THE ANTENNAL MOTOR SYSTEM OF THE ROCK LOBSTER: COMPETITIVE OCCURRENCE OF RESISTANCE AND ASSISTANCE REFLEX PATTERNS ORIGINATING FROM THE SAME PROPRIOCEPTOR

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SUMMARY

1. Skeletal, muscular and neural organization of the two distal joints (J2 and J3) of the antenna of the rock lobster *Palinurus vulgaris* has been described.

2. Motor innervation (nine motoneurones) of the two distal joints of the antenna has been determined by anatomical and physiological methods. Extensor and flexor muscles of J2 and J3 are each innervated by one specific excitatory tonic motoneurone. One excitatory phasic motoneurone is common to both the J2 and J3 extensor muscles, another to the J2 and J3 flexor muscles. The J3 extensor muscle also receives a specific phasic motoneurone. An accessory extensor muscle which spans J2 and J3 is innervated by one excitatory motoneurone. A common inhibitory motoneurone innervates the two flexor and the two extensor muscles of J2 and J3.

3. Movements of J2 and J3 are sensed by a proprioceptor (chordotonal organ). Reflex patterns involving this proprioceptor have been extensively studied. Sinusoidal extension-flexion movements imposed on the J3 joint induced intra-segmental reflexes (on the J3 muscle innervations) and inter-segmental reflexes (on the J2 muscle innervations) which exclusively involved the tonic excitatory motoneurones and the common inhibitory motoneurone.

4. Resistance reflexes (activation of the muscle stretched by the imposed movements) occurred whatever the excitability level of the animal and involved both flexor and extensor motoneurones. The motoneurones spiked at a higher frequency when the velocity of the imposed movement was increased. The common inhibitor motoneurone was activated during extension movements.

5. In preparations which became ‘more excitable’, assistance reflexes could be induced by joint stimulations which formerly induced resistance reflexes. Sometimes assistance reflexes could be induced by increasing the velocity of the movements imposed on J3. Assistance reflexes mainly involved extensor motoneurones.

6. The role of the tonic, phasic and inhibitory innervations and the functional significance of resistance and assistance reflexes are discussed in relation to the behavioural role of the rock lobster antenna.
INTRODUCTION

Stretch reflexes and resistance reflexes have been extensively studied since the work of Liddell & Sherrington (1924) upon vertebrates and the work of Eckert (1959) upon invertebrates. They are both induced by proprioceptors, the discharge of which determines the contraction of muscles stretched during a movement passively imposed on the joint at which the muscles operate. The main characteristic of these reflexes is to resist the imposed movement.

In vertebrates, the stretch reflex is produced by the muscle spindle sensory inputs. In invertebrates, particularly in Crustacea, the resistance reflex can be induced by similar sensory organs (i.e. sensory cells associated with special muscular structures) like the myochordotonal organ (Barth, 1934; Cohen, 1963a; Alexandrowicz, 1972) and the thoracicoxal receptor (Alexandrowicz, 1958, 1967; Alexandrowicz & Whitear, 1957; Bush, 1976, 1977) located in the walking legs. At the level of each joint of the cephalic and thoracic crustacean appendages resistance reflexes are also produced by chordotonal organs that provide sensory messages similar to those of the joint receptors of vertebrates.

It is well known that in vertebrates and invertebrates the gain of reflex loops is strongly modulated by various influences coming from the central nervous system and from the different sensory inputs, acting either on the sensitivity of the neuromuscular receptors by way of specific motor innervations, or directly on motoneurone and interneurone excitability. Therefore, it appears more and more probable that the effectiveness of the proprioceptive reflexes depends on the behavioural situation (Bassler, 1973, 1974) and particularly on the intended muscle activities (Hammond, 1956; Hagbarth, 1967; Evarts & Granit, 1976), this idea suggesting that a proprioceptor pool may be able to mediate reflex actions at different levels of the nervous system (Phillips, 1969; Lundberg, 1966; Shapovalov, 1975). The possibility that different and sometimes opposite reflex strategies could be induced by sensory fibres from the same origin has been considered but not definitively demonstrated in vertebrates, owing to the difficulty in individualizing the reflex contributions of the different kinds of kinaesthetic inputs. Thus, all the attempts to attribute the ‘shortening reaction’, first described by Wesphal (1877) in man and by Sherrington (1909) in the animal, to a paradoxal action of Ia, Ib or II afferent fibres remain unsatisfactory. In invertebrates the possibility of reversal of reflex effects has been clearly demonstrated by Bassler (1976).

