

THE PHYSIOLOGY OF A LEPIDOPTERAN MUSCLE RECEPTOR

II. THE FUNCTION OF THE RECEPTOR MUSCLE

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(Received 15 September 1965)

INTRODUCTION

One of the chief points of interest in muscle receptors generally is the ability which they confer on the C.N.S. to change the effective sensitivity of peripheral sensing elements which supply information concerning mechanical events. Physiological evidence indicating such efferent bias of stretch receptors was provided for cat muscle spindles by Leksell (1945). He found that stimulation of the small diameter (or gamma) efferent nerve fibres produced an increase in spindle afferent discharge frequency without the development of any recordable tension at the tendon. (By many authors the gamma efferents are termed fusimotor fibres. The muscle fibres of the spindle are currently termed intrafusal fibres, and those of the elements responsible for developing muscle tension are termed extrafusal muscle fibres. This terminology will also be used here where the context renders it helpful.)

The sensory terminations on the mammalian muscle spindle are of two types: primary or annulospiral and secondary or flower-spray endings. Boyd (1962) and others have described two types of intrafusal muscle fibres, the nuclear bag fibres and the nuclear chain fibres, both of which are found in single spindles. Boyd also described two types of gamma or fusimotor nerves, one having end-plate terminations and the other diffuse terminations. There is still uncertainty as to whether there are in fact two types of gamma fibre, but it is generally agreed that only one type goes to each intrafusal fibre (Matthews, 1964). The frog muscle spindle certainly has two types of motor innervation, fast and slow (Matthews, 1964); the motor axons of each type are common to both extrafusal and intrafusal muscle fibres (Gray, 1957).

The sensory responses of the crustacean abdominal muscle receptor organs (MRO) have been studied in considerable detail, and Kuffler (1954) described the effects of stimulating the receptor motor axon on the receptor muscle (RM) action potential, on its contraction and on the sensory discharge from these organs.

The literature concerned with reflex and central nervous effects on fusimotor activity in mammals is extensive and somewhat contradictory. While the excitatory effects of cutaneous stimulation and the inhibitory effects of squeezing the foot on fusimotor tone are well established (Hunt & Paintal, 1958), data on feedback reflex effects by spindle afferents on gamma efferents are confused. Similarly Hunt & Perl (1960) consider that a conservative view should be taken of the existence of the

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so-called 'gamma loop' (Granit, 1955). The suggested mode of operation of this loop is as follows. Stimuli, which at higher intensities evoke extrafusal reflex effects, at lower intensities cause changes only in the fusimotor tonic discharge. Then the resultant changes in spindle afferent discharge produce indirect reflex effects on the excitability of the extrafusal motoneuron pool. With this mechanism length adjustments would be independent of loading. Clearly such a role could not readily be ascribed to the amphibian spindle where extrafusal and intrafusal muscles are innervated by common axons.

Other effects which may be of considerable importance in the functioning of the gamma efferent system have been described by Matthews and Rushworth (1957, 1958) and Jansen & Matthews (1962). The former papers showed that selective gamma block by procaine results in reduction of the stretch reflex, and the latter showed that a central control over the magnitude of the 'dynamic' (or phasic) response in the spindle afferents is mediated via the gamma efferent system.

By contrast with the mass of data published on the vertebrate spindle, there are almost no studies of the central nervous use of RM systems by the arthropods. It is clearly important in the present work to know what indirect reflex effects could be mediated by the caterpillar MRO. For Critchlow & von Euler (1963) showed that in the cat fusimotor control permits a complete reversal in the pattern of spindle afferent discharge from the intercostal muscles.

MATERIALS AND METHODS

In the experiments in which the receptor motor axon was stimulated electrically very early pupae were used. Many of the muscle groups present in the caterpillar have degenerated by this stage (Finlayson, 1956). Since the RM axon has many branches which in the larva pass between the groups of dorsal longitudinal muscles, isolation of a functioning RM in this developmental stage was never more than partially successful. Furthermore, since lifting up the receptor strand in forceps damages its ends, the effects of RM stimulation must be examined with the MRO *in situ*. The RM axon can only be stimulated in company with a number of extrafusal axons and so it is necessary to have a preparation with a rigid integument which can be almost completely immobilized. These considerations necessitated using the pupa. The very early pupa was preferred because at this time the sensory responses to ramp-function stretch are most similar to those found in the caterpillar (Weevers, 1966*b*). Similarly, in the experiment where the sensory axon was stimulated electrically, the pupa again had to be used. Only in the pupa is there a sufficient length of single sensory axon for the stretch discharge to be blocked without killing so much of the axon that it can no longer be electrically stimulated.

Only those results which are shown in Text-fig. 7 were obtained from the caterpillar. Techniques of dissection and preparation were essentially the same as those described previously (Weevers, 1966*a*).

