REFLEX REVERSAL RESULTING FROM ACTIVE MOVEMENTS IN THE ANTENNA OF THE ROCK LOBSTER

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SUMMARY

1. In the rock lobster, *Palinurus vulgaris*, study was made of the effect of active flexion of the J3 joint of the flagellum upon the reflex produced by passive movement of this joint.

2. Active flexion was accompanied by activity of motoneurones to muscles assisting the movement.

3. Passive flexion not immediately preceded by active flexion was accompanied by activation of muscles to resist the movement (resistance reflex). When the passive movement followed slow active flexion ($7.5°/s$), there was some activity to assist the movement. If preceded by an active flexion of high velocity ($25°/s$), the assistance reflex predominated.

4. Passive extension produced a resistance reflex that was usually facilitated by preceding active flexion.

5. The functional significance of the reversal is discussed.

INTRODUCTION

In the invertebrates and vertebrates, a reflex may change from a resistance reflex to an assistance reflex or vice versa as a result of the physiological conditions. Thus, in insects (Bässler, 1976) and crustaceans (Vedel, 1980; DiCaprio & Clarac, 1981) it has been demonstrated that one proprioceptor can elicit either a resistance reflex or an assistance reflex in the same muscle according to the state of activity of the animal. In mammals, reversal of cutaneous reflex in limb extensor and flexor muscles has been observed, depending on the limb position (Grillner & Rossignol, 1978) or whether obtained during standing and walking (Lisin, Frankstein & Rechtmann, 1973).

During walking in the spinal cat (Forssberg, Grillner & Rossignol, 1975), in the decerebrate cat (Miller, Ruit & Van der Meche, 1977), in the intact cat walking on a treadmill belt (Forssberg *et al.* 1977; Forssberg, 1979) and in the freely moving cat (Duysens, Loeb & Weston, 1980), a phase-dependent reflex reversal has been described, showing that cutaneous or muscular afferents can induce opposite reflex effects according to the step phase during which they are stimulated. Phase-dependent reflex reversal has also been observed in other animal species, e.g. the intact eel (Grillner, Rossignol & Wallen, 1977) and dogfish (Wallen, 1980).

In the antenna of the rock lobster *Palinurus vulgaris*, passive movement of the joint can produce an assistance reflex (Vedel, 1980). The present study investigates whether this reflex pattern is present during, and just after, active movement of the flagellum.

MATERIALS AND METHODS

Experiments were performed on rock lobster *Palinurus vulgaris* of 400–600 g in weight.

Most of the methods have been described in a previous paper (Vedel, 1980).

Animals were fixed by rubber bands, dorsal side up, in a Perspex dish filled with oxygenated, refrigerated (16°) sea water. Fixation of the animal allowed spontaneous movements of the walking legs to ensure good circulation of the sea water in the branchial chamber. The right or left antenna was fixed in a holder with the J2 and J3 joints in complete extension. The cuticle was cut from the dorsal side of the S2 segment around the tendon of the J2 flexor muscle. The attachment of the J2 flexor tendon was cut, and the tendon was pulled back in order to carefully isolate the flexor and extensor nerves of the J3 muscle. 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.

Reflex response to passive movements (imposed movements) were studied just after active movements. In order to combine active and passive movement a small piece of iron was glued on to the flagellum 5 cm from its joint. During flagellum active flexion this piece of iron came into contact with an electro-magnet fixed to an electro-mechanical apparatus, which was used to impose a passive joint movement. In an experiment, the amplitude of the active movement being almost constant, the electro-magnet could be approximately positioned at the end of the active flagellum rotation and so the passive movement could be immediately imposed.

The amplitude of the passive movement was predetermined to be approximately the same as that of the active movement (10–30°, depending on the animal) and its velocity was equivalent to the higher velocity of the movement performed actively by the flagellum.

Activity of the extensor (E) and flexor (F) nerves of the J3 muscles was recorded by means of suction electrodes disposed *en passant*. J3 movements were recorded with a miniature submarine angle transducer (Marelli & Hsiao, 1976) and the imposed movement was recorded by means of a linear potentiometer linked to the electro-mechanical apparatus. All recordings were stored on tape.

