J. Physiol. (1970), **207**, *pp.* 747–759
With 3 plates and 3 text-figures
Printed in Great Britain

LENGTH CHANGES WITHIN ISOLATED FROG MUSCLE SPINDLE DURING AND AFTER STRETCHING

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(*Received 17 October 1969*)

SUMMARY

1. The length changes within the frog muscle spindle during stretch have been studied by stroboscopic photomicroscopy. Attention was focused on the length changes within the central reticular zone and these changes were related to the features of the receptor potential.

2. It was found that the length changes of the central reticular zone closely followed the applied stretch in time course and magnitude. The results suggest that the length changes of the polar zones are generally similar to those in the central zone.

3. There was no evidence of a relative shortening of the central zone in the early phase of maintained stretch, corresponding to the decline of the receptor potential from its dynamic peak to the static level.

4. Following release of stretch the central zone returned to its original resting length within a few msec. The rapid return of the spindle was in sharp contrast to the relatively slow exponential decay of the receptor potential. With strong or prolonged stretches the return became slower and resting length was not completely restored until 100–150 msec after release of stretch. No corresponding change in the decay of the receptor potential was seen.

5. The results suggest that the early adaptive fall of the receptor potential is not related to differential length changes between the central zone and the polar zones. It seems more likely that the contribution of mechanical factors to the early adaptation of the frog spindle have to be sought at the ultrastructural level.

6. The finding that the length changes closely follow the applied stretch suggests that the stimulus in terms of lengthening is transmitted to the endings with little distortion.

7. The results suggest that the elastic elements play a dominant role for

the transmission of the stimulus to the endings and for the return of the spindle to resting length after release of stretch.

INTRODUCTION

A central question in the physiology of mechanoreceptors is the mechanism of coupling between the external stimulus and the sensory nerve endings. In the Pacinian corpuscle Hubbard (1958) showed that the capsule acts as a mechanical filter which transmits fast mechanical transients relatively well but attenuates slow ones. The capsule thus appears to be responsible for the fast adaptation of the sensory response of the Pacinian corpuscle. This has been borne out by subsequent experiments of Loewenstein & Mendelson (1965) and Ozeki & Sato (1965).

In the muscle spindle the stretch stimulus is transmitted to the sensory nerve endings by the intrafusal muscle fibres and the connective tissue strands by which the endings are anchored to the muscle fibres. Since the structure of the intrafusal fibres is not the same throughout the spindle, the sensory endings in different zones could be differentially affected when the spindle is stretched. On the basis of ultrastructural studies on the frog muscle spindle Katz (1961) suggested that the dynamic component of the sensory response might arise from the central reticular zone of the intrafusal muscle fibres and the static component from the polar compact zones. Katz emphasized that one would have to know the stress/strain relations in the two zones before any definite conclusions could be made. Unfortunately such information appears to be technically difficult to obtain.

In the present study we have chosen another approach. The elongation of different regions of the spindle during passive stretch was observed by using a stroboscopic technique. The length changes could in this way be followed closely during the various phases of stretching. The results did not provide evidence for any systematic difference in distensibility between the central zone and the polar zones. The extension of the central zone and the polar zones closely followed the imposed stretch. After release of stretch the spindle rapidly returned to its zero position. The results suggest that the stimulus is equally distributed to the different regions during stretch.

A preliminary report of some of these results has been published (Ottoson & Shepherd, 1968).

METHODS

The principal aim of the present study was to measure the internal length changes of the muscle spindle during and after stretching and to relate these data to the transducer action of the spindle as represented by the receptor potential. The method employed was to take flash photomicrographs of isolated frog spindles at different times during and after controlled linearly rising stretches.

Isolation and mounting of the spindle. All experiments in the present study were carried out on muscle spindles isolated from the frog's toe muscle (m. ext. dig. long. IV). After isolation the muscle spindle was brought over into a small Ringer-filled chamber and mounted between two fine nylon rods. One of these rods was fixed while the other was attached to a loudspeaker coil (Philips AD 2300 BZ). The length of the spindle between the rods was adjusted to take up any slack. The spindle was carefully cleaned from external connective tissues and the sensory nerve was cut at its entrance into the capsule. This was done in order to obtain optimal conditions for photographing the intracapsular length changes.

