PRINCIPLES OF A BISTABLE ARTICULATION

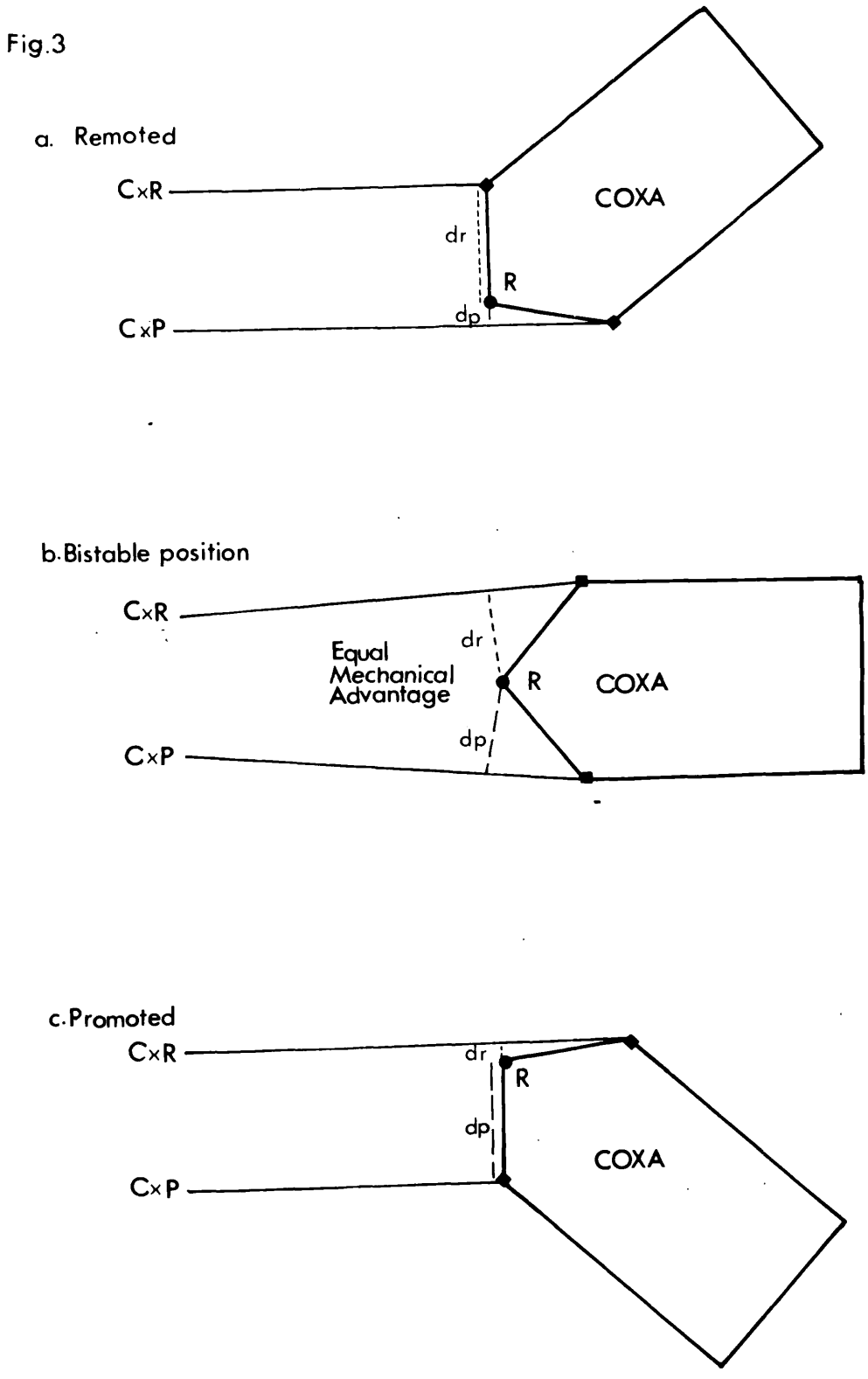
dr, mechanical advantage of remotion; dp, mechanical advantage of promotion; CxP, coxa promotor muscle; CxR, coxa remotor muscle; R, T-Cx pivot.

Figure 2b demonstrates that when the tension in the CxR and CxP is the same, the coxa is stable in two positions, one is when the T-Cx joint is fully remoted, fig. 3a when dr is greater than dp, and the other is when the joint is fully promoted, fig. 3c when dp is greater than dr. Calculation of the mechanical advantage (Fig. 2b) demonstrates that there is a point of equal mechanical advantage between the CxR and CxP which occurs when the joint is promoted to 28°. This situation is represented by fig. 3b, when dr equals dp. The point of equal mechanical advantage is a point of extreme instability and any slight increase in remotory or promotory force from muscles already under tension would swing the coxa in the appropriate direction, that is from b to a or c.

It is possible that this feature is used in producing the fast cheliped strike. The first situation, a, is equivalent to the position of the joint adopted in Full Threat. The third situation, c, is equivalent to joint positions adopted at the end of the strike. If the coxa could be moved to point b, the bistable position, a sudden increase of promotory tension would flip the joint in a promotory direction. Fig. 2b demonstrates that after this point of instability is exceeded the mechanical advantage of CxR decreases rapidly while that of the CxP continues to increase. Thus if the CxP continued to contract once this point is crossed, the coxa would be quickly promoted.

The crossing over of the point of instability could be achieved in one, or in combinations of three ways. Firstly the CxR could relax slightly and so allow the CxP to suddenly express its tension. Secondly, the CxP could produce an injection of extra promotory tension, such that it is now more powerful than its antagonist ; the point of instability will be exceeded and the coxa will be promoted. Thirdly, the beginning of coxal promotion could be achieved by the involvement of another muscle, giving an added promotory force to that already developed in the CxP. When this combined promotory tension exceeds that in the CxR, the limb will be promoted. In both of the last two instances, relaxation of the CxR after the point of instability is crossed would increase the speed of promotion.

Fig.3


a. Remoted
CxR
COXA
dr
R
dp
CxP
b.Bistable position
CxR
Equal
Mechanical
Advantage
dr
R
COXA
dp
CxP
c.Promoted
CxR
dr
R
dp
COXA
CxP

is crossed the mechanical advantage of the CxR decreases rapidly while that of the CxP continues to increase. Thus if the CxP continued to develop tension once the point of instability was crossed, the coxa would be quickly promoted.

It can be seen that when the coxa is fully remoted, the mechanical advantage of the CxP is far smaller than that of the CxR (Fig. 3a). This would mean that in this situation, the CxP could build up large amounts of tension which could be countered by a relatively small tension in the CxR. Thus the CxR would act as a muscular stop on promotion. When the tension in the CxP is equal to that in the CxR and the point of instability is reached, the coxa could be rapidly promoted in a strike movement by one, or a combination, of three ways. Firstly, the CxR could relax slightly and so release the muscular stop on promotion, allowing the tension in the CxP to be suddenly expressed. Secondly, the CxP could produce a sudden injection of promotory tension increasing its total tension over the antagonistic tension in the CxR; the point of instability would be crossed and the coxa would then flip in a promotory direction. The speed of this movement would be considerably increased if the CxR relaxed at the same time, or just after, the increase of CxP tension. Thirdly, the onset of promotion could begin by the action of another muscle which gives an added promotory force to that already developed in the CxP. The combined tension of the CxP and the "extra" muscle will then exceed the antagonistic tension of the CxR and the limb will be promoted as the cross-over point is exceeded. Again, the speed of promotion would increase if the CxR relaxed.

B. The BI Anterior levator muscle and the T-Cx, Cx-BI joints

The bifurcating nature of the Anterior levator muscle meant that the direction of force that it can exert was a resultant of its two components. To find the resultant it was first necessary to measure the forces that each muscle section could exert. It was not possible to measure these directly and so they were calculated using the equation below described by Alexander (1969):

Force exerted by a pinnate muscle = T Fn sin 2a.

where T = the surface area of one side of the muscle tendon.

Fn = force per unit initial cross sectional area of the muscle fibres.

a = angle subtended between the muscle fibres and the muscle tendon.

This is illustrated in figure 4. Fn was taken to be 1.7 kg cm^2, the value for the carpus extensor muscle of the striking limb in Squilla (Burrows, 1969), a value which is similar to insect skeletal muscle (Usherwood, 1962).

Force values were calculated for three sections of the A1 muscle using the above equation. The sections are indicated in Figure 5. Section 1 represents the muscle fibres attached to the wing of the tendon which runs posteriorly into the 4th pleural chamber, section 2 represents the muscle fibres attached to the wing of the tendon which runs medially into the 4th sternal chamber and section 3 represents the muscle fibres attached between the point of bifurcation and the tendon head. The calculated forces were 0.067 kg wt, 0.058 kg wt and 0.048 kg wt respectively.

Since the muscle was a complex shape, θ^{o} did not necessarily correspond to the anatomical divisions of the muscle. Instead the angles between lines drawn from the two origins to the insertion point were measured, as were the lengths of these in the 4 extreme positions of the joint. A large scaled graph was constructed on which was drawn the origin of sections 1 and 2 and the locus taken by the insertion from full levation to full depression. The resolved direction of force of the whole muscle could now be measured empirically by constructing a simple model on the large scale graph (Fig. 5).

Diagrams of the movement of the muscle insertion during joint excursion are shown in Figure 6a. Figure 6b indicates the mechanical advantage for such positions. Since it is known that the coxa and BI follow a humped elipsoidal course during the strike movement (Fig. 7, chapter 2), the changing mechanical advantage during a strike can be estimated and is represented by the dotted lines on figure 6b.

The mechanical advantage throughout depression alters considerably depending on the T-Cx joint positions. When the coxa is fully promoted the mechanical advantage of the A1 is less than when the coxa is remoted, over all degrees of BI depression. In the promoted situation the mechanical advantage decreases steadily while in the remoted situation the advantage is maintained at a high level over the first 20^{o} of BI depression. This is equivalent to the joint positions assumed in threat displays.

The course of the change in mechanical advantage during the strike shows that the decrease in advantage begins in the pre-strike stages and continues throughout the strike action. The advantage increases suddenly at the first stage of recovery and then rises more steadily over the remainder of this movement, as the limb is relevated and re-extended. Therefore if the A1 is to be used to its greatest mechanical advantage during a strike it should contract maximally during the period from threat to pre-strike when its advantage is at its peak, and then during the second phase of recovery when its advantage increases. The decreasing mechanical advantage shown during strike would mean that any residual

FIGURE 4

METHOD OF CALCULATION OF FORCE THAT MAY BE EXERTED BY A MUSCLE (ALEXANDER, 1969)

(a) Consider a pinnate muscle whose tendon has an area T on one side onto which the muscle inserts. When the fibres are at rest they make an angle a with the tendon. The cross-sectional area of the muscle on one side of the tendon measured at right angles to the fibres, value x, will be T sin a. Since there are 2 sides to the tendon the total area will be 2T. Therefore the total cross-sectional area of the muscle will be 2T sin a.

(b) Let the fibres contract to a fraction n of their initial length so that they make an angle a_n to the tendon. Let them exert a force Fn per unit cross-sectional area of muscle. They will now exert a total force of Fn 2T sin a on the tendon. The component of this force which acts along the axis of the tendon, y, is therefore 2T Fn sin a cos a_n.

The angles of pinnation of these muscles between the two extremes of movement, a and a_n, do not exceed 5^o. Therefore it will not introduce much error to assume cos a_n equals cos a. The force acting along the tendon is therefore 2T Fn sin a cos a. This is equivalent to T Fn sin 2a.

CHAPTER 4 FIGURE 4

Fig.4

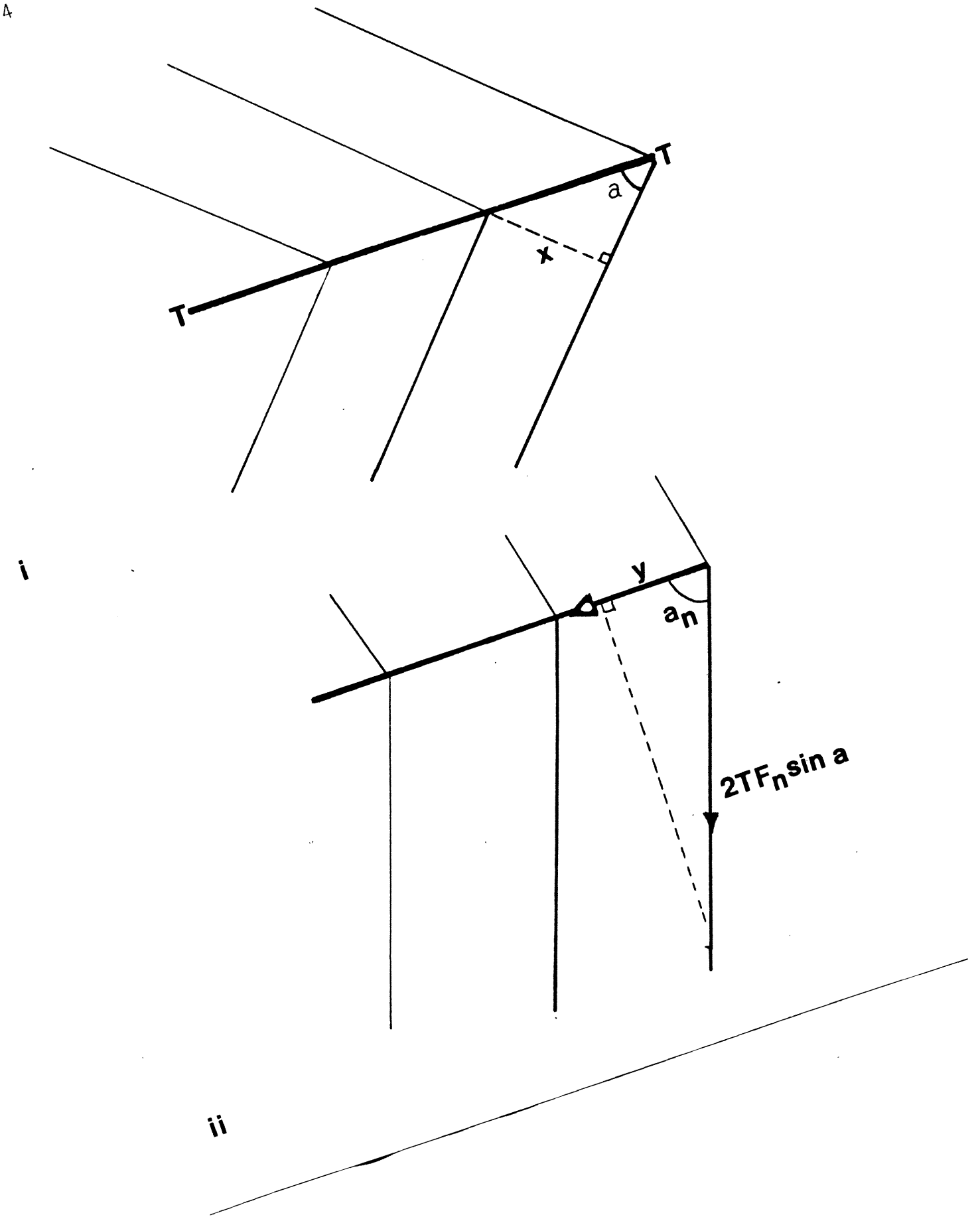


FIGURE 5

METHOD OF CALCULATION OF THE DIRECTION OF FORCE DEVELOPED IN THE BI ANTERIOR LEVATOR MUSCLE

Thick lines represent the situation when the BI is fully levated, thin lines when fully depressed. R represents the point of joint rotation. b represents the point of bifurcation of the muscle tendon. Line c-b represents the section of muscle which inserts onto the posteriorly running wing of the tendon in the 4th pleural chamber, a-b represents the section of muscle which inserts onto the medially running wing in the 4th sternal chamber, and b-X represents the remainder of the muscle. The joint moves from XL, fully levated, to XD, fully depressed.

To determine the direction of force of the whole muscle, the force capabilities of each section were calculated as shown in Fig. 4. A large scaled graph was drawn of the points and angles of the muscle origins and insertion at the extremes of joint movement. Using this graph a simple model was constructed which allowed empirical determination of the resolved direction of force.

Three sections of string were cut to the relative lengths of muscle and tied together in the Y shape of the whole muscle. The 2 ends representing the wing sections were placed over pins inserted through the points representing the origins, a and c. The third end was tied to a pin representing the insertion point X. Weights equivalent to the calculated force values were tied to the 2 free suspended ends of the string indicated by W on the figure.

If it is assumed that section 3 of the muscle contributes equally to the forces developed by sections 1 and 2, then the resolved direction of force exerted by the whole muscle will be in a line drawn as a continuation of line 3 when the model has reached equilibrium. Weights of 0.09 kg and 0.082 kg, that is the calculated forces for sections 1 and 2 plus half the total calculated force of section 3, were attached to the ends of the string suspended over points a and c respectively. The position of point b could then be accurately plotted onto the graph for different positions of X, along the locus. A line extended from this point to the locus was taken to be the resolved direction of force and allowed the measurement of the mechanical advantage as before. 2 values of d are shown, di is the advantage when the joint is fully levated and the direction of force lies along ML, while dii is obtained when the joint is fully depressed and the force is directed along line MD.

CHAPTER 4 FIGURE 5

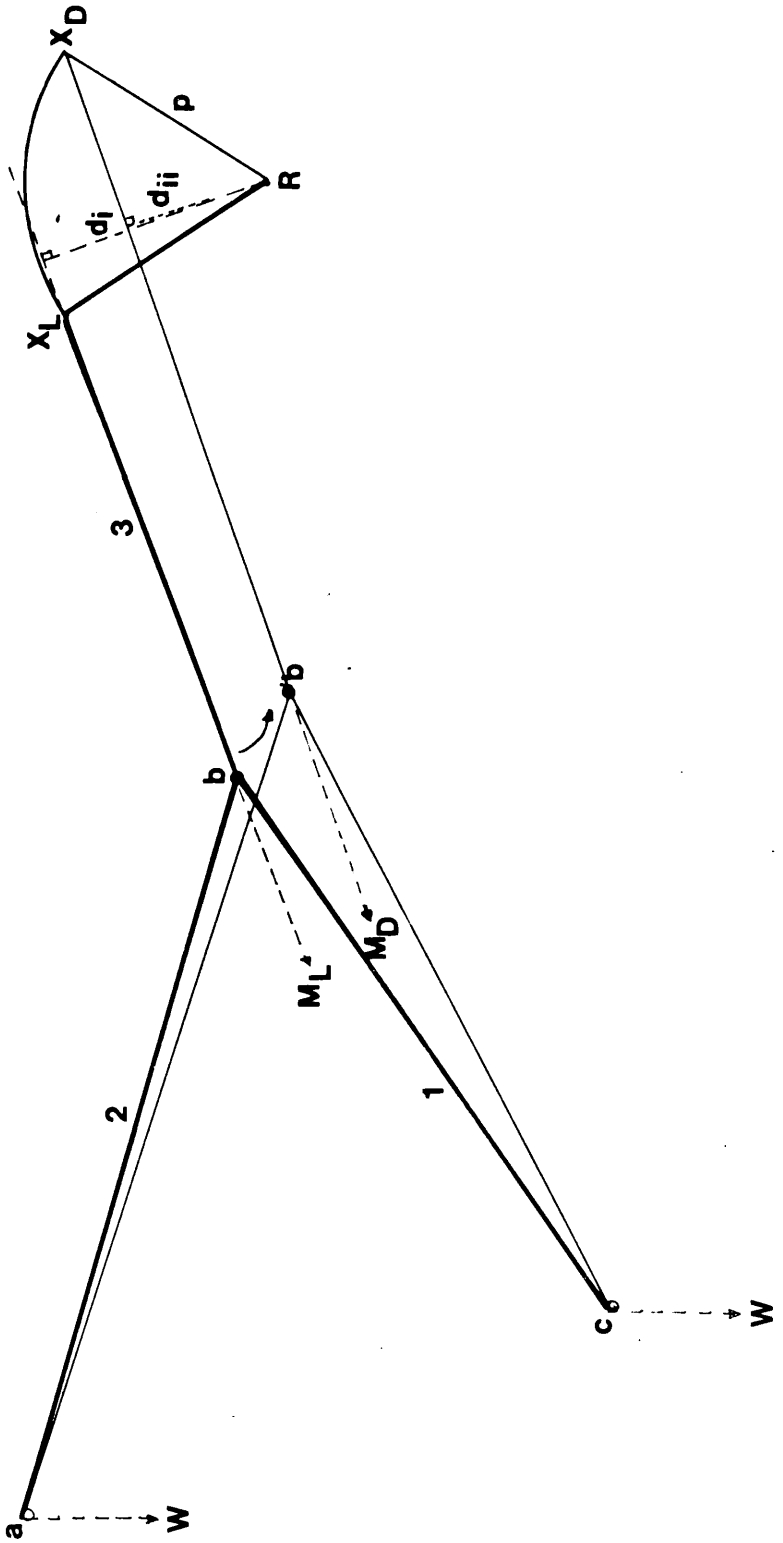


Fig.5

FIGURE 6

a. MOVEMENT OF THE BI ANTERIOR LEVATOR MUSCLE INSERTION DURING DEPRESSION OF THE BI SEGMENT

Thick lines represent the position when the BI is fully levated, thin lines when fully depressed. The resolved direction of force is shown by the discontinuous lines. 1 represents the situation when the coxa is held fully promoted and 2 when the coxa is held fully remoted.

4 representative values of d have been indicated when the joint is fully levated, at 0^{o}, and at angles of depression of 20^{o}, 40^{o} and 65^{o}, full depression. These are shown by 1, 2, 3 and 4 respectively.

It can be seen that when the coxa is fully promoted, d decreases throughout depression. When the coxa is fully remoted, the mechanical advantage increases for the first 20^{o} of depression and then decreases but to a less amount than in situation 1.

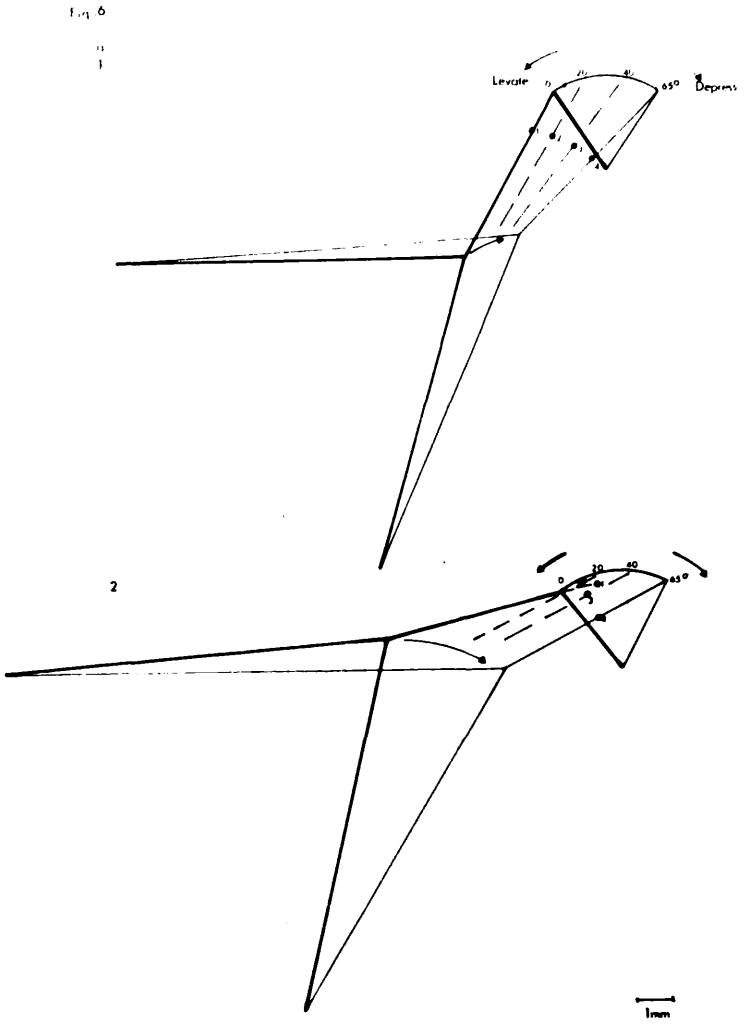
b. MECHANICAL ADVANTAGE OF THE BI ANTERIOR LEVATOR MUSCLE

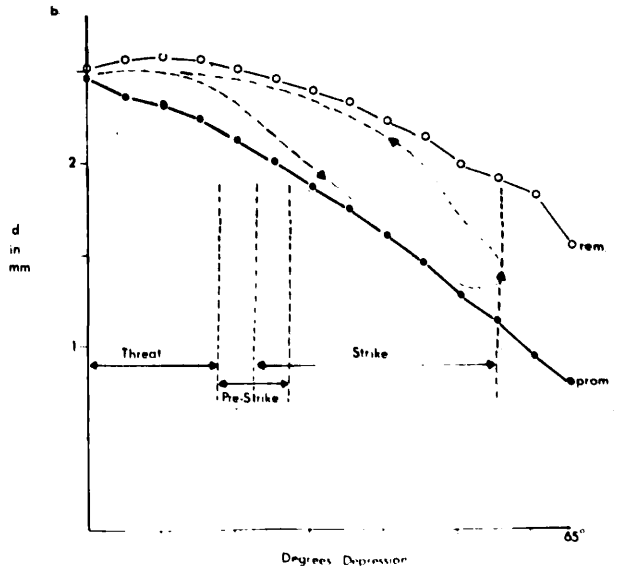
The mechanical advantage, in mm, is shown on the ordinate and the degrees of depression are shown on the abscissa. Thick lines, closed circles represent the advantage when the coxa is fully promoted and thin lines, open circles when the coxa is fully remoted.

The graph demonstrates the steady decline in mechanical advantage when the coxa is held promoted. When the coxa is held remoted the advantage is greater over all degrees of BI depression and increases slightly during the joint positions assumed during threat. It then decreases for the remainder of depression.

The mechanical advantage of the muscle during the whole strike action will lie within these two lines. The angle subtended by the Cx-BI joint during the strike and recovery movement have previously been measured (Fig. 5, chapter 2), and from these values the advantage of the muscle can be estimated. For example, it is known that the limb is fully levated and remoted in Full Threat, steadily promoted and depressed to pre-strike positions and then quickly depressed and fully promoted during a strike (Fig. 5, chapter 2). Strike recovery movements are initially remotory and depressory, then remotory and levatory. The projected mechanical advantage during the strike is indicated by the thin dotted lines within the two lines of mechanical advantage described above. The direction of the mechanical advantage is indicated by the arrows. This graph shows that the advantage is steady during threat but decreases rapidly during strike. The advantage increases steadily at the beginning of recovery and then rises more steadily to full threat positions of the joint. Throughout the recovery stage the advantage is greater than during the strike. The decreasing advantage shown during strike would mean that any residual tension in the Al during rapid cheliped flexion would not unduly slow the strike movement.

CHAPTER 4 FIGURE 6





tension in the Al during cheliped flexion would not unduly slow the strike movement.

C. The BI Anterior depressor muscle and the T-Cx, Cx-BI joints

The movement of the insertion of the Ad muscle and the mechanical advantage of the muscle is shown in figures 7a and 7b respectively. The mechanical advantage of the Ad also changes with the position of the T-Cx joint. The advantage increases from a maximum when the T-Cx and Cx-BI joints are remoted and levated, to reach a peak when the BI is depressed to 40° and the coxa remoted. When the coxa is promoted, a higher mechanical advantage is maintained over the first 25° of BI depression and then steadily decreases. Since the two lines of mechanical advantage on figure 7b represent all extremes of movement and there is not much difference between them, it is apparent that in the live crab the mechanical advantage would be relatively stable over a wide range of normal movement. If the Ad is to be used to its greatest mechanical advantage during depression of the cheliped in a strike, it should contract maximally between the period of overlap of pre-strike and strike, that is before the beginning of rapid coxal promotion.

D. The BI Posterior depressor muscle and the T-Cx, Cx-BI joints

The geometry of the Pd muscle is complicated by its possession of a flexible link between the tendon blade and tendon head. The small subdivisions of this muscle may alter the position of the heel, but it is not known if they contribute much to depression. In calculating the movement of the Pd about its joint, these muscles are considered to be passive although it is probable that they can alter the mechanical advantage of the main Pd muscle, Pd1. Thus the functional point of insertion of the Pd is taken to be the tip of the tendon blade rather than the BI rim.

The method of calculation of the direction of force and mechanical advantage is shown in figure 8. The movement of the Pd insertion is shown in figure 9a and the changes in mechanical advantage of Pd1 is shown in figure 9b. The mechanical advantage of the Pd is greater when the coxa is remoted and decreases during increasing angles of depression. Unlike the Ad there is a large difference, and change, in mechanical advantage between all extreme joint positions, and also the advantage decreases steadily. Therefore if only one depressor muscle is to be used to produce the depressory component of the strike it would appear to be more advantageous for the Ad to contract. The Ad not only has a higher mechanical advantage than the Pd but its advantage also increases during the initial stages of pre-strike. However if rapid depression is achieved by energy

FIGURE 7

a. MOVEMENT OF THE BI ANTERIOR DEPRESSOR MUSCLE DURING DEPRESSION OF THE BI

The thick lines represent the situation when the BI is fully levated and thin lines represent the situation when the joint is fully depressed. The muscle fibres act and lie directly along the tendon. 1 represents the situation when the coxa is fully promoted, 2 when the coxa is fully remoted. 4 values of d are represented by 1, 2, 3 and 4 when the joint is held at 0^{o}, 20^{o}, 40^{o} and 65^{o} depression respectively. When the coxa is held fully promoted the mechanical advantage of the Ad increases for the first 20^{o} of depression and then decreases throughout the remainder of joint movement. When the coxa is fully remoted, however, the advantage increases for the first 40^{o} of depression. It then falls slightly but less than in the equivalent position in situation 1.

b. MECHANICAL ADVANTAGE OF THE BI ANTERIOR DEPRESSOR MUSCLE

The legend is the same as Fig. 5b.

This graph illustrates that the mechanical advantage of the Ad increases at the beginning of depression of the BI segment when the coxa is held at both extremes of movement. The change in mechanical advantage over all degrees of depression is less than in the case of the Anterior levator muscle.

The projected mechanical advantage which would occur during a strike shows that the advantage increases up to the beginning of the strike and then decreases. Re-extension of the coxa during recovery causes the mechanical advantage to increase only slightly before it decreases again as the threat postures are resumed.

CHAPTER 4 FIGURE 7

Fig. 7. a

1.

2.

1 mm

7b.

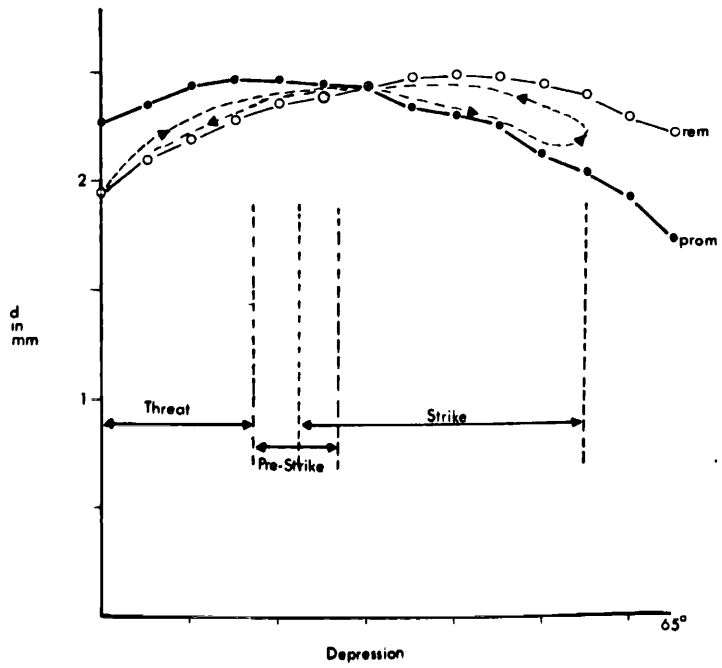


FIGURE 8

METHOD OF CALCULATION OF DIRECTION OF FORCE DEVELOPED BY Pd1

To estimate the movement of the BI Posterior depressor muscle and the direction of force exerted by Pd1, a single value θ^{o} could not be measured because of the flexible linkage between the tendon blade and heel shaped tendon head. Therefore a different method of calculation to the one explained in Fig. 1 was used.

The main tendon blade of the Pd muscle is represented by line Y-H. The fibres of Pd1 act and lie along this line. The heel shaped tendon head is represented by line H-X. H represents the flexible link between the tendon blade and heel. The excursion of joint movement is indicated by the locus XL, full levation, to XD, full depression. Two angles were measured to calculate the position of the origin of Pd. These were Zi between p and the heel, and Zii between the heel and tendon. These two angles were measured at full levation and full depression of the BI segment. The tip of the tendon blade acts as the functional point of insertion of Pd1. Therefore force will be developed along the line of the tendon. Between the two extremes of BI position the tendon tip moves along the line HL to HD. The actual position of this tip was estimated by drawing an arc equivalent to the length of the heel between successive degrees of joint movement, along the locus. The point at which this arc crossed line HL-HD was taken to be the point of the tendon tip. Extending lines from these points to the origin Y allowed value d to be measured as before.

The direction of force, M, is indicated for 4 positions of the joint when it is depressed to 0^{o}, 20^{o}, 40^{o} and 65^{o}. The 4 mechanical advantages at these positions are indicated by div, diii dii, and di respectively. It can be seen that as the joint depresses, the mechanical advantage decreases.

CHAPTER 4 FIGURE 8

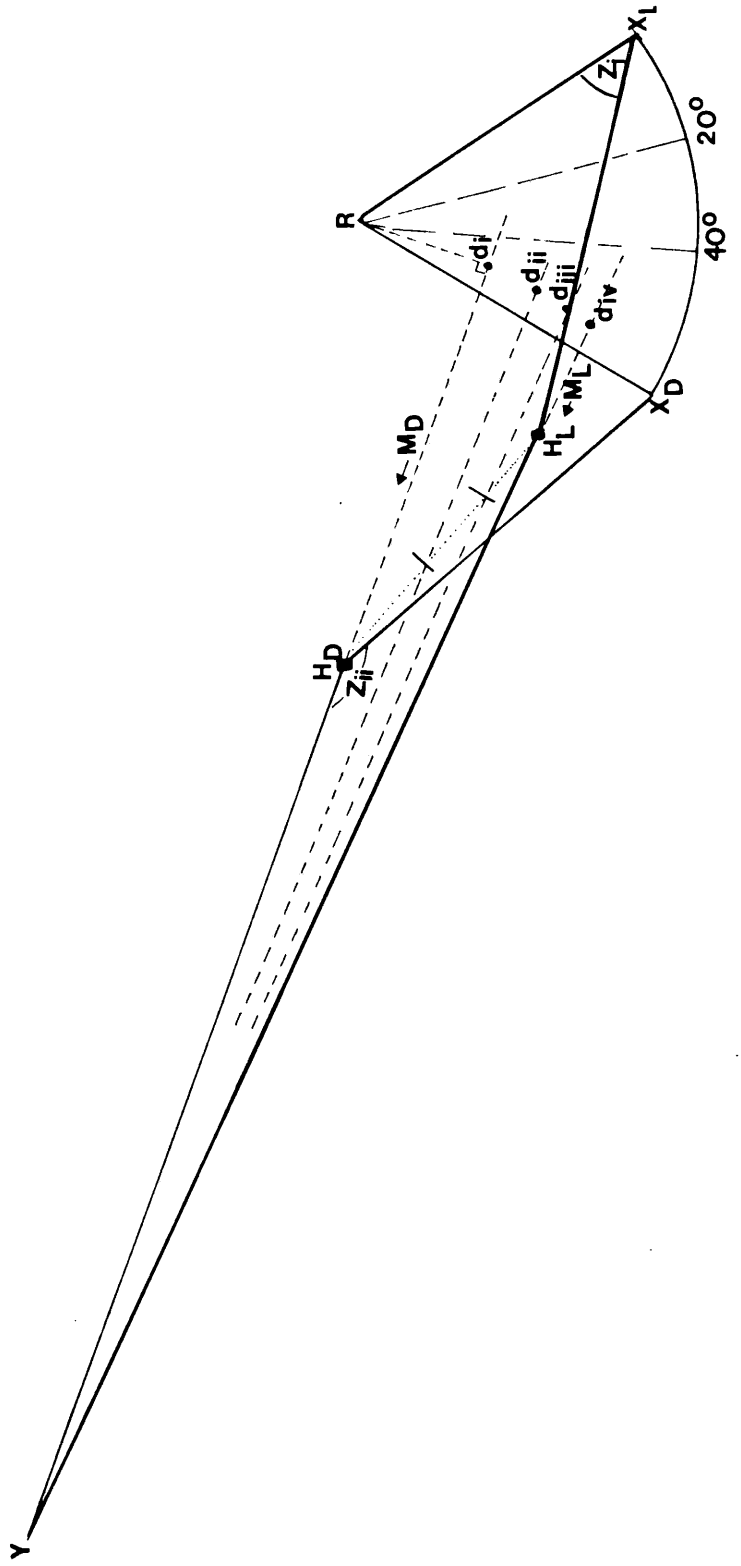


Fig.8

FIGURE 9

a. MOVEMENT OF THE BI POSTERIOR DEPRESSOR MUSCLE INSERTION DURING DEPRESSION OF THE BI

The legend is the same as in Fig. 5a. Fp represents the flexible point of attachment between the heel and tendon blade. The movement of this muscle was calculated as described in Fig. 7.

The 4 values of d plotted onto the diagrams show that the resolved direction of force has a steadily decreasing mechanical advantage throughout depression of the BI. When the coxa is held remoted, the advantages still decrease during depression but are greater than when the coxa is held promoted.

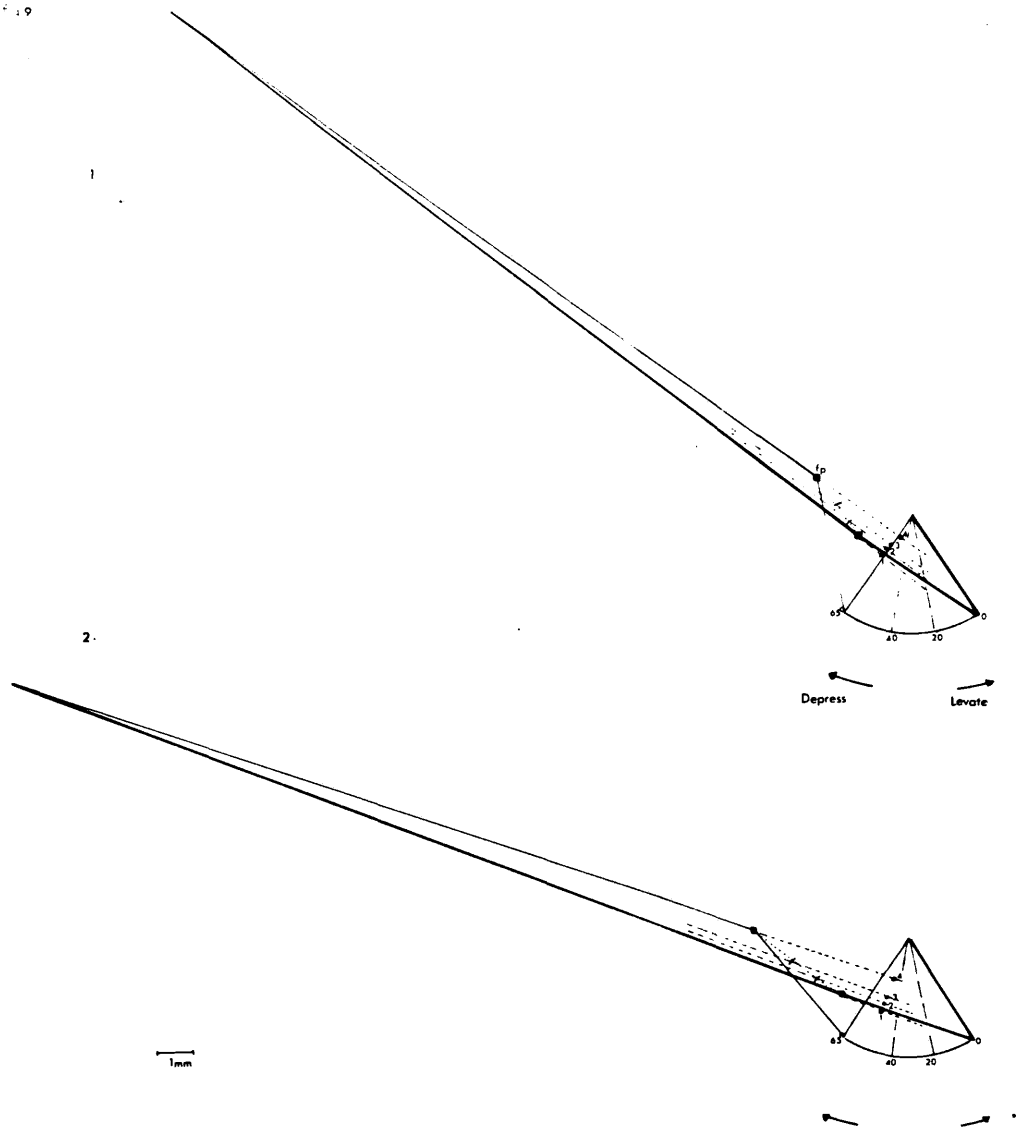
b. MECHANICAL ADVANTAGE OF Pd1

The legend is the same as in Fig. 5b.

Pd1 has a decreasing mechanical advantage as the BI is depressed and the greatest values occur when the coxa is remoted.

The mechanical advantages which would occur during a strike illustrate that the muscle will decrease in advantage throughout the strike but more rapidly at the beginning than at the end. Throughout the recovery from strike the mechanical advantage increases and is greater than the values achieved during the whole of strike and pre-strike.

CHAPTER 4 FIGURE 9



storage before the strike, then either depressor muscle could be used, providing it is counterbalanced by another muscle, such as the Al. In this situation it is more likely that the Pd would be used, since its mechanical advantage has similar values to , and follows the same increases and decreases as,that of the Al.

SECTION TWO

THE MECHANICAL ACTIONS OF THE BI MUSCLES

In most arthropod limbs, the muscles which insert onto any particular segment have their origins in the next proximal segment. For example, the muscles which open and close the dactylus, originate in the propus. They can therefore only exert a mechanical effect on the dactylus. This is not the case for some of the BI muscles of the cheliped in Carcinus. For example, the Al does not originate in the coxa but in the thorax. This gives these atypical BI muscles a dual mechanical effect and their contraction will not only cause movement of the BI but also of the coxa.

The principles behind this feature are illustrated in figures 10 and 12. The segments of the limb in question are depicted as three tubes. Segment 1 articulates with segment 2 along the vertical axis AA. This allows segment 2 to rotate anteriorly and posteriorly, equivalent to promotion and remotion. Segment 3 is attached to segment 2 along the horizontal axis BB which allows movement in a dorsal-ventral plane, equivalent to levation and depression (Fig. 10).

In a typical situation (Fig. 11A) a muscle attached to segment 3 originates in segment 2. Contraction of the muscle indicated in figure 11A will levate segment 3. The end elevation shows the line of force of this action, upwards along the vertical axis AA (Fig. 11A, c).

Three atypical cases can be demonstrated (Fig. 11B). One case is where the muscles originating in segment 1 pass directly along the dorsoventral midline YY (Fig. 11B, 1). A second case is where a muscle inserts posteriorly to the midline (Fig. 11B, 2) and a third case is where a muscle inserts anteriorly to the midline (Fig. 11B, 3).

In the first situation (Fig. 12A), the direction of force passes directly through the pivot of segments 1 and 2. If no other force is exerted on segment 2, contraction of the muscle in figure 12A will result in all the force being transmitted along the vertical axis AA, as shown in the end elevation (Fig. 12A, b). Therefore the muscle will only cause segment 3 to move, vertically upwards along the line F1.

FIGURE 10

MECHANICAL EFFECTS OF MUSCLES

Three segments of a limb are depicted as three tubes. Segment 2 articulates with segment 1 along the vertical axis AA. It can move in an anterior-posterior direction, the equivalent of remotion and promotion. The smallest segment, 3, articulates with segment 2 along the horizontal axis BB. It can move in a dorso-ventral direction, the equivalent of levation and depression.

CHAPTER 4 FIGURE 10

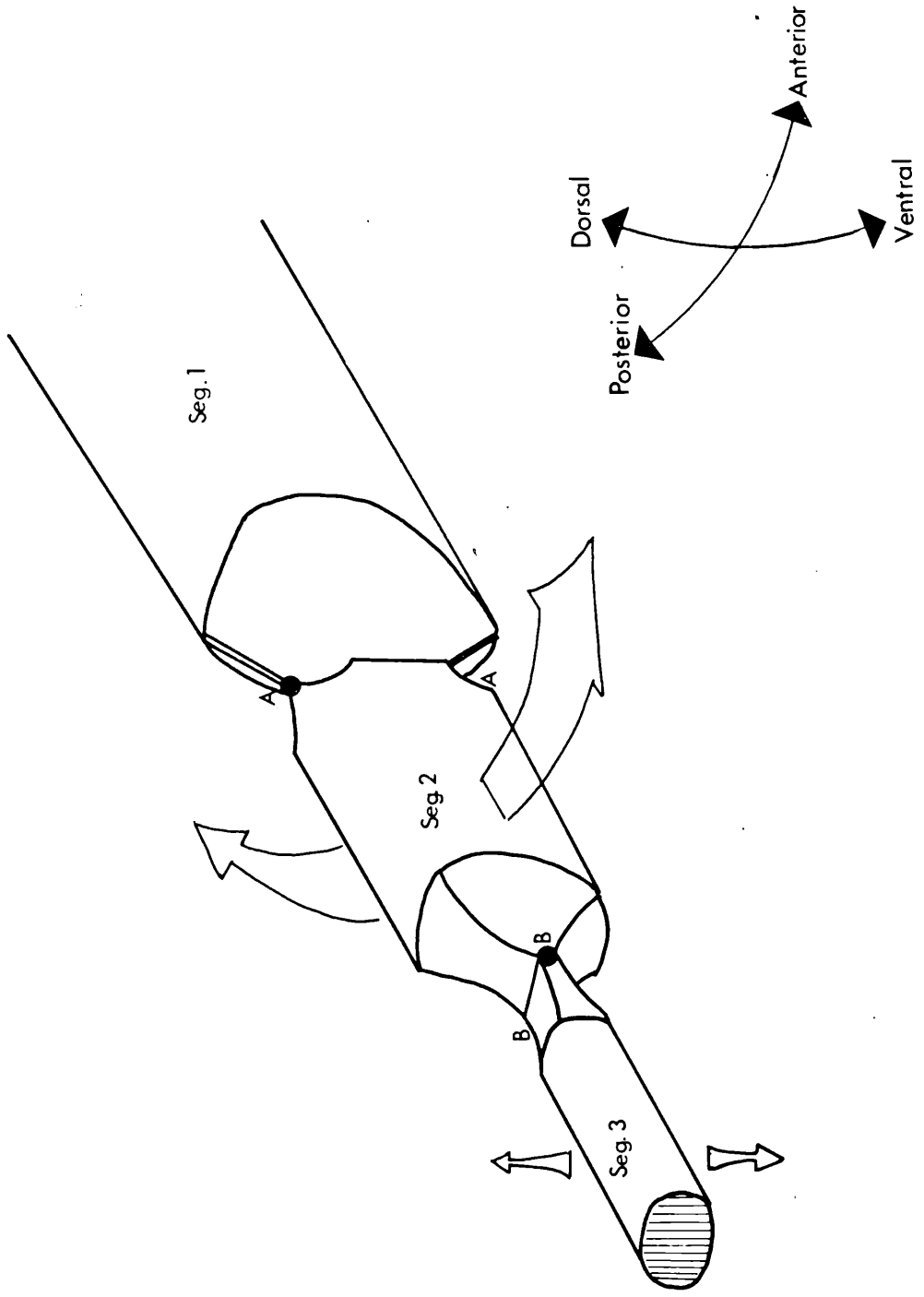


Fig. 10

FIGURE 11

A. THE NORMAL EFFECT OF A MUSCLE UPON A JOINT

In figures 11 to 17 open triangles represent no force in the muscle, closed triangles represent contraction of the muscle.

This figure represents a normal situation in which a muscle originating in segment 2, inserts onto segment 3. a and d represents the side elevation of the 3 segments, c the plan elevation and b the end elevation. The muscle is represented by line a-b from its insertion on segment 3 to its origin in segment 2.

If the muscle contracted it would act in the direction of line F, vertically along axis AA (Fig. c). This would have the effect shown in the side elevation, d, of levating the third segment.

B. THE EFFECTS OF MUSCLES WHEN THEIR ORIGINS ARE ATYPICAL

3 special situations are illustrated where the muscles which insert onto segment 3 do not originate in segment 2 but within segment 1. In each case they insert along arc CC. a represents the plan elevation and b the end elevation.

Muscle 1 inserts onto the middle of segment 3 and originates on the midline of arc CC. Muscle 2 lies more posterior to the midline, and muscle 3 lies more anterior.

CHAPTER 4 FIGURE 11

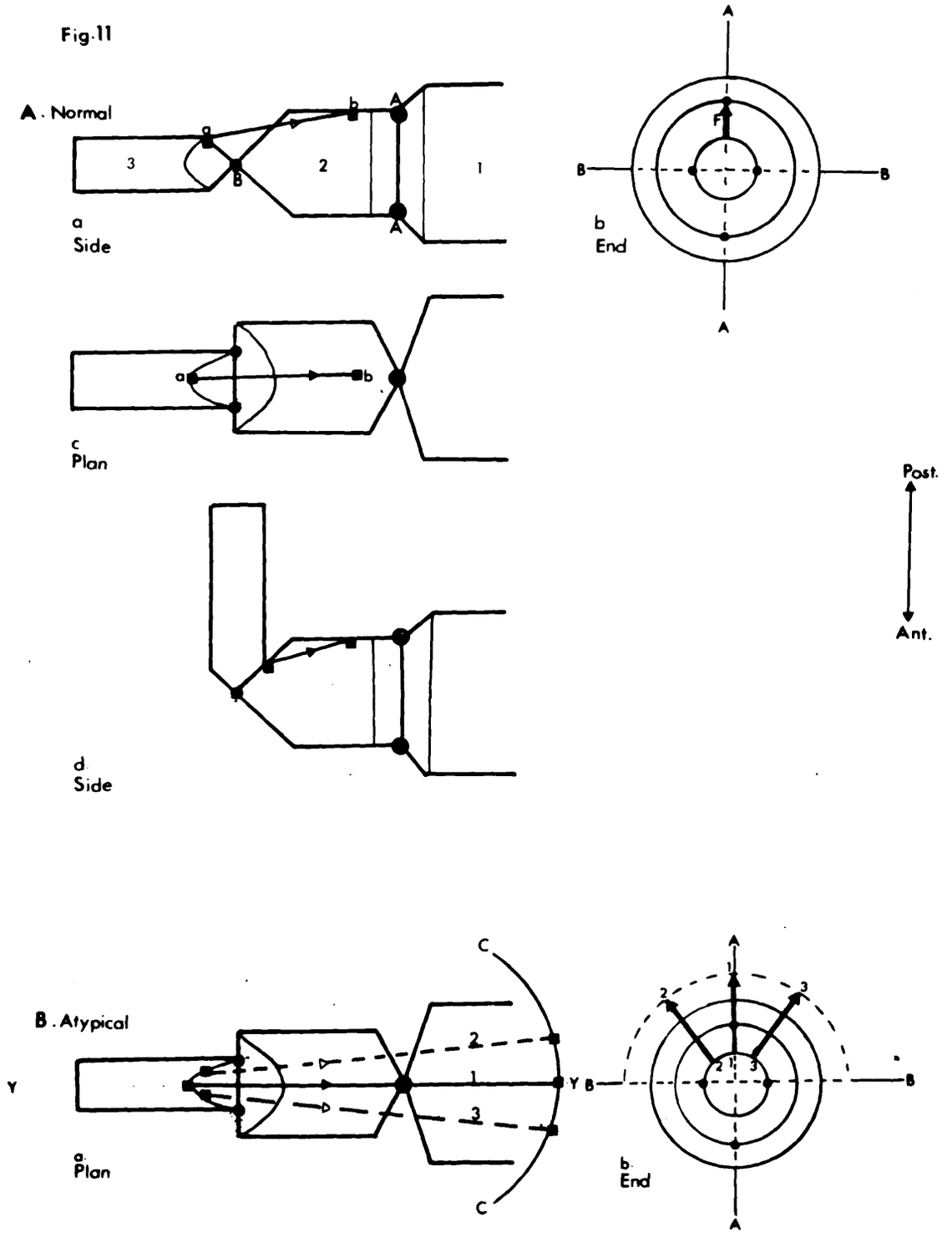


FIGURE 12

A. This illustrates the effect of muscle 1. a represents the plan elevation, b the end elevation and c the side elevation.

Muscle 1 lies in a vertical line which crosses through the pivot of segments 1 and 2 (Fig. a). Contraction of the muscle will cause segment 3 to be raised. The muscle cannot act on the pivot between segments 1 and 2 while its direction of force runs centrally through this pivot line. This is shown by line F1 on the end elevation b.

B. This illustrates the effects of muscle 2. a and c represent the plan elevation and b represents the end elevation.

Muscle 2 acts posteriorly to the midline YY. If it contracts it will not only cause segment 3 to be raised but will cause rotation of segment 2. The end elevation shows the direction of this force, F2. F2 can be resolved into a vertical component, Fv, and a smaller horizontal component, Fh. The former will act on segment 3 and the latter on segment 2. Therefore segment 3 will be raised and segment 2 rotated in a posterior direction.

C. This illustrates the effect of muscle 3. a and c represent the plan elevation and b represents the end elevation.

Muscle 3 acts anteriorly to the midline YY. If it contracts it will not only cause segment 3 to be raised but will cause segment 2 to be rotated. The force of this muscle, F3, can be resolved into its two components Fh and Fv. The end elevation shows that these forces will cause segment 3 to be raised and segment 2 to be rotated in an anterior direction when the muscle contracts (Fig. C).

CHAPTER 4 FIGURE 12

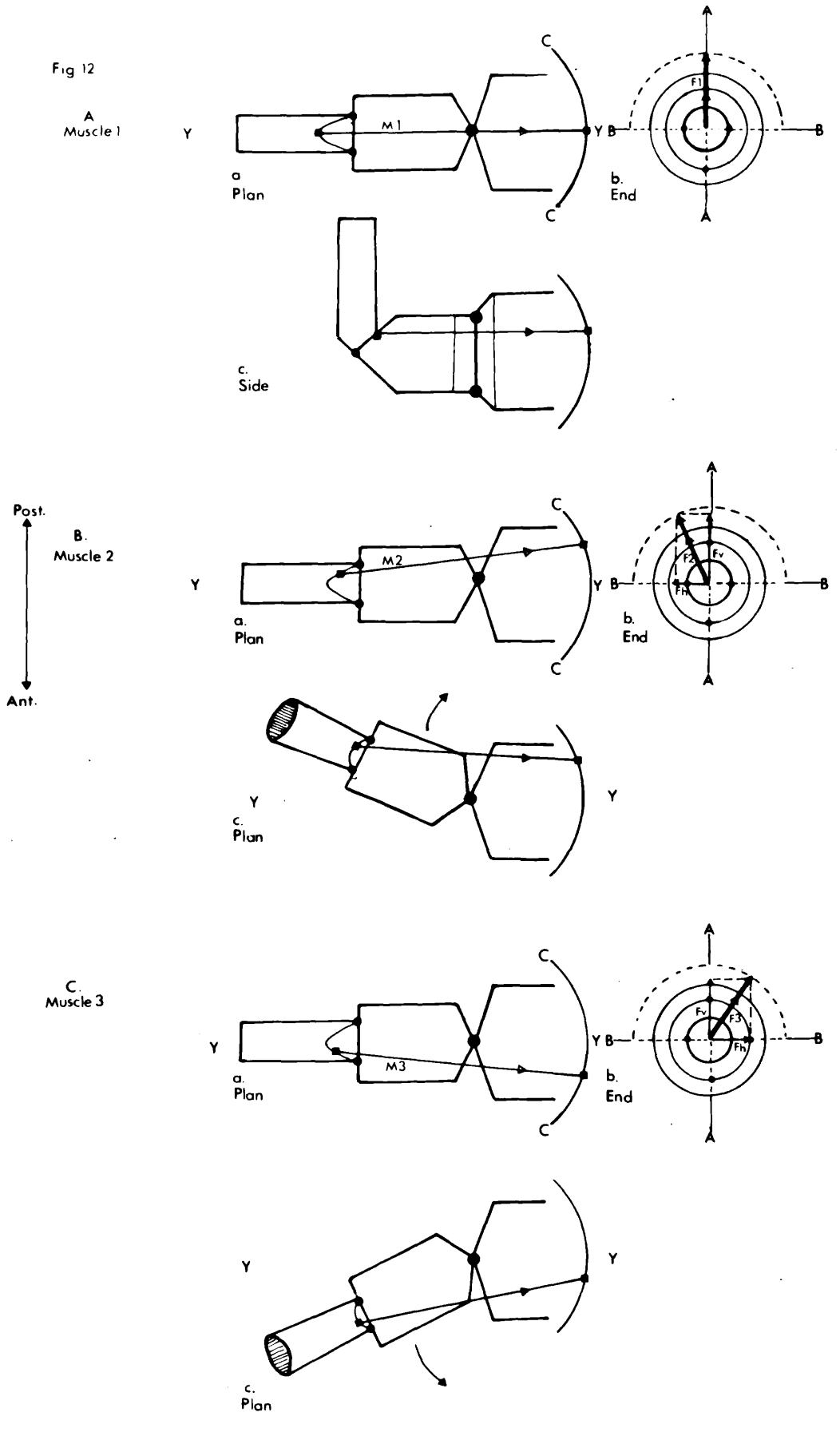


FIGURE 13

MECHANICAL ADVANTAGE OF A MUSCLE

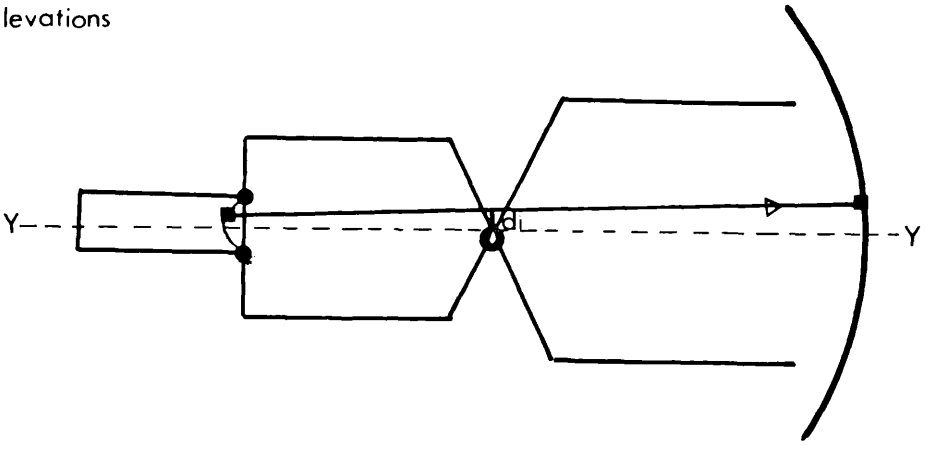
This diagram illustrates the principle of mechanical advantage and moments about a joint. As segment 2 rotates so line d, the perpendicular distance from the direction of force to the pivot of segments 1 and 2, increases. If the muscle were to exert a constant force the moment about the joint would increase as the mechanical advantage value d increased. This follows the rule of force x distance. Thus the moment of the muscle about the joint will increase from situation 1 to situation 3 as d increases from d1 to d3.

CHAPTER 4 FIGURE 13

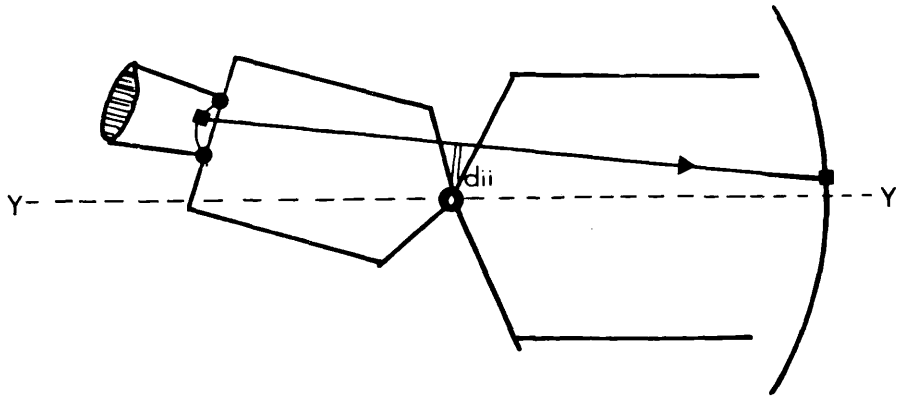
Fig.13

Plan elevations

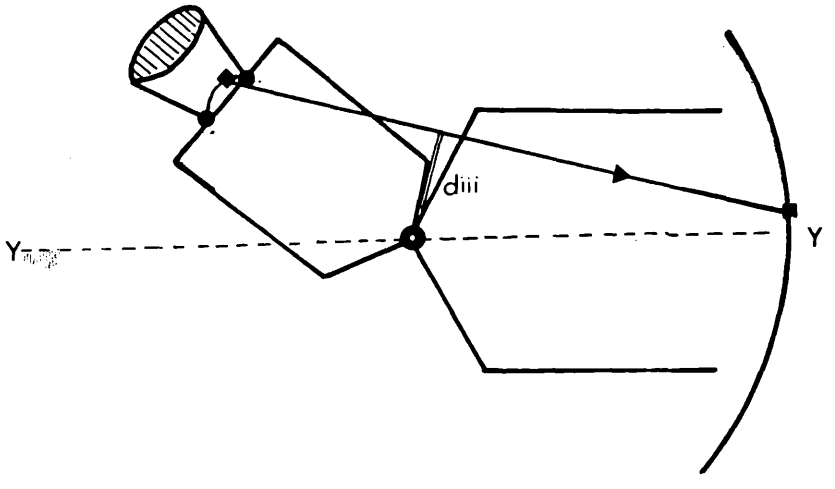
1.



2.



3.



In the second situation (Fig. 12B) the muscle originates and inserts posteriorly to the midline, YY. The end elevation shows the direction of force, F2, which will occur when this muscle contracts (Fig. 12B,b). The force can be resolved into its two components, horizontal and vertical. The action of this muscle will therefore not only be to vertically displace segment 3 but also to horizontally displace segment 2. Force Fv will levate segment 3 along axis AA, and force Fh will horizontally rotate segment 2 in a posterior direction along axis BB (Fig. 12B, c). It can be seen that the vertical component is initially larger than the horizontal. As the limb rotates posteriorly,the horizontal force component will increase as the distance between aX and Xb moves further from YY. For example, if the muscle gives a constant force of 100 gm and the perpendicular distance is 0.2 cm, the moment about the joint is force x distance, equal to 20 gm wt cms. Rotating the limb more posteriorly may increase the distance to 0.4 cm. The moment of the muscle about the joint now doubles to 40 gm wt cm (Fig. 13).

In the third situation (Fig. 12C), the muscle originates anteriorly to axis YY. In the same manner as the example above, the direction of the force F3 can be resolved into vertical and horizontal components. Contraction of the muscle will cause levation of segment 3 and will act on segment 2, rotating it this time in an anterior direction.

These principles explain the actions of these types of muscle origins. The BI Posterior levator and Lesser Posterior depressor muscles do not originate in the thorax but in the coxa. They will therefore have the action illustrated in figure 11A. Contraction of Pl will only cause levation of the BI while contraction of the Lesser Posterior depressor will only cause depression of the BI.

The Anterior levator muscle originates in the posterior side of the thorax equivalent to posteriorly to axis YY in the figures. When it contracts it will follow the principle illustrated in figure 12B, and will not only levate the BI but will rotate the coxa in a posterior direction. Thus it will have a remotory effect on the T-Cx joint. The Al therefore has the dual function of a BI levator and coxal remotor.

The Anterior depressor muscle originates in the anterior side of the thorax, equivalent to anteriorly to axis YY. When it contracts it will follow the principle illustrated in figure 12C, and will cause the BI to depress and the coxa to rotate in a promotory direction. Therefore the Ad also has dual functions, in this case of a BI depressor and coxal promotor.

The Posterior depressor muscle is more complicated; it inserts in the anterior side of axis YY but originates in the posterior side. It is further complicated by the possession of a flexible link between the main tendon blade and heel. Figure 14 illustrates the directions taken by the subdivisions of the muscle on the same plan of three tubes as before. Point X represents the flexible link. Pd1, Pd2, PdH5 and PdH6 all originate in the posterior side of the T-Cx axis while PdH3 and PdH4 originate in the anterior side of this axis.

The Pd can have two functional insertion points. One is from point X and would occur if muscles 2 to 6 can only move the tendon or heel and contribute no depressory effect. All the force will therefore be directed along the main tendon blade by Pd1. A second functional insertion would occur if these muscles also contributed towards depression, and would now be from the heel insertion on the BI rim. The direction of force would be along the resultant of lines aX and Xb. Since all the minor subdivisions of the muscles are so small and have been shown to be ill-aligned for depression, it is unlikely that they will contribute to any depressory force. It is more likely that their action is to alter the position of the heel and tendon blade and so alter the direction of force developed by Pd1. This latter effect is the case which is examined.

Figure 15 illustrates the situation that would occur if no tension was exerted in any of the minor muscles. Contraction of Pd1 would both depress the limb and cause the coxa to promote. In figure 16 the effects of PdH3 and PdH4 are considered. If these contracted they would pull the heel anteriorly, further away from the mid-line. Contraction of Pd1 would still rotate the coxa in a promotory direction but the initial mechanical advantage would be greater than that illustrated in the previous figure when PdH3 and PdH4 were passive (c.f. Fig. 15b and Fig. 16b). For an equal amount of force exerted by Pd1, the coxa would be promoted more when PdH3 and PdH4 contract, than if these muscles were passive. In the third situation (Fig. 17) the effects of Pd2, PdH5 and PdH6 are considered. If these contracted the heel and tendon blade would be pulled across the T-Cx pivot into the posterior side of the midline (Fig. 17b). Contraction of Pd1 would now cause the coxa to rotate in a remotory direction (Fig. 17c).