The reflex discharge of each motoneurone was analysed by the phase histogram method. Duration of the analysis phase was equal to that of the passive movement. Whatever its duration, the phase was divided into 15 bins. Spikes occurring in equivalent bins on ten successive repetitions of the same movement were summed. In the same manner the tonic motoneuronal activity was averaged during the same period after ten active movements not followed by a passive movement. Phase histograms were computed on a PDP 11/40 computer.
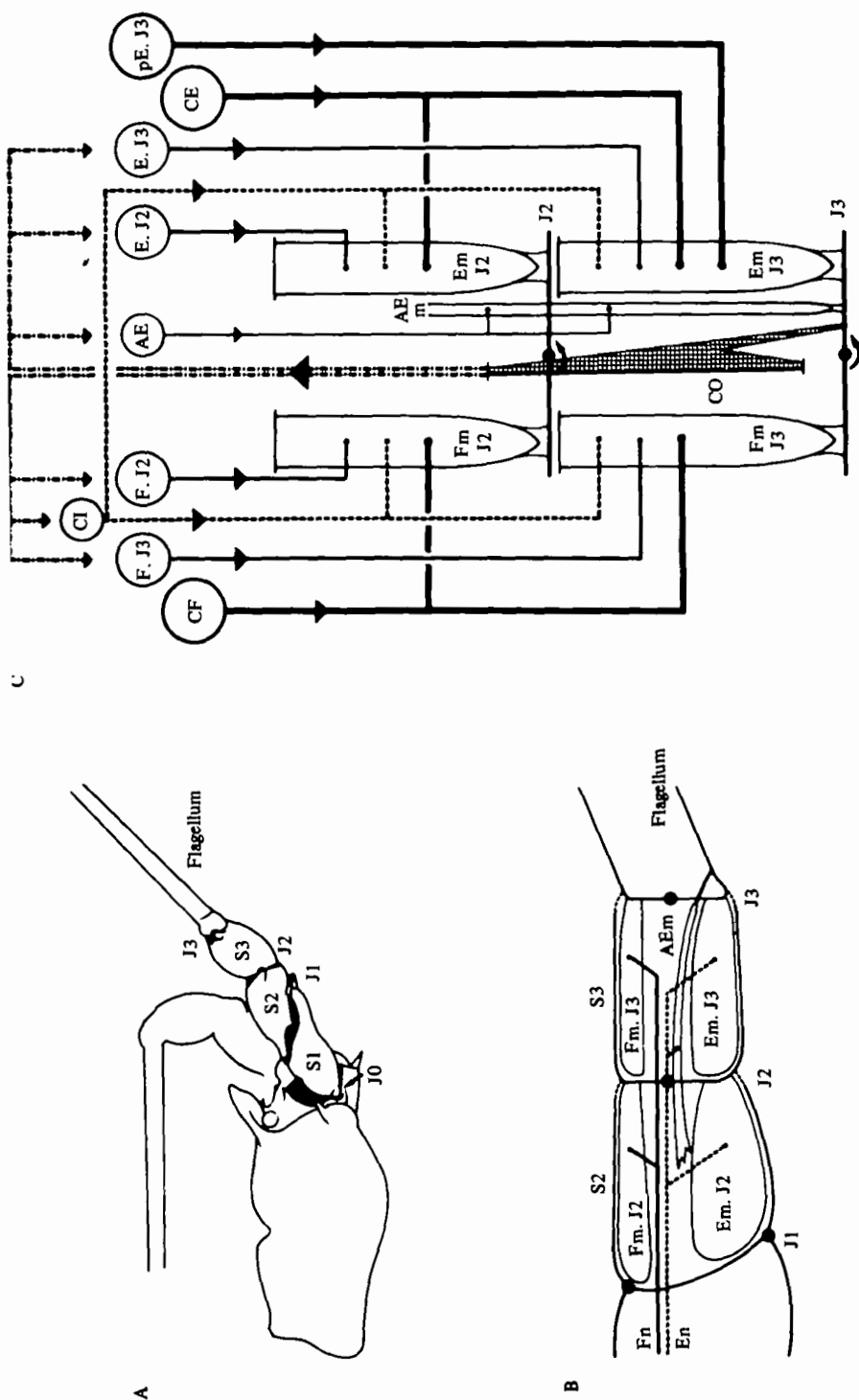
Fig. 1. Morphology and sensori-motor organization of the two distal joints (J2, J3) of the antenna of the rock lobster *Palinurus vulgaris*. (A) Morphology of the antenna. Segments (proximal to distal): S1, S2, S3, flagellum. Joints (proximal to distal): J0 (cephalothorax-S1), J1, J2, J3. (B) Muscular organization of the J2 and J3 joints. Flexor muscles: Fm, J2, Fm. J3; extensor muscles: Em. J2, Em. J3. AEm. Accessory extensor muscle; Fn, flexor nerve; En extensor nerve. (C) Motor innervation of the J2 and J3 joints. Excitatory motoneurones: F. J2, F. J3, E. J2, E. J3, CE, CF, pE. J3, AE. Inhibitory motoneurone: CI. CO, Chordotonal organ CO J2-J3 common to the two joints.
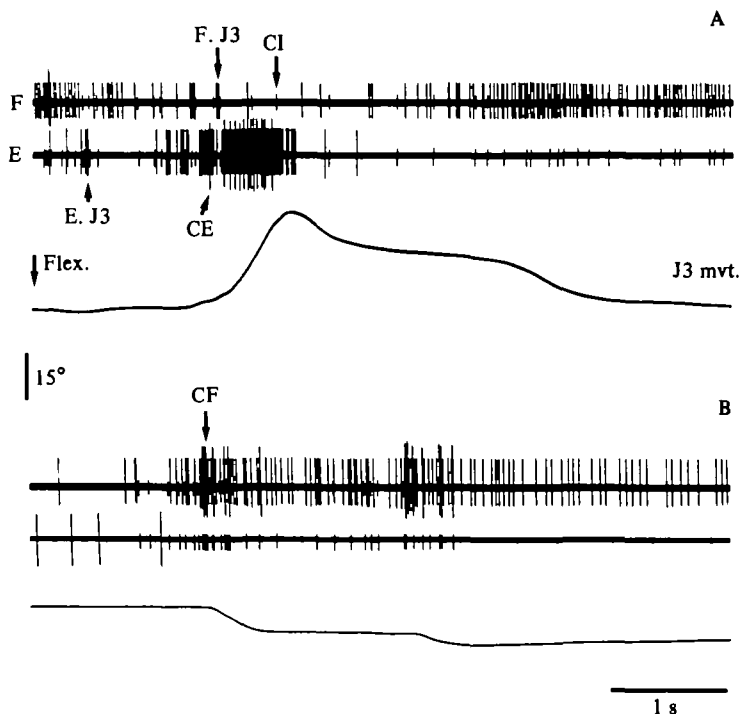
Fig. 2. Motoneuronal patterns during spontaneous extension (A) and flexion (B) move-
ments of the flagellum. Activity of the flexor (F) and extensor (E) motor nerves of J3 muscles
and the movement of the J3 joint (J3 mvt.) are simultaneously recorded. During each move-
ment, only the motoneurone of the contracting muscle fires. The common inhibitory
motoneurone (CI) is activated more during flexion than during extension. Tonic motoneurones:
F. J3, E. J3. Phasic motoneurones: CF, CE.

