THE PHYSIOLOGY OF A LEPIDOPTERAN MUSCLE RECEPTOR

I. THE SENSORY RESPONSE TO STRETCHING

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INTRODUCTION

There is an extensive literature concerned with various aspects of the sensory physiology of stretch receptors. This is especially true of the vertebrates, and to a lesser extent of the arthropods. The electrophysiological investigation of stretch receptors among the insects, however, is quite recent, dating from the description by Finlayson & Lowenstein (1958) of the receptors in four orders. Osborne & Finlayson (1962) extended the latter study with a description of receptors in a further seven orders. Among these only the sense organs of the Neuroptera, Trichoptera and Lepidoptera are true muscle receptors (MRO), with a separate motor innervation. Chordotonal organs are of much wider occurrence but only in a few cases have they been definitely shown to serve a proprioceptive function (e.g. Becht, 1958; Gettrup, 1962). Thus recent discoveries have shown that insects do not obtain all their proprioceptive information from sense organs in or on the cuticle, although the number of true stretch receptors in any one segment is small and none have been described in the legs. The suggestion by Pringle (1938) that the peripheral integration of strain information in insects may impose important limitations on their behaviour therefore still remains valid. These investigations showing the presence of stretch receptors, mostly slung between intersegmental membranes or between different points on the cuticle, provide useful topographical information. Finlayson & Lowenstein (1958) used methylene blue techniques to study the fine structure of some insect stretch receptors, and the electron microscopic investigation by Osborne & Finlayson (1965) gives details of the termination of the sensory dendrites. Information about the details of receptor processes of the kind provided by Eyzaguirre & Kuffler (1955a, b) for the crustacean abdominal MRO, is completely lacking.

Since the present series of papers is concerned with the behavioural functions of the caterpillar MRO, the aspect of its sensory physiology of greatest interest is the nature of the pulse-coded information which enters the c.n.s. and signals stretch. A number of studies partially or wholly concerned with the patterning of the afferent discharge have been published by authors working on the vertebrate muscle spindle (Katz, 1950; Lippold, Redfearn & Vuco, 1958; Bessou & Laporte, 1962; Jansen & Matthews, 1962; Matthews, 1963). Wiersma & Boettiger (1959) described the responses of a crustacean chordotonal organ; and Pabst & Schwartzkopf (1962) and Gettrup (1963) described the responses of a stretch receptor in the flight system of

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locusts. The only such study of an arthropod muscle receptor is that of Lowenstein & Finlayson (1960) on the lepidopteran pupal MRO, but the wave-forms which they used were only of one type. Moreover the relevance of their results to an investigation of the behavioural role of the MRO is limited owing to their use of an experimental medium yielding responses very different from those occurring in haemolymph (Weevers, 1966). The present work was undertaken to permit more precise evaluation of the way the movements of caterpillars are signalled by these receptors.

**MATERIALS AND METHODS**

The methods of dissection and preparation were essentially the same as those described previously (Weevers, 1966), except in one experiment (of which the results are shown in Text-fig. 14) where use of the early pupa required minor modifications. In all other experiments the afferent discharge was recorded from the MRO of a last instar larva, usually from that of the fifth abdominal segment, the largest receptor. The sensory axon is found in the second of the three nerves leaving the C.N.S. in each abdominal segment, here called nerve 2. Recordings were made just proximal to the spiracle after all afferent nerves other than that from the MRO had been severed and after nerve 2 had been pinched proximally to abolish the efferent discharge. Thus a single-unit discharge could be recorded with hook electrodes without pulling on the sensory cell body and producing a spurious elevation of discharge frequency.

The apparatus used to transmit controlled stretch stimulation to the MRO is shown in Text-fig. 1. Two types of stretching wave-form were used—sinusoidal length changes and ‘ramp-function’ length changes; the form of the latter stimulus is seen in Text-fig. 2. The figure also shows how far the tips of the forceps holding the MRO follow faithfully the rotation of the drive-shaft. The higher of the two stretch velocities shown is three times greater than any used to stimulate the MRO. The essential principle of the device used to generate sinusoidal and ramp-function rotations of the
drive-shaft was that a cam-follower made contact with appropriately shaped cams which could be rotated at different constant angular velocities. The cam-follower shaft was connected to the flexible drive shown in Text-fig. 1 either directly for sinusoids or via a clutch for ramp-functions.