These figures explain the principles involved when lines of forces cross over pivot points. In Carcinus the problem is further complicated since it occurs in 3-dimensions. The Cx-BI and T-Cx pivots are not at right angles to each other as suggested in figures 10 to 17 and the degrees of joint movement are not as extreme.

FIGURE 14

THE BI POSTERIOR DEPRESSOR MUSCLE

This diagram illustrates the nature of the BI Posterior depressor muscle and the attachment of the muscle's subdivisions. The plan elevation illustrated in all the figures (Fig. 14 to 16) is based on the situation of 3 tubes as before. The segments represent the thorax, coxa and BI, and the muscle subdivisions are represented by lines 1 to 6.

The heel attaches anteriorly to axis YY at point a. The tip of the heel is attached to the main tendon blade by a flexible link at point X. Pd1 originates at point b in the thorax. The heel has 4 muscles inserting onto its two faces. Two of these muscles originate on the anterior side of axis YY, that is PdH3 and PdH4, while two originate on the posterior side of arc YY, that is PdH5 and PdH6.

The main part of the muscle, Pd1, acts directly along the line of the tendon blade. Pd2 inserts onto the proximal end of the tendon and originates in the proximal region of the thorax, posteriorly to the midline.

CHAPTER 4 FIGURE 14

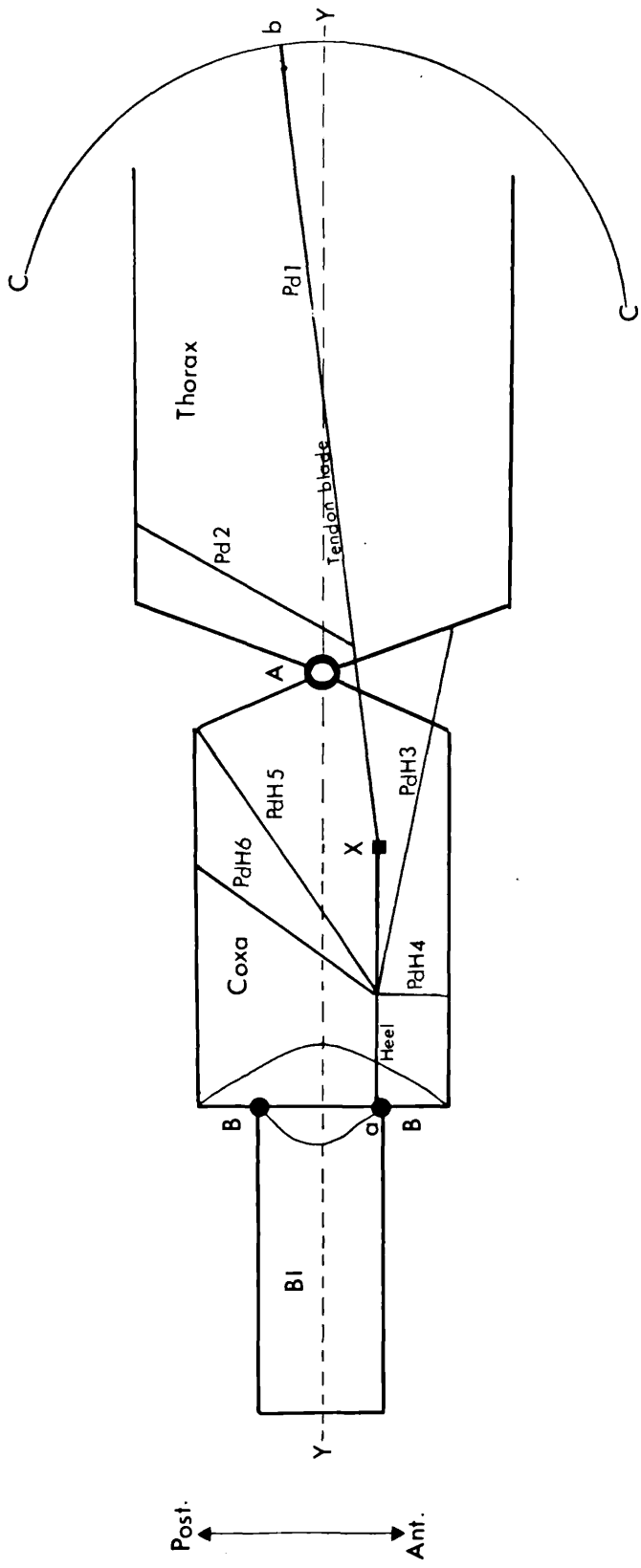


Fig.14

FIGURE 15

THE MECHANICAL ACTION OF Pd1

This diagram illustrates the mechanical action when Pd1 contracts with no interference from the other muscle divisions. In this situation the minor muscles are considered to be passive. The direction of force by Pd1 will act from point X, the link between the tendon blade and heel (Fig. a). Contraction of the muscle will depress the BI and also promote the coxa, because the line of force lies to the anterior of line YY, that is anterior to the T-Cx pivot (Fig. b).

CHAPTER 4 FIGURE 15

Fig.15

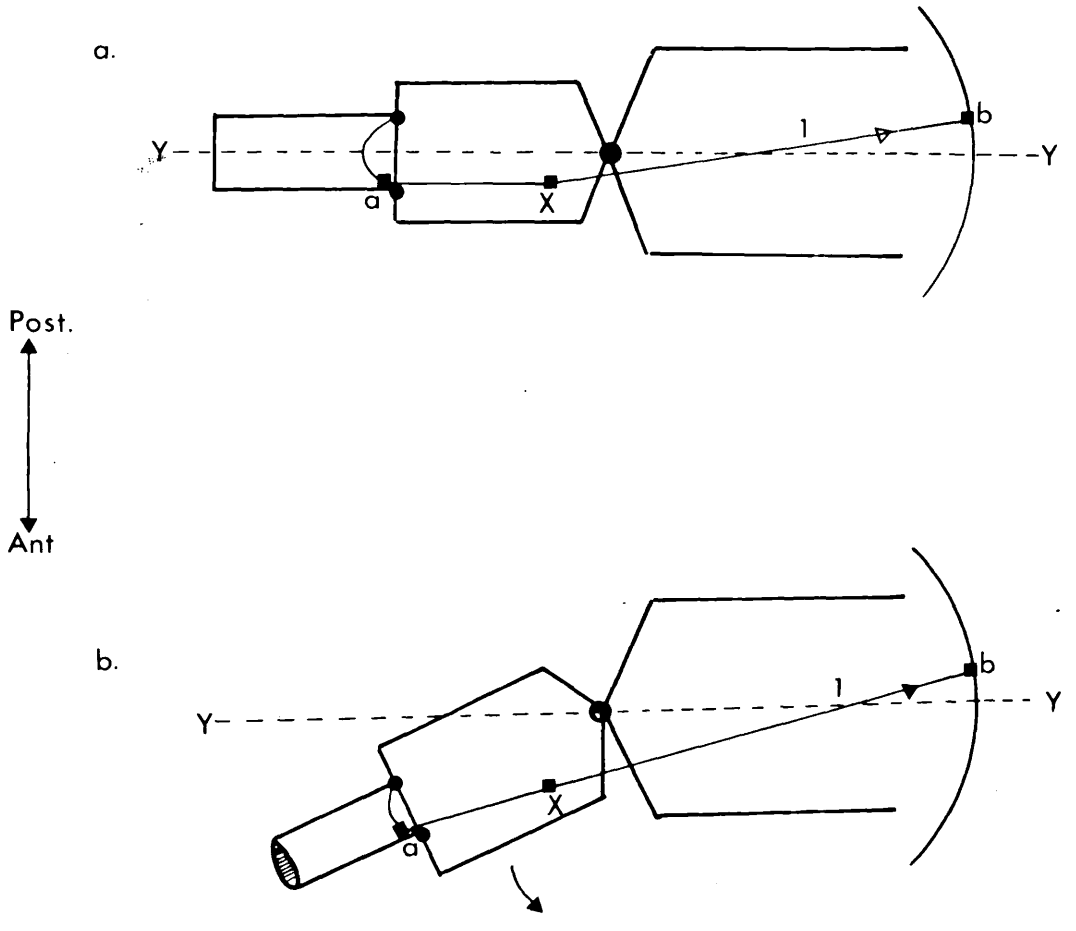


FIGURE 16

THE INFLUENCE OF PdH3 AND PdH4 ON THE MECHANICAL ACTIONS OF Pd1

These diagrams illustrate the possible influence of muscles PdH3 and PdH4 (Fig. a). If they exerted a force upon the heel they would pull this and the attached tendon more anteriorly from the midline (Fig. b). Subsequent contraction of Pd1 would cause a force to be developed along the new line X-b which lies anterior to the midline and the coxa will, therefore, be promoted (Fig. c). The mechanical advantage for promotion is initially large in comparison to the situation in Fig. 15 because of the influence of PdH3 and PdH4 (c.f. Fig. 15b).

CHAPTER 4 FIGURE 16

Fig.16

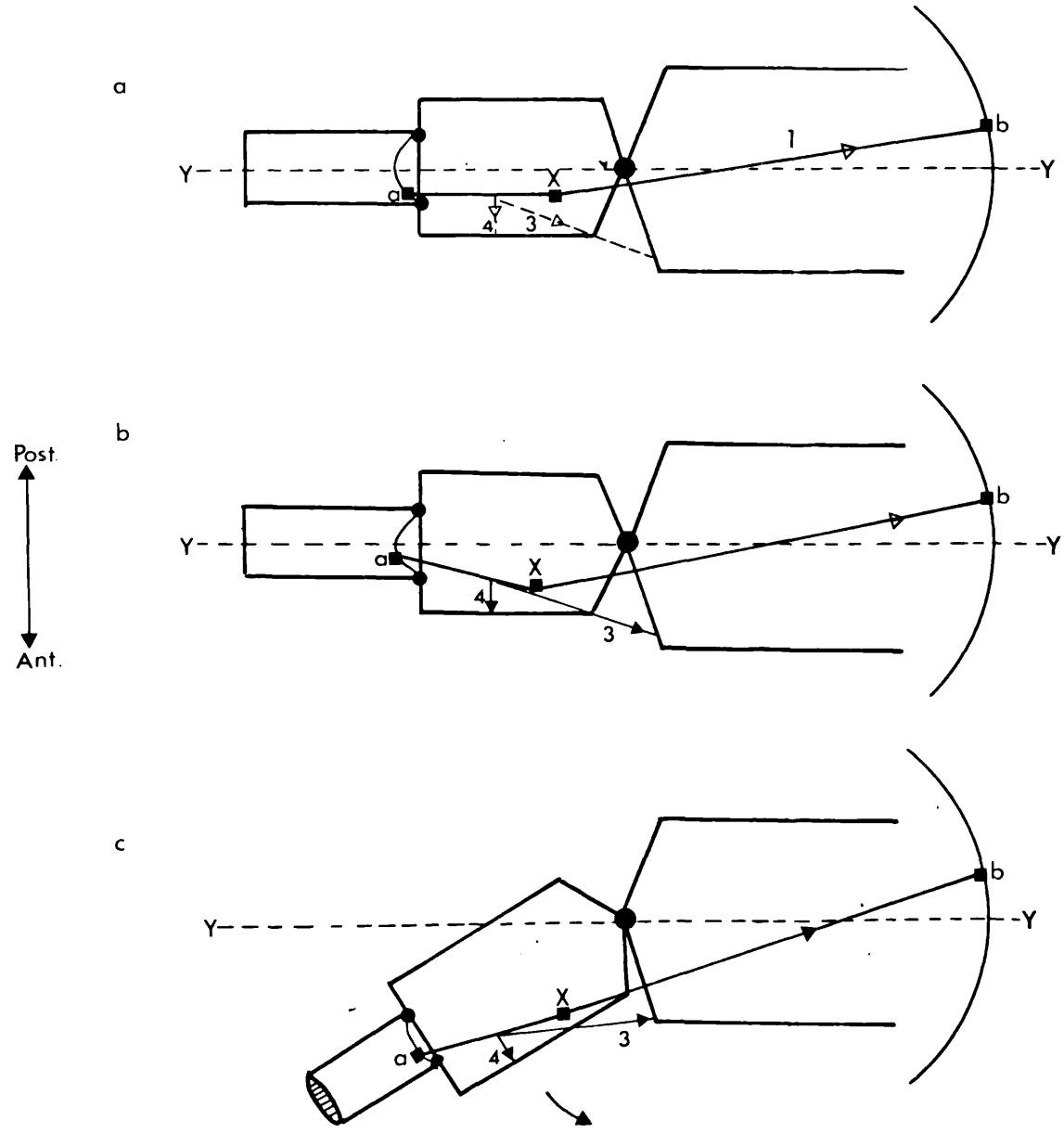


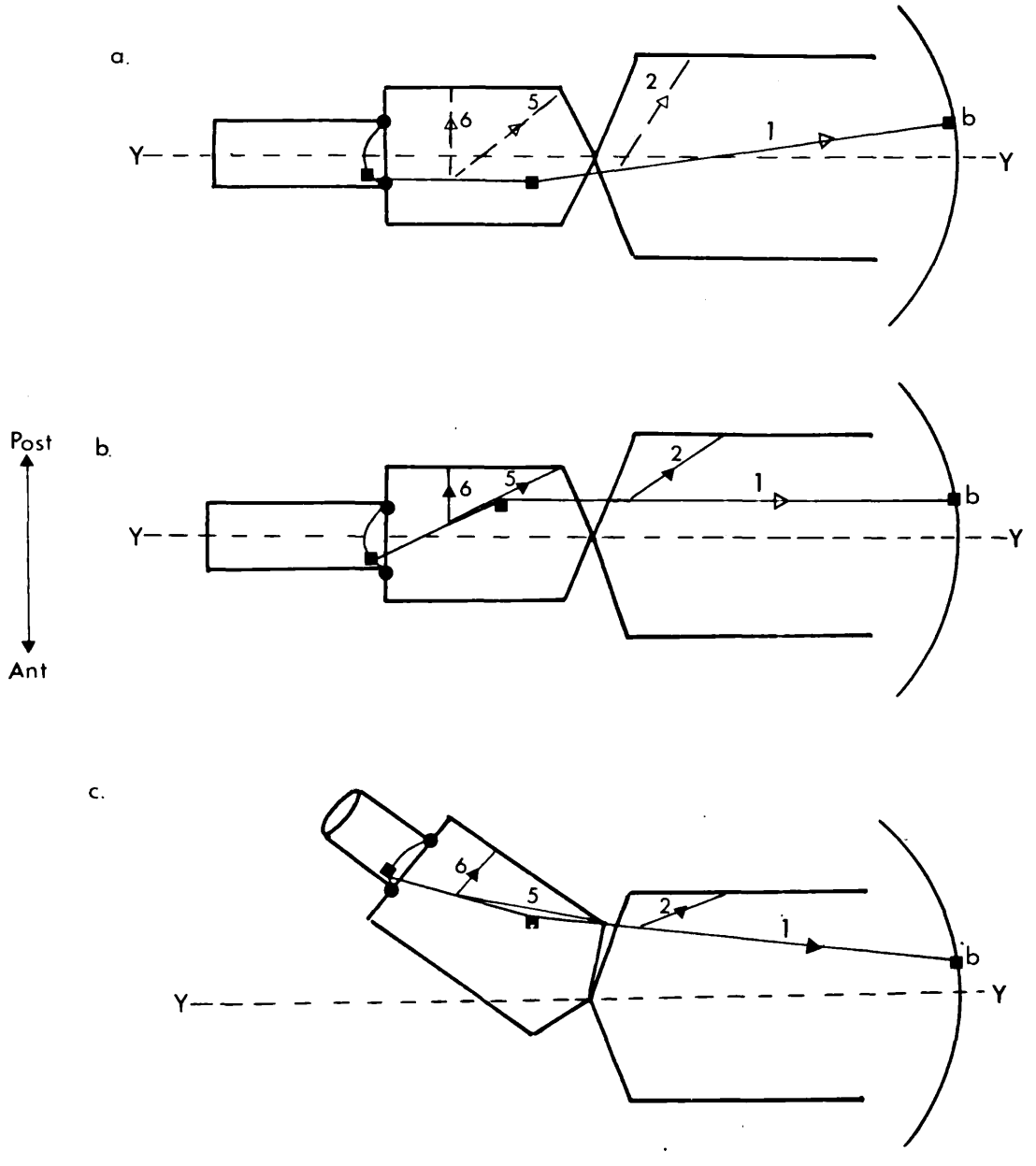
FIGURE 17

THE INFLUENCE OF Pd2, PdH5 AND PdH5 ON THE MECHANICAL ACTION OF Pd1

These diagrams illustrate the possible influence of muscles Pd2, PdH5 and PdH6 (Fig. a). If these muscles exerted a force upon the tendon and heel they would pull Pd1 across the T-Cx pivot (Fig. b). Contraction of Pd1 would now act along the new line X-b which lies posterior to the midline and therefore the coxa will be remoted. (Fig. c).

CHAPTER 4 FIGURE 17

Fig.17



Pd1 shortens through all degrees of BI depression when the coxa is held stationary. Therefore it is certainly a BI depressor muscle. However if the BI is held stationary and the coxa rotated, a different effect is observed. As the coxa is promoted, Pd1 shortens, as does Ad. This indicates that both muscles exert a promotory effect on the T-Cx joint. At a few degrees from full promotion, the flexible link between the Pd heel and tendon lies directly in line with the T-Cx axis. At this point any length change in Pd1 ceases. If it contracted in this position its effect would only be to depress the BI, as described in figure 12A. When the coxa is promoted by a few more degrees, the heel and flexible linkage suddenly flips over into the posterior side of the T-Cx axis, and Pd1 begins to lengthen. This indicates that it now has no promotory influence on the coxa,instead if it contracted it would rotate the coxa in a remotory direction. This increase in length continues to full promotion of the coxa. If the coxa is now moved back in a remotory direction, Pd1 begins to shorten, confirming its tertiary role as a coxal remotor. When the point of coxal rotation is reached at which the Pd tendon passes directly through the T-Cx axis, the length change of Pd1 stops again. Continued remotion of the coxa causes the heel and flexible link to flip back into anterior side of the T-Cx axis, and Pd1 begins to lengthen. It would therefore resume its role as a coxal promotor.

This feature was complicated even further. If the BI is held at increasing angles of depression during rotation of the coxa, the heel not only flips over earlier, but the length change of the remotory-acting Pd1 also increases, during depression of the BI. This indicates that the remotory action of Pd1 on the coxa will be greater as the BI is depressed. To explain this the limb was carefully removed from the T-Cx pivots and was viewed end on, down the arm (Fig. 18). As the BI is depressed part of the Pd heel insertion crosses over the T-Cx axis. This alone would tend to make the Pd less promotory because the mechanical advantage for promotion would progressively decrease with BI depression. When the decreasing advantage is coupled with the remotory role caused by the crossing over of the T-Cx axis, it is clear that the mechanical action of the Pd on coxal rotation is very complex indeed.

Therefore the BI Posterior depressor muscle is extraordinary in being capable of three different mechanical functions. It can depress the BI, it can promote the coxa and it can function as a coxal remotor within certain degrees of T-Cx joint. The point at which the last two functions change is also affected by the angles of BI depression. This is summarized on table 1.

FIGURE 18

This diagram illustrates the reason for a decrease in promotory mechanical advantage of the Posterior Depressor muscle during depression of the BI segment. Adt, Anterior depressor tendon head; Alt, Anterior levator tendon head; Ant, anterior; ap, Cx-BI anterior pivot; Cx, coxa; dp, T-Cx dorsal pivot; Pdt, Posterior depressor tendon head; Plt, Posterior levator tendon head; Post, posterior; pp, Cx-BI posterior pivot; vp, T-Cx ventral pivot. 1 represents the situation when the BI is fully levated, 2 represents the situation when the BI is fully depressed. The horizontal dotted line indicates the T-Cx pivot axis.

The cheliped was carefully removed from the T-Cx articulation and viewed end on. The figure is a scaled drawing of the situation when the BI is held levated and depressed. When the BI is levated,the Pd heel insertion lies anterior to the T-Cx axis. Contraction of the muscle would therefore cause promotion of the coxa. As the BI is depressed, the heel insertion moves progressively towards the T-Cx axis, therefore effectively decreasing the promotory mechanical advantage of the muscle. At full depression the midline of the insertion lies on the T-Cx axis, which would give a very small, if any, promotory mechanical advantage.

CHAPTER 4 FIGURE 18

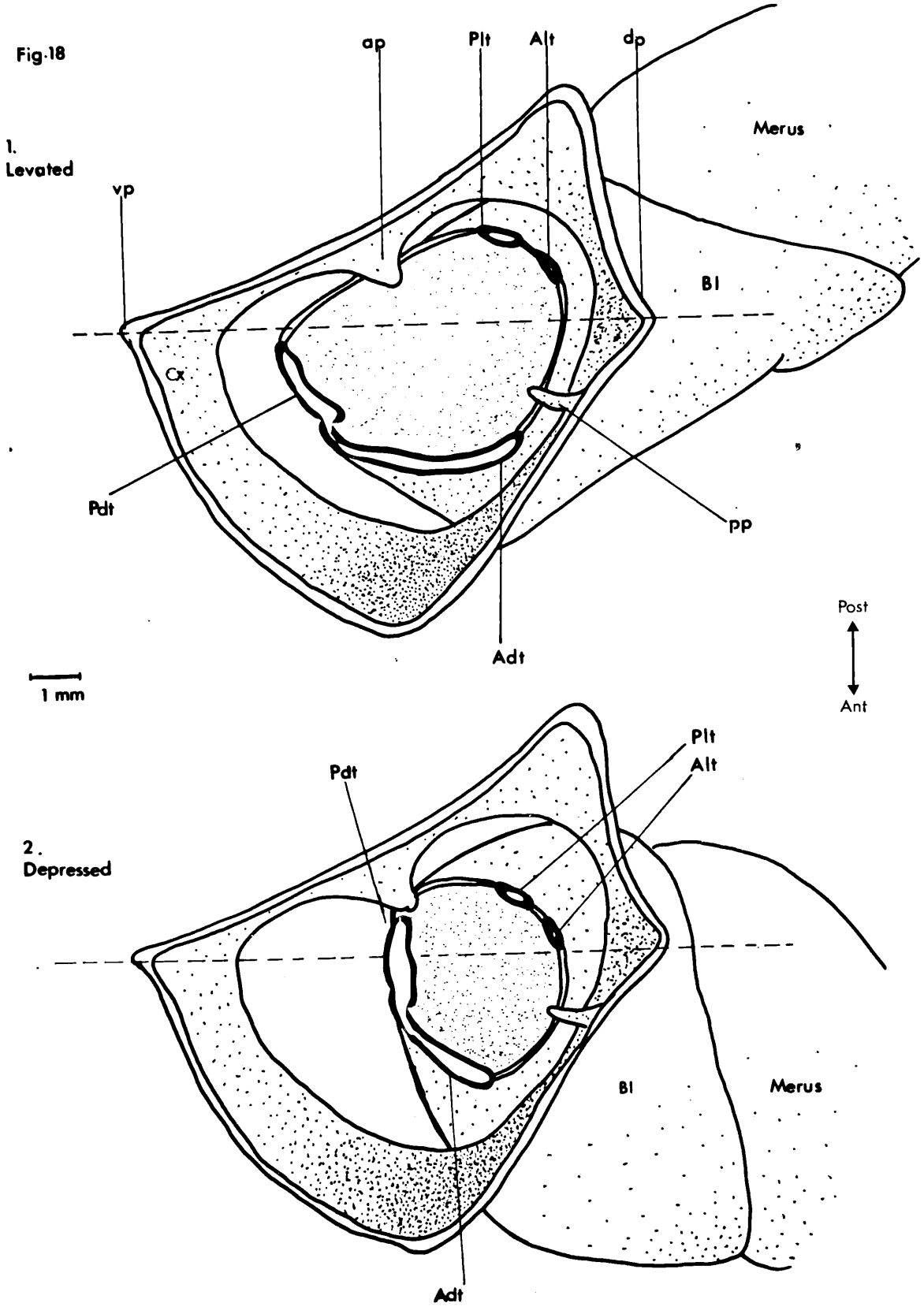


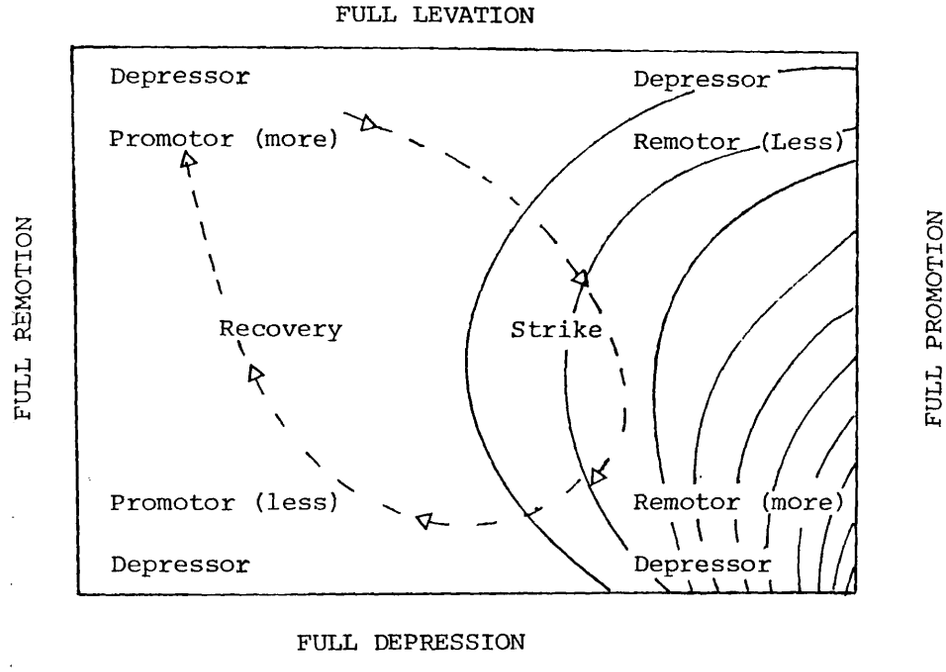
TABLE ONE

THE MECHANICAL ACTIONS OF THE BI POSTERIOR DEPRESSOR MUSCLE

DORSAL

COXA REMOTED
BI LEVATED
(Joint positions at threat)

COXA PROMOTED
BI LEVATED



COXA REMOTED
BI DEPRESSED

COXA PROMOTED
BI DEPRESSED
(joint positions at strike)

VENTRAL

This table illustrates the 3 actions of the BI Posterior depressor muscle during all the extremes of movement of the T-Cx and Cx-BI joints. The muscle always causes depression of the BI but, depending on the position of the T-Cx joint, it will have a promotory or remotory effect on the coxa. The extent of these 2nd and 3rd mechanical actions is dependent on the degree of BI depression. This is indicated in the table. The dashed lines indicate the direction these mechanical effects would take during strike and recovery movements. The curved lines indicate the area in the table at which the Pd would act as a coxal remotor. The amount of remotory influence is represented by the contours of these lines.

DISCUSSION

A summary of the mechanical actions of the coxa and BI is shown in table 2. From these results some suggestions can be made concerning the means by which a fast strike could be achieved. There may be the use of the bistable position about the T-Cx axis, there may be the use of the dually and triply functioning BI muscles or both. It is possible that they may both contribute in different parts of the strike behaviour.

The mechanical advantage values, d, were multiplied by the maximum muscle force values which were obtained during the neuromuscular analysis (Chapter 3, section 2). This allows the calculation of the moments about the joints, that is force x distance. It is accepted that the maximum values recorded from the experiments may not be the maximum forces that the muscles are capable of exerting, because the equipment used was not adequate for such estimations. However since all the muscles were tested using the same equipment and technique, all the values obtained should be relatively correct if not quantitatively correct. The maximum values obtained were:

Coxa remotor muscle, 10.0 gm
Coxa promotor muscle, 9.0 gm
BI Anterior levator, 7.75 gm
BI Anterior depressor, 9.25 gm
BI Posterior depressor, 9.0 gm

The moments of the BI muscles are shown individually on figure 19. The moments of the coxal muscles and the moments of the BI muscles which would occur during a strike are shown on figure 20.

Fig. 20, 1 shows that multiplying the mechanical advantages with the forces which the two coxal muscles can exert does not alter the feature of a bistable articulation, although the point of instability is now reached when the coxa is promoted to 38^{o}. Therefore the point of instability may still be used in the production of a strike. However if the CxR developed maximum tension before strike, the cheliped could not be promoted solely by the action of the CxP, the bistable condition would act as a stop upon promotion. That is, unless the T-Cx joint was promoted more than 38^{o}, a maximally contracting CxR muscle would prevent coxal promotion. This stop would be more effective if the A1 also contracted before a strike, since its remotory effect on the coxa would add to that of the CxR. This would further increase the remotory moment about the joint.

TABLE TWO

MUSCLE	PRIMARY ACTION	CONTRIBUTORY ACTION ON THE T-Cx JOINT
DORSAL COXA REMOTOR	Remotion of coxa	
VENTRAL COXA REMOTOR	Remotion of coxa	
COXA PROMOTOR	Promotion of coxa	
BI ANTERIOR LEVATOR	Levation of BI	Remotion of coxa
BI POSTERIOR LEVATORS	Levation of BI Autotomy of limb	
BI ANTERIOR DEPRESSOR	Depression of BI	Promotion of coxa
BI POSTERIOR DEPRESSOR	Depression of BI	Promotion and remotion of coxa
BI LESSER POSTERIOR DEPRESSOR	Depression of BI	

Therefore this leads to the question of what actually starts the strike. It may be that the CxR does not contract maximally before the strike. It would therefore have decreased moments about the joint. The moments of the CxP may then be greater than those of the CxR for a wider range of T-Cx joint position. If the moments of the CxP were greater over all degrees of coxal position, a strike could be produced simply by contraction of the CxP. However it has been demonstrated that the CxP develops tension slowly (Chapter 3, section 2), and therefore its action alone could not cause the limb to reach the known high angular velocities of the strike (Chapter 2, Fig. 6).

Figure 5, chapter 2, demonstrated that the limb is promoted slightly during pre-strike. If the moments of the coxal muscles exactly fitted the situation illustrated in figure 20, 1, then increasing promotion of the coxa would progressively reduce the difference between the promotory and remotory moments. It has also been shown that the limb is depressed slightly during pre-strike (Fig. 5, chapter 2). This may be due to relaxation of the levators or contraction of the depressors. If the depressors were active, they would influence the rotation of the coxa and cause promotion.

Therefore the dual mechanical action of the depressors could lead to the beginning of the strike. The combined promotory moments achieved when the Ad, Pd and CxP muscles contract may eventually exceed the combined remotory moments of the CxR and Al. Once the bistable position has been crossed the limb will be flipped in a promotory direction and a strike will begin.

If only one depressor muscle could be used to suddenly increase the promotory moment of the coxa, it would be advantageous for this muscle to have a high mechanical advantage and moment over the pre-strike period. As indicated in figure 20.2, this is only displayed by the Ad. Its moment increases during pre-strike and then decreases only at the beginning of coxal promotion.

The observed behaviour of pre-strike twitches supports this suggestion that the depressor muscles contract before the strike. From a Three-Quarters or Full Threat display, the chelipeds may be rapidly twitched forwards and downwards to pre-strike positions. If these movements were caused solely by the CxP generating sudden and extra tension, possibly due to the secondary spike responses and muscle twitch responses caused by the phasic axon, there would be no depressory component to the pre-strike twitch. It is more likely that these twitches are due to both contraction of the CxP and contraction of the depressors. The tension developing in

FIGURE 19

MOMENTS OF THE BI MUSCLES ABOUT THE Cx-BI JOINT

The abscissa represents the degrees of BI depression, the ordinate represents the moments of the 3 BI muscles about the Cx-BI joint in gram cm. The moment was calculated by multiplication of the measured maximum force capabilities of each muscle with the mechanical advantage value d. As before, thick lines, closed circles represent the situation when the coxa is held fully remoted, and thin lines, open circles represent the situation when the coxa is fully promoted.

The graphs indicate that the moments of the Ad are always greater than those of the Pd. Also the Ad moments increase for the first 25^{o} of BI joint depression whereas those of the Pd decrease throughout depression. The moments of the Al are always greater when the coxa is promoted than when it is remoted.

These graphs allow the calculation of the projected moments that would occur during the strike and recovery movements. The moments and directions are indicated by the dotted lines in the figures.

CHAPTER 4 FIGURE 19

Fig.19.

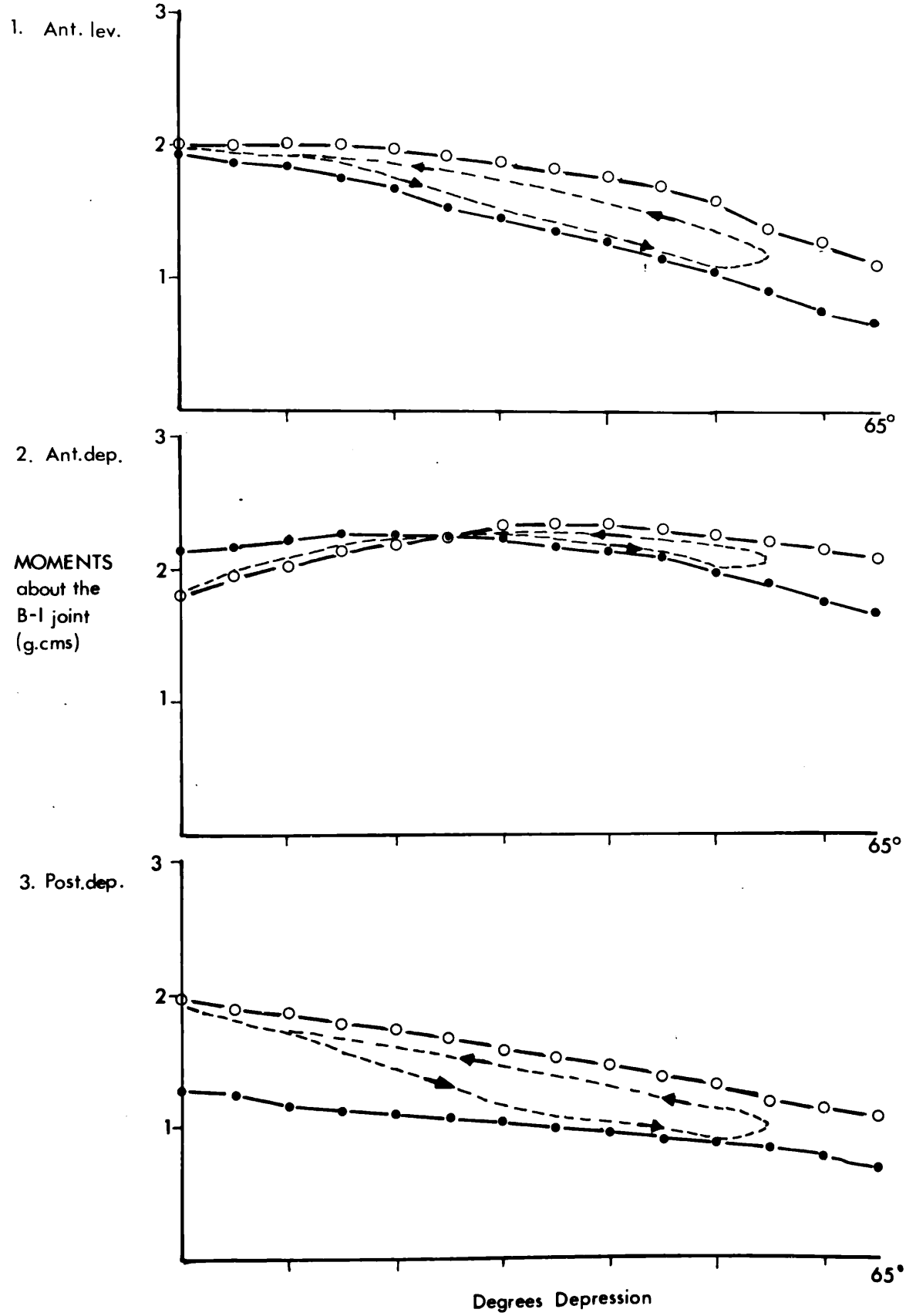


FIGURE 20

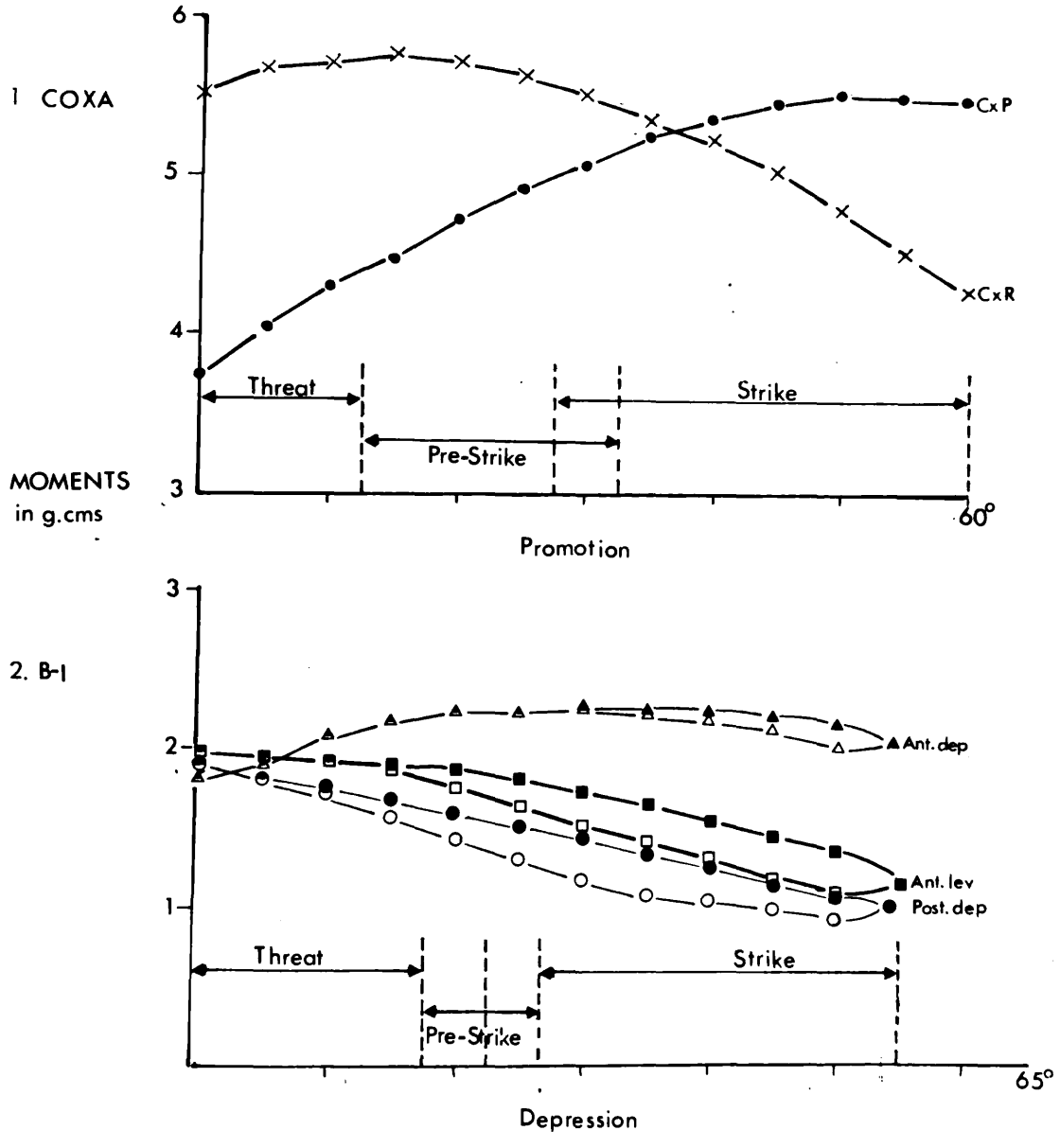
MOMENTS OF THE FIVE MAIN COXA AND BI MUSCLES

Graph 1 illustrates the moments of the coxal muscles about the T-Cx joint. The CxR has a high and increasing moment during the positions adopted in threat. At these stages the CxP has low but rapidly increasing moments. It can be seen that there is still a bistable position. This point may be used in the performance of a fast strike as discussed in the text.

Graph 2 illustrates the projected moments of the BI muscles which would occur during a strike and recovery action. The triangles represent the Anterior depressor muscles, squares represent the Anterior levator muscle and circles represent the Posterior depressor muscle. Open symbols are moments which occur in the direction of strike and closed symbols are moments which occur in the direction of recovery. Half closed symbols represent points where the moments of the two muscles co-incide. It can be seen that the Ad has the greater moment of the two depressor muscles. Its moments also increase to the positions of the joint which are adopted before a strike. The moments of the Pd decrease during the whole strike movement but are greater and increase during the recovery stage. It is therefore possible that its tertiary role as a coxa remotor may be used during the re-extension of the cheliped after the strike. The moments of the Al do not alter much during the positions of threat. This is similar to the moments of the CxR.

CHAPTER 4 FIGURE 20

Fig. 20.



the depressors may be sufficient to cause a slight movement to the cheliped at this stage in the behaviour, but not to cause the whole strike until peak tension levels have been achieved and the bistable point exceeded.

The pre-strike twitches also indicate that muscle tension in the depressors may not be generated smoothly but in sudden and short bursts. In this way the bistable point may not be reached and crossed gradually, but abruptly because of the sudden injection of extra promotory moments from the depressors.

The calculation of energy that is required to produce cheliped re-extention during recovery from strike, has shown that there must either be contraction in another coxal or BI muscle adding its force to that of the two remotors and two levators, or that there must be energy storage to produce the high angular velocities achieved during this movement. It is unlikely that the CxR could develop and store sufficient tension during the strike. If it was to do this it would have to contract maximally during the strike and would, consequently, considerably slow cheliped promotion. This is obviously not to the advantage of the crab because the whole behaviour is based on fast flexion and immediate re-extension of the cheliped.

Another fact which makes it unlikely that tension is developed in the CxR during a strike, is the duration of the behaviour. There is only 30 to 60 ms between the beginning of coxal promotion and the beginning of coxal re-extension. If the CxR was to relax, allowing fast promotion, and then contract to develop sufficient tension before re-extension, it would have to be an extremely fast muscle. It has been shown that this is not so (Chapter 2, section 2). The Al is unlikely to store energy for strike recovery for the same reasons.

Another possibility for producing the strike recovery movement, is the involvement of the Posterior depressor muscle. All three mechanical roles of this muscle, could contribute to the strike and recovery movements. If the muscle contracted during the strike it would aid in promoting the limb as well as depressing it. If tension was maintained after the Pd tendon had crossed over the T-Cx pivot, the Pd would continue to depress the BI but would now begin to cause remotion of the coxa.

This suggestion of Pd involvement is supported by the angular excursion taken by the coxa and BI at the end of coxal promotion. The BI continues to be depressed when the coxa has begun to re-extend (Figs. 6 and 7, chapter 2). Therefore the Pd may still be contracting at this stage. Thus it is very likely that all three roles of the Pd are used in the performance of a fast strike behaviour.

Muscles can contract isotonically or isometrically. In the former situation only one end of the muscle is firmly held. Thus the muscle is free to contract as it develops tension. The velocity of shortening is a function of the load, following Hill's characteristic equation and force-velocity curve (Hill, 1938). In an isometric contraction the muscle is firmly held at both ends and so little, if any, shortening occurs during tension developemnt. When the load preventing shortening is removed, the tension developed in the muscle will be suddenly released and the muscle can contract rapidly. This type of contraction was demonstrated by Gasser and Hill who termed the feature a quick-release contraction (Gasser and Hill, 1924). When a muscle is freely attached to a load and is excited, it will begin to contract isometrically until the tension produced by the muscle is equal to the load. It will then begin to shorten and move the load. From now on the load on the muscle, and therefore the tension developed, is constant and so the contraction is isotonic.

Loads, which prevent the shortening of a muscle, are often used to produce rapid limb movements. For example in Squilla the load is a skeletal click mechanism (Burrows, 1969) while in Alphaeus californiensis the load is produced by two discs located in the claw (Ritzmann, 1974). The load may also be muscular, when a muscle can contract against its antagonist. In this latter case a muscle which is beginning to develop tension, muscle A, may not be able to express its tension and, therefore, may not be able to contract freely if its antagonist, muscle B, was contracting more powerfully. Thus muscle A will develop tension isometrically. This will continue until muscle B relaxes in which case the load preventing muscle A from shortening is removed, and the muscle can contract rapidly by virtue of the quick-release mechanism.

This feature of co-activation of muscles allowing isometric contraction may be used in the rapid cheliped re-extension. If the Pd does continue to contract after coxal promotion, so exerting its remotory action on the coxa aiding strike recovery, the Al could begin to contract against this antagonistic load while the limb is still being depressed. Therefore the Al will be contracting isometrically. When the Pd finally relaxes, this isometric tension may be quickly released and the BI will be abruptly levated. Continued contraction in the Al will be isotonic and so will continue to levate the BI. This isometric contraction before the end of depression may ensure that the limb is raised as soon as depression stops. That is, there will be no pause at the end of the strike which may otherwise occur if the Al had to develop sufficient tension to lift the cheliped load by virtue of isotonic contraction only.

Therefore although there appears to be no skeletal stops allowing energy storage, as in Squilla (Burrows, 1969) or the locust (Bennet Clark and Lucey, 1967), or muscular specializations as in swimming crabs (Hoyle and Burrows, 1972), Carcinus could perform the fast strike behaviour by a combination of co-activation of antagonistic muscles and utilization of modified joint geometry. To co-ordinate these features and to produce a definite behaviour pattern which is the same from individual to individual, there must be a strict neural control on the sequence of muscle activity. This sequence of activity was examined in the next section using electromyographic techniques. These were employed in an attempt to solve the remaining questions concerning the cause of the fast strike action and the contributions of all the muscular and mechanical features which have been demonstrated in this and the preceeding chapters.

CHAPTER 5

THE ELECTROPHYSIOLOGY OF THE FAST STRIKE

INTRODUCTION

Electromyographic techniques have been widely used for investigations into regular patterns, such as locomotion, and other appendage movements, such as the rhythmic beating of the scaphognathite (Young, 1975). Electromyograms (EMG's) were recorded from the dactylus, propus and carpus muscles of the walking legs during normal walking in Cancer magister (Atwood and Walcott, 1965). Transducers, comprised of small wire coils, were fastened to the legs and allowed continuous monitoring of limb position. During unspecific movements, the patterns of electrical activity in the muscles was labile but during walking, regular patterns were observed and the muscle activity was more rigidly organized.

In slow walking movements it was found that muscle potentials recorded from the carpus extensor, propus extensor and dactylus opener muscles, were in phase during leg extension, whereas the potentials in the flexor muscles were in phase during leg flexion. There was little overlap of activity between antagonistic muscles at this slow speed of movement. In muscles innervated by both phasic and tonic axons, the latter was normally more active. There was marked inhibition at the beginning of bursts in the dactylus opener and propus extensor muscles with moderately fast walking.

A more detailed study on the crab Carcinus was undertaken by Clarac and Coulmance (1971), who studied both normal lateral walking and the effects on muscle activity and leg position during disruption of this pattern. EMG's were recorded from the carpus and BI Anterior levator muscles of the walking legs. It was found that sideways walking is accopanied by several features in muscle activity of the trailing and leading legs. Such features included the synchronous action of levation in the trailing legs, flexion of the distal segments and levation, extension and closing of the leading legs. Each movement in this series was achieved by alternation of antagonistic leg muscles.

When the normal walking patterns were disturbed, by securing the joints in various positions, different sequences of muscle activity and leg positions were observed. When the merus-carpus joint was fixed in an extended position, for example,the typical synchronous muscle activity from the BI Anterior levator and carpus flexor muscles in the trailing legs was prolonged, and the legs were levated more than usual. In the leading legs the opposite effect was observed. The leg remained depressed on

the ground and levator muscle activity was minimal. The authors established that the patterns of locomotion are dependant upon the sensory input from the chordotonal organs spanning the M-C joint, since these patterns disappear when these proprioceptors are destroyed. Thus there are proximally directed reflexes from the M-C chordotonal organs to the motorneurones governing the levator and depressor muscles of the coxal-BI joint.

EMG's have also been used for analysis of irregular, non-rhythmic behaviour patterns, such as escape, or defensive and aggressive movements. The use of EMG's in the rapid escape behaviour of Portunus sanguinolentus allowed the elucidation of the roles of specific parts of a muscle (Hoyle and Burrows, 1973). When this crab is suddenly startled it responds with a rapid, backward escape swimming movement. These movements were distinguishable from ordinary fast swimming as they were so powerful. The authors stated that attempts to grasp the crab often caused the animal to leap back out of the water. The physiological basis of the behaviour was described in Chapter 4.

The defensive behaviour of the snapping shrimps (Ritzmann, 1974) was also described in Chapter 4, and the predatory strike behaviour of Squilla was described in Chapter 2. In both of these agonistic interactions, EMG recording techniques were used to analyse the physiological basis of the behaviour, and showed that the rapidity of the movements is achieved by isometric contraction of muscles. Muscles which contract isometrically against skeletal locking mechanisms, utilize the characteristic force-velocity curve (Hill, 1938) and quick-release feature (Gasser and Hill, 1924) described in Chapter 4. Thus if a muscle can contract against a load it can continue to develop tension to maximum tetanic levels. When the load is removed, the full tension built up in the muscle can be rapidly released. It has previously been shown by cinematographic techniques that Carcinus maenas also performs a fast strike (Chapter 2). As in Squilla this happened too quickly to be achieved by muscles only beginning to contract at the beginning of the strike. Anatomical and mechanical investigations have shown that the effects of some of the BI muscles of the cheliped, are complex (Chapter 4), particularly their mechanical advantages and action upon the T-Cx joint. Before any conclusion could be made concerning the individual contributions of these effects, EMG techniques were employed to obtain the temporal sequence of muscle activity. In the following chapter the data concerning the fast strike is collated and suggestions are made as to how the fast strike is operated.

MATERIAL AND METHODS

Large, intact male crabs were obtained from the Marine Biological Station at Millport, Scotland. They were maintained in tanks of circulating sea water at 15°C in an aquarium.

Small lightweight plastic screws were stuck onto the dorsal carapace of the crab with a quick action epoxy resin (Devcon 5-minute Epoxy Resin), which allowed the crab to be suspended over a tank and angled mirror as previously described (Chapter 2). A small Perspex plate was inserted between a nut on the screw and the supporting rod..

Sub-miniature plugs and socket connectors (Radiospare Components, London) were inserted into holes drilled in the Perspex holder. The top end of the plugs were soldered to single core insulated wires. These could be separately connected to a low-impedance Pre-amplifier which was connected to the top beam of a Tetronix 502 A oscilliscope.

Lengths of Trimel coated 100 μm silver wire (Specialized Laboratory Equipment, Croydon, Surrey) were soldered into the lower end of the plugs. The wires were then cut so that they were bared at the tip. Any junctions between wires and connectors were insulated and made water tight by coating with a multi-purpose adhesive (Radiospare Components).

The Perspex plate could be manoeuvred and the lengths of wires adjusted, so that any muscle of the cheliped could be reached. The free ends of the wires were inserted through the arthrodial membranes between the joints and into the muscles. Correct placement of these electrodes was verified when recorded muscular activity co-incided with observed movement of the relevant segment. Occasionally the wires were cut from the plugs and the crabs subsequently dissected to confirm that they were in the correct muscle.

Since the BI Posterior levator muscle is comprised of 3 small groups (McVean and Findley, 1976), it was not possible to determine in which specific group the electrode was situated, without subsequent dissection or damage to each crab. Thus the term Posterior levator, Pl, in this and following chapters indicates the responses recorded from the muscle as a whole and not from specific groups of the muscle. Recordings from the BI Posterior depressor muscle were taken from Pd1.

Movement of the cheliped segments was filmed as before (Chapter 2), using a Beaulieu R16 ciné camera which was positioned in front of the tank. To heighten the definition during movement, white lines were painted onto the limb segments using Liquid Tippex.

A photodiode was placed behind the eye piece of the camera. This was connected, via a Pre-amplifier, to the lower beam of the oscilloscope. Each time the camera shutter opened, the photodiode registered an a.c. deflection on the oscilloscope trace. Therefore the position of the joint in each frame of film could be directly correlated to muscle activity. To conserve film, the ciné camera was only operated before an expected strike. Film speeds of 16, 25 and 32 fps were used. Movement of the segments about their joints was measured as before (Chapter 2), using enlargements obtained from the negatives.

A Ferrograph tape recorder, Series F, Model 722 allowed storage of the records. These were later recorded on film using a Telford camera. Analysis of the EMG's and spike counts were performed manually from these films, using an enlarger.

This method of correlating muscle activity with film meant that the crabs were not burdened with sensors or monitors on the limbs which may otherwise have impeded the strike. The only difference between this neurophysiological preparation and the previous behavioural one was the insertion of the thin wires into the cheliped muscles. As no difference in strike speed or angular excursion was found, it was concluded that the crab's behaviour was not disturbed by these wires.

In all the figures the following features are illustrated:

1. Recordings from individual muscles during the strike are shown on the upper beam of the EMG traces. The lower beam of each EMG shows the photodiode recording from the ciné camera which registers each time the camera shutter opens and therefore indicates each frame of film.
2. Below the EMG's is a line which indicates the portion of the trace shown in the enlargements.
3. The top graph is a frequency histogram of muscle impulses per second, ips, within the time occupied by each frame of film.
4. The second graph indicates the position of the limb joints. The upper graph represents the movement of the joint under study (thicker lines, scale in degrees on the left), and the lower graph represents the movement of the reference joint during the strike (thinner lines, scale on the right). This reference joint is the T-Cx except in figures 11 and 12, when it is the Cx-BI joint.
5. In all the figures except for those of the dactylus and merus, the third graph represents angular velocity (A.V) of the segment under study. This scale is in degrees per second. Positive values above zero represents movements in the direction of the strike, that is flexing and depressing movements, while negative values below zero represents movements of the

joint in the anti-strike directions of cheliped extension and levation.

6. The time of rapid coxal flexion, that is the strike mode, occurs within the 2 lines indicated below each trace and graph.

RESULTS

Representative EMG's from each muscle during a filmed strike are shown on figures 1 to 12. The positions of both the segments under study and the thorax-coxa joint in each frame of film are shown below the EMG's (thick and thin lines on the figures). The excursion of the T-Cx joint was used as a reference for each strike so that the time of coxal movement could be compared to the time of movement and position in the other joints. In the case of the two coxal muscles the "reference" graph is of the Cx-BI joint. Since the position of the BI-Merus joint could not be measured from the films, the position graph in the case illustrates the movement of the T-Cx joint only.

The EMG's were analysed and plotted in a histogram form of impulses per second (ips) within the time occupied by each frame of ciné film. The angular velocity of the joint under study is also shown on the figures. Samll enlargements of the traces show the muscle activity just before the strike, in greater detail.

One of the most significant results from this analysis was that a strike is certainly not achieved by simple rhythmic activity from antagonistic muscles. In all the muscles studied there was some overlap in antagonistic muscle activity, the extent of which varied considerably depending on the specific joint and muscle in question. Another significant feature was the similarity of the EMG's from crab to crab. At least 30 recordings during strikes were made from each muscle and in the case of the coxal and BI muscles considerably more, over 50 recordings for each muscle. These were all stored on tape and subsequently examined, and selected recordings were chosen for more detailed analysis. From these, one recording was selected as the most representative of the pattern of muscle activity. Although the number of spikes varied with electrode placement, the pattern and timing of muscle activity was rigid.

There are 4 clearly distinguishable modes of muscle activity and joint movement in the strike behaviour. These are the threat modes, both before and after strikes; the pre-strike mode, between the end of threat and the beginning of rapid flexion; the strike mode, during which the cheliped is rapidly flexed and depressed; and the recovery mode during which the cheliped is re-extended back to threat positions.

The muscles of the cheliped can be divided into 2 groups. These are termed "strike" and "anti-strike" muscles. The former category is given to the muscles which are involved in flexing and depressing the limb, the latter term describes the muscles which are involved in extending and levating the limb during threat and recovery movements. Each muscle will be examined in detail.

1. THE PROPUS-DACTYLUS JOINT (Fig. 1)

The P-D joint displayed the least amount of overlap of antagonistic muscle activity and also had the most labile pattern. During threat the dactylus opener muscle usually displays a high frequency tonic activity which increases during the pre-strike mode. This tonic activity ceases at the beginning of cheliped flexion. The muscle potentials are then greatly reduced in frequency for 100 to 150 ms until the claw is re-opened as the cheliped resumes the positions of threat.

The muscle potentials recorded from the dactylus closer increase in frequency during pre-strike and reach a peak frequency at the end of the strike when the cheliped is flexed. During this period, larger spikes in the EMG's indicate the introduction of new axons. When threat positions are resumed the closer muscle remains tonically active as the claw is maintained partially open at 35 to 45^{o}. Threat responses, before and after strike, are often accompanied by a sudden extra opening of the claw and an increase in the frequency of the opener muscle impulses together with a decrease in frequency of closer muscle activity.

2. THE CARPUS-PROPUS JOINT (Figs. 2 and 3)

During the threat displays the excitatory axon of the propus extensor muscle fires at high frequencies (fig. 2). Extra joint extension, which occurs when the crab displays from Three-Quarters to Full Threat, is accompanied by an increase in frequency of this unit. A further increase is seen at the beginning of the strike behaviour. Unlike the dactylus opener muscle, this high frequency activity does not continue to the end of pre-strike but is progressively reduced. The propus extensor muscle begins to increase in frequency again before the end of the strike and activity is continued throughout cheliped re-extension.

The propus flexor muscle fires at low frequencies during threat displays and is only increased in activity immediately before the strike behaviour (fig. 3). The frequency of muscle impulses increases rapidly to reach a peak 100 ms before the end of pre-strike, which is during the period of decreasing propus extensor muscle activity. It was demonstrated

FIGURE 1

THE PROPUS-DACTYLUS JOINT

In both cases the film speed was 16 fps. The time scale represents 1 s.

1. The dactylus opener muscle. This muscle shows a considerable increase in impulse frequency during pre-strike, which is suddenly reduced at the beginning of claw closure. A regular and maintained tonic activity is resumed when the claw is re-opened during the recovered threat displays.

2. The dactylus closer muscle. This muscle shows an increase in activity at the onset of a strike behaviour. The muscle impulse frequency increases during pre-strike to reach a peak during the strike mode. As the cheliped is re-extended and the claw re-opened, the tonic muscle activity decreases.

CHAPTER 5 FIGURE 1

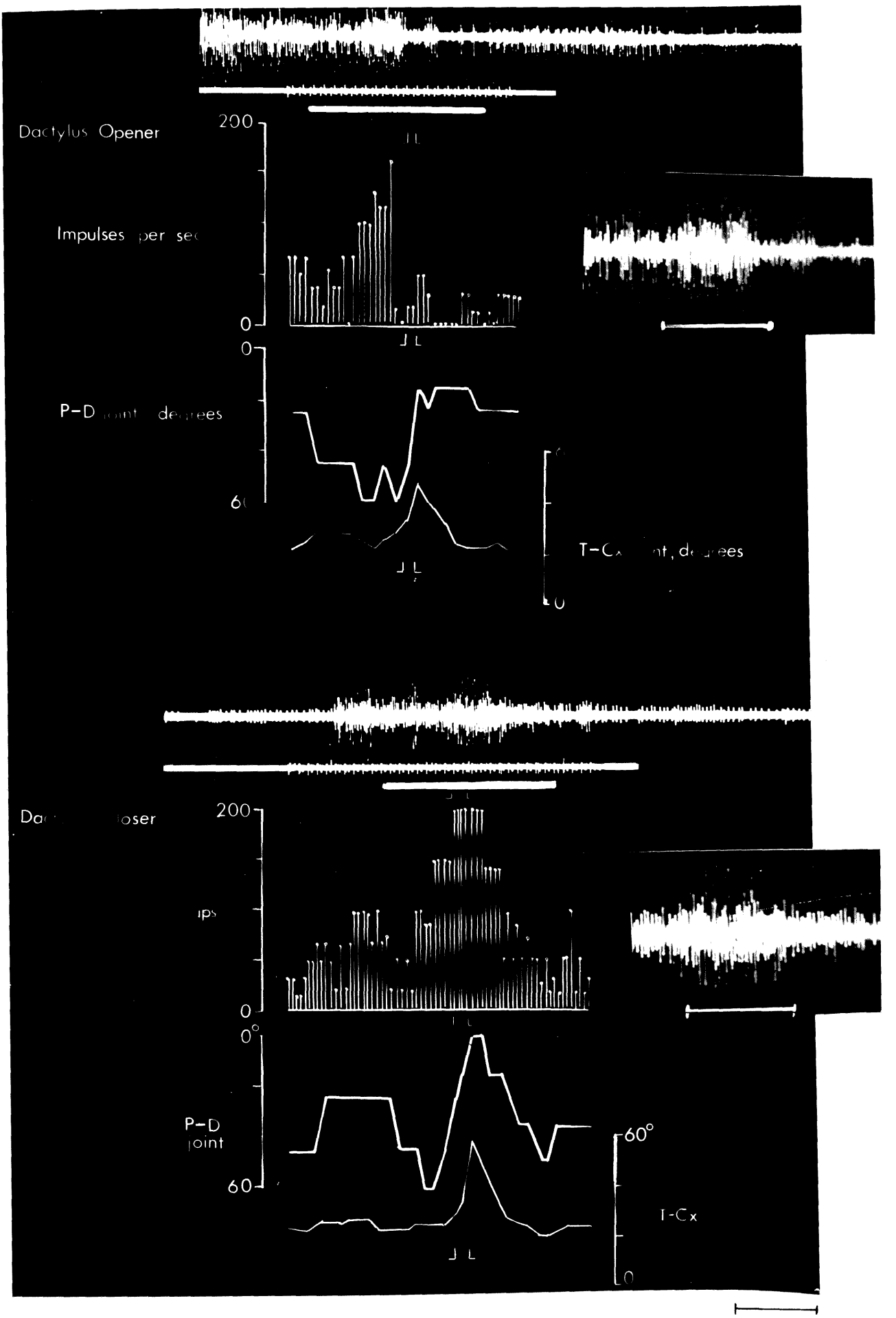


FIGURE 2

THE CARPUS-PROPUS JOINT

A. THE PROPUS EXTENSOR MUSCLE

The film speed was 25 fps. The time scale represents 1 s.

For a long time before the strike, the excitatory axon of the propus extensor muscle fires at a high frequency which increases in bursts as the threat displays are increased in intensity. At the beginning of a strike behaviour the impulse frequency rises considerably and reaches a peak at the beginning of pre-strike. After this the frequency falls suddenly. The muscle activity begins to increase again before the flexion of the joint has ended and is maintained throughout cheliped recovery.

The graph of the C-P joint angular excursion demonstrates the small re-extending twitch which is characteristic of the distal cheliped segments during a strike (Chapter 2, fig. 5). The peak strike angular velocities for the C-P joint are reached after the twitch.