The present work describes a relatively simple neural system that controls the two distal joints of the rock lobster antenna (Clarac & Vedel, 1975; Vedel & Clarac, 1975). It is demonstrated that one proprioceptor can be responsible for reflex strategies that are qualitatively different according to the reactivity level of the animal or the parameters of the mechanical stimulations imposed on the joints.

METHODS

Animals. Experiments were performed on rock lobster Palinurus vulgaris of 500–800 g in weight. This species adapts well to life in an aquarium, and spontaneous motor activities are readily obtained in free-moving experimental animals.
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*Anatomical methods.* The organization of the motor and sensory innervation and the structure of the proprioceptors were determined by methylene blue staining. The number and the diameter of the motoneurones in the flexor and extensor nerves were determined in transverse sections made at different levels of the nerves.

*Preparation.* Reflex actions were studied in animals fixed by rubber bands dorsal-side up in a perspex dish filled with 5 l of oxygenated sea water at 16 °C. The cephalothorax was secured on a strip of perspex in order to maintain the animal in a posture allowing the spontaneous movements of the walking legs. This appeared necessary to ensure a good circulation of sea-water in the branchial chamber.

*Dissection.* During dissection, the animal's excitability was reduced by lowering the sea-water temperature to approximately 7 °C, using a Peltier cooler.

The right or left antenna was fixed in a holder with J2 and J3 joints in complete extension. The cuticle was cut from the dorsal side of the S2 segment. The J2 flexor muscle was carefully removed in order to isolate the flexor nerve up to its connection with the J3 flexor muscle. Similarly, the extensor nerve was isolated up to its contact with the J3 extensor muscle; one of its branches selectively innervating the J2 extensor muscle was also isolated. Flexor and extensor muscles were completely denervated to avoid contractions during reflex activities.

All the sensory nerves related to the S2 and S3 segments and to the flagellum were cut except the nerve of the chordotonal organ common to the J2 and J3 joints. This sensory denervation permitted selective stimulation of the proprioceptor when extension-flexion movements were imposed on the flagellum.

*Mechanical stimulation.* Angular sinusoidal movements were imposed on the flagellum (J3 joint) by an electro-mechanical apparatus (Clarac & Vedel, 1971). The movement parameters were recorded by means of a linear potentiometer. Considering that J3 maximum rotation was limited to a range of 180°-120°, flagellum movement was imposed in a middle range from 165° to 135°. Reflex activities were generally studied during one bidirectional sinusoidal movement cycle, imposing successively either an extension-flexion pattern, or a flexion-extension one. Different cycle periods (1-3-4-5 s) corresponding to angular velocities of 46°/s to 13°/s, were used to test the physiological properties of the reflex loops.

*Recording methods.* Recordings were made from nerves by use of four suction electrodes. Two were positioned at the distal end of the extensor and flexor nerves (S3 level) in order to record from the motoneurones of the J3 muscles; the other two were located on nerve branches specifically innervating the extensor and flexor muscles of J2. Simultaneously, intracellular recordings were made from muscle fibres by means of glass microelectrodes (3 M-KCl), in order to correlate neuronal and muscular activity. Motor activities and movement parameters were recorded on tape.

*Averaging methods.* The reflex discharge of each motoneurone was analysed by the phase histogram method. Duration of the analysis phase was equal to the movement period. Whatever its duration, the phase was divided into 25 bins. Spikes occurring in equivalent bins on six successive repetitions of the same movement were summed. Mean frequency curves were plotted by calculating the mean frequency in any bin according to the bin duration and the number of movement repetitions. Phase histograms and mean frequency curves were computed on a PDP 11/40 computer.
Key to abbreviations used in the figures

S1, S2, S3, Flag. Successive antennal segments from the proximal to the distal segment

J0 Joint articulating S1 to the cephalothorax
J1 S2–S1 joint
J2 S3–S2 joint
J3 Flag.–S3 joint
En. S2 Extensor nerve at the S2 level
En. S3 Extensor nerve at the S3 level
Fn. S2 Flexor nerve at the S2 level
Fn. S3 Flexor nerve at the S3 level
Em. J2 J2 extensor muscle
Em. J3 J3 extensor muscle
Fm. J2 J2 flexor muscle
Fm. J3 J3 flexor muscle
AEm Accessory extensor muscle
E. J2 Specific excitatory motoneurone of the J2 extensor muscle
E. J3 Specific excitatory motoneurone of the J3 extensor muscle
F. J2 Specific excitatory motoneurone of the J2 flexor muscle
F. J3 Specific excitatory motoneurone of the J3 flexor muscle
pE. J3 Specific phasic excitatory motoneurone of the J3 extensor muscle
CF Excitatory motoneurone common to the J2 and J3 flexor muscles
CE Excitatory motoneurone common to the J2 and J3 extensor muscles
AE Specific excitatory motoneurone of the accessory extensor muscle
CI Inhibitory motoneurone common to the J2 and J3 extensor and flexor muscles