Extracellular hook electrodes were used to stimulate and to record from nerves, and potentials were led to amplifying, display and recording apparatus of the conventional type. Action potentials in the receptor muscle were recorded intracellularly with KCl-filled micropipettes.

RESULTS

The motor regulation of the afferent discharge

Oscillograph recordings of the effects of electrically stimulating the receptor motor axon are reproduced in Pl. 1. Simultaneous records from the RM and from the sensory axon are seen in *A*, and the sensory discharge alone from a receptor held at a greater length in *B*. Each stimulus was followed after a short delay by a transient increase in sensory impulse frequency. Records *C*, *D* and *E* show the excitation of a lightly stretched receptor by variously spaced pairs of stimuli to the RM axon. Each stimulus was again followed by a transient increase in sensory frequency; the total frequency increase was greater when the two stimuli were closely spaced. The excitatory effect of the second stimulus was in no case appreciably greater than that of the first, so although summation clearly occurred, there is no evidence of any facilitation.

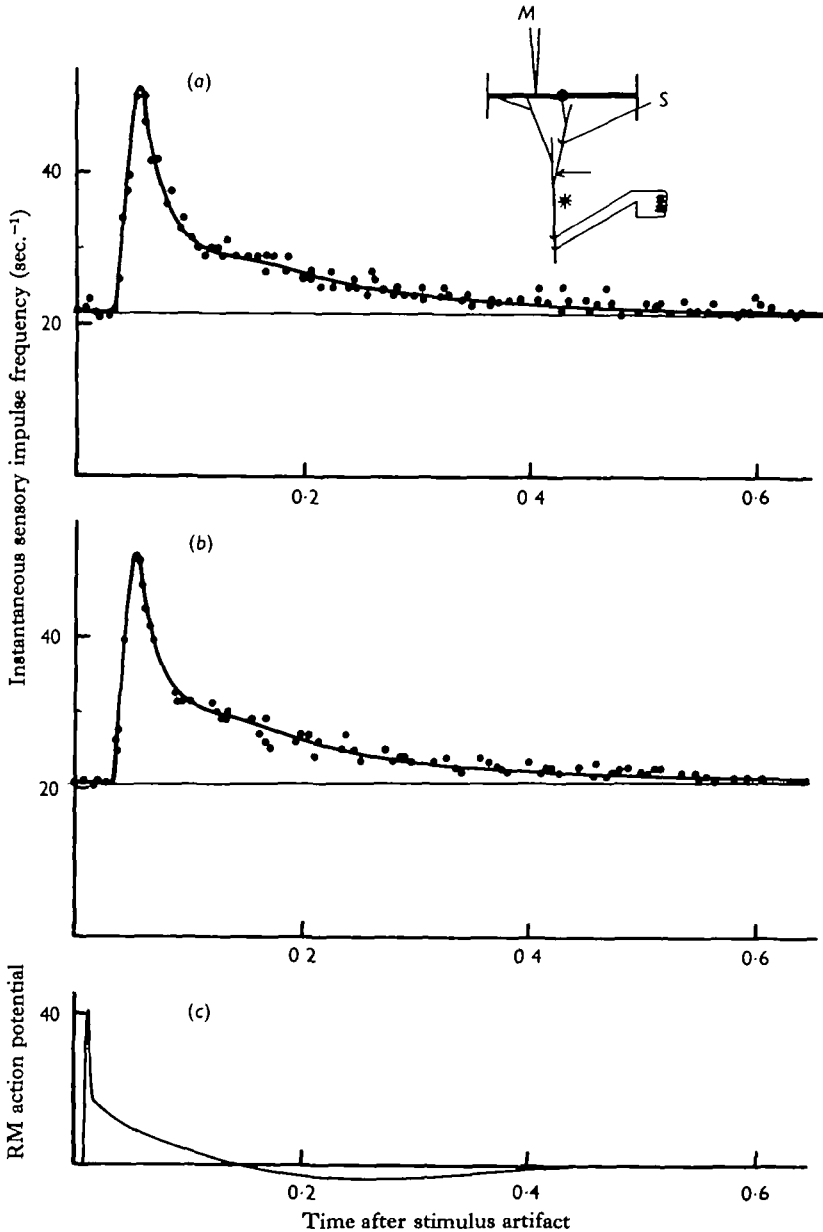
The intracellularly recorded RM action potential likewise showed no sign of facilitation at high frequencies of stimulation. It was always about 43 mV. or less, and like all other lepidopteran muscles from which records have so far been taken appears to be of the 'fast' type (Belton, 1958; van der Kloot, 1963; Weevers, 1966*a*). The active membrane response in the RM is larger than that recorded in the extrafusar muscles. This may be correlated with the fact that the frequency of impulses in the RM is usually higher than in the extrafusar muscles. When any of the five major branches of the motor nerve was cut, the intracellularly recorded RM action potential in the region innervated by that branch was reduced in magnitude but its shape remained the same. No evidence was obtained by recording from the different nerve branches for innervation of the RM by more than one axon.