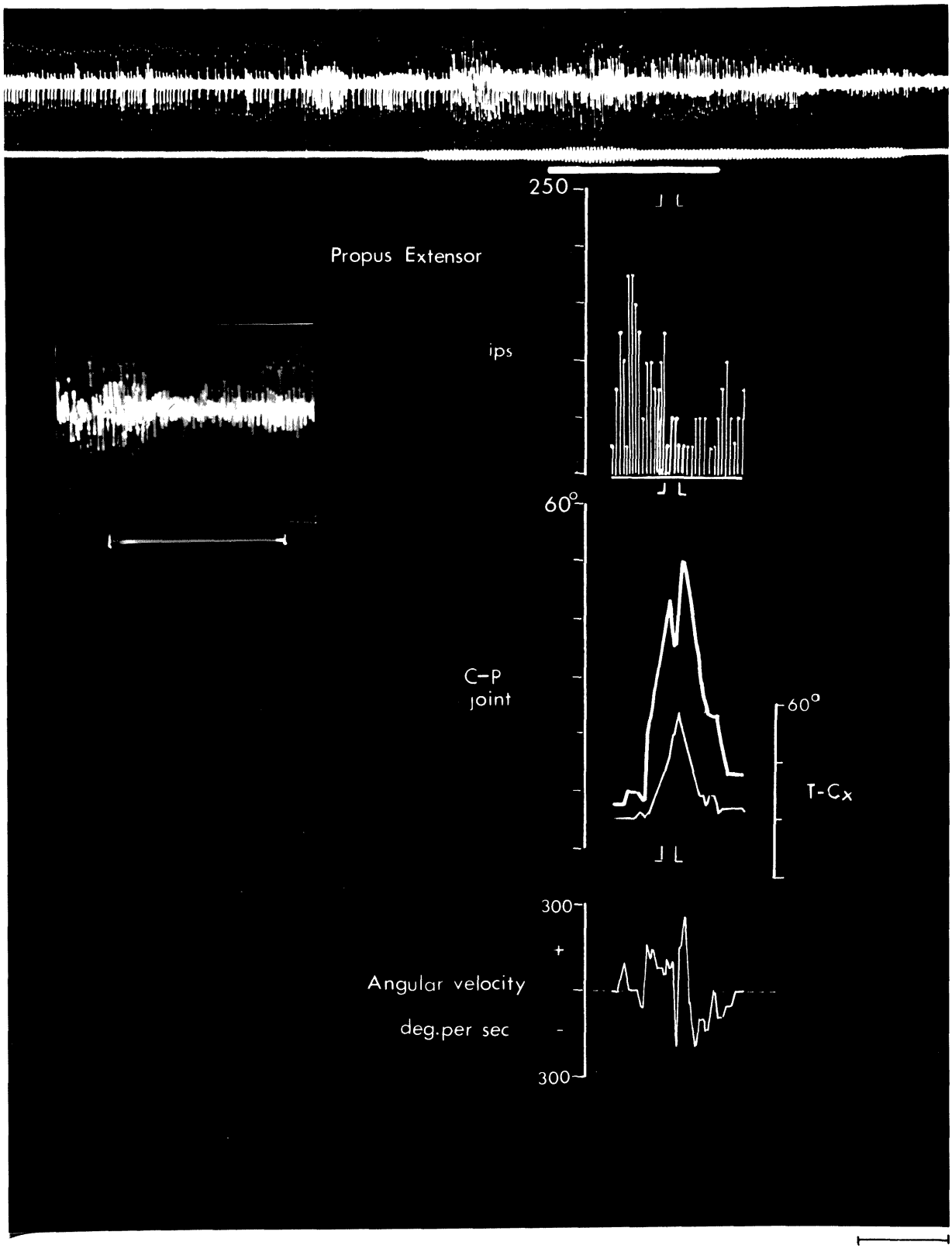

250
Propus Extensor
ips
60°
C-P
joint
60°
T-Cx
300
+
Angular velocity
deg.per sec
-
300

FIGURE 3

THE CARPUS-PROPUS JOINT

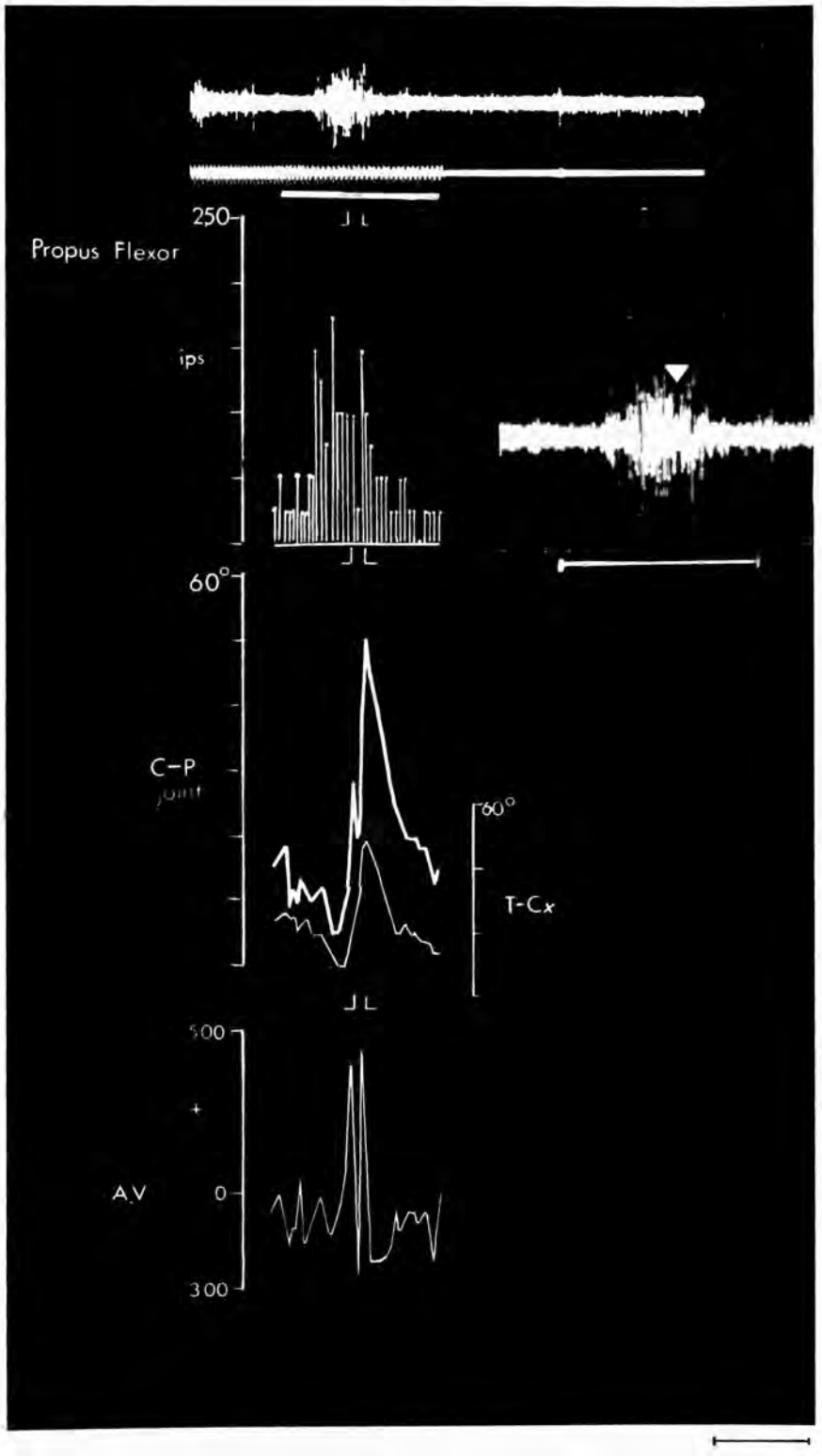
B. THE PROPUS FLEXOR MUSCLE

The film speed was 25 fps. The time scale represents 1 s.

The frequency of the propus flexor muscle impulse is low before a strike behaviour but increases considerably at the onset of pre-strike. The peak frequencies are reached when the T-Cx joint begins to flex. A momentary sharp decrease in frequency accompanies the re-extending twitch, indicated by the arrow on the enlarged EMG. Following this, high frequency activity is resumed for 50 ms, after which the muscle activity begins to decrease as the T-Cx joint re-extends for the resumed postures of threat.

The graph of the angular velocity at the M-C joint indicates 2 high peaks of strike velocity which occur before and after the short twitch.

CHAPTER 5 FIGURE 3



in Chapter 2 (fig. 5) that the distal joints of the cheliped often show a short re-extending twitch during the rapid coxa flexion. Figure 3 indicates that this twitch is accompanied by a momentary reduction in flexor impulse frequency. The frequency suddenly falls from 100 ips to 30 ips, indicated by the arrows on the enlarged EMG (fig. 3). As the C-P joint begins to flex again for the remainder of the strike movement, the carpus flexor muscle impulse frequency quickly increases to 150 ips. The frequency of excitation begins to decrease after the strike although the muscle is still active during the initial stages of T-Cx joint re-extension. This is because the C-P joint lags 30 to 60 ms behind the T-Cx joint and thus is still flexing when the coxa begins to remote. During this period of decreasing activity the propus extensor will begin to increase in frequency (fig. 2).

3. THE MERUS-CARPUS JOINT (Figs. 4 and 5)

The carpus extensor muscle, like the propus extensor, displays tonic activity during threat (Fig. 4). The frequency of the tonic unit in the carpus extensor increases considerably at pre-strike although this is quickly reduced as the M-C joint begins to flex during a strike and even reaches zero frequency. After this, muscle activity gradually increases to reach a peak frequency at the start of coxal re-extension. The impulse frequency is maintained at a low but regular level throughout the remainder of cheliped extension and the resumed threat displays.

The frequency of the tonic unit to the carpus flexor muscle increases gradually 150 to 200 ms before the beginning of the strike (fig. 5). This is during the first period of peak activity in the extensor muscle. Peak flexor muscle activity occurs just before the beginning of M-C joint flexion and large impulses are seen in the EMG's. After this, as the M-C joint begins to flex there is a steady decrease in the frequency of the carpus flexor muscle and the tonic unit stops firing 30 ms after the beginning of coxal re-extension, when the joint begins to re-extend.

A momentary and sharp decrease in the frequency of the carpus flexor muscle is displayed at the time of the re-extending twitch of this joint, and the impulse frequency falls from 200 ips to 30 ips. Resumption of rapid flexion accompanies a second increase in flexor muscle activity. This is similar to the pattern of activity shown in the propus flexor muscle during the twitch movement at the C-P joint, and is indicated on the enlarged EMG of figure 5.

FIGURE 4

THE MERUS-CARPUS JOINT

A. THE CARPUS EXTENSOR MUSCLE

The film speed was 25 fps. The time scale represents 1 s.

The carpus extensor muscle displays a regular tonic activity before and after the strike behaviour. This regular activity is disturbed at the onset of a strike and another unit is seen in the EMG's which fires at a high frequency reach a peak at pre-strike. The impulse frequency falls to zero at the beginning of rapid coxal promotion. After this the activity increases gradually to reach a second peak at the start of cheliped re-extension. The muscle activity is subsequently maintained at a low but regular level throughout the remainder of cheliped extension and resumed threat displays.

The graph of angular excursion at the M-C joint demonstrates the re-extending twitch which occurs during the strike. This brief movement produces two peaks of positive strike angular velocity, one before and one after the twitch.

CHAPTER 5 FIGURE 4

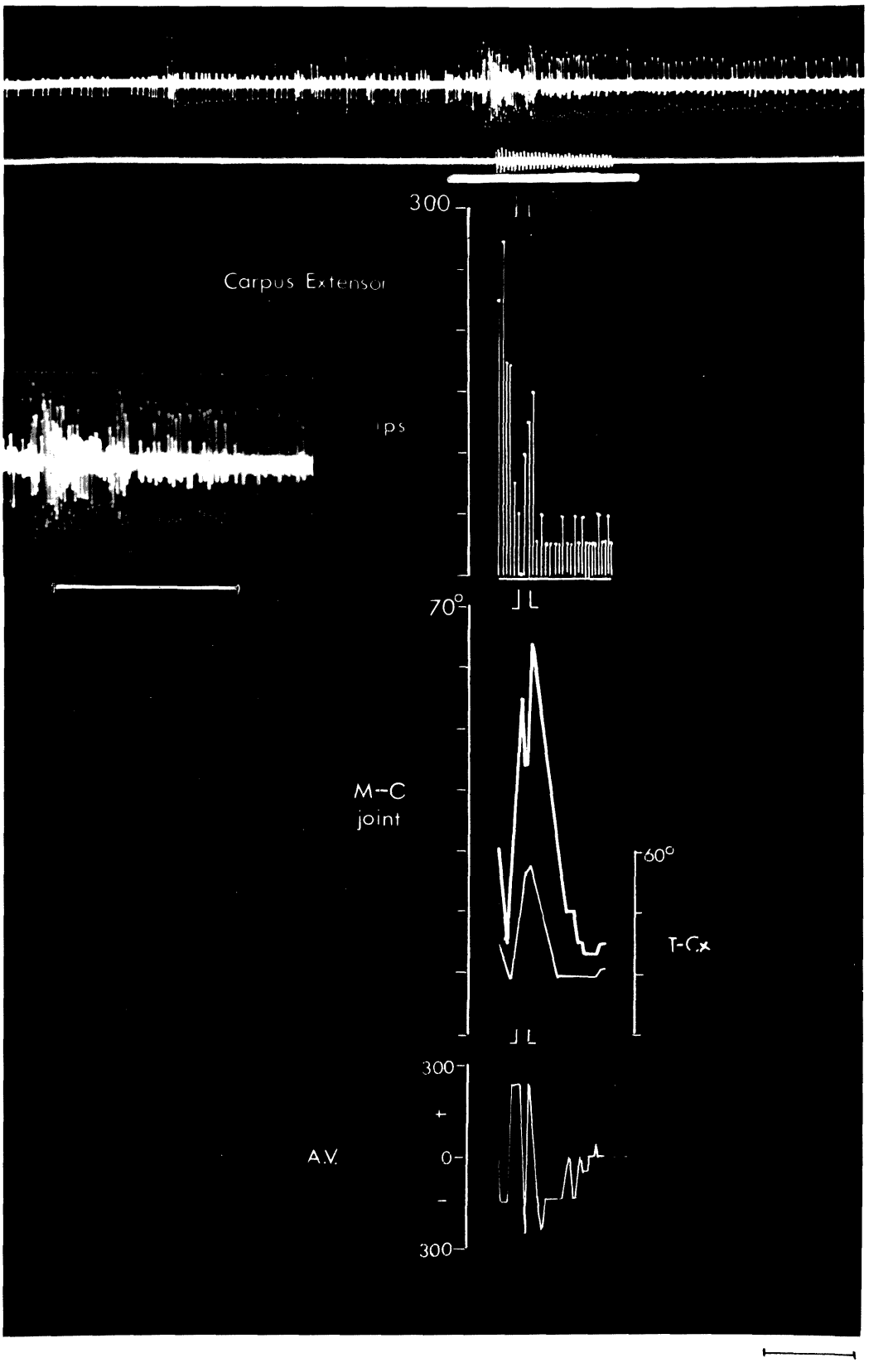


FIGURE 5

THE MERUS-CARPUS JOINT

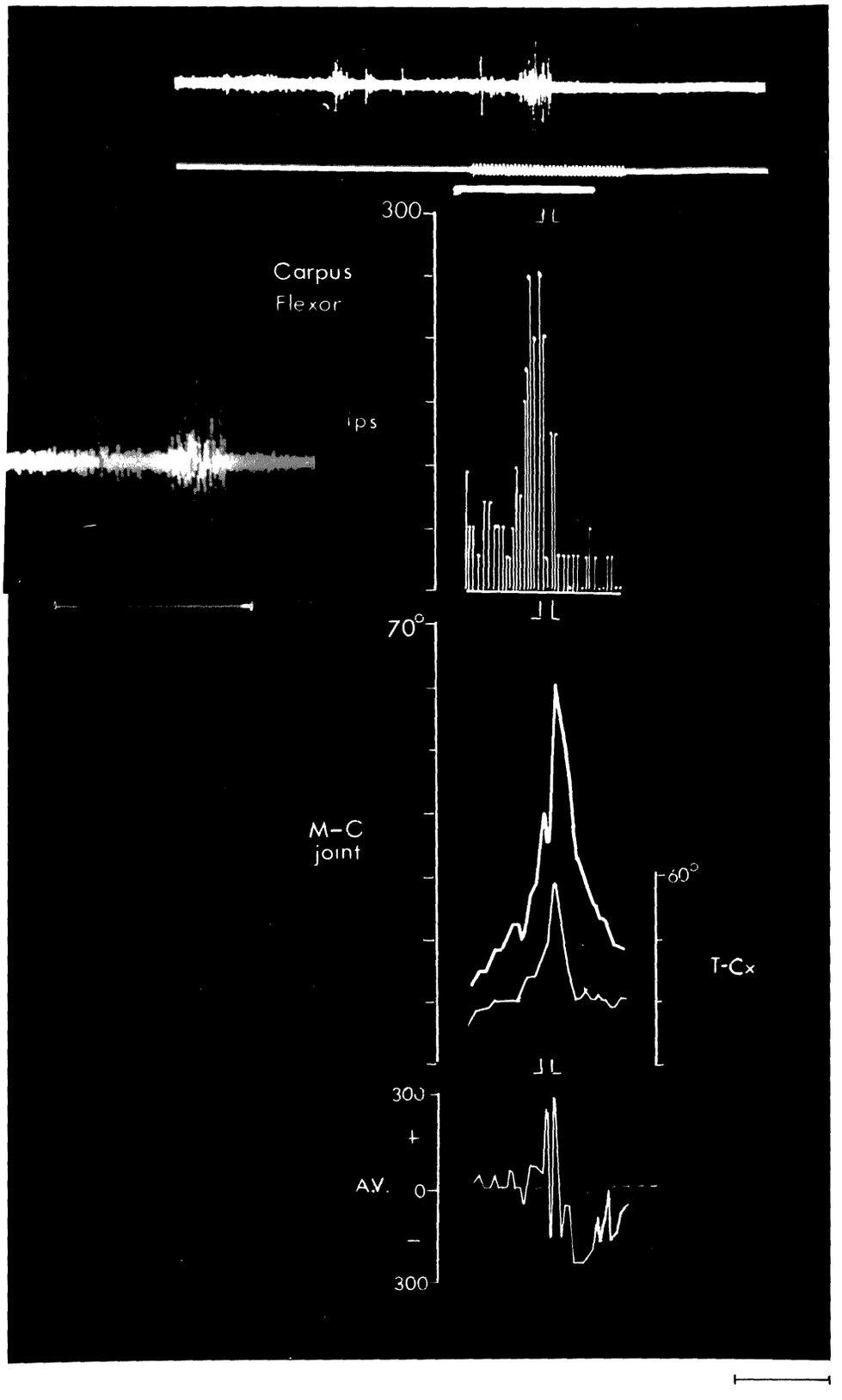
B. THE CARPUS FLEXOR MUSCLE

The film speed was 25 fps. The time scale represents 1 s.

The carpus flexor muscle shows an increase in impulse frequency before pre-strike and peak activity occurs just before M-C joint flexion when large impulses are seen in the EMG's. After this the frequency steadily decreases to fall to minimal levels at the beginning of cheliped re-extension.

A momentary decrease in excitation frequency accompanies the characteristic strike re-extending twitch at this joint. The frequency falls from 200 ips to 30 ips. The frequency of excitation is increased after the twitch when rapid flexion is resumed. As in figure 4, the twitch causes two peaks of positive strike angular velocity, one before and one after the movement.

CHAPTER 5 FIGURE 5



Thus like the two muscles operating the C-P joint, the carpus extensor and flexor muscles also display periods when they are both showing high frequency activation during the strike behaviour. This occurs mainly during pre-strike when the extensor fires at peak frequencies and the activity of the flexor muscle begins to increase.

4. THE BI-MERUS JOINT (Fig. 6)

The movement of the merus segment is limited to only 5^{o} about the BI. It can therefore have little importance in the strike action. However the merus extensor muscle normally displays a slight decrease in activity during rapid flexion of the cheliped and increases in impulse frequency during the resumed threat postures. This frequency is greatest 500 to 750 ms after the strike, when the cheliped is fully re-extended in threat.

5. THE COXA-BI JOINT

A. THE BI LEVATOR MUSCLES (Figs. 7 and 8)

The distinction and transition between the agonistic threat displays and strike behaviour are clearly illustrated in EMG's recorded from the Anterior and Posterior levator muscles. As described in Chapter 2, threat postures can be maintained for several minutes. The EMG's recorded from the levator muscles during strike behaviour demonstrate that any increase in intensity of threat position is accompanied by an increase in impulse frequency to the levator muscles. These increased frequency bursts can be seen after the strike in the EMG of the Anterior levator (fig. 7). Each burst is accompanied by the generation of a few larger muscle potentials which may indicate the recruitment of the 2nd phasic axon of the A1. Once a strike behaviour begins the regular muscle activity which is displayed during threat ceases, but once the strike has ended this regular activity is resumed.

At the beginning of the strike, when the rigid postures of threat displays end and the irregular pre-strike twitches are observed, the frequency of the A1 increases (fig. 7). Large muscle spikes indicate the introduction of the first phasic axon. This high frequency is not maintained, but occurs in several bursts of 100 to 200 ms duration. Between each burst the impulse frequency is decreased and levation of the BI is maintained by the small tonic impulses. The last burst of A1 pre-strike activity reaches a peak frequency 30 ms before the beginning of rapid cheliped flexion. During the strike itself, there is a marked reduction in frequency which continues until the beginning of BI levation, 30 ms after coxal re-extension. Large muscle spikes again indicate the introduction of the phasic axons. These axons fire for 250 ms after which muscle excitation is steadily decreased until the threat displays are

FIGURE 6

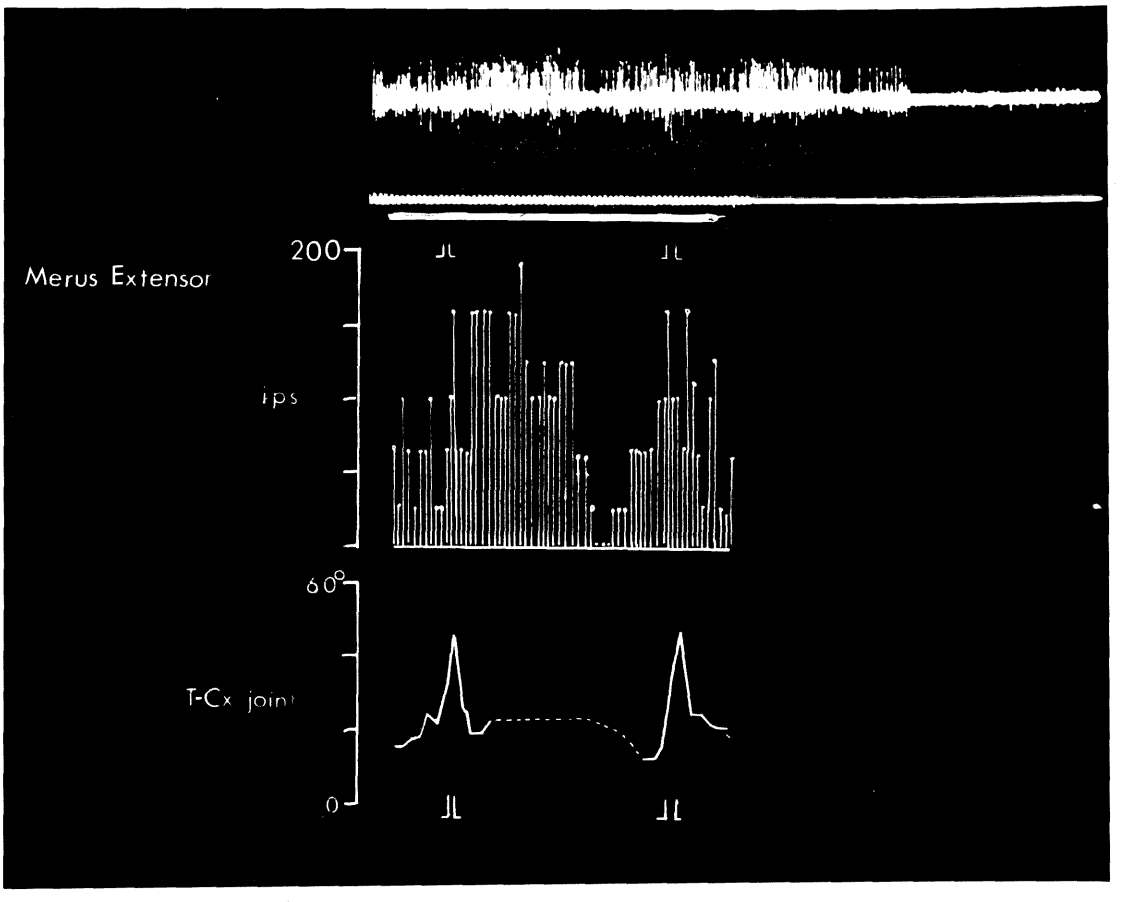
THE BI-MERUS JOINT

The film speed was 16 fps. The time scale represents 1 s.

It was not possible to measure the movement of the merus segment about the BI-merus joint, so the graph indicates the position of the T-Cx joint.

Two strikes are shown in this figure and both are accompanied by a slight decrease in merus extensor muscle impulse frequency during the rapid cheliped flexion. As the limb is re-extended in threat, the excitation frequency increases again to reach maximum levels, 500 to 750 ms after the strike.

CHAPTER 5 FIGURE 6



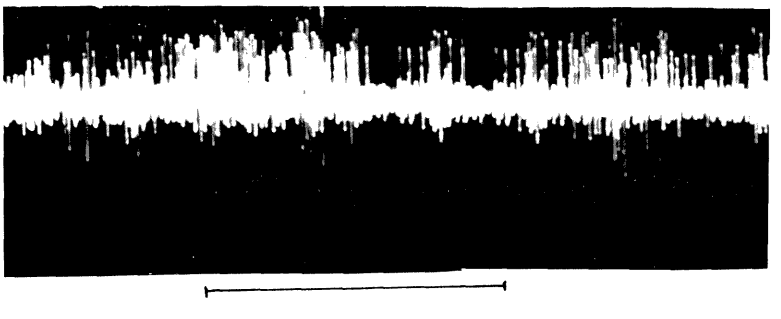


FIGURE 7

THE COXA-BI JOINT

A. THE ANTERIOR LEVATOR MUSCLE

The film speed was 32 fps. The time scale represents 1 s.

Before and after the strike, a regular frequency of tonic potentials is displayed in the Anterior levator muscle. At the onset of a strike behaviour this activity breaks into high frequency bursts of 200 ms duration. The last burst ends at the beginning of the strike mode. The muscle is active at considerably reduced impulse frequencies until the limb is re-levated, 30 ms after coxal re-extension begins. The large spikes which occur during the pre-strike bursts and also after the strike, indicate the introduction of one or both of the two phasic Al axons. After the strike, the threat postures are accompanied by a high frequency of large muscle potentials. These show sharp increases in frequency, which accompany the increase of threat displays.

CHAPTER 5 FIGURE 7

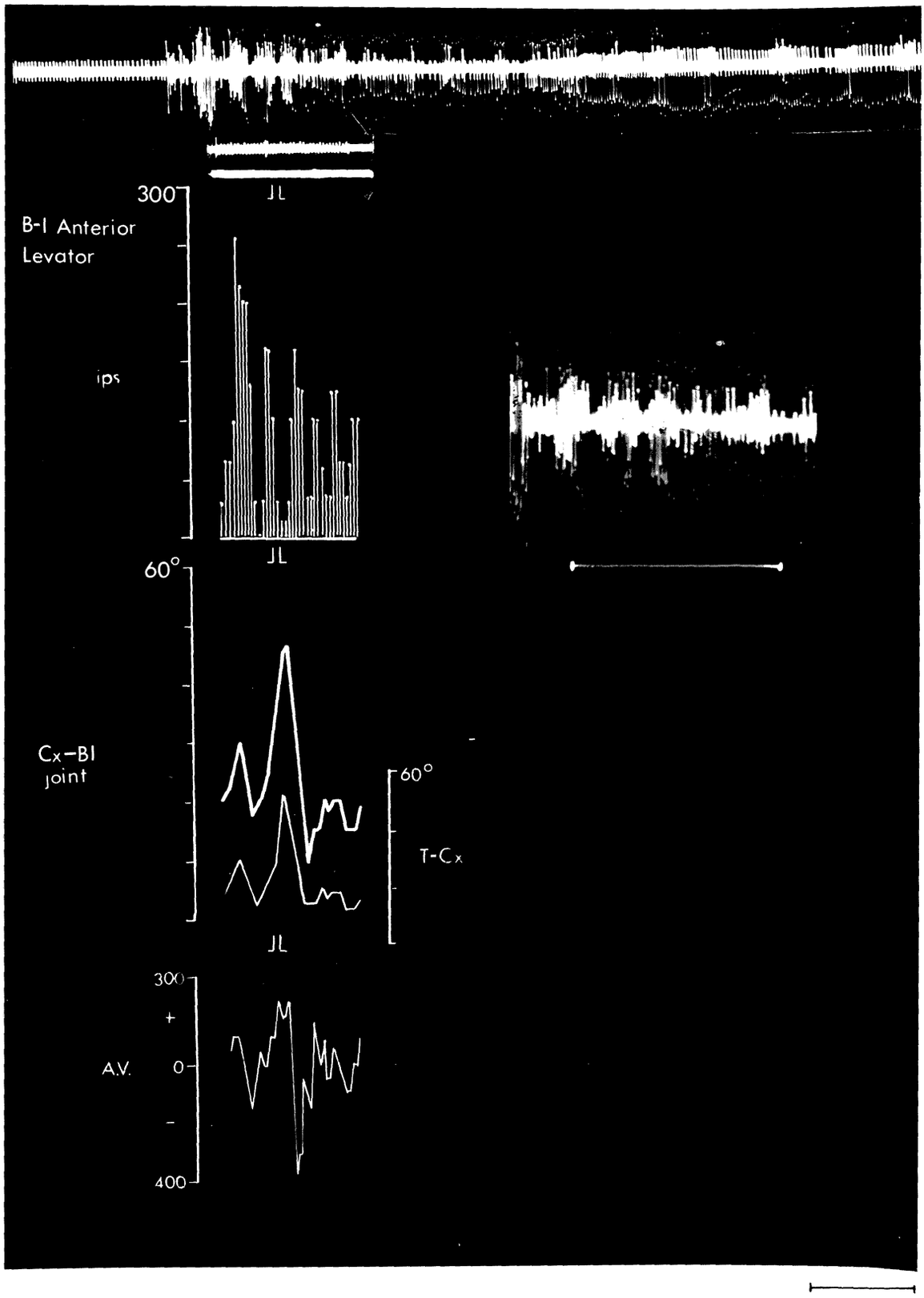


FIGURE 8

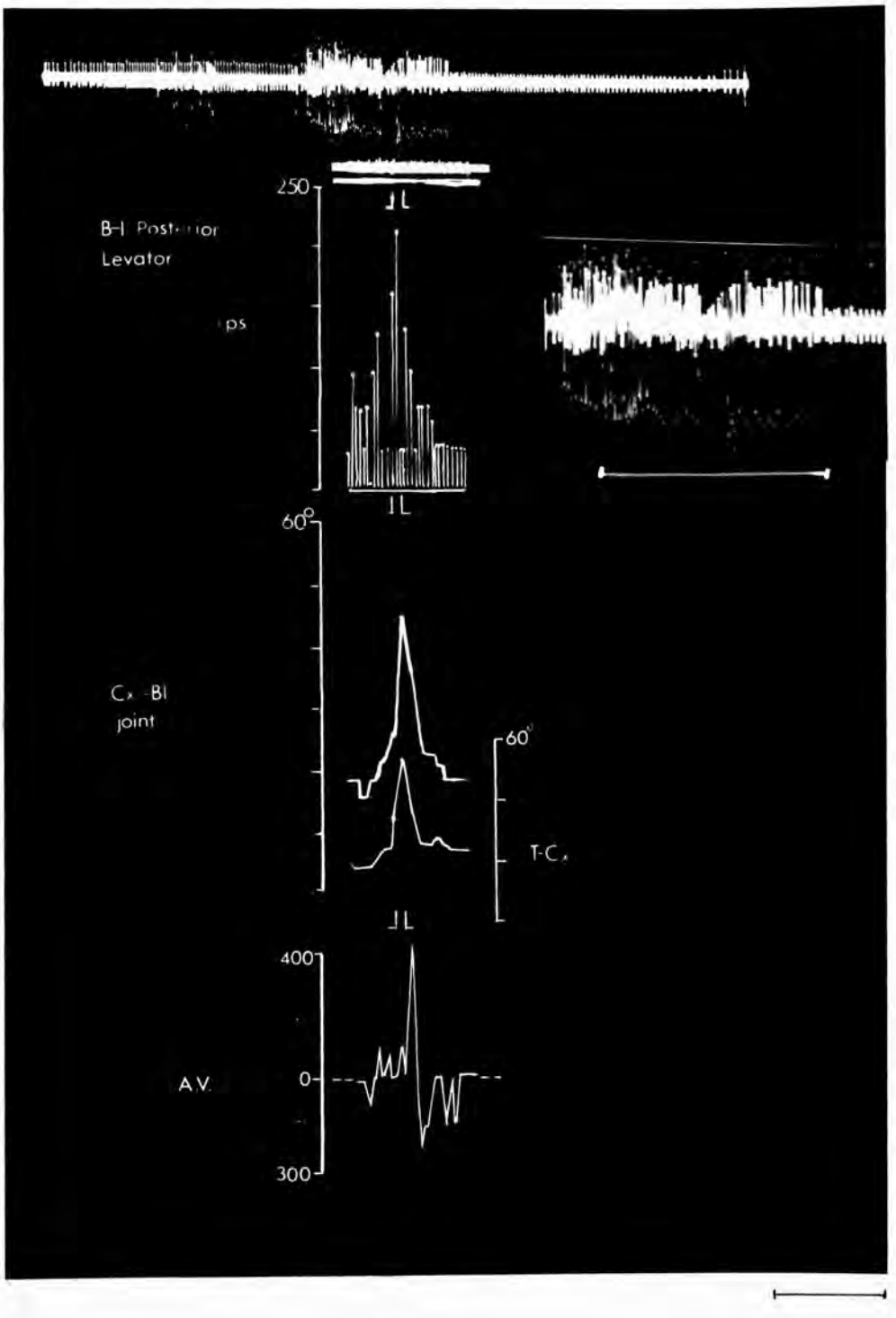
THE COXA-BI JOINT

B. THE POSTERIOR LEVATOR MUSCLE

The film speed was 32 fps. The time scale represents 1 s.

The frequency of the Posterior levator muscle impulses greatly increases at the onset of a strike behaviour and a new motor unit begins to fire, generating large muscle potentials. This second unit ceases to fire before pre-strike and muscle activity is maintained by smaller tonic impulses. The second unit is re-introduced during the strike mode itself and several large impulses are generated. After this, the frequency is slightly reduced until the cheliped begins to be re-extended after the strike. At this time the second unit is further increased in frequency until the threat postures are resumed and the smaller tonic activity is re-instated.

CHAPTER 5 FIGURE 8



resumed and tonic activity is re-instated.

The pattern of muscle activity in the Posterior levator is similar to the Al before and after the strike, but differs during the strike mode itself. At the beginning of a strike behaviour, when the rigid threat displays cease, the EMG of the Pl displays the introduction of large muscle spikes (fig. 8). This second unit stops firing during pre-strike and a low frequency tonic activity is displayed. However the second unit is suddenly re-introduced for 20 to 30 ms during the rapid flexion and depression of the cheliped, and generates a high frequency burst of large muscle impulses. Following this burst,the impulse frequency is slightly reduced until the coxa begins re-extension after the strike. At this point the large unit is increased in frequency again until the threat displays are resumed. When this occurs the large unit ceases to fire and muscle activity continues with low frequency small tonic potentials.

This is the first positive indication of a muscle being activated for a special purpose in the strike. The Pl displays a high frequency burst at the "wrong" time, that is when the limb is being rapidly depressed. The effect of the strike behaviour is primarily dependent upon the speed of its execution. Therefore this burst of levatory activity during rapid cheliped depression appears to be a paradox since it may serve to slow down BI depression during the strike.

B. THE BI DEPRESSOR MUSCLES (Figs. 9 and 10)

The two depressor muscles are silent during threat and are only activated at the onset of pre-strike. Like the levators, the temporal sequence of activity from the two depressor muscles differs within the strike mode. The activity recorded from the Anterior depressor during a strike does not last longer than 200 ms (fig. 9). All this high frequency occurs during pre-strike and ceases as soon as the cheliped begins to be depressed. The Ad then remains silent throughout the remainder of the strike behaviour. Occasionally one or two large muscle spikes may be generated during the oscillatory "bounce" movements at this joint, which occur after the strike.

The frequency of excitation in the Posterior depressor muscle also increases during pre-strike but at a lower level than in the Ad (fig. 10). However unlike the Ad, Pd activity is maintained throughout the strike and occurs in two discrete bursts. The first burst occurs in pre-strike and increases to a peak frequency 30 ms before the rapid depression of the BI. The EMG shows that different sizes of muscle potentials are generated during this burst which indicates the introduction of all 3 axons of the Pd. As cheliped depression begins the frequency is reduced and only small

FIGURE 9

THE COXA-BI JOINT

C. THE BI ANTERIOR DEPRESSOR MUSCLE

The film speed was 32 fps. The time scale represents 1 s.

The Anterior depressor muscle is silent during the threat displays and is only activated for 200 ms in a strike behaviour. During this time the muscle generates 6 to 10 large spikes, which all occur during pre-strike. The muscle activity then ceases, although the occasional spike may be generated during the oscillatory "bounce" movements which occur after the strike.

The Cx-BI joint reached a high positive strike velocity in this trace, over $600^{\circ}/s$. The strike movement itself was extremely rapid and occurred within 1 frame of the ciné film, that is 31.25 ms.

CHAPTER 5 FIGURE 9

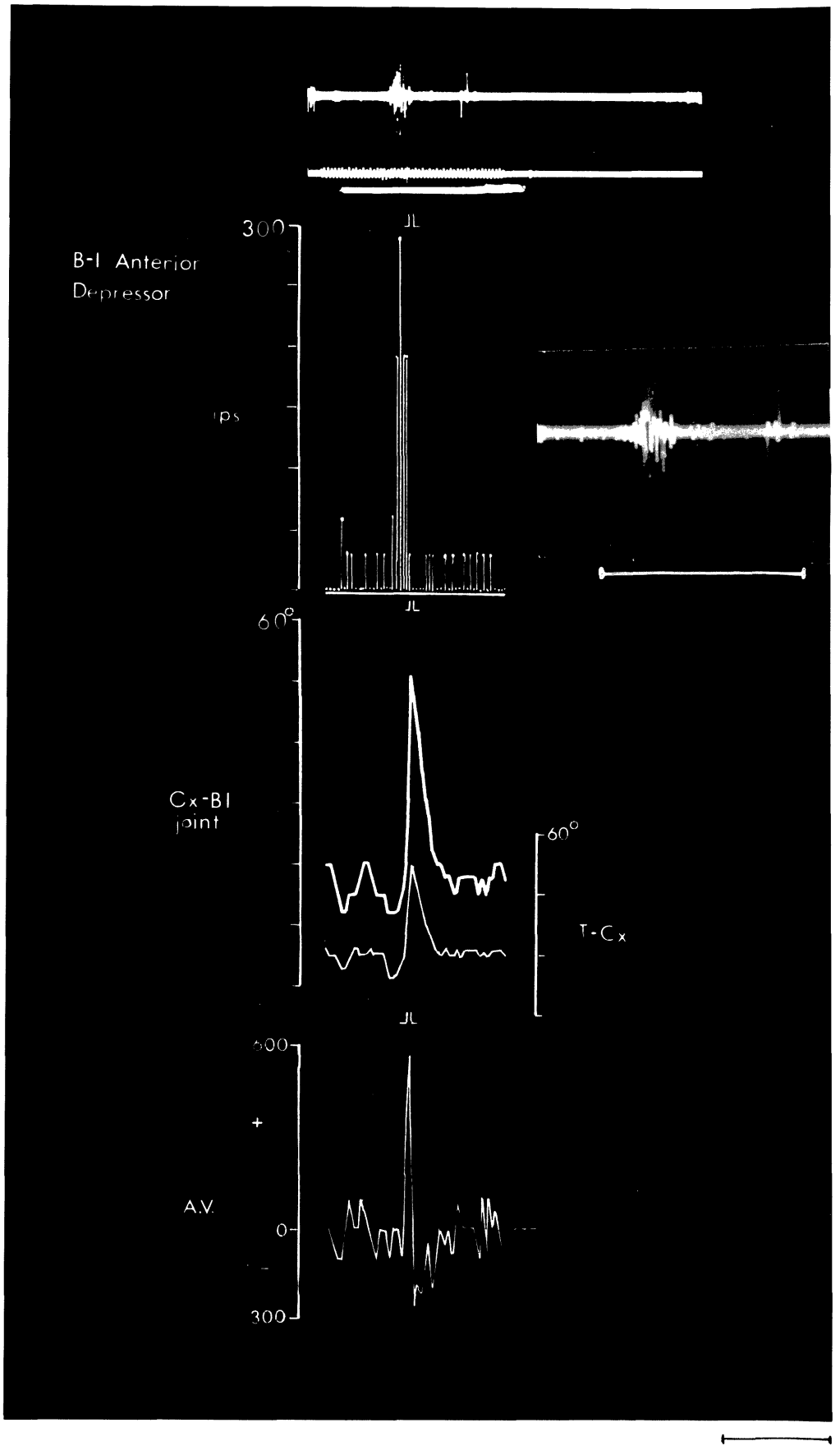


FIGURE 10

THE COXA-BI JOINT

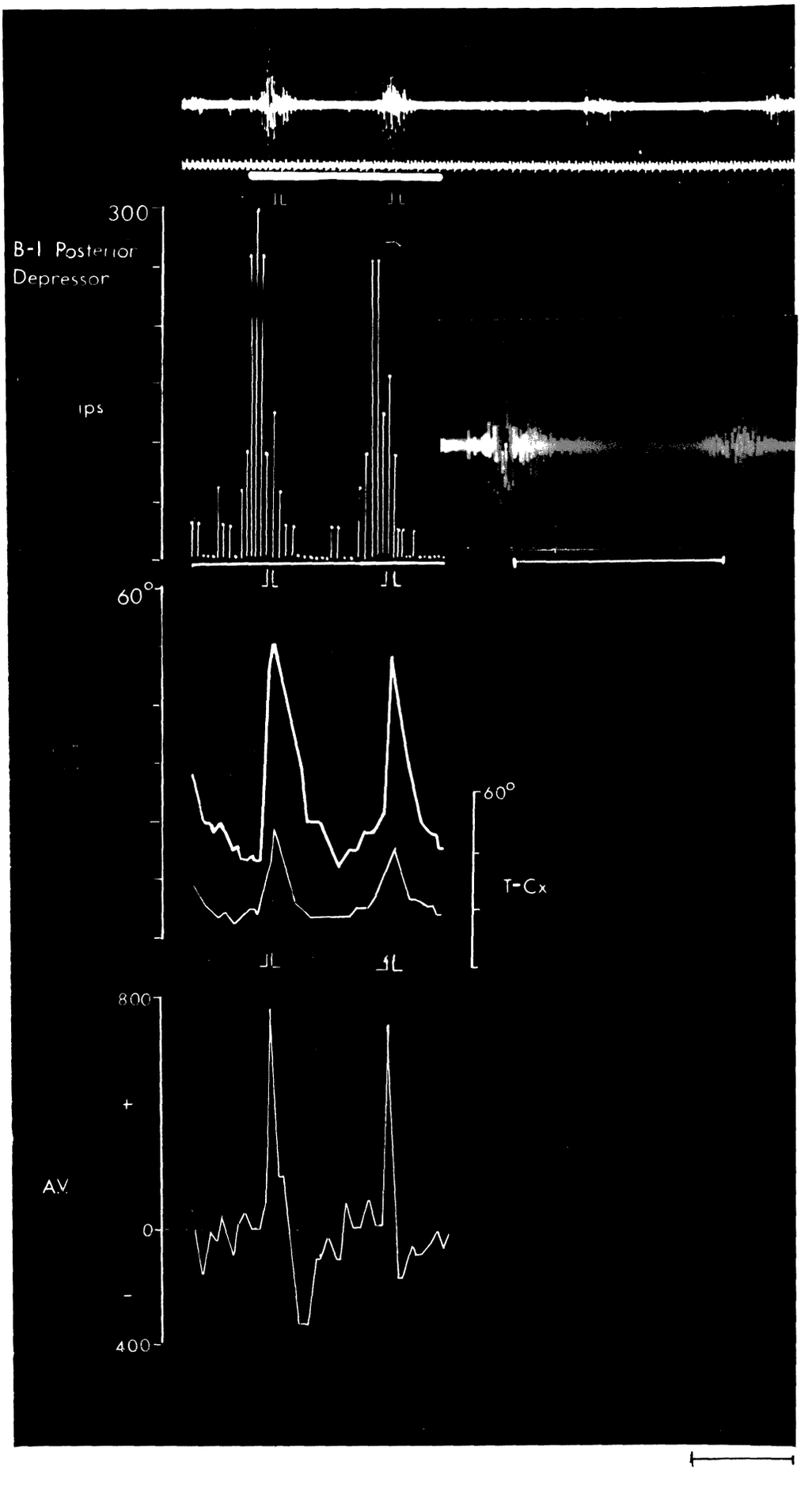
D. THE BI POSTERIOR DEPRESSOR MUSCLE

The film speed was 32 fps. The time scale represents 1 s.

Two strikes occurred within the period of recording. Both clearly demonstrate the two peaks of Posterior depressor impulse frequency during the strike behaviour. The first,and longer, burst of Pd activity occurs during pre-strike. The sizes of the muscle potentials in the EMG indicates that all 3 Pd axons fire during this burst. The burst ends at the beginning of coxal flexion, during which the Pd activity is maintained by small tonic impulses. The second burst occurs 10 ms before the end of coxal promotion and the large muscle impulses indicate the re-introduction of a second axon. This burst ceases 30 to 60 ms after the beginning of coxal re-extension.

The angular velocities achieved by the Cx-BI joint in both strikes illustrated on the figure, were exceptionally fast. The positive strike velocities in both strikes reached over 750 ^{o}/s.

CHAPTER 5 FIGURE 10



muscle potentials can be seen on the EMG.

The second burst of Pd impulses occurs 10 ms before coxal re-extension and continues for another 30 to 60 ms. The size of the muscle potentials in the EMG indicates that a second Pd axon is re-introduced which generates larger impulses.

Thus like the Ad, the Pd reaches peak excitation frequencies early in the strike behaviour, that is before maximum depression velocities have been achieved. However unlike the Ad, the Pd demonstrates a second burst of activity during the strike mode. This second, smaller burst was detected in all the EMG's recorded from the Pd muscle during the performance of fast strikes. Like the burst in the Pl, this also appears to indicate a muscle being activated for a special purpose in the strike behaviour. It would appear to be a paradox that the Pd, which functions as a strike muscle, should increase in frequency during the anti-strike movements of cheliped re-extension.

The levator and depressor muscles demonstrate a considerable amount of overlap in high frequency activity between antagonistic muscles. Both depressors increase in activity during the high frequency pre-strike bursts of the Al. The burst of the Pl during the strike mode, occurs when the Pd activity is maintained by small tonic impulses. The second burst of the Pd occurs at the end of the strike, when the Pl impulse begins to increase as the coxa re-extends. There may also be a slight overlap of muscle activity between the second Pd burst and the beginning of increase in Al excitation, which occurs as the BI is levated 30 ms after the end of coxal flexion.

6. THE THORAX-COXA JOINT (Figs. 11 and 12)

As in the traces recorded from the BI levators (Figs. 7 and 8), the distinction between threat displays and strike behaviour is clearly shown in EMG's recorded from the coxa remotor muscle. Before and after the initiation of a strike behaviour the cheliped is maintained in a rigid, extended position caused by medium frequency tonic activity in the CxR. Increased bursts in the CxR accompany increases in intensity of the threat display.

When the strike behaviour begins, the regular CxR activity breaks into irregular high frequency bursts similar to those in the Al (fig. 7). These are accompanied by the introduction of large muscle potentials which indicate the recruitment of other CxR axons or the generated secondary spike responses of the muscle fibres (fig. 11). The last burst occurs 50 ms before the strike, during the slow promotory pre-strike movements. The muscle is greatly reduced in impulse frequency during rapid coxal pro-

FIGURE 11

THE THORAX-COXA JOINT

A. THE COXA REMOTOR MUSCLE

The film speed was 25 fps. The time scale represents 1 s.

The regular frequency of coxa remotor muscle activity which occurs during threat displays, is abruptly disturbed at the onset of a strike behaviour. Like the Anterior levator, the beginning of strike behaviour is accompanied by high frequency bursts in the CxR, the last of which occurs at the end of pre-strike. During coxal promotion the muscle activity is considerably reduced. However the frequency of excitation is suddenly increased 10 ms before the end of a coxal promotion. This activity reaches peak frequences during the initial stages of coxal re-extension. As the limb resumes threat displays a regular tonic frequency is re-established in the CxR.

CHAPTER 5 FIGURE 11

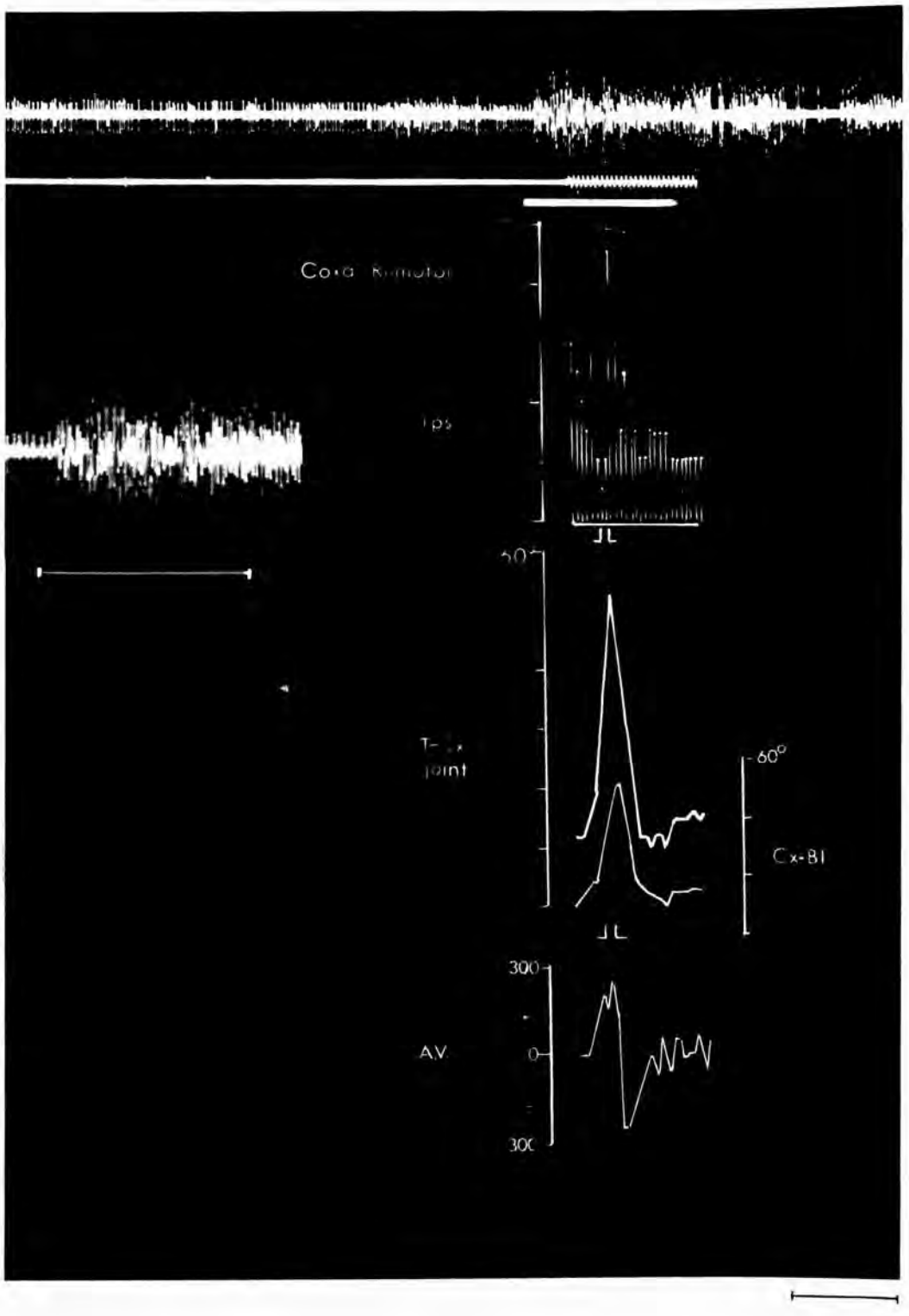


FIGURE 12

THE THORAX-COXA JOINT

B. THE COXA PROMOTOR MUSCLE

The film speed was 32 fps. The time scale represents 1 s.

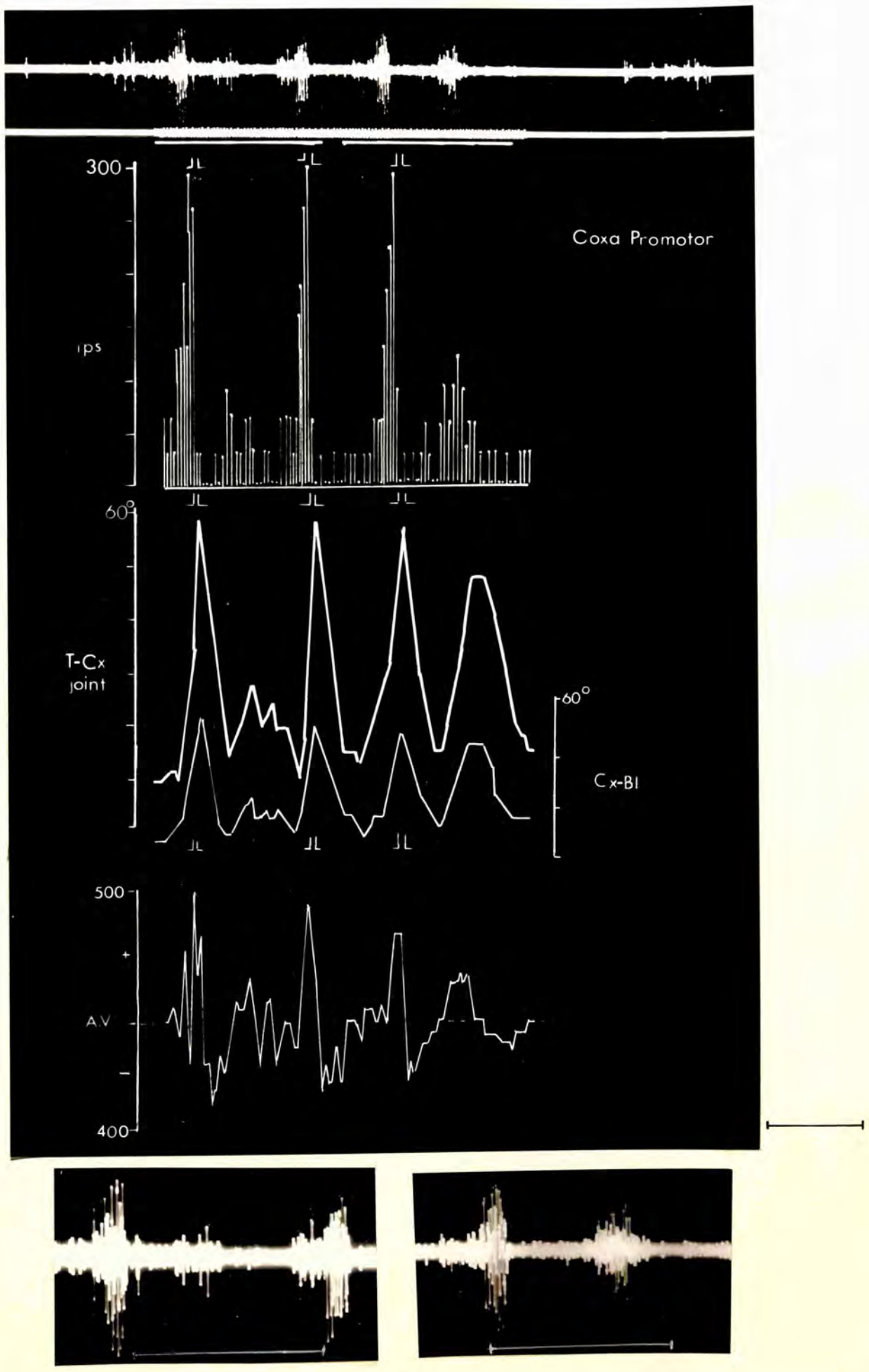
The crab used for this recording was particularly responsive and displayed 3 fast strikes, 1 slow strike, plus an aborted strike between strikes 1 and 2, during the period of cinematographic filming.

The CxP begins to increase in frequency of excitation at the first stages of pre-strike, 150 to 200 ms before the start of rapid coxal flexion. This increase gradually reaches a peak 30 ms before the strike mode. Subsequently the impulse frequency is considerably reduced before and during fast promotion. The CxP may therefore be releasing stored tension which was developed before the strike to enable the attainment of the high angular velocities and to achieve promotion in the short time of a strike.

The slow strike is characterised by a lower frequency of activity and a continuation of CxP excitation throughout the movement. There is also a pause in joint excursion between the end of flexion and the beginning of slow re-extension.

In an aborted strike the pre-strike twitches move the joint to the critical angles between strike and pre-strike positions, but instead of this angle being exceeded, so displaying a strike, the cheliped is rapidly remoted back into positions of threat.

CHAPTER 5 FIGURE 12



motion but suddenly increases in activity 10 ms before the beginning of coxal re-extension.

The recording from the coxa promotor muscle in figure 12, is interesting as it shows 3 fast strikes and 1 slow strike. It also shows an aborted strike between the first two strikes in figure 12. In an aborted strike the pre-strike twitches move the limb to the critical point of overlap between strike and pre-strike positions, but instead of this angle being exceeded, producing a strike, the limb is remoted back to the positions of threat. This promotion to the critical angle and countering rapid re-extension is an indication of antagonistic muscle tension being developed before the strike in these strike and anti-strike muscles.

The CxP appears to increase in activity and reach peak frequency levels at the wrong time in a strike behaviour. Increasing CxP activity begins in the initial stages of pre-strike, 150 to 200 ms before the strike mode, and normally reaches peak frequencies 30 to 60 ms before the strike begins. This activity is considerably reduced before, and during, rapid coxal promotion. This suggests that tension may have been developed prior to promotion, and achieved by isometric contraction against the tension in the CxR. Thus although there is reduced, or even no, excitation to the CxP during the strike mode, it may still be releasing stored promotory tension which was developed during pre-strike.

DISCUSSION

The use of EMG techniques has proved invaluable in determining the physiological aspects of the agonistic strike behaviour. Examination of muscle anatomy, joint geometry and mechanical effects were all prerequisities to a full understanding of the significance of the EMG's. The most likely method of operation of the strike, linking the preceding chapters with this one, is given in the following chapter.

It was shown in Chapter 2 that the strike cannot be produced simply by contraction of the coxa and BI strike muscles and relaxation of their antagonists. The fast time of the strike, 30 to 60 ms, is not sufficient to allow these muscles to produce the calculated energy requirements for the strike. Therefore there must be tension developed before the strike can proceed. The results in this chapter have demonstrated that this tension is developed by co-contraction of these strike muscles with their antagonists. Thus the strike muscles will be able to contract isometrically and when the antagonistic load is removed, the developed strike tension can be suddenly released.

Although the major force for promoting and depressing the cheliped must come from the coxal and BI muscles, moving the whole limb forwards and downwards, the distal muscles also display some periods of mutual high frequency activity during which the antagonistic muscle pairs may contract together. This may allow short periods of isometric tension development and so increase the speeds of the strike. For example, the propus extensor and flexor muscles are both active at the end of the strike (fig. 2 and 3), and so will be contracting together. When the flexor muscle impulse frequency is reduced at the end of C-P joint flexion, the activity in the extensor continues. Thus it will not only be contracting isotonically, but will be releasing any tension which it may have developed isometrically before the flexor relaxed. While rapid flexion is necessary to deter the approach of any potential predator or opponent, a rapid re-extension of the cheliped is equally important since it makes the crab appear as large as possible and displays its potential weapons; this should make the crab a less suitable prey or opponent. Rapid re-extension is also important since it re-establishes a position from which the crab can strike again. This short period of co-activation in the two propus muscles may be important in allowing faster speeds of re-extension to be achieved at the C-P joint.

The carpus extensor and flexor muscles also display periods of mutual increase in muscle activity, although this mainly occurs before the strike (figs. 4 and 5). In this situation the carpus flexor will begin to contract against the tension which has been developed in the carpus extensor during threat, and therefore the flexor may develop some tension isometrically during pre-strike. When the extensor begins to relax, due to decreasing frequencies of excitation, and the M-C joint is allowed to flex freely, this tension in the flexor will be expressed. During the strike, excitation to the flexor muscle is maintained, and so it will continue to contract isotonically. This short period of co-activity may be sufficient to ensure that the initial stages of the cheliped flexion are as fast as possible, that is, faster than could otherwise be achieved if the carpus flexor had to develop tension from zero levels at the beginning of M-C joint flexion.

The two carpus muscles also display a second period of co-activation, which occurs at the end of the strike when the extensor frequency begins to increase again. As in the propus muscles, this may be important to ensure that the re-extension of the M-C joint occurs immediately after flexion ceases. That is, the extensor muscles will not have to develop tension suddenly from zero levels, but instead the increase in frequency of

excitation before the re-extension begins, will produce extra extensor muscle tension which will add to the existing low levels maintained during the strike. Thus as soon as the flexor muscles relax, the extensor tensions will be displayed and the arm will be immediately re-extended.

The EMG's have demonstrated that the re-extending twitch which occurs in the distal cheliped joints during the strike, is accompanied by a decrease in carpus and propus flexor muscle frequency. This re-extension may, therefore, be passive and produced by the drag on the limb that occurs as it travels through the air. That is, when the flexor muscles relax, the arm is momentarily jerked backwards by the force of this drag as well as by continued acceleration of the rest of the arm. It has been shown in Chapter 2 and observed during the recordings in this chapter, that the re-extending twitch of the M-C joint is closely followed by a re-extending twitch in the C-P joint. This indicates that the timing of reduced activity in the propus and carpus muscles is closely linked and presumably under a fine neural control co-ordinating the 2 segments. Since this coupling of movement occurs in nearly all the recorded and observed strikes, it is likely that the twitch has an important function. As suggested in Chapter 2, this function may be to prevent the chelipeds from clashing together at the end of the strike which may otherwise occur if the two joints continued to flex rapidly, unchecked by this brief re-extending movement.

Although the EMG's demonstrate that tension is developed by the coxal and BI strike muscles before rapid promotion, by isometric contraction against their antagonists, the records do not give any definite evidence as to the actual causes of the beginning of the strike, that is the start of coxal promotion. The sequence of muscle activity shows that pre-strike is accompanied by increased impulse frequency in all 3 coxal-BI strike muscles and that the rapid coxal promotion is accompanied by reduced frequency in the CxR and A1. Thus the strike may be simply caused by the relaxation of remotory and levatory tension and the consequent release of promotory and depressory tension. The peak promotory angular velocity is achieved after the reduction of CxP frequency. This indicates that the dual mechanical roles of the BI depressor muscles, as coxal promotors, may also be used for aiding coxal promotion. Their timing of peak frequencies during the behaviour supports this suggestion. They are both active before promotion and continue to display high frequency activity up to the time of the peak promotory velocity at the T-Cx joint.

A second cause of the beginning of the strike may be due to the mechanical properties of the T-Cx joint. As shown in Chapter 4, the CxR

and CxP have a bistable moment about the T-Cx joint, and the coxa articulation may operate like a flip-flop mechanism. As the CxP, Ad and Pd develop tension the coxa is slowly promoted during pre-strike, and so the promotory moment about the joint will increase. The increased frequency of excitation to the CxR combined with the coxal remotory effect of the Al during this stage, will ensure that the remotory moment about the joint is maintained at a high level, and so the limb will not be released before peak strike tensions have been developed. However eventually the bistable moment will be exceeded and the limb will begin to rapidly promote by virtue of this flip-flop mechanism.

Coxal re-extension is almost as fast as the strike and may be achieved in a similar manner to that suggested above. When the promotor and depressors relax, the tension that is already developed in the Al and CxR will be expressed and the remotory moment about the T-Cx joint will rapidly increase. This tension will continue to rise as the frequencies of excitation to these anti-strike muscles increases. Once the bistable point is exceeded again, the coxa will overbalance, but this time it will flip in a remotory direction.

The four modes of strike behaviour rely unequally on the contributions of different muscles. The main contribution for the first mode, threat, is from all the anti-strike muscles but even within this mode the BI Anterior levator and coxa remotor contribute the major role. Their action not only holds the cheliped laterally erect but act as muscular stops against which the promotor and depressor muscles develop tension before a strike.

The second mode, pre-strike, is controlled by the coxa and BI muscles. Short high frequency bursts of activity in the levators and remotor are produced to prevent the tension being developed in the strike muscles from being released too early, that is before the optimum or maximum forces have been developed. This is achieved by coupling of increases in antagonistic muscle activity and by graded recruitment of the excitatory axons. As the tension in the strike muscles increase, the axons capable of causing the greatest anti-strike muscle tension responses, are introduced.

The increased impulse frequency seen before a strike in the phasic bursts of the already active CxR muscle, will generate secondary muscle spike responses. As demonstrated in Chapter 3, these cause the development of sudden and considerably increased tension in this muscle. This is necessary, since before a strike the CxR not only has to counter the tension developing in the CxP but also the promotory force developing in the depressors.

During the strike mode a brake is applied to both depression and promotion. The CxR suddenly begins to increase in activity 10 ms before the end of coxal promotion when the only active strike muscle is the Pd. At this stage the frequency of excitation to the Pd is not maximal and so it is probably not producing maximal levels of tension. Therefore the CxR could produce sufficient force to slow promotion. The brake on depression is unusual, in that it is not due to the main levator muscle, the Al, but to the smaller Pl. Again all the active depressory force at this stage is due to the Pd. The relatively small amounts of tension which the Pl would be capable of producing may be sufficient to slow down depression.

A brake on depression may be necessary for two reasons. Firstly the strike will be equally effective as a defensive deterrant whether the cheliped is fully or only partially depressed. The only difference will be in the time taken. It is likely that full depression of the BI will take a longer time to achieve than that for partial depression displayed during a strike. Since the visual effect of the strike is primarily based on speed, it will be more advantageous for the cheliped to be only partially depressed in this shorter time than in a longer time that would otherwise be necessary for a full depression.

The brake on depression may also be necessary to introduce the third mechanical role of the Pd. It has been shown that before full depression of the BI, when the coxa is promoted, contraction of the Pd causes the coxa to remote (Chapter 4). If the full depressory force of the Pd is partially antagonised by the levatory force of the Pl, tension in the Pd may be expressed more in its tertiary role as a coxal remotor than in its primary role as a BI depressor. This may cause a more rapid re-extension of the limb than if only the CxR was active.

The fourth mode, recovery, is primarily controlled by the CxR. It has been shown that the T-Cx joint begins re-extension 30 to 60 ms before any other joint. Such a feature would bring about the rapidly re-increasing visual size of the crab, after a strike, whether the rest of the cheliped was extended or not. That is, even if the distal joints remained flexed, the whole cheliped would be swung laterally, increasing the visual size. However the distal segments do re-extend and so produce an even greater enlargement of size.

Therefore it has been demonstrated that the fast strike of Carcinus is probably controlled by a neural programme which allows the behaviour to be identically reproduced in different individuals. The pattern of muscle activity is clearly separate from the preceding and following patterns of threat displays. Threat displays are accompanied by a steady and

regular discharge of muscle impulses which increase in frequency of threat. When a strike is "programmed", this regular sequence is abruptly disturbed as the tension of antagonistic muscles is primed for the rapid flexion and re-extension of the cheliped. The threat behaviour is examined in more detail in later chapters.

The EMG's recorded in this chapter have demonstrated that the main propulsive force for the strike is produced by co-contraction of the coxal and BI muscles. Suggestions have also been made as to the cause of the beginning of the strike. In the following chapter the sequences of muscle activity are correlated with the known physiological and mechanical properties of the coxal and BI muscles to explain the method of operation of the fast strike behaviour.

CHAPTER 6

OPERATION OF THE FAST STRIKE

Films taken of the fast strike of Carcinus maenas showed that the rapid flexing movement of the cheliped is completed in 30 to 60 ms. It is followed by an equally rapid re-extension and re-levation of the limb. During these movements, exceptionally high angular velocities are reached. Calculation of the energy required to propel the cheliped, indicated that there must be energy storage before the strike and some form of aid to the recovery movement.

Anatomical examination of the cheliped complexes around which the strike is organized, the thorax, coxa and BI, failed to reveal any skeletal click mechanisms which could facilitate energy storage. However, the origins of the three main BI muscles are far from simple. For instance, the Pd is subdivided into five small muscle groups and one large block which provides the major component of force. The minor subdivisions are ill-aligned for depression and would appear to influence the direction of force produced by the main muscle block.

Intracellular recordings from the main muscles of the BI, the Al, Ad and Pd, plus the two main coxal muscles, the promotor and Dorsal remotor, did not indicate any specializations for fast contractions, although each receives at least one phasic axon. Four of the muscles can also produce secondary generated spike responses in the fibres when stimulated at high frequencies, which causes extra large development of tension in the muscles.

