

SOME EFFECTS OF RECEPTOR MUSCLE CONTRACTION ON THE RESPONSES OF SLOWLY ADAPTING ABDOMINAL STRETCH RECEPTORS OF THE CRAYFISH

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INTRODUCTION

It has been known for many years that stimulation of the motor nerves to vertebrate muscle spindles leads to an increase in the frequency of discharge of the receptor afferent when the muscle is at a constant length (Matthews, 1933; Leksell, 1945; Kuffler, Hunt & Quilliam, 1951). Recently it has been found in muscle-spindle primary endings of cat and rabbit (Matthews, 1962; Emonet-Denand, Laporte & Pages, 1966) and in frog spindle afferents (Matthews & Westbury, 1965) that receptor muscle contraction may significantly change the dynamic response of the endings, i.e. their response to the rate of length change. For invertebrate stretch receptors Kuffler (1954) has demonstrated the effect of receptor muscle contraction on the responses of the fast-adapting and slowly adapting abdominal and thoracic stretch receptors of crayfish and lobsters when these are kept at a constant length. The present experiments on the slowly adapting stretch receptors of crayfish were carried out to see if receptor muscle contraction modified the responses of the receptor under dynamic as well as static conditions. A preliminary communication of some of the results has already been given (Brown, 1966).

METHODS

The experiments were carried out on twenty-three slowly adapting abdominal stretch receptors from sixteen fresh-water crayfish (*Astacus* sp.). The crayfish were kept in shallow tanks of continuously recirculated and charcoal-filtered tap water, and providing they were not crowded remained healthy for many weeks. The receptors were studied *in situ*. Early attempts at obtaining contractions from completely isolated receptors were unsuccessful, and this was probably because the fine motor fibres to the receptor were damaged during dissection. Fig. 1 shows diagrammatically the experimental arrangement which allowed adequate stretches to be given to the receptor but avoided damaging dissection. After removal of the flexor muscles and gut, and dissection of the nerve to the receptor from the ventral nerve cord, the abdomen was pinned ventral side down in crayfish saline and the carapace over segments 3 and 4 was carefully removed with scissors and forceps, followed by the layer of pigment tissue which immediately overlies the receptor and extensor muscles. The slowly adapting receptor inserts into tough connective tissue at the posterior end of the segment, and this was cut away from the shell and attached by a miniature chuck to an extension of

the stretching device. The medial superficial extensor muscle also inserts into this tissue and its most medial fibres were sometimes also attached to the stretcher.

Application of stretch. This was done with an electromagnetic puller (Goodman's V47) which was fed with ramp wave form currents of different rates of rise (to give different velocities of stretch) and of different final values (to give different length stretches). A full description of the stretcher is given in Brown & Stein (1966). In these experiments velocities of stretch from 0.05 to 10 mm./sec. were used with amplitudes of stretch from 0.1 to 0.5 mm. A linear phototransistor device (Machin, 1959) recorded the movement of the stretcher.

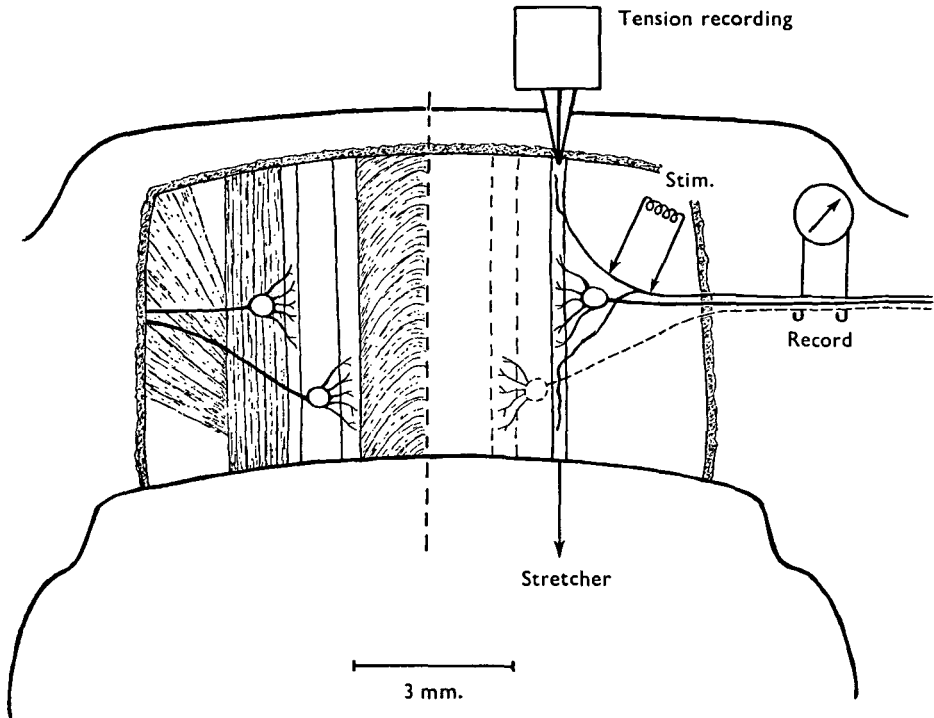


Fig. 1. Diagram of experimental arrangement. A single abdominal segment is seen from the dorsal side with the exoskeleton removed. The top of the diagram is the anterior end of the segment. The slowly adapting receptor is thinner than and lies lateral to the fast adapting receptor. Further description in text.