Finlayson & Lowenstein (1958) and Osborne & Finlayson (1965) showed that the sensory dendrites are confined to a connective tissue tube running parallel to the RM. The latter study also showed that the naked dendritic terminations which in the mammalian Pacinian corpuscle are the site of mechano-electric transduction (Lowenstein & Rathcamp, 1958) do not appear along the central non-muscular part of the receptor. Thus there is at least a possibility that the sensory dendrites are functionally in parallel with the muscular part of the receptor. In that case contraction by the RM would unload the sense organ and reduce its discharge frequency.

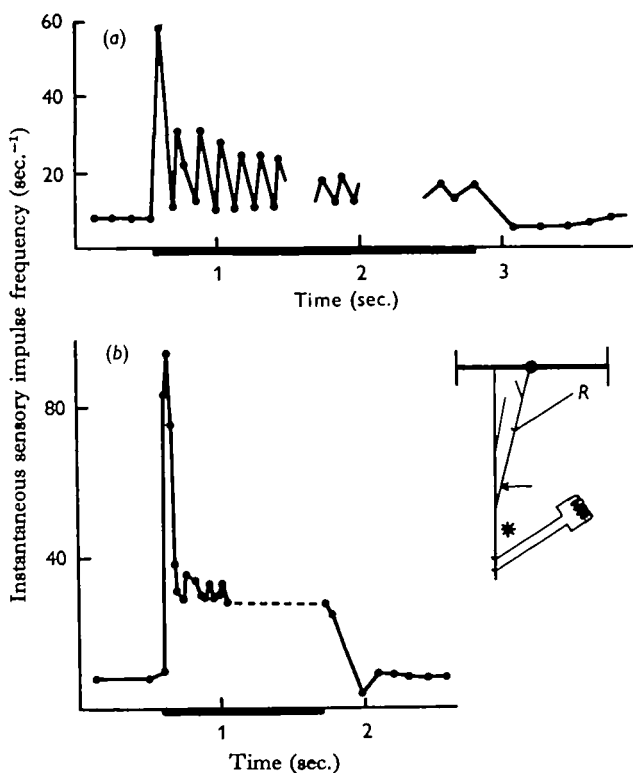
In view of this possible inference from the geometry of the receptor it was necessary to show that the increase in sensory frequency seen in Pl. 1 was not an artifact. For if during recording from the sensory nerve the receptor strand were pulled sideways in the middle so as to form a shallow V, RM contraction might produce MRO excitation by tension on the cell body. The latter form of stimulation would not occur *in vivo*.

Consequently in the experiment shown in Text-fig. 1, the sensory nerve from the MRO was cut just distal to the point where it joined the main tergal nerve, and great care was taken to avoid pulling on it during recording. Under these conditions single stimuli delivered to the RM still produced an increase in sensory frequency. This experiment was performed both in haemolymph and in pupal saline. The similarity between the graphs of instantaneous sensory frequency in these two media is a good confirmation of the adequacy of the pupal saline used.

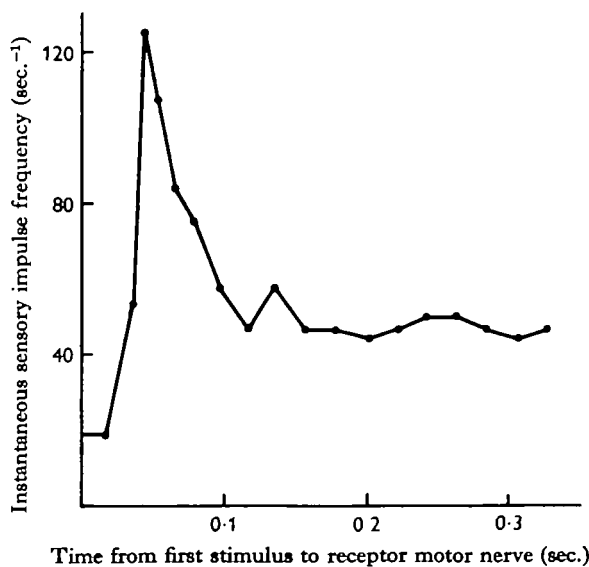
Text-fig. 2 shows examples of sensory responses to repetitive stimulation of the RM at two different frequencies. It is noteworthy that the fusion frequency as



Text-fig. 1. The changes in instantaneous sensory frequency during single contractions by the receptor muscle. Each point shows the reciprocal of the interval between a single sensory impulse and the previous one plotted at a time mid-way between the two. The response of the receptor was tested in two media, (a) haemolymph and (b) pupal saline; (a) shows the changes in sensory frequency during six RM contractions and (b) during five. (c) Shows the time-course of the intracellularly recorded RM action potential. The electrodes were located as shown in the inset diagram; *M* denotes an intracellular micropipette in the RM and *S* denotes an extracellular hook electrode under the sensory nerve. The stimulating electrodes were placed under nerve 2 proximal to the spiracle (shown by an asterisk) after connexions with the C.N.S. had been severed. The nerve branch containing the sensory axon from the MRO was severed at the arrow so that lifting it up on a recording electrode did not exert any tension on the cell body (see text). For simplicity only two branches of the receptor motor nerve are shown.