Different muscles had different rates of contraction and relaxation. For example, at peak frequencies of stimulation to the tonic axons of the CxR, this muscle displayed a slow production of tension. On the introduction of the phasic axon, tension increased stepwise and the decay from tetanic levels to zero was extremely rapid. The CxP displayed a slow rise to peak tension, when its tonic and phasic axons were stimulated. At the end of stimulation there was a maintained plateau of tension before the beginning of a slow decay. The Al also displayed a slow rise to, and decay from, peak levels of tension. However the recruitment of the two phasic axons, which generate large and small twitches respectively, could be used for development of sudden, extra bursts of tension in this muscle. The Ad demonstrated a very slow decay in tension after stimulation had ceased. The introduction of its phasic axon caused fast and sudden increases in muscle tension development. At maximum stimulation the Pd responded with a fast rise in tension and an even faster decay time.

Analysis of the geometry of the T-Cx and Cx-BI joints showed that there is a point of instability at which the mechanical advantage of the CxR and CxP are equal. As previously described in Chapter 4, this could be used as a "flip-flop" mechanism. The CxR has a high and steady mechanical advantage about the T-Cx joint over the positions adopted during threat. The CxP has a low advantage at threat which increases with promotion of the coxa.

The Al has a high and steady mechanical advantage about the T-Cx and Cx-BI joints when the cheliped is remoted and levated; that is for the full range of threat positions. The mechanical advantage subsequently decreases in pre-strike positions which will mean that any residual tension in the Al will not unduly slow the cheliped movement during strike. The Ad has an increasing advantage from threat to pre-strike positions and then decreases. It was suggested in Chapter 4 that maximum effect would be obtained from this muscle if it was active in the early pre-strike stages. The advantage of the Pd is unusual and unexpected as it decreases throughout the positions of strike but rises during recovery.

As described in Chapter 4, the BI muscles will also affect the position of the T-Cx joint. Contraction of the Al will not only levate the BI but will also remote the coxa. This is because the origin of the Al lies on the posterior side of the T-Cx axis. By a similar principle the Ad will depress the BI and also act on the T-Cx joint, promoting the coxa.

The Pd has a more complex role. It is unusual in that it has three distinct and separate effects. Its primary role is as a BI depressor but depending upon the degree of depression and position of the T-Cx joint, it will promote or remote the coxa. When the T-Cx joint is remoted and the BI levated, the Pd functions as a coxal promotor. As the BI is progressively depressed, its promotory effect is diminished. This is due to a reduction in promotory mechanical advantage caused by the movement of the Pd tendon head towards the T-Cx pivot axis. This, in turn, is due to the asymmetry of the T-Cx and Cx-BI pivots. When the coxa is fully promoted the Pd functions as a remotor and will continue to act in this way for several degrees of subsequent remotion. The actual angle at which this muscle changes in function, and the extent of its mechanical effect, depends upon the degree of BI depression.

The unusual mechanical actions of the Pd is enhanced by a flexible link between the tendon blade of the main muscle and the heel shaped tendon head. Movement of this link allows the force developed in the depressor to be directed either in the coxal remotory or promotory planes

of movement. It was shown that these two mechanical actions will occur even if the subsiduary muscles are passive, although their contribution will improve these two functions by alteration of the mechanical advantage of the Pd. It was suggested in Chapter 4 that all three actions of the Pd could be used in a strike. The muscle could contract during a strike, depressing and promoting the limb. Maintained activation would then begin coxal remotion, aiding any re-extending action from an activated CxR.

Both the CxR and Al have stable and high moments in the threat positions which precede the strike. It was suggested in Chapter 4 that this would be advantageous if these muscles were to be used as muscular stops against which their antagonists could contract. The use of combined EMG and cinematographic techniques revealed that these muscles could be used in this way.

The temporal sequence of muscle activity in all the cheliped muscles was determined by analysis of the EMG's. All the main cheliped muscle pairs show mutual increase in high frequency activity at times. This will allow isometric development of tension in the strike muscles which can contract against the antagonistic load developed by the anti-strike muscles. Co-activation varies from segment to segment. The least amount is shown by the dactylus opener and closer muscles, and only occurs before the claw is closed. Antagonistic activity occurs at the end of the strike movement in the propus extensor and flexor muscles. Since the extensor begins to fire before C-P joint flexion is complete, there will be no delay in joint re-extension after the strike which may otherwise occur if the muscle had to develop tension from zero levels at the end of the strike. In the carpus extensor and flexor muscles, the first overlap of muscle excitation occurs during pre-strike which might allow isometric tension development in the flexor muscle before the strike mode begins. A second overlap occurs before joint re-extension which should produce a more rapid re-extension in the manner described above for the propus muscles.

The BI muscles show clear periods of antagonistic activity. The regular discharge seen in the Al during threat, is disturbed shortly before the beginning of strike behaviour. The Al begins to fire in bursts and shows responses to all three axons, and at the same time the two depressors are activated. As the limb only depresses relatively slowly at this stage of pre-strike it can be assumed that the depressive force is being antagonised by the levatory action of the Al.

The Ad is only excited for a very short time during pre-strike, and ceases to fire during rapid cheliped depression. Only two muscles are highly active during the strike mode. One, the Pl, may act as a brake, to prevent full depression of the BI. The other muscle, the Pd, has two peaks of activity. The first, in pre-strike, is due to excitation of all

three axons, when tension will be developed against the levators. The second peak is due only to excitation from two tonic axons and occurs 10 ms before the end of the strike mode. It was suggested in Chapter 5 that this second peak may introduce the third, remotory function of the Pd, aiding fast recovery movements. It was also suggested that since the Pd is active during these initial stages of recovery exerting a remotory effect on the limb, the re-activating levators may begin to contract isometrically against this antagonistic tension.

The CxR is highly tonically active during preceding threat displays. Like the Al, this activity is broken into short irregular high frequency bursts at the beginning of strike behaviour. At this time, the CxP is excited, reaching peak frequencies during pre-strike. It is subsequently inactivated before the beginning of rapid coxal promotion. This suggests that the depressors must aid in flexion of the limb. The CxR, which is active at reduced frequencies during the strike mode, shows a sharp increase in frequency just before the beginning of coxal re-extension.

During rapid cheliped promotion, the CxR and Al will not relax completely. The EMG's demonstrate that they continue to be excited at low frequencies throughout coxal promotion, from activity in the tonic axons generating smaller muscle impulses. This should not slow the strike a great deal because the forces generated by the three strike muscles are so large, and also because of the feature of the flip-flop mechanism. Instead it will mean, that on subsequent increase of excitation after the strike, these anti-strike muscles will not have to develop tension suddenly from zero, but can add extra tension to existing levels.

All these features and results from previous chapters, can now be assembled to explain the most likely method of operation of the fast strike behaviour. The full sequence of muscle activity is illustrated on figure 1 and enlarged EMG's from the six main coxal and BI muscles are shown together on figure 2.

On the introduction of an appropriate stimulus, a displaying crab suddenly switches from a threat display behaviour to a strike behaviour. Whatever the trigger for this switch, the transition between the two agonistic patterns is distinct; from a rigidly maintained position in which the chelipeds are levated and extended, the arms are moved slightly inwards and downwards, and a small degree of flexion is displayed at all the joints. Once this action takes place the strike behaviour can be said to have begun. However, a fast strike is not always inevitable even at this stage. For example, this activity can also precede a slow strike. The behaviour may also be reversed without a strike occuring, if stimulation

FIGURE 1

CHELIPED MUSCLE ACTIVITY DURING A FAST STRIKE

The activity of the cheliped muscles during fast strikes was analysed from all the EMG recordings. From these, a typical sequence of muscle action was established. These were assembled together with reference to time and are indicated on figure 1. The width of the bars represents the intensity of excitation to each muscle. Thus the largest widths indicate the maximum muscle impulse frequency. The widths are not comparable between individual muscles and do not represent tension development, but indicate the sequence of events for each particular muscle.

The abscissa represents time in ms before and after the strike.

The vertical dotted lines indicate the time of each strike mode. For example the first threat mode begins 500 ms, and ends 250 ms, before the end of rapid cheliped promotion.

The upper graph represents the angular excursion of the T-Cx and Cx-BI joints during the fast strike. The T-Cx is represented by a continuous line, the Cx-BI is represented by a thicker dotted line. The lower graph indicates the angular velocities of these two joints during the strike. The T-Cx is represented by triangular symbols, the Cx-BI by circles.

The activity of the muscles demonstrates the features described in the text. These include:

1. Co-activation of all muscles, which allows muscles to contract against antagonistic loads.
2. Muscles showing reduced activity apparently early in the strike behaviour. For example the Ad and CxP are inactivated before peak depression and promotion velocities are reached. This indicates their development of tension before the strike.
3. Muscles operating at apparent wrong times in the strike behaviour. For example the Pl is excited during limb depression and the Pd maintains activity during the re-extending recovery movement of the cheliped.

CHAPTER 6 FIGURE 1

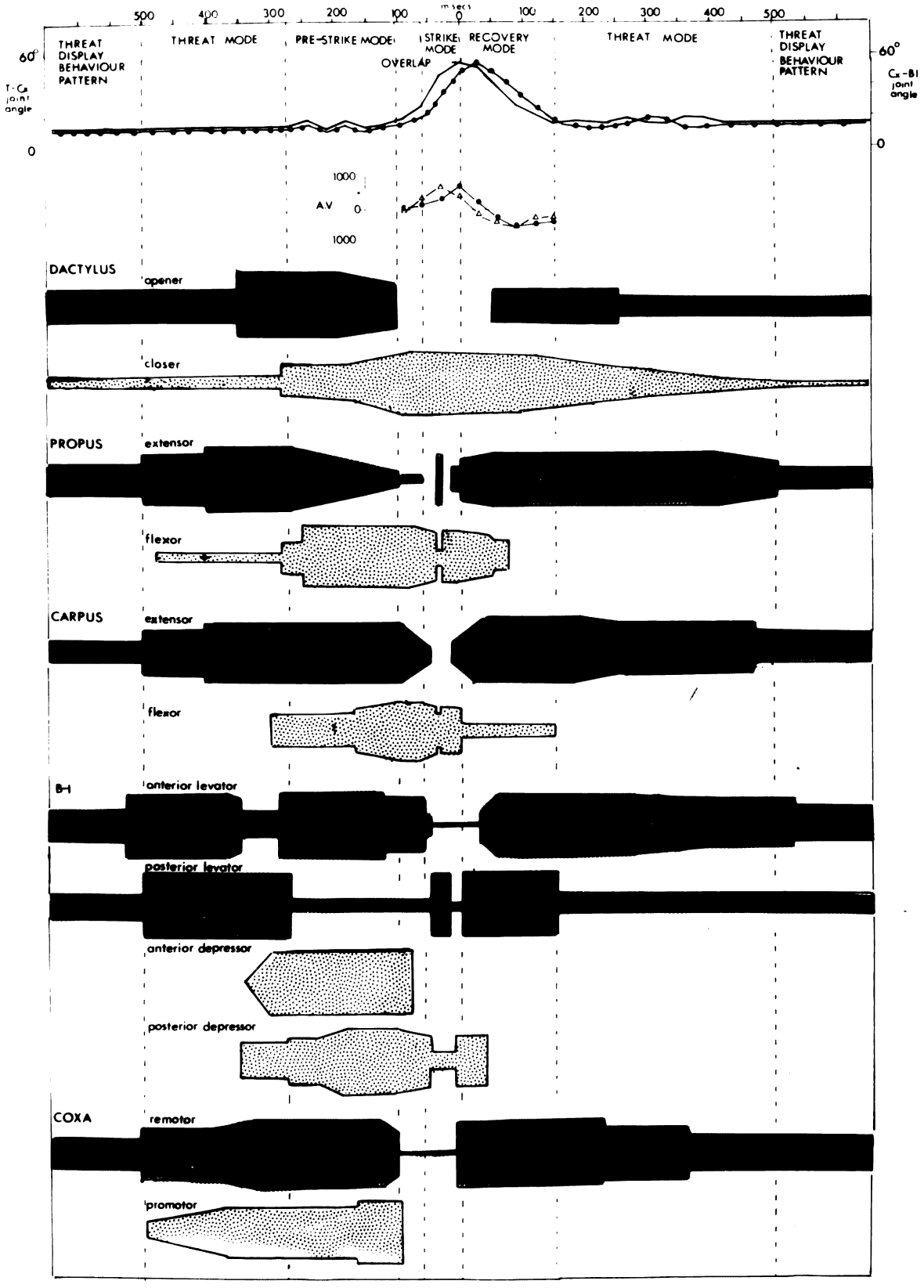


FIGURE 2

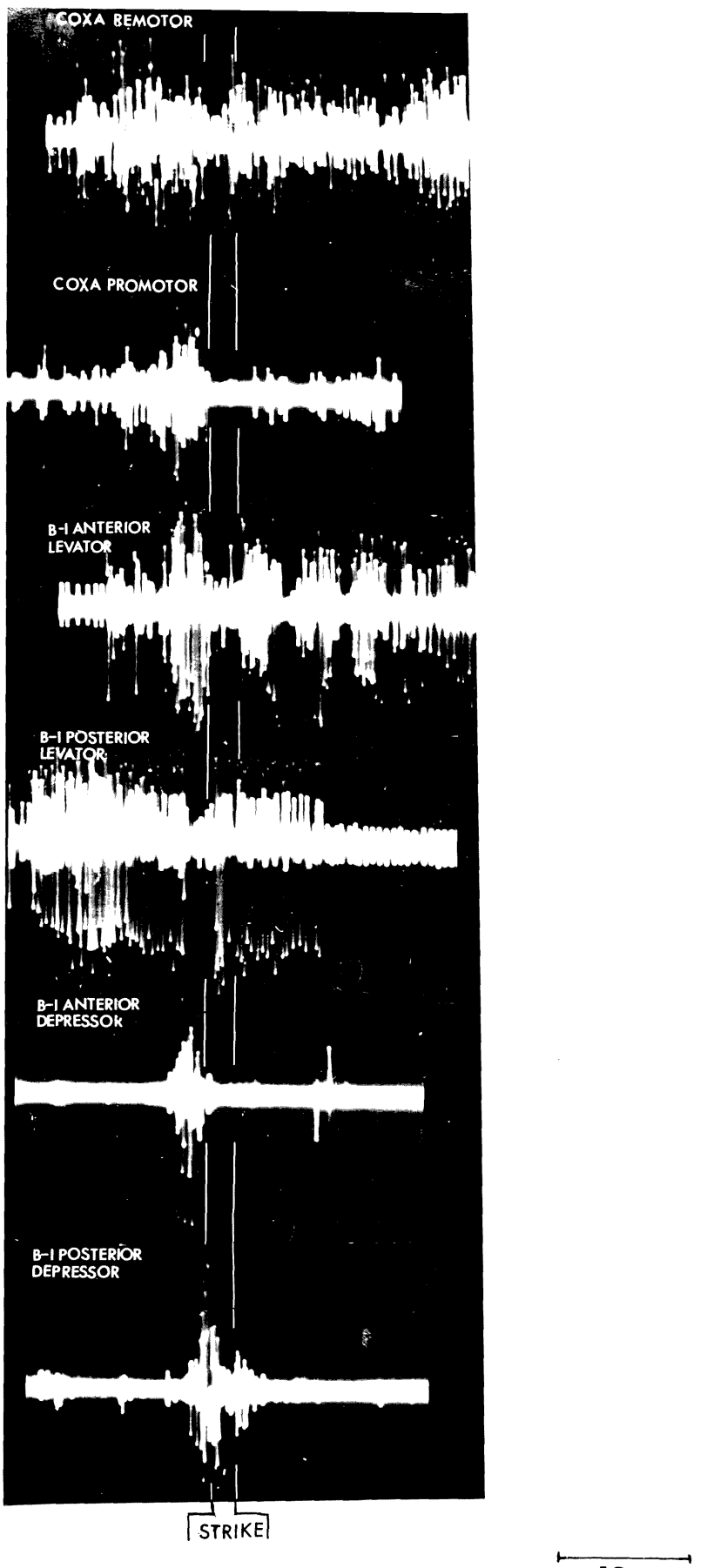
THE ACTIVITY OF THE COXAL AND BI MUSCLES DURING A FAST STRIKE

EMG's recorded from the 6 main coxal and BI muscles during typical fast strikes were assembled together with reference to time. This is indicated in Fig. 2. The activity of each muscle during the strike can be directly compared vertically.

The EMG's demonstrate several features described in the text. These include:

1. The brief antagonistic phase of the BI Pl and Pd during the strike. This may serve to act as a brake on depression, allowing the third mechanical effect of the Pd, remotion of the coxa, to be displayed.
2. The high frequency burst of muscle impulse in the CxR and Al before the strike. This will progressively increase the tension developed in these muscles to counter the increasing tension which develops in the strike muscles. The effect of this is to prevent the release of the cheliped before peak strike muscle tensions have been achieved.
3. The sudden injection of muscle spikes from the Ad.
4. The "early" relaxation of the CxP and Ad before the peak strike velocities are achieved.
5. The continuation of Pd activity into the recovery mode due to a second burst of small impulses.
6. The phasic nature of strike muscle activity compared with the tonic-phasic nature of the anti-strike muscles.

CHAPTER 6 FIGURE 2



is ceased; the crab will then resume a threat position. The crab may also perform a series of aborted strikes, moving the arm gradually to the critical strike angles, but then rapidly re-extending it.

When pre-strike twitches are observed, a fast strike is almost inevitable. At this stage the muscles which provide the propulsive force, that is the main coxal and BI muscles, show a mutual increase in high frequency activity. This muscular tug-of-war is displayed as these small, quick remotory-promotory and levatory-depressory twitch movements.

The first increase in strike muscle tension begins in the CxP. Its antagonist, the CxR, shows high frequency bursts. In these initial positions of the strike behaviour, the CxR has its greatest and most stable moment about the T-Cx joint. The CxP has a low moment which gradually increases as the limb is promoted. This latter feature is ideal for allowing the CxP to develop increasing tension before the beginning of rapid promotion. Prior development of tension in this muscle is also necessary because the CxP develops tension slowly. Hence, the CxP will slowly develop increasing tension during these positions of low promotory mechanical advantage. At this time the CxR appears to be excited by its four axons, maintaining this muscle at peak tension levels and producing a muscular load against which the CxP can contract.

150 to 200 ms after the CxP begins to develop tension, the BI depressors are activated. The levators show a disturbance to their regular tonic activity which occurs during threat. Both levators display a considerable increase in impulse frequency of excitation. The remotory effect of the A1 will aid the CxR in countering development of promotory tension. Like the CxR, the A1, the main levator muscle, is excited in short bursts. Between each burst, caused by the recruitment of its two phasic axons, the tonic unit maintains its activity.

The end of the pre-strike mode is characterised by reduced excitation in both the CxR and CxP muscles. It is not known how the strike is triggered. One possible trigger could be proprioceptive. When the BI and coxal joints reach critical angles, this could be proprioceptively relayed into the thoracic or cerebral ganglia. This may activate interneurones which could lead to the reduction of CxR excitation allowing the force stored in the CxP to be suddenly released. The trigger may also involve mechanical features. As the depressors develop tension they will exert a force on both the BI and coxa. There will be a point at which the combined promotory force of these three proximal strike muscles exceeds the antagonistic remotory force of the two anti-strike muscles. Once this point is exceeded the arm will begin to promote faster by virtue of the

flip-flop mechanism. At this point, proprioceptive information may then lead to reduction of CxR and A1 excitation, allowing the full promotory force to be expressed and generating the rapid promotion.

By whatever means the fast strike begins, reduced activity in the CxR accompanies the first stages of promotion. Therefore the CxP will be able to release the stored tension developed during pre-strike and will begin to promote the limb. Shortly after the CxR is reduced in frequency, excitation to the CxP ceases.

As predicted in the analysis of mechanical advantages (Chapter 4), the Ad is maximally active during pre-strike when its moment is greatest. Like the CxP, the Ad will develop tension before the strike by co-contraction with its antagonist, the levator muscles. The Ad is inactivated only a few ms after the CxP, during the initial stages of depression, before the peak depressory velocity is reached. Although the Ad only displays a few extremely large spikes during the strike, the neuromuscular analysis of this muscle showed that, even at low rates of stimulation, tension generated by the phasic axon is considerable and increases rapidly (Chapter 3).

The Pd is also active before rapid depression begins, and its promotory effect will be added to the other two strike muscles. The differences in peak frequency, times of inactivation and neuromuscular properties of these strike muscles ensures a continuous rapid promotory movement. In the first stage of the strike mode, the Pd is the only highly active proximal cheliped muscle; excitation to the CxR and levator muscles is reduced. This is just after the time of peak promotory velocity, and just before the time of peak depressory velocity. At this stage, most of the stored CxP tension will probably have been expended. As the Ad is inactivated slightly later than the CxP, it will probably still be releasing its stored tension, but its effect will be split between promotion and depression. This may account for the subsequent decrease in promotory velocity. The later depressory velocity may be due to the later peak activity time of the Pd, adding its effect to that of the Ad.

During the middle of the strike mode, the second unit of the Pl is re-introduced generating large muscle impulses. This activity will probably act as a brake on depression of the BI. It has been suggested that the brake is necessary to introduce the third effect of the Pd, as a coxal remotor, and also to save valuable recovery time which may otherwise be wasted on superfluous depressory movements. That is, it is advantageous for the crab to show that it can strike fast, but equally advantageous to regain threat postures. It will be advantageous to apply this brake if

by stopping the strike several degrees short of full depression without altering the startling and sudden visual effect of a strike, the crab gains extra time for recovery.

The second peak of Pd impulses occurs 10 ms before the end of the strike mode. The peak co-incides with the rising mechanical advantage of this muscle. By maintaining activity, the Pd will suddenly switch from acting as a strike muscle to an anti-strike muscle, although it will still cause depression. An overlap of depression and remotion has been shown to occur in the graphs of angular excursions of the coxa and BI joints. At this time, excitation to the CxR is suddenly and considerably increased. The remotory effect of the Pd will add to that of the CxR and so produce an even more rapid re-extension to the limb.

It has been suggested that any residual tension in the Pd may be utilized by the Al for co-contraction and fast tension development. The EMG's show that there is a few ms overlap between the increased excitation to the Al and maintained activity of the Pd. However as it has been shown that the Pd has a very fast tension decay rate (Chapter 3), it is unlikely that this short co-activation could have much, if any, effect on tension development in the Al; instead it is more likely that the small levator muscle, the Pl, contributes again, aiding re-levation of the BI. Unlike the Al which does not receive maximum excitation until 30 ms after cheliped promotion is complete, the Pl fires at a high frequency immediately at the end of flexion. It may be able to generate sufficient tension to aid the main levatory force developing in the Al. Once excitation frequencies to the Al are increased, its remotory effect will add to the CxR. Peak recovery velocities occur after this time, and as figure 1 shows, these values are reached 60 to 90 ms after the beginning of recovery.

Although the proximal cheliped muscles provide the main propulsive force for the strike, the distal muscles are certainly not passive elements in the behaviour. They also display mutual increase in frequency of activity at times. The propus extensor and flexor muscles both show a high frequency activation at the end of the strike (Chapter 5, Figs. 2 and 3). It was suggested in Chapter 5 that this co-activation may allow some isometric tension to be developed in the extensor muscle before the C-P joint begins to re-extend and will also mean that strike recovery follows immediately after flexion, since the extensor will not have to develop tension from zero levels. This reflects the importance of this joint in making the crab bigger again as soon as possible after the strike, which is necessary since the propus is a long, broad segment, extension of which doubles the apparent length of the cheliped.

The carpus extensor and flexor display two period of co-activation (Chapter 5, Figs. 4 and 5), one during pre-strike and a second just before the end of the strike mode. It was suggested in Chapter 5 that the first period of mutual increase in high frequency activation may allow the flexor to contract isometrically before the strike and so ensure that the beginning of M-C joint flexion is as fast as possible. This is important since the carpus is comparable to an elbow, flexion of which will propel the propus medially whether the latter exerted any additional flexion force or not. The second period of co-activation will function in a similar manner described above for the propus muscles. It will ensure that the M-C joint is rapidly extended immediately after flexion and will not delay strike recovery which may otherwise occur if the extensor had to develop tension from zero levels.

COMPARISON WITH OTHER SYSTEMS INVOLVING RAPID MOVEMENTS

It has been shown that in order to perform the strike, Carcinus maenas uses a variety of physiological modifications. Unlike rapid movements in some other arthropods, it does not appear to have concentrated on extreme specialization of any one particular facet, but rather relies upon contributions from several.

The agonistic cheliped snapping behaviour of Alphaeus heterochelis is achieved by modification to pivot points and special muscles. The rapid claw closure is produced by the P-D joint being locked open until a separate, small closer muscle contracts to release the lock. This allows the tension in the large closer muscle, which was developed during the time of lock at the P-D joint, to be suddenly released and so snaps the claws shut (Ritzmann, 1974). In Carcinus the subdivisions of the Pd muscle do not act as locks or releasers of locks but may change the mechanical effect of the main muscle block. Their activity will make the Pd act as a coxa promotor or remotor but would not allow the development of tension prior to movement. This function is achieved by co-contraction of antagonistic muscles.

The strike of Squilla lasts for only 4 to 8 ms (Burrows, 1969), over eight times as fast as the strike of Carcinus. This reflects the extreme specialization and simpler limb movement found in Squilla. The raptorial leg of Squilla is propelled forwards ballistically, while in the cheliped of Carcinus all segments of the limb are involved during a strike. The cheliped is not simply moved forward like a harpoon but is flexed at all the joints in a clutching posture. By flexion of the distal joints, the midline of the body is reached in a shorter time.

The time course of the defensive fast strike in Carcinus may be compared to the defensive tail flick of the crayfish. This latter action takes 70 to 80 ms (Wine and Kranse, 1972). However there is only 10 ms between the introduction of a tactile stimulus and the beginning of flexion. This is due to the lateral giant fibres which initiate the reflex. The flexor muscles are fast and massive, and can produce flexion quickly without prior development of tension. Thus the crayfish has two specialized mechanisms allowing rapid movements, a giant fibre system and large muscles. This means that not only will the movement be rapid, but there will be a minimal time of latency between the stimulus releasing the behaviour and the rapid movement. The importance of this reflex is not the action itself but the time taken to begin it. In Carcinus the reverse is true. The crab is already defensive in threat, the strike is an exaggeration of this defensiveness. It therefore displays a time lag, during which the strike muscles can develop peak tension, between the initiation of a strike behaviour and the actual movement itself.

In locusts, a similar feature of time lag is displayed and like Carcinus, the rapid movement relies upon isometric muscle contractions. However, there is considerably more specialization in the jumping leg geometry of locusts, and leg extension takes only 20 ms. In order to develop peak power, the tibial extensor muscle of the jumping leg must develop tension isometrically before the jump. As the flexor muscle is considerably smaller, there must be specializations to the joint allowing this build up and as explained in Chapter 4, these specializations include an unusual joint geometry and the possession of a skeletal projection, Heitler's lump (Heitler, 1974). The modified joint geometry gives the flexor muscle a much larger mechanical advantage over the extensor muscle when the limb is flexed; a ratio of 21 to 1. However when the tibia is extended the mechanical advantage ratio is reduced to 1.5 to 1. This has the advantage that jump extension will not be slowed down by residual flexor tension.

In Squilla, the rapid strike is achieved by co-activation of antagonistic muscles and a skeletal click mechanism (Burrows, 1969). Operation of the click mechanism gives the smaller carpus flexor muscles of the raptorial limb a 900 to 1 mechanical advantage over the larger extensor muscles. The principle of changing mechanical advantage is also used in Carcinus. In this crab the muscles which provide the main propulsive force do not have such widely different mechanical advantages seen in Squilla and the locust. On the contrary, the fast strike begins from a position in which the antagonistic CxP and CxR muscles have equal mechanical advantages, the point of instability about the T-Cx joint. This means that the coxa

can be operated as a flip-flop mechanism.

The coxa is stable in two positions, fully remoted and fully promoted. At the point of equal mechanism advantage the coxa is extremely unstable when the tension in the CxR is equal to that in the CxP; any slight increase in remotory or promotory force will flip the limb in the appropriate direction. This is likely to be the main cause of the sudden promotion of the coxa. The CxP gradually develops tension by contracting against the CxR. In the initial positions of the strike behaviour, the mechanical advantage of the CxR is far greater than that of the CxP and so large amounts of developing promotory tension could be countered by relatively small amounts of remotory tension. However, as shown on all the graphs of T-Cx joint excursion, the strike movement itself does not begin from a fully remoted position of the coxa, but from a pre-strike angle of about 30^{o} at the T-Cx joint. If at this stage in the behaviour the CxR and CxP were producing maximum tension levels, then their moments would be quite close as shown in figure 20, Chapter 4.

The EMG's indicated that before the strike the two coxal muscles receive high frequency excitation and therefore will be producing almost maximum tension. It has been shown that when these muscles produce maximum tension the bistable point about the T-Cx joint is reached at 38^{o} promotion (Chapter 4, Fig. 20), an angle which occurs during the strike mode itself. Thus, if the two muscles were producing maximum tension at any angle less than 38^{o} and no other muscles were influencing the coxal position a strike could not occur; instead the limb would be remoted.

Therefore, for a strike to occur with both coxal muscles fully active, the point of instability must be crossed. This could be achieved in two ways. One way is by relaxation of the CxR. The tension developed in the CxP will now be released and the limb promoted. The second possibility is by the introduction of an additional extra promotory force developed by the CxP or from another muscle. If this extra force is sufficient to raise the total promotory moment over the total remotory moment, the point of instability will be crossed and the limb flipped in a promotory direction.

The EMG's indicate that the latter suggestion is the more likely method by which the strike is produced and that this extra force is produced by the two depressor muscles which develop tension during pre-strike. The A1 is also active during pre-strike and so its remotory effect on the coxa will add to the CxR. This will further increase the total remotory moment about the T-Cx joint, and also indicates that the CxP must receive even more extra promotory force to propel the coxa forwards. Thus the effect of the depressors on the coxa will add to that of the CxP, pro-

gressively raising the moment of promotion. At some stage the bistable point will be crossed and the coxa flipped in a remotory direction. Subsequently, partial relaxation in the CxR and Al ensures that the cheliped movements will not be unduly slowed by their antagonistic action. The removal of any impedance on promotion is aided by the decrease in moment of the CxR about the T-Cx joint and the Al about the T-Cx and Cx-BI joints, which occurs for positions of the joints taken during strike.

It has been shown that the CxR and Al will not be completely relaxed during the strike; there is still low frequency excitation in these muscles. This means that the recovery action will be faster than if these muscles were otherwise completely relaxed. That is, when the frequency of motor excitation increases these muscles will not have to develop tension from zero levels, but instead will be able to add extra tension onto existing levels. This ensures that limb re-extension and re-levation will follow immediately at the end of the strike mode, permitting a smooth and continuous action throughout. If the anti-strike muscles had to suddenly develop tension from zero at the end of the strike mode, the arm would be jarred to a halt before beginning to slowly remote and re-levate as recovery muscle tension developed.

The re-extension of the coxa may employ the bistable properties of this joint. The bursts of CxR impulses would have the effect of injecting sudden and increasing amounts of remotory force on the coxa. Thus the moment of remotion about the T-Cx joint will quickly climb to the point of instability. Once this point is crossed, the arm will flip in a remotory direction and the velocity of coxal remotion will increase. The remotory effect of the Al and the third role of the Pd, as a coxal remotor, will add to that of the CxR. Consequently the point of instability will be reached even quicker than if the CxR was active alone.

In locust, the muscles which produce rapid limb extension in a jump can be divided into power producers and power controllers (Heitler and Burrows, 1977). The power producer muscle is the extensor tibia while the power controller muscle is the flexor tibia. Once maximum force is achieved by the extensor muscle, the controlling flexor muscle relaxes and allows the force in the extensor to be released and so produce rapid leg extension.

A similar division of muscles is seen in Carcinus. Separation of these two roles will increase the accuracy of the timing of the strike. If the CxP had no controlling stop against which it could produce tension, the strike duration would depend purely on the muscle's physiological properties. It has been shown that the CxP has a slow tension rise time. The resultant "strike" would therefore be slow, even if the promotory effects of the two

depressors were added on to it. However in Carcinus a strike does not occur until peak muscle tensions have been developed. Development of these tensions is controlled by activity in the CxR and levators. When the trigger for a strike is released, the power controlling muscles relax, and the full force in the power producing CxP, Ad and Pd muscles will be expressed.

The Pl muscle may also act as a power controller. The Pl shows a high frequency burst during the strike mode. Since the Pl is comprised of small muscle groups, it is probably not capable of producing much levatory tension. Instead this burst may function as a power control, and may slow down depression. As suggested previously, this control on BI depression may be necessary to introduce the third role of the Pd, as a coxal remotor.

The Al has two functions, as a power producer for levation before and after the strike, and as a power controller for the promotory-depressory movement, allowing the strike muscles to develop tension before the strike. Similarly, the Pd has both power controlling and power producing functions. The main muscle block, Pdl, produces the main depressory-promotory force. Selective activation of the subsiduary muscles may control its power and effect.

There must be a motor programme co-ordinating the strike movements and muscle action, as all strikes are similar in form and muscle activity. However it is probably not a simple circuit; there is likely to be considerable feedback of proprioceptive information from the limb positions, indicating whether the cheliped is in the correct position for a strike and producing the stereotyped positions adopted during pre-strike.

Several possible programmes for the locust jump were suggested by recording from the motorneurones (Heitler and Burrows, 1977). Tibial flexion always precedes a jump. When this occurs the fast extensor tibiae motorneurones may begin to spike, which initiates a series of events resulting in the co-activation of flexor and extensor muscles. The series begins with an increase in excitation to the slow extensor tibiae motorneurones and excitation to the flexor motorneurones. This ensures that the flexor muscle tension is high and the tibia remains flexed as the extensor muscle begins to develop tension. As this occurs, an excitatory reflex is evoked due to strain receptors in the distal femoral cuticle.

The actual trigger to the jump, when the co-contraction is terminated, the flexor excitors inhibited and the flexor inhibitors excited, is not known. It was suggested that it could be due to a measure of tension in the femoral muscles. This was considered to be unlikely since abortive kicks, when muscle tension will be the same as in an actual jump, do not

show trigger activity. Also synchronous kicks in the two legs can occur when spike frequency and presumably muscle tension, is different in the two legs. The authors suggested that this indicated that the trigger action is controlled by a central command.

The trigger releasing the strike in Carcinus is similarly unclear. It may be due to the excitatory neurones reaching specific frequencies which will indicate the correct and optimum development of tension in the relevant muscles. It may also be purely mechanical when the combined promotory moments exceed the antagonistic remotory moments. Even so, once this mechanical trigger has been released a neural circuit must be started by which the CxR and A1 are partially relaxed allowing the developed strike tensions to be released. If this is the trigger, the initiation of the strike mode may be due to the Ad. It is only active for 150 to 200 ms and could provide an injection to the CxP, sufficient to raise the promotory moment over the remotory moment and so set the flip-flop mechanism into action.

Direct proprioceptive information is another possible trigger. However when the joints reach their critical pre-strike angles, a strike does not always immediately follow. There is usually a pause during which the development of maximum tensions takes place. If the achievement of specific joint angles was the trigger, it would involve a very complex series of neural circuits which would have to receive and assimilate information from all the limb joints. It is therefore unlikely that joint position actually releases the strike action.

It is suggested that the strike controlling programme consists of a number of circuits which are activated in a sequence, relying on various inputs. Appropriate stimulation will prime these circuits and cause the crab to switch from a threat display behaviour pattern to a strike behaviour. This may lead to increased excitation of the CxR and A1, generating increasing tension levels in these muscles. The recruitment of phasic axons or secondary generated muscle spike responses may lead to a second circuit being activated, exciting the CxP. Feedback mechanisms could further excite the A1 and CxR, ensuring the generation of maximum tension levels in these anti-strike muscles. The injection of tension from the Ad would increase the promotory moment and may cause the beginning of rapid flexion, when the Ad has reached its optimum tension levels. The resulting movement of the limb may be received proprioceptively and cause the reduction of excitation frequencies to the anti-strike muscles, allowing the full strike muscle tension to be released. When the Ad is inactivated, a circuit controlling the re-excitation of the P1 could be introduced. The consequent

reduction of depressory velocities could also be proprioceptively received and cause increased excitation to the CxR together with the second peak of the Pd. Decreasing tension or levels of excitation in the Pd may lead to the increased excitation in the A1 which would start the main levatory component of the recovery movement. Other circuits could similarly control and co-ordinate the movement and activity of the distal segments and muscles.

CHAPTER 7

THE ELECTROPHYSIOLOGY OF THE SLOW STRIKE

INTRODUCTION

It has been shown that the fast strike behaviour of Carcinus is not due to any one particular specialized mechanism, such as a click-joint, but is due to the combined effects of muscular and mechanical modifications. These include co-contraction of muscles, allowing isometric tension development and the use of unusual joint geometry. EMG analysis was performed on records obtained from crabs which displayed slow strikes to compare the muscle activity patterns in the slow and fast strikes, in an attempt to define the physiological differences between these two agonistic behaviours.

A slow strike is normally performed when a food particle, such as a piece of fish, is placed in front of the crab. The crab moves towards the stimulus and then displays a slow strike, clutching the food between the claws at the end of cheliped flexion. If it manages to catch the stimulus the crab retreats slowly, with chelipeds raised and extended, to a corner of the tank where it ingests the food. If the crab misses the food, it may repeat another slow strike or simply retreat in a threat display. Slow strikes were also performed by the crabs in the experimental preparation. In these instances the claws usually grasp the object of stimulation, which was normally a thin plastic tube waved in front of the crab. Sometimes the object was not siezed but simply hit by the closed claws. After several ms the cheliped is re-extended into positions of threat and the claws re-open to release the stimulus.

A slow strike is similar to a fast strike but has a longer time course, and generally lasts for 250 ms. This duration is not as rigidly fixed as in the fast strike and can vary from 500 to 100 ms. Even at its fastest speeds it is possible to distinguish between the two behaviours. A slow strike involves less flexion of all the cheliped joints especially at the M-C joint. There are no pre-strike twitches before the movement and no oscillatory "bounces" after. During cheliped flexion there are no reversed twitches in the distal segments. Before the cheliped is re-extended there is usually a pause at the final positions of flexion.

Before the slow strike begins, there is a period of preparatory slow flexion of all the limb joints. During this phase the arms are gradually positioned for catching the stimulus. When the appropriate joint angles are reached, the strike begins. At the end of flexion the two chelipeds remain together for 50 to 200 ms during which time any food or other stimulus,which may have been caught by the claws, is firmly held. The

chelipeds are then slowly re-extended to positions of low intensity threat displays. Although this is termed a slow action, it is still fast when compared to many others, such as normal locomotion, although it is unlikely that the sequences of muscle activity are as complex as those displayed during a fast strike.

Comparison of the two strike patterns can provide further support for the suggestions made in the previous chapter concerning the operation of the fast strike. Various parameters can be compared. These include the sequence of muscle activity, joint angular excursion, frequency of muscle excitation, occurrance of co-contraction of muscles and the presence or lack of any trigger mechanism.

MATERIALS AND METHODS

The crabs were prepared as described in Chapter 5. The recordings were examined as before and representative ones were selected for detailed analysis. At least 30 recordings were made from each muscle during a slow strike. In all the figures the following features are common:

1. The upper beam of the EMG trace illustrates the individual muscle responses during slow strike action.
2. The lower beam of the EMG trace illustrates the photodiode register of the ciné camera as described in Chapter 5.
3. The first graph represents the muscle impulses per second, ips, calculated from the EMG traces.
4. The second graph illustrates the joint position in degrees, during the slow strike. The upper, thicker lines indicate the excursions of the joint under study and the lower, thinner lines indicate the reference joint. In all, except for figure 7, this is the T-Cx joint. In figure 7 the reference joint is the Cx-BI joint. Movement of the BI-merus joint was not measured and, as before, the positional indicator graph represents the movement of the T-Cx joint during the recorded slow strike.
5. The slow strikes occurred between the arrowed lines below the EMG's and graphs.

RESULTS

The most apparent difference between the fast and slow strike behaviour is the relative lability of the latter. A fast strike always lasts between 30 and 60 ms and is followed by immediate re-extension of the joints. A slow strike can last from 100 to 500 ms with various periods of pause between flexion and re-extension. The muscle pairs will be examined and compared to their performance in the fast strike.

1. THE PROPUS-DACTYLUS JOINT (Fig. 1)

The muscles operating the dactylus do not contribute to any great extent in the fast strike. The trace of the dactylus opener muscle is comparable to the fast strike EMG in pattern of activation (Chapter 5, Fig. 1). The difference is in the time at which the muscle begins to relax. In the slow strike the opener muscle does not show any reduction in impulse frequency until 150 ms after the beginning of cheliped flexion (Fig. 1).

The activity of the dactylus closer muscle is also similar in both strike behaviours although again the timing of activity is altered slightly. The main period of increased muscle excitation frequencies occur at the end of the strike movement (Fig. 1) and not during the beginning (Chapter 5, Fig. 1).

2. THE CARPUS-PROPUS JOINT (Fig. 2)

The patterns of activity in the two propus muscles are considerably different in the 2 strike behaviours. There is no overlap of high frequency muscle activity in the slow strike and no reversed twitches. The frequency of the propus extensor muscle impulses is high before a slow strike during the preparatory flexion stage (Fig. 2). This high frequency stops 50 ms before the flexion of the C-P joint. During the strike itself, the muscle is active at low levels and may even reach zero frequencies. A low frequency of tonic activity accompanies joint re-extension.

The main increase in propus flexor muscle impulse frequency occurs during cheliped flexion. Unlike the performance of this muscle in the fast strike there is no large increase in muscle activity before the joint begins to flex (Chapter 5, Fig. 3). The tonic activity begins to decrease in frequency as the joint is slowly re-extended.

The angular excursion of the C-P joint is less extreme in a slow strike than in the fast strike. In Figure 2 the joint is not flexed beyond 50°, whereas in the fast strike the C-P joint typically flexes to 55 or 60° after which it is immediately re-extended.

3. THE MERUS-CARPUS JOINT

Again the difference between carpus muscle activity patterns in the two strike behaviours is in the onset of increased activity. In the fast strike the main increase in carpus extensor muscle activity occurs in pre-strike (Chapter 5, Fig. 4). During the slow preparatory flexion stage before a slow strike, the extensor muscle is only active at low frequencies (Fig. 3) and only small impulses are displayed in the EMG. This motor unit increases slightly in frequency during the joint flexion. At the beginning of coxal remotion a second unit fires generating larger impulses. These reach peak frequencies as the M-C joint begins to re-extend. As

FIGURE 1

THE PROPUS-DACTYLUS JOINT

The time scale represents 1 s. The film speed was 8 fps in the EMG of the dactylus opener muscle and 16 fps in the EMG of the dactylus closer muscle. The dactylus opener muscle is greatly increased in impulse frequency before a slow strike action. This high frequency continues during the beginning of coxal promotion. After this the frequency is reduced and the muscle remains tonically active until the cheliped is re-extended in positions of threat.

The dactylus closer muscle displays maximum impulse frequencies at the end of the slow strike. This corresponds to the period of reduced opener muscle activity. As the claw is re-opened in threat, the closer muscle is considerably reduced in activity.

CHAPTER 7 FIGURE 1

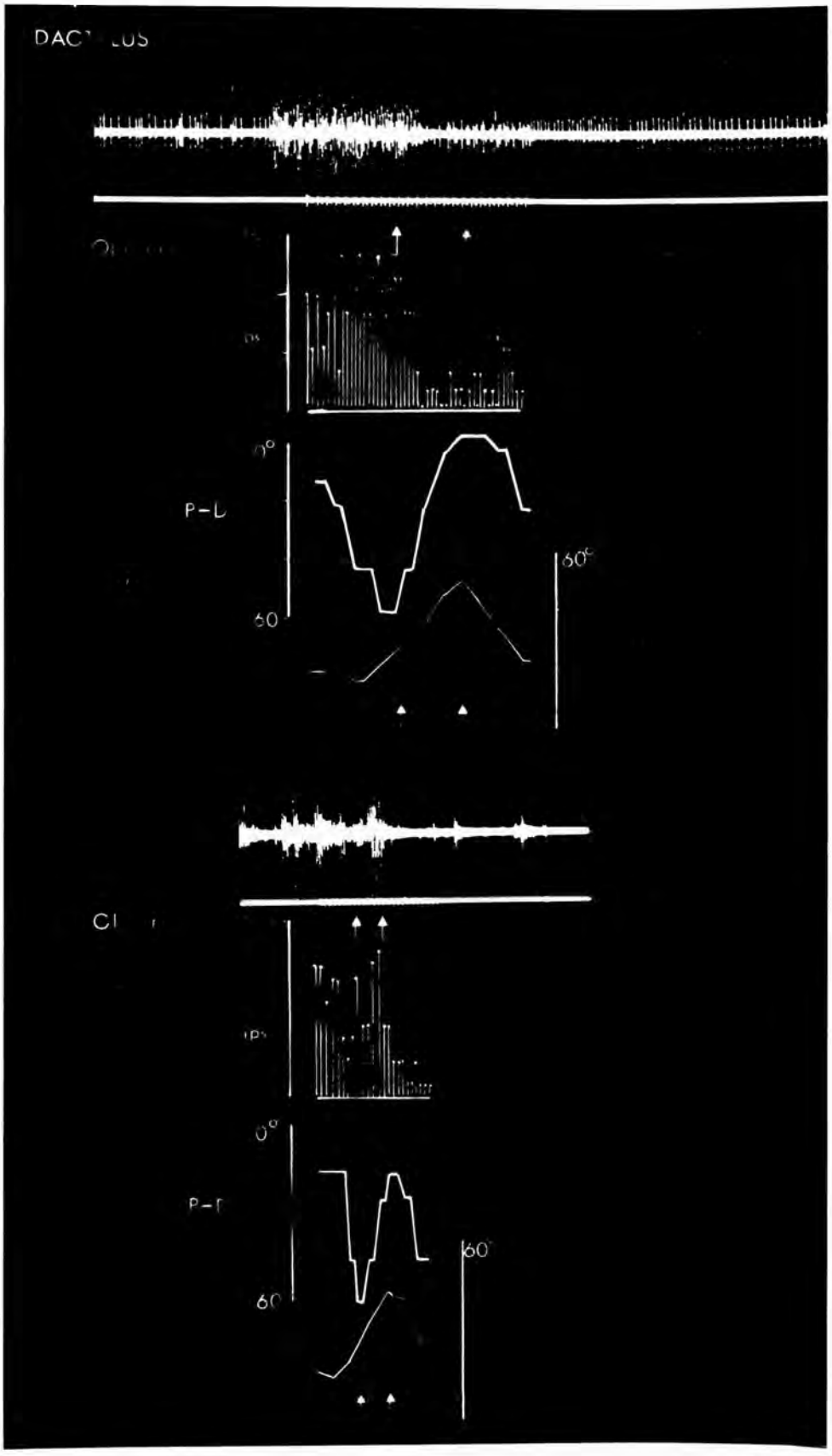


FIGURE 2

THE CARPUS-PROPUS JOINT

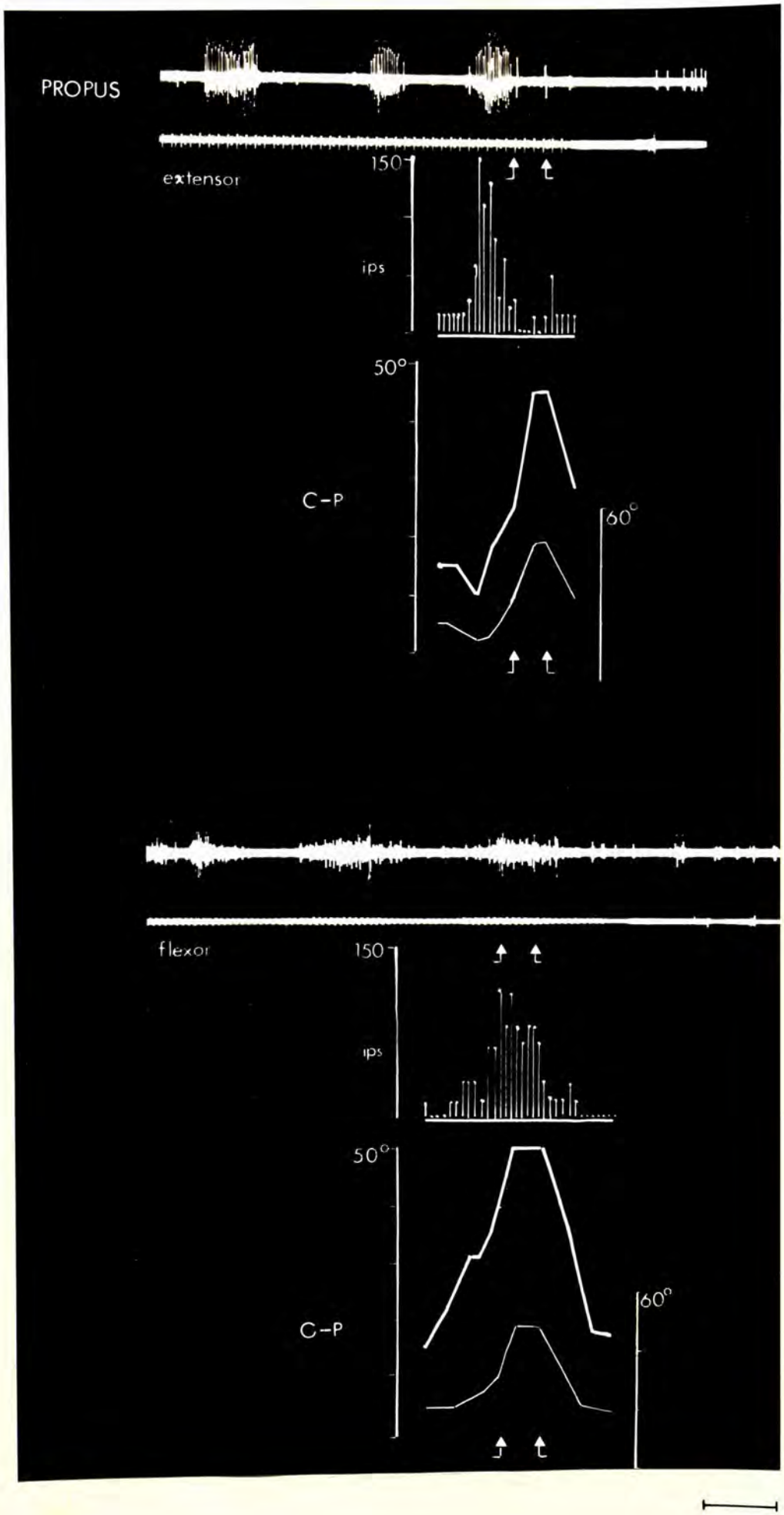
The time scale represents 1 s. The film speed was 8 fps in the EMG of the propus extensor muscle and 16 fps in the EMG of the propus flexor muscle.

The propus extensor muscle displays an increase in muscle excitation during the slow preparatory flexion stage of the slow strike. This frequency is considerably reduced 50 ms before the beginning of C-P joint flexion and reaches zero frequency during the slow strike. Three slow strikes were displayed during the period of recording; graphs have been drawn for the last one.

The propus flexor muscle increases in activity during cheliped flexion, and this excitation continues for 75 ms after the end of the strike. 2 slow strikes were displayed in the trace; graphs have been drawn for the second strike.

In both the illustrated slow strikes, the joint displays a pause between the end of cheliped flexion and the beginning of re-extension. This joint is flexed to a maximum angle of 50^{o}, whereas in the fast strike C-P joint flexion typically reaches 55 to 60^{o} and is then immediately re-extended.

CHAPTER 7 FIGURE 2



this movement progresses the large unit ceases to fire and smaller tonic impulses are displayed which fire at low frequencies.

The main difference in activity patterns of the carpus flexor muscle in the two strike behaviours is the frequency of excitation and the maintenance of activity throughout the movement. In the fast strike the frequency of excitation to the carpus flexor is reduced immediately at the end of coxal flexion (Chapter 5, Fig. 5), whereas in the slow strike carpus flexor muscle activity continues for 100 to 200 ms after coxal re-extension, although at a reduced frequency (Fig. 3). The muscle activity increases before the slow strike begins, before the first arrow on the EMG (Fig. 3) and then displays a second increase during the pause between extension and flexion, between the 2 arrows in figure 3. Following this second burst, muscle activity is gradually reduced until the joint is re-extended when the impulse frequency is reduced even further.

The angular excursion of the limb is quite different in the two strike behaviours; M-C joint flexion reaches 60^{o} in a fast strike but rarely exceeds 45^{o} in a slow strike.

4. THE BI-MERUS JOINT (Fig. 4)

The merus extensor was shown to increase in frequency of excitation during the threat stages of the fast strike action, while during the strike itself the muscle is not as active (Chapter 5, Fig. 6). A similar pattern is displayed in the slow strike (Fig. 4). The muscle impulse frequency is greatly reduced and even reaches zero during the strike, while in the preceding and following threat postures the activity is increased.

5. THE COXA-BI JOINT

A. THE BI LEVATOR (Fig. 5)

The Anterior and Posterior levator muscles display similar activity patterns in both types of strikes, but differ in the duration of reduced impulse frequency. The Al increases in excitation at the beginning of the slow preparation flexion stage of the strike (Fig. 5). This does not take the form of short bursts as in the fast strike (Chapter 5, Fig. 7), but rather a maintained high frequency. The muscle begins to reduce in activity 200 ms before the main depressory movement of the slow strike and continues at this level until re-levation of the BI. The beginning of levation is accompanied by a high frequency as in the fast strike, but this lasts longer in the slow strike, 500 ms instead of 200 ms.

The frequency of impulses from the Posterior levator also increases during the preparatory flexion stage and large muscle spikes can be seen in the EMG (Fig. 3). However unlike the Al, this high frequency activity continues for 75 to 125 ms during the faster depression of the BI. After this

FIGURE 3

THE MERUS-CARPUS JOINT

The time scale represents 1 s. The film speed was 25 fps in the EMG of the carpus extensor and 16 fps in the EMG of the carpus flexor muscle.

The small tonic impulses in the carpus extensor increase slightly in frequency during the preparatory slow flexion stage of the slow strike. This activity is maintained throughout the strike. At the beginning of coxal re-extension a second unit fires, generating larger muscle impulses, and reaches peak frequencies at the beginning of M-C joint extension after the characteristic pause following cheliped flexion. Re-extension of the joint continues with a reduced but regular frequency from small muscle impulses.

The carpus flexor muscle begins to increase in activity 200 ms before the beginning of flexion at the M-C joint. A second increase of impulse frequency can be seen between the 2 arrows below the EMG and occurs when the carpus is flexed to its maximum slow strike angle. The muscle activity continues at a reduced frequency until the joint is re-extended, when the frequency is reduced even further.

In both of the illustrated strikes the joint did not exceed 45^{o} flexion and no re-extending twitches were displayed. In a fast strike, M-C joint flexion reached 65^{o} (Chapter 5, figs. 4 and 5).

CHAPTER 7 FIGURE 3

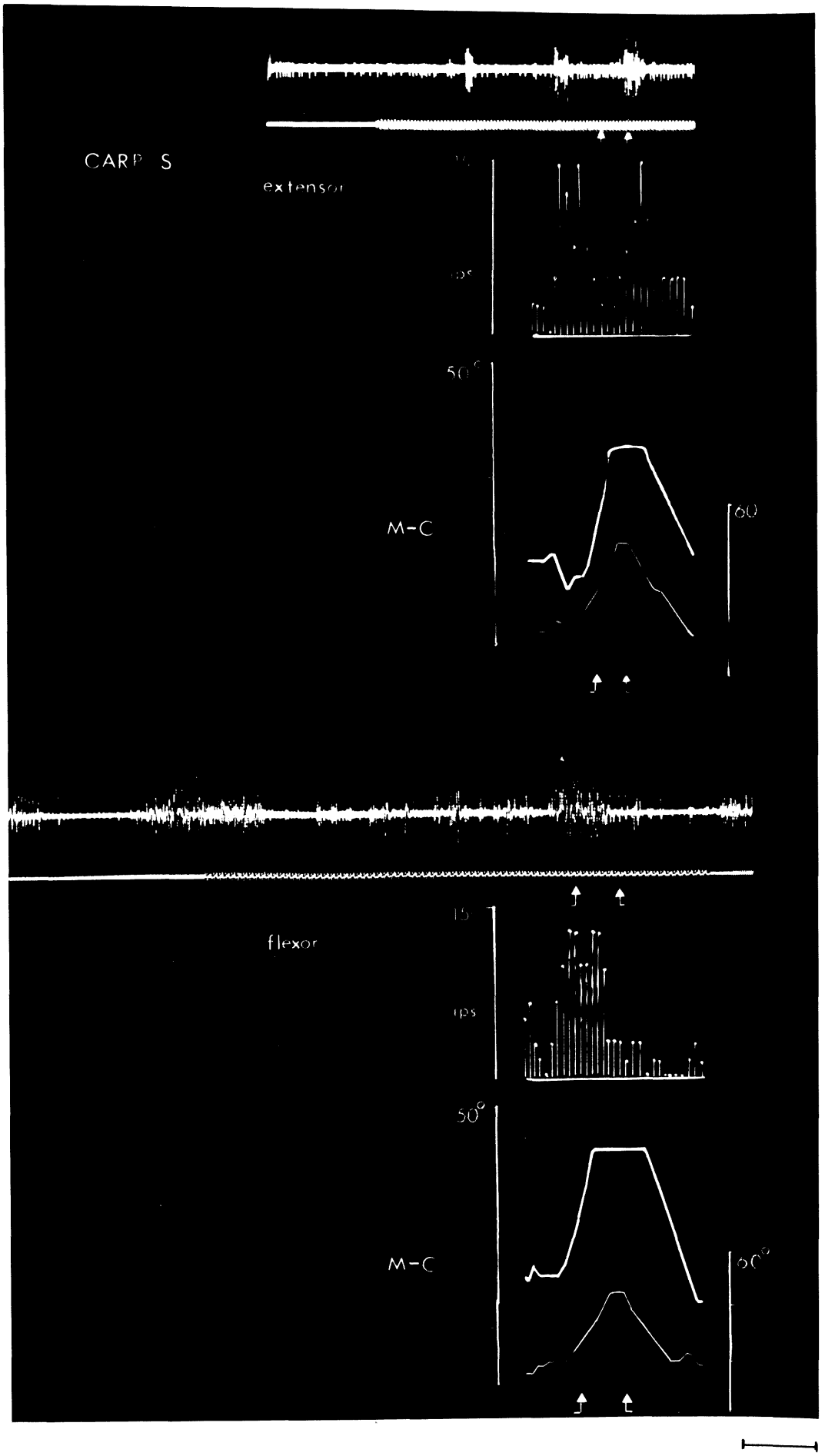


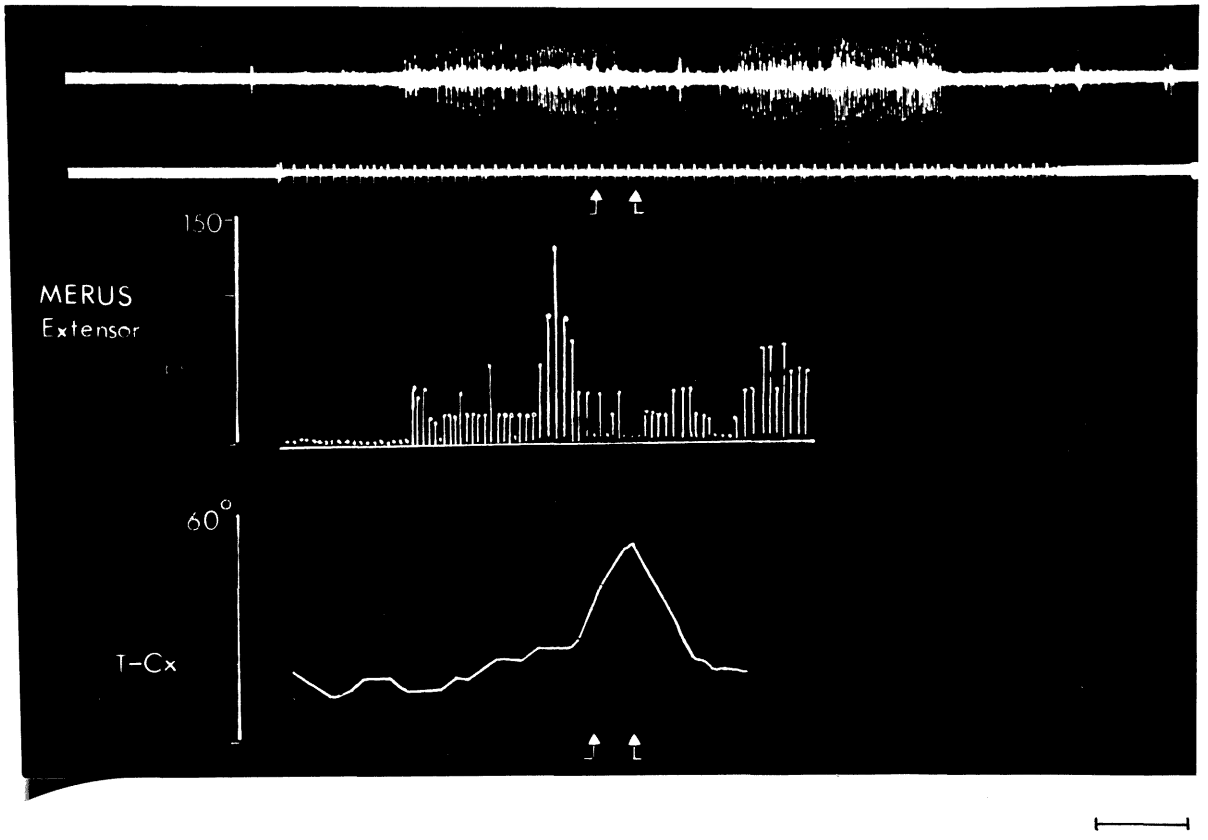
FIGURE 4

THE BI-MERUS JOINT

The time scale represents 1 s. The film speed was 8 fps.

The pattern of activity in the merus extensor muscle is similar in both strike behaviours. The muscle displays a high frequency of impulses in the threat displays which precede and follow the strike. During cheliped flexion and subsequent re-extension the muscle is active at a considerably reduced level and even reaches zero frequency levels.

CHAPTER 7 FIGURE 4



and for the remainder of the strike, the large unit stops firing and only small tonic impulses are displayed in the EMG's. As the joint is re-levated the large unit is re-introduced but at a reduced frequency than before the strike. Resumption of threat postures are accompanied by low frequency activity from large and small muscle impulses.

B. THE BI DEPRESSOR MUSCLES (Fig. 6)

The Anterior depressor muscle displays a high frequency burst during a slow strike (Fig. 6) but the duration of this burst is almost twice as long as that during a fast strike (Chapter 5, Fig. 9). Although the peak excitation frequency is reached just before the strike begins, muscle activity does not stop before depression but continues during the slow strike for 50 to 100 ms. In a fast strike the Ad characteristically generates only a few large spikes in a short time, whereas in slow strikes more large spikes are displayed over this longer time. After this burst the Ad is not completely inactive, as occurs in a fast strike, but instead small low frequency tonic impulses are displayed which continue for 50 to 75 ms after the beginning of re-levation.

Before a slow strike the Posterior depressor muscle also increases in excitation (Fig. 6) and like the Ad, the high frequency activity continues during the beginning of depression. After this, the muscle activity is considerably reduced. There is no second burst of impulses before the beginning of coxal remotion which is characteristic of a fast strike (Chapter 5, Fig. 10) and, therefore, it is unlikely that its tertiary function as a coxa remotor is used in the behaviour.

The cheliped is not depressed as far in slow strikes and depression rarely exceeds 45°, whereas it typically reaches 50 to 52° in a fast strike. Re-levation of the BI is also much slower.

6. THE THORAX-COXA JOINT (Fig. 7)

Like the Anterior levator, the coxa remotor muscle displays a pattern of altered activity in the 2 types of strike. The slow strike is preceded by an increase in impulse frequency but this does not take the form of bursts, characteristic of fast strikes (Chapter 5, Fig. 11). The duration of reduced activity is also much longer, 350 to 250 ms in a slow strike compared to only 50 ms in the fast strike. This reduction in frequency begins 75 to 100 ms before coxal promotion in the slow strike, whereas it occurs 25 to 50 ms before the start of the fast strike. At the beginning of slow coxal re-extension, the CxR increases in activity but again this does not take the characteristic burst form of a fast strike. Instead the muscle is active for 500 ms to 1 s after the end of coxal flexion (Fig. 7).

FIGURE 5

THE BI COXA-BI JOINT

A. THE LEVATOR MUSCLES

The time scale represents 1 s. The film speed was 16 fps in the EMG's of both muscles.

The Anterior levator muscle displays a similar pattern of activity in both types of strike but differs in the duration of reduced muscle impulse frequency. In the slow strike the muscle activity is reduced 250 ms before the beginning of depression, whereas in the fast strike the last burst of the Al continues to the beginning of the strike (Chapter 5, Fig. 7). After the slow strike the muscle activity increases and fires for 500 ms. In the fast strike there is also an increase in frequency after promotion but this takes the form of short bursts of 200 ms duration.

The Posterior levator muscle increases in activity during the preparatory slow flexion stage of the slow strike and reaches a peak impulse frequency just before the limb begins to depress. A second unit, which generates large impulses, stops firing as the limb is depressed and only small tonic impulses are displayed. As the limb is re-extended, the large unit is re-introduced but at a lower frequency than before. Regular tonic activity from the smaller unit accompanies the resumed threat postures.