RESULTS

Sensory-motor organization of the J3 joint

Sensory-motor organization of the J2 and J3 joints has been described in detail
in a previous paper (Vedel, 1980).

The J2 and J3 joints (Fig. 1A) each moves about 60° in the same plane, allowing
the flagellum about 120° of antero-posterior rotation. Proprioception of the J2 and J3
joints is ensured by a common sensory organ, the chordotonal organ CO J2–J3.
Their flexor (Fm. J2, Fm. J3, Fig. 1B) and extensor (Em. J2, Em. J3, Fig. 1B)
muscles receive specific tonic motoneurones (E. J2, E. J3, F. J2, F. J3, Fig. 1C) and
common phasic motoneurones (CE, CF, Fig. 1C). In addition the J3 extensor muscle
receives a specific phasic motoneurone (pE. J3). A common inhibitory motoneurone
(CI) innervates the two extensor and the two flexor muscles (Fig. 1C). Only the
motor innervation of the J3 joint is concerned in the reflex studied here.

Motor patterns during active flagellum movements

When the flagellum was left to move freely, the animal could spontaneously per-
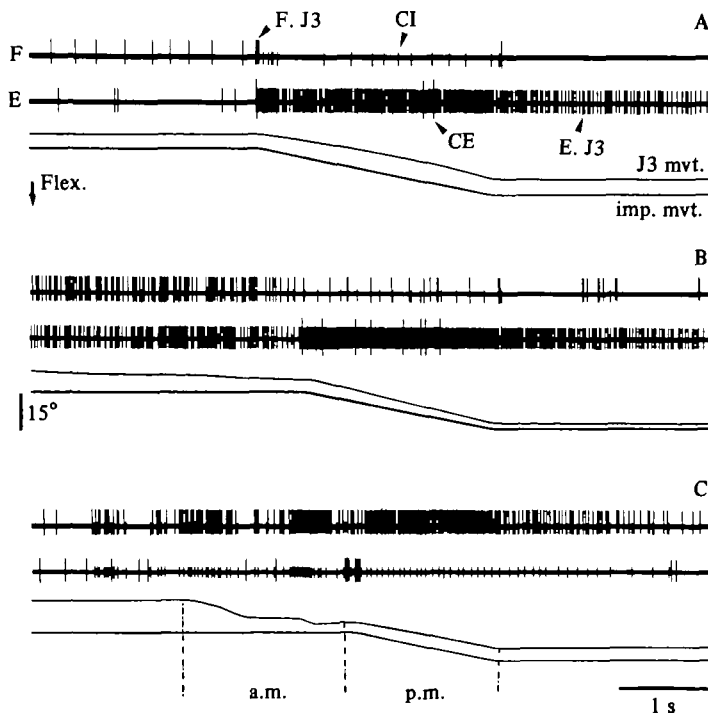form J3 flexion and extension (Fig. 2). During these movements the motoneuro

Fig. 3. Flagellum motor patterns induced by different kinds of stimulation. Activity of the extensor (E) and flexor (F) motor nerve of the J3 muscles, movement of the J3 joint (J3 mvt.) and joint movement imposed by an electro-mechanical device (imp. mvt.) are simultaneously recorded. (A) Extensor resistance reflex occurring during passive flexion of the J3 joint when the animal is spontaneously immobile. (B) Increase of the extensor reflex response to passive J3 flexion consecutive to coactivation of the extensor and flexor motoneurones induced by scratching the dorsal surface of the cephalothorax. (C) Motoneuronal patterns during successive active flexion (a.m., 11°/s) and passive (p.m.) flexion of the J3 joint. Passive flexion imposed immediately after an active flexion induces a flexor assistance reflex. Extensor resistance reflex previously obtained during passive flexion (A) has completely disappeared. The common inhibitory motoneurone (CI) is strongly activated during active and passive movements. Tonic motoneurones: E. J3, F. J3. Phasic motoneurone: CE.

innervating the contracting muscle were activated, while the motoneurones of the stretched muscle were completely silent.