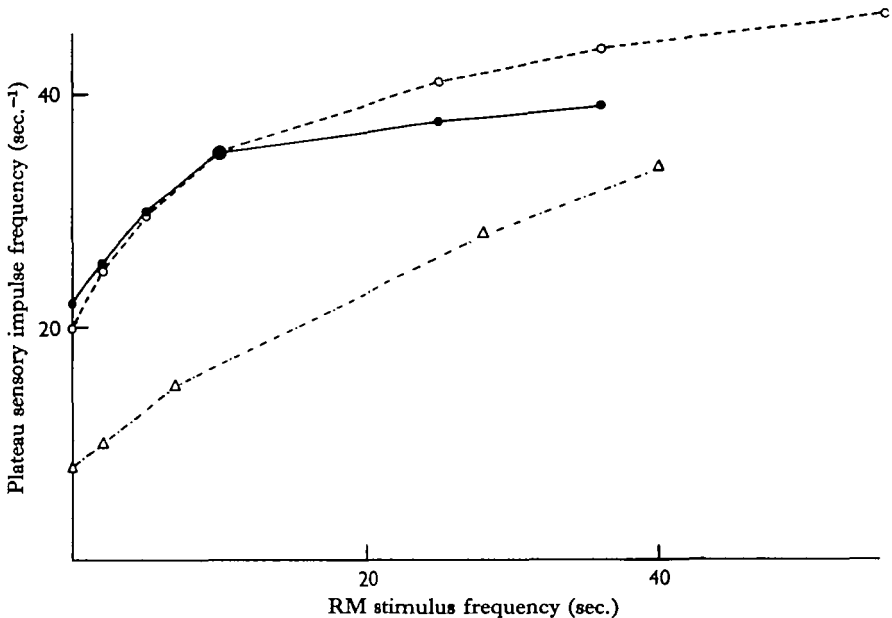


Text-fig. 2. The sensory discharge during trains of stimuli to the RM. A heavy line below the abscissa shows the duration of the stimulus. (a) Stimulus frequency 7/sec. (b) Stimulus frequency 28/sec. The same conventions are followed in the inset diagram as with Text-fig. 1.



Text-fig. 3. The effect of high-frequency stimulation of the RM on the sensory discharge. The frequency of stimulation was 60/sec.

detected by the sensory discharge (around 10 stimuli/sec.) is similar to the lowest frequencies commonly recorded in the RM when it was connected to the C.N.S. In Text-fig. 3 the response of another receptor may be seen. The frequency of stimulation was equal to the highest which had been recorded in the RM with its central connexions intact. The time-scale is expanded compared with Text-fig. 2 in order to show in more detail the changes in instantaneous frequency at the start of RM stimulation. This figure is strikingly similar to plots of the sensory discharge following rapid constant-velocity stretch (Weevers, 1966*b*).



Text-fig. 4. The steady elevated sensory frequency plotted against the frequency of RM stimulation during stimulus trains of long duration (longer than 2 sec.). Circles show the responses of one preparation: ●, in haemolymph; ○, in pupal saline. Triangles show the response of a different preparation where the receptor was held at a lower level of stretch.

The 'plateau' sensory frequencies produced in different conditions by long trains of stimuli delivered to the RM are shown in Text-fig. 4. The curves for one preparation in haemolymph and in pupal saline are again similar, though not identical. A characteristic feature of the 'plateau' discharge was that even high-frequency stimulation could not evoke a maintained sensory impulse frequency much higher than 45/sec., irrespective of how much the receptor was stretched. This is similar to the maximum 'position' or tonic discharge frequency (Weevers, 1966*b*).