RESULTS

(I) Morphology of the rock lobster antennae

The paired cephalic antennae of rock lobsters differ in morphology and motor activities from those of other crustaceans. They appear to be specialized for the tactile location of nearby objects. Each antenna is composed of a distal flagellum, which is longer and more rigid than in other species, and three basal segments. According to the terminology of Paterson (1968) for *Jasus lalandii* and of Hartman & Austin (1972) for *Panulirus interruptus*, the three basal segments are named (starting with the proximal one) S1, S2 and S3 (Fig. 1A, B). They are articulated by the joints J1 (S1–S2 joint), J2 (S2–S3 joint) and J3 (S3–flagellum joint). It is here proposed to give the name J0 to the joint articulating S1 to the cephalothorax.

Movements of each joint are uniplanar: J0 moves S1 in a dorso-ventral plane, J1 moves S2 in a medio-lateral plane, J2 and J3 act approximately in the same plane extending the flagellum forwards from the cephalothorax, or flexing it back towards the cephalothorax. The combined movements of J2 and J3 allow the flagellum about 120° of anterior–posterior rotation, each contributing about 60° of movement.
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(II) Motor organization of the J2 and J3 joints

1. **Muscles**

J2 and J3 are each moved by one flexor (Fm. J2, Fm. J3) and one extensor muscle (Em. J2, Em. J3) located in S2 and S3, respectively (Fig. 1C). Flexor muscles are found in the dorsal section of the segments, extensor muscles being in the ventral part. The extensor muscles are greater in volume than the flexor muscles.

In addition, an accessory extensor muscle (AEm, Fig. 1C) lies on the dorsal surface of the extensor muscles spanning J2 and J3. Proximally, it is attached to the middle of the exterior side of the S2 exoskeleton; distally, it terminates in a thin tendon inserted on the ventral part of the flagellum cuticle. Owing to its small size this muscle, named accessory extensor because of its anatomical organization, appears unable to induce joint movements. Indeed, its diameter never exceeds $500 \mu m$ in *Palinurus vulgaris* while the J2 and J3 extensor muscles are 10 mm broad.
Lateral view

Fig. 2. Anatomical organization of the chordotonal sensory organ (CO) associated with the J2 and J3 joints of the rock lobster antennae. The chordotonal organ is composed of a large elastic sheet lengthened and shortened by J2 and J3 movements. About 400 sensory neurones are distributed along the sheet in three groups, g1, g2 and g3. The lateral view shows that CO is closely connected to the dorsal ridge of the tendon of the J3 extensor muscle (Em tendon). Sn: sensory nerves.

(2) Proprioceptors

There is no evidence that the AEm of the rock lobster has a proprioceptive role, although a similar accessory flexor muscle seems to have such a function in the American lobster antenna (Sigvardt, 1977).

According to Hartman & Austin (1972), sensory information relating to J2 and J3 movements is mainly provided by a chordotonal organ common to the two joints (Fig. 2). Located between the extensor and flexor muscles, this sensory organ appears as a large elastic sheet (Fig. 2, CO) attached proximally to the exterior side of the S2 exoskeleton near the lateral condyle of J2. Spanning J2 obliquely it terminates distally on the medial side of S3 near the medial condyle of J3. A thin strand connects the middle of the sheet to the ventro-medial side of the flagellum. A complex network of thin strands connects the CO ventral surface to the dorsal ridge of the tendon of the J3 extensor muscle (Fig. 2).

Approximately 400 sensory cells are distributed in three groups along the sheet: one proximal (g1) and one distal group (g3), and one medial group (g2) in which the cell bodies are more diffusely distributed. The CO sensory cells can be divided into two clearly distinct physiological categories (C. Rossi & J. P. Vedel, in preparation): those exclusively sensitive to angular position changes (dynamic sensitivity) and those...
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Fig. 3. Identification of the motoneurone impulses and of their neuromuscular junction potentials. (A) Identification of the motoneurones innervating J2 and J3 muscles by simultaneous recordings of flexor and extensor nerve branches at different levels. Among the nine neurones histologically identified, only 6 discharge spontaneously when the flagellum is not moving. J2 and J3 motoneuronal activities are recorded from the common flexor nerve (Fn. S2) and from the specific Fm. J3 nerve branch (Fn. S3). Confirmation that F. J3 motoneurone discharge occurring in the two flexor nerve recordings reaches Fm. J3 selectively is given by the absence of its activity in specific Fm. J2 nerve branches. In the same way, recordings of the Fm. J2 nerve have been used to confirm the innervation of this muscle by the common inhibitor motoneurone (CI). (B) Competitive occurrence of EJP’s and IJP’s in one Em. J3 muscle fibre related to E. J3 and CI impulses. (C) In a same muscle (Em. J3) the fibres do not all seem to be innervated by CI. (D) EJP’s recorded in AEm muscle fibres are correlated to the smaller impulses recorded in the J3 extensor nerve. IJP’s are never observed in AEm muscle fibres. (E) Simultaneous occurrence of EJP’s (F. J3) and IJP’s (CI) in a flexor muscle fibre (Fm. J3).