During such active movements the activity of the proprioceptive afferents which are normally responsible for resistance reflex occurring in the stretched muscle when the joint is moved passively (Fig. 3A) may be speculated upon. Are these proprioceptive afferents completely inhibited or are they associated by a 'reversal process' with the central motor command contributing to the organization of the active movement? In other words, during an active movement of the flagellum, may the proprioceptive action be switched from resistance to assistance reflex patterns as has been observed in other conditions (Vedel, 1980)? Considering the difficulty in distinguishing the peripheral action from the central action in a motoneuronal burst, the modification of the reflex pattern eventually induced by an active movement has been studied by comparing the flexor motoneuronal response obtained with passive move-

ments imposed immediately after the end of an active movement to response induce
with the same passive movements but imposed independently of any active motor
action.

Movements spontaneously performed by the animal being unpredictable, active
movements have been obtained by various methods. Cuticular and appendage stimu-
lation allow modification of the activity of the motor innervation of the extensor and
flexor muscles of J3, each kind of stimulation giving rise to a stereotyped effect.
Scratching the dorsal surface of the cephalothorax induces a coactivation of the
flexor and extensor tonic motoneurones of J3 (F. J3, E. J3, Fig. 3B). Generally this
effect does not induce a flagellum movement and does not qualitatively modify the
extensor resistance reflex previously obtained during passive flexion (Fig. 3A).
Nevertheless, cuticular stimulation increased the reflex discharge frequency of the
tonic (E. J3) and phasic (CE) motoneurones (Fig. 3B) during the passive movement,
but the difference between frequency of the tonic discharge before and during the
passive movement is not significantly increased (compared with Fig. 3A).

Fig. 3C illustrates the effect obtained when repetitively moving the uropods
laterally. This stimulation induces a selective activation of the flexor motoneurones
of J3, which produce an active movement of flexion (a.m., Fig. 3C) when the flagellum
is able to move freely. Simultaneously the discharge of the common inhibitory moto-
neurone (CI) is strongly increased as can be observed in the two physiological recor-
dings of Fig. 3C. The flexion movements produced in this condition have a constant
angular amplitude in the same animal (10–30°). Selective activation of the tonic flexor
motoneurone (F. J3) induces slow movements whose velocity never exceeds 10°/s.
When the stimulation also activates simultaneously the phasic flexor motoneurone
(CF) the movement velocity can increase up to 40°/s. It has to be noted that discharge
of the phasic motoneurone never occurs without a background of activity in the tonic
motoneurone.

Qualitative modification of the extensor reflex pattern by active flagellum movements

In an animal in which activity is depressed by the low temperature of the sea water,
the most common effect obtained during imposed joint movement is the resistance
reflex characterized by an activation of the motoneurones of the stretched muscle.
Passive flexion of the flagellum regularly activates the tonic extensor motoneurone
(E. J3, Figs. 3A, 4B), the reflex response of the phasic motoneurone (CE) depending
on the level of reactivity of the animal.

Immediately after an active flexion movement at high velocity (10–30°/s) (a.m.,
Figs. 3C, 4A), the same passive movement (p.m., Figs. 3C, 4A) does not induce a
resistance reflex but produces an activation of the tonic flexor motoneurone and
sometimes of the phasic flexor motoneurone (CF, Fig. 4A). This effect can be con-
sidered as an assistance reflex and reveals qualitative modifications of the reflex
loops consecutive to the active movement. This reversal of the reflex pattern can
persist for several seconds after an active movement performed at high velocity and
can involve not only the tonic and phasic flexor motoneurones (Fig. 4A) but also the
extensor motoneurones (compare in Fig. 4A and B the motoneuronal responses to
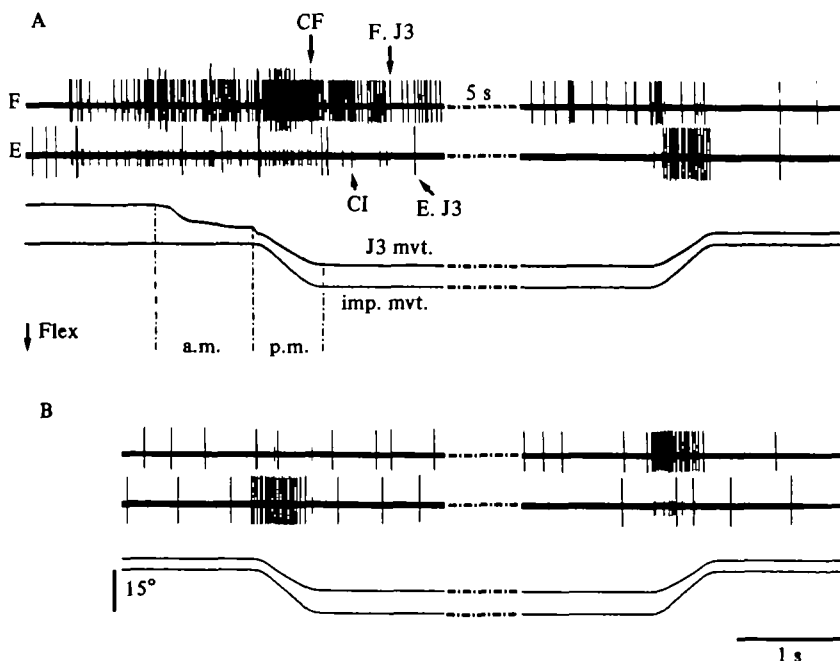passive extension movements).