CHAPTER 7 FIGURE 5

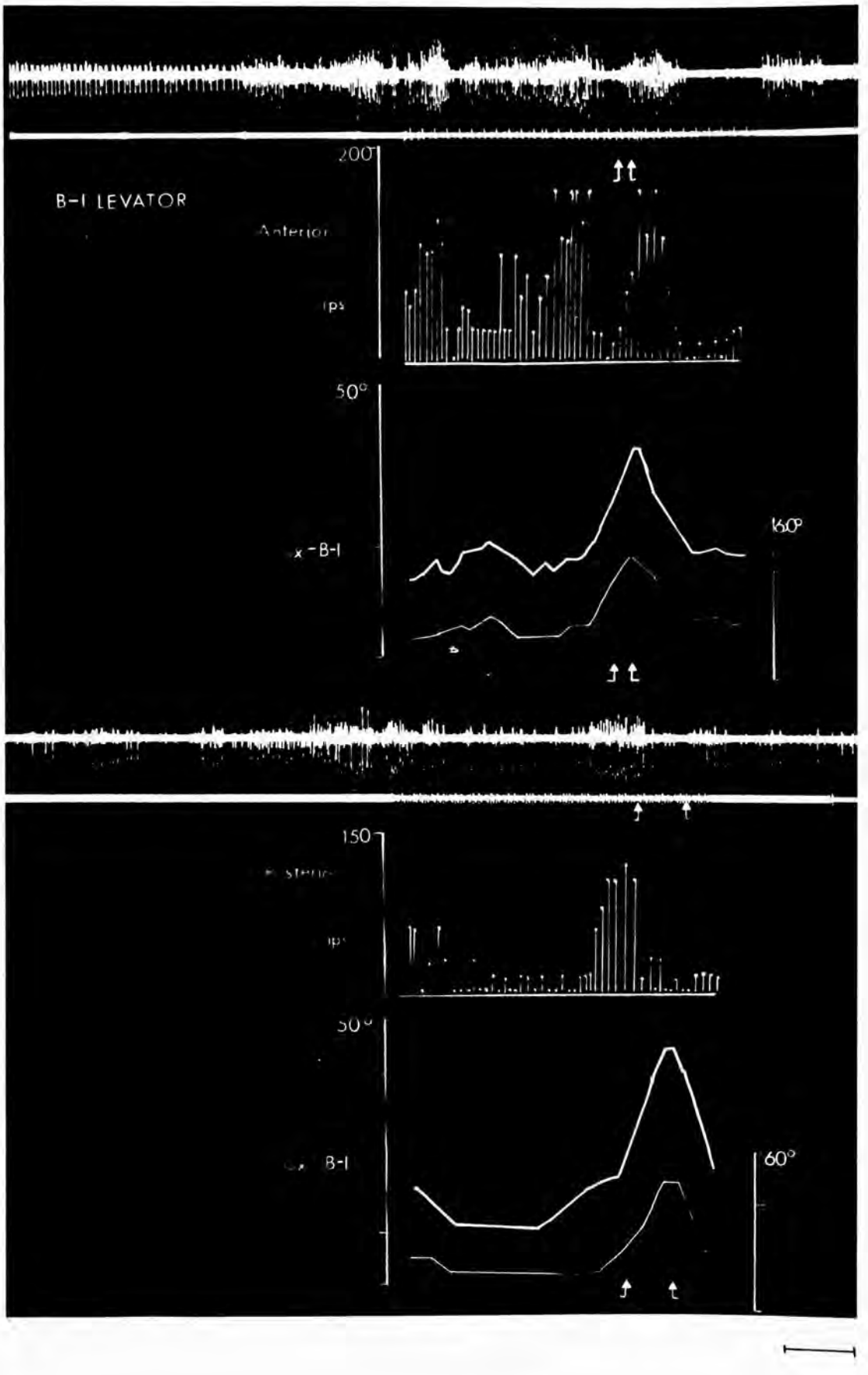


FIGURE 6

THE COXA-BI JOINT

B. THE DEPRESSOR MUSCLES

The time scale represents 1 s. The film speed was 32 fps in the EMG's of both muscles.

A short frequency burst of impulses from the Anterior depressor muscle accompanies the slow strike. The duration of this burst is almost twice as long as that displayed in a fast strike (Chapter 5, Fig. 9), and continues during depression of the BI. The muscle fires at low frequencies throughout the slow strike and begins to reduce in activity 50 to 75 ms after the end of the strike.

The Posterior depressor muscle also displays a high frequency burst before a slow strike. There is no second burst of activity which is characteristic of a fast strike (Chapter 5, Fig. 10). Therefore it is unlikely that the third function of the Pd, as a coxal remotor, is used in the performance of a slow strike.

CHAPTER 7 FIGURE 6

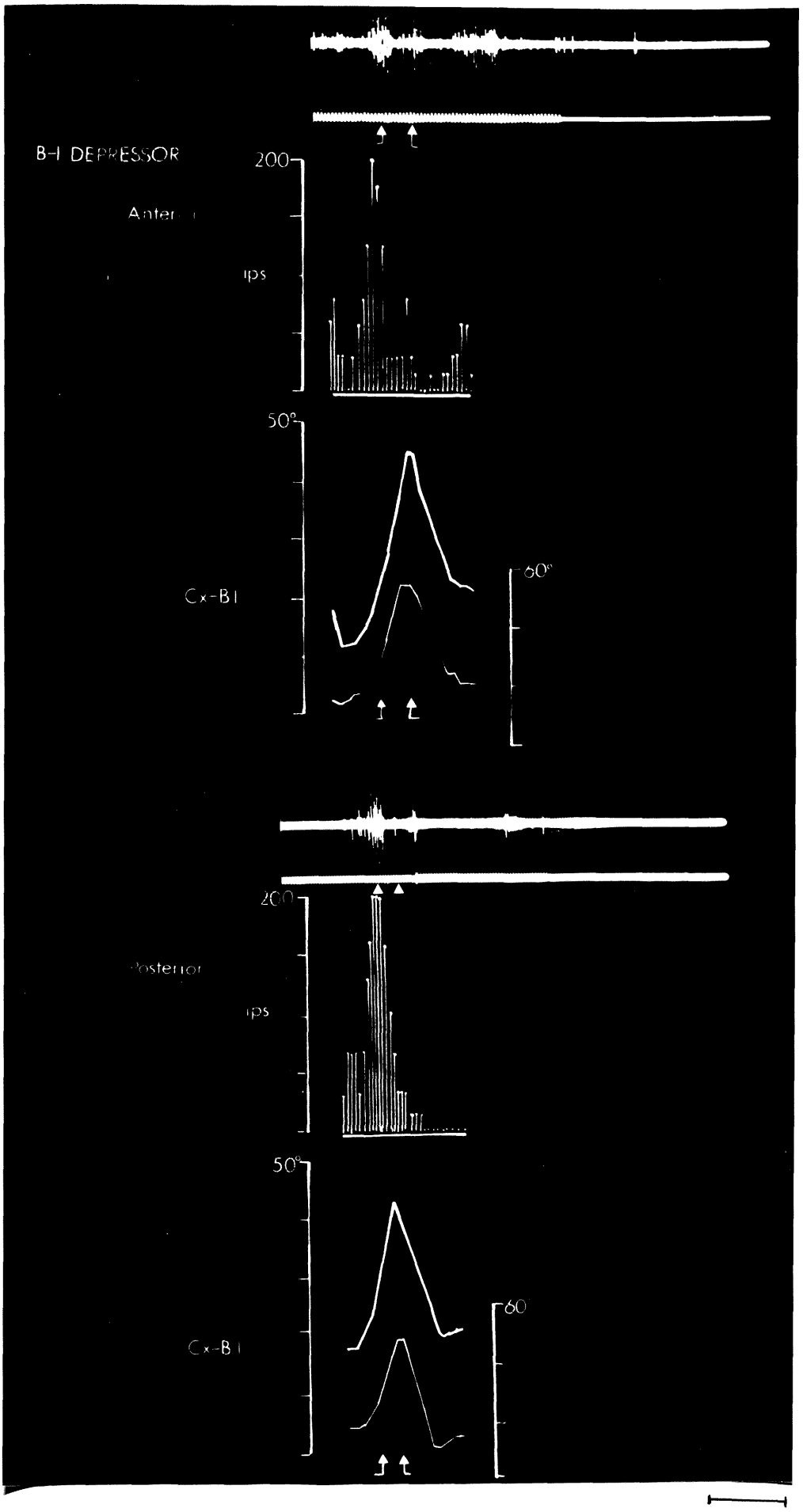


FIGURE 7

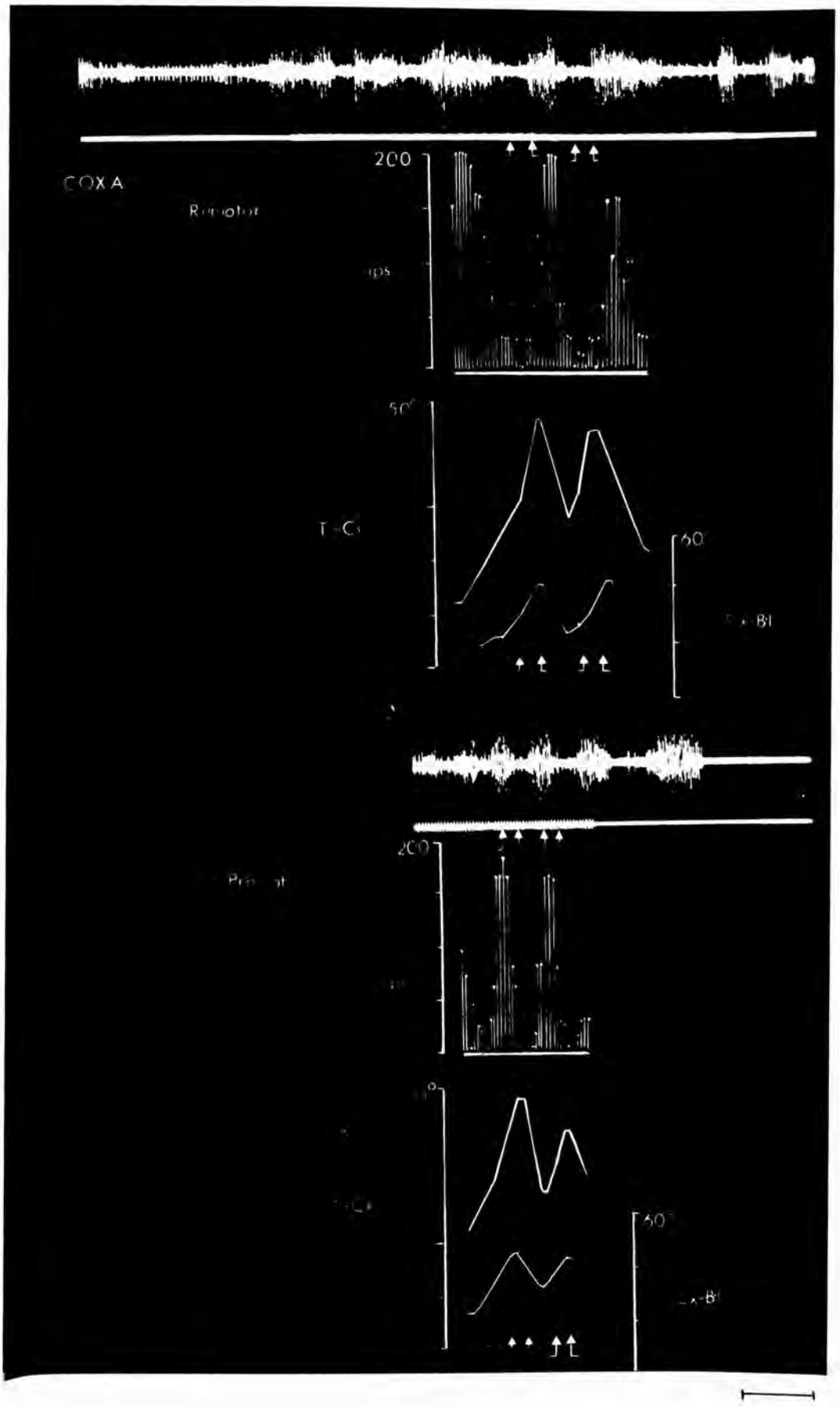
THE THORAX-COXA JOINT

The time scale represents 1 s. The film speed was 32 fps in the EMG of both muscles.

The coxa remotor muscle displays a considerable increase in frequency of excitation 1 s before a slow strike. Unlike its performance in a fast strike (Chapter 5, Fig. 11), this high frequency does not take the form of bursts. The muscle is subsequently reduced in activity 75 ms before the slow strike and remains at a low frequency throughout coxal promotion. A gradual increase in impulse frequency accompanies the slow re-extension of the coxa. As the threat positions are resumed, the muscle displays a low frequency of tonic impulses with short bursts of larger impulses accompanying increased intensities of threat display.

The coxa promotor muscle is increased in impulse frequency for a longer period in a slow strike, almost twice as long as in a fast strike (Chapter 5, Fig. 12). The muscle activity also differs by maintaining a high frequency of excitation during the first stages of coxal promotion. Three slow strikes were displayed during recording, graphs have been drawn for the first two. The third occurred at the end of filming with the ciné camera. After this the crab completely flexed its chelipeds in a resting position, folding the distal segments in front of the mouth. This was accompanied by a longer burst of CxP activity, which is displayed at the end of the trace.

CHAPTER 7 FIGURE 7



The coxa promotor muscle increases in frequency of excitation before the slow strike (Fig. 7), but unlike the pattern of muscle activity in the fast strike (Chapter 5, Fig. 12), this high frequency continues during the beginning of coxal promotion. The peak frequencies occur at the start of the slow strike and not 30 to 60 ms before the start of the flexion, as displayed in fast strikes.

The angular excursion of the T-Cx joint conforms with the pattern of reduced flexion of all the cheliped joints. Coxal flexion does not exceed 50^{o} in a slow strike whereas it is almost completely flexed in a fast strike.

DISCUSSION

The EMG's of the slow strike indicate that this behaviour is not caused by the same mechanisms which produce the fast strike. It does not appear that muscles contract isometrically before the strike. Thus although the slow strike may be divided into two parts, an initial slow flexion stage and the slow strike itself, there is no indication that the first stage has the same function as pre-strike, that is for tension development. Instead the first stage probably functions to direct the chelipeds toward the stimulus which is to be attacked and allows the joints to be positioned in the appropriate angles.

The periods of mutual activity in the CxP and CxR, and the BI levators and depressors is not sufficient to allow much, if any, isometric tension development in the strike muscles. For example, the CxR is reduced in activity 75 to 100 ms before coxal promotion. This is at the same time as the CxP begins to increase in impulse frequency. Therefore the promotor muscle could not develop tension against its antagonist. This means that instead of utilizing the flip-flop property of the T-Cx joint to produce promotion, the slow strike is caused simply by isotonic contraction of the CxP and relaxation of the CxR.

In a similar manner, the depression of the BI could not be achieved by isometric contraction of the depressors against the levators. Although the depressors begin to fire before the slow strike, the Al is reduced in activity and therefore could not provide much, if any, antagonistic force against which the depressors could contract isometrically. Thus the levels of tension developed by the depressors may be considerably less before a slow strike than those developed by co-contraction with the levators before a fast strike. This means that not only will cheliped depression be slower but also coxal promotion will be slower because the promotory action of the depressors will be less effective. Both depressor muscles display a longer period of high frequency activation before the slow strike, which continues

during depression. This indicates that without the feature of co-contraction, the depressors may require longer periods of excitation to develop sufficient tension, isotonically, to produce the speed of a slow strike.

The large unit of the Pl muscle is introduced in the middle of the performance of a fast strike. It was suggested in the previous chapter that this may sufficiently slow BI depression to allow the third role of the Pd, as a coxal remotor, to be expressed so aiding rapid coxal re-extension. In a slow strike the large unit of the Pl fires at a high frequency at the beginning of BI depression. This may slow the speeds of depression from the start of the strike and not during the middle, and so may allow the movement of the cheliped to be more finely controlled and directed towards the object of stimulation. The Pl does not display a second burst of high frequency activity at the start of the slow BI re-levation, which is characteristic of the fast strike. Therefore the force to levate the limb must be derived from the Al in a slow strike. Consequently the time course for levation may be slower. The graphs of angular excursion on Figure 5 and 6 indicate that this is the case, and levation takes almost three times as long in a slow strike than in a fast strike.

Rapid coxal re-extension in a fast strike is produced by combined activity in the CxR, Al and Pd. In a slow strike there is no second burst of muscle impulses in the Pd and its frequency of excitation is reduced at the end of the strike. Therefore it cannot be used in its third role as a coxal remotor.

In a fast strike the frequency of excitation to the CxR and the Al is maintained at a low level during rapid coxal promotion. Therefore these anti-strike muscles will retain some tension throughout the strike. Rapid coxal re-extension is accompanied by an increase in excitation frequency to the Al and CxR which will increase the existing levels of muscle tension. The remotory role of the Al together with the action of the CxR will quickly move the coxa to the bistable point of the T-Cx joint and subsequently overbalance the joint, flipping the coxa in a remotory direction. After a slow strike the Al and CxR do not fire in bursts which would rapidly increase the remotory moment about the T-Cx joint, but display a more gradual increase in impulse frequency. Consequently muscle tension will be developed more slowly and smoothly. This indicates that the flip-flop properties of the T-Cx joint may not be used for coxal remotion after a slow strike. Instead the re-extension of the limb may simply be started by gradual isotonic contraction of these 2 anti-strike muscles.

The distal muscles of the chelipeds also show differences in muscle activity between the two strike behaviours. The dactylus opener muscle

maintains a level of high frequency activity during the beginning of coxal promotion in a slow strike while the increase in the activity in the dactylus opener occurs mainly at the end of the strike. This indicates the different function of the claws in the slow strike. They are actively used to grasp the stimulus during the movement. Thus the dactylus remains open by activity in the opener muscle, until the stimulus is positioned close to the claws. At this stage the dactylus closer muscle increases in activity, which shuts the claw and allows the stimulus to be held.

In the fast strike there is an overlap of high frequency activity in the two muscles of the propus, which occurs at the end of coxal promotion. This is not shown in the slow strike. As the re-extension at the C-P joint is much slower in a slow strike, this supports the suggestion made in the previous chapter, that the period of mutual high frequency activation displayed by the propus extensor muscles at the end of rapid cheliped flexion, is sufficient to significantly increase the velocities of C-P joint re-extension after the strike.

The two muscles of the carpus do not display any periods during which tension could be developed isometrically during a slow strike, and both flexion and re-extension of the M-C joint is slower than in fast strike. This also supports the suggestion made in the previous chapter, that the periods of mutual high frequency activation in the two carpus muscles before a strike, aids in the performance of rapid flexion at the M-C joint.

The M-C joint is not flexed as far in a slow strike as in a fast strike. Since the carpus is comparable to an elbow, this feature will allow objects which are further away from the crab, to be reached by the claws. The EMG's of the carpus flexor show two peaks of increased muscle activity, one before the first arrow on the trace and one between the 2 arrows (Fig. 3). The first burst may position the limb into the appropriate angle, directing the claw towards the stimulus. The second burst may be necessary to firmly hold the M-C joint while the claw is involved in clutching the stimulus.

Thus by alterations to the frequency, duration and onset of cheliped muscle activity, two distinct but similar agonistic behaviours can be performed, the slow and fast strike. Although both are produced by the same muscles they are not produced by the same mechanical properties of the cheliped joints. The fast strike utilizes the unusual features of the bi-stable moment about the T-Cx joint and dually or triply functioning BI muscles, together with isometric contraction of antagonistic muscle pairs. This behaviour must require a neural programme which will control and co-ordinate sequences of muscular activity. The slow strike relies more upon

typical rhythmic patterns of muscle activity with only short periods of overlap. However the form of the behaviour is similar from individual to individual and therefore it probably also requires a controlling neural programme which is separate from the fast strike programme. The initiation of the fast strike motor programme allows an action to be performed which is at least three times as fast as that caused by the initiation of a motor programme controlling a slow strike.

The patterns of muscle activity displayed in both strike behaviours differs from that which occurs during the threat display behaviour. The remainder of the thesis is concerned with the analysis of threat displays using EMG and nerve recording techniques. By presenting various stimuli to the crabs, the effects of several parameters were examined. The experiments were devised to test the physiological processes which produce the observed different intensities of threat display and also the cause of the sudden switch from one level of display to another.

CHAPTER 8

THE THREAT DISPLAY BEHAVIOUR: EMG AND CINEMATOGRAPHIC RECORDINGS

INTRODUCTION

It has been shown in the previous chapters, that the fast and slow strike behaviours of Carcinus are produced by a strict sequence of muscle activity. This activity is clearly distinct from that recorded during the preceding and following threat display behaviour. In the next two chapters the muscle activity recorded during threat displays is analysed and the stimulus parameters which affect the displays are examined.

As described in the General Introduction, the threat displays of Carcinus are similar to those displayed by many brachyuran crabs (reviews by Schöne 1968, Wright 1968). Carcinus responds to stimulation by displaying the Aufbäumreflex (Bethe, 1897) or Lateral Merus Display (Wright, 1968). This involves a rapid movement of the chelipeds laterally and vertically, and is often accompanied by postural changes. Displaying crabs may rear up, so that the body axis is at 45^{o} from the substratum with the anterior end of the body higher than the posterior end. The walking legs may be stretched out in such a way that the animal assumes a stable posture and may maintain this rigid display for long periods of time.

In the natural environment of the crab, the threat display will probably be directed towards other crabs of the same species and also towards predators. Carcinus has many predators which attack the animal when it is in water and also when it is on the shore. The invertebrate predators of Carcinus include the octopus and cuttlefish. Fish predators include eels, cod, bass, flounders and dogfish. Aquatic mammals also prey on Carcinus and include some whales, seals and otters. Young and medium sized crabs are often eaten whole by sea birds, when they are exposed on the shore. Bird predators include mallards, herring gulls and cormorants. Other predators are listed by Crothers (1968).

Films taken of displaying crabs and general observation, revealed that Carcinus has various intensities of threat display, demonstrated by the adoption of different positions of the chelipeds and different postures of the body (Chapter 2). Crabs which are not particularly alert or are fatigued, respond to stimulation with Shallow Threat displays. In this display the crab remains lowered on the substratum and only weakly raises its chelipeds; they are tucked in towards the mouth from M-C joint. More alert crabs respond to stimulation with Half Threat displays, in which the body is slightly raised from the substratum and the chelipeds are levated and extended more from the T-Cx and Cx-BI joints. The claws are directed

medially from the C-P joint.

If the crabs are even more responsive, they may display a Three-Quarters Threat posture, in which the animal rears up anteriorly and the chelipeds are almost fully extended and raised at all joints. Continued stimulation may cause the fourth display, Full Threat, to be performed. This extreme display usually occurs from a Three-Quarters display, and the movement from one display to the other takes only 10 ms to achieve. Full Threat displays are not maintained for long periods and the crabs soon re-adopt Three-Quarters postures.

Stimulation may cause the crab to move directly from a resting posture to a Three-Quarters Threat display without adopting the intervening postures. The whole action can be extremely fast and can take less than 30 ms to be completed. When stimulation ceases,the crabs usually gradually adopt successively decreasing intensities of display until a rest posture or Shallow Threat display is maintained.

Each display is probably used to indicate an extent of aggressiveness or defensiveness by the displaying crab. For example, when the distant approach of a predator is perceived,the crab may respond with a Shallow Threat display. As the predator moves nearer, the crab may respond with a Half or Three-Quarters Threat display. This will make the crab appear much larger and will display its potential weapons, the claws. If these rigid displays are insufficient to deter the approach of the predator the crab may rapidly twitch its chelipeds into a Full Threat display, which suddenly makes it appear even larger and more threatening.

In this chapter the muscle activity accompanying threat behaviour was examined using EMG and cinematographic techniques. In this way a temporal pattern of muscle activity that occurs during threat displays can be assembled. Also the physiological basis of the different intensities of threat displays is examined.

MATERIALS AND METHODS

Large male crabs were prepared for EMG recordings as before. In the first series of experiments, they were suspended over a tank containing an angled mirror,the tank filled with sea water. The crabs could then be filmed from any angle by adjustment of the position of the ciné camera. Film speeds of 2 and 8 fps were used. As in the previous chapters, the films were analysed using an enlarger. The different intensities of threat display could subsequently be directly correlated with any recorded alteration in muscle activity.

In the second series of experiments, the animals were allowed to move freely in a tank, and were partially covered with cooled sea water. Simultaneous activity from two muscles could be recorded using both beams of the oscilloscope. The occurrence of any particular behavioural activity during recording was noted with reference to the digital counter of the tape recorder.

In all the experiments the crabs were stimulated manually. The experimenter's hand was moved towards and away from, the face of the tank. This meant that the crab only received visual stimulation and not mechanical; the glass front of the tank prevented the introduction of any tactile stimulation fromair sources. Mild stimulation was produced by slow movements of the hand, passing the crab's field of vision in a horizontal arc. More vigourous stimulation was produced by quickly flicking an open hand towards the crab in the centre of its field of vision.

It has been previously demonstrated that threat responses from muscles are most clearly shown in recordings from the extending-levating muscles used for anti-strike actions. Therefore only recordings from these muscles are used in most experiments. These muscles can now be termed "threat" muscles.

RESULTS

SECTION 1 - EMG's AND CINEMATOGRAPHY

Muscle activity recorded during threat displays is shown in figures 1 and 2. The lines below the traces indicate the time of stimulation and resulting change in threat posture. Closed triangles represent movements from Three-Quarters to Full Threat, and open triangles represent movements from Half to Three-Quarters Threat display postures. The muscle activity which follows stimulation is termed the threat response.

The traces demonstrate that an increase in threat display corresponds to an alteration to the pattern of muscle activity. The extent of excitation to the muscle reflects the intensity of the display. A high frequency of activation accompanies the high intensity displays while lower frequencies of activation accompany lower intensities of display. All the threat muscles respond in a similar manner. There may be recruitment of new axons, generating larger muscle spikes, increased frequency of existing tonic activity, or both.

When the claw is fully opened in a display, there is a marked increase in tonic activity and the introduction of a second excitatory axon response, in the trace of the dactylus opener muscle (Fig. 1). In the illustrated EMG the crab was initially in Shallow Threat positions and the muscle displayed only low frequency activity. At the beginning of stimulation, the

crab rapidly moved in Full Threat postures. These postures were accompanied by a sudden increase in impulse frequency. The crab then gradually re-adopted Half Threat displays and impulse frequency was reduced. A second stimulus caused the crab to change back to Three-Quarters Threat postures, and the tonic activity was slightly increased in frequency but there were no large spikes.

The propus extensor muscle activity associated with threat displays, shows an increase in existing tonic impulse frequency (Fig. 1). The greater the intensity of the threat display, the greater the frequency of muscle impulses. In the illustrated trace, the facilitation of the impulses is clearly demonstrated. The final stimulus, which caused the crab to respond with a Full Threat display, not only accompanied considerable facilitation to the impulses but also accompanied an increase in muscle activity. Both of these features are greater than in the preceding response in which the crab responded with a Three-Quarters Threat display.

Muscle responses to different threat displays are clearly distinguishable in recordings made from the carpus extensor muscle. At the beginning of the illustrated trace the crab was in a Shallow Threat posture (Fig. 1). As soon as stimulation began, the crab responded with a sudden change to a Full Threat display. This was accompanied by an increase in frequency of tonic activity plus the generation of large spikes indicating the recruitment of a second axon. Following this, a high frequency activity was maintained as the crab remained in Three-Quarters Threat. Subsequent stimulation caused the crab to respond back into Full Threat and the muscle responses were the same, with large spikes and an increase in frequency. As the crab became less responsive, the muscle threat responses were greatly reduced in frequency.

At the beginning of the illustrated trace for the merus extensor muscle, the crab was completely at rest with the chelipeds tucked in front of the mouth, and there was no recorded muscle activity (Fig. 1). When stimulation began, the crab slowly adopted increasing intensities of threat display. This was associated with an increase in muscle activity with peak frequencies accompanying the Full Threat display.

The most dramatic muscle response to threatening stimuli is shown in recordings from the BI Anterior levator muscle. The illustrated trace in figure 2 demonstrates the A1 responses which accompany threat behaviour. At the beginning of the trace the crab was in Shallow Threat and only a low frequency tonic activity was apparent. When stimulation began this tonic pattern was disturbed; phasic muscle responses quickly twitched the limb into increased postures of threat and the frequency of muscle activity was

FIGURE 1

This figure illustrates representative EMG's recorded from the distal cheliped threat muscles. The crab was stimulated and the threat displays filmed with the ciné camera. The time of stimulation is indicated by the lines below the camera photo-diode register on the lower beam. The response recorded from the muscles, the threat response, is indicated by the triangles below these lines. Closed triangles indicate movements to high intensities of threat display and open triangles indicate movement to lower intensities of threat display. The film speed was 2 fps in the first three traces and 8 fps in the fourth. The time scale represents 1 s.

The trace of the dactylus opener muscle illustrates the increase in activity and introduction of a second axon which is characteristic of threat responses in most of the cheliped threat muscles. At the beginning of the EMG, the crab was in a Shallow Threat posture and the muscle was active at low frequencies. The first stimulus caused the crab to respond with a Full Threat display and the claw was fully opened. Larger muscle spikes and a greatly increased frequency of excitation is evident. Following this, the crab gradually resumed Half Threat postures. The second stimulus caused the crab to change back to Three-Quarters Threat display. This was also accompanied by an increase in muscle impulse frequency but it was not as high as previously and fewer large spikes are seen. The third stimulus caused the crab to twitch into a Full Threat posture and the claw was fully opened again. The frequency of excitation was increased but was not as high or as long as the first threat response.

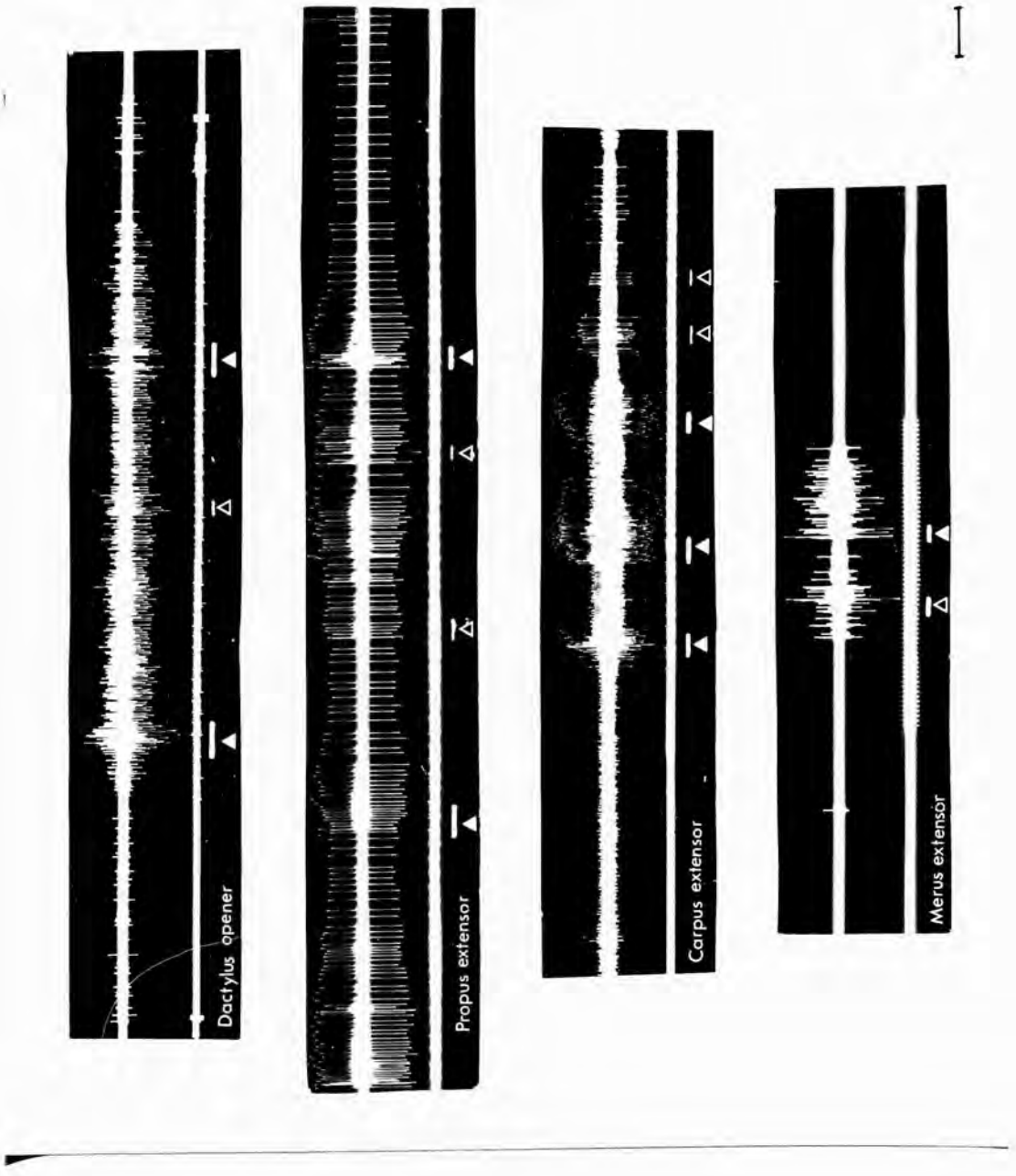
The propus extensor muscle activity during threat display shows an increase in frequency of the muscle impulses. At the beginning of the trace the crab was in a Three-Quarters display. The level of muscle impulse frequency decreased as the intensity of display was slowly reduced. The first stimulus caused facilitation of muscle impulses and an increase in frequency for 500 ms as the crab displayed in Full Threat. Following this the crab moved through Three-Quarters to Half Threat postures. This was accompanied by an increase in interspike interval. The second and third bouts of stimulation only caused the crab to respond with a Three-Quarters display and the resultant muscle responses are different from the preceding and following ones in which the crab adopted Full Threat. The bursts of activity were shorter, of lower frequencies and less facilitation of muscle impulses is evident. After the final response, stimulation was stopped and the crab slowly lowered and flexed its chelipeds to end in

a Shallow Threat posture. This was accompanied by low frequency tonic activity.

The response of the carpus extensor muscle is quite dramatic. Increased postures of threat are accompanied by the introduction of a second excitatory axon, together with a considerable increase in ongoing activity. At the beginning of the trace, the crab was in a Shallow Threat display. The first stimulus caused the crab to move directly into Full Threat. This was associated with an increase in muscle activity plus the generation of large spikes, indicating the recruitment of a second axon. The crab then adopted Three-Quarters Threat, accompanied by a maintained increase in tonic impulse frequency in the muscle. The second stimulus again caused a Full Threat display which was maintained for longer and corresponded to the generation of a greater number of large spikes over a longer period than before. The third display was not maintained as long and there were fewer large spikes. The final two displays were reduced in intensity and were accompanied by a considerable reduction in threat response activity, and fewer large spikes were generated. Finally the crab readopted the Shallow Threat posture. At this stage the original frequency of excitation was resumed.

At the beginning of the illustrated trace of the merus extensor muscle, the chelipeds were tightly tucked around the mouth as the crab was completely at rest; there was no recorded muscle activity. Stimulation caused the crab to slowly adopt increasing threat displays. This was accompanied by an increase in impulse frequency. Initially the displays reached a Three-Quarters display and then the crab readopted Half Threat. The second stimulus caused a Full Threat display and a sudden, higher frequency of activity is shown. Muscle activity ceased when Shallow Threat postures were adopted at the end of cinematographic filming.

CHAPTER 8 FIGURE 1



considerably increased. Repeated stimulation caused the responsive crab to display with Full Threat postures, almost every time. The phasic nature of this extreme display is reflected in the phasic nature of the muscle response.

The A1 was found to represent the most consistant and reliable muscle indicator of threat displays. The muscle impulse frequency is low when the intensities of display are low, and high during the more extreme displays. Each increased display posture corresponds to a brief phasic burst of activity in the muscle. Movements to Half and Three-Quarters Threat positions are accompanied by the generation of fewer large spikes and a smaller increase in impulse frequency, than movements to Full Threat.

After each phasic burst accompanying the Full Threat display, the muscle activity is reduced for several ms before regular high frequency activation is re-established as the chelipeds resume Three-Quarters Threat positions. Thus the phasic activity in the muscle will twitch the chelipeds above the angles of Three-Quarters Threat, to Full-Threat. When the phasic activity ceases, the arm adopts the original Three-Quarters Threat display and a regular high frequency muscle activity is resumed.

The BI Posterior levator fulfils its function as an aid to A1 action in this behaviour as well as in that of the strike. It is excited when the behaviour switches from a low intensity to a higher intensity of display. When the increased displays are maintained, the frequency of P1 activity is progressively reduced. At this stage, levation of the limb is presumably achieved by A1 action alone. Thus the P1 will aid the A1 in rapidly moving the limb upwards from one level of display to another, but is reduced in frequency when these increased postures are reached and maintained (Fig. 2).

The different displays are also reflected by differences in the duration of the increased activity in the coxa remotor. The lowest intensities of threat are due to long bursts of CxR activation, and the muscle shows responses to excitation from at least two of its axons (Fig. 2). The more intense displays are accompanied by a shorter burst of higher frequency activity and usually a few large phasic spikes are generated.

SECTION 2 - SIMULTANEOUS RECORDINGS FROM TWO CHELIPED MUSCLES

Simultaneous recordings were made from the same muscle of both chelipeds. Representative traces are shown on figures 3 and 4. Figure 3 demonstrates that although the occurrence of muscle impulses may not be identical in both A1 muscles, the overall impulse frequency is similar. Figure 3a was recorded from a crab which was in a Shallow Threat posture; low frequency muscle activity accompanied this display. The remaining three

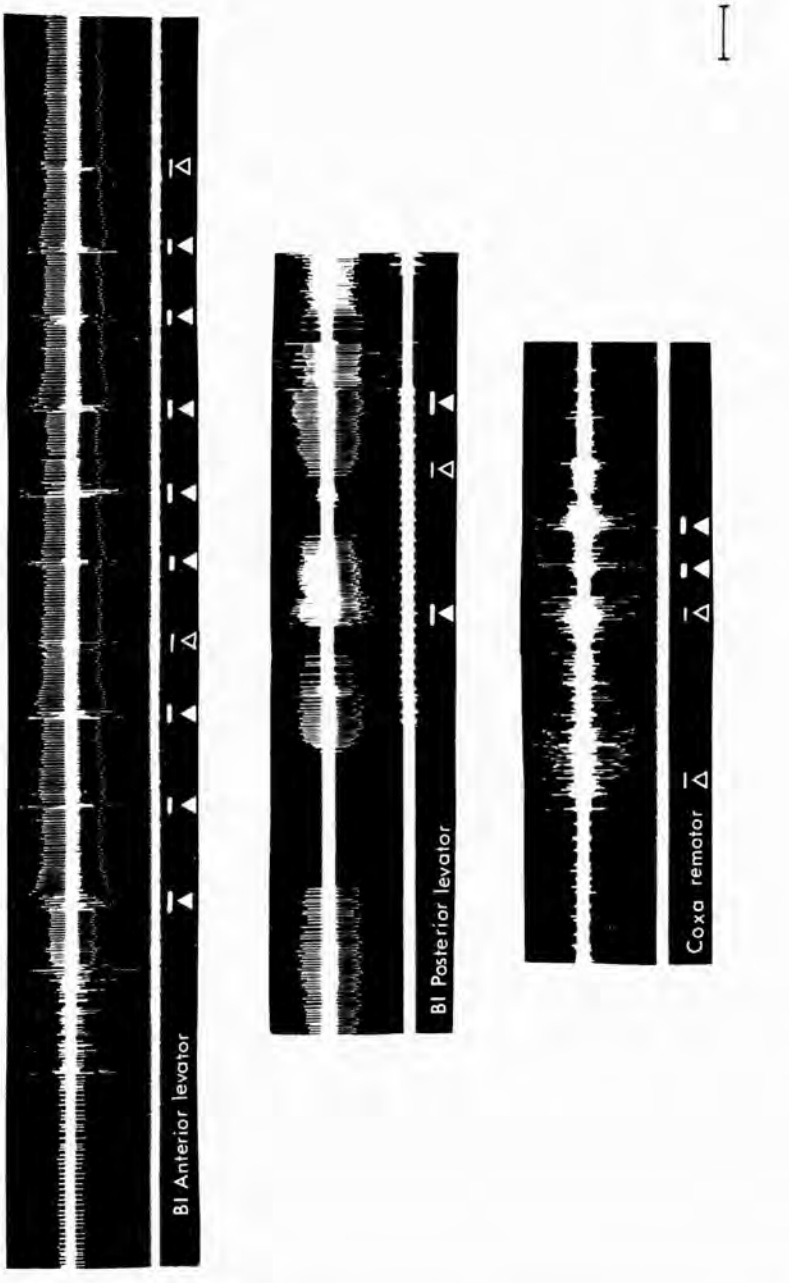
FIGURE 2

This figure illustrates representative EMG's recorded from the proximal cheliped threat muscles during filming with the ciné camera. The symbols are as described in figure 1. The film speed was 2 fps and the time scale represents 1 s.

At the beginning of the trace for the BI Anterior levator muscle, the crab was in a Shallow Threat Posture. This was accompanied by a low frequency tonic activity in the muscle. When stimulation began, this pattern was disrupted and large phasic muscle spikes quickly twitched the limb into increasing positions of threat display. 2.5 s after the beginning of cinematographic filming, the crab had adopted a Three-Quarters Threat display and the frequency of muscle activity was considerably increased. Repeated stimulation caused the responsive crab to display with a Full Threat almost every time for 11 s. These displays corresponded to the generation of large muscle spikes, indicating the recruitment of the second phasic Al axon, together with a further increase of impulse frequency. The two stimuli which released only Three-Quarters Threat are clearly distinct from the more extreme responses and were accompanied by a lower increase in impulse frequency and the generation of fewer large spikes. The BI Posterior levator functions as an aid to the Al and is excited when the behaviour changes from a low intensity display to a higher intensity display. At the beginning of the trace the crab was moving from a Three-Quarters to Half Threat display and the Pl was reduced in frequency of excitation until it was finally silent. Just before the beginning of cinematographic filming, the limb was relevated to Three-Quarters Threat and the Pl was excited. This posture was subsequently maintained and Pl activity was reduced. The first stimulus caused the crab to display with a Full Threat and was accompanied by a sudden resumption of high frequency Pl activity. This continued for 1.5 s after the crab re-adopted Half Threat. The second stimulus released only a Three-Quarters Threat display and the re-introduced Pl activity occurred at a lower frequency than before. The third stimulus followed shortly after this and caused a Full Threat display, and was accompanied by a further increase in Pl activity. After cinematographic filming had ended, the crab resumed Half Threat displays.

The coxa remotor fires at a lower frequency than the Al during maintained threat displays and responds to stimulation with a longer burst. In the illustrated EMG, the first two stimuli caused Three-Quarters Threat displays and corresponded to a burst of muscle impulses. The different sizes of the impulses indicate the recruitment of at least two of the CxR axons. In the last two responses, the crab displayed with Full Threat. This was accompanied by a shorter burst of higher frequency impulses and a few large phasic spikes are evident in the last burst.

CHAPTER 8 FIGURE 2



traces of this figure are a continuous record from the same crab after it had been mildly stimulated. The crab now assumed a Half Threat position, increasing the levation of the chelipeds. This is reflected by the increased muscle activity.

A feature in trace b2, indicated by the arrow, strongly suggests that increased excitation which accompanies threat displays, is received at the same time in both chelipeds. At the indicated point the crab changed from Half to Three-Quarters Threat positions. The onset of the increase in activity is identical in both muscles. Figure 4 demonstrates the simultaneous activity in two other threat muscles, the coxa remotor (Fig. 4a), and the carpus extensor (Fig. 4b). This feature of mutual increase in frequency in the same muscle of both chelipeds was seen many times in the EMG's. It can therefore be concluded that neural excitation controlling the threat displays, is received at the same time by muscles of both chelipeds.

A series of experiments was performed to examine whether the muscle activity is co-ordinated in the cheliped. This was achieved by simultaneously recording from two threat muscles of the same cheliped. One result is shown in figure 4c, and illustrates several relevant features of threat. At the beginning of the trace, when the crab was in a Shallow Threat position, the main activity is from the CxR. As the distal joints are partially flexed in this display, the carpus extensor frequency is low. The first stimulus caused the crab to respond with a Half Threat display which corresponded to an increase in CxR activity and peak frequencies of excitation were reached just as the impulse frequency begins to increase in the carpus extensor. This sequence of activity reflects the behavioural display of Half Threat in which the cheliped is extended laterally from the coxa before the distal joints are extended. However once this display is maintained, the M-C joint is extended more laterally than the T-Cx joint, which is reflected by the continued high frequency activity in the carpus extensor and reduced activity in the CxR.

The next stimulus caused the crab to further increase the display to a Three-Quarters Threat posture. There was not such a marked difference between peaks of activity in the two muscles. This again reflects the behavioural display, in which all the joints are extended rapidly and together. After this, stimulation was stopped and the crab gradually moved through the intervening stages of threat to end in a Shallow Threat posture. The muscle activity clearly reflects the display postures. Both muscles are reduced in activity as the joints are progressively flexed from Half to Shallow Threat display positions.

FIGURE 3

SIMULTANEOUS RECORDINGS FROM ONE THREAT MUSCLE IN BOTH CHELIPEDS

Recordings were made from the A1 muscle in both chelipeds to determine whether threat responses are symmetrical. The results indicate that excitation is received at almost the same time by both muscles. Although the recorded frequency of excitation is slightly different, the onset of the increased burst is simultaneous.

The time scale represents 1 s.

In trace a the crab was in a Shallow Threat posture. The chelipeds were lowered, and consequently A1 activity was low. Traces b1 to b3 are a continuous record from the same crab which had adopted a Half Threat posture. The activity in both muscles had increased by the same amount. The arrow in trace b2 indicates the point at which the crab responded to stimulation by moving from Half to Three-Quarters Threat postures. The onset of the increase in msucle impulse frequency was the same in both muscles.

CHAPTER 8 FIGURE 3

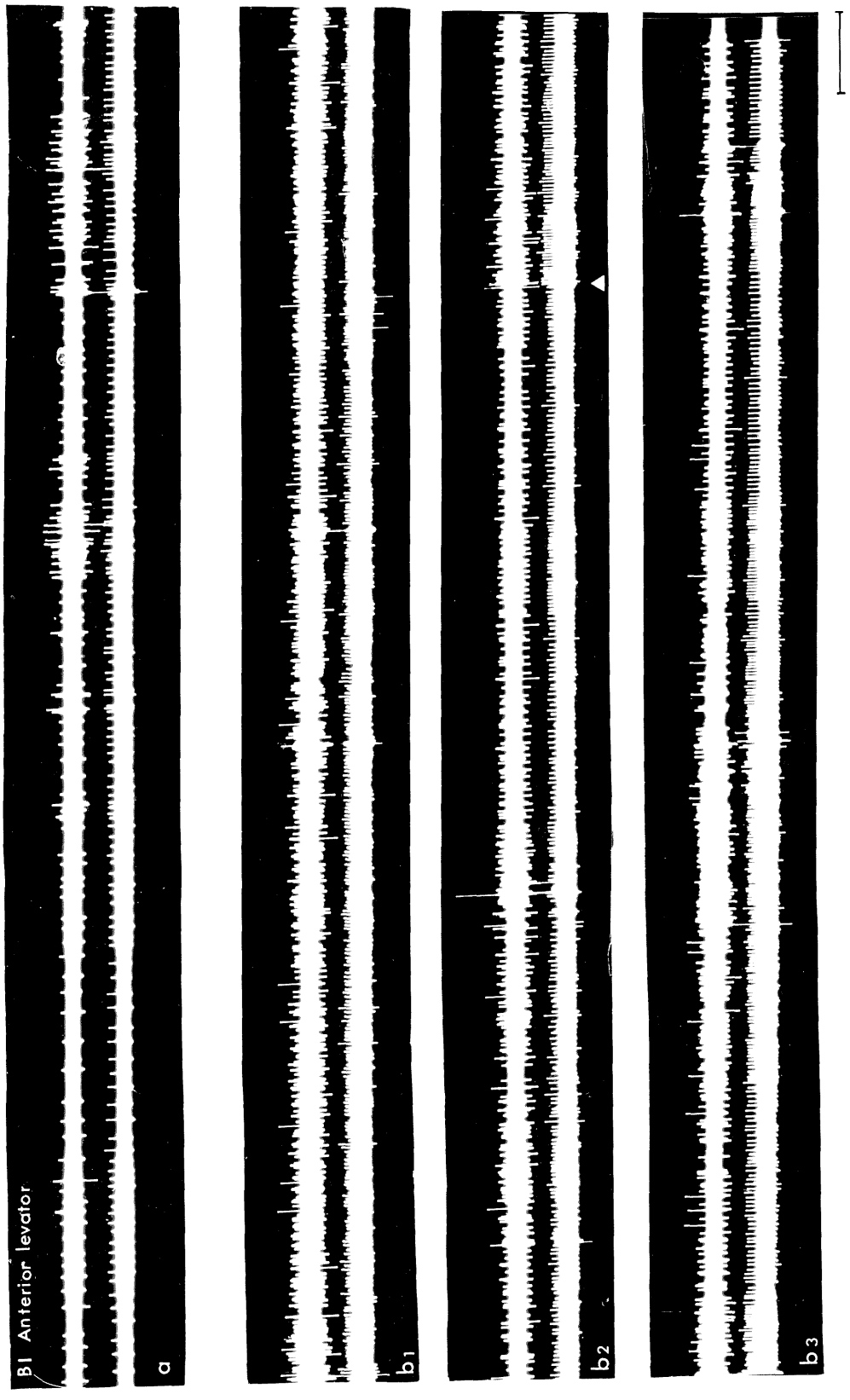


FIGURE 4

Traces a and b demonstrate simultaneous recordings from one muscle in both chelipeds. Trace c demonstrates simultaneous recordings from two muscles in one cheliped. The time scale represents 1 s.

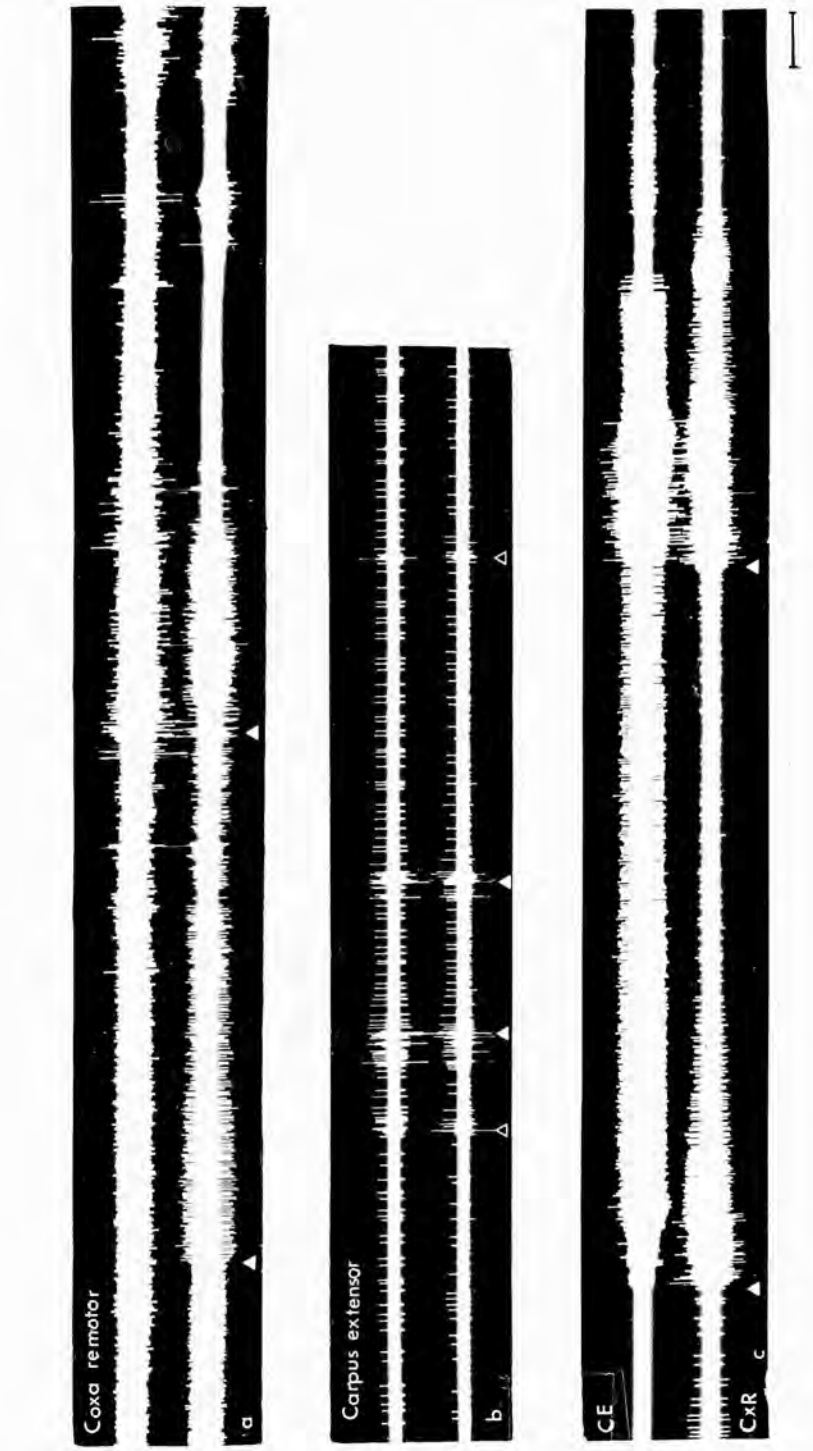
Traces a and b support the suggestion that the chelipeds receive excitation at the same time during the threat responses. The arrows indicate the times of increased threat displays.

Trace a is a recording from the coxal remotor muscles of the two chelipeds. At the beginning of the trace the crab was in Half Threat display posture. Stimulation caused the crab to respond with a Three-Quarters display, and was accompanied by synchronous increase in CxR activity. The second arrow indicates the point at which the crab responded with a Full Threat display. Again the onset of increased activity in both muscles was identical.

Trace b is a recording from the carpus extensor muscles of the two chelipeds. The first and fourth stimuli caused Three-Quarters Threat while the second and third caused Full Threat displays. However in all four, the onset of increased muscle frequency occurred at the same time.

Recordings were made from two muscles of the same cheliped to determine the sequence of muscle activity during threat displays. One such recording is shown in trace c. The upper beam is from the carpus extensor muscle and the lower beam is from the CxR. At the beginning of the trace the crab was in Shallow Threat postures with the distal cheliped segments flexed. This was accompanied by low frequency activity in the carpus extensor. The first stimulus caused the crab to respond with a Half Threat display, and corresponded to an increase in CxR activity followed by an increase in carpus extensor activity. This reflects the behavioural display, as the T-Cx joint is extended before the distal limb segments. However once this threat position is maintained, the M-C joint is extended more laterally than the T-Cx joint. This is reflected by the continued high frequency activity in the extensor and reduced activity in the CxR. The crab responded to the second stimulus with a Three-Quarters Threat display, and was accompanied by an almost simultaneous increase in frequency in these two threat muscles. Again this reflects the behavioural display position, as all the cheliped segments are rapidly extended together. After this, stimulation was stopped and the crab moved from Three-Quarters, to Half, to Shallow Threat postures. The progressive flexion of the cheliped joints is reflected by the gradual decrease in carpus extensor and CxR activity.

CHAPTER 8 FIGURE 4



By various other combinations of simultaneous recordings it was found that the CxR and BI levators increase in excitation at almost the same time in movements from Three-Quarters to Full Threat displays, while Al activity precedes carpus extensor activity. In movements from lower intensities of display, the CxR increases in frequency before the levators, which in turn are increased in activity before the carpus extensor.

In another series of experiments, simultaneous recordings were made from threat and anti-threat muscles of the same cheliped. Two representative traces are shown on figure 5. Trace 5a illustrates the pattern of activity in the two coxal muscles. Each burst in the CxR corresponds to an increased threat display. It is apparent that between each burst there is a brief activity in the promotor muscle. This accompanied the observed, slight promotion of the cheliped from high to less intense threat displays.

Figure 5b indicates simultaneous recordings from the BI Al and Pd. The distinction between the activity of these antagonistic muscles is even more apparent. The crab was in a Half Threat posture at the beginning of the trace and subsequently switched to Three-Quarters Threat display. This was accompanied by the introduction of a second unit in the Al generating larger spikes. When stimulation was stopped, the crab resumed Half Threat postures which corresponded to a momentary inactivation of the Al and a sudden introduction of Pd activity. When the Half Threat position had been reached, the Pd was inactivated and the Al resumed tonic activity. From these and similar results, it was concluded that the anti-threat muscles are actively involved in causing the reduction of threat displays.

Simultaneous recordings were also made from the anti-threat muscles to determine their sequence of activity during movements from high to low threat displays. These sequences conformed to the expected pattern. When the arm is moved from Full to Three-Quarters Threat positions, the CxP is activated before the BI depressors, which in turn are activated before the carpus flexor. When the displays move from Three-Quarters to Half Threat positions, the frequency of activation in the carpus flexor is increased, reflecting the increased degree of flexion at the distal joints of the cheliped during this movement. A summary of muscle activity and threat posture is shown in figure 6.

DISCUSSION

This preliminary study of the threat displays of Carcinus demonstrate that there is a distinct alteration of muscle activity accompanying each alteration of threat display. The lowest intensities of threat are produced by low frequency tonic activity in the threat muscles. As the display is increased, the limb is further extended and levated due to increased

FIGURE 5

THE ACTIVITY OF THE ANTI-THREAT MUSCLES

Simultaneous recordings were made from antagonistic muscle pairs of the same cheliped to determine whether movement from a high to low intensity of threat display, is passively or actively achieved. Two representative traces are shown in the figure. In trace a, the upper beam is a recording from the CxR and the lower beam is a recording from the CxP. In trace b these recordings are the Al and Pd respectively. The time scale represents 1 s in both.

Each burst of the CxR in trace a corresponded to an increase in threat display. Between each, the arm was moved back to a display of a lower intensity. The traces demonstrate that this movement is achieved by active introduction of the CxP and is not simply a passive movement.

This active involvement of the anti-strike muscles is even more apparent in trace b. The crab was initially in Half Threat postures and responded to stimulation with a Three-Quarters Threat display, accompanied by the generation of large spikes in the Al. The subsequent movement, from Three-Quarters to Half Threat, was accompanied by a momentary inactivation of the Al and activation of the Pd. When Half Threat postures were reached, the Pd was inactivated and the Al resumed tonic activity.

CHAPTER 8 FIGURE 5

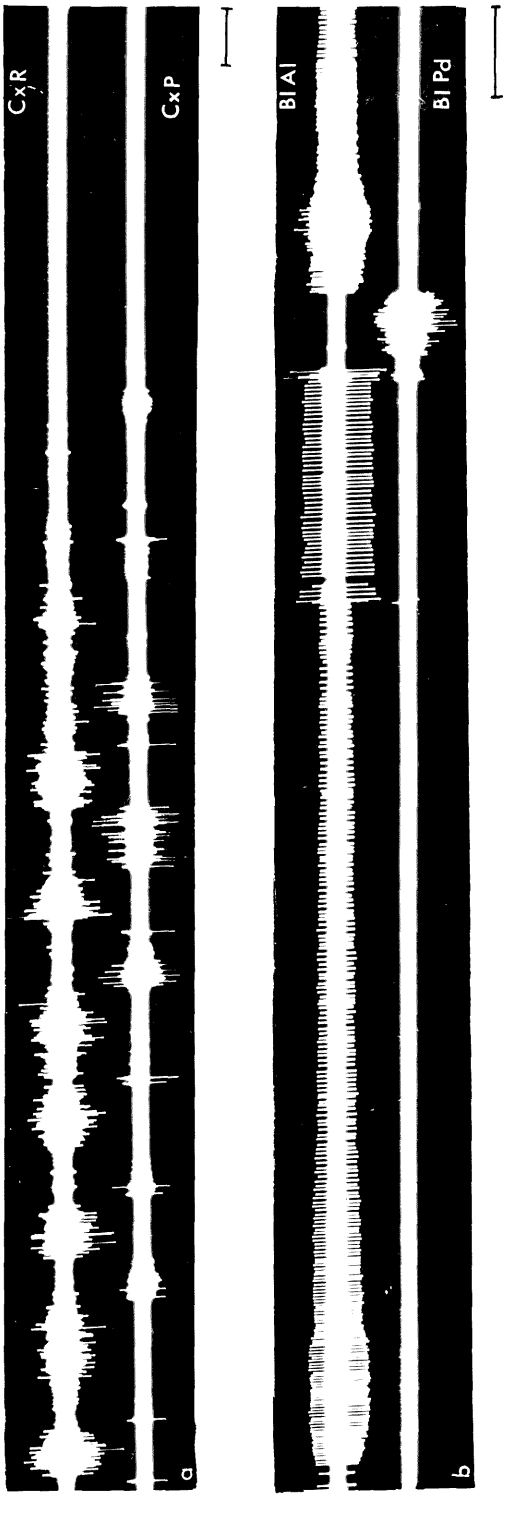


FIGURE 6

THE THREAT DISPLAYS AND MUSCLE ACTIVITY

Legend: C.e, carpus extensor; C.f, carpus flexor; CxP, coxa promotor; CxR, coxa remotor. 1 represents Full Threat, 2 represents Three-Quarters Threat, 3 represents Half Threat and 4 represents Shallow Threat.

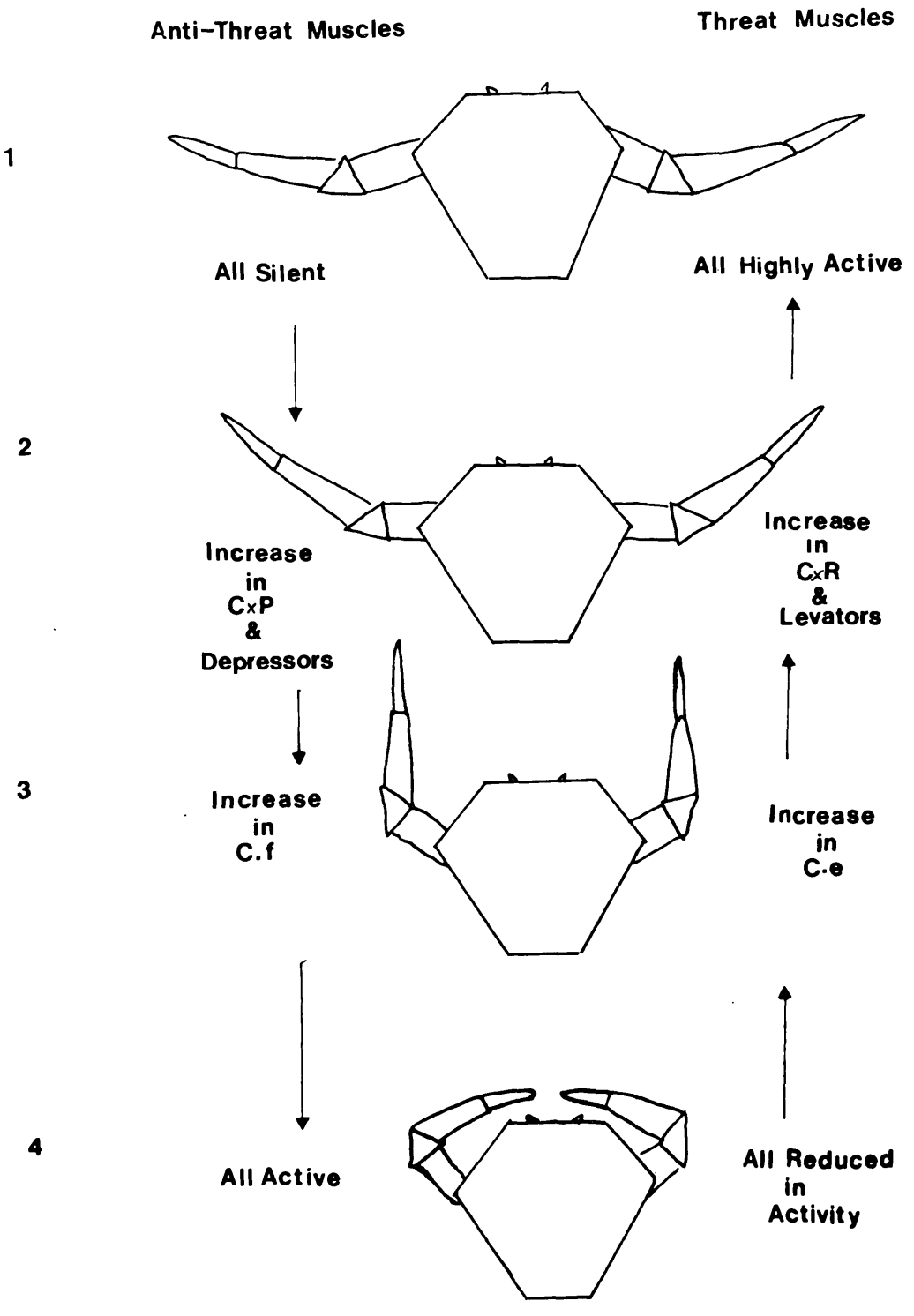
The action of the anti-strike muscles is indicated on the left hand side of the figure, as the threat displays are decreased, while the action of the threat muscles is indicated on the right hand side, as the threat displays increase.

As the chelipeds are moved from high to low intensities, 1 to 4, the anti-threat muscles are activated. Movement from stage 1 to 2 is primarily accompanied by activity in the coxa promotor and BI depressors, as the arm is promoted and lowered. Stage 3 is mainly produced by activation of the carpus flexor which directs the distal limb segments anteriorly and medially. At the final stage, all the anti-threat muscles are active at low frequencies, causing the limb to be partially flexed at all the joints of the cheliped.

A similar but reversed pattern is shown by the threat muscles when the displays increase in intensity, 4 to 1. Movement from stage 4 to 3 is primarily produced by activation of the carpus extensor directing the distal joints forward. The movement from stage 3 to 2 primarily involves remotion and levation, and so the coxa remotor and BI levators contribute more than the carpus extensor muscle, although the extensor is active in maintaining the display posture. In the extreme Full Threat display all the threat muscles are highly active, causing extension and levation at all the joints of the cheliped.

CHAPTER 8 FIGURE 6

Fig.6



activity in these muscles. The final stage of the displays, Full Threat, is not maintained for long periods. It can be termed a phasic behaviour and is caused by phasic muscle responses; it is accompanied by brief high frequency muscle activity and often new phasic axons are introduced.

DeLong (1971) considered that for a movement to be co-ordinated, three requirements must be fulfilled by the central nervous system. Firstly, the appropriate muscles must be selected. This is the spatial aspect of the movement. Secondly, each particular muscle must be activated or inactivated in a correct temporal pattern relative to the others. Thirdly, the appropriate amount of excitation or inhibition must be exerted on each muscle. This is the quantitative aspect of the movement.

The results obtained in this chapter show that the movements of threat fulfil these requirements and therefore the threat displays may be considered to be co-ordinated movements. The appropriate muscles are selected for all stages of the movement, shown in figures 1 and 2, which fulfils the first requirement. The fulfilment of the second requirement is shown in the EMG's of figures 4 and 5. That each individual posture of display is exactly reproducible in and between individuals, shows that the third, quantitative, requirement is fulfilled. That is, each muscle must receive the appropriate amount of excitation to produce the stereotyped postures of threat displays.