The frequency–time plots were all constructed in the same way. The mean impulse frequency was measured during successive intervals of an arbitrary duration. These intervals were sufficiently short that consistent peaks in frequency were not obscured. The resultant graphically integrated frequency measurement was plotted at a time mid-way between the limits of each interval.

The larval and pupal salines used were the same as those described previously (Weevers, 1966).

RESULTS

The tonic response

Finlayson & Lowenstein (1958) showed that insect stretch receptors signal both tonic and phasic parameters of the stimulus. The magnitudes of both of these components vary with the ionic constitution of the saline. Thus Text-fig. 3 is included to show the nature of the tonic or ‘position response’ of a caterpillar MRO in the present saline. Apart from its slope, the shape of the curve is similar to that reported by Finlayson & Lowenstein.

The phasic response. Stimulation by ramp-function stretches

(1) The component parts of the response

When a receptor is stretched at a constant velocity, even a very low velocity, the discharge throughout the period of stretching is consistently higher than would be expected on the basis of the position response seen in Text-fig. 3. Text-fig. 4 shows the relative contributions of the tonic and phasic components to the overall discharge during low-velocity stretching and releasing.

The responses may be considered as the algebraic sum of: (1) a positive-going and a
Text-fig. 3. The adapted sensory impulse frequency of a larval receptor plotted against its length. The discharge was allowed to adapt for 4 min. at each new length. The horizontal lines show the largest and the smallest length changes used in sinusoidal stimulation (Text-figs. 8–13).

Text-fig. 4. The complex response of an MRO to slow constant-velocity stretching and releasing (full line) compared with the changes in adapted impulse frequency over the same length range plotted on the same time-scale (dashed line). A heavy line above the abscissa in this and subsequent figures indicates stretching and a heavy line below the abscissa indicates releasing. The dashed line will be termed the position response; $\Delta F_1$ will be termed the movement response; $\Delta F_2$ will be termed the acceleration response (see text).
negative-going ramp-function, here called the position response; (2) a positive and a negative step-function corresponding in time to the periods of stretching and releasing, here called the movement responses; and (3) one positive and two negative delta-functions or spikes, corresponding to one positive and two negative accelerations of indeterminate magnitude, here called the acceleration response. Oscillograph records of the sensory discharge during a similar low-velocity ramp-function may be seen in Pl. 1, fig. 1 A and B.

Text-fig. 5. The response of an MRO to the same amplitude of stretch delivered at different (constant) stretch velocities. The time-scale is expressed as a percentage of the duration of the stretching wave-form. Stretch velocities (cm./sec.) were as follows: •, 0.032; △, 0.10; ▲, 0.20; ○, 0.36; ■, 1.60.

(2) The effect of increasing the rate of stretch

As the rate of movement is increased the form of the sensory response to ramp-functions changes considerably. It is perhaps not surprising that during rapid releasing the discharge ceases entirely. This is probably partly a consequence of a purely neural post-excitatory silence and partly of a failure by the sensory strand, due to its viscous properties, to 'follow' the forceps holding it. The neural contribution to this silent period may be gauged from the duration of a similar cessation of orthodromic discharge following a train of antidromic impulses in the sensory axon, Pl. 1, record 1 C. The response to stretching, seen in Text-fig. 5, is quantitatively
related to the stimulus over a considerably wider range than the drop in impulse frequency during releasing. As the velocity of stretch increases so also do both the movement response and the acceleration response.

