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TENSION CHANGES IN CRAYFISH STRETCH RECEPTORS

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Although much is known about various stretch receptors no information seems to be available on their mechanical properties; yet these properties are often considered to be responsible for certain characteristics of the nervous response of the receptor to stretch (e.g. Matthews, 1931, 1933; Loewenstein, 1956; Finlayson & Lowenstein, 1958; Lippold, Nicholls & Redfearn, 1960; and many others). It therefore seemed of some interest to examine the stretch–tension relation of crayfish stretch receptors, which can be isolated and whose behaviour in many respects has already been analysed in great detail (Wiersma, Furshpan & Florey, 1953; Kuffler, 1954; Eyzaguirre & Kuffler, 1955; Florey, 1956). A brief report of our results has already appeared (Krnjević & van Gelder, 1960).

METHODS

All the stretch receptor organs were taken from specimens of *Astacus fluviatilis* (subvariety *torrentium*). During the dissection the preparation was kept submerged in crayfish saline, and after isolation the receptor organs were transferred in a platinum spoon, together with a small volume of fluid, to the recording chamber. Inside the glass-bottomed Perspex chamber the receptors remained floating in saline (0·5–1 ml.) throughout the experiment. The saline was derived from van Harreveld's (1936) well-known solution, and had the following composition (mM): Na^+ 202, K^+ 5·0, Ca^{2+} 9·4, Mg^{2+} 2·3; Cl^- 220, and Tris acid maleate buffer 10·5; with a pH of 7·1–7·2. In some experiments 4·7 mM L-monosodium glutamate was also present.

Tension measurements. One end of the receptor bundles was held by the closed tips of a watch-maker's fine forceps. The other end of one or both receptor organs was tied with 50 μ silver wire to a fine glass hook attached to the movable anode of an RCA 5734 mechano-electric transducer. The forceps and the transducer were both mounted on a horizontal threaded shaft, and they could be separated in a predictable manner by rotating this shaft (Fig. 1).

The stretch receptors are quite small; the slow-adapting organ, in particular, can have a diameter of 50 μ. Their mechanical properties are apparently comparable with those of muscle in general, so that the total tension developed during stretch is in the order of only a few milligrams (cf. Kuffler, 1954). As the RCA 5734 transducers are very sensitive to

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changes in temperature and in voltage supply, two were used differentially to minimize drift caused by these factors.

The natural frequency of the transducer with the glass hook attached was in the order of 100 c/s, more than adequate to deal with the relatively slow changes of tension produced in these experiments. To calibrate recorded tensions accurately known weights were suspended from the glass hook of the transducer held at the appropriate angle. The output was linear over the relevant range of tensions. The compliance of the system was negligible; to displace the hook by 100 μ required a force of 200 mg.

Nerve impulses. The saline in the recording chamber was covered with a layer of liquid paraffin. The saline was earthed through an Ag-AgCl electrode covered with gauze or agar-agar. Afferent impulses from the nerve were recorded either in a monopolar fashion with one 50 μ silver wire on the nerve in the paraffin, or differentially with two such leads.

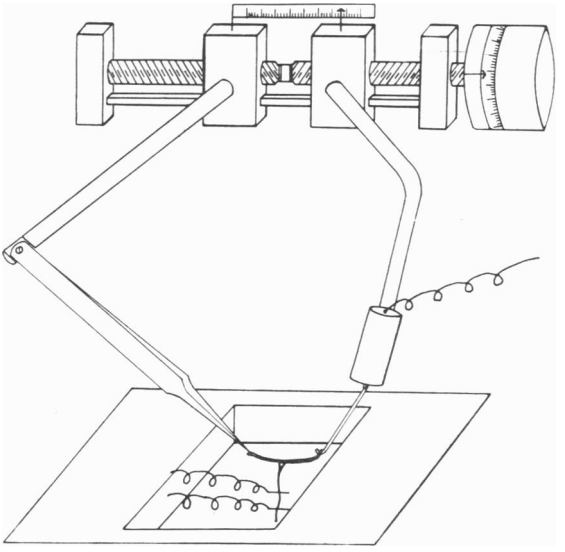

Fig. 1. Diagram of experimental set-up. One end of receptor organ is tied to fine glass hook connected to movable anode of transducer valve. Recording silver leads are in contact with nerve branch containing axon of receptor neurone.

Procedure

In most cases, in order to reduce handling, the two receptor organs (fast- and slow-adapting) were first mounted together. When initial observations had been completed, the thicker bundle of the fast-adapting receptor was disconnected on one side or cut from the forceps and observations were repeated while stretching only the thin bundle. In several cases one of the two organs (usually the thicker) was left untied from the beginning, so that only one exerted any appreciable tension. The two receptors are in very close relation to one another and so cannot be freed completely without great risk of damaging one or both. As has already been shown by Wiersma *et al.* (1953), even after cutting a bundle the corresponding receptor may be activated if the remaining bundle is stretched sufficiently (see below). Useful observations were made on sixteen isolated preparations, kept at room temperature (18–22° C).