The third feature, which ensures that the postures of display are the same between individuals, is particularly important in the threat behaviour. It will enable other crabs viewing the display, to correctly receive the displaying information and act accordingly. The purpose of an agonistic display is to minimize physical contact. The whole effect would be lost if the cheliped was not held in the "expected" positions.

When a stimulus must reach a certain level of intensity to cause a behaviour, it is termed a "releaser". The releaser for the threat behaviour in Carcinus is primarily visual, although mechanical stimuli can also release the displays. The next chapter of the thesis was concerned with investigating the parameters of stimulation which release and affect the threat behaviour. This was performed by applying various stimuli to the crab and recording the muscle response. Comparison of the recordings with the known activity patterns obtained from this chapter, allows an estimation of stimulus effectiveness.

CHAPTER 9

ANALYSIS OF THE THREAT BEHAVIOUR

INTRODUCTION

It has been shown that Carcinus maenas responds to rapidly approaching stimuli by extending and levating the chelipeds. This is termed the threat display and can be divided into four categories of intensity; Full, Three-Quarters, Half and Shallow Threat. The most extreme display is a phasic behaviour and, unlike the others, is not maintained. Movements from low to high intensities are extremely rapid while movements in the reverse direction can take much longer. The increased intensities are accompanied by an increased frequency of activation in the muscles which cause extension and levation to the cheliped, the threat muscles. When the crab reduces its threat display, the anti-threat muscles, the flexors and depressors, are activated as their antagonists are inactivated.

A study of the defence reflex of the crayfish was performed by Glantz (1974, a.b.c.). The preliminary study of this reflex was concerned with the muscle responses to presentation of various stimuli (Glantz, 1974a). From this study the author was able to correlate the recorded muscle responses with activity recorded from elements in the optic nerve (Glantz, 1974b). From these results he extracted the importance of different visual stimulus parameters which are necessary to evoke the defence reflex.

When the crayfish is stimulated with an approaching target, it generally responds by raising and directing its chelipeds towards the object of stimulation. EMG recordings were used to determine the onset of muscle activity after the beginning of stimulation (Glantz, 1974a). The first series of experiments performed by Glantz were concerned with stimulus repetition rate and habituation. It was found that properties of the reflex are dissimilar to most observations concerning habituation. Repeated stimulation usually causes a decrease in a behaviour; this is termed habituation (Hinde, 1970). However,Glantz found that fast rates of repeated stimulation caused the reflex to be maintained, and he suggested that the enhanced response was due to facilitation of one of several pathways in the neural circuit controlling the reflex.

Glantz performed other experiments which showed that the rate of habituation decreased with the effectiveness of stimulation; that is, more effective stimuli produced less habituation and so the reflex was maintained for longer periods. Effective stimuli included increased stimulus repetition rate, objects presented to the front of the animal and rapidly approaching objects. A habituated animal could be dishabituated by

increasing the stimulus effectiveness, by mechanical stimulation to the carapace and also by slightly moving the axis of the stimulus target. It was found that moving the target axis by only 5^{o} was sufficient to produce substantial response recovery.

From these preliminary studies, Glantz was able to suggest which parameters of stimulation are most likely to release the reflex. Subsequently he recorded from the optic nervous system to determine which elements in the optic nerve respond in the same way as the muscles (Glantz, 1974b).

The presence of separate intensities of threat display in Carcinus indicates that certain parameters of stimulation may be more effective in releasing the behaviour than others. To examine this, a series of experiments was designed to analyse the muscle response in detail when the crabs are subjected to different parameters of stimulation. These parameters include stimulus presentation rate, approach and angular velocity and dishabituation. To ensure that the behaviour patterns were as normal as possible, the crabs were tested in a freely moving situation.

The stimulus parameters were chosen to represent stimuli that may affect the crab in its natural environment. For example a predator may repeatedly attempt to attack the crab; a sea bird, for instance, may repeatedly peck at the crab. This feature was examined by altering the rate of stimulus presentation to the crab. The effect of the speed of repeated approach by an attacking predator was examined by altering the approach velocity of the stimulus presented to the crab. A predator may also be large or small. The effect of this feature was examined by presenting the crab with stimuli of various visual angles. Examination of dishabituation stimuli was chosen to represent the effect of a predator suddenly changing its attack rate, approach velocity or actually hitting the crab.

MATERIALS AND METHODS

As previously described, the experiments were performed on large male Carcinus. The crabs were prepared for EMG recording as before but instead of being suspended over a tank, they were allowed to move freely in a rectangular tank. The tank was partly filled with cooled sea water, which was changed regularly. The front of the tank was transparent while the other three sides were painted black. The tank was mounted on a table, separate from the other equipment. A light was placed behind and above the tank, directed forwards.

The threat display stimulator was composed of a piston which could be moved towards and away from the crab. The piston rod was housed in a smooth Perspex cylinder which was rigidly clamped. One end of the piston

was attached, via a pivot pin, to a long flat Perspex bar. This, in turn, was attached via a screw, to the radial arms of the top of a large kymograph drum. This coupling provided a rotational movement to the Perspex bar as the drum revolved. Since this was coupled to the piston rod, movement of the drum pulled the rod in and out of the cylinder with each revolution, which produced approach and retreat strokes of the stimulus. The piston and tank were covered by a black cowl to prevent the crab from observing any other visual stimuli which may affect the response.

White discs of varying sizes could be attached to the free end of the piston. The arrangement produced an illumination of 9 ft candles when the disc was closest to the crab and 6 ft candles when farthest away. Altering the disc diameter allowed the alteration of visual angles of stimulation presented to the crab. The angular velocity of stimulation was altered by varying the speed of the kymograph motor and, therefore, changing the speed of target approach. The angular velocity was calculated as indicated below:

$$\text{Angular velocity} = \frac{VA_2 - VA_1}{td}$$

where VA_1 = visual angle of disc at beginning of piston travel

VA_2 = visual angle of disc at end of piston travel

td = time of disc travel

The approach, or transitional velocity, was calculated as shown below:

$$\frac{\text{Distance of disc travel}}{\text{Time of disc travel}}$$

Alteration of the speed of a freely rotating drum also allowed the alteration of stimulus presentation rate. Alternatively, the drum could be stopped at the end of each approach and retreat stroke by the application of mechanical stops. This was produced by attachment of a metal rod, horizontally, on to the spindle of the kymograph. Another rod was flexibly and vertically attached to the kymograph motor. When the two rods met, the drum was halted. Disengaging the flexibly attached rod allowed the drum to rotate again. All the rods were covered with rubber to minimize the force of contact and consequent jarring of the machine. The drum could also be rotated manually to obtain faster speeds than could be achieved by the kymograph motor.

The movement of the piston was measured in one of two ways. In some experiments small metal markers were attached to the base of the kymograph spindle. As the drum rotated the markers opened a microswitch which was attached to the motor. This switch could be connected to the lower beam of the oscilloscope. If the piston position for the first recorded marker

was noted, the subsequent positions could be readily and accurately measured by reference to this first, and following, markers recorded on the traces. In this way, recorded muscle activity could be correlated with disc position. The position of the piston was also measured by use of a photodiode. This was placed below the drum and could be connected to the lower beam of the oscilloscope. A series of bars were arranged, radially, across the drum base. When a light source was directed through the drum, the photodiode did not register. As the drum rotated, the bars interrupted the light beam and the photodiode registered a deflection on the oscilloscope trace. One bar was made wider than the others and consequently produced a longer photodiode response. In this way the position of the piston at any specific time in the records could be measured.

Control runs were made without a disc attached to the end of the piston to test that the crabs were not responding to mechanical stimuli. In no instance was there any evidence of mechanical artifact responses.

The crabs always orientated towards the disc at the beginning of stimulation. They remained in this position until movement of the disc ceased. Most EMG recordings were taken from the BI Anterior levator muscle since this has been shown to be the most reliable muscle indicator of threat displays (Chapter 8). Some recordings were also made from the coxa remotor muscle for comparison of its responses with those of the A1. The EMG's were stored on tape and filmed directly from the oscilloscope for analysis. This was performed using an enlarger as before. The data was treated in two ways. Firstly, the latency between the beginning of stimulus movement and the achievement of peak muscle response frequency was measured. Secondly, the muscle response frequency, M.r.f., was calculated for each stimulus presentation. This was performed in several steps:

1. The frequency of muscle impulses recorded five seconds before and five seconds after stimulation, was measured. This was converted into impulses per second.
2. From these values a mean, unstimulated resting frequency of muscle activity could be calculated. This was termed value A.
3. The frequency of impulses that were recorded during the presentation of the stimulus was also measured and converted into impulses per second. This was termed value B.
4. The above procedure enabled the calculation of a standardized muscle response frequency, M.r.f. This value allowed direct comparison of muscle response accompanying stimulation between crabs, because it accounted for any differences in recorded resting activity. The M.r.f. was calculated by dividing value B by value A. When the muscle activity is increased by the

FIGURE 1

THE THREAT DISPLAY STIMULATOR

A crab, wired for EMG recordings, was placed in a tank partly filled with cold sea water. The front of the tank was transparent while the other three sides were painted black. A light was positioned behind and above the tank, directed forwards. The stimulator consisted of a piston, housed in a smooth Perspex cylinder. The cylinder was rigidly clamped to a table. One end of the piston rod was attached, via a pivot pin, to a long Perspex bar. This was coupled, via a screw, to the top of a large diameter kymograph drum. As the drum revolved, the bar was pulled around. This transmitted a push and pull movement to the piston rod. Consequently, the rod was moved towards and away from the crab, in approach and retreat strokes with each revolution of the drum.

The drum was allowed to freely rotate at different speeds producing different velocities of travel (translational velocity). Manual movement of the drum achieved faster speeds than could be generated by the motor.

Discs were attached to the free end of the piston rod. By varying the disc diameter, different visual angles of stimulation could be produced. By varying the kymograph speed, different angular velocities could be produced.

Marking of stimulus position was performed in two ways. Firstly, small metal rods could be attached to the base of the kymograph spindle. These opened and closed a microswitch, which was attached to the motor of the kymograph, as the spindle rotated. The switch could be connected to the lower beam of the oscilloscope. If the initial position of the rod was noted before recording, the subsequent positions could be accurately measured with reference to the recording markers.

A second method of position marking was achieved with the use of a photodiode placed below the drum. This could also be connected to the oscilloscope. Bars were placed radially across the drum base. When a light was directed through the drum, the photodiode did not register. As the drum rotated, the light beam was interrupted and the photodiode produced a deflection of the oscilloscope trace. One bar was made wider than the others and produced a longer photodiode response. Thus the position of piston travel at any time could be measured by reference to the photodiode registers on the recordings.

A metal bar was attached horizontally to the kymograph spindle. Other bars were flexibly and vertically mounted around the kymograph motor. When the drum revolved, the two bars met, stopping the travel of the drum and piston. Releasing the stop allowed the drum to revolve again. By placing the stops at different points around the spindle, the piston travel could be halted at the end of the threat and approach strokes.

The piston and tank were covered with a black cowl to prevent the influence of any other visual stimulation which may influence the response of the crab.

CHAPTER 9 FIGURE 1

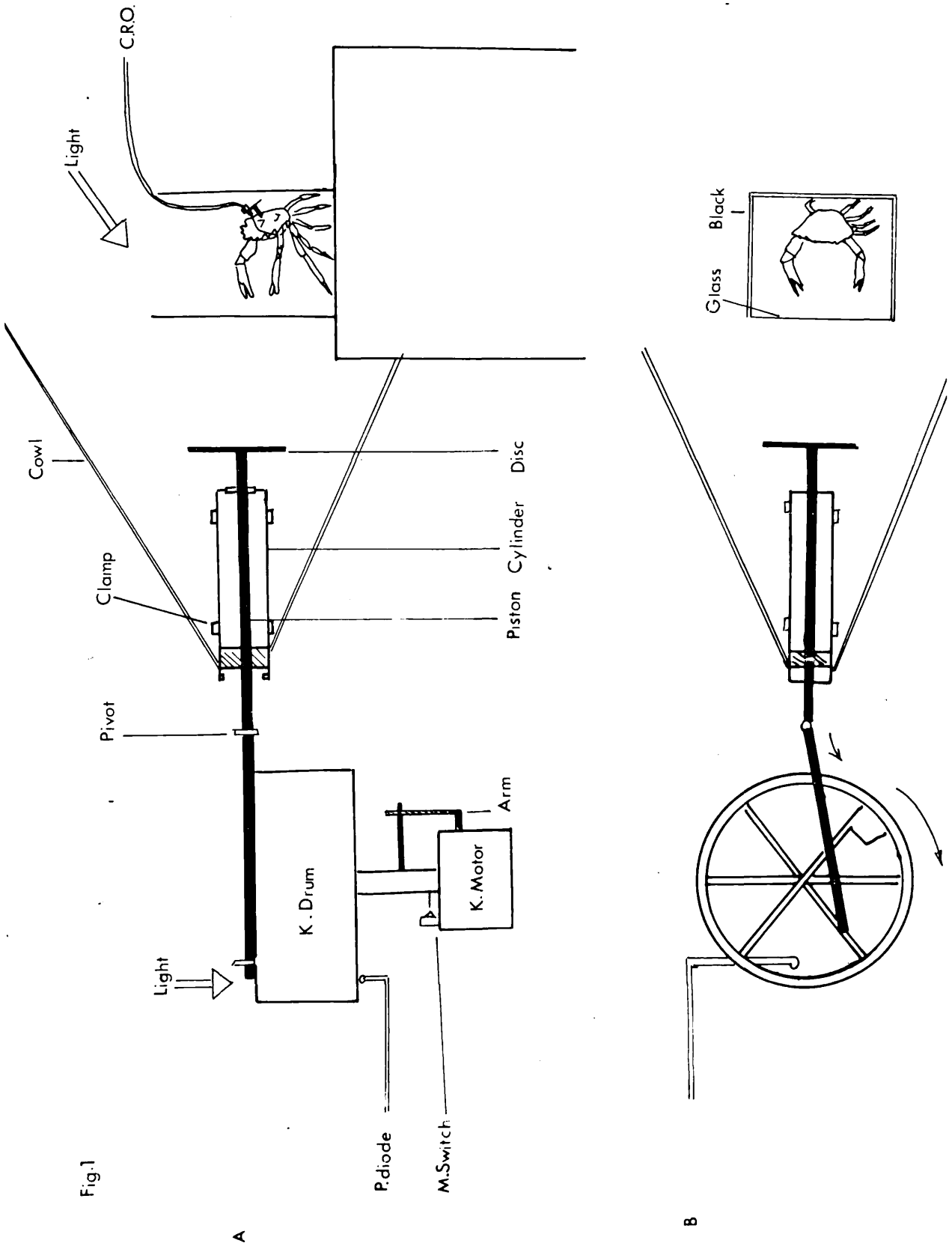


Fig.1

stimulation, the M.r.f. will be larger than 1. The greater the muscle response increase, the greater will be this value. When there is no observable change in muscle activity the value will be 1. At this stage, habituation of the response was assumed to be complete.

For example, the resting frequency, value A, may be 10 ips. On the first presentation of the stimulus, the frequency may rise to 20 ips. The resultant M.r.f. is 20 ÷ 10 = 2. As stimulation continues the crab may respond less, and value B may decrease as will the resultant M.r.f. For example, after five stimuli value B may be 15 ips, and therefore the M.r.f. will be 1.5. After n stimuli there is no change in frequency of muscle activity. Value B is now 10 ips, and the M.r.f. is 10 ÷ 10 = 1. This method of estimating and calculating muscle response to stimulation allowed the responses from each crab to be standardized and compared with other crabs. It also allowed data to be pooled.

RESULTS

At the beginning of stimulation the freely moving crabs orientated to face the moving disc. They then responded by raising the chelipeds and often reared towards the stimulus. The intensity of the display released by stimulation depended upon the effectiveness of the stimulus and also upon the responsiveness of the individual crab.

1. Types of threat response

In the previous chapter it was shown that each display intensity is paralleled by a distinct muscle response. Before any conclusions can be made as to the importance of various stimulus parameters, the overall effectiveness of the whole experimental procedure had to be assessed to determine whether it released a typical threat display. Crabs, which varied in responsiveness, were placed in the experimental tank and allowed to settle. The disc was then moved manually, producing an angular velocity of 65°/s; a translational velocity of 25 cm/s. Results from representative crabs are shown in figures 2 and 3.

The first series of three EMG's in figure 2 indicate the BI Anterior levator muscle response to stimulation. In the previous chapter it was shown that increased threat displays correspond with the brief introduction of the second phasic Al axon. More muscle spikes are generated by the axon as the intensity of the display increases. Following each burst, there is usually a momentary reduction in impulse frequency before the postures of threat are rigidly maintained. This is also the situation found in this present experiment (Fig. 2). In trace 1 of figure 2, the crab responded to stimulation by movement from Shallow to Half Threat display positions, which was accompanied by a relatively small increase in frequency

of muscle activation, and a long latency between the beginning of stimulation and peak M.r.f. In figure 2.2, the crab responded by twitching its chelipeds from Half to Three-Quarters Threat display. The increase in impulse frequency was greater and the latency between the beginning of stimulus movement and peak muscle activity was shorter. After the phasic burst, the crab readopted Half Threat and the muscle activity returned to the frequency displayed before stimulation. In figure 2.3, the crab responded with a Full Threat display. This corresponded to a further increase in impulse frequency and the generation of more large phasic spikes. Peak frequencies occurred only 50 ms after the stimulus began to move.

This indicates that the muscle and behavioural responses to a moving disc are comparable to those obtained previously (Chapter 8). The difference lies in the more transient nature of the increased display. In the previous chapter stimulation was uncontrolled,and the crabs responded both to the moving hand stimulus and to the experimenter's body. In the present experiment, the stimulus was more controlled and effectively stopped as soon as the disc stopped moving. Instead of remaining in increased positions of threat, the crabs tended to respond to stimulation with briefer movements; the chelipeds were rapidly raised upwards and were then moved back down to the original display posture when stimulation ceased. This more rapid movement was especially evident in the more alert crabs which moved from Three-Quarters to Full Threat display positions.

Figure 2 a to c, indicates the recorded responses from the coxa remotor muscle. The three EMG's represent responses from crabs which moved from Shallow to Half Threat, trace a; Shallow to Three-Quarters Threat, trace b; and Half to Full Threat, trace c. As in the levator recordings, the more controlled nature of the stimulus is reflected by the more phasic response recorded from the muscle.

In figure 3, the responses of the distal cheliped muscles are shown. These also conform to the patterns described in the previous chapter. In all three traces the crabs responded to both approaching and retreating stimuli with movements from Half to Three-Quarters Threat display posture. Again, increased frequencies of muscle activity are only shown when the disc moves and original frequency levels are rapidly resumed when stimulation stops.

These results show that the experimental technique releases threat responses which are comparable to those observed in the previous chapter. Thus it may be assumed that any alterations in muscle activity accompanying manipulations made to the stimulus parameters, should reflect responses displayed during normal behaviour, as well as those displayed during these experimental situations.

FIGURE 2

This illustrates the muscle responses of the BI Anterior levator and coxa remotor muscles to a single presentation of the stimulus. At the end of the approach stroke, the travel of the disc was stopped mechanically. In all the traces the lines below the EMG's represent disc travel and were obtained by reference to the kymograph position markers. The translational velocity was 25 cm/s and the angular velocity was 65^{o}/s.

The time scale represents 1 s.

Traces 1 to 3. These illustrate the A1 response. In trace 1, the crab responded to stimulation by movement from Shallow to Half Threat positions. This was accompanied by a relatively small increase in muscle impulse frequency and a long latency of 700 ms, between the beginning of stimulus travel and peak muscle frequency. The crab adopted Shallow Threat soon after stimulation ceased.

In trace 2, the crab rapidly moved from Half to Three-Quarters Threat. This corresponded to an increase in muscle impulse frequency and the generation of a few large spikes, indicating the recruitment of the second A1 phasic axon. There was only a 150 ms latency between the peak impulse frequency and the beginning of stimulation. Subsequent to this burst, muscle activity was reduced until the crab readopted Half Threat postures.

In trace 3, stimulation caused the crab to respond with a Full Threat display. This was accompanied by a brief latency, only 50 ms, between the beginning of target movement and peak impulse frequency. After this phasic burst, the crab readopted a Three-Quarters Threat display posture.

Traces a to c. These illustrate the CxR response. The three traces also illustrate three intensities of threat display. In trace a, the crab moved from Shallow to Half Threat postures. This was accompanied by a slight and brief increase in CxR activity.

In trace b, the crab moved from Shallow to Three-Quarters Threat. This corresponded to a sudden high frequency in the muscle. When stimulation stopped, the crab quickly assumed a Half Threat display and impulse frequency decreased.

In trace c, the crab responded to stimulation by displaying Full Threat. This corresponded to a greater and more prolonged increase in impulse frequency. After the first phasic burst,the crab assumed a Three-Quarters Threat display and the frequency of muscle impulses was gradually decreased.

CHAPTER 9 FIGURE 2

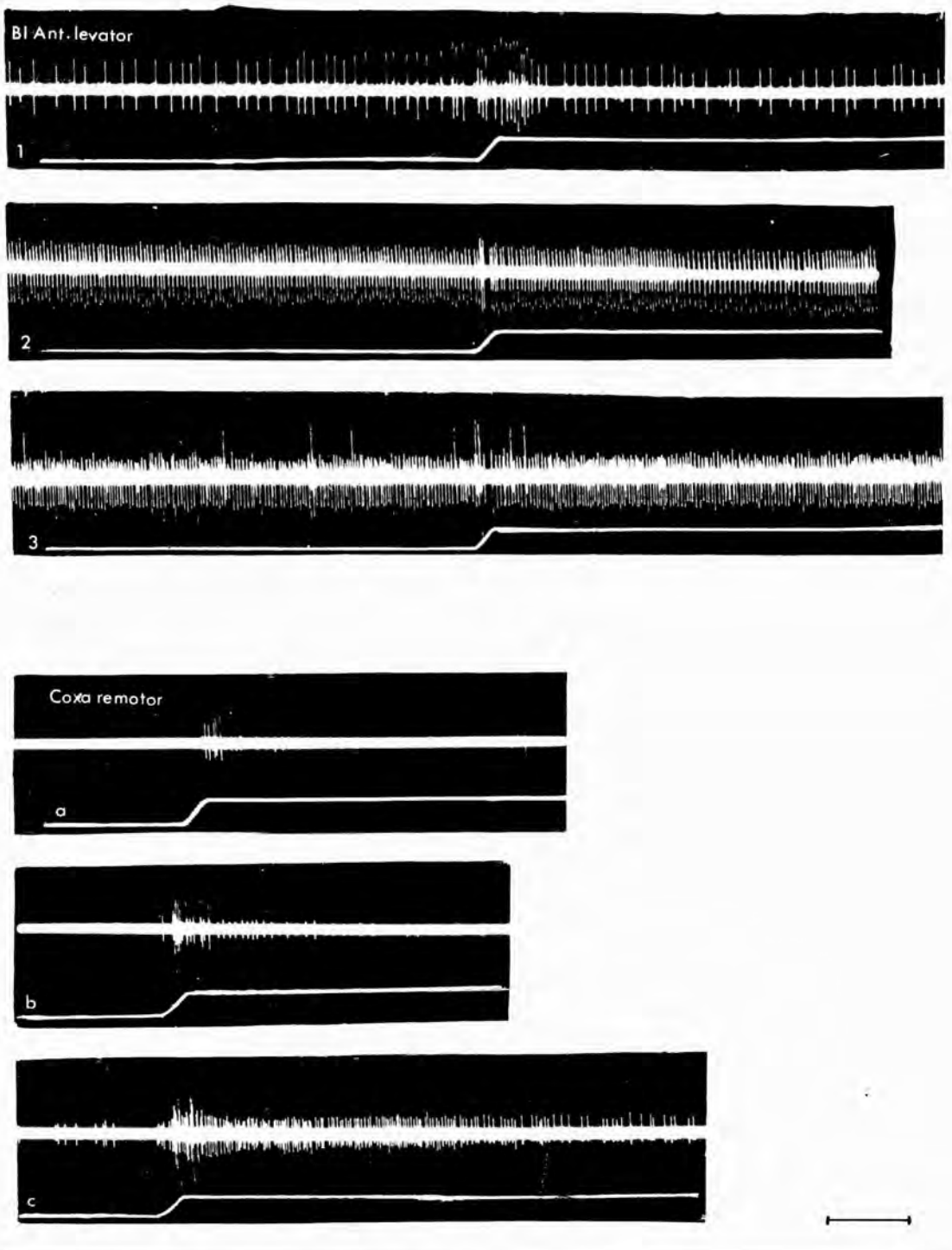


FIGURE 3

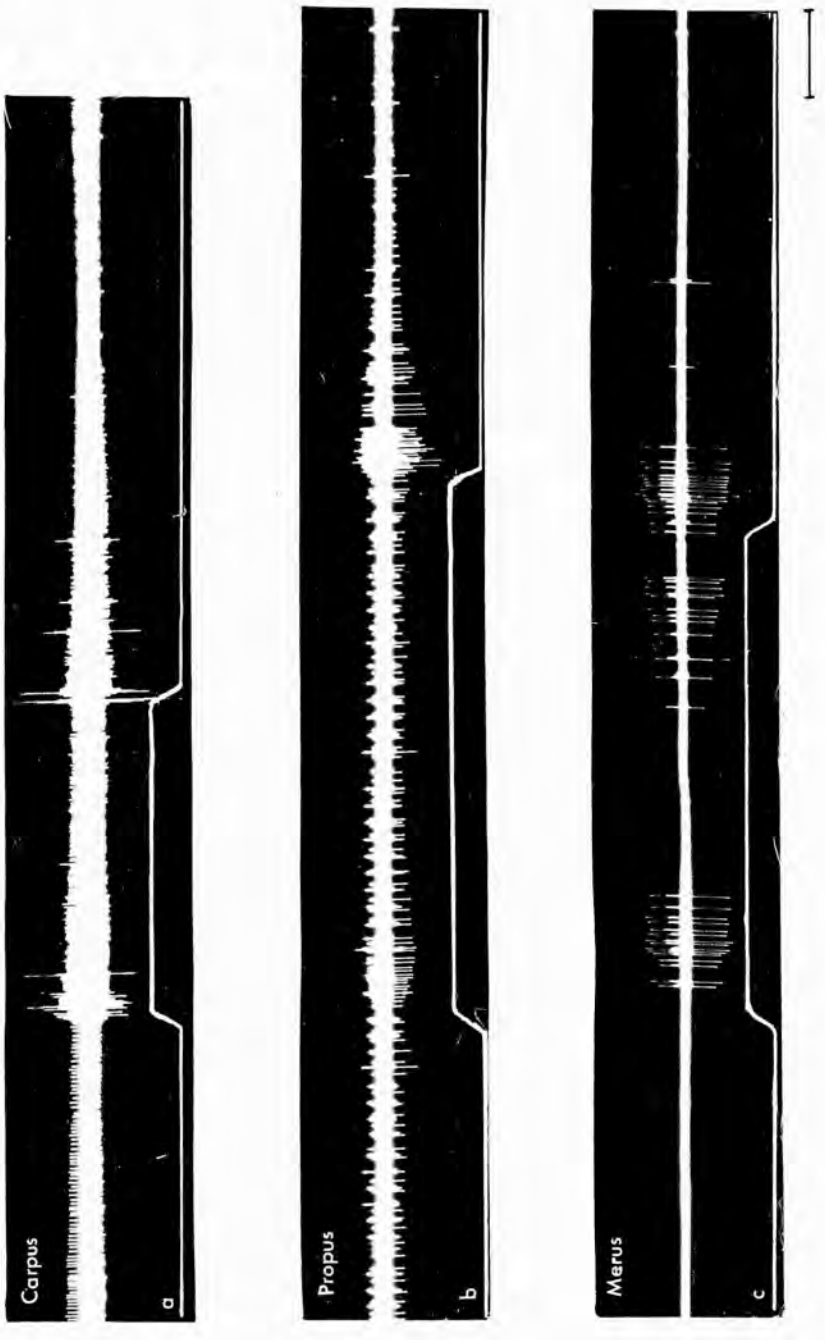
This illustrates the responses from the distal cheliped muscles to presentation of the stimulus. At the end of each half revolution of the drum the disc travel was stopped. This produced an approach and retreat stimulus, and is indicated below the EMG's. The time scale represents 1 s.

Trace a demonstrates the responses recorded from the carpus extensor muscle. The approach and retreat of the stimulus was accompanied by the introduction of large muscle spikes and an increase in existing frequency of muscle activity.

Trace b demonstrates the response recorded from the propus extensor muscle. The movement of the disc corresponded to an increase in existing tonic activity.

Trace c demonstrates the response recorded from the merus extensor muscle. After a long latency between the approach of the stimulus and the beginning of muscle response, the merus extensor showed a brief increase in frequency of activation. There was a shorter latency when the stimulus was retreated.

CHAPTER 9 FIGURE 3



2. The influence of stimulus presentation rate and stimulus velocity on the muscle response

The disc size used in this experiment produced a visual angle which increased from 22^{o} to 70^{o}. The experiment was designed to examine the effects on the threat response when predators repeatedly approach the crab at a constant velocity and rate. The influence of approach velocity and repetition rate of attack was examined by altering the rate of presentation of the stimulating target to the crab. Four kymograph speeds were used to test the influence of altering stimulus presentation rate and velocity, together. The results are shown on figures 4, 5 and 6.

Figure 4A illustrates the decrease in BI Anterior levator muscle response as the stimuli are repeated. The rate of habituation is indicated by the decrease in muscle response frequency from values above 1 to values of 1. When the latter is reached, it is assumed that habituation is complete. It is apparent that the number of stimuli necessary to cause habituation of the response is less at the slower rates of stimulus presentation and velocities. Only four presentations were needed at a rate of 1 stimulus every 5 s, whereas habituation had not occurred after twelve presentations at the fastest rate.

Figure 6a and b, illustrate EMG recordings from the A1 when the crab was stimulated at the second and third rates of presentation indicated on figure 4. The traces demonstrate the decrease in muscle impulse frequency as habituation occurs with repeated stimulation.

Figure 5 and figure 6c, d, illustrate the responses to stimulation recorded from the coxa remotor muscle. The EMG's indicate that whereas the A1 is highly active maintaining threat displays (Fig. 6a, b) levating the cheliped, the CxR is less active during maintained positions but suddenly increases in frequency when the cheliped is rapidly twitched into more extreme display postures.

The CxR displays a faster rate of habituation than the A1 at the higher rates of stimulus presentation and velocities (Fig. 5). Although the rate is steeper than the A1 response, the time before habituation is completed, is longer. As in figure 4A, the rates of habituation demonstrated by the CxR are similar at all three tested rates of stimulus presentation. However the fastest rate of presentation accompanied a M.r.f. value which was almost three times as high as that shown for the slower rates, unlike the situation displayed by the A1 (Fig. 4A).

FIGURE 4

A. This illustrates the muscle response frequency of the Anterior levator to different stimulus presentation rates and consequent approach velocities.

The kymograph was allowed to rotate freely at four speeds. The disc size produced a visual angle of 22° when the piston was fully away from the crab, and 70° when the piston was at its other extreme of movement, nearest to the crab. The four speeds used produced the following stimuli:

SPEED	PRESENTATION RATE	ANGULAR VELOCITY	TRANSLATIONAL VELOCITY	SYMBOL
1	1 stimulus every 0.8 s	60°/s	22.5 cm/s	Closed circles
2	1 stimulus every 1.2 s	40°/s	15 cm/s	Open triangles
3	1 stimulus every 2.0 s	29°/s	9 cm/s	Closed squares
4	1 stimulus every 5.0 s	9.6°/s	3.6 cm/s	Open circles

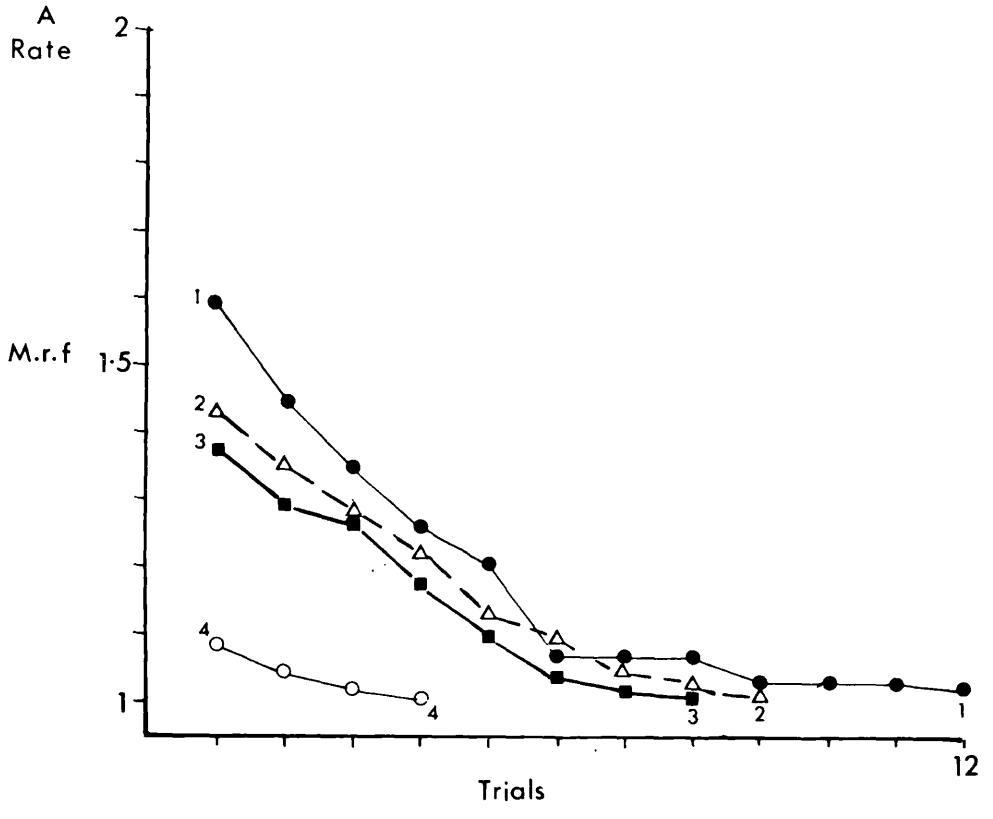
The points plotted on the figure are mean values obtained from the pooled data of all the crabs which were tested in this way. At least six crabs were tested with each rate of stimulus presentation. The ordinate represents the muscle response frequency,M.r.f., for each presentation of the stimulus, that is for one complete revolution of the drum producing approach and retreat strokes. The abscissa represents the number of presentations of stimuli. The figure demonstrates that less stimuli are required to produce complete habituation of the recorded threat response at the slower presentation rates and velocities. The rate of habituation is similar for all four presentation rates, but the M.r.f. values are dissimilar, being initially higher at the faster rates of stimulus presentation and velocities.

B. This illustrates the rate of habituation plotted against time.

When the curves of habituation, obtained fromgraph A, are plotted against time, it is apparent that although more stimuli are needed before habituation is completed at the fastest rates of stimulus presentation, the time for this to occur is less than that for the slower rates. That is, at the fastest rate of stimulus presentation, habituation was complete in 10 s, whereas at the slower rate, habituation was only complete after 20 s.

CHAPTER 9 FIGURE 4

Fig. 4



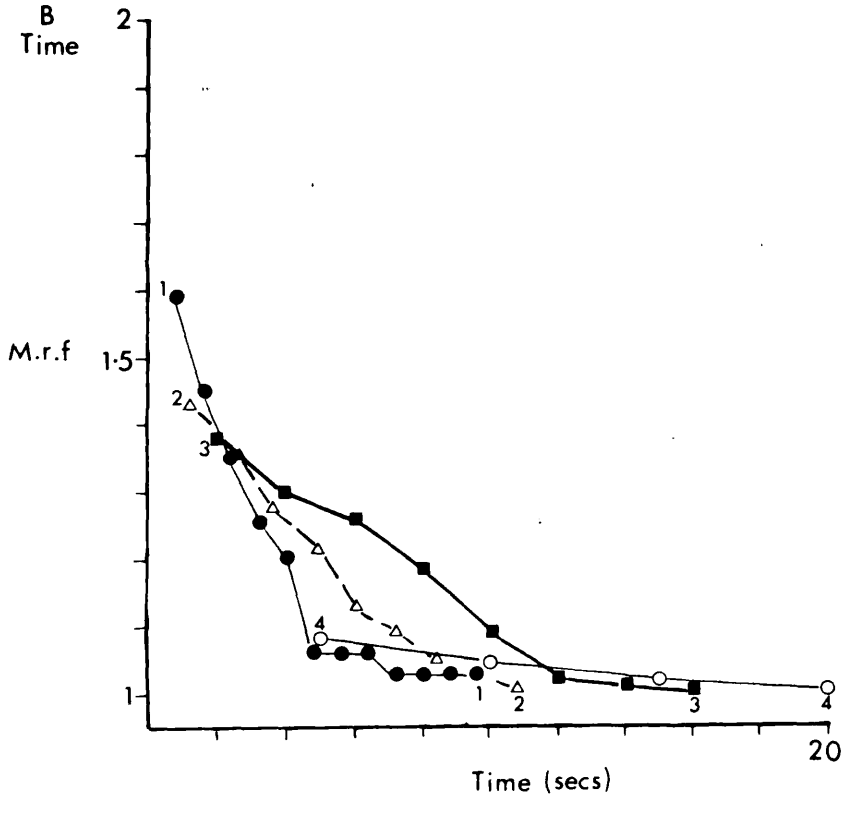


FIGURE 5

This illustrates the effect of altering stimulus presentation rate on the response recorded from the coxa remotor muscle.

Three rates of stimulation presentation rate were used and correspond to speeds 1, 2 and 3 in figure 4. Five crabs were used in all three experiments. The points plotted on the graph are mean values obtained from pooled data. The ordinate and abscissa are as before in figure 4A.

This figure shows that the overall muscle response frequency of the CxR is greater than that calculated for the Al (Fig. 4). The rates of habituation are similar at all three rates of stimulus presentation, however the M.r.f. is dissimilar and is higher at the fastest rates of stimulus presentation. Habituation of the response takes longer to be completed at the faster rates of stimulation than that shown in the Al (Fig. 4).

CHAPTER 9 FIGURE 5

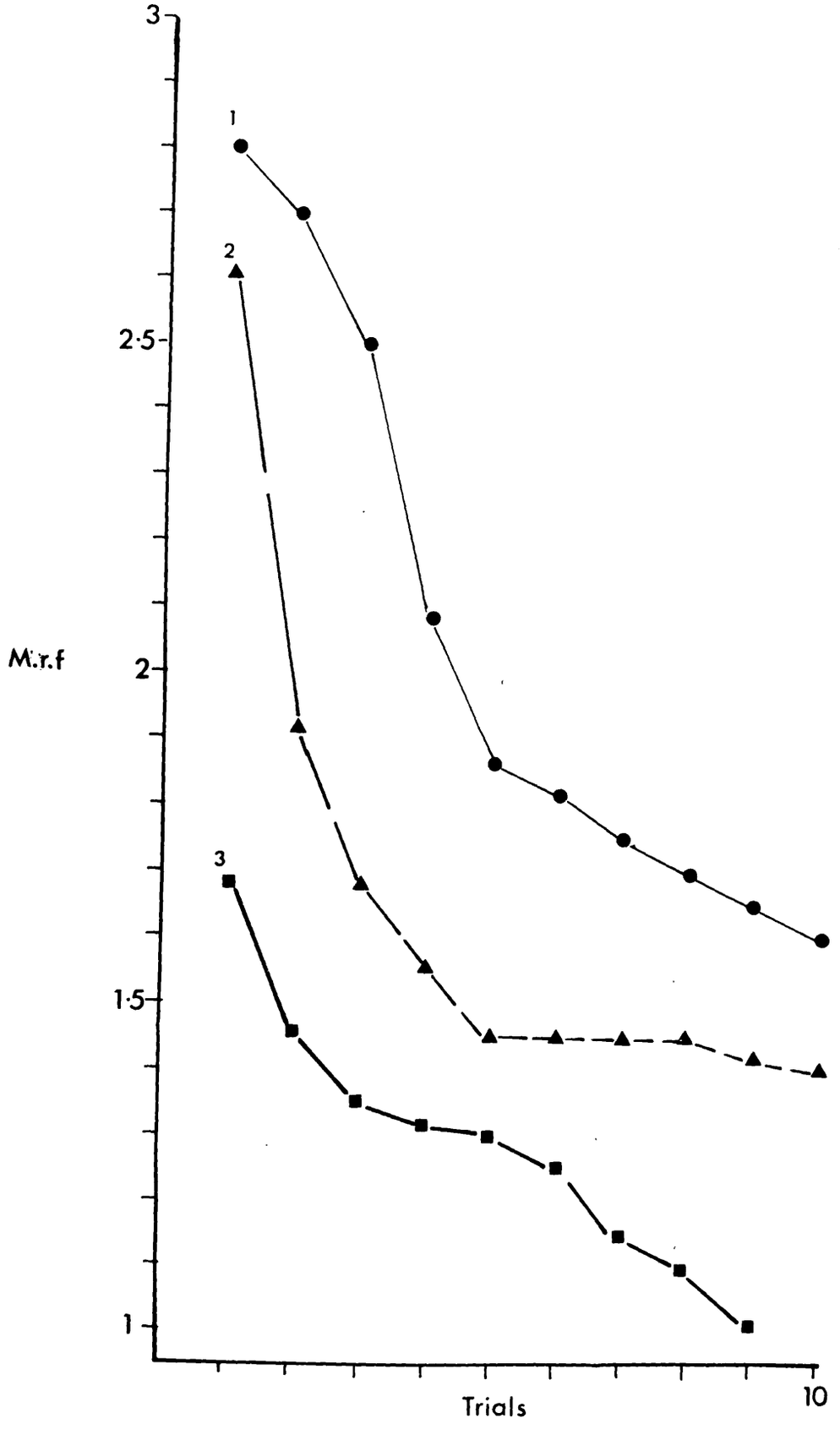
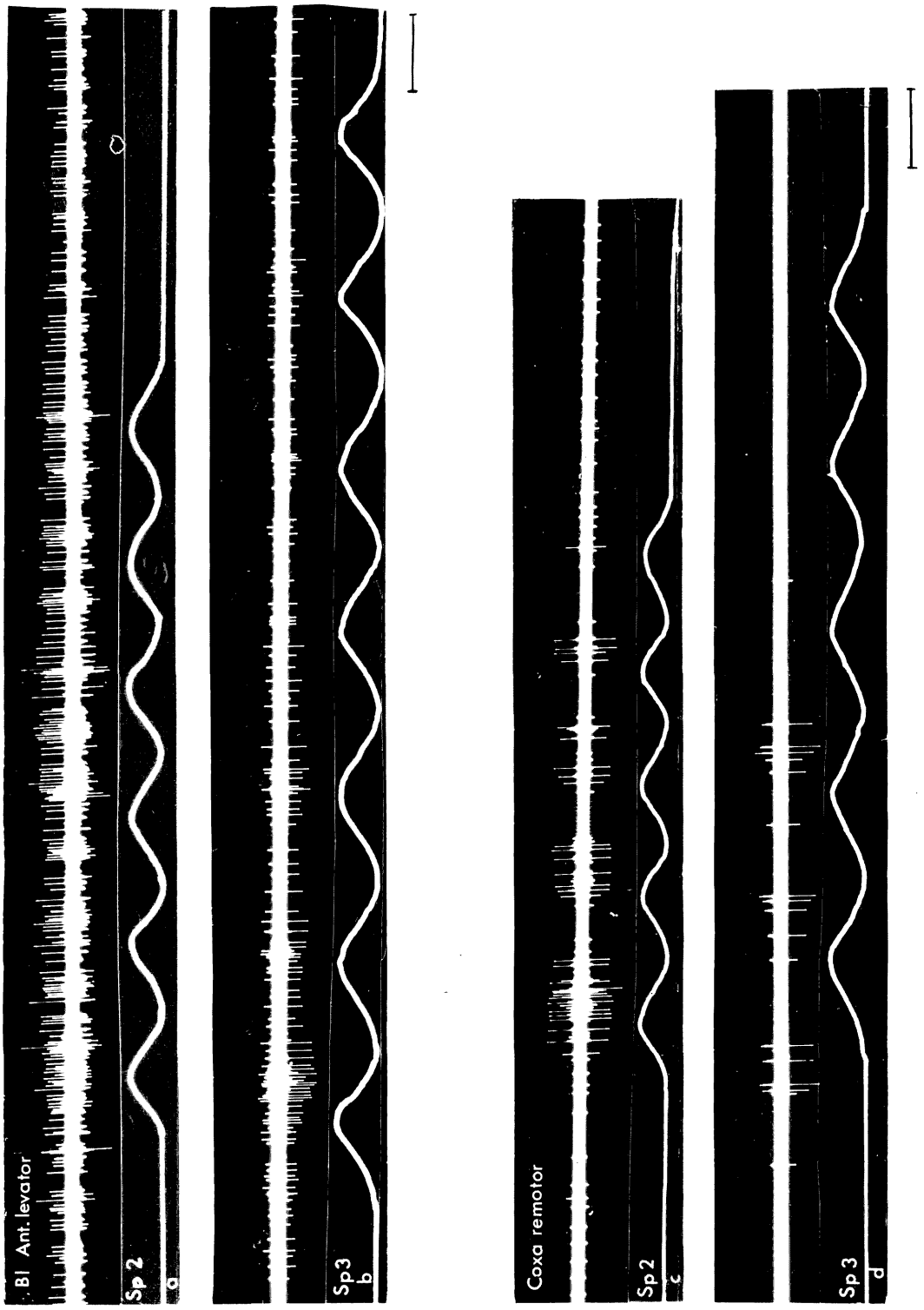


FIGURE 6

This illustrates muscle responses to stimulation at two rates of stimulus presentation and velocities. Traces a and b are recordings from the Anterior levator; traces c and d are recordings from the coxa remotor. Sp.2 indicates a presentation rate of 1 stimulus every 1.2 s and Sp.3 indicates a presentation rate of 1 stimulus every 2.0 s and correspond to the same rates shown in figure 4. The lines below the EMG's indicate the approach and retreat of the disc, which was measured by reference to the stimulus markers. The time scale represents 1 s.

The traces demonstrate that these two threat muscles respond to the approach of the stimulus with an increase in frequency of activation. The bursts of increased frequency are progressively reduced as the response habituates. The traces of the CxR indicate the greater change in impulse frequency between the presentation of the stimulus and unstimulated periods. This produces a higher M.r.f. than that calculated for the Al.

CHAPTER 9 FIGURE 6



3. The influence of stimulus presentation rate and stimulus velocity on habituation

Although figure 4A appears to indicate that habituation takes longer to occur at the faster rates of stimulation, this is not so. Habituation is certainly influenced by stimulus presentation but is also influenced by time. Only four stimuli are necessary to produce habituation of the response at a presentation rate of 1 every 5 s. Thus habituation is complete in 20 s. However at the faster presentation rate of 1 every 1.2 s, nine stimuli are needed before habituation occurs. This only represents a time of 10.8 s, almost half that for the slower rate. This is shown on figure 4B.

Therefore it appears that, in Carcinus, habituation follows the typical principles explained in the introduction; that is, higher rates of repetition cause a faster rate of habituation. However the following experiment shows that when the two variable stimulus parameters of presentation rate and stimulus velocity are separated, habituation of the response is atypical.

4. The effect on habituation of maintaining the same stimulus velocity while varying presentation rate

To distinguish between the effects of the two parameters, stimulus presentation rate and approach velocity, a series of experiments was performed with a constant velocity and varying stimulus presentation rate. This was designed to examine the effect of a predator which approached the crab at a constant velocity while altering its rate of attack. Altering the rate of presentation was achieved by using mechanical stops to halt the movement of the kymograph and disc at the end of each approach and retreat stimulus. The drum could be set to a single speed so producing the same velocity each time, while the time between successive stimuli could be altered.

The results are shown on figures 7 and 8. The kymograph speed was set, such that the stimulus produced an angular velocity of 43.7^{o}/s and translational velocity of 16.4 cm/s. Figure 7 indicates that when the approach velocity is kept the same while the rate of stimulus presentation is altered, habituation takes a different form than in the previous experiment in which both stimulus parameters were altered together. Habituation now takes longer to be completed, and in one instance a crab was tested at a presentation rate of 1 stimulus every 15 s for 10 min and still displayed threat responses at the end of this time. The zigzag nature of the graphs is due to the slightly decreased effectiveness of a retreating stimulus, although it still accompanies an increased M.r.f.

FIGURE 7

This demonstrates the effect on habituation of maintaining the same stimulus approach velocity while altering the stimulus presentation rate,on the responses recorded from the BI Anterior levator muscle. The kymograph was set to produce a constant and fast velocity to the stimulus. The travel of the disc was mechanically stopped at the end of each approach and retreat stroke. The stops could be manually released at set times which allowed the alteration of stimulus presentation rate.

The kymograph speed was set, such that the travelling stimulus produced an angular velocity of 43.7°/s and translational velocity of 16.4 cm/s. Three stimulus presentation rates were used. These were:

1. 1 stimulus every 5 s; represented by circles.
2. 1 stimulus every 15 s; represented by squares.
3. 1 stimulus every 30 s; represented by triangles.

Open symbols represent responses to retreating stimuli, closed symbols represent responses to approaching stimuli. Five crabs were tested in each case. The ordinate and abscissa are as before. The points plotted on the graph are mean values from pooled data.

The zigzag nature of the lines is due to a slight decrease in effectiveness of a retreating stimulus. Comparison of this figure with figure 4A, demonstrates the effect on the threat response of maintaining the same stimulus approach velocity while altering the stimulus presentation rate. Unlike the results shown in Fig. 4A, separating these two stimulus parameters increases the time before habituation is complete and also accompanies maintained higher M.r.f. values.

It is interesting to note that the faster and slowest rates of stimulation accompany higher M.r.f. values than the intermediate presentation rate.

CHAPTER 9 FIGURE 7

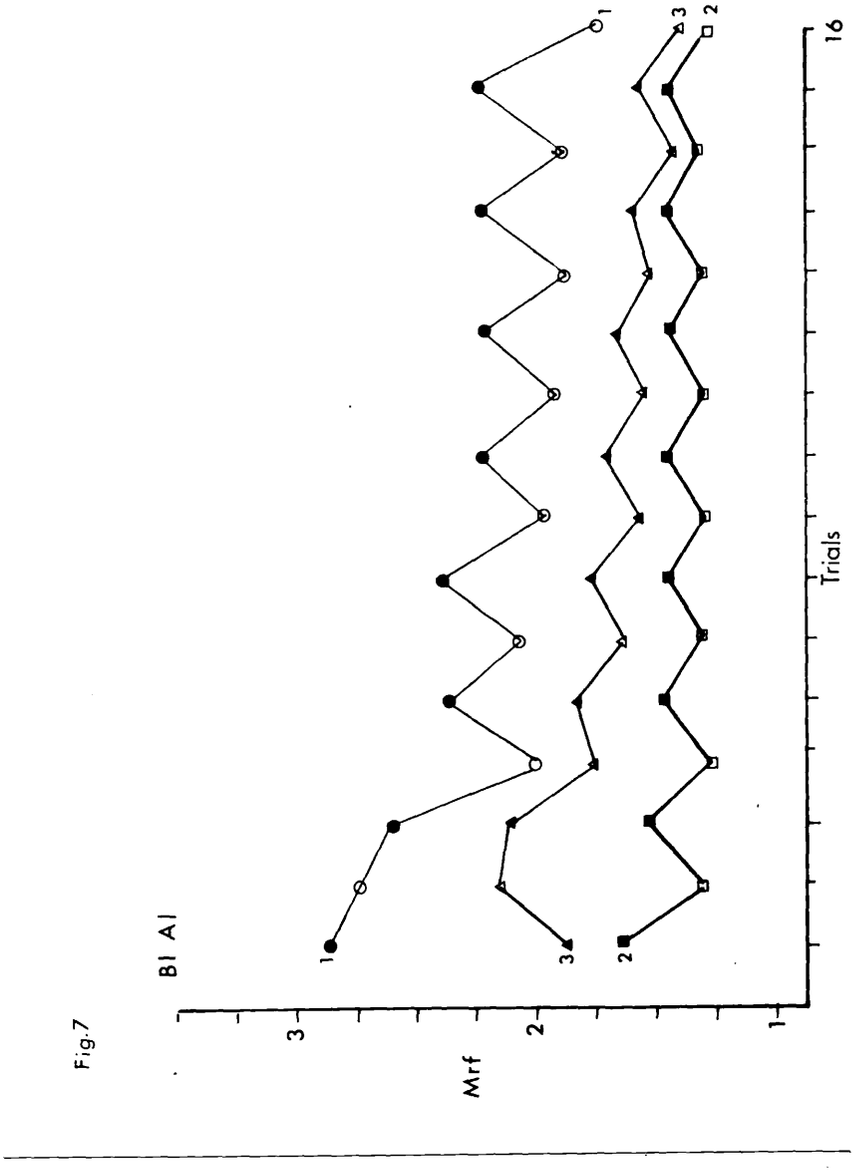


Fig.7

FIGURE 8

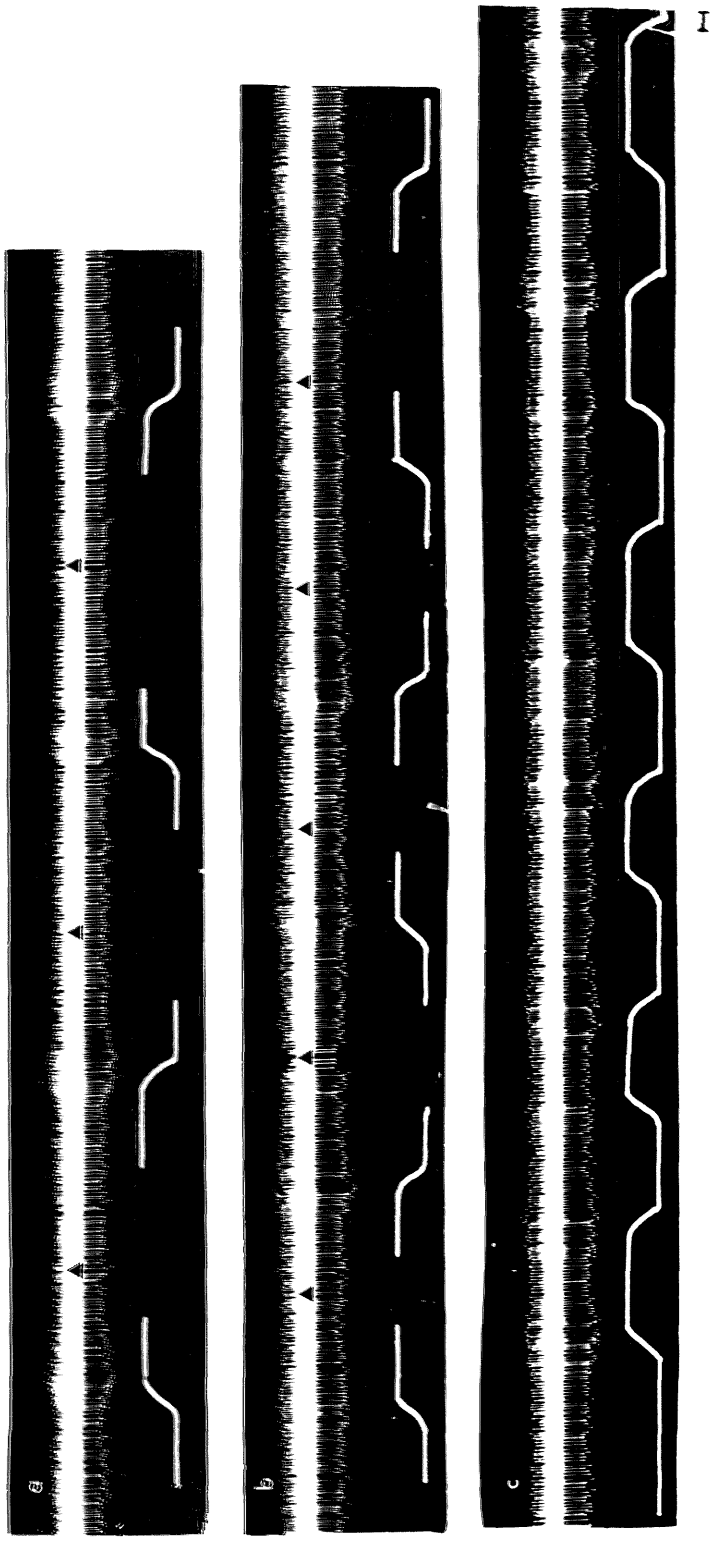
THE INFLUENCE ON MUSCLE RESPONSES OF MAINTAINING THE SAME STIMULUS VELOCITY WHILE ALTERING STIMULUS PRESENTATION RATE

Traces a to c are sections of recordings made from the Anterior levator of one crab which was tested at three stimulus presentation rates. Between each trial the crab was allowed to rest for at least 5 min. The tape recorder was stopped between each stimulus at the slower rates of presentation indicated by the arrows on the EMG's. The lines below the EMG's represent the disc movement. The time scale represents 1 s.

The kymograph speed was set, such that the travelling stimulus produced an angular velocity of 43.7°/s, and translational velocity of 16.4 cm/s. The crab was stimulated at a presentation rate of 1 stimulus every 30 s in trace a, 1 stimulus every 15 s in trace b, and 1 stimulus every 5 s in trace c.

The traces demonstrate that at the fastest rate of stimulus presentation, trace c, the increase in frequency of muscle activity is greater than for the other two rates. Comparison of these traces with figure 6 a and b, clearly demonstrates the effect on the muscle response of maintaining the same high velocity while varying the stimulation rate. Not only is the frequency of muscle response higher, but habituation takes longer to be completed.

CHAPTER 9 FIGURE 8



The results appear to indicate that there are two optimum presentation rates for releasing, and maintaining, the threat response. At the faster stimulus presentation rates, 1 every 5 s, the M.r.f. was high and it took longer for habituation to be complete. It may be expected that at the slowest rate, 1 stimulus every 30 s, the M.r.f. would be least. However this was not the case and instead this slowest presentation rate accompanied a higher M.r.f. than the intermediate presentation rate of 1 every 15 s. This suggests that the crabs may be able to discriminate between fast, slow and intermediate rates of stimulus presentation rates. The fastest and slowest rates appear to be more effective in releasing increased threat responses.

Figure 8 a to c, shows EMG's recorded from the A1 muscle of one crab which was stimulated at presentation rates of 1 stimulus every 30, 15 and 5 s respectively. Between each trial, the crab was allowed to recover for at least 5 min. The EMG's demonstrate the effect shown on figure 7A, that is, the increased frequency of muscle response activity when stimulus presentation rates are fastest.

5. Dishabituation

It has been shown that higher M.r.f. values and lower habituation rates accompany stimuli which are presented at fast rates and at fast velocities. A series of experiments was designed to test the effect of altering stimulus effectiveness on a habituated crab. These experiments represent the effect of an attacking predator altering its rate of attack, velocity of approach and actually hitting the crab.

In the first series of experiments,the kymograph drum was allowed to rotate freely to produce a slow presentation rate and slow velocity. This was subsequently altered to produce a faster rate and velocity. A representative result from one crab is shown in figure 9A. As soon as the presentation rate and velocity were increased, indicated by the horizontal dashed line, the M.r.f. was raised almost threefold. Following this sharp increase, the frequency rapidly decayed as the response rehabituated. The dotted horizontal line represents the trend of habituation which would occur without the increase in rate of presentation and was obtained previously from the same crab without manipulating the stimulus rate.

In a second series of experiments, the effect of maintaining the same velocity while only altering the rate of stimulus presentation rate, was examined. This was achieved by halting the disc travel as before using the mechanical stops. A representative result is shown on figure 9B. The drum was set to produce an angular velocity of 43.7^{o}/s.

FIGURE 9

THE EFFECT OF DISHABITUATION ON THE THREAT RESPONSE

All the graphs were obtained from recordings taken from the BI Anterior levator muscle. The ordinate and abscissa are as before.

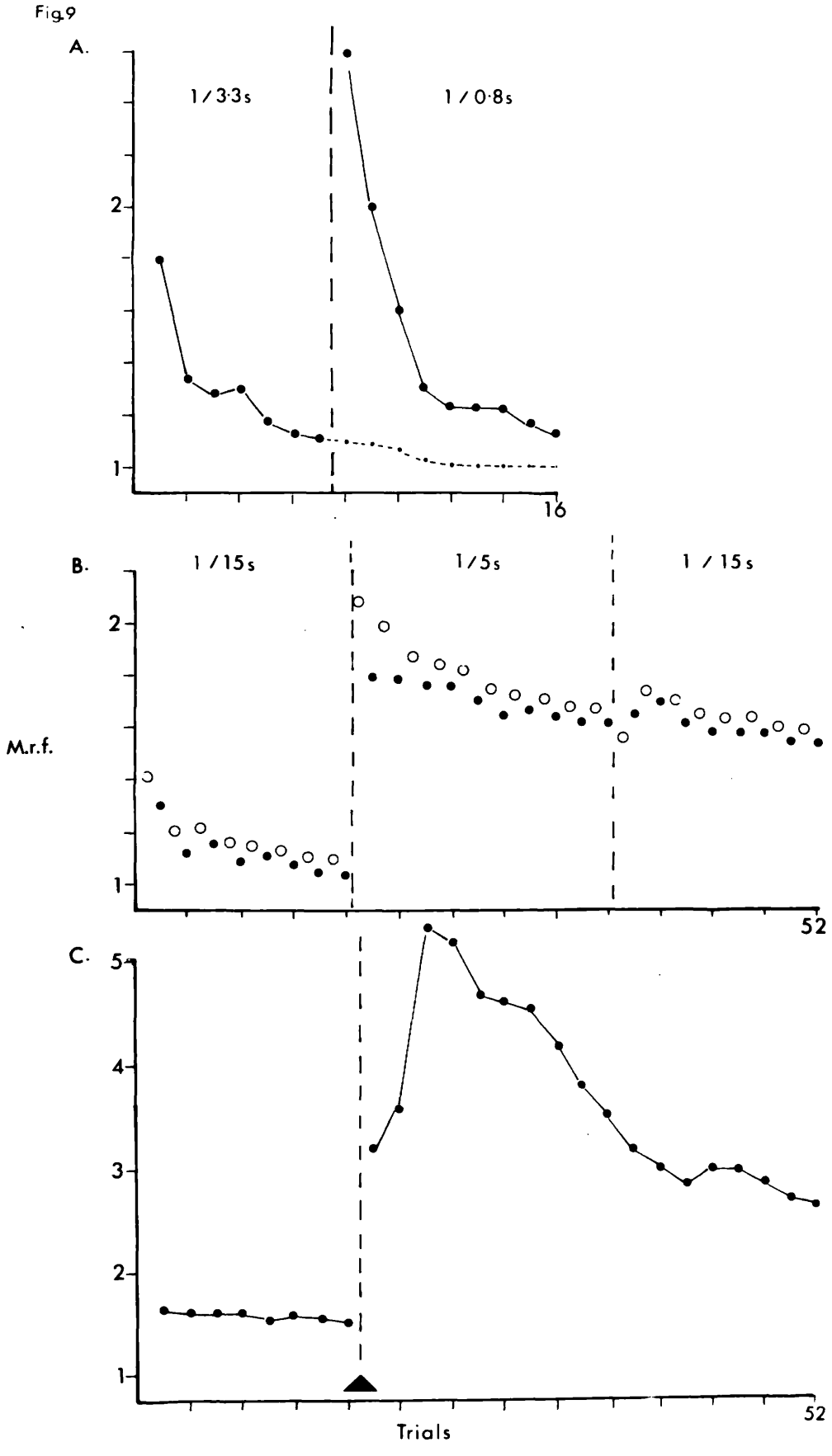
A. The drum was allowed to rotate freely to produce 1 complete stimulus every 3.3 s; that is, approach and retreat strokes. After seven presentations, the rate was increased to 1 every 0.8 s, indicated by the horizontal line. This greatly increased the M.r.f. Subsequent presentations of the stimulus accompanied a decrease in frequency back to original levels of activity, as the threat responses re-habituated. The dotted line indicates the rate of habituation which occurred previously in the same crab without manipulating the presentation rate.

B. The kymograph was set to produce a translational velocity of 16.4 cm/s. By using mechanical stops as before, the presentation rate could be altered. The closed circles represent responses to retreating stimuli and open circles represent responses to approaching stimuli.

After 16 presentations at a rate of 1 stimulus every 15 s, the presentation rate was increased to 1 stimulus every 5 s, indicated by the first dotted line. The M.r.f. increased and was maintained at a higher level for the following 20 stimuli. After this the presentation rate was slowed back to 1 every 15 s, indicated by the second dotted line. The increased level of M.r.f. was maintained for several minutes.

C. The crab was mechanically prodded at the indicated point after 16 presentations of the stimulus at a rate of 1 stimulus every 5 s. The dishabituating stimulus accompanied a five-fold increase in M.r.f. This level fell only gradually and was still twice as high as the original level, 3 min after dishabituation even though the stimulus presentation rate was maintained at 1 every 5 s. Only the responses to retreating stimuli are shown for clarity.

CHAPTER 9 FIGURE 9



When the stimulus presentation rate was increased from 1 every 15 s to 1 every 5 s, the crab responded with an increased display which accompanied an increased M.r.f. This higher frequency was maintained for the remainder of stimulation at this increased rate. After 20 presentations, the stimulus rate was reduced back to 1 every 15 s. The increased M.r.f. continued for several more stimulus presentations and only gradually decayed back to the original level.

Dishabituation could also be achieved by mechanically prodding the crab. The effect of this dishabituating stimulus was greater than the previous two experiments, as shown on figure 9C; note the reduced scale of the ordinate. The M.r.f. increased to a level almost five times as high as before the dishabituation, even though the rate of stimulus presentation was maintained at 1 every 5 s throughout the period of recording.

These experiments indicate that dishabituation of the threat response greatly increases the frequency of excitation to the muscle and can be caused by altering stimulus effectiveness; that is by increasing stimulus velocity and rate. The more effective the dishabituating stimulus, the longer the time required for subsequent rehabituation. Thus mechanically prodding the crab is a more effective stimulus than increasing the presentation rate while maintaining a high velocity. This, in turn, appears to be more effective than increasing both presentation rate and velocity together.