At the end of the period of stretching there is invariably a brief cessation of sensory impulses before the slowly adapting tonic discharge begins. At low stretch velocities this drop in frequency is very nearly equal to the rise at the start of stretching (see Text-fig. 4). This is probably the negative analogue of the initial acceleration peak, less in apparent magnitude because a negative transient cannot reduce the impulse frequency to less than the reciprocal of the duration of the transient. It is possible that at the end of stretching the forceps 'overshoot', but the upper mechanogram in Text-fig. 2 shows little sign of this. Moreover it is not necessary to postulate such overshoot since the orthodromic discharge from a fully stretched receptor ceases briefly following a high-frequency train of antidromic impulses; thus post-excitatory depression could account for the drop in frequency. The pauses following stretching and antidromic stimulation are clearly seen in Pl. 1, fig. 2 A and B.

(3) The relation between the phasic response and the rate of stretch

The phasic responses of the MRO are summarized in Text-fig. 6, where the magnitudes of the acceleration and movement responses are plotted against the rate of stretch on a log.-log. scale. The movement response is very nearly linearly related to the square root of the rate of stretch, whereas the acceleration response shows a more complex relationship. It is however possible that this relationship would be
simpler if the acceleration were more precisely controlled. In theory the start of any ramp-function, however slow, should occur with infinite acceleration. The real departure from infinite acceleration is due to the limitations of the mechanical linkage, which might well not be simply related to the velocity of stretch. However, in view of the square-root law apparently governing the movement response, this acceleration peak could not be produced by a delay in the initiation of movement followed by more rapid movement, a waveform which might easily result from imperfect transmission of the stimulus to the receptor.

Text-fig. 7. The response of an MRO to a sudden change in stretch velocity compared with its response to sudden initiation of stretching. The fast stretching phase took place at about six times the velocity of the slow stretching phase. The full lines show the responses to slow followed by fast stretch; the dashed lines show the response to the same stimulus with the slow stretch omitted. When stimulated by fast stretch alone the unstretched length of the receptor was increased by an amount equal to the amplitude of the slow stretching phase. The heaviest full and dashed lines show the responses to stretch at 0.005 and 0.03 cm./sec., the medium lines to stretch at 0.03 and 0.20 cm./sec., and the thinnest lines to stretch at 0.11 and 0.64 cm./sec.

(4) The acceleration response

Jansen & Matthews (1962) stated that the analogous (though smaller) initial peak in the frequency–time curve of the mammalian muscle spindle, when it is subjected to ramp-function stretch, should not be termed an acceleration response. They found that when the rate of stretch was changed in the middle of a ramp-function from 0.1 to 0.3 cm./sec., this response did not appear. In short it was a 'starting-to-move' response. Text-fig. 7 and Pl. 1, 3A and B show the results of a similar experiment.
performed on the caterpillar MRO. (The initial slow stretch was produced with a hand-cut spiral cam of a lower pitch than the main cam and placed alongside it. The low rate of stretch was not perfectly constant, but the forceps were already moving at the start of rapid stretch.) Under these conditions, the ‘change-of-rate’ response is only slightly less than the ‘starting-to-move’ response, so that the caterpillar receptor is certainly capable of signalling acceleration.

**Stimulation by sinusoidal stretch**

The ramp-function data give a good qualitative description of the complex phasic-tonic response of the MRO. Sinusoidal stimulation on the other hand would be expected to yield results more amenable to quantitative treatment.

Text-fig. 8 shows an example of oscillograph records from an experiment where the same receptor was stimulated with three different amplitudes of sinusoidally varying stretch. For further analysis plots were constructed of sensory frequency against the phase angle of the stimulus. Text-fig. 9 is one such plot for the lowest cycle frequency. The points on this graph show the impulse frequencies recorded for a given stimulus amplitude and phase; the curves are calculated sine curves of appropriate amplitude fitted to the data by eye. The phase-angles of the peak responses were measured from the curves.