Photomicroscopy. Photomicrographs of the spindle at different instants of time during stretch were taken under dark field illumination by high speed photography using a stroboscope (General Radio Strobotac 1531-A). The spindle was subjected to a given stretch and a photographic exposure was made with the flash at a chosen delay during stretching. The same stretch was then repeated and another photograph taken at a different flash delay. The procedure was repeated for as many different delays as desired. In this way a sequence of pictures of the spindle during stretch at intervals of 1 msec or less was obtained, i.e. the results corresponded to high speed photography at 1000–2000 pictures/sec. A key to this analysis was the high reproducibility of the spindle response (Shepherd & Ottoson, 1965) and this was borne out by the photographic results.

The flash was recorded with a photocell and monitored on an oscilloscope which also displayed the stretch (see below). The timing of each flash could thus be obtained from measurements of the oscilloscope recordings. Before each run the dark field illumination was arranged so as to give a clear picture of the intracapsular structures. By adjusting the optical apparatus different structural features could be brought out. For each run the apparatus was set to bring out as clearly as possible some particular landmarks. The run was often repeated with another setting of the optical apparatus so that other landmarks were seen. Measurements from these runs in general gave consistent results. The single exposures were taken on 35 mm film (Kodak) and enlarged prints ($\times 6{\cdot}5$) were used for measurements of the length changes.

Measurements of length changes

Criteria for landmarks. In the photographs of the spindle taken under dark field illumination some structures were brought out more clearly than others. Myelinated branches of the sensory fibre were usually clearly recognized as was also the capsule, while the intrafusal fibres were less distinct. For the measurements of the length changes only landmarks which could be clearly identified as being *intracapsular* were chosen. Within the central region of the spindle the capsular landmarks could easily be distinguished from the intracapsular ones while in the polar regions the distinction was less clear. It was felt therefore that the measurements of displacement of polar landmarks had a lower degree of confidence than those from central regions. Usually the relative movements of some 15–30 landmarks were studied in each spindle. Most of these landmarks were located in the central region, but polar as well as extrapolar landmarks were also used. In general the results obtained by measuring between different intracapsular landmarks were consistent. This would indicate that the displacements of the chosen landmarks were representative for the length changes of the spindle. The present report will be limited, however, to the length changes of the central zone since the measurements of the landmarks in this region were more accurate than those in the polar regions. Another reason for restricting the analysis to the central zone is that this region is functionally the most interesting part of the spindle. With respect to the hypothesis of a mechanical basis for the differentiation of the response (see Discussion) the greatest length changes during dynamic stretch would be expected to occur in the central zone.

Within the central zone the landmarks which were most distinctly seen in the photographs could be identified as myelinated branches of the sensory fibre. After its entrance through the capsule the afferent fibre breaks up into finer branches. These branches are myelinated down to the terminal sensory endings. With the present method it was not possible to see the unmyelinated endings. The measurements were therefore made from small myelinated branches. The landmarks chosen usually had a size of a few microns. Most often the outer contours or edges of the landmarks were used but in some cases measurements were also made from the centre of a landmark to the centre of another. A basic assumption of the method used is that the landmarks chosen move in direct relation to the extension of the central zone. This assumption is based on anatomical evidence showing that the nerve branches are myelinated down to the terminal chains which are anchored to the intrafusal fibres (Katz, 1961; Karlsson, Andersson-Cedergren & Ottoson, 1966). The smaller myelinated branches which were generally used as landmarks may therefore be assumed to move in close relation to the sensory terminals.

Errors in measurements. A criterion for the landmarks used was that they should be distinctly recognized in all phases of stretch. Landmarks which had distinct contours in the non-stretched spindles but which became indistinct during stretching were rejected. The length changes between landmarks were measured to within 0·1 mm on enlarged prints of the negatives, which was equal to 0·7 μ in the spindle. The measurements were made independently by the two authors. These measurements as well as those of repeated measurements by the same author at different times were generally accurate within 0·2 mm, i.e. approximately 2 μ.

An important point in the measurements of the length changes was the distance between the landmarks. The smaller the distance the greater was the error when the displacements of the landmarks were converted into per cent length changes. For this reason landmarks at the outer borders of the central zone were generally chosen. As shown in electronmicroscopical work (Karlsson *et al.* 1966) the sensory nerve demyelinates at the boundary of the central zone. This fact facilitated the definition of the central zone. The length of the central zone as measured between the regions where myelinated fibres could no longer be identified in the photographs was usually 150–200 μ. These values are somewhat higher than that obtained in electronmicroscopical studies. The difference may be explained as due in part to shrinkage in the fixed preparations. It is also possible that the landmarks used actually extended into the polar regions. If so this fact did not appear to affect the results since measurements over distances which could clearly be defined as not extending into the polar zones gave the same results as when the polar regions were also included.