6. The effect of stimulus velocity on the threat response

A large predator will produce a higher angular velocity when it approaches the crab quickly, than when it approaches slowly. To examine the effect on the threat response of different sized predators attacking the crab, so producing different angular velocities, the data from the first set of experiments (section 2), where both parameters of velocity and presentation rate were variable, was subjected to further analysis. The M.r.f. and latency between the movement of the first stimulus presentation and peak M.r.f., was plotted against stimulus velocity. The four speeds of the kymograph that were used, produced angular velocities from 9 to 60^{o}/s and equivalent translational velocities of 3 to 22 cm/s. The results are shown on figure 10.

These results indicate that as the angular and translational velocities increase, the M.r.f. increases and the latency between the beginning of stimulation and peak impulse frequencies, shorten. Thus the highest M.r.f. and shortest response latencies would accompany a large object rapidly approaching the crab.

FIGURE 10

THE INFLUENCE OF ANGULAR AND TRANSLATIONAL VELOCITIES

The data from the responses of the Anterior levator muscle in figure 4A, was subjected to further analysis. The M.r.f. to the first presentation of the stimulus was plotted against the different angular, and consequent translational, velocities. The latency between the beginning of the first stimulus and the first M.r.f. peak was also measured and plotted against velocity.

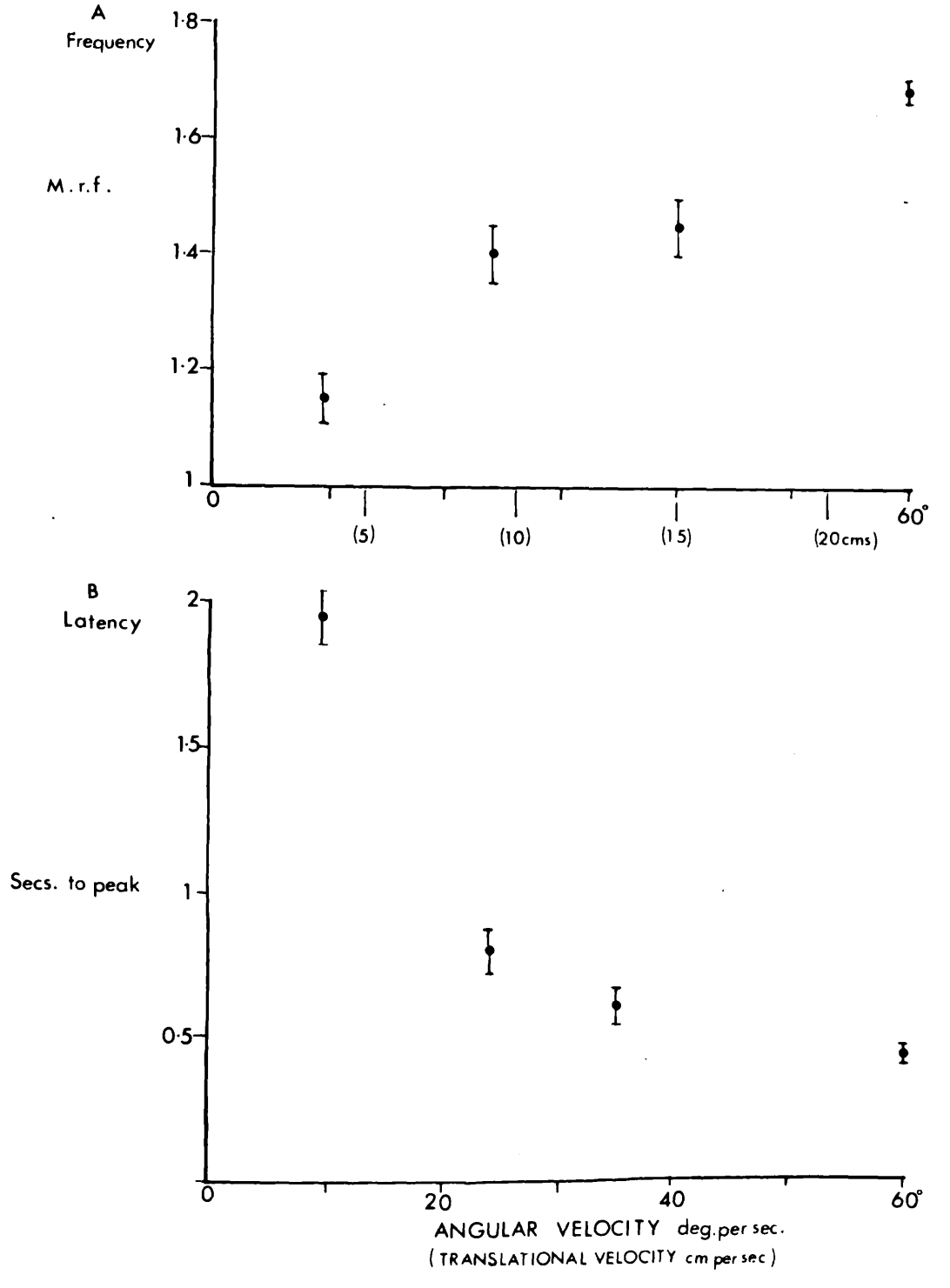
The two graphs indicate the mean and standard errors calculated for the responses to four speeds of the kymograph. The four speeds produced angular velocities of 60, 40, 23 and 9^{o}/s. The translational velocity values are indicated in the brackets on the abscissa.

A illustrates the influence of stimulus velocity on the M.r.f. As the velocity increases, the initial M.r.f. increases.

B illustrates the influence of stimulus velocity on the latency between the movement of the first stimulus and the first M.r.f. peak. As the velocity is increased, the latency is decreased. There are not enough points to conclude whether this is a straight line or curve relationship. However it is evident that at the faster velocities the latency was four times as short as that for the slowest velocity. These results indicate that the most effective stimulus, reflected by high M.r.f. values and short latencies, will be produced by the rapid approach of a large object, since the larger the object, the greater the angular velocity.

CHAPTER 9 FIGURE 10

Fig.10



Although positive conclusions cannot be made concerning the optimum effectiveness of angular velocity, the trend is demonstrated in these results. A rapidly approaching or retreating visual stimulus accompanies the greatest M.r.f. values and shortest response latencies, and so will probably release the most extreme threat displays from a crab.

7. Release of pre-strike behaviour

The above experiments indicated that a large fast moving object is the most effective threatening stimulus. To determine whether the threat display behaviour can be switched to a strike behaviour, maximal stimulation was produced by placing a very large disc on the end of the piston. This was left in front of the crab for a few minutes to allow the crab to fixate on the disc, and was then rapidly withdrawn by manually moving the drum. The resultant translational velocity was 70 cm/s. One side of the cowl around the apparatus was removed to allow observation of the response. The most alert crabs responded with a promotory-depressory twitch of the chelipeds rather than an extending-levatory twitch.

In order to confirm that this was a pre-strike twitch rather than a passive movement of the chelipeds, recordings were made from the coxal and BI strike and BI anti-strike muscles. Representative results are shown on figure 11. It can be seen that these muscles are activated when the stimulus is rapidly withdrawn.

Several observations support the suggestion that these are pre-strike twitches and not movements from a high to lower intensity of threat displays. For example, one observation is that the Al did not respond with the momentary reduction in activity after the phasic burst which is characteristic of a threat response (Fig. 2). If the cheliped movements were due to decreased threat intensities, the Al would be inactivated as shown in the recordings from the previous chapter (Chapter 8, Fig. 5). If the movements are true pre-strike twitches, there will be no inactivation, instead tonic activity will continue, to counter any strike muscle tension development as described in Chapters 5 and 6.

A second observation is in the activity of the strike muscles. This is clearly different from the responses recorded during movements from high to low intensities of threat display (Chapter 8, Fig. 5). A movement producing a decreased display involves a longer period of anti-threat muscle activation and not just the generation of a few large spikes which is characteristic of pre-strike activity (Chapter 5).

FIGURE 11

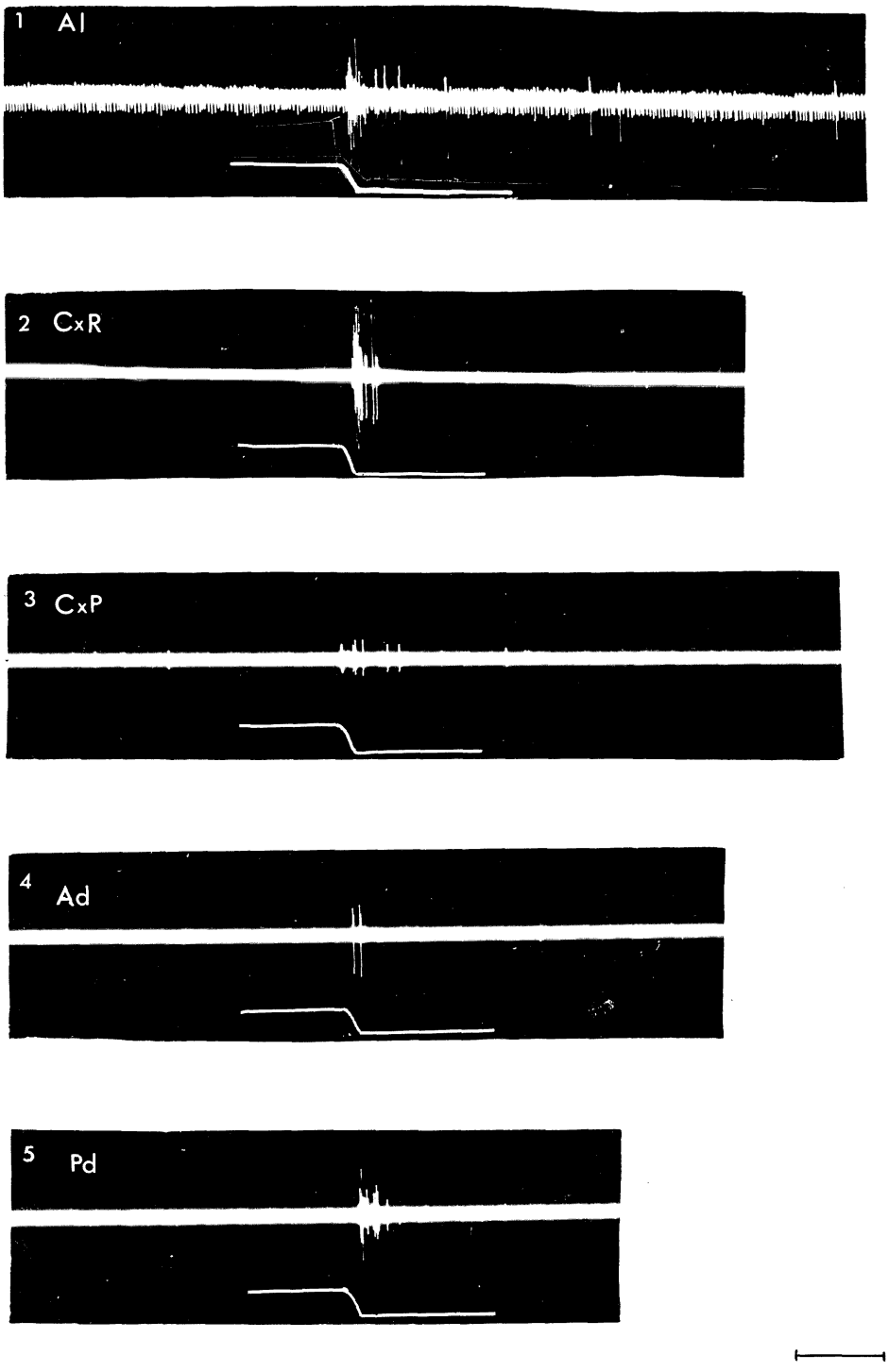
THE RELEASE OF PRE-STRIKE BURSTS OF MUSCLE ACTIVITY

When the most effective stimulus, that is a large, fast moving disc, was presented to alert crabs, the crabs did not respond with an increased threat display but with a pre-strike twitch. This was clearly distinct visually; the pre-strike response was due to promotion and depression of the chelipeds rather than an upward extending twitch produced during increased threat displays.

The traces illustrate the muscle activity recorded from the five main coxal and BI muscles. Presentation of the stimulus corresponded to short bursts of activity in the strike muscles, the coxa promotor and BI Anterior and Posterior depressors, together with increased frequency in the anti-strike Anterior levator muscle and a burst of activity in the coxa remotor muscle. All these phasic bursts correspond to the brief pre-strike activity which precedes the main component of strike muscle tension development which occurs before a fast strike is performed.

The time scale represents 1 s.

CHAPTER 9 FIGURE 11



A third observation is in the timing of muscle activity . Results from the previous chapter showed that the threat and anti-threat muscle pairs are activated in opposition to each other without any overlap (Chapter 8, Fig. 5). In this present experiment the onset of muscle activity was almost the same in all the muscles, between 50 to 75 ms after the beginning of stimulation. This is the situation seen in pre-strike activity when all the muscles are active together allowing isometric tension development in the strike muscles (Chapter 6, Fig. 2).

Therefore it can be concluded that the most effective stimulus for releasing threat responses, that is large, rapidly moving objects, can cause the sudden twitch of behaviour from a threat display to a pre-strike pattern. However, in no case was a complete strike behaviour released. Presumably there are other stimulus parameters necessary to trigger the full strike behaviour which were not fulfilled in this experiment.

DISCUSSION

The experiments have demonstrated that the threat display of Carcinus is released by the movement of targets producing increasing or decreasing visual angles. Threat responses are recorded from all the threat muscles of the chelipeds when controlled stimuli were presented and are comparable in pattern of activity to recordings made in the previous chapter when stimulation was less controlled. Muscle responses accompanying controlled stimulation are more phasic in nature than muscle responses which accompany the more uncontrolled stimulation of a moving hand.

Manipulation of the stimulus parameters of presentation rate and velocity suggested several indications of the importance of these parameters in releasing the threat responses. For example, when the presentation rate and stimulus velocities are low, few stimuli are needed to cause habituation (Fig. 4A). However habituation takes longer to be completed at these low rates and velocities, than when stimulation rates and velocities are high (Fig. 4B). This is in accord with typical observations on habituation (Hinde, 1970). Animals tend to ignore fast repeated stimuli more quickly than slow repeated stimuli. In the first series of experiments (section 2), the stimulus parameters of presentation rate and velocity were altered together. When these were separated in the second series of experiments (section 4), it was apparent that the rate of habituation alters from that observed in the first series. When the velocity is maintained at a high level, not only is more time required before habituation is completed at any presentation rate, but M.r.f. values are greater at the fastest rates of stimulation (Fig. 7).

The explanation of this atypical feature of habituation, that is greater motor responses accompanying high rates of stimulation, may lie in the particular behaviour which is being studied. When a crab is exposed on the beach it is vulnerable to attack by sea birds, for instance. An attacking bird may break open the carapace by repeated strong pecking movements. The results obtained in this chapter have suggested that as soon as the crab detected an approaching bird it would respond with a threat display. As the bird began to approach more rapidly in order to attack the crab, the crab should increase its display, because it would respond to the increase in angular velocity of the approaching predator. The increased display and apparent increase in visual size of the crab, may cause the predator to retreat slightly, but if hungry enough, it would re-continue its advance. If the crab rapidly habituated to constant approaching and retreating stimuli, the bird would eventually be able to reach its prey. However, the results of this chapter suggest that the behaviour of the crab is not determined in this way. As shown on figure 7, constant approach and retreat of fast stimuli do not cause habituation, instead the M.r.f. is maintained at a high level and each approaching stimulus accompanies an addition to this level. Thus each approach of the bird would release an increased threat display.

Obviously there are strategic methods by which the bird could reach its prey. It could move exceptionally slowly towards the crab, releasing only Shallow or Half threat displays. Alternatively the predator could be very small, releasing low intensities of display and accompanying low M.r.f. values due to the decreased angular velocity of the stimulus. Neither of these are likely to occur in the natural situation.

Maintaining a high and constant translational and angular velocity, demonstrated another interesting facet of the behaviour. The three rates of stimulus presentation used were representative of fast, slow and intermediate rates of predator approach. It may be expected that since the fastest rate accompanies the greatest M.r.f., successively slower rates would accompany less muscle activity. This did not appear to be the case. Of all five crabs tested, the responses to the intermediate rate were slightly below those shown to presentations of the slowest rate. It is apparent that the crabs can distinguish between stimulus repetition rate.

Again, this may be important to the behaviour. A predator may become less interested in the crab if, with each attacking approach, the crab responds with a threat display. The predator may begin to tire and approach less often. It is advantageous for the crab to respond equally well to this new slower rate. The results obtained in the experiments show that

the crab should respond almost as well to slow rates of approach as to fast rates, and so will continue to display.

The experiments concerning dishabituation may also be relevant in the threat behaviour. A situation may occur in nature which is the reverse of the above. A tired predator may suddenly have a few final attempts to catch the crab. It may therefore speed up its rate of attack. Figure 9 indicates that any sudden increase in the approach rate or velocity would have the effect of dishabituating the crab and increase the M.r.f., so enhancing the threat display. This should further deter the predator from attacking the crab. This can be caused by a change in rate of approach (Fig. 9B), a change in angular velocities (Fig. 9A) or both (Fig. 9A). Furthermore, if the predator actually struck the crab, the frequency of excitation to the muscle should increase even more (Fig. 9C).

The experiments concerning alterations of visual angle demonstrated another stimulus parameter which influences the threat response. Increasing angular velocities accompanies an increase in M.r.f. A crab will respond with the extreme threat displays to large and rapidly approaching objects. When the approach and angular velocities are low, the latency between the beginning of stimulus movement and peak M.r.f., is long (Fig. 10b). As the approach velocity is raised, these latencies decrease; there is less than 500 ms between the beginning of stimulus movement and the maximum M.r.f. when the stimulus is presented at an angular velocity of 60^{o}/s (Fig. 11b).

This may also be an important facet of the threat display behaviour. It is likely that a large predator will be capable of more damage to the crab, than a small predator. If the large predator approaches quickly, not only will the crab respond rapidly, but the M.r.f. will be high and so the intensity of the display will be more extreme. There were not enough experiments performed to examine whether a small, rapidly approaching predator would also release the more extreme threat displays.

In no instance was a fast strike evoked. However when the most effective stimuli were presented, pre-strike twitches were observed in alert crabs. This demonstrates the sudden switch from a threat display behaviour to a strike behaviour, which was also seen in the analysis of strike EMG's (Chapter 5). There was apparently not enough stimulation to generate a complete fast strike behaviour. Presumably the stimulus parameters which release the strike were not fulfilled in these experiments.

These results have demonstrated several stimulus parameters which affect the release and intensity of the threat displays. It can be concluded that the behaviour is released by visual input. The released

displays are influenced by the approach and angular velocities of the stimulus and the rate of stimulus presentation. Increasing these parameters increases the effectiveness of the stimulus, and consequently increases the intensity of the M.r.f. and adopted threat display posture.

In the following chapter, recordings were made from circumoesophageal connective nerves to determine whether distinct patterns of nervous activity also accompanies the presentation of threatening stimuli, and possibly the means by which stimulus parameters are encoded. Subsequently simultaneous recordings were made from the connectives and threat muscles to examine their patterns of activity during the threat and strike behaviours.

CHAPTER 10

THREAT RESPONSES RECORDED FROM THE CIRCUMOESOPHAGEAL CONNECTIVE NERVES

INTRODUCTION

The crayfish responds to approaching objects with a defence reflex in which the chelipeds are raised and directed towards the stimulus. Examination of EMG's recorded from the cheliped levatory muscles, indicated that the response is enhanced at the muscular level by fast rates of stimulus presentation (Glantz, 1974 a). Glantz suggested that this enhancement was due to a facilitation of the neural circuit which controls the reflex. Recordings were also made from neural elements in the optic nerve to determine their involvement in the reflex control pathway (Glantz, 1974 b) Examination of sustaining units, dimming units and motion detector units, under stimulus conditions associated with the defence reflex, revealed that only the motion detectors exhibited responses which parallel the muscle activity which accompanies the reflex. For example, when stimuli were presented at low rates, 2 to 4 stimuli per minute,the recorded motion detector activity exhibited a time course of habituation and spontaneous recovery similar to that observed behaviourally. Simultaneous recordings from motion detectors and cheliped levatory muscles, revealed a significant number of positive correlations between their activities.

In a third study of the reflex, it was found that the behaviour is evoked after a criterion change in stimulus visual angle (Glantz, 1974 c). This suggested that the initiation of the controlling programme may be due to either the change in visual angle, or angular velocity of the approaching stimulus. It was found that the probability that a stimulus will evoke a defence reflex increased with the velocity of target approach. Motion detector activity exhibited strong responses to approaching targets and both mean discharge rate and number of interspike intervals per stimulus increased linearly with the angular velocity of the stimulus. From these results, Glantz proposed that a fixed number of motion detector impulses or interspike intervals, may provide the visual trigger for the initiation of the defence reflex.

Fraser examined the properties of several large interneurones in the circumoesophageal connective of Carcinus maenas (Fraser, 1974 a, b). Five giant fibres were identified, termed cells 1 to 5 (Fraser, 1974 a). Cells 1 and 3 responded phasically to movement in the visual field and to touch over the whole carapace and bases of the walking legs. Cell 2 responded to the same stimuli but with a reduced discharge rate. Cell 4 had similar responses to cells 1 and 3 but showed a sustained tonic discharge to prolonged mechanical stimulation, and this discharge outlasted the duration

of the stimulus.

Extracellular recordings were made from freely moving crabs. Although it was not possible to positively distinguish the activity of individual fibres, Fraser stated that the large units could be recognised by their characteristic discharge. No obvious correlation of activity between any of the fibres with behaviour, was observed. Agonistic rearing behaviour, for example, could be evoked without any conspicuous activity from these fibres. However the visual tracking of stimulating objects by the crab, did evoke giant fibre activity. Fraser concluded that the identified fibres do not control the basic rearing reflex, instead it is more likely that they are only part of a large group of neuronal elements necessary to initiate and maintain the complete behaviour.

A second study of the connectives was performed with particular emphasis on the statocyst fibres (Fraser, 1974 b). Five interneurones were identified in Carcinus which respond directly to rotation of the animal. Each appeared to be activated by the direction of fluid flow in one statocyst canal. These fibres showed characteristics which could activate and control, positional and locomotory reflexes. For example, one fibre, termed cell A, may control the stability of the back legs. In the rearing behaviour of the crab, input to this cell is provided by upward movement of the leg joints and head up rotation of the body. Fraser suggested that activity from this fibre could control the activity of the hind legs during this behaviour. Swimming movements can be produced by providing input to the eyes, legs and statocysts. This excited two other fibres, C and D. Fraser suggested that it is likely that activity from these fibres controls the initiation of the swimming reflex. He found that stimulation of cell C produced the full swimming reflex. Further studies of the activity of these five statocyst fibres suggested that cells A, C and D provide integrated information on leg and body positions during walking, and cells B and E could control steering errors.

The thoracic nerve cord of Orthoptera contains a number of large and conspicuous visual units. These fall into three groups (Rowell, 1971). The first consists of at least one pair, that is one axon per connective, of units unaffected by input to the compound eyes but producing "off" responses when stimuli cross the ocellar field. The second group of visual neurones contains a number of mixed units which have wholly visual or mixed visual and mechanoreceptive inputs. The third group contains two pairs of units, the descending contralateral movement detectors and the descending ipsilateral movement detectors. These two groups are collectively termed descending movement detectors, DMD's. Although several investigations have been made concerning the properties of DMD's,there is little evidence as to

their actual function in the animals (review by Rowell, 1971). It is unlikely that DMD's participate in the optomotor response of insects, since they are insensitive to movement across the whole visual field, convey no reliable directional information, are phasic and rapidly habituate (Rowell, 1971).

Burrows and Rowell (1973) recorded from the thoracic motorneurones involved in the back leg kick of the locust, and showed excitatory post-synaptic potentials, EPSP's, which were directly correlated with spike activity of the DMD units. However the EPSP's were not sufficient to cause spike activity in the motorneurones and were not visible as overt behaviour.

It is possible that although the DMD's do not directly elicit escape behaviour, they may have a "warning" function (Rowell, 1971). This is made likely since they are large in size, have thoracic terminations and are sensitive to small moving objects which suddenly appear in the visual field. Rowell (1971) suggested that DMD activity may prime the thoracic ganglion for subsequent activity, such as escape behaviour, though not itself elicit any direct motor response.

The previous chapter demonstrated that the threat display behaviour of Carcinus is released by the approach of an object such as a disc. The behaviour is influenced by manipulating stimulus parameters. An enhanced threat response is evoked by the most effective stimuli, such as fast angular and translational velocities, and fast stimulus presentation rates.

In this present chapter, recordings are made from the circumoesophageal connectives of freely moving crabs, to determine the characteristic features of nervous activity which accompanies threat behaviours. Nervous and muscle activity was then compared to examine whether there is any obvious correlation between the two, when threat and other agonistic behaviours are displayed.

MATERIALS AND METHODS

Small, lightweight plastic screws were stuck onto the dorsal carapace of large crabs as before. 50μm Trimel coated wire electrodes were soldered into one end of the miniature plug and socket connectors. The other end of the plug was connected to a pre-amplifier and oscilloscope.

The crabs were placed ventral side up, in a Perspex clamp, for dissection. The clamp was placed in a bowl of cold sea water which covered the animal. The third maxillipeds were removed by an incision across their bases. The oesophagus was released from its attachment around the rim of the mouth. It was not cut further but was allowed to retract by virtue of its elasticity. Subsequent removal of other mouth parts displayed the two large connective trunks which run from the brain to the thoracic gang-

lion. The connective sheath surrounding the trunks was carefully removed so that other nerves branching from the connective, were not destroyed.

This technique could be performed in a short time and, if successful, did not appear to disturb the crab's behaviour. In most instances the operation was only performed on one connective, and in these crabs only one side of the mouth was exposed. The electrodes could be inserted into the connectives with the aid of a binocular microscope. They were bared at the tip and cut back so that only 1 or 2 μm of unshielded wire was exposed. The stiffness of the wire was sufficient to allow penetration of the connectives without tearing or splitting them. The remainder of the electrode, to the connecting plug, was folded over the top of the carapace between the eyes so that it could not be easily reached by the chelipeds.

After the operation the crabs were replaced in the aquarium for recovery. They were viable for several days and still performed normal behaviour patterns. Connective tissue was eventually laid around the operation scar, further reducing the effects of the dissection. The nerve cells which were penetrated by the electrodes, did not always survive as long as the crab. Thus the wires were generally removed after the experiments had ended. Subsequent replacement was quicker than initially, as it was easier to find the semi-exposed connectives.

The experimental crabs were placed in glass tanks which had three black sides as before. A light was placed behind and above the tank, directed forwards. The tank and light was situated in a closed cardboard box which had a hinged front for access. The inside front of the box, that is the side facing the crab, was coloured white. All the other surfaces were black. A longitudinal slit, measuring 1 cm by 14 cm, was cut into the centre of the white card. The tank was arranged such that the slit was in front of the crab's field of vision. The light was directed towards this slit (Fig. 1).

Four different sizes of black arrows were painted onto separate strips of white kymograph paper (Fig. 2a). The paper was wrapped around a kymograph drum which was positioned in front of the slit in the white card. Thus when the drum was rotated, the crab viewed a stimulus which represented an increasing visual angle (Fig. 2). This was equivalent to an approaching stimulus. Alteration of the kymograph speed produced different velocities of stimulation to the viewing crab, by increasing or decreasing the time that it viewed the arrow as it moved across its visual field. Stimulus markers were attached to the kymograph spindle as described in the previous experiment. The crabs could also be stimulated manually by the movement of a hand passing in front of their field of vision, as before.

FIGURE 1

A crab which had 50 μm silver wire electrodes implanted into the circumoesophageal connective nerves, was placed in a tank of cold sea water. This was placed inside a black cardboard box. One inner surface of the box was painted white. This was the side facing the crab. A light was positioned behind and above the experimental tank, directed towards the white face. A narrow longitudinal slit was cut into the white card and measured 1 cm by 14 cm.

A kymograph drum was positioned in front of the slit. Four large black arrows were painted onto pieces of white paper which could be wrapped around the drum. As the drum revolved, the crab viewed an increasing visual angle stimulus as the arrow moved across its field of vision. This represented a stimulus of an approaching target and is shown in Figure 2b.

Positional markers for the kymograph were arranged as in the previous experiments using small metal markers on the kymograph spindle, or a photodiode below the kymograph drum.

CHAPTER 10 FIGURE 1

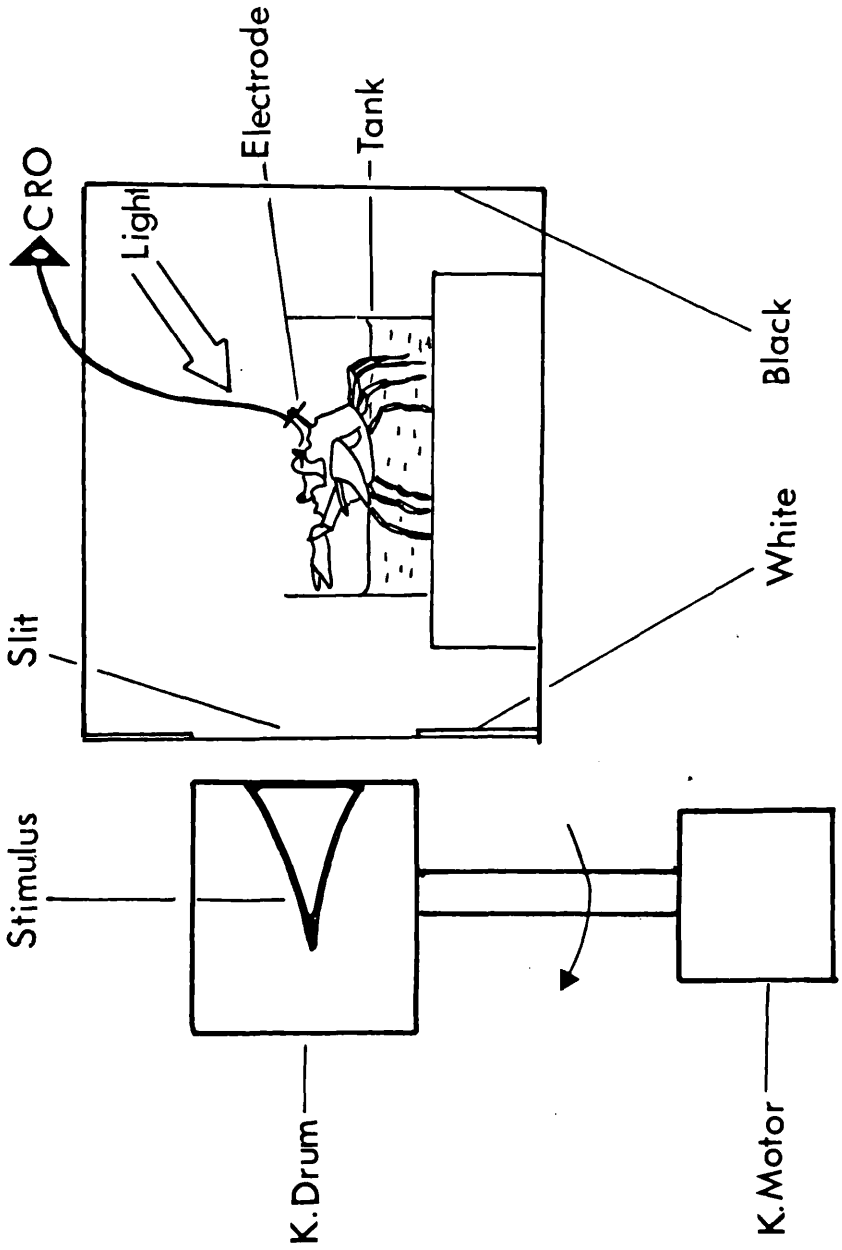


Fig.1

FIGURE 2

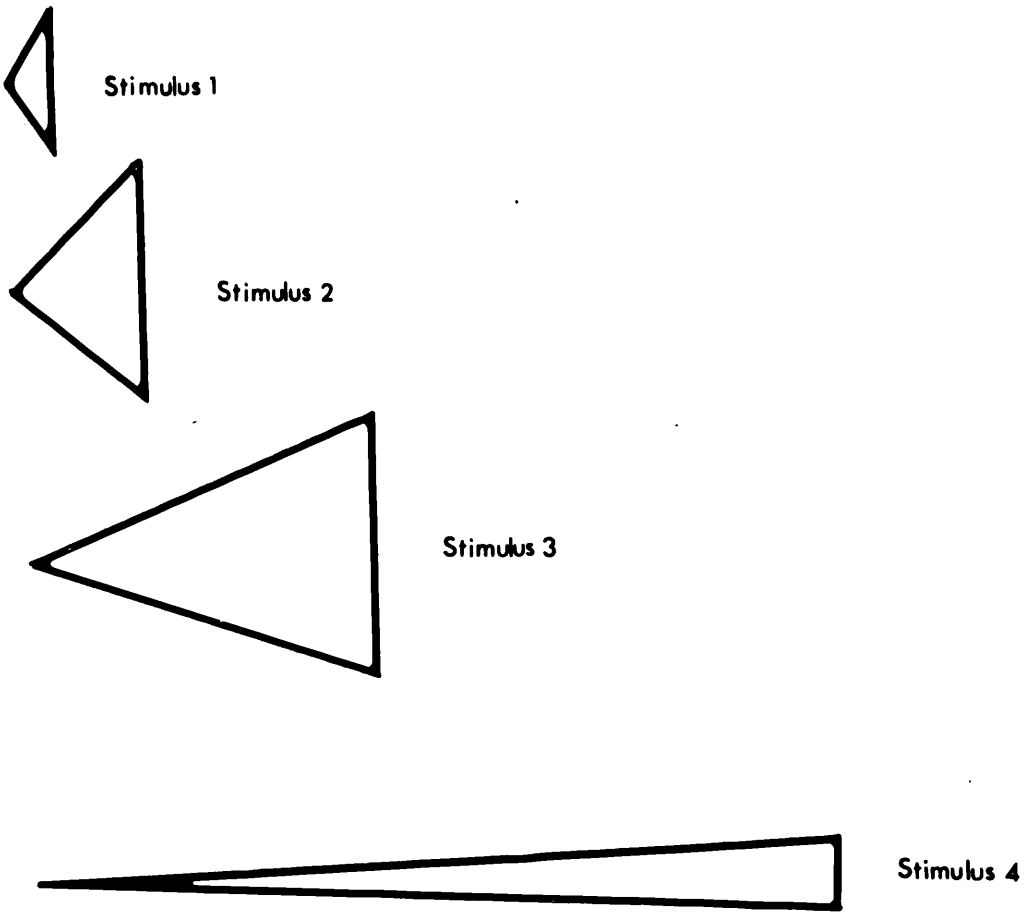
a. This illustrates the representative shapes and sizes of the stimuli. At any speed of drum rotation, stimulus 1 presented the sharpest change in visual angle; stimulus 2 was less extreme, stimulus 3 was even longer and more tapered; stimulus 4 presented very little change in visual angle at any speed of drum rotation.

b. The kymograph drum was positioned, such that the crab viewed the movement of the arrows between the slit in the white card at the front of the box around the experimental tank. As the drum revolved the arrow gradually filled more of the crab's visual field. This would give the impression of an approaching object. By varying the speed of drum rotation, and size of the stimulus, a range of different angular velocities could be produced.

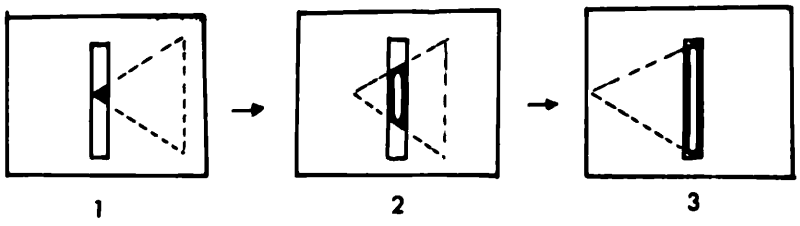
CHAPTER 10 FIGURE 2

Fig. 2

a



b



Activity recorded from the connectives when stimuli were presented to the crab, was stored on tape and filmed for analysis. Any activity which typically accompanied threatening stimuli is termed the connective threat response.

RESULTS

1. Connective activity which accompanies visual stimulation

Before the specific effects of any stimulus parameters can be examined, the responses from the connectives to gross visual stimulation must be assessed. The front of the enclosing box was removed and the crabs were manually stimulated in two ways. Firstly, the experimenter's hand was rapidly moved towards the crab, a form of stimulation which has been shown to be reliable although uncontrolled. Secondly, the experimenter's hand was slowly moved in a horizontal arc, 30 cm in front of the crab, from one side of its body to the other.

Results from three crabs are shown on figure 3. Traces 1a and b of this figure are from one crab as are traces 2a and b. Trace 3 demonstrates the recorded activity when the electrode penetrates only one fibre in the connective. Lines below the traces indicate the time of stimulation. In 1a, 2a and 3, a photodiode and light beam was arranged 25 cm in front of the tank. When the moving stimulus interrupted the beam, the photodiode registered on the oscilloscope.

The results demonstrate several features which were characteristic of the recorded "threat response" from the connective which accompanied the presentation of threatening stimuli to the crab. When the crab responds to fast moving stimuli (Fig. 3, traces 1a, 2a and 3), a brief burst of high frequency activity may be recorded from the connectives. The burst typically includes the generation of large spikes. These spikes are only present for 100 ms and occur at the beginning of the response burst. As shown in trace 3, if only one fibre which produces these large phasic spikes is penetrated, connective activity is silent after this burst. When activity from several different fibres is picked up by an electrode (Fig. 3, traces 1a and 2a), the recorded burst generally includes the presence of medium sized spikes, which only fire during the time of stimulation. When stimulation ceases, recorded activity in the connectives is typically maintained by fibres generating smaller spikes. These impulses gradually reduce in frequency until the next stimulus is presented to the crab. It is proposed that the fibres which generate the phasic, large spikes will be termed type A fibres; those which generate the phasic-tonic medium sized spikes, will be termed type B fibre; and those which generate the tonically active smaller sized spikes, will be termed type C fibres.

FIGURE 3

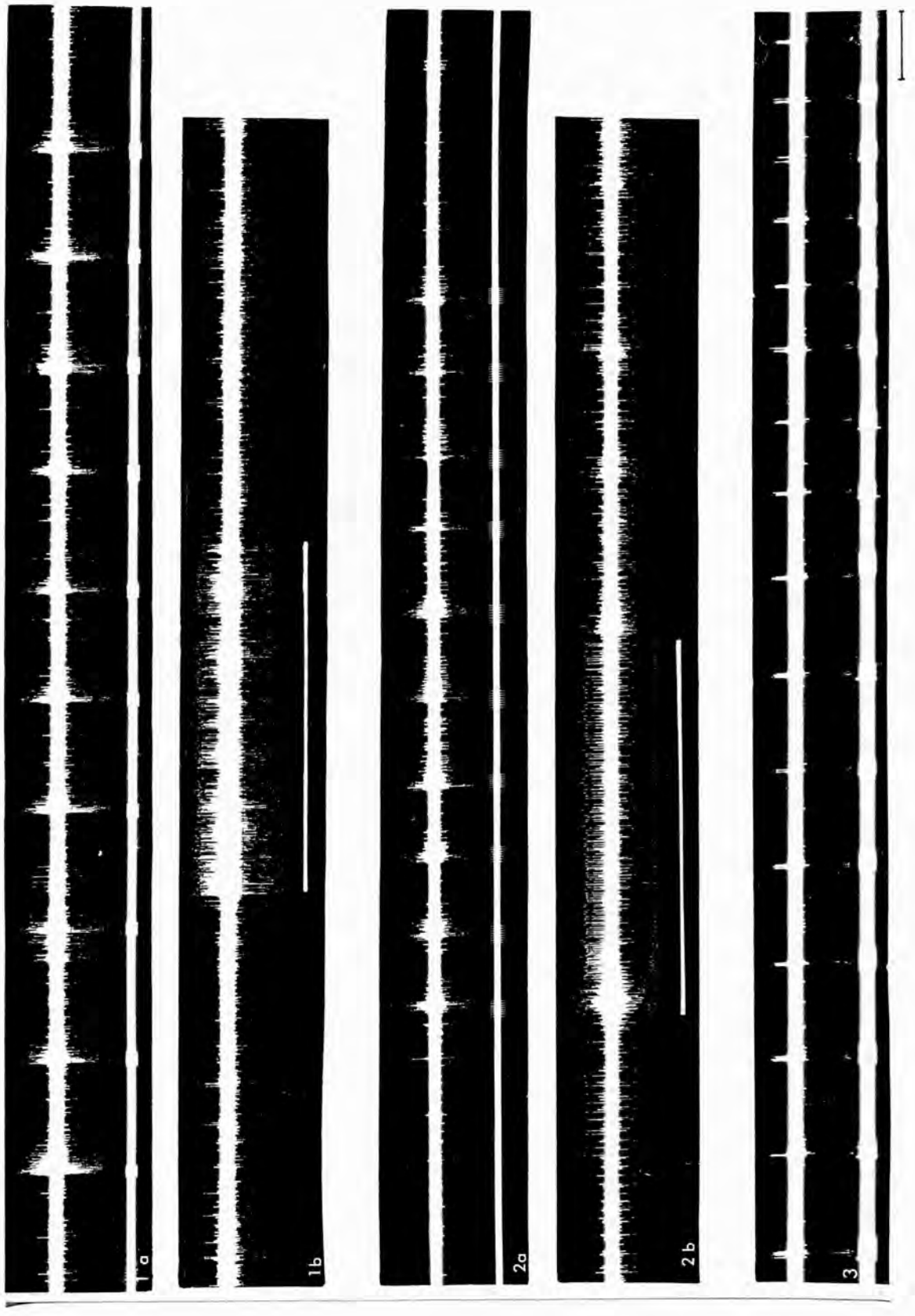
RESPONSES RECORDED FROM THE CONNECTIVE DURING THE PRESENTATION OF THREATENING STIMULI

Traces 1a and b are from the same crab, as are traces 2a and b. Activity from only one fibre was picked up in trace 3 and demonstrates the phasic element of the "threat response" which may be recorded from the connective. The time scale represents 1 s. The stimulus presented during recording of traces 1a, 2a and 3, was a fast moving hand which travelled from 30 cm to 20 cm, towards the crab. The stimulus marks below these traces register the point at which the stimulus interrupted a light beam shining onto a photodiode situated 25 cm in front of the crab.

The stimulus for traces 1b and 2b was a slow horizontal movement of a hand 30 cm in front of the crab, from one side of it's visual field to the other. The duration of stimulation is represented by the bar below the trace.

Each fast stimulus corresponds to the generation of a few large spikes, recorded from fibres in the connectives termed type A. This is particularly clear in trace 3. When activity from several fibres is picked up by the electrodes, stimulation is accompanied by the production of medium sized spikes, from fibres termed type B. These fibres are usually active during the time of stimulation. When stimulation stops, recorded activity is typically maintained by the generation of small tonic potentials which gradually decrease in frequency until stimulation recommences. These small tonically active impulses are produced by fibres termed type C fibres.

The onset of slower stimulation, traces 1b and 2b, correspond to an immediate generation of large phasic spikes. These reduce slightly in frequency as stimulation continues and the recorded activity is maintained by the excitation of type B fibres, generating the medium sized phasic-tonic impulses. When stimulation ceases, the activity of the type B fibres also ceases.


1a
1b
2a
2b
3

When stimulation is slower, this is usually accompanied by a maintained activity of the medium sized spiking fibres (Fig. 3, trace 1b and 2b). Some large spikes may also be produced and usually occur at the beginning of stimulus movement. Both fibre types discharge at highest frequencies during the beginning of stimulation. When stimulation stops, their activity ceases.

2. The influence of stimulus repetition rate on the connective threat response

Crabs were tested with all four stimuli at four speeds of the kymograph motor. This provided stimulus presentation rates of 1 every 800 ms, 1 every 1.2 s, 1 every 2 s and 1 every 3 s. Representative recordings from the connectives are shown in figures 4 and 5.

In figure 4, recordings were made from the same crab as Fig. 3, trace 3. The crab was presented with the second stimulus (Fig. 2a) at all four stimulus presentation rates. The recordings clearly demonstrate the phasic element of the threat response from the connectives which accompanies stimulation. The production of phasic, large spikes, produced by the A fibres, is typically confined to the duration of stimulus movement, indicated by the arrows below the traces and usually occurs at highest frequencies at the beginning of stimulus movement.

The traces in figure 4 demonstrate that although more spikes accompany the slower rates of stimulus presentation, their frequency is less than that associated with the faster presentation rates. The records also demonstrate the influence of stimulus presentation rate on the habituation of the connective activity. This is illustrated by the decrease in frequency of the spikes as the stimuli are repeated. It is apparent that habituation of the connective threat responses takes longer to achieve at the faster rates of stimulus presentation. In trace a, figure 4, large spikes still accompanied stimulation after 100 stimuli had been presented to the crab.

Figure 5 shows recordings made during stimulation at other rates of presentation. Traces 1a to c of this figure were recorded during stimulation with stimulus 1 (Fig. 2a) at rates of 1 every 800 ms (trace a), 1 every 1.2 s (trace b) and 1 every 2 s (trace c). As before they demonstrate the phasic element of the connective threat response. Trace 1a illustrates that when stimulus 1 is presented at fast rates, the recorded response rapidly habituates and, typically, no responses are recorded from the connective after four or five presentations of this stimulus at this fast rate. Comparison of trace 1b with 1c clearly show that the frequency of both the large and medium sized spike activity is higher when the

FIGURE 4

CONNECTIVE NERVE RESPONSES WHICH ACCOMPANY CONTROLLED STIMULATION: 1

These recordings were made from the same crab as figure 2.3. They are recorded responses made when stimulus 2 was presented at rates of:

trace a, 1 stimulus every 800 ms

trace b, 1 stimulus every 1.2 s

trace c, 1 stimulus every 2 s

trace d, 1 stimulus every 3 s

The duration of stimulation at each rate is indicated below the traces by the open triangles. The position of the stimuli was obtained by reference to the positional markers which were recorded on the lower traces. The time scale represents 1 s.

The results demonstrate the phasic element which typically forms the first part of the connective threat response. The traces also illustrate that although more spikes accompany the slower stimulus presentation rates, the frequency of these spikes is less than that which is associated with faster rates of stimulus presentation. The traces also show the influence of stimulus presentation rate on habituation of the recorded connective activity. This is illustrated by the decrease in frequency and number of spikes which comprise each connective threat response. It is apparent that it takes longer for habituation to occur at the faster rates of presentation with this stimulus.

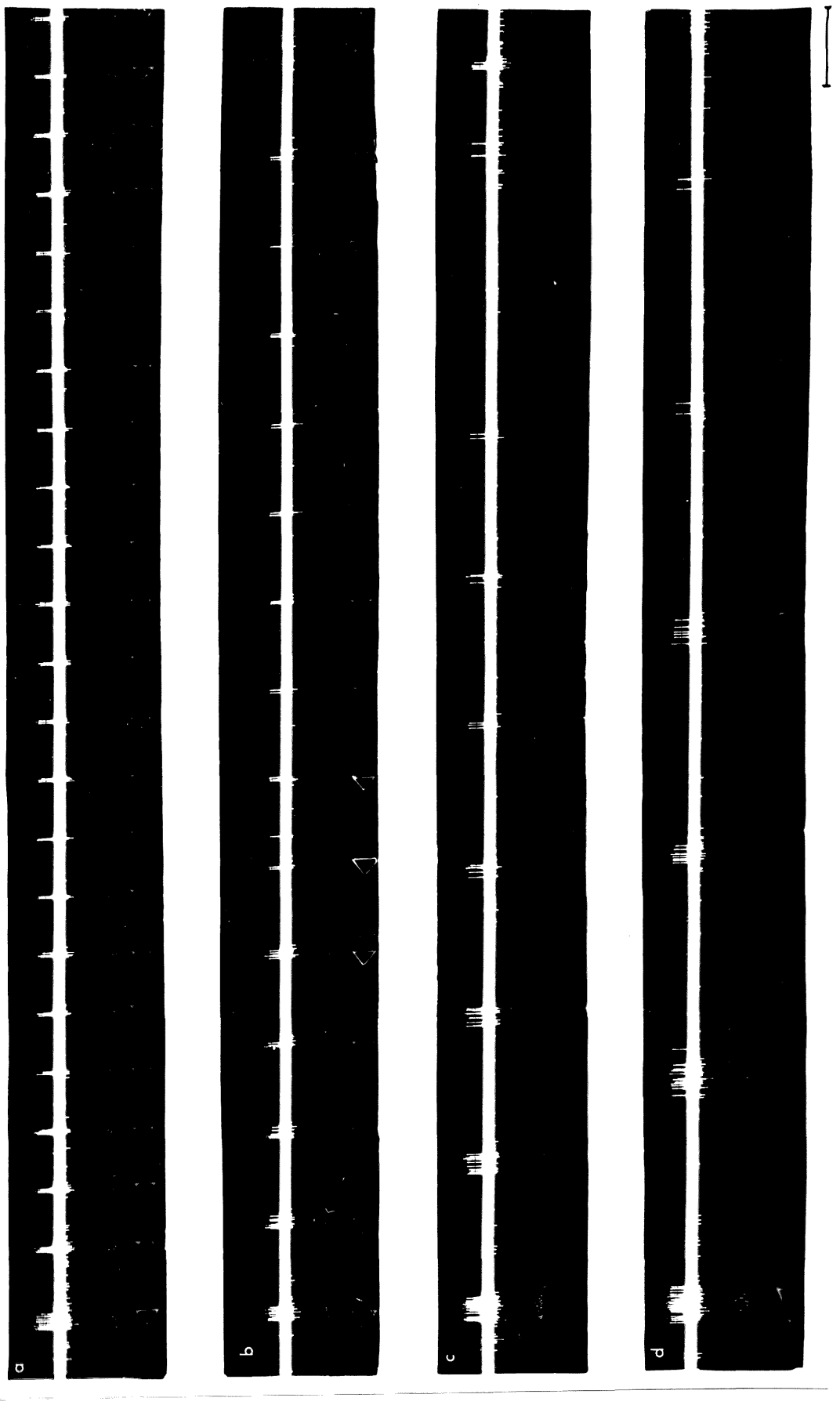

a
b
c
d

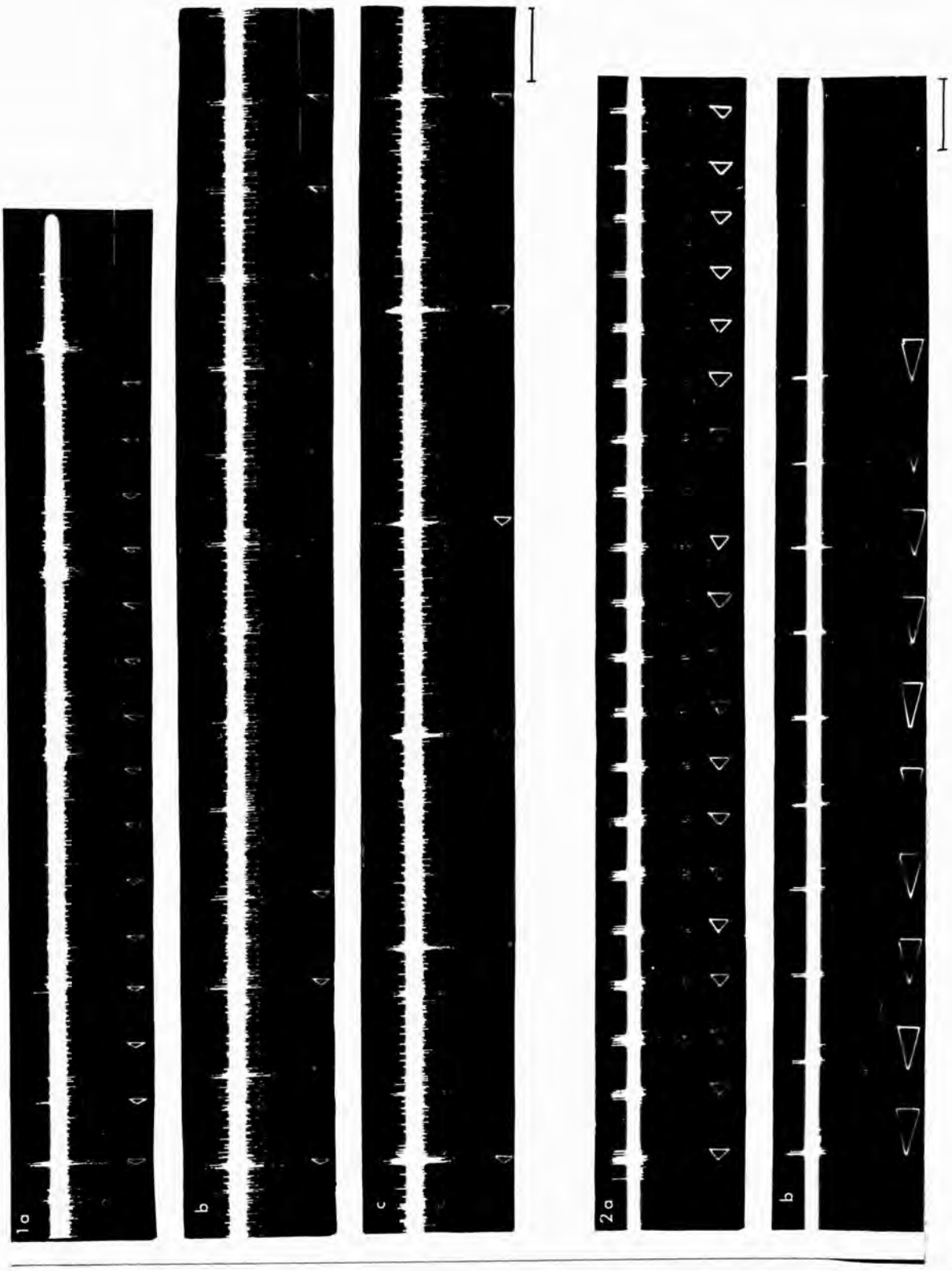
FIGURE 5

CONNECTIVE NERVE RESPONSES WHICH ACCOMPANY CONTROLLED STIMULATION: 2

Traces 1a, b and c are recordings made from the same crab as in figure 1.2. Traces 2a and b are recordings made from the same crab as in figure 2. The traces illustrate connective responses when stimuli 1, 3 and 4 were presented. The time scale represents 1 s. Traces 1a, b and c were made during presentation of stimulus 1 at rates of 1 stimulus every 800 ms, 1 stimulus every 1.2 s and 1 stimulus every 2 s respectively. They demonstrate the phasic element of the connective threat response. They also include the feature of habituation which typically accompanied the presentation of this brief stimulus at the fast rates. There was a sharp decrease in recorded activity with the faster rates of stimulus repetition. Comparison of traces b and c shows the higher frequency of both large phasic and medium tonic-phasic sized spikes which accompany the faster rate of stimulation.

Traces 2a and b indicate connective activity which accompany the presentation of stimulus 3 at a rate of 1 stimulus every 800 ms and stimulus 4 at a rate of 1 stimulus every 1.2 s, respectively. It can be seen that presentation of stimulus 3 corresponds to higher frequency activity from the large spikes. These spikes decrease in frequency during the bursts as stimulation is repeated.

CHAPTER 10 FIGURE 5



stimulus presentation rates are higher.

Traces 2a and b (Fig. 5) were recorded from one crab which was stimulated at rates of 1 every 800 ms with stimulus 3, and 1 every 1.2 s with stimulus 4 respectively. It is apparent that more large spikes accompany the presentation of stimulus 3. Again the influence of repetition rate on habituation of the response is demonstrated in trace 2a. The frequency of spikes is considerably reduced by the end of the recording.

3. Connective and muscle responses which accompany threatening stimuli

It was observed that although this form of stimulation, which represented approaching objects, was sufficient to evoke activity from the connectives, many crabs did not respond with full postural displays of threat. Instead only small levatory and extending twitches of the chelipeds were observed. To examine whether the muscles respond at the same time as the connective during stimulation, simultaneous recordings were made from the connective and BI Anterior levator muscle. A small part of the box was cut away to allow observation of the crab during stimulation. A representative result is shown in figure 6a.

Stimulus 3 (Fig. 2a) was presented at a rate of 1 every 800 ms. The crab responded to the initial stimulus by moving from Shallow to Half Threat display positions. This took the form of a sudden twitch and was not maintained. With the following stimuli, the muscle response was decreased in frequency and was not perceptible after five presentations. At this point, postural twitches were not detected although the characteristic threat responses from the connectives were still evident for the remainder of stimulation.

Although this form of stimulation was less effective in releasing full postural threat displays than that shown in the previous chapter, muscle threat responses may still be detected at reduced frequencies. The onset of the muscle responses closely follow the occurrence of the threat responses recorded from the connectives.

4. Symmetry of the threat response recorded from the connectives

Simultaneous recordings were made from both connectives to examine whether the activity which accompanies stimulation, is simultaneously transmitted along the two connectives. Figure 6b to e, indicates that this is so.

In figure 6b and c, the crabs were stimulated manually. Each recorded threat response is simultaneous in both connectives with respect to onset and duration of activity. In the middle of trace b, the stimulus was changed from a rapid movement to a slower movement of the hand. This was associated with a change in recorded activity from a phasic to more tonic frequency in both connectives.

FIGURE 6

a. SIMULTANEOUS RECORDINGS FROM ONE CONNECTIVE AND THE BI ANTERIOR LEVATOR MUSCLE

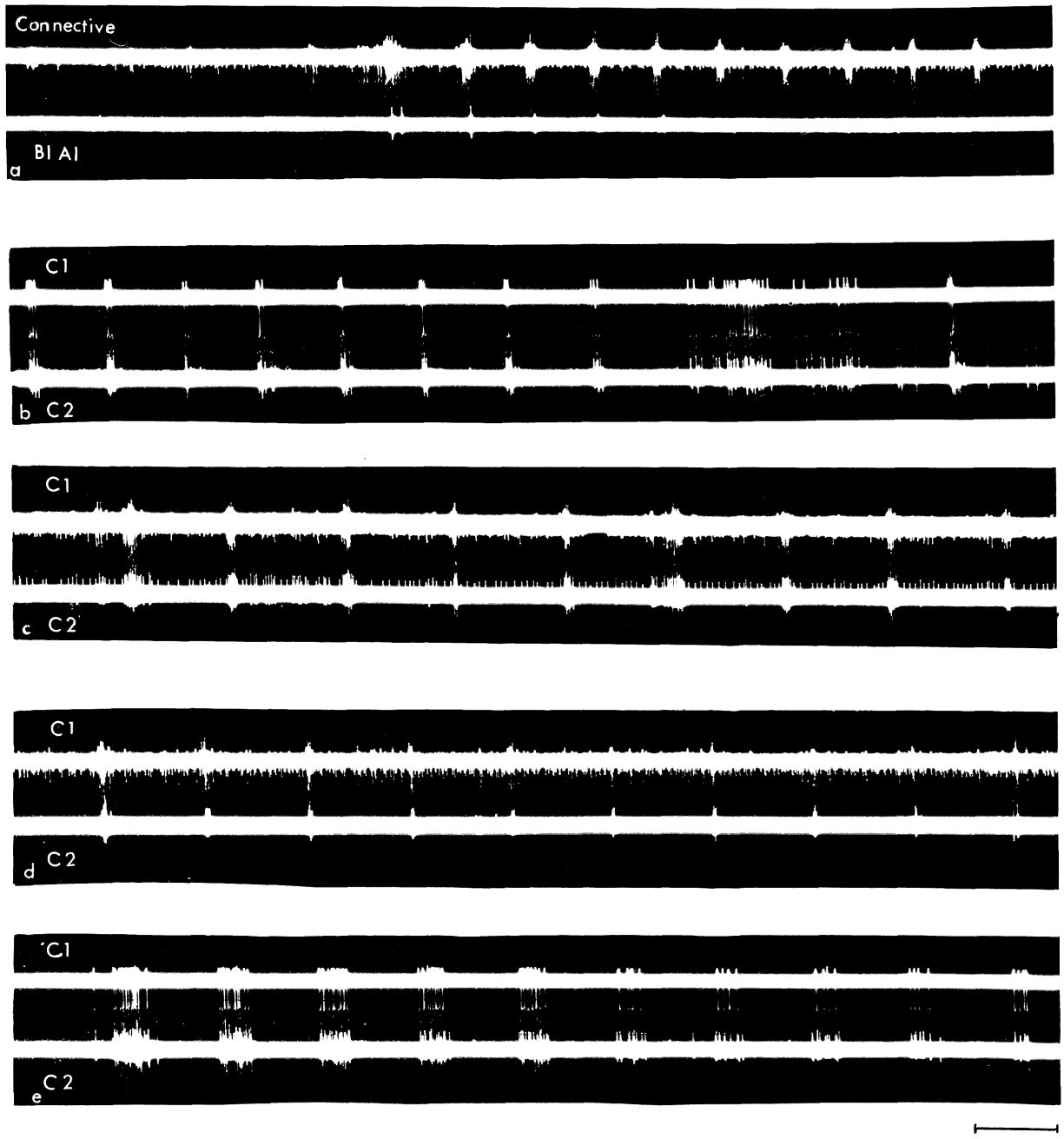
The activity from the connective during stimulation is shown on the upper beam of the trace and the activity recorded from the muscle is shown on the lower beam. The crab was stimulated with stimulus 3 at a presentation rate of 1 every 800 ms. The time scale represents 1 s.

The traces demonstrate that although this method of stimulation which represents approaching objects, was less effective in producing the high frequency muscle activity characteristic of responses accompanying the actual approach of objects shown in the previous chapter, muscle responses are still displayed. The muscle responses occur at a reduced frequency and for shorter periods when the stimuli are presented in this experimental set-up than in the previous arrangement. The onset of these muscle responses closely follow the recorded connective responses which accompany stimulation. The muscle responses habituate before the connective responses.

b-e SIMULTANEOUS RECORDINGS FROM BOTH CONNECTIVES OF ONE CRAB

In traces b and c the crabs were stimulated manually. The onset, duration and frequency of the recorded responses are all identical in both connectives. Towards the end of trace b, stimulation was slowed. This altered speed of stimulation accompanied a longer discharge of large spikes in both connectives.

In traces d and e, the crabs were stimulated by the kymograph apparatus at a rate of 1 stimulus every 1.2 s with stimulus 2 and 3 respectively. The results further indicate that connective activity recorded during the presentation of stimuli, is simultaneously transmitted along both connectives.


Connective
a B1 A1
C1
b C2
C1
c C2
C1
d C2
C1
e C2

In traces d and e (Fig. 6), the crabs were stimulated with the kymograph apparatus at presentation rates of 1 every 1.2 s with stimulus 2 in trace d and stimulus 3 in trace e. Again the symmetry of the recorded threat response is evident. Thus the results in these traces indicate that responses to threatening stimuli are simultaneously transmitted along each connective, which may explain the symmetry of the postural threat display response.

5. The influence of stimulus angular velocity on the connective threat response

Each rate of stimulus presentation with the four different arrows, produced different angular velocities of stimulation as viewed by the crab. To examine the effect of stimulus angular velocity on the threat response, the latency between the beginning of the first presentation of each stimulus at each rate and the first large spike response recorded from the connective, was measured. The latency, measured in ms, was plotted against the angular velocities produced by the stimuli. The results are illustrated in figure 7. The values plotted on the graph are the mean and standard errors of data obtained from all the crabs which were tested with the kymograph apparatus.

The graph demonstrates that as the angular velocity of stimulation increases, the latency between the initiation of the connective threat response and the beginning of stimulus movement, decreases. This is comparable with the results obtained in the previous chapter concerning muscle responses (Chapter 9, Fig. 10), although the velocities produced in the present experiment were much faster than those produced previously.

The results indicate that from 0 to 100^{o}/s, there is little change in the response latency. After this, the latency is considerably reduced, until at the fastest angular velocities, there was only 60 to 70 ms latency between the onset of stimulation and the initiation of the typical connective threat response.

DISCUSSION

These experiments indicate that presentation of threatening stimuli to the crab, is associated with characteristic patterns of activity which may be recorded from the connective nerves of *Carcinus*. This activity typically takes the form of a short high frequency burst of large, phasic spikes generated by fibres termed type A. These spikes accompany the beginning of stimulation and are usually followed by activity from a second group of fibres, termed type B, which produce medium sized spikes which are tonic-phasic in nature. The activity of these fibres is typically

FIGURE 7

THE INFLUENCE OF ANGULAR VELOCITY ON THE LATENCY OF THE CONNECTIVE THREAT RESPONSE

The latency between the beginning of stimulus movement and generation of the first large spike recorded from the connectives, was measured for each stimulus and presentation rate. The latency was measured in ms and is represented on the ordinate scale. The abscissa represents the angular velocities which were produced by each stimulus at each presentation rate. The angular velocities produced by the stimuli ranged from 2 to 766^{o}/s. The values plotted on the graph are mean and standard errors of response latency for each velocity obtained from pooled data of all the crabs.

The graphs demonstrate that as the angular velocity of stimulation increases,the latency between the beginning of stimulation and the initiation of the characteristic connective threat response, decreases; a feature which is comparable to that found in the previous chapter (Chapter 9, Fig. 10). The results indicate that varying the angular velocity between 0 and 100^{o}/s has little influence on the initiation of the recorded connective response to the initial presentation of the stimulus. However, higher angular velocities accompany considerably reduced response latencies.