RESULTS

Changes in tension caused by stretching

When a receptor organ is gradually pulled out, the tension initially rises only very slowly. Zero length was therefore a somewhat arbitrary length, determined partly by inspection with the microscope (showing that the resting folds had straightened out) and partly by evidence that the tension was beginning to increase. Resting length *in situ* was not used for comparison, since the length *in situ* varies considerably with the degree of

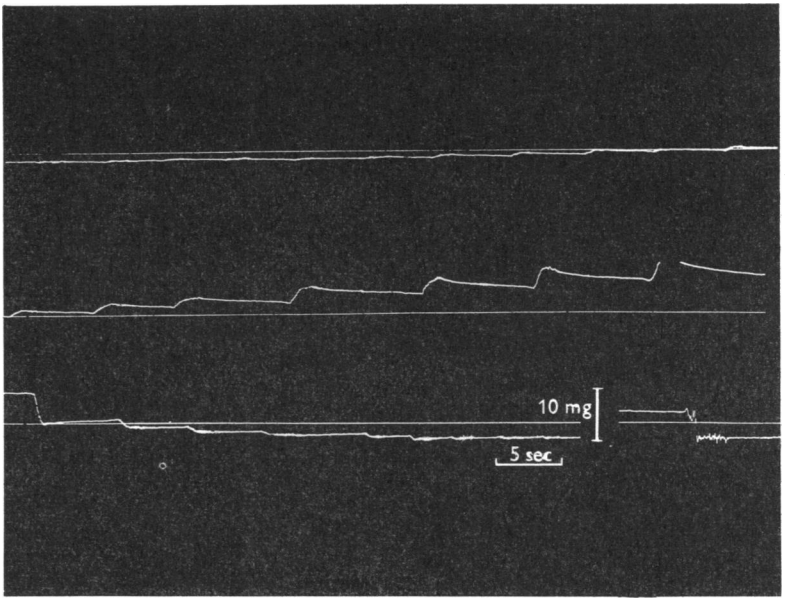

Fig. 2. Tension changes produced by stretching slow-adapting receptor organ in steps of 0·1 mm up to a maximum of 1·8 mm; in bottom row, length was reduced in steps of 0·2 mm. Zero length was 2·7 mm. Sequence to the right of calibration lines shows abolition of tension when moderately stretched receptor was cut with scissors at end of experiment.

abdominal flexion; in any case, the thinner bundle is not straight *in situ*, being attached at several points. In practice, the zero length was within the range of 1–3 mm.

In Fig. 2 a complete sequence of tension changes is illustrated. The bundle was stretched in steps of 0·10 mm, up to a maximum extension of 1·8 mm (i.e. an increase of 2/3 over the zero length). Several features are evident which were characteristic of all our observations. The tension did not increase linearly, but more and more steeply. At each increment in length there was a tendency for the tension to reach a peak that was not

maintained: this was seen especially clearly when the stretching exceeded 1 mm. The tension fell away from its peak value at first rapidly and then more slowly.

On reducing the length of the stretched bundle the tension falls suddenly, although it may creep up again somewhat before the next step down, as is shown in Figs. 2, 5 and 9. This phenomenon of a creeping up of tension was always much less evident than the corresponding creeping down during stretching.

The tensions measured in these experiments were so small that appreciable changes in tension were sometimes produced with no tissue attached, presumably by the surface tension of films of water between the forceps and the glass hook. For this reason controls were performed regularly, such as the demonstration at the end of the experiment that cutting the bundle abolished the tension and then repeating sequences of stretch and relaxation. A control cut is shown at the end of Fig. 2. It is clear that the tension produced by a moderate stretch of the same bundle disappeared when the bundle was cut. Although an appreciable amount of tension could sometimes be produced spuriously, at its greatest this amounted to only 14 % of the tension developed by stretching a bundle in the same experiment.

From traces like those in Fig. 2 plots were made of tension against stretch. In fifteen cases the plots gave rather similar curves, concave upwards and showing nearly always a distinct though variable hysteresis (e.g. Figs. 4, 7 and 10). There was no qualitative difference between observations made while stretching both receptors simultaneously or either independently. For instance, in Fig. 3 curves are shown of the tension changes caused by first stretching both bundles (open circles) and then stretching the thin bundle only (after cutting the thicker one). The thicker bundle is much larger than the thin one but its fibrils are usually folded rather loosely, so that although it is much thicker it seldom contributed as much as 50 % to the total tension when both were pulled together.

It is clear that the receptors did not obey Hooke's law. They behaved, in fact, very much like many other tissues (e.g. Stacy, 1957) and like vertebrate muscle fibres in particular (Ramsey & Street, 1940; Buchthal, 1942; Buchthal & Rosenfalck, 1957).