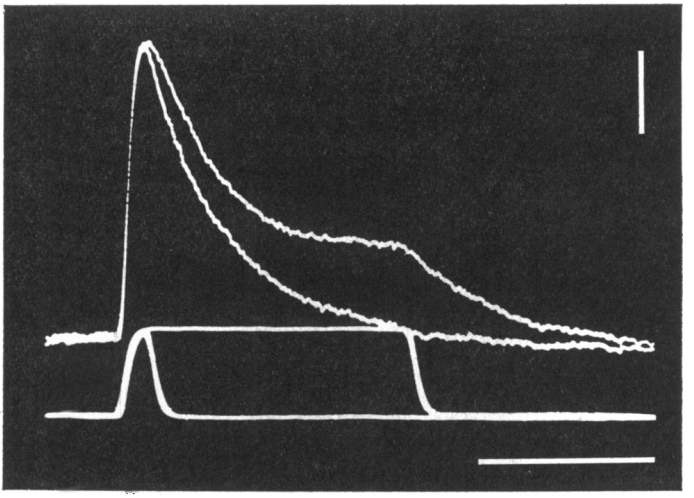
Receptor potential. The receptor potentials used in the present study for comparison of the transducer action with the length changes were recorded from spindles other than those used for the photomicroscopy. These spindles were treated with 0·18% lignocaine (v/v) in order to block the conducted impulses. Recordings were made with calomel half-cell electrodes connected to the spindle through Ringer-agar bridges. The potentials were fed into a DC amplifier and the responses were displayed on an oscilloscope. Controlled stretches with the same parameters as those in the photomicroscopical part of the study were used.

Stretch. The spindle was subjected to linearly rising stretches. The lengthening of the spindle was monitored on the oscilloscope beam by means of a high-sensitivity capacitance-meter (Haapanen, 1962) which measured the movement of the pulling rod. There was close agreement between the stretch monitor and the movement of the rods as measured in the photographs. It may be noted that the rates of stretch and release in the experiments illustrated in the results were high, of the order of 100 mm/sec. The measurements made in spindles subjected to slower dynamic

stretches did not differ in any significant respect from the measurements during the fastest dynamic stretches. The fastest stretches were of primary interest, because such stretches give the maximum dynamic effect in the response, and hence provide optimal conditions for revealing differential length changes in the spindle. Similarly, the rapid rate for release of stretch provides the optimal condition for testing the ability of the spindle to return to rest by the action of its passive mechanical properties alone.

RESULTS

The main characteristics of the response of the muscle spindle to applied stretches are illustrated by the records in Text-fig. 1. In this Figure the responses to a brief and a sustained stretch have been superimposed. In



Text-fig. 1. Receptor potentials of an isolated frog muscle spindle. Superimposed recordings (above) of responses to brief and sustained stretches (monitors shown below) of same amplitude. Time (horizontal) bar: 25 msec. Recording calibration (vertical) bar: 1 mV.

both cases the applied stretch had a fast rising phase which caused a rapid dynamic rise of the receptor potential. Following the brief stretch the potential fell from its dynamic peak toward the base line with an exponential time course. When stretch was maintained the dynamic potential decayed somewhat more slowly toward a relatively static level. Following the static stretch the receptor potential fell toward base line with an exponential time course; the rate of decay was similar to that for the decay following the brief stretch. The detailed characteristics of the receptor potential response in the isolated spindle have been described by Ottoson & Shepherd (1965). The responses in Text-fig. 1 show the typical depolarization of the sensory nerve endings caused by structural changes in the

spindle imposed by brief and maintained stretches. In the following we will relate these features of the transducer action to the underlying length changes within the spindle as revealed by stroboscopic photomicroscopy.