Recording of tension. The tension in the receptor muscle was recorded with a myograph very similar to that used by Atwood, Hoyle & Smyth (1965). It consisted of an R.C.A. 5734 transducer valve with a fine forceps tips attached to the anode pin. Even when under saline the myograph was underdamped and to avoid recording oscillations at its natural frequency (130 cyc./sec.) the output was deliberately restricted by a simple low-pass R-C filter with a turn-over frequency of 50 cyc./sec. Unfortunately in most cases attaching the myograph to the receptor made the contraction weaker (cf. Weevers, 1966) and so in some experiments the myograph was not used. It was also hard to isolate the receptor at the anterior end of the segment, and the tensions recorded passively would often consist of more than the tension in the receptor muscle. In some cases, too, the myograph was attached to the receptor via connective tissue

with unknown elastic properties. The myographic results therefore have serious quantitative limitations.

Recording afferent discharge. The discharge from the receptor was recorded monophasically with a pair of fine silver electrodes which lifted the cut end of the receptor nerve into liquid paraffin which had previously been equilibrated with crayfish saline (van Harreveld, 1936). The receptor itself was just covered with the solution, the temperature of which ranged from 17 to 20° C. The amplified action potentials triggered a circuit which gave a direct display of the instantaneous frequency of discharge (Matthews, 1963). Each action potential caused a momentary brightening of the spot of a cathode-ray tube. The deflexion of the spot in the Y-axis was proportional to the reciprocal of the time interval since the immediately preceding action potential. To prevent either the shock artifacts or the antidromically conducted potentials in the motor fibres (see Fig. 1) from triggering the instantaneous frequency meter, a pulse height analyser circuit was used. This was set to pass potentials only in a narrow band which encompassed the peak of the action potentials in the sensory axon. The critical setting of this 'window circuit' meant that small fluctuations in size of the sensory action potential could lead to failure of triggering of the frequency meter: occasional apparent halving of the instantaneous frequency due to loss of one action potential might thus occur (see Figs. 2 and 4), but as the receptors fire very regularly this did not obscure the pattern of discharge. A similar failure of triggering of the instantaneous frequency meter could be brought about by the simultaneous occurrence of the wanted action potential, for which the window was set, and a larger unwanted shock artifact. This was more likely to occur with higher stimulation rates. The output of the frequency meter, the length transducer and the myograph were displayed on two double beam oscilloscopes, and were photographed together with 1/sec. time marks and a signal light from the stimulator on slowly moving recording paper (1.22 or 1.82 cm./sec.).

Stimulation. 100 μ sec. square pulses, or pulses (total duration 1 msec.) from a relaxation oscillator, were applied through an isolating transformer and fine bipolar silver wire electrodes insulated for all but their tips. The electrodes were placed with their tips just under the surface of the thin film of crayfish saline. It was usually found possible to excite the motor branches to the receptor alone, without also directly exciting the axon of the sensory cell, by placing the stimulating electrodes to one or other side of the main nerve running towards the receptor; the fine motor twigs usually diverge from the main nerve and run towards the poles of the receptor muscle before the sensory cell is reached. This is shown diagrammatically in Fig. 1.

Movements of the receptor and its nerve during stretches of up to 0.5 mm. were not found to reduce the effectiveness of the stimulation of the motor fibres. If the stimulus intensity was gradually increased with the receptor at a constant length, excitation of the motor fibres, with subsequent contraction of the receptor and firing of the sensory cell, occurred in an all-or-none manner. This finding fits with that of Fields & Kennedy (1965) who found in *Procambarus* that only one, and at the most two, of the five motor fibres to the superficial extensor muscles innervates the slow receptor muscle. Thus in these experiments, provided there was any excitation it was at a maximum, and failure of stimulation could be immediately seen by a rapid drop in the frequency of the sensory cell.

Although the electrodes probably directly stimulated only branches of the main motor fibre to the receptor, direct observation showed that the receptor contracted at both poles which suggests either that the particular branch ramified widely over the receptor or that impulses spread antidromically into other branches to achieve overall excitation of the motor fibre.

Analysis of results. The frequency at various times before, during and after stretch was measured directly from the film. Time could be resolved to the nearest 25 msec., and frequency, with accurate calibration curves for the frequency meter, to within 1 impulse/sec.