Fig. 4. Substitution of resistance reflex pattern by assistance reflex pattern induced by active flexion movement of the flagellum. Activity of the flexor (F) and extensor (E) motor nerves of J3 muscles, movement of the J3 joint (J3 mvt.) and joint movement imposed mechanically (imp. mvt.) are simultaneously recorded. (A) Passive flexion (p.m.) following active flexion (a.m.) at high velocity ($12°/s$) produces a flexor assistance reflex (increased activity in F during p.m.). (B) Passive flexion not preceded by active flexion produces an extensor resistance reflex. Reversal of the reflex patterns persists for several seconds and can concern not only the extensor resistance reflex but also the flexor resistance reflex (compare in A and B the responses to extension movements). Tonic motoneurones: F. J3, E. J3. Phasic motoneurone: CF. Inhibitory motoneurone: CI.

Passive movements that induce the flexor assistance reflex also activate the discharge of the common inhibitory motoneurone, which is silent most of the time when the flagellum remains still.

Quantitative modulation of assistance and resistance reflex by the active movement

When the active movement is carried out at low velocity there is only partial substitution of the resistance reflex by an assistance reflex (Fig. 5A). Almost complete substitution is found after high-velocity active movement (Fig. 5B).

Fig. 6 quantifies this effect. The histograms in the left column illustrate the averaged responses of the tonic flexor (F. J3) and extensor (E. J3) motoneurones to ten identical passive movements imposed at $25°/s$ after ten active movements whose mean velocity was about $7·5°/s$. Histograms in the right column show in the same manner the response of F. J3 and E. J3 to $25°/s$ passive movements imposed after active movements performed at about $25°/s$.

Comparison of the two series shows the increase of the assistance reflex (F. J3 response) and the decrease of the resistance reflex (E. J3 response) according to the
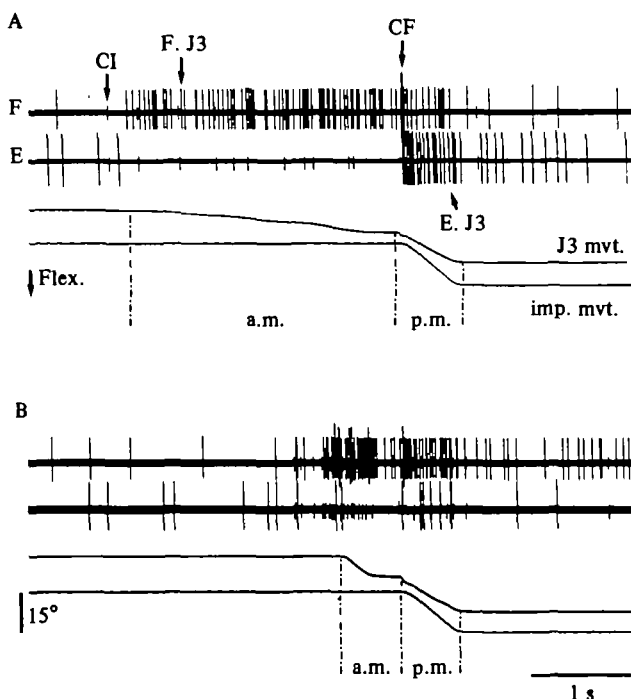
Fig. 5. Competitive occurrence of the resistance and assistance flexor reflexes according to the velocity of the preceding active movement. Activity of the flexor (F) and extensor (E) motor nerve of J3 muscles, movement of the J3 joint (J3 mvt.) and joint movement imposed mechanically (imp. mvt.) are simultaneously recorded. Comparison of the recordings A and B shows that during passive movement the extensor resistance reflex remains predominant after an active movement (a.m.) performed at low velocity (A) whereas the assistance flexor reflex predominates after a high-velocity active flexion (B). Tonic motoneurones: F. J3, E. J3. Phasic motoneurone: CF. Inhibitory motoneurone: CI.

active movement velocity. Histogram F. J3(a) and F. J3(b) illustrate the tonic activity of the flexor motoneurone, which follows respectively $7.5°/s$ and $25°/s$ active movements without imposition of passive movement to J3. Tonic activity was also averaged after ten active movements. These histograms permit estimation of the reflex effect depending on passive movements in the right and left F. J3 histograms.

E. J3 hatched histogram shows the averaged resistance reflex pattern (response to ten passive flexion at $25°/s$) obtained independently of any active movement. It permits evaluation of the quantitative modulation of the resistance reflex consecutive to active movements.