The receptor organs could be stretched by about 100 % of the initial length without any obvious damage, although inspection of curves suggested that there was some irreversible loss of resistance to extension if the length was increased by much more than 50 %, as in the case of muscle fibres (Buchthal, 1942).

The extent to which a dynamic phase (overshoot) of tension was observed depended on the rate of stretching. At the fastest rate of stretching that could be managed conveniently (0·4 mm/sec) the peak tensions exceed the plateau very substantially. Hence, if a series of such quick stretches is compared with a sequence of very slow stretching (at 0·01 mm/sec) a

marked excess of tension is immediately evident (Fig. 4, *A* and *B*). It can also be seen that the very slow stretching prevented the appearance of any pronounced hysteresis (in Fig. 4*B*).

Although the amount of overshoot of tension during the dynamic phase was related to the rate of stretching, for a given rate of stretching the overshoot was an approximately constant fraction of the final increment of plateau tension (Table 1). Hence, in general, the greater the increase in tension, the greater was the corresponding overshoot.

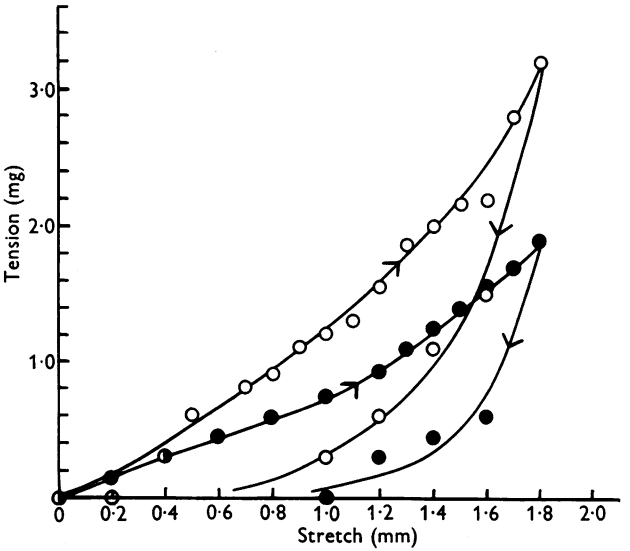

Fig. 3. Stretch–tension relation of (*a*) fast and slow-adapting receptor organs together (○—○), and (*b*) slow-adapting receptor organ after cutting fast-adapting one (●—●).

The tensions developed by various receptors at a given stretch differed considerably, owing at least partly to differences in zero length and variations in the thickness of individual organs. This could not be assessed with accuracy, since the receptors did not have a constant thickness and shape at different points along their length. The tension developed by a 1·0 mm stretch varied by a factor of nearly 30 in a series of twelve different trials with slow-adapting receptors: the mean tension was 1·8 mg, with a range of 0·3–8·5 mg. Four trials with fast-adapting receptors gave a mean tension of 1·1 mg (range 0·8–1·5 mg) at a stretch of 1·0 mm.

There was somewhat less variation between the rates of change of tension (dF) with increasing stretch (dl) in different preparations. In Table 2 are given representative values of dF/dl at 4 degrees of extension, for three slow-adapting and two fast-adapting receptors.

As the receptors did not obey Hooke's law, it is not possible to calculate an elastic modulus that will describe the elastic properties over more than a limited range. Nevertheless, it may be of some interest to compare the elastic modulus in a given range with values obtained for ordinary muscle. The principal source of inaccuracy is due to some uncertainty about the cross-sectional area. In the present calculations it is assumed that the receptors were circular in cross-section. Five slow-adapting receptors, measured as accurately as possible with a magnification of 80 times, had diameters within the range 30–50 μ. Values of the elastic modulus (E) were

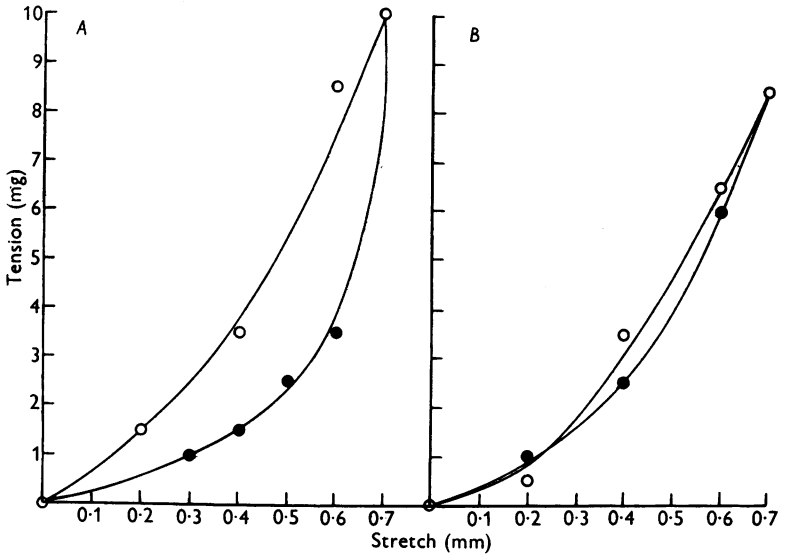

Fig. 4. Stretch–tension relation of slow-adapting receptor organ when stretched in steps, A, at relatively quick rate of 0·4 mm/sec, and B at slow rate of 0·01 mm/sec.