Text-fig. 10 shows a similar plot of impulse frequency against stimulus phase for the highest cycle frequency. The curve is fitted to the filled circles in the same manner as in Text-fig. 9. The presence of harmonic components other than the fundamental of the stimulus cycle frequency indicates that there are substantial non-linearities in the responses to the two larger stimulus amplitudes (Machin, 1964). The smallest stimulus amplitude also evoked a harmonically distorted response but to a considerably lesser extent. Further difficulties of interpretation are introduced by the fact that at
and above this stretch frequency the receptor strand was observed to become slack after peak stretch and to jerk when re-stretched. This may be responsible for introducing some of the harmonic components during the stretching phase, and probably does not represent the real behaviour of the sense organ in vivo, where a

Text-fig. 9. Sensory impulse frequency plotted against the phase of sinusoidal stretch. Three amplitudes of stimulus were used, as in Text-fig. 8: ▲, 0.037; ■, 0.027; ●, 0.014 cm. peak-to-peak. The cycle frequency was 0.0045 cyc./sec. Each point gives the mean of the impulse frequencies at a particular stimulus phase in two successive stretch cycles. The data for 0.014 and 0.027 cm. stretch were obtained from one receptor and that for 0.037 cm. from another.

Text-fig. 10. As Text-fig. 9 but with a stimulus cycle frequency of 0.79 cyc./sec. Here each point gives the mean of the impulse frequencies at a particular phase in six successive stretch cycles. The responses were all from a single receptor.
tonic discharge to the receptor muscle is almost always present. Consequently no attempt was made to study the effects of sinusoidal stimulation at higher frequencies than 0.79 cyc./sec.

(2) Non-linearities over the range of stimulus cycle frequencies

Text-fig. 11 shows the changes in response to sinusoidal stretching of low amplitude as the frequency of stimulation is increased. Up to 0.79 cyc./sec. the harmonic distortion is slight; i.e. the response is truly sinusoidal, and in this respect gives no evidence of non-linearities which would prevent further analysis of the data (Machin, 1964; Fender, 1964). But when the peak-to-peak frequency excursion is plotted against the amplitude of sinusoidal stimulation as in Text-fig. 12, it becomes apparent that the relationship between stimulus and response is far from linear, at any rate for stretch amplitudes greater than 0.014 cm.
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(3) The frequency response of the caterpillar MRO

The steady-state responses of the caterpillar MRO to stimulation by sinusoidal stretch are summarized in Text-fig. 13. In Text-fig. 13a the phase-angle between peak stretch and peak sensory impulse frequency is plotted against the cycle frequency of sinusoidal stimulation on a logarithmic scale. Text-fig. 13b shows the manner in which the peak-to-peak amplitude of the response is related to the cycle frequency for each of three stimulus amplitudes. The amplitude of response is expressed as the gain relative to the position response obtained from Text-fig. 3, or \(20 \log_{10}(\Delta F/\Delta F_0)\), where \(\Delta F_0 = \text{‘static’ impulse frequency excursion and } \Delta F = \text{impulse frequency excursion at a particular stimulus cycle frequency. This method of depicting the frequency response of a ‘black box’ is known as the Bode plot, and for a linear device defines the transfer function } \phi, \text{ where } \phi = \text{magnitude of output/magnitude of input (Machin, 1964). The non-linearities in the response of the MRO preclude linear transfer function analysis of the present data; nevertheless certain qualitative features of Text-fig. 13 are worthy of note.}

First, it is clear that these non-linearities are rather subtle in nature; although Text-fig. 12 clearly indicates their presence, Text-fig. 13a does not. For a linear

\[ \text{Text-fig. 12. The relation between the magnitudes of stimuli and MRO responses over the range of cycle frequencies. } \bullet, 0.0045 \text{ cyc./sec.}; \triangle, 0.07 \text{ cyc./sec.}; \blacksquare, 0.22 \text{ cyc./sec.}; \blacklozenge, 0.79 \text{ cyc./sec.} \]
response the phase-shift at a given stimulus cycle frequency should be independent of the amplitude of the stimulus (De Barr, 1962; DeVoe, 1963). For the range of stimulus amplitudes shown in Text-fig. 13a this criterion is not violated. Furthermore, as mentioned in connexion with Text-fig. 11, the harmonic content of the sinusoidal response is low—again little indication of non-linearities. Secondly, it is quite clear from Text-fig. 13a that the dominant mode of behaviour of the MRO is similar to that of a phase-advance element yielding at least a first differential component in the response, since the phase-advance reaches and may exceed 90°. This is quite unlike the behaviour of the cockroach tibial spine as reported by Chapman & Smith (1963), where over the range of stimulus cycle frequencies producing impulse frequency modulation the phase-advance was essentially constant.