responding to maintained angular positions (static sensitivity). Some cells respond to either J2 or J3 movements, some others to J2 and J3 movements, depending upon their position on the sheet.
The distribution and diameters of the motoneurones that were found in the extensor and flexor nerves to J2 and J3 are shown in Table 1.

Electrophysiological recordings showed that when the flagellum was stationary, six motoneurones discharged spontaneously (Fig. 3 A). Four of these neurones, one in each nerve, fired tonically with large spikes (E. J2, E. J3, F. J2, F. J3, in Fig. 3 A). Correlations between axonal discharges and muscle fibre membrane potentials show that these neurones induce large EJP’s in their corresponding muscle (Fig. 3 B, C, E). A fifth motoneurone firing spontaneously (CI) is characterized by small impulses occurring simultaneously in the four muscle nerves. This axonal activity is responsible for IJP’s (Fig. 3 B, E) in the two extensor and two flexor muscles but apparently not in AEm. In one muscle (Em. J3) this common inhibitory motoneurone does not seem to reach all the muscle fibres (Fig. 3 C). A sixth motoneurone (AE) discharges more irregularly from one experiment to another. Its activity is characterized by very small spikes which are recorded in the nerve branches innervating Em. J3 and AEm and which are correlated to EJP’s in the accessory extensor muscle fibres (Fig. 3 D).

The three other motoneurones shown by histology are mainly activated during fast antennal movements like those occurring during escape behaviour. Each of them induces EJP’s. One of them (CF) innervates the two flexor muscles; another (CE), the two extensors; and the third (pE-J3) innervates the J3 extensor muscle (Fig. 4).

From the above data, and that of Clarac & Vedel (1975), the muscle innervation can be modelled as shown in Fig. 4.
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Fig. 4. Motor innervation of the two distal joints (J2, J3) of the antenna of the rock lobster 
*Palinurus vulgaris*. Motoneurones concerned with the chordotonal organ (CO) reflex actions 
are indicated by their relation to sensory afferences. Excitatory motoneurones: F. J2, F. J3, 
CF, E. J2, E. J3, CE, pE. J3, AE. Inhibitory motoneurone: CI. Flexor muscles: Fm. J2, 

(III) Reflex modulation of the motoneurone activities induced by 
the chordotonal organ

As described in Methods, complete S2, S3 and flagellum sensory denervation, 
keeping only the chordotonal organ centrally connected, permits selective stimulation 
of this proprioceptor by flagellum movements. Reflex effects have been systematically 
tested by means of two sinusoidal movement patterns imposed on J3, extension–flexion 
movement and flexion–extension movement.

(1) Tonic reflex effects

Static discharge of the motoneurones innervating J3 muscles depends on the 
angular position imposed on the flagellum. E. J3 is more active during maintained 
flexion and F. J3 discharges at higher frequency during maintained extension. Spon-
Fig. 5. Intra-segmental (on J3 motor innervation) and inter-segmental (on J2 motor innervation) resistance reflexes induced by (A) flexion-extension and (B) extension-flexion sinusoidal movements imposed on the flagellum. F. J2 and F. J3 flexor motoneurones are activated during the extension phase of the movements, E. J2 and E. J3 during the flexion phase. The activity of the common inhibitory motoneurone (CI) increases exclusively during extension movements.

Simultaneous static activities of these motoneurones change as a function of the animal's state but never exceed 20 impulses/s. Static discharge of the J2 muscle motoneurones are hardly ever influenced by flagellum positions. When J2 is maintained completely extended during experiments, F. J2 is generally more active than E. J2.

Whatever the J3 angle, the discharge frequency of CI and AE is very variable; in fact the activity of these two motoneurones seems to depend mainly on central influences.

(2) Resistance reflexes

Dynamic movements imposed on the flagellum strongly modulate the discharge of most of the motoneurones spontaneously active under static conditions: E. J2, E. J3, F. J2, F. J3 and CI.