TABLE 1. Ratios of maximal change in tension (measured at peak) to final change (measured during plateau at a fixed time after peak). Receptor organs were all stretched in steps at approximately same rate (about 0·1 mm/sec). In each column values are in order of increasing stretch. Note that A, E and F were slow-adapting receptors, B, C and D fast-adapting

	A	*B*	*C*	*D*	*E*	*F*
	1·5	1·0	3·0	2·0	2·0	2·0
	1·25	1·2	4·0	1·5	3·0	1·5
	1·4	1·8	1·6	3·0	2·0	1·5
	1·5	2·1	2·0	2·0	2·0	2·0
	—	1·5	4·0	2·0	2·0	2·0
	—	1·6	2·2	2·0	1·5	1·8
	—	—	3·0	2·0	1·2	2·5
	—	—	—	1·7	1·8	2·3
	—	—	2·8	—	—	—
Mean	1·4	1·5	2·8	2·0	1·9	1·9

thus calculated for the three slow-adapting receptors *A*, *B* and *C* (cf. Table 2), by means of the given values of dF/dl for a stretch of 0·5 mm and 1·5 mm respectively, and equation 1:

$$E = \frac{dF}{dl}\frac{l}{\pi r^2}, \tag{1}$$

where l is the total length, and r the bundle radius at zero length corrected to allow for a reduction in cross-sectional area during stretch (assuming that the bundle volume remains constant). The calculated values of E at 0·5 mm (i.e. in the region 120–130 % of zero length) are $0{\cdot}7–7{\cdot}0 \times 10^6$ dyn/cm^2. They agree fairly well with values of E for resting frog muscle given in the literature (e.g. $0{\cdot}98 \times 10^6$ (Wöhlisch, 1932); $2{\cdot}5 \times 10^6$ (Sichel, 1934); $0{\cdot}5 \times 10^6$ (Buchthal, 1942), all in dyn/cm^2).

For a greater stretch of 1·5 mm (in the region 170–180 % of zero length) the slopes of dF/dl were much steeper and the respective values of E correspondingly larger, 7·6–57 dyn/cm^2.

TABLE 2. Changes of tension per unit stretch (dF/dl) at different degrees of extension: values were calculated from tangents to curves such as those in Figs. 3, 4, 5 and 10. Receptors *A*, *B* and *C* were slow-adapting, *D* and *E* fast-adapting

l (mm)	0·5	1·0	1·5	2·0
A	0·35	0·6	2·0	—
B	3·5	5·5	8·0	—
C	3·5	7·0	15	28
D	1·0	1·5	2·5	7·0
E	1·5	2·5	6·0	45

Properties of slow- and fast-adapting receptors

The data already presented show that there is little qualitative or even quantitative difference between the thin (slow-adapting) and thick (fast-adapting) receptor bundles, at least in so far as their more obvious mechanical properties are concerned. The curves of tension against stretch are much the same (compare Figs. 3 and 10); and values of the tension (see above) and of dF/dl at different degrees of extension (Table 2) are well within the same range for the other type of receptor. However, since the fast-adapting receptors are much thicker, it follows that they must have a much lower coefficient of elasticity. In fact, the values of E calculated as above for the two fast-adapting receptors in Table 2 (*D*, *E*) are 0·14 and $0{\cdot}21 \times 10^6$ dyn/cm^2 at a stretch of 0·5 mm, and 0·68 and $1{\cdot}6 \times 10^6$ dyn/cm^2 at a stretch of 1·5 mm respectively. These values are consistently less than the corresponding values of E for the slow-adapting receptors already given.

One other feature should perhaps be mentioned. The dynamic phases of tension change were sometimes more pronounced when stretching the

thicker bundles than the thinner. In other words, the tension tended to fall off from the peak to a greater relative extent. This is noticeable in some of the figures given in Table 1. However, as can also be seen in Table 1, there was a good deal of overlap between the two groups, and it is not at all certain that this is a systematic difference.

Relation between stretch and nerve discharge

It is of some interest to know whether the observed acceleration in the discharge is related to the change in length or to the change in tension.

Slow-adapting receptors. Parts of a typical sequence of changes in rate of firing and tension during stretching in steps are shown in Fig. 5. Individual steps during stretch or release can also be seen enlarged in Fig. 6. Examination reveals a certain correspondence between the discharge and the tension, both showing at each step a dynamic phase which was not maintained. If we plot values of tension and of the firing frequency (during the relatively steady plateaus) against stretch, curves are obtained similar to those in the lower half of Fig. 7. They show that, like the tension, the firing rate increases progressively faster with increasing stretch. The general resemblance between such curves suggests that the tension and the firing rate may be simply related to each other. This is found to be the case if firing rate is plotted against the measured tension for the same receptor, as in the upper half of Fig. 7.