RESULTS

Stimulation with the receptor at a constant length

Frequencies of stimulation between 1 and 90/sec. were studied and the responses from two different receptors are shown in Fig. 2. The contractions were more powerful for the receptor in B and the individual contractions of the muscle appear as

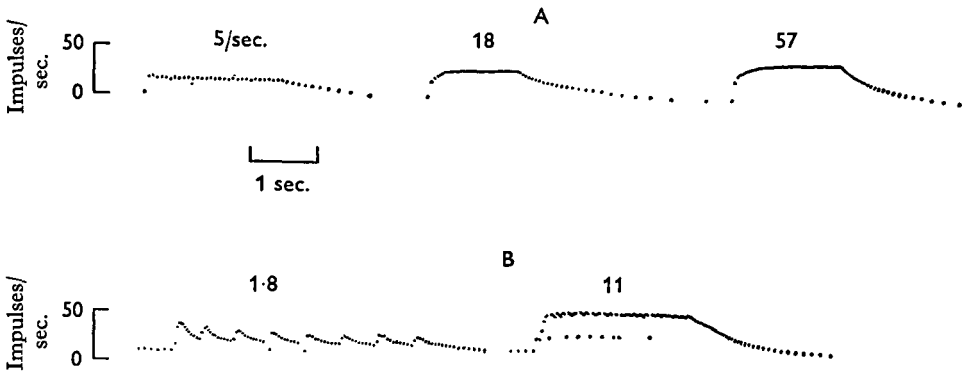


Fig. 2. Stimulation of the motor fibres with the receptor at a constant length. In this figure and figs. 4 and 6, each action potential is represented by a dot, and its vertical displacement is proportional to the reciprocal of the time interval since the previous action potential (i.e. the instantaneous frequency in impulses/sec.) The calibration bars represent 0-50 impulses/sec. Results from two experiments (A and B). Frequency of stimulation is given above each response. For explanation of missed impulses (gaps in frequency record) see methods.

rhythmic modulations of the discharge frequency at the stimulation rate (cf. Kuffler, 1954). These modulations are only just visible at 5/sec. in A but can still be seen at 11/sec. in B. They were never seen with stimulation rates above 11/sec. In agreement with this apparent low 'fusion frequency' it is found that although the sensory response increases with stimulation rates up to 50 or 80/sec., the response is often 70% of maximal with stimulation at 11 or 18/sec. A graph of the relationship between stimulation frequency and frequency of firing of the sensory cell is shown in Fig. 3 for the receptor illustrated in Fig. 2A.

The maximum frequency found in different receptors ranged between 20 and 70 impulses/sec. but was usually about 50 impulses/sec. Fig. 2 also shows that the frequency remains fairly constant throughout the period of stimulation, and that the frequency rises much more quickly to a plateau at the beginning of stimulation than it decays from it at the end of stimulation, due to a slow decay in tension (cf. Fig. 8).

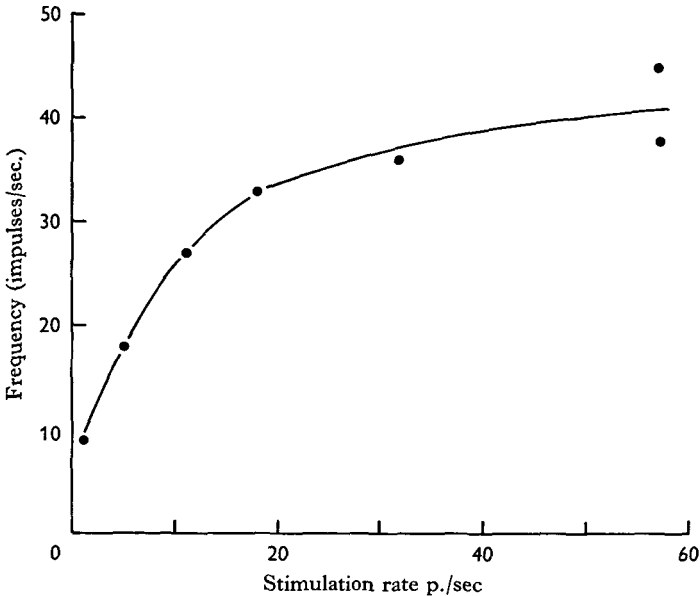


Fig. 3. Relationship between stimulation rate (abscissa) and frequency of receptor firing (ordinate). From experiment partly illustrated in Fig. 2A.

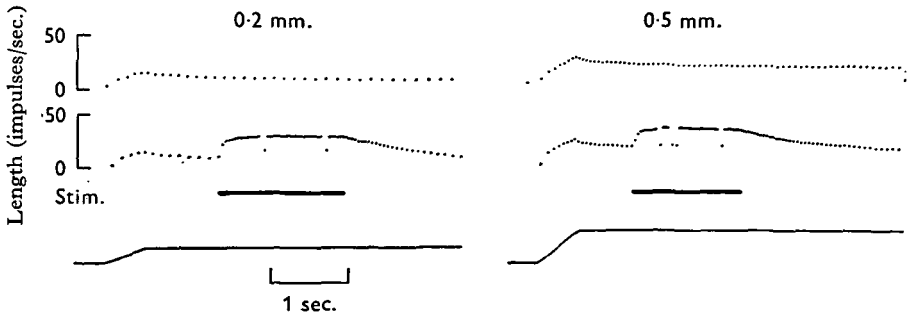


Fig. 4. Responses to two different lengths of stretch. Top records from passive receptor. In the middle records the motor fibres were stimulated at 18/sec. for the periods marked by the black bars. The bottom records are the output from the length transducer. In the top two rows frequency is recorded as described in methods and in the legend of Fig. 2.