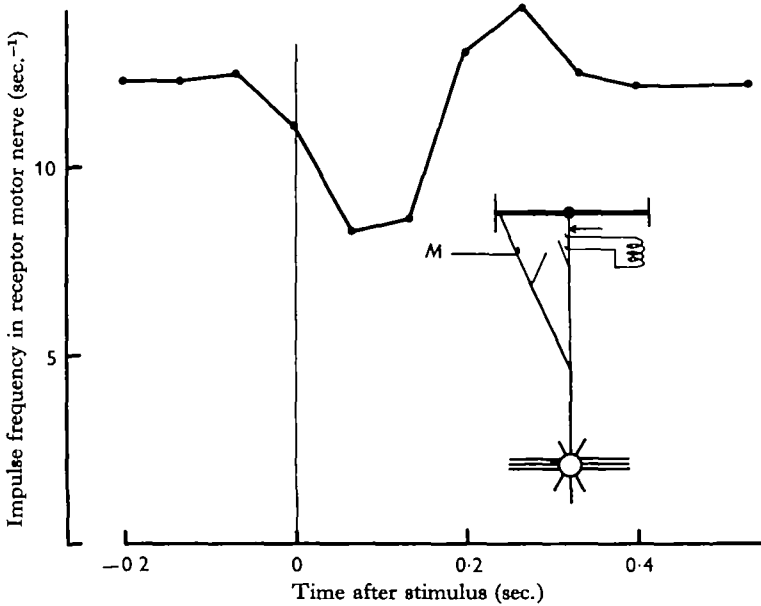
Feedback reflex control of the RM

Stretching the MRO was the only form of sensory stimulation used in the present study so reflex effects of other afferent pathways on the normal discharge to the RM will not be described.

As mentioned under 'Methods', it is possible in the pupa to block the stretch discharge by pinching the MRO axon lightly where it leaves the sense cell. There is

then a length of about 1 mm. of this single axon under which stimulating electrodes can be hooked. (The same experiment in the larva of this species is very difficult to carry out.) Under these conditions, with no impulses entering the C.N.S. along the MRO sensory axon, any reflexes affecting the tonic RM discharge should disadapt completely. Then electrical stimulation of the MRO axon should excite reflex effects to an abnormally intense degree, so rendering their detection easier.

This expectation was confirmed by the results shown in Text-fig. 5. Even single sensory impulses markedly inhibited the steady discharge in the RM axon. The

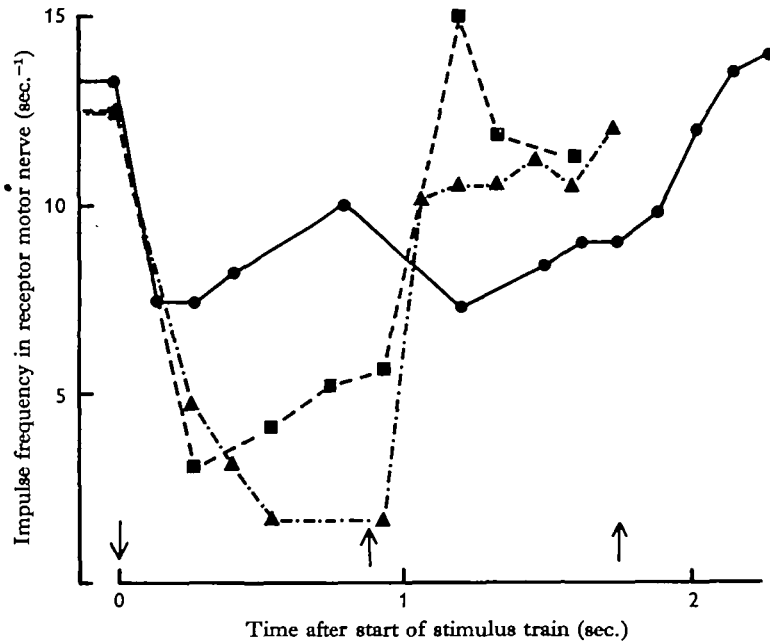


Text-fig. 5. The inhibitory negative-feedback reflex in a pupal RM with intact central connexions. The sensory nerve was pinched at the arrow on the inset diagram to abolish the stretch discharge and stimuli were delivered to the single MRO sensory axon. The changes in the spontaneous efferent discharge to the RM were then recorded at M in the inset diagram. The graph shows the mean of the responses to six successively evoked impulses which reached the C.N.S. at 5 sec. intervals. The thin vertical line shows the time when the stimulus was delivered. The mean RM impulse frequency was measured during successive intervals of 67 msec. duration. This facilitated averaging of the responses to several stimuli.

expected adaptation of the reflex is probably reflected in the rebound excitation before the RM discharge settled down again. Text-fig. 6 shows the results of a similar experiment where trains of stimuli were delivered to the MRO sensory axon. Again the RM discharge was inhibited. Typically there was some recovery from inhibition while the stimulus continued; and for low-frequency trains the inhibition was often followed by a rebound excitation. Thus there is every indication that under more normal conditions the reflex would be phasic.