CHAPTER 10 FIGURE 7

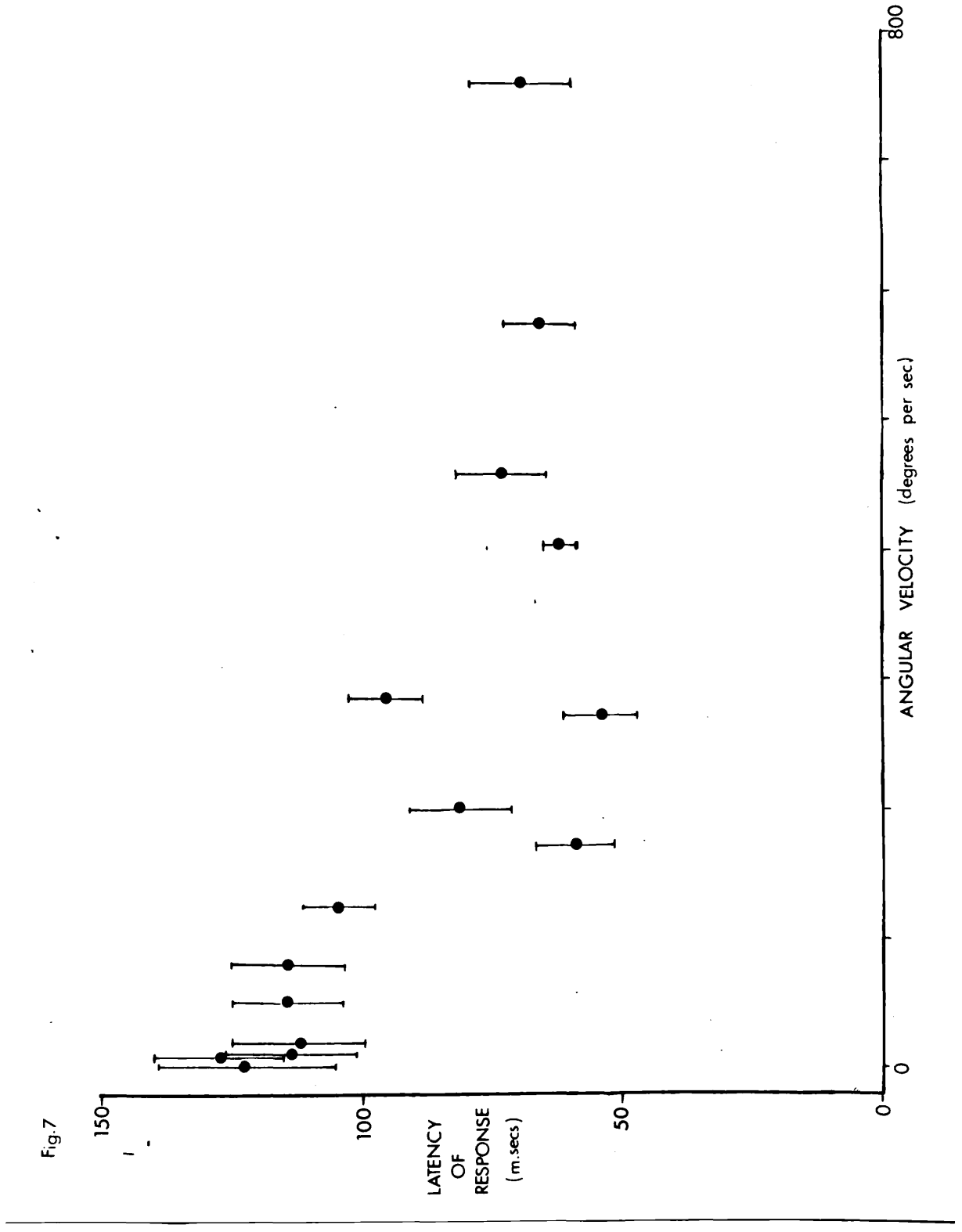


Fig.7

confined to the duration of stimulation. A third group of fibres, termed type C, produce tonically active small spikes, which are usually produced at low frequencies between stimuli.

The connective threat responses have many similarities with the muscle threat responses which were recorded in the previous chapter. Figure 6a indicated that the connective response occurs at the same time as muscle threat responses when stimuli are presented. It has been shown that, like the muscle responses (Chapter 9, Fig. 3), the connective response displays habituation of activity as stimuli are repeated. Also, like the muscle threat response (Chapter 9, Fig. 10) the latency between the beginning of stimulation and the initiation of the connective threat response decreases as the stimulus angular velocity increases. Figure 6 demonstrated that the response is simultaneously transmitted along both connectives. This may explain the synchrony of muscle and postural response which are associated with the approach of threatening stimuli, described in previous chapters.

The shortest recorded muscle threat response latencies were 500 ms when the velocities of stimulation were high (Chapter 9, Fig. 10). However the longest measured response latency in the connectives was only 137 ms while the shortest latency was only 55 ms (Fig. 7). This indicates that although connective and muscle responses are similar with respect to the onset of increased response activity when stimuli are presented, the recorded connective activity may not act directly on the muscles, causing their typical threat responses, but may trigger activity in other neural circuits which control the muscle excitation. In this respect the activity recorded from the connectives in these experiments may be compared to DMD activity. The connective responses may be subthreshold events which form the basis of any "warning" activity which precedes the beginning of agonistic behaviours.

The connective threat responses are similar in activity pattern to the motion detector responses of the crayfish defence reflex (Glantz, 1974 b), especially the output of type A fibres. It is possible that the activity of the large, phasic spikes is preceded by visual input which triggers motion detectors or similar elements in the optic nerve of the crab. These elements may transmit their information to the brain. This may then be received and added to by other inputs, before it is transmitted along the connectives in the characteristic form of the recorded threat responses. This sequence of activity was also suggested to occur in the crayfish by Glantz (1974 c). He suggested that the motion detector output was not the sole trigger of the reflex, but rather one labile process in a pathway that may contain several.

It has been shown that there is activity in the connectives which may be compared in form and character to threat responses recorded from the cheliped muscles. It was observed that the connective response was usually accompanied by postural changes, especially when stimulation was extreme. Certain elements in the connectives, such as the large, phasic spikes, suggest that the recorded responses may be involved in neural pathways controlling the threat displays.

The following chapter is concerned with simultaneous recordings from connectives and muscles in freely behaving animals. This enabled the nervous activity to be directly compared with motor output and behaviour in an attempt to establish whether the characteristic muscle activity displayed during agonistic interactions, such as pre-strike bursts and the phasic threat bursts, is associated with any distinct patterns of nervous activity.

CHAPTER 11

SIMULTANEOUS RECORDINGS FROM THE CONNECTIVE NERVES AND COXAL-BI MUSCLES DURING AGONISTIC BEHAVIOUR

INTRODUCTION

Only a few studies have been made concerning the neural control of agonistic behavioural patterns. One such study of prey capture was performed in the aplysian mollusc, Navanax (Woollacott, 1974). The sequence of muscle contractions during the predatory behaviour was correlated with intracellular recordings obtained from neurones of the buccal ganglion in an attempt to determine the neuronal basis of muscular activity during a complex behaviour.

The prey capture response of Navanax is completed within 100 ms and involves a rapid swallowing of the prey. The behaviour was elicited by placing small nudibranchs and opisthobranchs near the opening of the oral cavity. The behaviour was difficult to evoke in the whole animal preparations and was achieved by electrical stimulation of the cerebuccal connective nerves.

It was found that the muscles were activated in a co-ordinated sequence. The pharynx was initially protracted and then expanded by twitch contractions in the radial pharyngeal muscles. Sequential contraction of the circumferential muscles caused a swallowing action. Simultaneous activity in muscles controlling the anterior and mid sections of the oesophagus, forced material into the posterior half of the oesophagus. This cycle was repeated if the prey was too large to be swallowed by the execution of one contraction sequence.

Identified buccal ganglion neurones were observed to modulate their pattern of firing during a contraction cycle, and were classified according to their response patterns. Three classes were described. These were cells which fired during pharyngeal expansion and were related to the motor control of radial muscle contraction; cells which fired during contraction of the circumferential muscles and elicited pharyngeal constriction; and cells which slowed in activity during specific phases of the contraction cycle. Activity in the latter group was not associated with muscle contraction.

The author identified the neurones as motorneurones since they fulfilled several requirements. For example, each intracellularly recorded spike was associated with a spike recorded from the nerve trunk connecting the buccal ganglion with the pharynx. Each spike was also associated with a twitch response in the appropriate muscles, and a muscle impulse could be detected by EMG electrodes. The neurones also participated in the response cycle in isolated, deafferenated ganglion preparations.

It was demonstrated that the action potentials in the motorneurones exhibited sequences of bursts which were accompanied by muscle contractions which caused the swallowing action. Activity from certain motorneurones, such as the radial motorneurones which mediate pharyngeal expansion, appear to synchronize the bursts of action potentials in other motorneurones, especially those which mediate swallowing. The firing pattern of buccal motorneurones was identified in whole animal, pharynx-ganglion and isolated buccal ganglion preparations. It appeared that peripheral feedback is not a necessary component in determining the pattern of activity which occurs during the prey-capture response, although Woollacott suggested that in the intact animal, sensory input may initiate the response.

Results from previous chapters in this thesis, have demonstrated that activity may be recorded from the connectives of Carcinus which has similar characteristics to responses recorded from the cheliped threat muscles associated with the presentation of threatening stimuli. It has been suggested that the responses recorded from the connectives may not act directly on the motorneurones which cause the threat responses, but may either have a warning function or may trigger the activation of other neural circuits which control the agonistic displays.

It has been shown that the presentation of threatening stimuli accompanies a characteristic threat response in muscle activity which comprises a sharp increase in tonic frequency of activation and often the recruitment of phasic axons. The presentation of similar stimuli accompany a characteristic pattern of activity which may be recorded from the connectives. This comprises the generation of a phasic burst of large spikes, typically followed by the production of tonic-phasic, medium sized impulses.

In this chapter, muscle and neural recordings were performed simultaneously to examine their sequence and pattern of activity which accompanies agonistic interactions in freely moving crabs.

MATERIALS AND METHODS

Large male crabs were prepared for recording as described previously. Two electrodes were used. One was positioned in a selected coxal or BI muscle and the other was implanted in a connective. Recordings were only made from the five main strike and anti-strike muscles, that is, the coxa remotor and promotor together with the BI Anterior levator, Anterior depressor and Posterior depressor muscles.

The crabs were allowed to recover after electrode placement. In most cases, normal behaviour patterns were displayed soon after the operation, indicating that the placement of the electrodes did not unduly disturb the crab.

The animals were placed in a glass tank which was partly filled with sea water. The presentation of threatening stimuli was produced manually. Although this did not provide such a controlled situation as in the preceding chapters, it ensured that stimulation was maximally effective and released all the facets of the strike and threat behaviours.

RESULTS

Representative recordings from the connective nerves and muscles are shown in figures 1 to 5. In each figure, the top trace illustrates recordings from the connective and the lower trace illustrates EMG's from the selected coxal and BI muscles.

1. The BI Anterior levator muscle

Figure 1 shows records from the BI Anterior levator muscle and a connective. Figures 1a and b, and 2a and b are continuous recordings from two crabs. The A1 muscle produced the most comparable pattern of response activity between muscle and connective because it typically responds phasically to stimulation.

Figure 1a, traces 1 and 2,is a continuous recording from a crab which maintained a Half Threat display. The activity recorded from the A1 parallels that recorded from the connective; there is high frequency tonic activity in both. When the frequency of activity in the connective increased slightly, there was a similar increase in muscle impulse frequency. This is demonstrated in the middle portion of trace a (Fig. 1). When the frequency of connective activity decreased, as occurred at the beginning of trace a (Fig. 1), muscle activity was similarly reduced in frequency.

In trace a2 (Fig. 1), the crab was presented with a slowly approaching stimulus. This was accompanied by an increase in frequency of spikes recorded from the connective and was followed by a substantial increase of A1 activity. The crab responded to stimulation with a Three-Quarters Threat display which was maintained until the approach rate of stimulation was suddenly increased. This sudden change in approach rate was associated with the characteristic threat responses recorded from the connective and muscle. The connective response comprised a high frequency burst of large spikes and the muscle response similarly comprised a high frequency burst of phasic activity. The crab responded to the increased stimulus approach rate by displaying a Full Threat posture. After this, the crab readopted Three-Quarters Threat display positions.

These recordings demonstrate that the characteristic muscle activity associated with threatening stimuli are reflected in recordings made from the connectives. This is also seen in traces b1 and b2 in figure 1. Trace b1 (Fig. 1), illustrates the recorded response from a crab which displayed

FIGURE 1

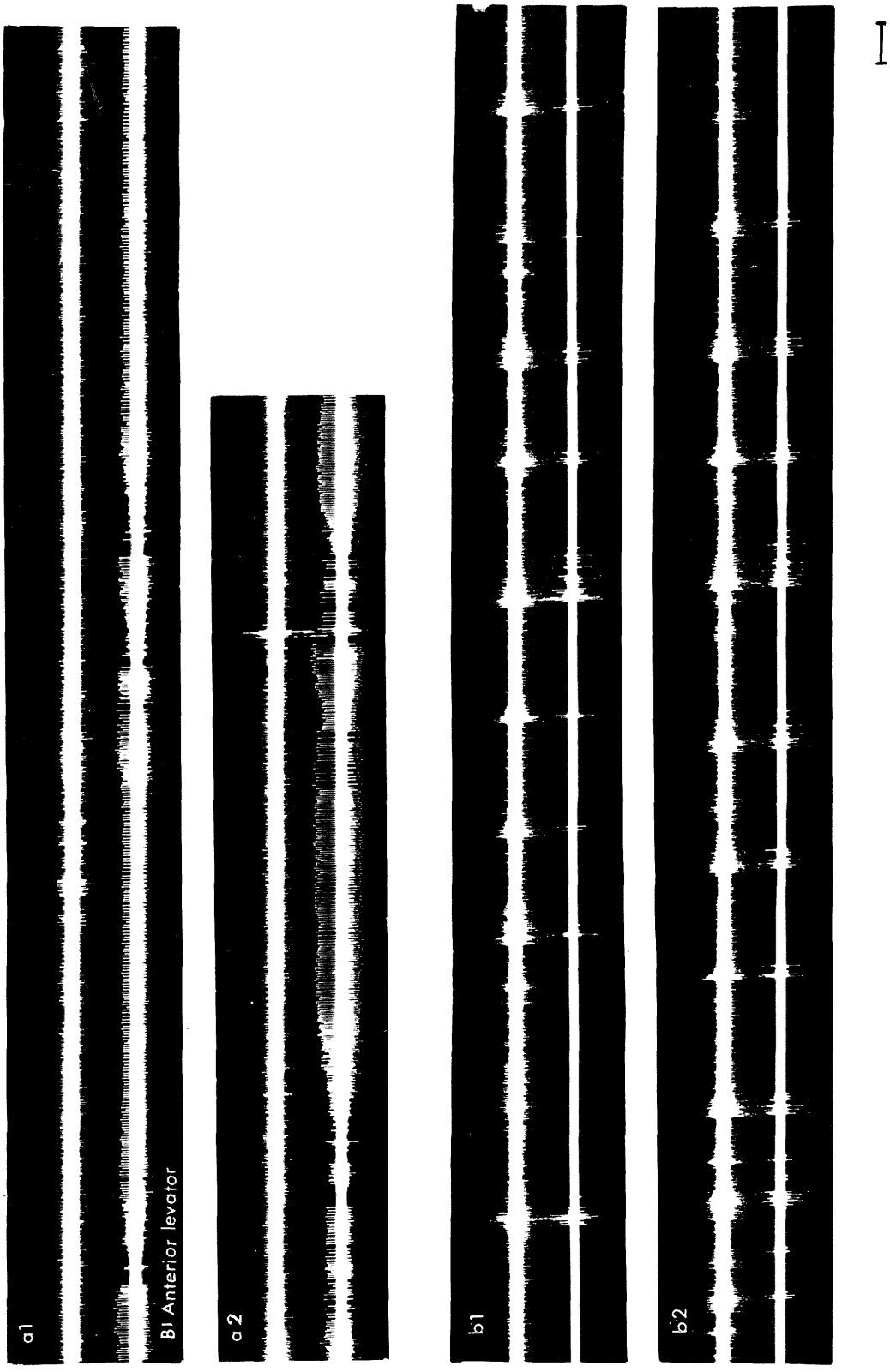
SIMULTANEOUS RECORDINGS FROM THE CONNECTIVE AND BI ANTERIOR LEVATOR MUSCLE: 1

Trace a, 1 and 2 is a continuous record from one crab. At the beginning of recording the crab was positioned in a Half Threat display. This was associated with a tonic frequency of activity recorded from the connective and BI Anterior levator muscle. At the beginning of trace 2, the crab adopted a Three-Quarters display. This change in display position was reflected by an alteration in frequency of connective and muscle activity; both increased in frequency. Near the end of this trace, the sudden approach of a stimulus caused the crab to twitch its chelipeds upwards. This was associated with the characteristic threat response from both the connective and muscle; that is, both showed a phasic burst of high frequency large impulses.

Trace b, 1 and 2 is a continuous record from one crab which responded to each rapid approach of a stimulus with a brief levatory twitch of the chelipeds from a Half to Full or Three-Quarters Threat display. Almost every display was associated with a phasic burst of connective and A1 activity, the characteristic threat responses. As described in chapters 8 and 9, the intensity of the display is reflected by the frequency of A1 activity. The first stimulus released Full Threat and corresponded to a high frequency burst from the A1, while the next three stimuli accompanied a reduced A1 burst frequency and only released Three-Quarters Threat displays.

The time scale represents 1 s.

CHAPTER 11 FIGURE 1



to the presentation of a rapidly moving stimulus with a brief levatory twitch of the chelipeds from Half to Three-Quarters or Full Threat postures. Almost every display corresponded to a phasic burst of activity recorded from the connective and a phasic burst of large impulses from the A1 muscle.

As demonstrated in chapters 8 and 9, the intensity of the postural display is reflected by the frequency of the A1 impulses. The highest frequency of burst activity in the A1 accompany Full Threat displays while reduced burst frequencies accompany Three-Quarters Threat displays. This is shown in trace b (Fig. 1) in which the crab responded to the first stimulus with a Full Threat display while the following three stimuli only released Three-Quarters Threat displays and corresponded to a reduced A1 response. The fifth stimulus released Full Threat again, and accompanied an increased frequency of A1 impulses.

Figures 2 and 3 show a series of recordings made from one crab over 30 mins. Traces d and e are continuous. Trace a (Fig. 2) was recorded while the crab was recovering from electrode placement. The crab assumed a resting posture with the chelipeds flexed and depressed in front of the mouth. The trace illustrates that this posture is accompanied by low frequency tonic activity recorded from both the connective and muscle.

Trace b (Fig. 2) was recorded 15 mins after the operation. The crab responded to mild stimulation with slow movements of the chelipeds, from rest to Shallow or Half Threat positions. This low intensity of display is reflected by the recorded responses. That is, there are fewer large spikes and the duration of the bursts from both muscle and connective are longer than the responses recorded in Figure 1b when Full Threat was displayed.

Trace c (Fig. 2) was recorded after a further five minutes. The crab was more alert and responded to stimulation with more rapid movements of the chelipeds to Three-Quarters Threat positions. The burst responses recorded from the muscle and connective reflected these increased and more rapid displays; the recorded response activity is generally shorter in burst duration. Between traces c and d, the crab performed a series of fast strikes. These are illustrated in figure 3. The shorter traces illustrate the respective strikes filmed at double speed. The time of the beginning of rapid cheliped promotion is indicated by the arrows.

In trace a (Fig. 3), the crab responded to the approaching stimulus by rapidly moving from Half to Full Threat positions and then suddenly performed a fast strike. The muscle activity conformed to the expected pattern as described in chapters 5 and 6. There were short, high frequency bursts with the generation of large phasic spikes in the ultimate burst before rapid cheliped promotion. During the strike mode, the muscle activity was reduced in frequency. Increasing frequencies accompanied

cheliped re-extension and took the characteristic burst form again.

The activity in the connective is comparable to the muscle activity. As shown in trace a2 (Fig. 3), each muscle burst of pre-strike was preceded by the generation of large spikes in the connectives, which occurred in irregular bursts similar to the pattern of A1 activity although they were not quite as distinct. Recorded connective activity was maintained throughout the strike by high frequency discharge from medium sized spikes and the large spike activity ceased at the beginning of cheliped promotion. The medium sized spike activity continued until cheliped recovery movements were established, when the frequency of connective activity was decreased.

In trace b (Fig. 3), the crab maintained a Three-Quarters Threat display before the fast strike. This is reflected by the recorded high frequency discharge in the A1 muscle. The display was also accompanied by tonic activity in the connective. As pre-strike behaviour began, after the beginning of trace b2, the muscle activity displayed the characteristic pre-strike bursts again. As in trace a, cheliped promotion and the initial stages of re-extension were associated with a tonic discharge from the large phasic spikes. Following the strike, the crab assumed a resting posture. This was reflected by a sudden decrease in A1 activity, and was accompanied by a considerable reduction in frequency of the medium sized spike activity recorded from the connective.

The third strike, illustrated in trace c (Fig. 3), was also associated with the same pattern of recorded muscle and nerve activity. Following the strike, the crab displayed with a Shallow Threat display. This is shown in figure 2, trace d which was recorded shortly after the third strike. The crab did not respond to stimulation with an observable cheliped twitch. However stimulation still corresponded to increased activity in the connective, indicated by the three arrows on the trace. Following the third stimulus, the crab froze in a Shallow Threat posture and all the limbs were held rigid. This is reflected by the lack of recorded A1 activity and, from the third arrow of trace d to the first arrow of trace e, the crab was motionless. The recorded frequency of connective activity was also substantially reduced and only small spikes are evident in the traces.

At the first indicated point in trace e (Fig. 3), the crab suddenly lifted its body from the floor of the tank and began to retreat with raised chelipeds in a typical escape behaviour. After retreating to the back of the tank, it settled into a corner where it readopted a Shallow Threat display. The second transition in behaviour is indicated by the second arrow on trace e.

FIGURE 2

SIMULTANEOUS RECORDINGS FROM THE CONNECTIVE AND BI ANTERIOR LEVATOR MUSCLE: 2

These traces represent parts of a record obtained from one crab which was continually examined for over 30 min. Traces d and e are continuous. The time scale represents 1 s.

Trace a. The crab was recovering from implantation of the electrodes. It adopted a full rest posture with the chelipeds depressed and tucked around the mouth. This was accompanied by a low frequency of activity from the connective and muscle.

Trace b. 15 min after the operation the crab responded weakly to stimulation and each stimulus released only Half Threat displays. These displays were associated with the generation of relatively long bursts of response activity in the connective and muscle.

Trace c. After a further 5 min the crab was more alert and each stimulus released a rapid levatory twitch to a Full or Three-Quarters Threat display position. These rapid movements were reflected by a reduced duration of increased connective response frequency and high frequencies of Al response activity.

Traces d and e. After the crab had performed three fast strikes (Fig. 3), it remained in a Shallow Threat posture. Although stimulation corresponded to increased activity recorded from the connective, indicated by the three arrows, no muscle or postural responses were observed. After the third stimulus the crab froze in a Shallow Threat posture. No activity was detected in the Al while the connective activity was considerably reduced in frequency. At the first arrowed point in trace e, the crab suddenly levated its chelipeds and began to retreat in an escape behaviour pattern. This escape behaviour was accompanied by only a slight increase in connective activity while high frequency irregular bursts of large impulses can be detected in the recording from the Al. At the second indicated point, the crab had retreated into a corner of the tank and now assumed a Shallow Threat posture. This corresponded to a more regular tonic discharge from the Al.

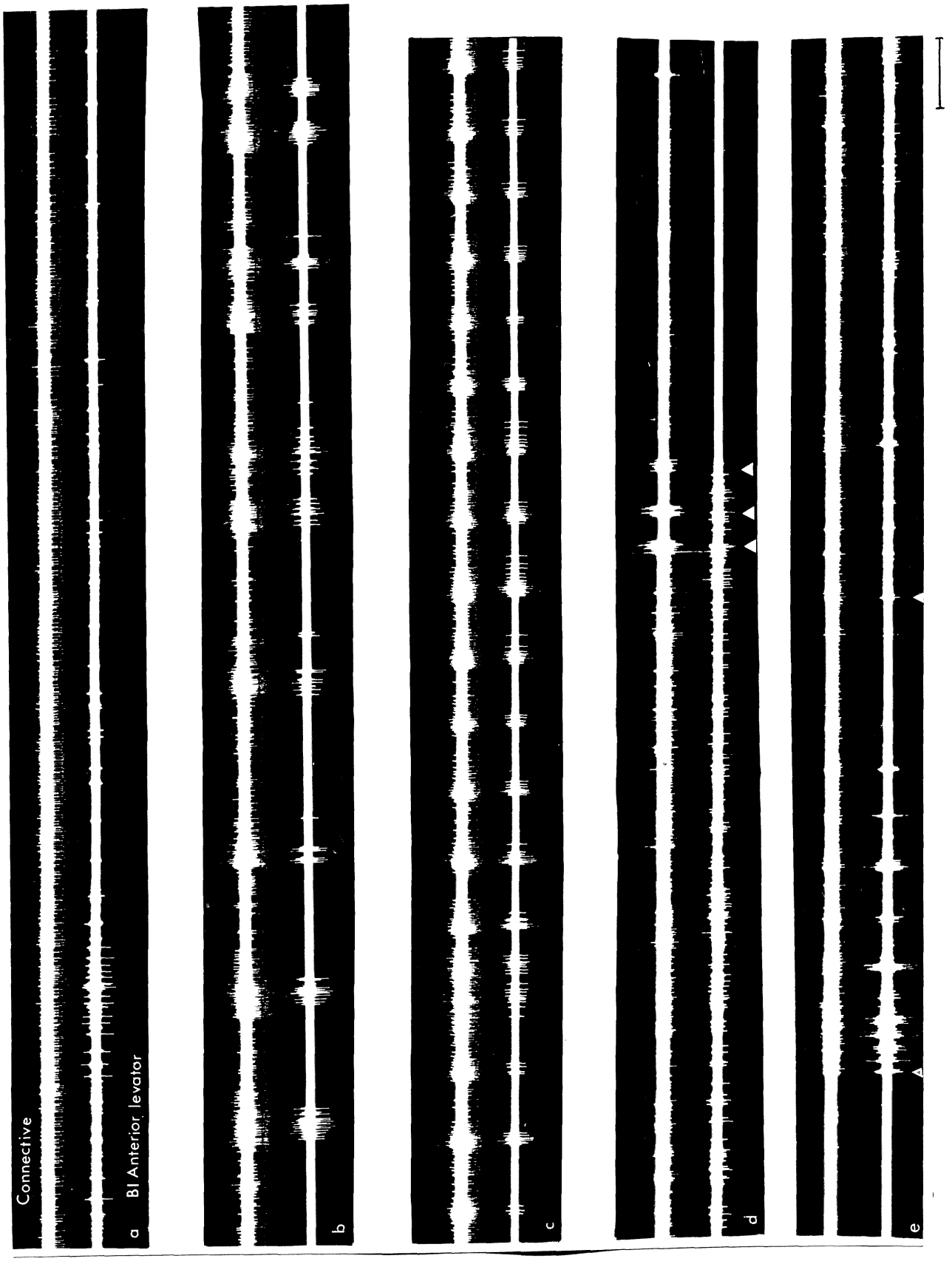

Connective
a BI Anterior levator
b
c
d
e

FIGURE 3

STRIKE ACTIVITY RECORDED FROM THE CONNECTIVE AND BI ANTERIOR LEVATOR MUSCLE

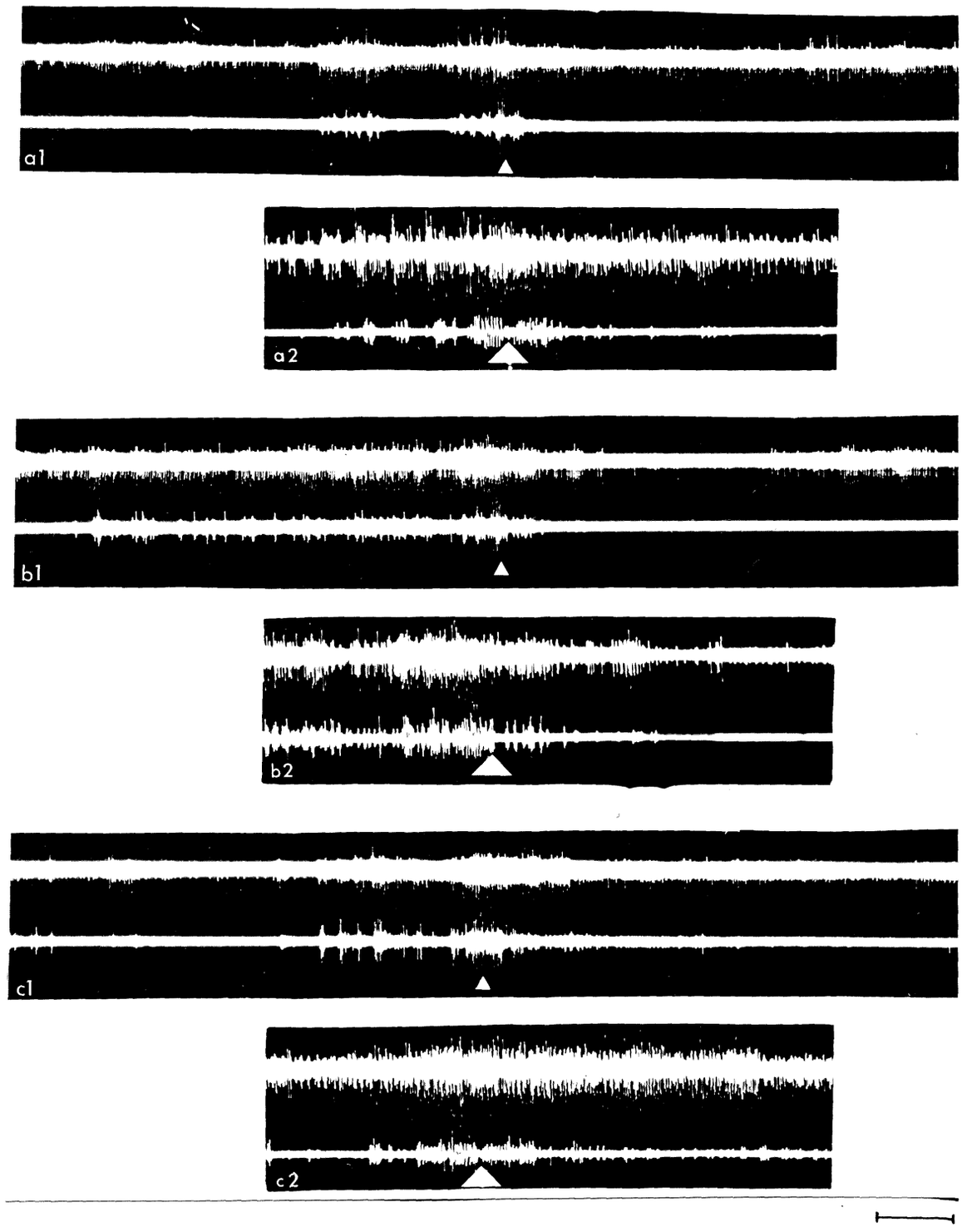
Between traces c and d of figure 2, the crab performed three fast strikes. These are shown in traces a, b and c of this figure with the recorded strike activity below each trace filmed at double speed. The arrows indicate the beginning of rapid cheliped promotion. The time scale represents 1 s in traces a1, b1 and c1 and 500 ms in traces a2, b2 and c2.

Trace a. The fast strike was extremely sudden. The crab reared to Full Threat before performing a strike. Each characteristic pre-strike burst in the A1 was preceded by a high frequency burst of activity from the connective during which several large spikes were generated. The production of these large spikes ceased before rapid cheliped promotion began, at which point the A1 frequency of activation was considerably reduced. High frequency, medium sized spike activity was recorded from the connective throughout the strike. This activity was reduced in frequency as the cheliped was re-extended in strike recovery movements.

Trace b. The crab assumed a Three-Quarters Threat display posture at the beginning of the trace. This was maintained until the strike behaviour was initiated. At this point, the muscle showed the typical pre-strike burst activity. After the strike, the crab assumed a resting position which was accompanied by a decrease in A1 activity. As before, pre-strike was associated with the generation of large spikes in the connective which ceased at the beginning of cheliped promotion. After the strike the frequency of medium sized spike activity recorded from the connective was reduced considerably.

Trace c. Several pre-strike twitches were displayed before the strike and are reflected by several high frequency A1 bursts of large impulses in trace c1 before the strike. Many large phasic spikes were displayed in the A1 recording before the cheliped was promoted. After the strike, cheliped recovery was slow and A1 activity was maintained at a low frequency for 3 s before it was reduced even further as the crab assumed resting postures. As before, cheliped promotion was accompanied by a maintained discharge of medium sized spikes from the connective, which reduced in frequency after cheliped recovery.

CHAPTER 11 FIGURE 3



2. The coxa remotor muscle

Two traces recorded from a connective and coxa remotor muscle of one crab during the presentation of threatening stimuli, are shown in figure 4, traces a and b. In trace a the crab responded to stimulation with a low intensity threat display. These displays corresponded to the generation of a few low frequency impulses in the CxR and a slight increase in connective activity.

In trace b (Fig. 4), the crab responded to stimulation with a Full Threat display. This increase in display was reflected by an alteration in connective and muscle activation compared to that shown in trace a (Fig. 4) when only low intensity threat positions were displayed. The increase in threat display in trace b corresponded to a greater increase in activity recorded from the connective and a higher frequency of burst activity recorded from the CxR. Between each threat response the crab maintained a Half Threat display, which was accompanied by a low frequency of CxR activity.

3. The coxa promotor muscle

The crabs which were tested with simultaneous coxa promotor and connective recordings, showed two patterns of activity associated with the presentation of threatening stimuli. These are represented in figure 4, traces c and d, which were recorded from the same crab. When stimulation released threat displays, each burst of characteristic connective threat response activity occurred between CxP tonic activity. The CxP was typically reduced in activity as the connective produced its phasic threat response activity. After these phasic bursts, tonic excitation to the CxP recommenced. This resumption of CxP activity corresponds to movement of the chelipeds back to positions of lesser intensities of threat display. Thus, this pattern of activity recorded from the CxP represents the active contribution of the anti-threat muscles in producing reduced threat display postures as described in chapter 8.

The second pattern of CxP activity occurred when alert crabs responded to stimulation with pre-strike twitches. Each pre-strike twitch accompanied an increase in connective activity. However, each connective response was now immediately followed by a brief increase in CxP activity and not a reduction shown when stimulation releases a threat display (trace c, Fig. 4). This is shown in the first part of trace 4d (Fig. 4).

FIGURE 4

SIMULTANEOUS RECORDINGS FROM THE CONNECTIVE AND COXAL MUSCLES

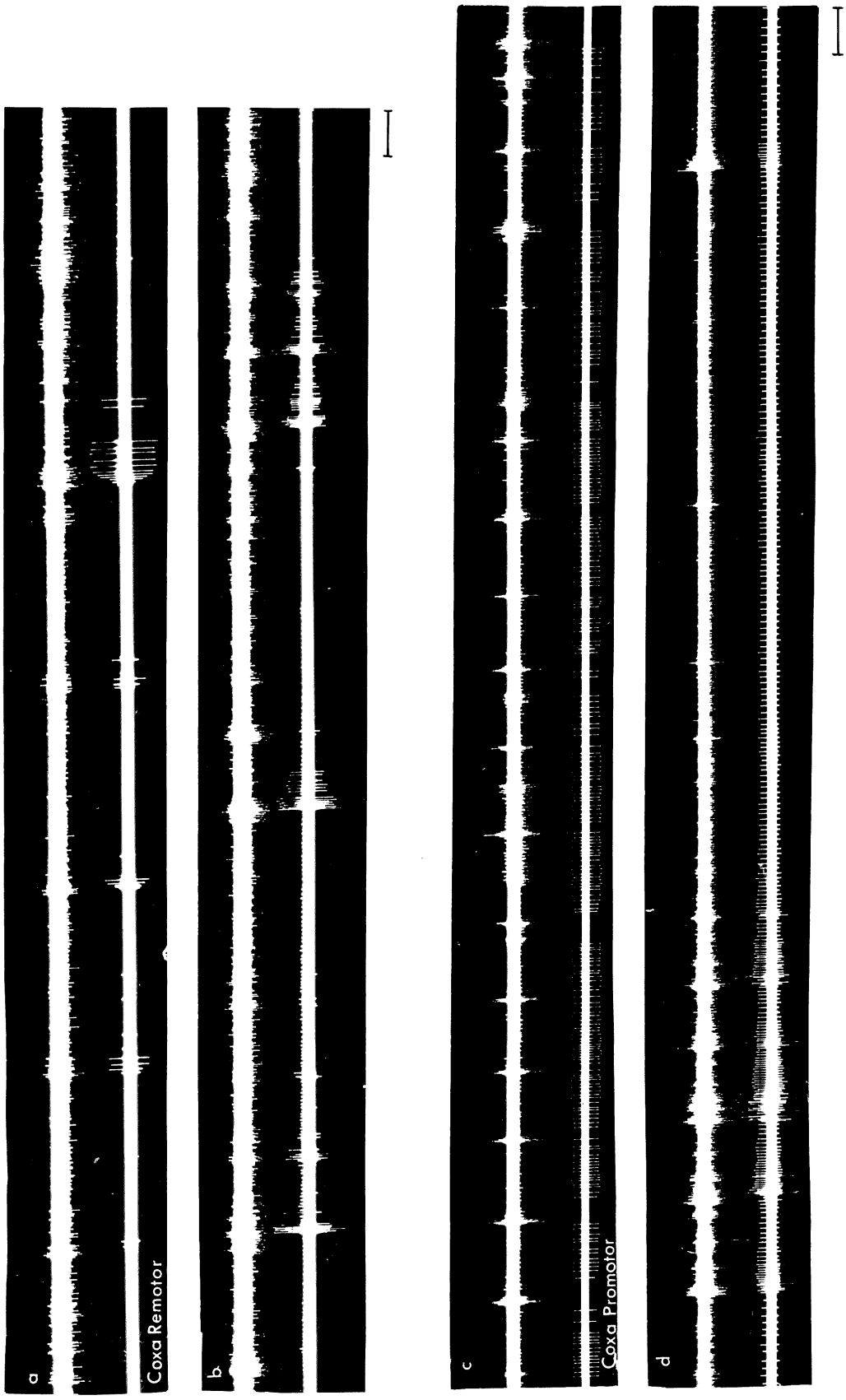
Traces a and b. These are recordings made from the connective and coxa remotor muscle of one crab. In trace a, the crab responded to stimulation with low intensity threat displays. These were accompanied by low frequency nerve and muscle activity. In trace b, the crab responded to stimulation with Full Threat displays. The increased displays corresponded to the generation of more muscle spikes which occurred at a higher frequency than in trace a. The response to stimulation recorded from the connective was also of a higher frequency and more large spikes were produced.

Trace c and d. These are recordings from the connective and coxa promotor muscle of one crab. They demonstrate the two characteristic CxP muscle responses to threatening stimuli. In trace c, the crab responded to stimulation with threat displays, which corresponded to the characteristic connective threat responses. Between each phasic burst,the CxP activity was considerably reduced or even absent. Increasing muscle impulse frequencies recommenced when the limb was re-established in positions of lesser intensities of threat displays.

In trace d, the crab responded to stimulation with pre-strike twitches, and the pattern of CxP activity was quite different. Each stimulus corresponded to an increase in connective activity. When the crab responded with pre-strike twitches, these phasic bursts were simultaneous with increased CxP activity. This is shown at the beginning and end of the trace. However when the stimuli released threat displays, as occurred in the middle of the trace, the CxP impulse frequency was not increased while the increased connective response activity was shorter in duration.

The time scale represents 1 s.

CHAPTER 11 FIGURE 4



4. The BI Anterior depressor muscle

Traces from the BI Anterior depressor muscle and connective of one crab are shown in figure 5, traces a and b. Trace b2 is a section of b1 filmed at double speed. In trace a (Fig. 5), stimulation caused the highly responsive crab to perform pre-strike twitches. Each twitch corresponded to the characteristic pre-strike activity of the muscle; the generation of one or two large spikes. These occurred just after the peak frequency of connective spike activity which also accompanied the pre-strike twitches.

In trace b (Fig. 5), the crab performed a fast strike, indicated by the arrow. The pattern of Ad activity conformed to previous results (Chapters 5 and 6). The Ad showed a sharp increase in frequency of activity for 200 ms before the strike, during which time several large phasic spikes were produced. These stopped when the cheliped was rapidly depressed. The activity recorded from the connective during the strike was slightly different from that recorded in figure 3. Although the production of large spikes still ceased before cheliped promotion, there was not such a marked activity from the medium sized spikes throughout the strike behaviour as seen in figure 3.

5. The BI Posterior depressor muscle

Trace c (Fig. 5) is a continuous record from one highly responsive crab. Each stimulus released a pre-strike twitch almost every time, although the twitches decreased in strength as stimulation was repeated. The recordings reflect the progressive decay of the twitches from the presentation of the first to the last stimulus.

It has been shown that a pre-strike twitch is accompanied by the generation of several large impulses in the Posterior depressor muscle (Chapters 5 and 9). The traces of figure 5c show that as the intensity of the twitches decreased, the frequency of muscle activity also decreased. The first postural response to stimulation was a relatively large twitch, depressing the cheliped by almost 10^{o}. The degree of depression gradually reduced upon repeated stimulation, until by the end of the recording the twitches were extremely small. This is reflected by the reduced activity from the Pd muscle. It is interesting to note that the reduction in Pd impulse frequency accompanying the pre-strike twitches is also reflected in the recorded connective response activity. As the Pd burst frequency is reduced, the connective burst response is slightly reduced in frequency and duration.

FIGURE 5

SIMULTANEOUS RECORDINGS FROM THE CONNECTIVE AND BI DEPRESSOR MUSCLES

Traces a and b are recordings made from the connective and BI Anterior depressor muscle of one crab. Trace b2 is a section of b1 filmed at double speed. The time scale represents 1 s in traces a and b1 and 500 ms in trace b2.

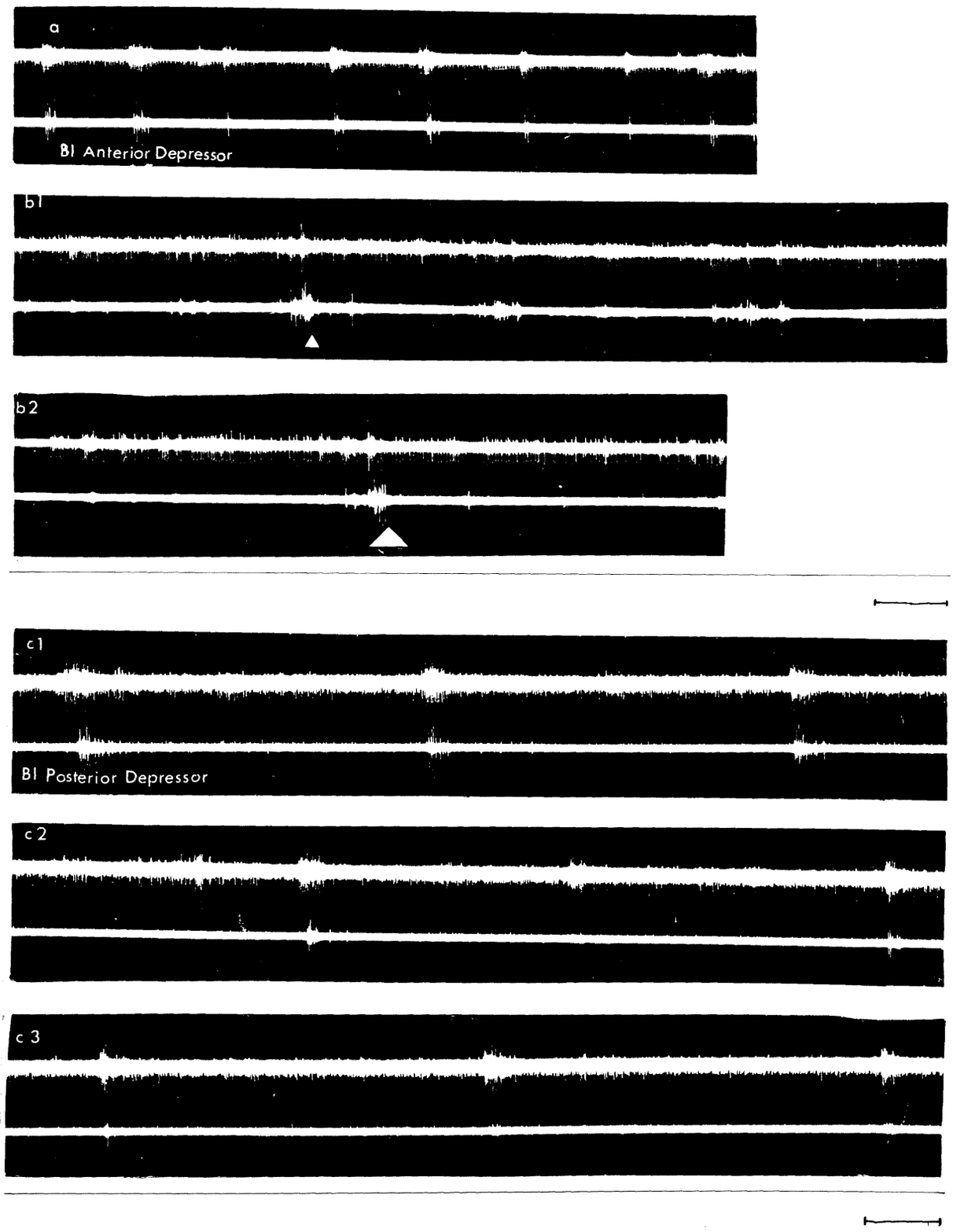
Trace a. The alert crab responded to stimulation with pre-strike twitches. These twitches corresponded to relatively long bursts of medium sized spike activity in the connective. The muscle activity associated with the pre-strike twitches conformed to the expected pattern (Chapters 5 and 9) and a few large phasic spikes were generated.

In trace b, a fast strike was performed, indicated by the arrow. Trace b2 shows the recorded strike filmed at double speed. The activity recorded from the muscle conformed to the pattern described in the analysis of the fast strike (Chapter 5); that is, the muscle was active at a high frequency for 200 ms before cheliped depression. The recorded activity from the connective was slightly different from that shown in figure 3. Fewer large sized spikes were produced throughout the strike, although the generation of large spikes still ceased before cheliped promotion.

Trace c, 1 to 3 is a continuous record made from the connective and BI Posterior depressor muscle of one responsive crab. Almost every stimulus presentation released a pre-strike twitch. These corresponded to the characteristic Pd strike activity of high frequency bursts during which several large spikes were generated. As stimulation was repeated, the intensity of the pre-strike twitch decreased. This is reflected by the reduction of the Pd response, until by the end of recording, the pre-strike twitches were barely perceptible and the stimuli were only associated with a slight increase in Pd activity. It is interesting to note that the reduction in Pd impulse frequency with repeated stimuli is also associated with a reduction in frequency and duration of the corresponding connective response.

The time scale represents 1 s.

CHAPTER 11 FIGURE 5



DISCUSSION

These results indicate that there is a more or less distinct pattern of neural activity which accompanies the threat responses recorded from the muscles and also the behavioural threat displays. Several correlations between muscle and connective activity have been demonstrated, but it is unclear whether the recorded neural activity accompanying the agonistic behaviour is causal of, or simply parallel to, the motor activity. Also if the connective responses should prove to be the cause of motor output, it is unclear whether the connective activity connects directly with the motorneurones which control the agonistic display movements or whether the responses simply trigger activity in other neural circuits which control motorneurone excitation.

The correlations between recorded neural and muscle activity includes the simultaneous generation of phasic bursts in the threat muscles and connectives which accompany the rapid approach of threatening stimuli. Each typical muscle threat response is usually accompanied by the generation of several large spikes from the type A fibres in the connectives. These are often preceded and followed by the generation of medium sized tonic-phasic spikes from type B fibres. In many instances, the more intense and rapid threat displays corresponding to the most phasic muscle threat responses, also correspond to the highest frequencies, and shortest durations, of increased connective activity. This is shown in figure 1, trace b; figure 2, trace c; and figure 4, trace b.

The recordings shown in figure 2 and 3 show that the connective activity recorded during agonistic and other behaviours, has several comparisons with Al activity. For example, resting behaviour was accompanied by reduced activity in the connective and muscle (Fig. 2a). Low intensities of threat display were associated with a relatively low frequency of muscle and connective response activity, and few large spikes were generated in the connectives (Fig. 2b). As the intensity of threat displays were increased, this accompanied a shorter duration of connective response activity and the frequencies of the spikes were generally higher, as were those in the muscle.

The pre-strike behaviour corresponded to burst activity in the Al and large spikes in the connective. Rapid cheliped promotion was not only associated with the typical reduction in Al activity, but also the cessation of large spike activity in the connective. Threat or resting postures adopted after the strike were accompanied by a reduced frequency in connective and muscle activity (Fig. 3).

The transition from threat to escape behaviour patterns, corresponded to a sudden and almost complete reduction of A1 activity, together with a considerable reduction in recorded connective activity (Fig. 2d). As the crab retreated, the chelipeds were raised and the A1 displayed brief high frequency bursts. There were no large spikes evident in the connective trace, although the frequency of activity was increased slightly.

Figure 5b demonstrates another comparison between connective and muscle activity. Repeated stimulation caused the gradual decay of pre-strike twitches shown by the crab. This decay was reflected by reduced Pd pre-strike responses. The reduction in the degree of depressory twitch was also associated with a reduction in recorded connective response; that is, the connective activity generally decreased in frequency and duration.

The agonistic behaviour also appears to be reflected by the extent of simultaneous CxP and connective activity. In the first six threat responses shown in trace d, figure 4, pre-strike twitches were displayed by the crab. These were accompanied by short high frequency bursts in CxP and connective activity. The following three stimuli released threat displays and were associated with shorter high frequency bursts from the connective but no simultaneous increase in CxP activity. The final stimulus released another pre-strike twitch. Consequently, the muscle impulse frequency was increased and was also accompanied by a relatively longer burst of activity recorded from the connective.

The results illustrated in figure 2d and e, appear to indicate that the agonistic behaviour of escape may not be directly associated with connective activity; that is, the motor responses appeared to be spontaneous in the trace without any obvious alteration in connective activity, such as the generation of large spikes which may indicate some form of controlling function. Command fibre activity which can inhibit or suppress behaviour have been demonstrated in crustaceans (Wilkens et al., 1974). In the crayfish, it was found that stimulation of one command fibre could entirely freeze the whole animal, including the appendages and abdominal segments, into any position that the crayfish assumed between stimulations (Bowerman and Larimer, 1974).

The results in this chapter form the basis of a preliminary survey into examining the sequence and pattern of neural and muscular activity associated with the production of complex agonistic behaviours. It may be that the recorded connective responses act in a manner suggested for the DMD's, that is they may have a warning or priming function. They may initiate a pattern of events which eventually lead to the agonistic displays, rather than actually controlling the displays. Various correlations have

been described between neural and muscular activity associated with the threat and strike behaviours. However it is unclear whether the recorded nervous activity is directly causal of the responses recorded from the cheliped muscles, whether it triggers other neurones which control the muscle excitation, or whether it is simply parallel activity. It is apparent that more detailed studies must be made into identifying the interneurones in the connectives and analysing their response properties, as well as examining motorneurone activity in the cerebral and thoracic ganglia, before any positive conclusions can be made concerning the neural control of the agonistic behaviour.

CHAPTER 12

DISCUSSION OF THE POSSIBLE CONTROLLING MECHANISMS FOR THE STRIKE AND THREAT BEHAVIOURS

This thesis has examined some aspects of the underlying neuromuscular basis of three complex behaviours, the fast and slow strike actions and the threat display behaviour of Carcinus maenas. All three behaviours utilize the same muscular elements, the muscles of the cheliped, but rely upon different sequences of activation and co-ordination in these muscles for the performance of the different motor actions, characteristic of each behaviour. However, it is not clear whether these three agonistic interactions share the same neuronal elements which may directly control the motor output or trigger activity in other, separate neural circuits which control excitation to the motorneurones of the cheliped muscles.

The presence of command neurones, stimulation of which can elicit complete or partial behaviours, was first described by Wiersma (1938) in an analysis of crayfish escape behaviour, although the term "command fibre" was not used until later, in studies of the swimming movements in the crayfish (Wiersma and Ikeda, 1964). When command fibres are driven at relatively low frequencies and in unpaired trains, partial or complete behaviours can be released. These behaviours range in complexity from control of heartbeat (Wilkens et al., 1974) to the performance of complex agonistic displays, such as escape behaviours (Wiersma, 1952). The wide variety of other command driven behaviours is reviewed by Larimer (1976).

It is a generally accepted rule that command neurones do not synapse directly upon motor output (Larimer, 1976). Instead, various forms of driver interneurones appear to be interposed between the command and final output. The existence of such intermediate cells has been demonstrated by Kovac (1974) in the neuronal control of crayfish abdominal movements. Kovac established that a command interneurone is responsible for producing abdominal movements. It was found that stimulation of the driver units, termed flexor drivers, which are situated bilaterally in each abdominal connective, produces a single, complete cycle of motor output in lower ganglia that has the same phase and burst period as that produced by the command fibre itself. He suggested that coupling between flexor driver units may account for intersegmental co-ordination displayed during the behavioural movements.

A complete behaviour often requires the participation of several simultaneous commands, but some movements can be released by stimulation of single command fibres. In one example, multiple and complex behavioural movements were found to be released when a specific command fibre was

stimulated over a range of frequencies (Atwood and Wiersma, 1967). In this study when the command fibre, CM4 from the circumoesophageal connective of the crayfish was stimulated at 2 Hz, there was remotion of the 5th pereiopod. When the stimulus frequency was increased to 4 Hz, the abdomen was flexed, the telson was extended and the swimmerets also moved. At 10 Hz, the claws were extended and raised in a defence reflex position.

Animals commonly employ the same group of muscles in different co-ordinated patterns during different behaviours (Wilson, 1962; Larimer and Kennedy, 1969; Clarac and Coulmance, 1971). It appears that each motor output released by command fibre stimulation, is unique to the group of command elements which are stimulated; that is, little or no redundancy apparently exists. This suggests that the command elements may be used in groups to produce variations of movements within a single behavioural action. This feature was described by Larimer and Kennedy (1969) who studied the complex motor system that controls the movement of the uropods in the crayfish. The tonic muscles of the crayfish uropods regulate movements in the three axes of extension-flexion, promotion-remotion and rotation. A bilaterally symmetrical output accompanies abdominal movements, while the appendages can also move asymmetrically during "steering" actions.

Most of the movements of the tail appendages are combined movements, that is they depend upon the action of two or more sets of muscles that move the appendage in different planes. The authors termed such muscles which fire together in a same phase of movement, semi-agonists. In the crayfish, semi-agonistic muscles include the abdominal rotators and flexors. It was envisaged that two methods of control of combined movements could be produced by command activity. Firstly, several command elements, each one specific for a given plane of movement, could be activated simultaneously. Alternatively, a single command fibre might release activity in motor-neurones to produce the combined movements. A series of experiments was performed to show that the latter is in fact the case, and related series of movements could be produced by a single command element, (Larimer and Kennedy, 1969). When the command fibres were stimulated, antagonistic muscles responded in a reciprocal fashion. The authors suggested that this indicated the presence of a motor score (Wilson, 1968) in which a fixed set of motor output connections are activated by specific interneurones.

The relationships between the semi-agonistic muscles of the crayfish uropods did not appear to be rigidly controlled; their synergism could be broken by the activity in particular command fibres (Larimer and Kennedy, 1969). This indicates that their relationships could not be entirely due to connections at the motorneurone level, instead the connections necessary for the appropriate motor output must be pre-synaptic to the motorneurones.

It was concluded that the "combined movements" were encoded in the connections made by single command interneurones and that the performance of such movements would not require activity in a whole set of interneurones, each concerned with a specific part of the motor output. Instead movements utilizing a diverse combination of muscle groups may be triggered by single interneurones. The authors proposed that the use of single interneurones to produce combined movements may be a typical feature of muscle control and not restricted to a few behaviour patterns which require specific triggers, such as the defence reflex of the crayfish (Wiersma, 1952). However the variety of movements in a single behaviour pattern may be larger than the number of command fibres, which necessitates that command elements may be used in groups.

Muscles which have two functions were described by Wilson (1962) in the thorax of grasshoppers. It was found that some of the thoracic muscles are used to move the wings and legs; these were called bifunctional muscles. Elsner (1974) investigated the bifunctional muscles of the grasshopper, Stenobothrus rubicundus, in an attempt to determine whether there is bifunctionality in the motorneurones as well. This grasshopper stridulates successively with the hind wings and hindlegs. Some of the motorneurones which are involved in wing stridulation participate in later stages of leg stridulation, and the main part of downward leg movement is characterised by phasic activity of motorneurones which are involved in wing stridulation. These motorneurones are, therefore, bifunctional. It was found that they were remarkably output-pattern specific, that is they were activated at the same rate during leg stridulation as during wing stridulation. Consequently, frequencies of muscle activity characteristic of wing beat, appear in leg stridulation when these bifunctional motorneurones are activated.

The use of one group of motorneurones for producing two different movements provides an example of neural economy; that is, the grasshopper is able to produce elaborate leg stridulation, wing stridulation and flight, with only a small number of controlling motorneurones. This is possible not only because the behaviour involves bifunctional motorneurones but also because the movement involves bifunctional muscles. It is possible that such a system of neural economy may exist in the control of the strike and threat behaviours of Carcinus on two levels.

The first level of economy may occur with the performance of one behaviour, the strike. For example, there may be a single control element operating on each of the bifunctional muscles of the BI, producing their activity and inactivity at the appropriate stages of the strike so utilizing their different mechanical actions. In the case of the BI Posterior depressor,

continued excitation from a single motorneurone throughout the strike could not only produce movements of depression of the BI and promotion of the coxa, but would also cause the coxal remotory function of the Pd to be expressed during the initial stages of strike recovery. A single neurone controlling the activity of the Anterior depressor muscle may not only cause the muscle to develop tension before the strike, which allows the fast velocities and short duration of the strike to be achieved, but may also be the trigger for rapid coxal promotion. That is, when the tension produced by the Ad is sufficient to raise the total promotory moment over the total remotory moment about the T-Cx joint, and so sets the flip-flop mechanism into operation which may begin rapid promotion.

The second level of neural economy may be within the performance of two agonistic interactions, the strike and threat behaviours. Since a strike always occurs from a position of threat, it is conceivable that a single group of command elements may be involved in both behaviours. It is possible that the motor output of the cheliped muscles may be dependant on the frequency of excitation from command elements. Thus a certain frequency of command fibre excitation may produce the motor output characteristic of threat display positions, while other frequencies may produce the positions of threat which precede the strike behaviour.

Some of the muscles involved in the strike may be considered as semi-agonists (Larimer and Kennedy, 1969). These include the coxa promotor and BI depressors, and the coxa remotors and BI levators. Since their action also produces combined movements, it is possible that their activity is controlled in a similar manner as that suggested for the crayfish semi-agonist muscles (Larimer and Kennedy, 1969). Any command elements may not act directly on the motorneurones controlling these muscles, but may impinge on driver circuits. If a single command element connects to several drivers, which are activated in sequence, the feature of neural economy may still be displayed. Since both the threat and strike behaviours are co-ordinated, it is possible that there is a series of controlling circuits which are activated sequentially to co-ordinate activity in the cheliped muscles, producing the combined movements displayed during threat and strike.

It is apparent that the threat displays are triggered by relatively simple visual stimuli (Chapter 9), while the specific parameter which triggers the fast strike remains unclear. In attempting to explain this, the problems outlined by Hinde (1970) described in the General Introduction, are particularly applicable. An ethologist would infer that a strike will be released when the threshold of defensiveness in a crab reaches a

certain level. That is, at some point the crab "decides" that threat displays are insufficient to deter the predator or opponent and so switches its behaviour to the performance of a more startling and active, fast strike. Where the strike-decision centre lies in the neural elements controlling the strike, can only be suggested. However it is unlikely that any strike-decision centre will be simple. Most stimulated crabs will threaten, but fewer will follow this with a fast strike. It appears that an important factor for releasing the strike is the responsiveness of the crab. The degree of responsiveness can be described using behavioural terminology. For example, a crab requiring a great deal of stimulation before it performs a strike may be said to be less motivated towards a strike than a crab which readily strikes. However describing these features using neurophysiological terms is far more difficult, especially when such a complex behaviour is concerned. In a simpler behaviour, one may be able to express the responsiveness of an animal in terms of frequencies of muscle or neuronal excitation, while in the complicated movements necessary for a strike this would be impossible.

The central trigger for the initiation of a strike behaviour is also unclear. It may be due to a criterion number of nervous impulses reaching a central command circuit, similar to the method of crayfish defence reflex trigger suggested by Glantz (1974c). Once the required number or frequency of nervous impulses is reached, the strike behaviour may then proceed by virtue of sequential excitation to driver units. Larimer and Kennedy (1969) also proposed the existence of several sets of driver interneurones which control the sequence of uropod movement shown in the crayfish. They suggested that the variety of motor output shown during the combined movements, would require either a large number of driver interneurones, a heirarchy of them, or a situation in which there is a more modest number of drivers and certain command fibres may make by-pass connections directly with some motorneurones.

The central trigger activity for the actual strike mode may also be coded in frequency of nervous impulses in the connectives or in the motorneurones to the strike muscle. The involvement of the connectives was suggested by the results in the previous chapter (Chapter 11, fig. 3 and 5). The large spike activity recorded from the connectives, ceases just before rapid coxal promotion begins. This activity may be, or reflect, command fibre activity which precedes the strike. Whether the control is direct onto one muscular element, such as the Ad providing the feature of a trigger muscle, or whether the control acts on all the strike semi-agonistic muscles, remains unclear. The central trigger for threat displays is also unidentified. Again, activity recorded from the connectives in chapters

10 and 11, reflect that each display could be due to a change in frequency of excitation from command elements, or possibly the excitation of intervening driver units.

It is unlikely that a single behavioural trigger of the strike can be defined; there are too many variables. For example, crabs of between 5 and 7 cm carapace width were observed to strike more readily than smaller or larger crabs. Very large crabs rarely tend to strike at all, but often remain in threat positions, while smaller and female crabs tend to adopt other agonistic postures such as egg-protection positions and escape. There may be hormonal reasons which limit the extent of aggression in females. Similarly young or fully grown males may lack a hormone or other factor, such as neurosecretion, which appears in the medium sized aggressive crabs. However, large and small crabs do threaten, and the latter threaten quite readily, and so cannot totally lack all "aggressive-factors". Instead other features may prevent the performance of strikes in these crabs. A small crab may be more likely prey than a larger crab. Thus its behaviour should be adapted for this. That is, instead of remaining still and exposed in a threat position, it would be more strategic to escape and hide. A fully grown male crab may be a less likely prey than a smaller one, and so a Full Threat display may suffice to deter most predators without expending the extra energy necessary to perform a fast strike.

The extra energy necessary to move large chelipeds in a fast strike may also limit the number of strikes shown in fully grown males and has interesting implications in the operation of strike control systems. In the analysis of crayfish uropod movements it was found that command interneurones could produce asymmetrical responses in the appendage muscles of the two sides of the body (Larimer and Kennedy, 1969). For example command fibre stimulation could produce; ipsilateral excitation and contralateral inhibition, the reverse, symmetrical inhibition, or contralateral excitation without ipsilateral inhibition. This feature of asymmetrical response may be important in the control of the strike in Carcinus. Since the chelipeds move symmetrically during a strike, it is likely that there is bilateral control. However this control must take into account the fact that adult crabs possess chelipeds of different sizes, that is one cheliped, especially the propus and dactylus segments is usually larger than the other. The unequal sizes will mean that the rotational energy, Ek, necessary to move the two limbs will be different for each side of the body.

The cheliped used for the calculation of Ek in chapter 2, was the smaller of the two. It was calculated that the moment of inertia of this limb was 511.0784 $g.cm^2$. The moment of inertia of the larger cheliped was

calculated to be 1015.862 $g.cm^2$, almost double. However the three strike muscles, the CxP, Ad and Pd, did not weigh twice as much in this limb, but totalled only 2.08 gm compared with 1.67 gm in the smaller limbs. Using the insect flight muscle energy production values of $6x10^5$ ergs/gm (Machin and Pringle, 1959) the muscles of the large cheliped could produce:

$$(6x10^5 \text{ ergs}) \times 2.08 \text{ gm/s}$$
$$= 12.48 \times 10^5 \text{ ergs/s}$$

This compares with 10.02×10^5 ergs/s calculated for the muscles of the smaller cheliped (Chapter 2).

Since the strike is symmetrical the angular velocities should also be the same, and it may be assumed that the maximum angular velocity of the Cx-BI complex will be 940^o/s in the larger limb (Chapter 2). The rotational energy of this larger cheliped will, therefore, be:

Ek = 0.5 x Moment of inertia x Angular Velocity in radians

= 0.5 x 1015.862 x 269.12

Therefore the rotational energy = 1.367×10^5 ergs.

The rotational energy of the smaller limb was 0.688×10^5 ergs. At the calculated level of energy production of $.01248.10^5$ ergs/ms these muscles of the larger cheliped would require almost 110 ms to produce the known energy requirement of 1.359×10^5 ergs, 50 ms longer than the maximum strike duration. This compares to almost 70 ms needed by the smaller cheliped muscles to produce their known energy requirement. Using the energy production values of skeletal muscle of a toad (Hill, 1949), the larger cheliped muscles would require over 800 ms to produce the energy necessary for a strike, as compared to over 500 ms for the muscles of the smaller cheliped (Chapter 2).

These calculations suggest that there must also be feedback mechanisms controlling the strike trigger. That is, the time of optimum tension development may not be reached at the same time in the two chelipeds, due to the different Ek requirements necessary to achieve the strike. Any central trigger should only be activated when information received regarding the extent of muscle tension development reached optimum levels in both arms. This further supports the suggestion that the trigger may be due to sudden extra activity in a trigger muscle, such as the Ad. That is, when the strike muscles have reached their peak tension levels in both arms, the trigger mechanism may be activated, releasing simultaneous excitation to the Ad of both limbs, providing the injection of extra promotory tension required to operate the flip-flop mechanism.

Indirect evidence strongly supports the role of command fibre activity during normal behaviour. However, as stated by Bowerman and Larimer (1976), it is still unclear whether movements in freely behaving animals are normally driven by action of appropriate command fibres. Although activity in giant fibres has been shown to accompany swimming movements for example (Bowerman and Larimer, 1974; Fraser, 1974b), there is a lack of information concerning the role of command systems in normally behaving animals using chronically implanted electrode recording techniques. In one study cited by Larimer (1976) it was found that attempts to stimulate and record from command elements in intact animals did not generate clearly reproducable behaviours. It was assumed that this stimulation technique failed because the input was artificial and out of context with ongoing voluntary commands.

The preliminary survey performed in Chapters 10 and 11 concerning the neural activity that may be recorded from the connectives of Carcinus during the presentation of threatening stimuli, shows many features which may reflect command activity, such as phasic bursts of large spikes accompanying threat displays. Larimer and Kennedy (1969) proposed that in order to understand the control of motor output by command neurones, it is desirable to work with a set of identified cells that meet certain requirements. The output must be complex temporally and spatially in order to establish the uniqueness of the controlling elements and to place maximum restraint on any control models which may be drawn. At the same time the output must be highly stereotyped. Although the presence of command fibres has not been identified in this thesis, it is clear that the above requirements are fulfilled by the threat and strike behaviours; they are both complex and stereotyped. These agonistic interactions may, therefore, be considered as possible candidates for further elucidating the role of command fibres in complex behaviours.

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