When the receptors were stretched very slowly, there was no overshoot of tension and the firing rate also had no dynamic phase, but there was a slow decline in the frequency of firing over several minutes; thus the receptors as a rule do show some slow-adaptation. Measurements of plateau tension and of the corresponding firing rate at different lengths during release also fell about the same straight line usually, except when the fully stretched state was maintained for several minutes, since the frequency of discharge declined more quickly than the usual creeping down of tension.

The slopes of firing against tension varied considerably in different experiments. The full range of ten estimates was 2–35 impulses/sec/mg. Receptors with a low elastic modulus tended to give a relatively steep relation between firing and tension. For instance, receptor *A* from Table 2, with low values of dF/dl, increased its rate of firing by 13 impulses/sec for every milligram increase in tension, whereas receptor *C*, with high values of dF/dl, accelerated by only 2·5 impulses/sec/mg.

The receptor whose behaviour is illustrated in Fig. 8 was an interesting example of the fact that, even after cutting a slow-adapting receptor bundle, its neurone may be caused to fire by stretching sufficiently the remaining fast-adapting receptor bundle (because of interconnecting

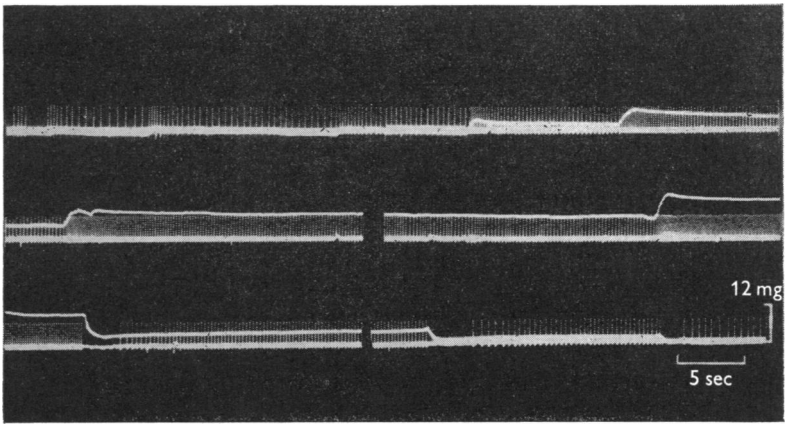

Fig. 5. Impulses in slow-adapting receptor axon and tension exerted by same receptor organ while being stretched in steps of 0·1 mm up to a maximum of 2·2 mm. Length was then reduced in steps of 0·1 mm. Only parts of complete sequence are illustrated. Zero length was 2·1 mm. Spikes had an amplitude of 200 μV.

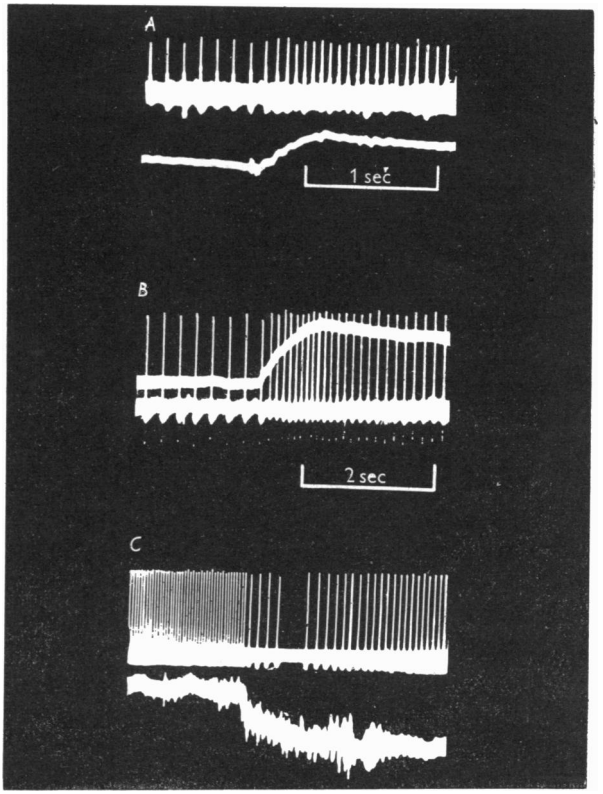

Fig. 6. Magnified traces showing tension and impulses, in *A* and *B* during stretch of 0·1 mm, in *C* during release by 0·1 mm. Traces have been retouched.

strands of tissue in the region of the neurones, as shown by Wiersma *et al.* 1953). However, this is evidently an inefficient method of activating the neurone; hence the very moderate inclination of the lower straight line in Fig. 8 corresponding to a change in frequency of only 0·25 impulse/sec/mg, i.e. only 1/10th of the lowest value observed in other receptors. Presumably not more than 1/10th of the tension developed in the thicker bundle is transmitted to the slow-adapting neurone via the connecting strands.