The effect most commonly and regularly obtained is the well-known resistance reflex which increases the J2 and J3 extensor motoneurone discharges during a flexion movement, while the flexor motoneurone activity is increased during a flagellum extension (Fig. 5, 6). When this reflex pattern occurs selectively, each motoneurone completely stops firing during the movement in the opposite direction to that responsible for the resistance reflex.

Since imposed movements are limited to the flagellum and their effects are observed in the J2 and J3 motoneurones, it appears that resistance reflexes act by way of intra-segmental loops (on E. J3 and F. J3) as well as inter-segmental loops (on E. J2 and F. J2), their actions being nevertheless quantitatively different in the two cases. Individual phase histogram analysis of the different motoneuronal discharges,
Fig. 6. Resistance reflexes. Individual phase histogram analysis of the reflex activity of the J2 and J3 motoneurones during (A) extension—flexion and (B) flexion—extension flagellum movements. Movements were bidirectional and sinusoidal. Spikes occurring in equivalent bins on six successive repetitions of the same movement were summed in each histogram. Cycle duration (i.e. movement duration): 4.3 s. Bin duration: 172 ms. Black rectangles before each phase histogram indicate the level of the motoneuronal static discharge averaged over the 10 s preceding the movement. Intra-segmental reflexes (F. J3, E. J3) are generally more powerful than the inter-segmental ones (F. J2, E. J2) and moreover, resistance reflexes appear stronger when they are induced in the first part of the movement.
Fig. 7. Assistance reflexes induced by extension–flexion movement of the flagellum. The histograms of this figure are to be compared with those of the Fig. 6A. Fig. 6A and Fig. 7 show data from the same preparation. When the preparation becomes more active, extensor assistance reflexes occur (E. J2, E. J3 activation during the extension phase of the movement). Simultaneously, the flexor resistant reflexes (F. J2, F. J3) induced by the same movement are strongly depressed. During the flexion phase of the movement, extensor resistance reflexes persist.

CI and AE reflex discharges are not significantly different in the two experimental situations illustrated in Fig. 6A and Fig. 7.

Illustrated in Fig. 6 shows that the predominant effect exerted by J3 stimulation is upon E. J3 and F. J3, i.e. the intra-segmental reflexes are stronger than the inter-segmental reflexes. Moreover, it appears in this figure that the resistance reflexes are often more efficient when they are induced in the first part of the bidirectional movement imposed on the flagellum (compare F. J3 burst during extension–flexion and flexion–extension movements in Fig. 6).

CI is also activated by dynamic movements of the flagellum but more weakly than the excitatory motoneurones. Its discharge increases during the extension phase like that of the flexor motoneurones (Figs. 5, 6).

AE discharge, which is generally very low and variable when the flagellum is maintained immobile, increases slightly at the beginning of the dynamic movement, whatever the initial direction (extension or flexion). AE activity is never significantly modulated during the bidirectional movements.

(3) Assistance reflexes

When the animal remained unmoving for several hours, the excitability of the central nervous system spontaneously changed. These different states of the preparation are correlated with modifications of the motoneuronal static discharges, with quantitative
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Fig. 8. Effect of the velocity of the flagellum movement on the reflex patterns induced by the chordotonal organ. In active animals, when the extensor assistance reflexes do not appear during flagellum extension–flexion imposed a low velocity, they can be obtained by shortening the movement duration without changing the angular course amplitude. Discharge of the extensor motoneurones (E. J2, E. J3) increases progressively during the extension phase of the movements, whereas flexor motoneurone activities (F. J2, F. J3) simultaneously gradually decrease.

modulations of the resistance reflexes (static and reflex activity increases when the excitability increases) and sometimes with the appearance of new reflex strategies.

Though it was very difficult to quantify the central nervous system reactivity, it appeared that resistance reflexes were selectively induced when the state of the preparation was very stable and somewhat depressed. These conditions occur momentarily after the dissecting phase of the experiment or when the sea water temperature was maintained very low (5–8 °C).

If the animal became spontaneously more active, the bidirectional flagellum movements, which previously induced exclusively resistance reflexes, could also be responsible for assistance reflexes.

This reflex pattern involved predominantly extensor motoneurones and produces E. J2 and E. J3 activation during the extension phase (Fig. 7) of the movements, but only when the extension precedes the flexion (i.e. during an extension–flexion movement) (Fig. 7). During the flexion phase the extensor resistance reflexes persisted and remained stronger than the assistance reflexes when the imposed movements were slow.