Length changes during stretch

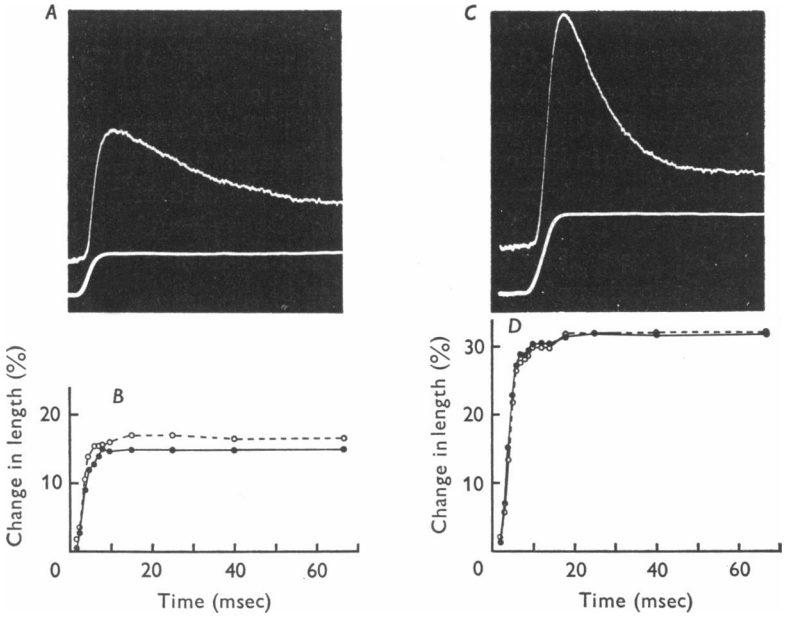
The photographs in Plate 1 illustrate the sequence of length changes during stretch. In this experiment a step stretch was maintained for about 70 msec. The photographs show the spindle at different critical times during this stretch. The first photograph, *A*, in this series shows the spindle before stretch was applied; photographs *B* and *C* were taken during and at the peak, respectively, of the dynamic stretch, while the final pictures *D* and *E* show the spindle at two times during maintained stretch. Two intracapsular landmarks near each end of the central zone have been chosen to illustrate the length changes within the central region of the muscle spindle. These landmarks were clearly small myelinated branches of the sensory nerve fibre. The fine white lines connecting the landmarks in the different photographs allow the qualitative conclusion that the elongation of the central zone is proportional to the movement of the rod.

Measurements between two landmarks at many times during stretch of the spindles are plotted in Text-fig. 2*B*. Filled circles show the over-all increase in length of the spindle as measured from one rod to the other during different times of stretch. During the first ten milliseconds there was a linear dynamic increase in length to about 16 % of the resting value followed by a maintained static elongation of the spindle at that length. The open circles plot the percentage increase in distance between the two intracapsular landmarks. It can be seen that the displacements of these landmarks closely followed the magnitude and time course of the applied stretch. For comparison the receptor potential response to a corresponding stretch in another spindle is shown above (Text-fig. 2*A*). It can be seen that in the length changes of the central zone there is no indication of the peak and decline of the dynamic receptor potential.

Similar results were obtained with stronger stretches as is shown in Text-fig. 2*D*. The stretch rose linearly to 32 % of the resting length of the spindle and the elongation of the central zone closely followed the over-all length changes of the spindle and the applied stretch. The receptor potential response to a similar stretch is shown above in Text-fig. 2*C*. At this amount of stretch it may be considered that the maximum dynamic potential has been obtained (Ottoson & Shepherd, 1965). Again, there is no indication in the movement of the central zone of a structural change related to the peak and fall of the sensory response.

Measurements were also made during strong steplike stretches of up to 40 % of the resting length of the spindle. The results were similar to those

illustrated in Text-fig. 2. In some cases, however, the relative increase in length of the central zone was less than that of the over-all lengthening of the spindle. There appeared to be a tendency with stronger stretches for the central zone to lengthen relatively less than the polar zones of the spindle. This would suggest that the central zone is slightly stiffer than the polar regions, which would be in agreement with the view that the central zone is protected by its dense connective tissue against overstretching which could cause damage to the nerve and muscle fibres.



Text-fig. 2. *A*. Receptor potential response (above) to step stretch (below) corresponding to that in *B*. *B*. Measured distances between two landmarks near edges of central zone (filled circles, continuous line) and between the two rods holding the spindle (open circles, dashed line) during step stretch of approximately 16 % of resting spindle length. *C*. Receptor potential response to step stretch corresponding to that in *D*. *D*. Measured distances as in *B* during step stretch of approximately 32 % of resting length.