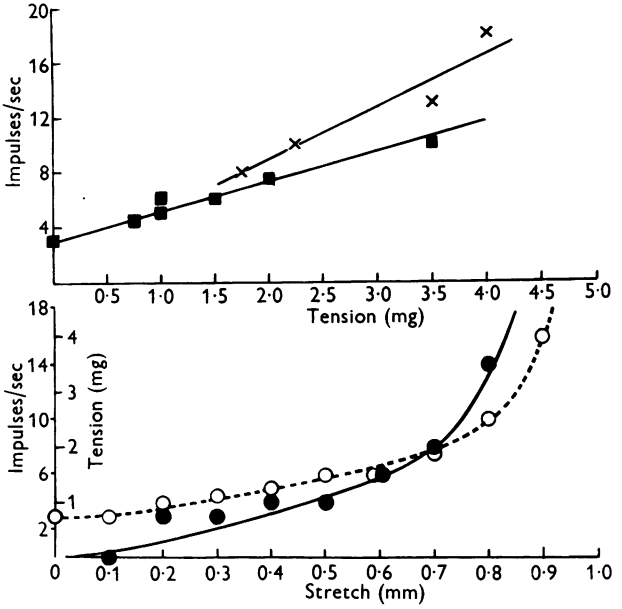

Fig. 7. Above: ■, relation between discharge of receptor and tension during plateau of tension after each increment in length; ×, corresponding relation for peak values of dynamic phase of tension. Below: ●, relation between tension and stretch of slow-adapting receptor organ; ○, relation between receptor discharge and stretch.

It therefore seems that over short periods of time the rate of discharge of the slow-adapting receptor may be determined principally by the tension in the receptor organ. The correspondence in time between the dynamic phases of tension and firing might suggest that the same simple relation holds throughout. But if one plots the peak firing rate against the peak tension one finds that, though the two variables are again related linearly, in the majority of cases the slope is substantially steeper (cf. the two sets of straight lines in Figs. 7 and 9).

Fast-adapting receptors. A typical sequence of changes in firing and tension while stretching in steps of 0·1 mm is shown in Fig. 9. As already

stated, the tension changes were not grossly different from those seen with slow-adapting receptors (see also Fig. 10). But the discharge adapted much more rapidly, so that it usually ceased altogether within a number of seconds. On the other hand, if the peak rate of discharge was plotted against the peak tension a linear relation was again found (Fig. 10); in three experiments the slopes had values of 3–5 impulses/sec/mg, near the lower end of the observed range for slow-adapting receptors.

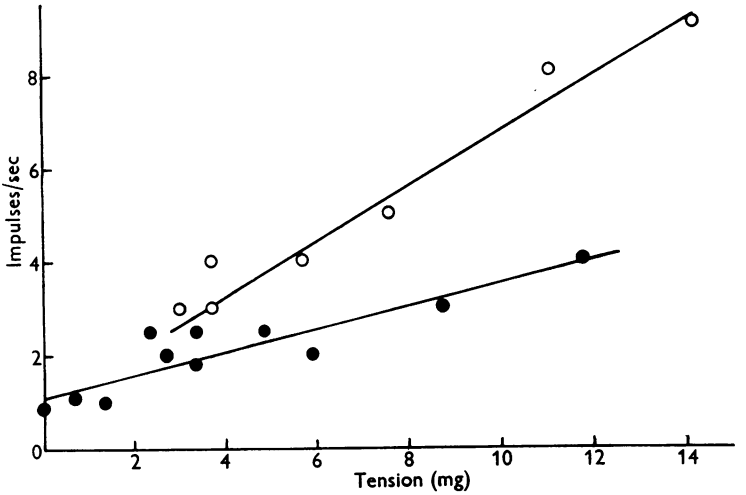

Fig. 8. Changes in firing rate of slow-adapting receptor caused by tension changes in adjacent fast-adapting receptor, transmitted via interconnecting strands. ●, values obtained during plateau after each stretch; ○, values at peak of dynamic phase of tension.

DISCUSSION

It is not surprising that the stretch receptors should have mechanical properties very similar to those of muscle, since somewhat modified muscle makes up the bulk of the receptor bundle (Alexandrowicz, 1951; Florey & Florey, 1955). Like muscle, therefore, the receptors behave in a manner characteristic of bodies with both damped and undamped elements. In this respect the slow- and fast-adapting receptors are qualitatively very similar. However, unlike the slow-adapting receptors, the fast-adapting organs have a substantially smaller resistance to stretching, with a smaller elastic modulus than is common for muscle.