This activation of E. J2 and E. J3 during the flagellum extension was accompanied
Fig. 9. Individual phase histogram analysis of the J2 and J3 motoneurone activities during flagellum extension-flexion movements applied at different velocities. In A, B and C the movement duration (cycle period) was respectively of 4.3, 2.3 and 1.3 s. Extensor motoneurone activities (E. J2, E. J3) increase progressively during flagellum extension, these assistance reflexes becoming stronger than the resistance reflexes occurring during the flexion phase of the movement. Simultaneously flexor resistance reflexes (F. J2, F. J3) decrease substantially. AE and CI discharge patterns are quantitatively unmodified by the movement velocity.
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![Graph](image)

Fig. 10. Analysis of the mean discharge frequency of E. J3 (left) and F. J3 (right) motoneurones during resistance reflexes induced by flagellum movements imposed at different velocities. Movement duration: A, 1.5 s; B, 2.5 s; C, 3.5 s; D, 4.5 s. Mean frequency curves reveal that when they are induced under the same conditions (in the first part of the sinusoidal movement) E. J3 and F. J3 reflex discharges are differently influenced by the movement velocity. The discharge frequency of the extensor motoneurone appears closely dependent on this movement parameter, but this is not the case for the F. J3 reflex response.

by a decrease in the resistance reflexes which were induced simultaneously by the same movement in the flexor motoneurones (compare F. J2 and F. J3 histograms in Fig. 6 A and Fig. 7, i.e. either with or without extensor assistance reflexes). If the assistance reflexes did not appear during slow flagellum extension, they could be obtained by increasing the movement velocity without changing the angular displacement. Such an experimental situation is illustrated in Fig. 8 and 9, where three extension-flexion movements of different durations have been applied to the flagellum. Thus, assistance reflexes progressively appear as movement velocity is increased, and become more important than the resistance reflexes (Fig. 8 C, 9 C). Simultaneously flexor resistance reflexes gradually decrease (F. J2, F. J3, Figs. 8, 9).

CI and AE response patterns to flagellum movements remained qualitatively unmodified compared to those observed when J3 extension-flexion induced only resistance reflexes.

Flexor assistance reflexes were sometimes observed during flexion-extension movements, but were always weaker and less reproducible than the extensor ones.
Fig. 11. Modulation of the E. J3 discharge frequency by the velocity of the flagellum movement during assistance and resistance reflexes. During assistance reflex induced by flagellum extension (left) the E. J3 discharge frequency increased strongly with the movement velocity. Comparison in the same experiment of E. J3 responses to flagellum flexions when the animal is in different states of excitability shows that the resistance reflex is sensitive to the movement velocity when it occurs selectively (right), but tends to remain constant when it is preceded by an assistance reflex (left). Movement durations: A, 1-3; B, 2-3; C, 4-3 s.

(4) Modulation of motoneuronal discharge frequency by J3 movement velocity

Mean frequency analysis of motoneuronal activities revealed a differential sensitivity of the extensor and flexor motoneurone responses to the velocity of the flagellum.

During the resistance reflexes, the discharge frequency of E. J3 attained a higher maximum when the cycle duration was shortened, i.e. when the mean velocity of the movement increased. By contrast, whatever the movement duration, F. J3 discharge frequency usually remained constant (Fig. 10). A similar, but less clear-cut effect, was also found in the E. J2 and F. J2 intersegmental resistance reflexes.

During assistance reflexes, the maximum discharge frequencies of E. J3 (Fig. 11) and E. J2 also depend closely on movement velocity. During the extension phase of an extension–flexion movement, this increase of the assistance reflex activity was followed, during the flexion phase, by an extensor resistance reflex characterized by a discharge frequency independent of movement velocity (Fig. 11). When an assistance reflex did not occur during such a series of extension–flexion flagellum movements, the extensor resistance reflex increased with movement velocity (Fig. 11).

The CI reflex discharge also depends on the duration of the movement (Fig. 12) but maximum frequency of CI usually remained much lower than that of the extensor motoneurones discharge induced by the same movement (cf. Fig. 10).
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**DISCUSSION**

Many studies have been devoted to the neural mechanisms underlying rhythmic motor outputs, but it seems that neural processes related to non-cyclic motor activities and particularly to voluntary movements have not raised such interest. However, some invertebrate structures, such as the rock lobster antennae, seem to provide good preparations in which to study this kind of neural control system.

The structure of the antennae provides one advantage, for each joint moves in only one plane, facilitating the analysis of the processes which coordinate movements of the joints. Neural organization is also relatively simple, with few motoneurones to each muscle. Proprioceptors are also readily isolated experimentally and thus their respective sensory activities and reflex actions can be easily studied.