Text-fig. 13. Graphical summary of the responses of the MRO to sinusoidal stimulation (Bode plots). (a) The phase angle between peak input and peak output, plotted against cycle frequency expressed in octaves above the lowest frequency used. (b) The relative amplification of the MRO (log. scale) plotted against stimulus cycle frequency, also on a log. scale as above (see text). The different symbols indicate the amplitude of the sinusoidal stimulus; •, 0.014 cm.; ■, 0.027 cm.; ▲, 0.037 cm. Three different receptors were used to obtain these data.

Text-fig. 13b is very difficult to interpret. Although a curvilinear plot of this form could be a segment of many different curves, there is no indication of an asymptotic slope greater than about 3 dB./octave. Yet, a single differentiating element in a phase-advance network generates an asymptotic gain slope equal to 6 dB./octave and both the ramp-function data and Text-fig. 13a indicate that the response contains zeroth, first-, and quite likely second-order differential components of the stimulus. This anomaly could either be a consequence of the non-linear relation between stimulus and response or it may indicate that the stimulus cycle frequency range was insufficient to evoke the asymptotic gain slope. Presumably the lower gain with larger stimulus amplitudes in Text-fig. 13b is a reflexion of the non-linearities in Text-fig. 12.
Prediction from maintained stretch and ramp-function data of the response to sinusoids

It is also of interest to examine qualitatively the extent to which the response to ramp-function stimuli can be used to predict the frequency response of the MRO. Text-fig. 3 shows a linear relation over the physiological range between length and the position response. Text-fig. 6 on the other hand indicates that the velocity response may be related to a fractional power of the rate of movement. The acceleration response may be neglected because the acceleration during all but the highest cycle frequencies of sinusoidal stimulation is very much less than at the start of ramp function stretch. Assuming that the position response and the velocity response combine additively (an assumption which may be justified by the observation that the curves in Text-fig. 5 are essentially parallel to one another and to the position curve) one might indeed predict a non-linear relation between stimulus and response. The asymptotic gain slope would be a fraction of 6 dB./octave, and the phase-advance would tend to 90° and would be considerable even at very low stimulus cycle frequencies, as found experimentally. However the prediction falls short in one rather important respect. The changes in sensory impulse frequency resulting from sinusoidal changes in length would be non-sinusoidal and Text-fig. 11 clearly shows that this is not the case.

Sensory adaptation following electrical step-functions

One property of a sense organ that indicates the extent to which it responds to differential components of the stimulus is its adaptation following a step-function. Stretch step-functions could not be achieved using the present apparatus, but the ramp-function data certainly indicate initial rapid adaptation followed by a slower decline in frequency, properties which the lepidopteran MRO shares with the ‘slow’ abdominal muscle receptors of decapod Crustacea.

It was suggested earlier that purely neural properties are sufficient to explain the post-excitatory pause following stretching ramp-functions and during releasing. Therefore the MRO was stimulated with direct current in order to examine the extent of neural adaptation, as distinct from adaptation resulting from the visco-elastic properties of the receptor strand. The MRO was dissected as usual. Then, held in the stretching forceps, it was lifted, together with a length of sensory nerve, into mineral oil. The sensory nerve was hooked over the usual type of recording electrodes and saline-agar-filled pipettes were placed on the receptor strand as shown in the inset diagram of Text-fig. 14. In order to avoid polarization the stimulating current was carried by chlorided silver wires dipping into the pipettes.

Dual time constant of adaptation

When a cathodal step-function change in potential was applied to the sensory soma, the discharge frequency suddenly rose and then declined during the remainder of the stimulus. Text-fig. 14 is a plot of impulse frequency against time on a logarithmic scale following such a stimulus. The points are fitted by two regression lines so two time-constants of adaptation may well be involved. The slopes of these regression lines may be somewhat below those obtaining under ideal conditions since the stimulus current did not rise as an ideal step-function. This was the result of high
electrode capacity and the high impedance of a long thin column of lepidopteran saline which contains low concentrations of ions.