CI histograms show that the response of the common inhibitory motoneurone during passive movements imposed after $7.5°/s$ (left histogram) and $25°/s$ (right histogram) active movement is slightly increased compared to its response obtained independently of any active flexion (CI hatched histogram).
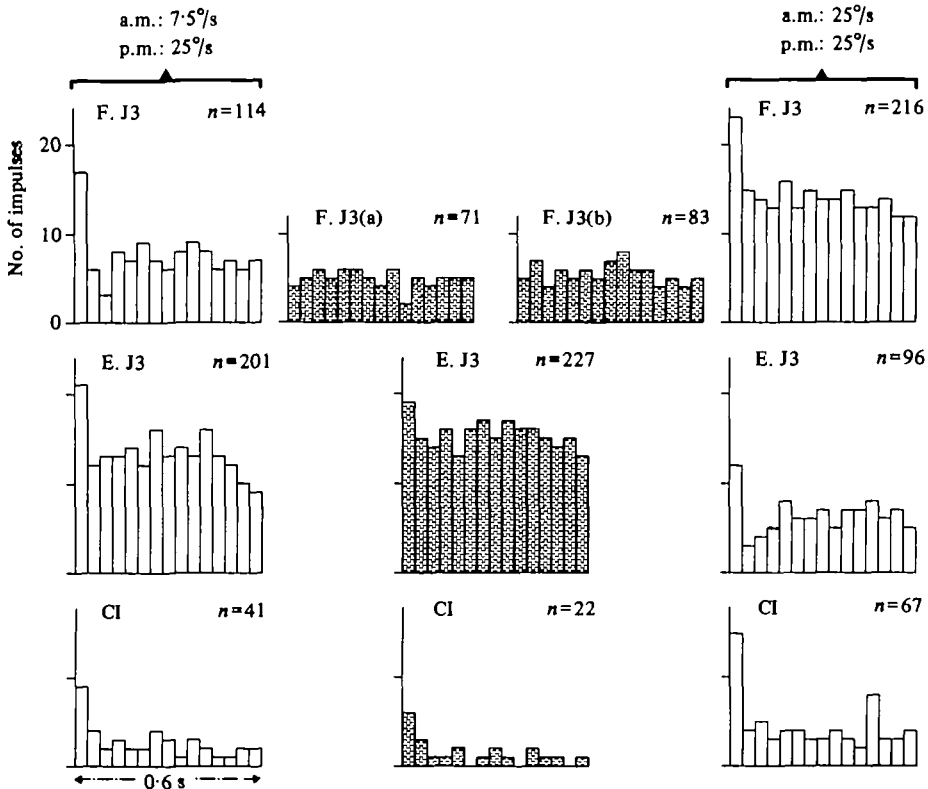
Fig. 6. Individual histogram analysis of the extensor and flexor motoneuronal reflex responses to passive movements imposed after low- and high-velocity active movement of the flagellum. Spikes occurring in equivalent bins on ten successive repetitions of the same passive movement were summed in each histogram. The analysis time corresponded to the passive movement duration (0·6 s), the bin duration was 40 ms. In the left and right column (white histograms) the passive flexion (25 °/s) was applied after active flexion whose mean velocity was respectively 7·5°/s and 25°/s. Comparison of the two columns shows the predominance of resistance reflex (left E. J3 histogram) after low-velocity active flexion and the predominance of assistance reflex (right F. J3 histogram) after high-velocity active flexion. F. J3 (*a*) and F. J3 (*b*) histograms show the tonic flexor activity occurring respectively after 7·5°/s and 25°/s active flexion when passive flexion was not imposed on the flagellum. E. J3 hatched histogram illustrates the extensor resistance reflex obtained independently of any active movement. CI histograms show that the response of the common inhibitory motoneurone during passive movement imposed after 7·5°/s (left histogram) and 25°/s (right histogram) active flexion is slightly increased compared to its response obtained independently of any active flexion (hatched histogram). *n*, Total number of spikes.

Reflex pattern evoked by passive movement imposed in the opposite direction to the preceding active movement

An active flexion preceding a passive extension movement does not always modify qualitatively the induced resistance reflex (flexor pattern) as described in Fig. 4. Most of the time, the active movement facilitates the flexor resistance reflex by increasing the discharge frequency of the tonic flexor motoneurone (F. J3) and sometimes by inducing a reflex response of the phasic flexor motoneurone (CF) (Fig. 7A) which is frequently silent when the passive movement is imposed alone (Fig. 7B).
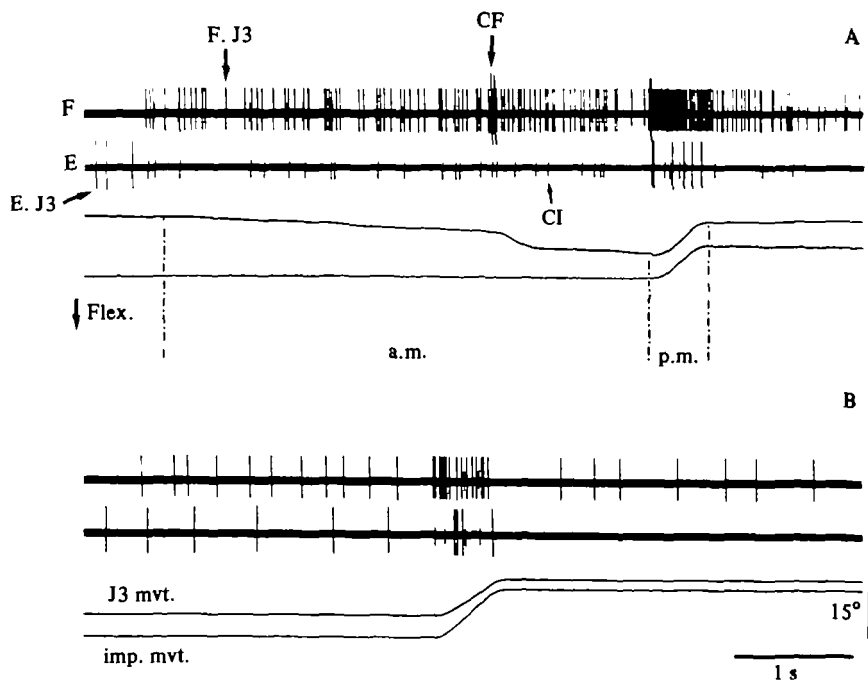
Fig. 7. Increase of the flexor resistance reflex as a result of a preceding active flexion of the flagellum. Activity of the flexor (F) and extensor (E) motor nerves of J3 muscles, movement of the J3 joint (J3 mvt.) and joint movement imposed mechanically (imp. mvt.) are simultaneously recorded. An active flexion (a.m.) preceding a passive extension movement (p.m.) increases the resistance reflex response of the tonic flexor motoneurone (A) compared to that produced by passive movement (B) and sometimes induces an activation of the phasic flexor motoneurone (CF) which is normally silent. Tonic motoneurones: F. J3, E. J3. Phasic motoneurone: CF. Inhibitory motoneurone: CI.