A similar experiment was performed on the last instar larva, but here the sensory nerve was left intact and was excited by stretching the receptor. The changes in the RM discharge in the two receptors of a segment were then recorded intracellularly with micropipette electrodes. The afferent response to the same stimulus was monitored later. Text-fig. 7 shows that under these more normal conditions the reflex

was almost wholly phasic. During stretching, when the sensory frequency was about 90/sec., the RM frequency in the stretched MRO dropped. The contralateral receptor was little affected at this time. At the end of stretching when the sensory frequency fell to about 40/sec., the RM discharge in both receptors underwent a phasic rebound excitation. The RM discharge in the stretched receptor was slightly inhibited while the stimulus continued. Finally, on releasing, when the sensory discharge dropped to zero and gradually rose again to 6/sec., the RM discharge in both receptors again showed a phasic excitation



Text-fig. 6. The reflex inhibition of the tonic discharge to a pupal RM by trains of impulses in the MRO sensory axon. The electrodes were located as in the inset diagram of Text-fig. 5. The symbols signify three different frequencies of stimulation applied to the sensory nerve: ●, 8/sec.; ■, 23/sec.; ▲, 35/sec.

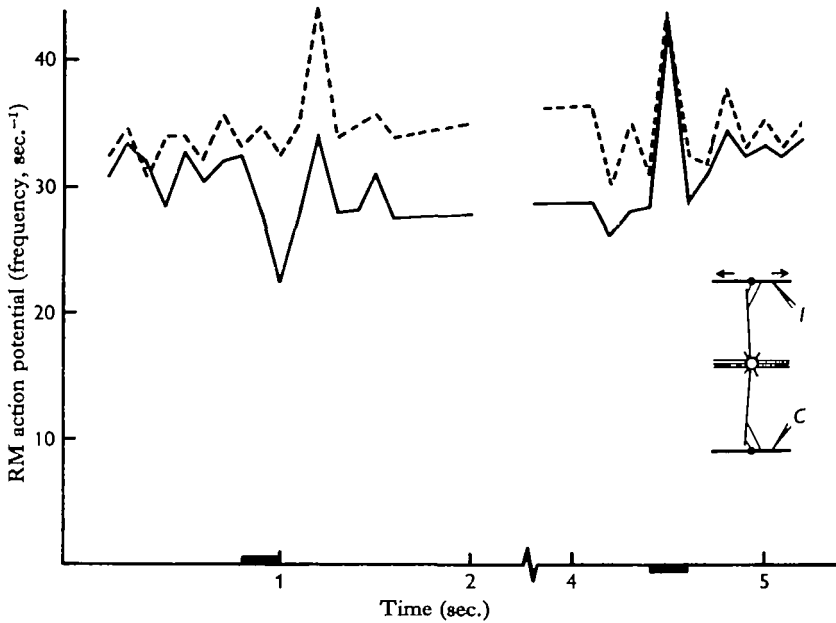
This is a negative feedback reflex and would normally tend to reduce rapid changes in sensory frequency. It should be noted therefore that in this experiment the feedback loop is inevitably opened; for the process of lifting the MRO in forceps in order to stretch it so weakens the RM contractions that they have little effect on the sensory discharge.

No reflex effects of stretching the MRO were seen in the RM of receptors in adjacent segments.

DISCUSSION

The lepidopteran MRO, like the vertebrate spindle and the crustacean abdominal MRO, shows an increased sensory discharge frequency when the RM is stimulated. As mentioned earlier, the morphology of the receptor might lead one to expect unloading by RM contraction. Finlayson & Lowenstein (1958) proposed that the central giant nucleus of the lepidopteran receptor might function in a manner analo-

gous to that suggested for the nuclear bag of the vertebrate muscle spindle. Thus RM contraction would extend the equatorial region and excite the sensory discharge. But the finer branches of the sensory dendrites continue toward either end of the lepidopteran MRO, quite unlike the primary endings on the nuclear bag of the muscle spindle. Moreover the fine naked tips of the dendrites do not leave the connective tissue tube (Osborne & Finlayson, 1965), and could not therefore be squeezed by



Text-fig. 7. The changes in the spontaneous efferent discharge to the two MRO of one segment in a caterpillar where one of the receptors was subjected to ramp-function stretch (0.15 cm. amplitude at 0.6 cm./sec.). A heavy line above the abscissa signifies stretching and a heavy line below it signifies releasing. *I* and *C* on the inset diagram show the location of the ipsilateral and contralateral recording electrodes. The full line shows the frequency of impulses recorded in the RM of the stretched receptor, and the dashed line the frequency in the contralateral RM of the same segment. Each curve is the mean of the responses to three identical stimuli.

contraction of the RM. A simple model of the mode of excitation by stretch and RM stimulation can be constructed only if shear between the muscular and tendinous parts of the MRO is the adequate sensory stimulus. In such a model the central nuclear region would have to be the most compliant part of the receptor to permit relative movement between the RM and the connective tissue tube of an excitatory kind both during stretching and during RM contraction (T. Weis-Fogh, personal communication).