(2) Interference by excitation of the receptor muscle

Several workers have used d.c. electrical stimulation to excite sense organs to discharge (e.g. Edwards, 1955; Lowenstein, 1955; Lippold et al. 1960) and in most cases have assumed a close relation between the artificial stimulus and the receptor potential which occurs naturally. The present situation is complicated by the presence of a receptor muscle, which after electrical stimulation might show a decline of tension with a characteristic time-constant due to fatigue. For several reasons it is unlikely that this actually happened. When an MRO is lifted up in forceps the ends are damaged and it becomes progressively harder to evoke contractions of the receptor muscle by any means. At the start of the present experiment the stimulating current required to produce visible contraction of the receptor muscle was $10^{-6}$ A., ten times the current used later to stimulate the sense organ. Further, when the cathode was moved along the receptor to a position on the far side of the sensory soma and the same distance from it as the anode, higher currents were needed to produce any sensory excitation. Presumably the sensory dendrites on one side are hyperpolarized by the same amount as they are depolarized on the other, so that the net effect at the soma is nil, though the receptor muscle should still be excited to the same extent. Finally, as shown in Pl. 1, record 4, an anodal pulse inhibits the sensory discharge and once again the inhibition is not constant in amount, but recovery occurs while the stimulus continues. Only a direct action on the sense cell could have this effect.

Thus some of the differentiation of the stimulus by the MRO results from adaptation occurring in the pacemaker mechanism of the sense cell so that the impulse frequency would decline with time even if the receptor potential remained constant.
DISCUSSION

Sinusoidal stimulation

The use of simple harmonic stimuli as an analytical tool in investigating the response of the caterpillar MRO to stretch encountered certain difficulties, some of which were technical, and some of which may be inherent in the nature of the sense organ.

(1) Departures from 'small signal' analysis

It was found that the peak-to-peak impulse frequency excursion was not proportional to the magnitude of the sinusoidal stimulus for the range of amplitudes from 0.014 to 0.058 cm. stretch. This non-linearity is reflected in other aspects of the responses shown. DeVoe (1963), in a study of the receptor potentials in the wolf-spider eye, found that for small incremental and decremental stimuli, the potential changes were linearly related to the amplitude of the stimulus. However, the linear range was limited to stimuli eliciting small responses.

It is possible that if sinusoidal stimuli less in amplitude than 0.014 cm. were applied to the caterpillar MRO, the response might be linearly related to the magnitude of the stimulus. It would certainly become possible to extend the measurements over a greater range of cycle frequencies. Unfortunately the apparatus used to transmit stretch waveforms to the MRO in this study could not easily be modified to give such small stimuli. For this purpose it would probably be better to use a loudspeaker movement or a servogalvanometer and an electronic function generator, as did Chapman & Smith (1963). The failure of the ramp-function data to predict the sinusoidal responses may also tentatively be ascribed to departure from 'small signal' analysis.

(2) Information loss inherent in the genesis of a pulsatile discharge

Another technical problem which would probably be encountered when using such small stimuli lies in the nature of the response recorded. The genesis of a pulsed afferent discharge, the parameter recorded here, might incorporate non-linearities; it is certainly responsible for some of the differentiation of the MRO (see Text-fig. 14). Spontaneous fluctuations in frequency would be appreciable compared with the total impulse frequency excursion; this would necessitate averaging the responses in a large number of cycles for a high enough 'gain' to be obtained graphically. Thus at low stimulus cycle frequencies the preparation might deteriorate appreciably during the measurements. Finally, at low impulse frequencies actual information loss may occur in the process of spike initiation. For instance, on releasing after intense excitation the membrane potential might rise above the firing level; no change in impulse frequency could occur during this period, although the graded receptor potential would be changing all the time. It would in some respects be more satisfactory to record the receptor potential directly. However no success was obtained in many attempts to penetrate the receptor cell body; in any case, it is more relevant to the present study to know how sensory information enters the C.N.S. than how it arrives at the spike-initiating locus of the sense cell.