In this condition it also appears that the level of facilitation of the reflex response of the flexor motoneurones depends on the velocity of the active movement. When this parameter is high a light extensor assistance reflex can occur during the facilitated resistance reflex (Fig. 7 A, recording E).

DISCUSSION

In these experiments it appears that a movement actively performed by the animal is able to modify reflex patterns and can even lead to a complete reversal of the motor effects induced by proprioceptive loops.

Reflex modulation has been observed in the period succeeding active movement and so does not really demonstrate the contribution of peripheral actions to central programs during the performance of a joint movement. Nevertheless, the effects obtained reveal a reorganization of the proprioceptive inputs so that they act in the same way as the central motor command. Active flexion leads to a flexor assistance reflex during passive flexion and sometimes to an increase in the flexor resistance reflex during passive extension. There was thus a proprioceptive assistance pattern

During the passive movement, and it is possible that this was also present during the preceding active movement.

It has been observed that after an active flexion movement the flexor resistance reflex induced by a passive extension can be either increased (Fig. 7) or reversed, an extensor assistance reflex occurring in this condition (Fig. 4). These different effects also illustrate the functional plasticity of the reflex loops when an active movement is carried out.

It has to be noted that in a previous study (Vedel, 1980) it was shown that increase of the central reactivity of the animal and passive movements imposed at high velocity resulted in the extensor assistance reflex being elicited. The experimental situation used in the present work demonstrates that this kind of reflex effect can also concern the flexor motoneurones. As in a previous study (Vedel, 1980), all sensory nerves related to the S2 and S3 segments and to the flagellum were cut, except the nerve of the chordotonal organ common to J2 and J3 joints. This permitted selective stimulation of the proprioceptor by extension–flexion movements of the flagellum and demonstrated that the different reflex patterns observed have the same peripheral origin. So, it can be suggested that the reversal effect obtained depends on the switching of the reflex pathways of particular afferents, attributable to central actions. Occurrence of such a switching process has been extensively discussed by Matthews (1972) with regard to the appearance of decerebrate rigidity in cats by development of autogenetic excitation on stretching a muscle. Recent work (Jankowska *et al.* 1981*a–c*) on proprioceptive spinal connexions have greatly enlarged our knowledge of the possibility of synaptic actions on motoneurones, revealing notably the existence, for the same afferents, of several autogenetic effects and suggesting a real functional plasticity of the reflex pathways.

In invertebrates several examples of switched reflex pathways have been described. Wilson & Davis (1965) first observed such a phenomenon in crustaceans, then Bässler (1973, 1974, 1976, 1977) described complete reversal of a proprioceptive reflex in an insect and suggested the term 'assistance reflex'. Ayers & Davis (1977, 1978), observing in the walking legs of the lobster *Homarus americanus* that muscles could be excited by the movements they normally cause, proposed comparing these reflexes to positive-feedback reflexes demonstrated by Davis (1969) in the muscle of the swimmerets in the same animal.

It may be suggested that reflex reversal results in the disappearance of the resistance reflex in the stretched muscle during flagellum movement actively performed by the rock lobster. Absence of resistance reflex has also been observed by DiCaprio & Clarac (1981) during stereotyped motor behaviour in the crab. If the proprioceptive afferents responding to flagellum flexion really do activate the flexor motoneurones during an active flexion, this effect could be considered as a system of regulation of the muscular contraction taking continuously into account the parameters of the ongoing movement. However, the function of an assistance reflex induced by a passive flexion movement during an active flexion is not clear. In this condition the response is a flexor reflex which amplifies the ongoing flexion movement and so can disturb the central motor command. In other words, occurrence of the assistance reflex suppresses the process of load compensation normally attributed to the resistance reflex. Rein-

forcement of flexor resistance reflex observed when a passive extension is impose
after an active flexion can be understood as a compensation of disturbance opposing
the active flexion.