The similar excitation of the sensory discharge by RM contraction in the lobster MRO is more readily explained since the sensory dendrites, as with the primary endings of the mammalian muscle spindle, are restricted to a non-contractile region in the centre of the receptor (Alexandrowicz, 1951). Kuffler (1954) was able to provide an explanation of the elevation of sensory discharge frequency by RM contraction in the crayfish, for in this animal, although there is no intercalated

tendinous region as in the lobster, the sensory dendrites are confined to the equatorial region of the receptor. Kuffler observed that when local regions of the 'fast' receptor are subjected to tension, only these regions contract following stimuli to the RM. Therefore, in decapod Crustacea, morphology and physiology are in agreement; the 'in series' behaviour actually observed can be predicted from the structure of the receptors.

It is only for the secondary endings of the mammalian muscle spindle, as for the lepidopteran MRO studied here, that difficulty is experienced in reconciling the morphology of the receptor with the observed sensory responses to stretch and RM stimulation (see Matthews, 1964). Bessou & Laporte (1962) clearly showed that the secondary endings are excited by contraction of the intrafusal muscle; yet the sensory dendrites lie over the contractile polar region of the spindle.

The phasic sensory response to stretch and to stimulation of the RM

Kymograph recordings (Weevers, 1965) showed that the rate of extension of single segments during peristaltic locomotion in intact caterpillars did not exceed 0.1 cm./sec. Furthermore it is unlikely that this rate of extension would be reached as rapidly as during experimentally imposed ramp-function stretch, owing to various series compliances. It is possible that attack by predators might produce higher extension rates. The results in the first half of this paper indicate a marked phasic response by the MRO at the beginning of trains of stimuli to the RM. Thus the caterpillar may only utilize the high phasic sensitivity of its muscle receptor to the full at the start of high-frequency trains of RM impulses. There may also be an enhancement of phasic sensitivity during RM activity in the manner shown by Jansen & Matthews (1962) for the mammalian muscle spindle. All attempts to investigate such effects resulted in damage of the RM when it was held in the stretching forceps.

The reflex control of the RM

(1) Control by other afferent pathways

The data presented in the second half of this paper show one kind of reflex modulation of RM tonic discharge. The changes in the frequency of stimuli to the RM would tend to protect a receptor when it was stretched violently and would also take up the slack when it or its contralateral homologue was suddenly released. It is likely that further investigation would reveal the existence of a wide variety of other reflex effects. For example, if one of the dorsal tufts of cuticular hairs is stimulated in either the same segment or in segments adjacent to the one under test, both RM frequency and extrafusal frequency show a transient inhibition followed after about $\frac{1}{2}$ sec. either by recovery or by excitation. This forms a striking parallel with the effects of cutaneous stimulation on mammalian fusimotor discharge (see Introduction). It also suggests that further functional parallels may be found.

(2) Feedback reflexes

The only previous work on feedback reflexes in the MRO of arthropods is that of Eckert (1961 *a, b*). He found that passive stretch of a single crayfish MRO resulted in reflex inhibition of the stretched receptor, of its contralateral homologue, and of the

receptors in adjacent segments. The effects were seen up to three segments away from the stimulated MRO and were mediated by the accessory fibre of Alexandrowicz (1951). Eckert (1961*a*) encountered difficulty explaining the significance of this auto-inhibition. He argued that it could not be a sensory contrast mechanism, since the stimulated receptor was inhibited as much as adjacent ones, and in any case the crayfish abdomen flexes as a unit.

However, stretch of a single MRO also resulted in a slight inhibition of extensor discharge, and interaction between adjacent receptors strongly facilitated this response. Eckert discussed the possibility of a reflex mechanism, based on these two responses, which could reinforce the swimming movements of the evasive reflex and possibly even effect rhythmic repetition. He abandoned this interpretation after observing that nearly normal movements occurred following denervation of the MRO. Under these conditions accessory fibre excitation and extensor inhibition still accompanied flexor activity. Indeed, even after denervation of the abdominal muscles, these neural correlates of swimming were still seen. Thus the MRO's appear to fulfil a relatively minor co-ordinatory role. The only function Eckert (1961*b*) could attribute to them was control of streamlining. He suggested that the cessation of the centrally originating accessory fibre discharge towards the end of flexion would result in an intense MRO afferent burst which would prolong extensor inhibition. Simultaneously, the accessory fibre would be reflexly excited, thus inhibiting the sensory discharge, and, after a short delay, releasing the extensors from inhibition. The start of extension would then continue the process of reducing MRO afferent discharge. It is noteworthy in relation to the results presented in a subsequent communication that extrafusal muscle activity in the crayfish, in contrast to the caterpillar, is thus under the control of a positive feedback reflex. Extension is accompanied by a 'melting' of tension, not a resistance reflex. This is somewhat analogous to the 'clasp knife' reflex of decerebrate mammals, mediated by the Golgi tendon organs.