As pointed out in Methods, measurements were made between many landmarks in each of our spindles. The amount of relative increase in length varied for different combinations of landmarks in different regions, but in all cases the time course of the length changes was similar to that of the applied stretch. Except for the relation to strong stretches cited above we could find no systematic differences between the distensibility of central and polar zones comparing different spindles. But we would emphasize that this point is not conclusive because of the relative lack of clarity of

the landmarks in the polar zones with the present combination of photographic and microscopic methods.

Length changes following release of stretch

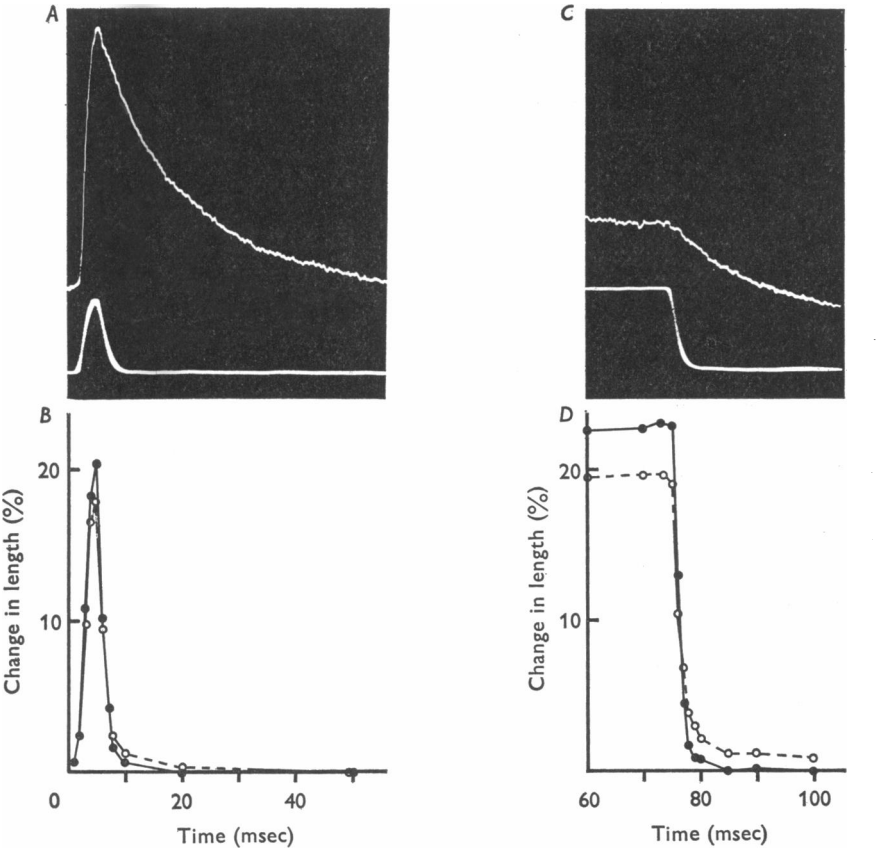
As illustrated in Text-fig. 1 the response of the sensory endings declines exponentially toward the base line after the release of a brief stretch. After release of a prolonged stretch there is a similar decline of the response, though in this case the potential falls from the lower relatively static level. The time for return to base line after release of the brief dynamic stretch is about 40 msec. The time for return after release of static stretch is about 25 msec (D. Ottoson & G. M. Shepherd, in preparation). We wished to know whether the spindle, and particularly the central zone, returns to its resting length with a time course similar to the fall of the receptor potential.

The photographs in Plate 2 show the spindle during and after release of a brief stretch. The photograph in *B* shows the spindle during the dynamic phase of extension; in *C* stretch has reached its peak and the pulling rod thereafter returns rapidly to its zero position *E*. It may be noticed that there is no indication of slackness or curling of the spindle in *E*. Measurements of the length changes taking place during the stretch illustrated in Plate 2 are plotted in Text-fig. 3*B*. The open circles show the length changes of the central zone as indicated by the thin white lines in Plate 2. When stretch was released the central zone shortened with the same time course as that of the pulling rod in returning to zero position. The receptor potential elicited by a similar stretch can be seen in Text-fig. 3*A*. The slow decay of the receptor potential contrasts with the rapid return of the spindle to its zero position.