Static stretch

To investigate the relationship between impulse frequency and length, the receptors were stretched to different final lengths (the ramp rise-time for all the stretches being the same). In Fig. 4 are sample records for stretches of 0.2 and 0.5 mm. The increase in instantaneous frequency over that at the initial length (the initial length was set so that the receptor fired at about 1 impulse/sec.) was measured at a series of fixed times after the end of the dynamic phase of stretch. A series of curves relating impulse frequency to length was thus obtained whose slopes decreased as the frequencies were measured at progressively later times. Crayfish receptors continue to 'adapt' for up to 2 min. (Florey, 1956; Wendler, 1963; Brown & Stein, 1966), and although they do not adapt to zero the fully adapted relationship between frequency and extension is

small, and was not determined. In Fig. 5 the lower curve (open circles) gives the increase in instantaneous frequency 2 sec. after ramp stretches plotted against the increase in length. The relationship is approximately linear, a result which has been found before (Wendler & Burkhardt, 1961; Terzuolo & Washizu, 1962; Brown & Stein, 1966) but this is not always so (Krnjevic & van Gelder, 1961; Brown & Stein, 1966).

The maximum amplitude of stretch used was 0.5 mm. which for an average receptor represents an increase of 17% over its minimum *in situ* length. Inspection of receptors *in situ* during flexion of the abdomen suggests that the maximum natural

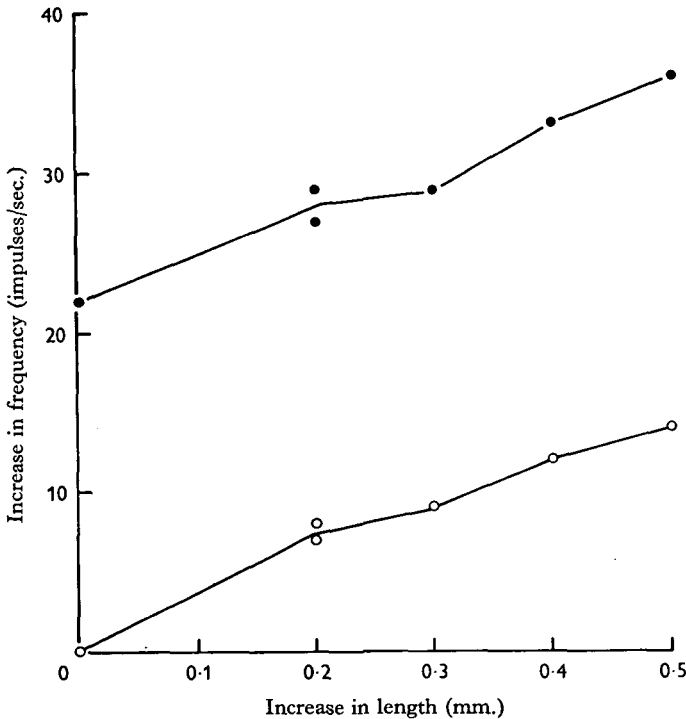


Fig. 5. Relationship between length of stretch (abscissa) and frequency of firing (ordinate). Open circles are the results from passive receptor. The filled circles are the results from the same receptor during stimulation of the motor fibres at 18/sec. Results from experiment partly illustrated in Fig. 4. The frequencies are the instantaneous frequencies measured 2 sec. after the application of the stretch from which have been subtracted any frequency occurring before the application of stretch (see text).

increase in length is 35% of the minimum (Brown & Stein, 1966), but in these experiments stretches larger than 0.5 mm. could lead to failure of stimulation (see methods).

The effect of receptor muscle contraction on the frequency/extension relationship was studied by giving the same stretches as before and, when the receptor had reached the new length, stimulating the motor fibres (cf. Crowe & Matthews, 1964), as is illustrated in the lower records of Fig. 4. The stimulation in each case was begun at approximately the same time after the stretch. The upper curve of Fig. 5 plots the results of this experiment, again for frequencies 2 sec. after the dynamic phase of stretch. The passive and active curves run closely parallel indicating, as can be seen in Fig. 4, that the contraction at each length added about the same increase in frequency.

Thus receptor muscle contraction does not seem to alter appreciably the slope of the frequency/extension relationship when determined in this way, and this result was found in the nine experiments where it could be adequately studied.

Dynamic stretches

The frequencies in a receptor stretched 0.3 mm. at two different velocities are shown in Fig. 6. In the top row of records there was no motor nerve stimulation, but in the bottom row the motor fibres were stimulated at 18/sec. starting about a second before the stretches began and continuing during and after the dynamic phase of stretch. During the dynamic phase of stretch the increase in frequency (the difference between the frequency before the stretch and the peak frequency) is greater in the bottom records, and also the frequency decays more quickly after the ramp.