The motor activities of the antennae appear more varied than those in other crustaceans. The large size of the basal segments and the rigidity of the flagellum allow the antennae to exert more force on surrounding objects than can the antennae of other species. This enables the antennae to be used as 'threatening' and defensive organs in addition to providing sensory information.

**Excitatory motoneurones**

The existence of excitatory motoneurones common to the synergistic muscles of the J2 and J3 joints (CE common to the two extensor muscles, CF common to the two flexor muscles) demonstrates that the movements of these two joints are closely linked.
to produce large extension and flexion movements of the flagellum. Since CE and CI are activated during high velocity movements, it appears that this anatomical coupling of J2 and J3 motor commands may be used for phasic actions. The lack of reflex activation of these common motoneurones is consistent with the observations of Sigvardt (1977) on the American lobster antenna and suggests that their activities are mainly dependent on central commands. Nevertheless, previous work (Vedel & Clarac, 1975) suggests that, in the rock lobster, this kind of motoneurone should become sensitive to reflex actions when imposed joint movements are combined with other sensory stimulations. The absence of reflex activation of fast motoneurones has also been observed in the PD and CP muscle innervations of the crab (Spirito, Evoy & Barnes, 1972).

The poorly facilitating EJP's of the four motoneurones (E. J2, E. J3, F. J2, F. J3), each innervating one of the J2 and J3 muscles, seem to be similar to those observed in slow-acting muscle fibres by Atwood (1965, 1977) and thus could be responsible for slow contractions and consequently for slow movements. Thus, by their anatomical distribution these neural commands of J2 and J3 muscles appear to be more differentiated than the phasic ones and suggest a greater independence of the motor activities of the two joints during slow movements.

In view of their spontaneous tonic discharges it may be expected that these motoneurones assume control of the muscular tone and postural activities of the flagellum. In this way, two motor systems can be clearly distinguished in the flagellum neural command, a tonic one and a phasic one. Their sensitivity to proprioceptive inputs appears very different, and the coordination of their activities has to be examined during spontaneous flagellum movements.

**Inhibitory motoneurone**

The existence of inhibitory axons innervating crustacean striated skeletal muscles has been convincingly demonstrated in the work of Wiersma since 1933. However, while crustacean preparations have provided detailed information about mechanisms of action of inhibitory axons on muscle, their functional significance remains unclear, especially when the same neurone innervates several muscles and more particularly antagonistic muscles as has been observed in most of the crustacean limbs (Wiersma, 1941; Wiersma & Ripley, 1952; Cohen, 1963a).

Considering the common inhibitory innervation (CI) of J2 and J3 muscles of the antennae in the rock lobster, it has been previously observed (Vedel & Clarac, 1975) that during spontaneous dynamic motor activities, CI is strongly activated whatever the direction of the flagellum movement, in extension or in flexion. These results indicate that IJP's occur simultaneously in the contracting muscle (i.e. the muscle producing the movement) and in the antagonistic muscle which is stretched and generally electrically silent. CI could be involved in control of the movements in two ways. Firstly, CI could modify contractile properties of the muscle fibres (Kennedy & Takeda, 1965a, b; Kennedy & Evoy, 1966). This supports the very important idea suggested by Florey (1977) that ‘the same motor program can produce different movements when the responsiveness of the muscles fibres is altered’. Secondly, CI
Reflex patterns in the rock lobster antenna

Build control muscle relaxation by suppressing the resting tension which can persist in a muscle fibre even when excitatory motoneurones are silent (Hoyle, 1968).

In contrast with its patterns of discharge during spontaneous movements, CI is activated during reflex actions by flagellum extension movements and thus opposes the flexor resistance reflexes which occur simultaneously. During extensor assistance reflexes its inhibitory action on flexor muscles acts jointly with the depressing effect directly exerted upon flexor excitatory motoneurones.

It is interesting to note that inhibitory axons have not been found in the two distal joints of the American lobster antenna (Sigvardt, 1977). This difference of motor innervation may be related to the different behavioural involvement of the antenna in the two species.

Resistance reflexes

In each crustacean appendage all the chordotonal and neuromuscular receptor organs are able to induce resistance reflexes during imposed joint movements (Bush, 1963, 1965; Spirito, 1970; Clarac & Vedel, 1971; Spirito et al. 1972; cf. Mill, 1976).