It remains possible, even if these difficulties were overcome, that the response of the MRO would still be related to a non-linear function of receptor length. In that
case, non-linear systems analysis would have to be used in formulating a mathematical model of the receptor response (Fender, 1964). A consideration which might lead one to expect non-linearities is the probability that on occasion it may be a considerable advantage to the animal to process some aspects of information before it enters the C.N.S.—(cf. lateral inhibition in the eye of Limulus, Hartline, Wagner & Ratliff, 1956; and mechanical strain integration in the insect leg, Pringle, 1938).

**Adaptation of neural origin**

Lippold *et al.* (1960) applied electrical and mechanical step-function stimuli to the mammalian muscle spindle. They found that the extensive adaptation present in the response to mechanical stimuli was very nearly absent, at least during the first 2 sec. following excitation by electrical step-functions. In the lepidopteran MRO, although the adaptation following an electrical step-function is probably much less initially than after mechanical stimulation it is nevertheless present, and its later time-course is very nearly identical with the time-course of adaptation following stretching of the same receptor. Such neural adaptation is presumably occurring somewhere in the chain of events between the receptor potential and spike initiation, but in the absence of further experimental evidence it is probably not profitable to speculate precisely where.

Thus while Matthews (1964) could attribute the ‘dynamic response’ of the mammalian spindle to the viscous properties of the intrafusal fibres, this does not appear to be possible for the lepidopteran MRO. Its mechanical properties are undoubtedly important but the phasic response of the latter receptor is also influenced by neural adaptation.

**Economical use of the afferent pathway**

In conclusion it should be pointed out that the caterpillar MRO is perhaps an extreme example of the tendency for proprioceptors to generate a ‘quiet’ afferent signal, a characteristic which was the subject of comment by Pringle (1962). Thus the afferent discharge is extremely regular and in the animal’s own haemolymph has a basic adaptation rate which is lower than those of either the crustacean MRO or the vertebrate muscle spindle. As a consequence, just two receptors per segment can rapidly supply exact information about their owner’s movements. The manner in which this information is used by the C.N.S. will be the subject of a future communication.

**SUMMARY**

1. The afferent discharge from the lepidopteran MRO provides complex information to the C.N.S. on the parameters of movements occurring at the periphery.
2. Not only ‘position’ but also ‘movement’ and ‘acceleration’ components are present in the response.
3. While the position response is very nearly linearly related to the length of the receptor, the movement response is related to the square root of the rate of stretch. The acceleration response bears a more complex relation to the stimulus.
4. The responses of the sense organ to stretching are discussed in relation to the possibility of using methods of linear systems analysis. The observed non-linearities preclude such treatment of the present data.
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REFERENCES


EXPLANATION OF PLATE

The effects of various stimuli on the afferent discharge from muscle receptors. Only record 4 is taken from a pupal sense organ, the rest are from last-instar larvae. Spikes are lightly retouched. 1 A, Low-velocity stretching, and B releasing (0-06 cm./sec.). The vertical line gives the scale of the mechanogram as do similar lines to the left of records 2 A, 3 A, B. Records 1 A and B are consecutive. C, The silent period in the discharge from a lightly stretched MRO following a train of antidromic impulses (20/sec.) produced by electrical stimulation of the sensory nerve proximal to the recording electrode. The horizontal line below this record and below 2 B shows the duration of antidromic stimulation. 2 A, High-velocity stretching (1-2 cm./sec.). B, Antidromic stimulation at 120/sec. of a fully extended MRO. 3 A, The acceleration burst (arrow) at the start of a period of high-velocity stretch in a sense organ which was previously motionless. B, The similar acceleration burst when the same high-velocity stretch (0-38 cm./sec.) was preceded by a period of low-velocity stretch (approximately 0-06 cm./sec.). 4, The inhibition by direct current passed through the sense cell of the discharge from a lightly stretched pupal MRO. The anode was located on the cell body. The time-scale of each record or group of records is shown on the left.