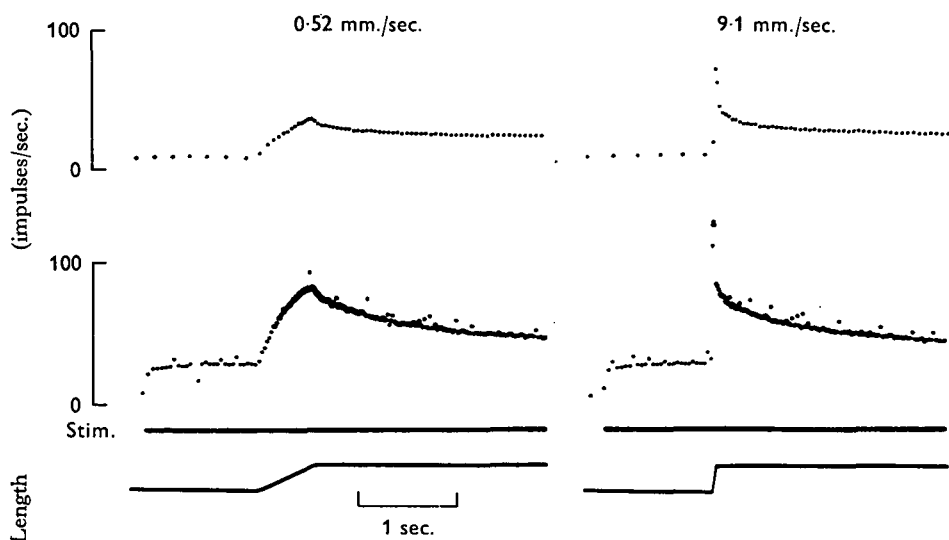


Fig. 6. Responses to different velocities of stretch. Top row of records from passive receptor. In the middle row the motor fibres were stimulated at 18/sec. for the periods marked by bars. The bottom row is the output from the length transducer. Length of stretch was 0.3 mm. Recording of frequency as described in methods and the legend of Fig. 2.

These two points are further illustrated in Fig. 7. Increases in frequency are plotted as the ordinate against velocity of stretch. The open circles give the differences between the peak frequencies at the different velocities and the frequencies before the stretch for the passive receptor, and the filled circles do the same for the active receptor (motor nerve stimulation at 18/sec.). For the active receptor the rise in frequency during the dynamic phase of stretch is roughly double that for the passive receptor. The square points in Fig. 7 give the increases in frequency over the initial frequencies measured 2 sec. after the end of the dynamic phase of stretch (open squares, passive receptor; filled squares, active receptor). Not only are the frequencies measured at this time independent of velocity, but because of the faster decay of frequency in the active receptor there is also now little difference between the results in the two situations. In other words the contraction increased the dynamic sensitivity of the receptor, for in the active receptor the greater increase in frequency generated during the

dynamic phase of stretch was not maintained into the static phase of the stretch, and after 2 sec. the rise in the frequency due to the stretch was the same for the passive and active receptor.

This result has been found on every receptor, but the size of the effect varied considerably. On the whole, where contraction had a powerful action with the receptor at a constant length the action in increasing the dynamic sensitivity was larger than average. The receptor illustrated in Fig. 6 demonstrates an effect which was about average. In no receptor was there a decrease in dynamic sensitivity.

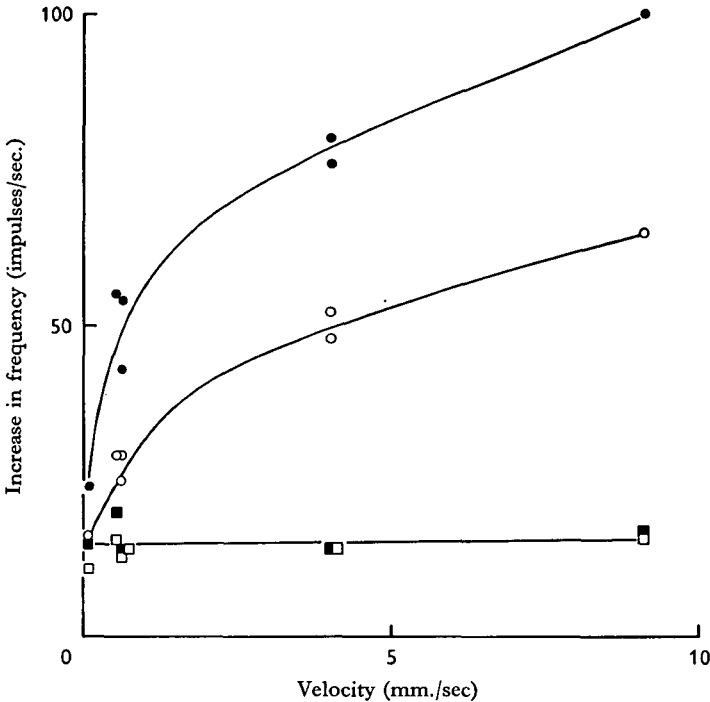


Fig. 7. Relationship between velocity of stretch (abscissa) and frequency of firing of the receptor (ordinate). Circles are the peak frequencies, the open circles being the results from the passive receptor and the filled circles being the results obtained during motor-fibre stimulation at 18/sec. The squares are the frequencies 2 sec. after the end of the dynamic phase of stretch; the open squares from the passive receptor, the filled squares from the contracting receptor. The frequencies are the instantaneous frequencies from which have been subtracted any frequency occurring before the application of stretch. Results from experiment partly illustrated in Fig. 6.