The reflex changes in accessory fibre discharge in the crayfish exert a negative feedback control over the MRO sensory discharge. In the caterpillar the weak phasic inhibition by MRO stretch of RM tonic discharge has a similar effect. It would be interesting to know whether a tonic discharge is present in the crayfish RM and if so whether this is inhibited by MRO stretch. Eckert (1961*b*) pointed out that the central modulation of the sensory discharge during swimming renders the crayfish MRO very different from a simple length-measuring device. He suggested that its potential role as a length detector might only be fulfilled during activities other than swimming.

At first sight negative-feedback reflex modulation of the afferent discharge might appear likely to lessen the sensitivity of the MRO to extension. However, even in the limiting case of infinite negative feedback gain, where the sensory discharge would be completely stabilized at one frequency, length detection could still be achieved from a 'knowledge' of the changes in frequency in the fibres exerting the negative feedback control. This is essentially the process involved in measuring electrical resistances with a Wheatstone's bridge. Similar considerations apply to both sensory inhibition in the crayfish and to RM inhibition in the caterpillar.

(3) *Adjusting the set point of a fixed length servomechanism*

Merton (1951) was the first to suggest that the stretch reflex in mammals has many properties in common with a fixed length servomechanism stabilizing muscle length. The fusimotor discharge would then establish the length at which the muscle was to be stabilized. Muscle length could thus be set indirectly by means of this gamma servo loop. Hunt & Perl (1960) preferred to regard the fusimotor system as a mechanism for maintaining afferent signals during shortening by extrafusal muscle. Matthews (1964) discussed the merits of the two theories.

In the caterpillar no evidence was obtained for use of the MRO in a manner analogous to that postulated for the vertebrate gamma loop. As pointed out by Hunt & Perl (1960) and Matthews (1964), one way of proving the servo theory would be to show that changes in the excitability of intrafusal motoneurons precede changes in the excitability of the extrafusal motoneurons by an interval greater than the delay-time of the gamma loop. It was shown previously (Weevers, 1965) that during reverse peristaltic movements in a pinned-out preparation of a caterpillar, changes in RM discharge frequency always lagged somewhat behind changes in discharge frequency in those extrafusal muscles which normally unload the receptor. Thus here the RM discharge was tending to prevent cessation of afferent signals in the sensory nerve from the MRO; it was not being used to activate the extrafusal muscles indirectly via the stretch reflex.

It is interesting to speculate on the adaptive advantage conferred by an RM system which functions only to 'take up the slack'. When the MRO is fully extended, the RM tonic discharge may be somewhat inhibited to avoid sensory overstimulation. On the other hand when the MRO is very short, the RM discharge will not be subject to reflex inhibition and will tend to take up the slack or even increase the sensory discharge frequency to a higher level. Therefore it seems likely that one important function of the RM is to extend the useful range of lengths and velocities of movement over which the MRO can operate, thus fulfilling the same function as that suggested by Cohen (1963) for 'range fractionation' by the chordotonal organs of decapod Crustacea.

SUMMARY

1. Stimulation of the pupal receptor muscle via its nerve resulted in an increased sensory discharge frequency from the MRO.
2. The extent of this excitation was similar in haemolymph and in pupal saline.
3. Stimulation of an MRO whose connexions with the C.N.S. were intact resulted in a transient reflex inhibition of the tonic discharge in the RM of the stimulated receptor. Cessation of sensory stimulation resulted in a transient elevation of RM tone in the stimulated receptor. These changes would tend to protect the sense organ during rapid stretching and would also 'take up the slack' when it was released.
4. A slight crossed intrasegmental RM reflex is described which would normally reinforce the ipsilateral reflex. No RM reflexes were found in adjacent segments.
5. These results are discussed in relation to the nature of the deformation occurring in the sensory dendrites, and in relation to the function of RM systems generally.

I am very grateful to my supervisor, Prof. G. M. Hughes for his guidance during the course of this work and to the D.S.I.R. for financial support in the form of a Research Studentship.

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EXPLANATION OF PLATE

The effect of stimulating the RM on the afferent discharge from the MRO. Afferent spikes are lightly retouched

A, Simultaneous recordings from the sensory nerve and the RM, the latter being intracellular. The electrodes were located as shown in the inset diagram of Text-fig. 1.

B, The sensory discharge from a receptor under somewhat higher stretch during RM contraction.

C, D, E, The sensory discharge following paired stimuli to the RM. Intervals between the stimuli were: *C*, 400 msec.; *D*, 100 msec., *E*, 20 msec. In *B, C, D* and *E* the time of each stimulus is marked by a dot. The upper time-mark refers to record *A* and the lower one to the rest of the records.