From equation (1) it can be seen that the change in length needed to produce a given change in tension per unit area of cross-section is proportional to l/E. The length of the fast-adapting receptor *in situ* is about 20 % greater than that of the slow-adapting receptor. If one takes a representative figure of 1/10 for its elastic modulus, the fast-adapting receptor

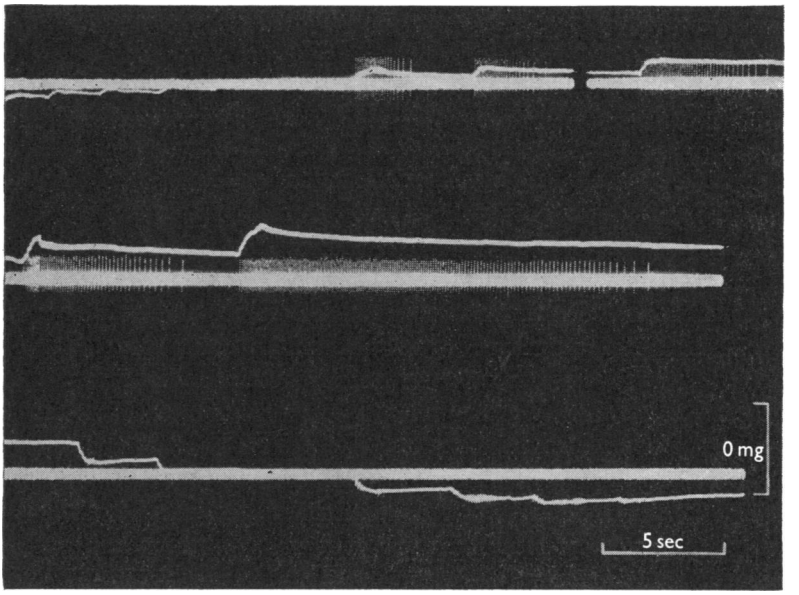

Fig. 9. Traces showing changes in firing and tension during stretch of a fast-adapting receptor organ in steps of 0·1 mm up to a maximum of 2·3 mm. Length was then reduced in three steps of 0·1 mm and four further steps of 0·5 mm. Zero length was 2·0 mm. Spikes had an amplitude of 120 μV.

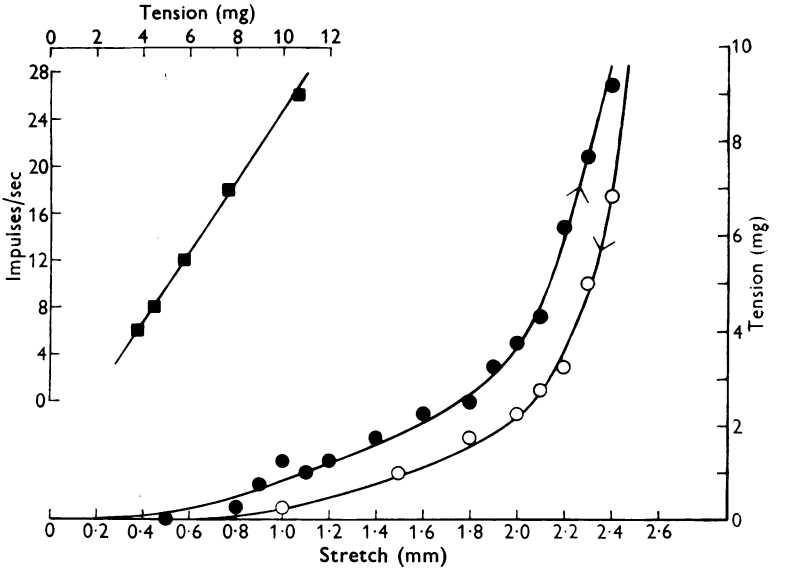

Fig. 10. Closed and open circles indicate tension exerted by fast-adapting receptor organ during stretch and relaxation in steps. Straight line through squares gives relation between discharge of receptor and tension at peak of dynamic phase.

would require an elongation twelve times greater to produce a given change in tension per unit area. The great difference between the amounts of extension needed to excite the two types of receptors *in situ* (cf. Wiersma *et al.* 1953; Florey & Florey, 1955) may be caused largely by their different mechanical properties. Some differences in neuronal characteristics, such as the electrical threshold (cf. Eyzaguirre & Kuffler, 1955) or the orientation of dendrites (Florey & Florey, 1955) may, of course, also play a part.

The different rates of adaptation of the fast and slow receptors cannot easily be ascribed to their mechanical properties: the slight tendency of the tension of fast-adapting receptors to fall more rapidly does not seem either sufficiently pronounced or regular in its occurrence (Table 1) to account entirely for the consistently quicker rate of adaptation. In other experiments (unpublished observations) we have found that the rates of adaptation of individual receptors to d.c. polarization are rather similar to the rates of adaptation observed after stretching. Moreover, we have also found that under the influence of certain drugs (which do not alter the mechanical properties) fast-adapting receptors may become slow-adapting. It seems that the principal factor in determining the rates of adaptation of the two kinds of receptors must be the electrical properties of the respective neurones.