It will be seen that for the fast stretches (9 mm./sec.) in Fig. 6 the peak frequency consists only of one or two impulses at the peak rate, often well separated from any comparably high-frequency impulses, and the usefulness of attaching any significance to the frequency corresponding to only one or two impulses may be questioned. In fact these isolated points were repeatable, in keeping with the regularity of the receptors, and from the descriptive point of view are therefore significant. A rate of stretch of 9 mm./sec. is well within the physiological range. Flash photography of crayfish swimming during the escape reaction shows that the receptors may be extended at least as fast as 30 mm./sec.

Tension and frequency

Two aspects of the relationship between tension and frequency are of current interest. The first question is whether the frequency is linearly related to receptor tension. The second is, whatever the relationship between tension and frequency, is there a constant relationship between any one tension and any one frequency; that is, does the receptor adapt to a constant tension? Both these points have been studied previously (Wendler & Burkhardt, 1961; Krnjevic & Van Gelder, 1961; Brown & Stein, 1966) in experiments where only the passive tensions generated by stretch were used.

Unfortunately (see methods) the tensions recorded in these experiments provide only qualitative information, and so cannot help to answer the first question. The general correspondence between tension and frequency during stretch with contraction of the receptor (stimulation at 5/sec.) is shown in Fig. 8. The individual contractions and the general shape of the tension record are mirrored in the frequency.

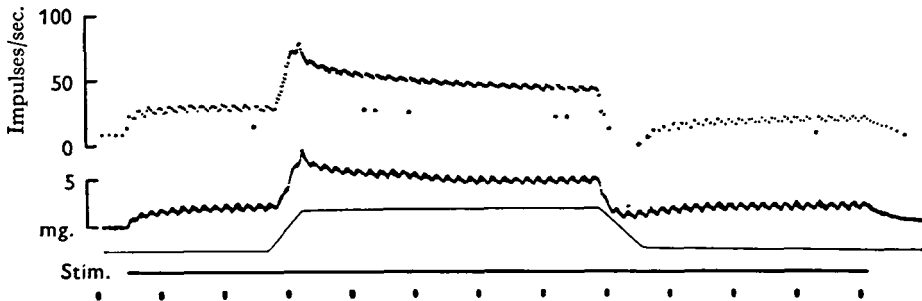


Fig. 8. Relationship between frequency and tension. Top row, instantaneous frequency recorded as described in methods and legend of Fig. 2. Second row, tension in the receptor muscle. Third row, output from length transducer. During period marked by black bar the motor fibres were stimulated at 5/sec. Time marks, 1/sec.

However, it can also be seen in Fig. 8 that a particular tension is not associated with only one frequency, for on release of stretch the frequency falls to zero, but the tension is still above the initial tension where the frequency was already 10/sec. Part of the explanation in this case may be 'fatigue', leading to a general reduction in frequency, but it seems that the frequency is partially dependent upon the rate of change of tension as well as on the tension itself. Thus, before stretch begins (and before many impulses have been fired) it can be seen that although the tension continues to rise very slowly the frequency flattens off. But whereas the response to rate of change of length (the dynamic sensitivity) is immediately obvious in Fig. 8 the adaptation to a constant tension appears to be small, and it may be accounted for by the small but definite adaptation of the firing region of the sensory cell to constant-current stimulation (Brown & Stein, 1966). It should be noted that the fastest rate of rise of tension obtainable by motor nerve stimulation is not very great, and so any response to rate of tension change might be expected to be small. The application of step changes in tension presents greater technical difficulties than the application of step changes in length. Wendler & Burkhardt (1961) with such step tension changes did find a considerably greater adaptation than has been suggested by the present results, but they

also found much more adaptation to constant-current stimulation than was found by Brown & Stein (1966), and it therefore is still uncertain whether it is necessary to postulate an adaptation of the generator potential to a constant tension in addition to the adaptation of the impulse-generating region to constant currents. It does seem to be clear from Fig. 8 that the major cause of the receptor response to dynamic stimuli lies in the properties of the receptor muscle.