The relationships between the velocity of the active movement and the reograniza-
tion of the proprioceptive pathways reveal a modulated action of the central command
upon the reflex connexions and demonstrate that such an effect can also induce a
competition between several kinds of afferent actions which could well illustrate the
functional plasticity of combined central and peripheral motor actions.

REFERENCES

AYERS, J. C. & DAVIS, W. J. (1977). Neuronal control of locomotion in the lobster *Homarus americanus*.
II. Types of walking leg reflexes. *J. comp. Physiol.* **115**, 29–46.

AYERS, J. C. & DAVIS, W. J. (1978). Neuronal control of locomotion in the lobster *Homarus americanus*.
III. Dynamic organization of walking leg reflexes. *J. comp. Physiol.* **123**, 289–298.

BÄSSLER, U. (1973). Zur stenerung aktiver Bewegungen des Femur-Tibia-Gelenkes der Stabhenschrecke
Carausius morosus. Kybernetik **13**, 38–53.

BÄSSLER, U. (1974). Vom Femoralen chordotonalorgan gestenerte Reaktionen bei der Stabhenschrecke
Carausius morosus: Messung der von der Tibia erzengten Kraft im aktiven und inaktiven Tier.
Kybernetik **16**, 213–226.

BÄSSLER, U. (1976). Reversal of a reflex to a single motoneuron in the stick insect, *Carausius morosus.
Biol. Cybernetics* **24**, 47–49.

BÄSSLER, U. (1977). Sensory control of leg movement in the stick insect *Carausius morosus. Biol. Cyber-
netics* **25**, 61–72.

DAVIS, W. J. (1969). Reflex organization in the swimmeret system of the lobster. I. Intrasegmental
reflexes. *J. exp. Biol.* **51**, 547–563.

DICAPRIO, R. A. & CLARAC, C. (1981). Reversal of a walking leg reflex elicited by a muscle receptor.
J. exp. Biol. **90**, 197–203.

DUYSENS, J., LOEB, G. E. & WESTON, B. J. (1980). Crossed flexor reflex responses and their reversal
in freely walking cat. *Brain Res.* **197**, 538–542.

FORSSBERG, H. (1979). Stumbling corrective reaction: a phase dependent compensatory reaction
during locomotion. *J. Neurophysiol.* **42**, 936–953.

FORSSBERG, H., GRILLNER, S. & ROSSIGNOL, S. (1975). Phase dependent reflex reversal during walking
in chronic spinal cats. *Brain Res.* **85**, 103–107.

FORSSBERG, H., GRILLNER, S. & ROSSIGNOL, S. (1977). Phasic gain control of reflexes from the dorsum
of the paw during spinal locomotion. *Brain Res.* **132**, 121–129.

GRILLNER, S. & ROSSIGNOL, S. (1978). Contralateral reflex reversal controlled by limb position in the
acute spinal cat injected with clonidine i.v. *Brain Res.* **144**, 411–414.

GRILLNER, S., ROSSIGNOL, S. & WALLEN, P. (1977). The adaptation of a reflex response to the ongoing
phase of locomotion in fish. *Expl Brain Res.* **30**, 1–11.

JANKOWSKA, E., McREA, D. & MACKEL, R. (1981a). Pattern of 'non-reciprocal' inhibition of moto-
neurones by impulses in group IA muscle spindle afferents in the cat. *J. Physiol., Lond.* **316**, 393–409.

JANOWSKA, E., McREA, D. & MACKEL, R. (1981b). Oligosynaptic excitation of motoneurones by
impulses in group Ia muscle spindle afferents in the cat. *J. Physiol., Lond.* **316**, 411–425.

JANKOWSKA, E., JOHANNISSON, T. & LIPSKI, J. (1981c). Common interneurones in reflex pathways from
group Ia and Ib afferents of ankle extensors in the cat. *J. Physiol., Lond.* **310**, 381–402.

LISIN, V. V., FRANKSTEIN, S. I. & RECHTMANN, M. B. (1973). The influence of locomotion on flexor
reflex of the hindlimb in cat and man. *Expl Neurol.* **38**, 180–183.

MARELLI, J. D. & HSIAO, H. S. (1976). Miniature angle transducer for marine arthropodes. *Comp.
Biochem. Physiol.* **54**A, 121–123.

MATTHEWS,, P. B. C. (1972). *Mammalian Muscle Spindle Receptors and Their Central Actions*. London:
Edward Arnold.

MILLER, S., RUIT, J. B. & VAN DER MECHE, F. G. A. (1977). Reversal of sign of long spinal reflexes
dependent on the phase of the step cycle in the high decerebrate cat. *Brain Res.* **128**, 447–459.

EDEL, J.-P. (1980). The antennal motor system of the rock lobster: competitive occurrence of resistance and assistance reflex patterns originating from the same proprioceptor. *J. exp. Biol.* **87**, 1–22.

WALLEN, P. (1980). On the mechanism of a phase-dependent reflex occurring during locomotion in dogfish. *Expl Brain Res.* **39**, 193–202.

WILSON, D. M. and DAVIS, W. J. (1965). Nerve impulse patterns and reflex control in the crayfish claw motor system. *J. exp. Biol.* **43**, 193–200.