Relation between tension and firing

Our observations have shown remarkably consistently a linear relation between the tension exerted by the receptor when stretched, and the rate of discharge. We have here a receptor which clearly does not provide a logarithmic-to-linear transformation of signals in keeping with Fechner's law. (If firing is plotted against length, a linear relation might conceivably be found between the logarithm of the *discharge* rate and the length, but certainly not the reverse.) As stretch-receptor mechanisms have proved in general to be remarkably similar in a wide variety of living forms, it would be surprising if they differed very radically in this respect. One cannot help wondering whether the linear relation observed between the logarithm of the load and the discharge frequency of stretch receptors in vertebrate muscle (e.g. Matthews, 1931, 1933; Fessard & Sand, 1937) is really a property of the actual receptors; when a large muscle is stretched by a given load, much the greatest part of the tension is exerted by the bulk of the muscle, and this tension may not be simply related to the tension in individual receptors.

Our results are consistent with the linear relation observed between cat muscle length and spindle discharge rate by Eldred, Granit & Merton (1953). In their experiments the muscle was extended by not more than 25 % of its resting length. The authors point out that within this range an

indistinguishable result would be achieved if spindle frequency were proportional to the logarithm of the length. The converse is also true: within this range the results would probably be similar if the logarithm of the discharge were proportional to the length. For instance, in Fig. 7 the relation between extension and firing rate is approximately linear up to 0·7 mm (this is equivalent to a 30 % change in length). The lack of linearity between firing rate and extension is shown clearly in the experiments of Eldred *et al.* (1953) after de-afferentation (in their Figs. 2 and 3), when the spindle was allowed to discharge over a much greater range of frequency.

According to Florey & Florey (1955) the dendrites of the receptor neurones ramify extensively within the central region of the receptor organ over a length which may be as much as 0·5 mm. Since the muscular component does not extend continuously through the central part of the receptor (Alexandrowicz, 1958) the load on the dendrites cannot be reduced by parallel contraction of the muscle. Kuffler (1954) thus found that excitation of the efferent nerves to the muscle did not produce a silent period in the afferent discharge. Contraction of the muscle always caused an acceleration of neuronal firing, and he concluded that the dendrites were effectively in series with the muscular component. Changes in bundle tension, therefore, should be transmitted directly to the dendrites, and in the steady state the load on the dendrites should bear a simple relation to the tension exerted by the whole receptor organ. The linear relation between the rate of discharge and the tension suggests that the decisive stimulus is the tension exerted on the dendrites. It is of interest that the generator potential is apparently also simply related to the final rate of discharge (Burkhardt, 1959).

However, if the viscous properties of the dendrites differ from those of the rest of the bundle, the tension changes in the dendrites during a quick extension will be correspondingly greater or smaller than the tension changes in the bundle as a whole. It is likely that the steeper relation between firing and receptor tension during the dynamic phase is due to greater viscosity of the dendrites. (A similar explanation was put forward by Matthews (1933) to account for the dynamic phase of discharge of the vertebrate muscle spindle.)

The possibility that stretch causes a temporary depolarization by increasing the membrane capacity of the dendrites (cf. Katz, 1950) seems unlikely in our experiments, in which the rate of stretching was relatively slow compared with the probable electrical time constant of the membrane.

SUMMARY

1. When isolated abdominal stretch receptors of the crayfish (*Astacus fluviatilis*) are stretched in steps, and then released, the changes in tension are not linear, and they show marked hysteresis, as in ordinary muscle.

2. The two kinds of receptors have similar mechanical properties, but the fast-adapting organ has a lower coefficient of elasticity, and so needs a greater degree of extension to produce a given change in tension per unit area. This may account for its high threshold.

3. The steady rate of discharge of the slow-adapting receptor is a linear, and not a logarithmic, function of the tension exerted by the receptor. The peak of discharge of the fast-adapting receptor is also linearly related to the tension.

4. Immediately after stretching both the tension and the discharge show a dynamic phase (or overshoot), which can be ascribed to viscous elements in the receptor organ.

5. The quicker adaptation of the fast-adapting receptor is probably not a consequence of its mechanical properties.

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Note added in proof. In a recent paper L. Wendler & D. Burkhardt (1961; Zeitlich abklingende Vorgänge in der Wirkungskette zwischen Reiz und Erregung (Versuche an abdominalen Streckreceptoren dekapoder Krebse). *Z. Naturf.* **16***b*, 464–469) describe measurements of the relation between the discharge and the tension of crayfish stretch receptors and also some effects of electrical polarization. Although their observations in general agree with ours, they conclude that adaptation of the receptor neurone is partly responsible for the decay of activity after the peak of the dynamic phase of discharge.