Transfer functions

It has been found empirically (Brown & Stein, 1966) that following fast ramp stretches ('step' changes in receptor length) the frequency of isolated receptors decays according to a power function of time; and where the frequency is a linear function of receptor length, which seems frequently to be the case, the total frequency response of slowly adapting receptors to a step stretch can be expressed by

$$f = ax^{1-k} + bx + c, \quad (1)$$

where f is the instantaneous frequency, x is the receptor length, t is the time since change in length, and a , b , c , and k are constants. The transfer function for the time-dependent (phasic) component of the frequency has been calculated (Chapman & Smith, 1963) and is

$$F(s) = a\Gamma (1-k)s^k. \quad (2)$$

It was used to predict the response to ramp stretches and to sinusoidal stretches. The constants a and k determined from steps, ramps and sinusoids were compared and the only significant inconsistency found was that the value of k determined from the peak frequency during ramp stretches was too high. This finding may be related to the fact that at very early times the frequency decay following steps falls faster than predicted by the power function of equation (1). It seemed of interest to see if this convenient mathematical summary of the response of slowly adapting receptors could still be applied during receptor muscle contraction, and if so by alteration of which of the 4 constants a , b , c , or k .

In a previous section it has been shown that receptor muscle contraction does not alter the slope of the frequency/extension relationship, and therefore of the two time-independent constants only c , which represents the background frequency which is independent of length as well as time, is increased by receptor muscle contraction. Constants a and k which together determine the form of the phasic part of the response were obtained for passive and active receptors from two sets of data: the frequency change following rapid ('step') stretches, equation (1), and from the relationship between peak frequency of firing and velocity of stretch for which the transfer function predicts that

$$f_{\text{peak}} = \frac{ax^{1-k}v^k}{1-k} + bx + c, \quad (3)$$

where v = velocity of stretch in mm./sec.

In both these methods the time-independent part of the frequency has to be subtracted from the total to obtain the phasic portion of the response. It has been assumed that the frequency before the application of stretch (the background frequency, c) represents virtually all of this non-phasic component of the response, because as explained on p. 449 the true fully adapted length-dependent frequency is very small

for the passive receptor, and as the receptor muscle contraction does not change the slope of the frequency/extension curve, the same must be so for the active receptor. It can be seen from Fig. 2. that the background frequency during stimulation remains reasonably constant. If following 'step' stretches equation (1) is obeyed it can be seen that a plot of the phasic part of the frequency against time on double logarithmic co-ordinates will give a straight line of slope $-k$, a being easily calculated from the frequency occurring at time $t = 1$. Similarly, from equation (3) it can be seen that if phasic peak frequency is plotted against velocity of stretch on double logarithmic co-ordinates a straight line of slope k should be obtained, a being calculated from the frequency at $v = 1$ mm./sec.

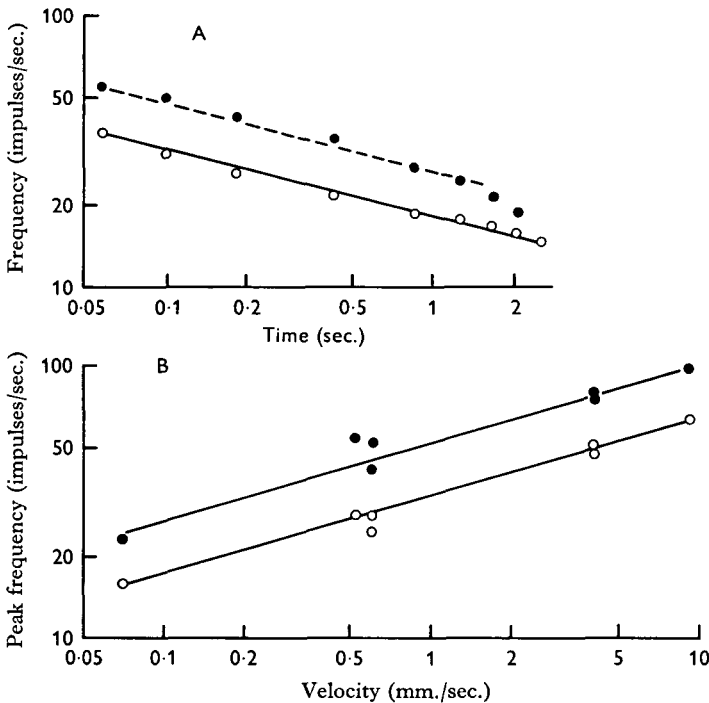


Fig. 9. A. Decay of impulse frequency following a 'step' stretch, plotted on a log-log scale. Open circles, results from passive receptor, filled circles results obtained during motor-fibre stimulation at 18/sec. The frequencies are the instantaneous frequencies, and in both cases any frequency occurring before the application of the stretch has been subtracted. Results for 9.1 mm./sec. stretch of Fig. 6. Length of stretch 0.3 mm. Lines drawn by eye (see text). B. Relationship between peak frequency and velocity of stretch plotted on a log-log scale. From experiment partly illustrated in Fig. 6. Open circles, results from passive receptor; filled circles, results obtained during motor-fibre stimulation at 18/sec. In both cases any frequency occurring before application of stretch has been subtracted. Lines drawn by eye.