While the role of both resistance reflexes in invertebrates and of myotatic reflexes in vertebrates clearly appears to be to maintain a centrally programmed posture by compensating for external disturbances, their functions during voluntary joint movements are less obvious, since they oppose the movement. In invertebrates, during normal walking or spontaneous movements, resistance reflexes are apparently absent (Barnes, Spirito & Evoy, 1972; Vedel, Angaut-Petit & Clarac, 1975). However, during walking, imposed joint movements are able to produce resistance reflexes: this leads Barnes et al. (1972) to suggest that they may act to compensate for any changes in loading which may occur during normal locomotion on a rough substrate.

As has been described for the motor command of the claw of the crab (Bush, 1962, 1965) and for the activities of the walking legs of the American lobster (Ayers & Davis, 1977), the reflex discharge frequency of the extensor motoneurones of the flagellum increases with the velocity of the imposed movement. In contrast, the flexor reflex discharge is not modulated in this way. This difference could be related to the behavioural role of the extension and flexion movements of the flagellum: extension movements are mainly responsible for mechanical probing of the environment and so require constant adjustments of the velocity and force parameters during the performance of the movement, whereas flexion movements appear mainly involved in postural motor activities generally effected at constant velocity.

Assistance reflexes

The occurrence of assistance reflexes (under certain conditions) raises the problem of the functional plasticity of the reflex loops.

In invertebrates, Wilson & Davis (1965) first observed in the chela of Procambarus that activity of the excitatory opener motoneurone could increase during passive opening movements. The term 'assistance reflex' was suggested by Bässler (1973, 1974, 1976) when he obtained a complete reversal of a proprioceptive reflex according to the state of the animal. His work demonstrated that ramp-wise stretching of the
femoral chordotonal organ of the stick insect leg induced an extension of the femur-tibia joint in ‘inactive’ animals and a flexion of the same joint in ‘active’ animals. Electrophysiological study showed that the extensor motoneuronal activity increased in the first case and decreased in the second case (Bässler, 1976). Ayers & Davis (1977) observed in the walking leg of the lobster *Homarus americanus* that at the level of the CB and TC joints, elevator and depressor (CB muscles) and retractor (TC muscle) muscles are excited by the movements they normally cause. The authors compare these reflexes to the positive feedback reflexes which occur in the muscles of the abdominal swimmerets during imposed cyclic movements (Davis, 1969).

Qualitative modifications of reflex actions have also been observed in vertebrates on changing the central state of the preparation. By the method of conditioning and test stimuli, Holmqvist & Lundberg (1961) demonstrated in the cat that muscular afferents such as joint afferents are able to increase, decrease or to not modify the monosynaptic reflexes (test stimuli) according to the preparation used: spinal, decerebrate or mid-pontine lesion. Several authors (Forssberg, Grillner, Rossignol & Wallen, 1976; Forssberg, Grillner & Rossignol, 1977; Miller, Ruit & Van Der Meché, 1977), have observed that tactile stimuli can provoke opposite effects on the limb reflex activity in the cat, according to the phase of the step cycle during which they are applied.

In the rock lobster, the excitability of the animal can determine whether assistance or resistance reflexes occur in the extensor motoneurones E. J2 and E. J3, and can influence the production of assistance reflexes when the velocity of movements imposed upon the flagellum is increased.

It appears that sensory information from the J2–J3 chordotonal organ can induce different reflex strategies. The depression of the flexor resistance reflexes correlated to depression of the extensor assistance reflexes shows that this reflex reorganization affects the whole of the J2 and J3 motor commands.

The major threat/defensive movement of rock lobsters is forward extension of the antenna which may explain the predominance of extensor-based assistance reflexes. The assistance reflex should be considered as a reinforcement of a defence reaction; the reflex pattern being preferentially selected by the central command to assist voluntary extension movements in free moving animals.

The possibility of obtaining different reflex strategies from the chordotonal organ enhances the idea that extensor and flexor sensory informations originating from a proprioceptor are largely distributed to the extensor and flexor motoneurones which assume the command of each joint. Thus, one can suppose that a central motor program for a given behaviour would be able to select the reflex pattern which would contribute most efficiently to its realization. According to the observation of Ayers & Davis (1978) on the reflex patterns during locomotion in *Homarus americanus*, assistance reflexes could be considered as positive feedbacks used to amplify the central motor commands during the power stroke of the movement.

In order to go further in the study of the antennal motor system it will be necessary to resolve the role of the accessory extensor muscle. Details of the motor command (AE motoneurone) to the AE muscle, as well as mechanical properties and possible proprioceptive functions of this muscle remain completely unknown. Nevertheless, it is very important to determine whether AEm is or is not a neuromuscular recepto
In order to complete the schema of the sensory-motor organization of the J2 and J3 joints and to progress in the understanding of the reflex mechanisms on these two levels.

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REFERENCES