As an example of the findings the results from the experiment illustrated in Figs. 6 and 7 are shown in Fig. 9, where in A frequency (from which has been subtracted the time-independent frequency) following a 'step' stretch is plotted against time on double logarithmic co-ordinates, and in B the peak frequency (minus the background time-independent discharge) is plotted against velocity of stretch also on double logarithmic co-ordinates. In Fig. 9A the lower line (open circles) is for the passive receptor, and in agreement with results from isolated receptors the points do fall on a straight

line on this graph, giving a slope $k = 0.24$ and $a = 57$ impulses $\text{mm.}^{-1} \text{sec.}^{k-1}$. The points above (filled circles) are for the same stretch applied during motor-nerve stimulation at 18/sec. Towards 2 sec. the frequency tends to drop below a line which might be drawn through the earlier points. This may be an exaggeration of the tendency for the response of passive receptors to fall away at about this time, and which has been attributed (Brown & Stein, 1966) to electrical adaptation. This effect is perhaps more likely to appear following the higher frequencies produced by stretch when these are applied on a background excitation due to contraction. This has been the general finding for the frequency decay following step stretches during receptor contraction, and clearly it detracts from the use of the simple formula (1) as a complete description of the response. However, for comparison with results from the ramp stretches, lines have been drawn through points for the first 1.5 sec., and in most experiments a good fit can be obtained, and a and k determined. For Fig. 9 this gives a value for k equal to that found for the passive receptor (0.24), but with an increase in a to 81 impulses $\text{mm.}^{-1} \text{sec.}^{k-1}$. This is a typical result, there being no consistent change in k in other experiments but always an increase in a .

In Fig. 9B, which shows the circle points of Fig. 7 replotted on double logarithmic co-ordinates, the lower points are from the passive, and the upper from the contracting, receptor. Straight lines of identical slope ($k = 0.29$) fit both sets of data. This value for k is slightly higher than the figure found from the step responses. In the passive case, a is 57 impulses $\text{mm.}^{-1} \text{sec.}^{k-1}$ (i.e. the same as the value found from steps) and in the active a is 89 impulses $\text{mm.}^{-1} \text{sec.}^{k-1}$ (81 for steps.)

It has been a general finding that there is agreement (sometimes not as close as in the example given) between the values of a and k determined in these two ways and also that k is not changed appreciably by receptor contraction but that a is increased. For determinations from the peak frequency/velocity relationship the mean change in k as a result of receptor muscle contraction was $+0.009 \pm 0.047$ (S.D.), $n = 7$, and the mean change in a was $+34 \pm 19$ (S.D.). For determinations from step changes in length the mean change in k was $+0.025 \pm 0.045$ (S.D.), $n = 10$ and the mean change in a was $+33 \pm 16$. It seems that the main effect of receptor contraction on the transfer function is to add a background frequency, c , and to increase the value of a .

DISCUSSION

The results show that receptor muscle contraction increases the dynamic sensitivity of the slowly adapting receptor and although only cautious comparison with the findings from vertebrate species should perhaps be made, it seems that the motor fibre to the receptor muscle is analogous to the dynamic fusimotor fibres of cats and rabbits and to the small motor fibres of frogs, and not to the static fusimotor fibres.

The function of dynamic fusimotor fibres in mammals is not clear. Matthews has suggested that they may alter the damping of the stretch-reflex arc by controlling the size of the velocity feedback from the muscle spindles (Jansen & Matthews, 1962) and/or that they may serve to increase the phasic 'gain' of the stretch reflex (Brown & Matthews, 1966). Similar roles can be proposed for the motor fibre or fibres to the crayfish receptor, as Fields & Kennedy (1965) and Fields (1966) have shown that the slowly adapting cell evokes a reflex contraction in the muscles in which it lies.

The failure of receptor contraction to change the slope of the frequency/extension relationship is surprising, because in most striated muscles the tension/extension curves in the passive and active state are not parallel, the active curve being steeper as well as displaced upwards on the tension axis. The means of recording tension were not adequate to decide if the receptor muscle was atypical in this property. A possible explanation for the results assuming a normal tension/extension relationship may lie in the finding (Brown & Stein, 1966) that with higher tensions the slope of the frequency/tension curve for receptors tends to decrease, a greater rise in tension being needed at higher tensions to produce a given increment in frequency.

SUMMARY

1. Stimulation of the motor fibres innervating the slowly adapting abdominal stretch receptors of the crayfish was carried out under the following circumstances:

2. With the receptors at a constant length the frequency of stimulation was varied. A maximal response from the receptors, which averaged about 50 impulses/sec., was obtained with stimulation rates of 50–80/sec. But low rates of stimulation (e.g. 10/sec.) had a powerful excitatory action, often 70% of maximal.

3. With the receptors stretched different amounts the motor fibres were stimulated at a constant rate. The increase in the receptor discharge caused by the contraction was the same over the range of lengths studied.

4. The receptors were stretched at a series of constant velocities (0.05–10 mm./sec.) to the same final length with and without motor-nerve stimulation. The contraction increased the frequency rise during the dynamic phase of stretch and increased the amount by which the frequency decayed at the end of the ramp.

5. The phasic response of the de-efferented receptor has previously been described by the following transfer function $Fs = a\Gamma(1-k)s^k$, where a and k are constants. To a first approximation the effect of receptor contraction on this phasic response was to increase the value of the constant a , but to leave k unaffected.

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