Following release of stretch after a maintained stretch the shortening of the central zone had a time course similar to that following a brief stretch, as illustrated in Plate 3. The photographs, *A* and *B*, show the spindle at the end of a static stretch with a duration of 75 msec. The subsequent photographs, *C* and *D*, were taken during the return of the rod to its zero position. In *D* the spindle can be seen to be slightly curled indicating that the elastic elements had not yet pulled the spindle back completely to its resting length. Measurements of the length changes of the central zone of the spindle in Plate 3 are shown in Text-fig. 3*D*. In the first msec of release the shortening of the central zone appeared to be as rapid as the movement of the rod but thereafter the rate of shortening slowed. In the final phase of return the central zone was slightly more elongated than at comparable times following brief stretches, and the time for return was also prolonged. The receptor potential response to a comparable static stretch is shown in Text-fig. 3*C*. The time course of decay of the receptor potential is considerably slower than the rapid early return of the central

zone towards its resting length. The central zone thus shows a rapid return toward its resting length similar to that after brief stretch. There is also a second prolonged period for return to final resting level.

The return of the spindle to rest was also observed during release of static stretches of longer duration (up to 300 msec) and also during release of stretches of higher amplitudes (up to 40% of resting length). In a typical experiment using a stretch of 24% maintained for 300 msec, the time course for return of the rod was similar to that shown in Text-fig. 3*D*. However, the initial phase for return of the central zone was not quite as



Text-fig. 3. *A*. Receptor potential response and decay during and after brief dynamic stretch corresponding to that in *B*. *B*. Measured distances between edges of central zone and between rods as in Text-fig. 2. Brief dynamic stretch as in *A*. *C*. Receptor potential response and decay during and after release of static stretch corresponding to that in *D*. *D*. Measured distances as in *B* during and after static stretch. Amplitude of stretch approximately the same as in *B*. Duration of stretch approximately 77 msec, as in *C*.

rapid and the final phase was characterized by a slightly greater residual distension over a period of more than 150 msec. The decay of the receptor potential following such a long stretch is generally similar to that following a shorter static stretch, which contrasts not only with the initial rapid return of the central zone but also with the greatly prolonged final phase of return. The effects of higher amplitudes of stretches were similar to those of increasing duration of stretch, i.e. a slowing and prolongation of the time course of return of the central zone. With regard to other regions of the spindle our measurements suggested that they also followed a time course of return to resting length which was generally similar to that for the central zone. With the longest and strongest stretches, however, one or other of the polar zones near its attachment to one of the rods tended to return to rest more slowly than the rest of the spindle. It was our impression that under these conditions the mechanical structure of those zones had been subjected to an unphysiological stress.

DISCUSSION

The differentiation of the response of the muscle spindle into a dynamic and a static component is generally attributed to structural differences between the central zone and the polar zones (Matthews, 1931; Katz, 1961; P. B. C. Matthews, 1964). According to this hypothesis the central zone would extend relatively more than the polar zones during dynamic stretch, while during maintained stretch the extension of the central zone would diminish because of the viscosity of the polar zones. Adaptation of the spindle response would thus be a result of the differences in elastic and viscous properties of the central zone and the polar zones. Several models have been advanced for the frog spindle (Houk, Cornew & Stark, 1966; Toyama, 1966) based on these differences.

The present results do not lend support to this hypothesis in the frog muscle spindle. When the spindle was subjected to a steplike stretch the central zone closely followed the imposed stretch and there was no indication of a relative shortening which would correspond to the adaptive fall of the receptor potential during the early period of maintained stretch. Furthermore, the results did not provide evidence for any significant difference in distensibility between the central zone and the polar zones. The observation that the relative elongation was more or less the same in different zones and closely followed the imposed stretch suggests that the stimulus in terms of lengthening of the intrafusal fibres is transmitted to the endings without any appreciable distortion.

The fact that the measurements did not reveal differential length changes between the central zone and the polar zones does not rule out the

possibility of a mechanical origin for the differentiation of the response. As shown by Katz (1961) and Karlsson *et al.* (1966) some of the sensory endings are anchored to the muscle fibres by connective tissue strands while others are lying more or less free in the lymph space. Differences in attachment of the endings might very well lead to a differential transmission of the stimulus. It is also possible that the ultrastructure of the central zone provides for a rate-sensitive distortion of the sensory endings even though the relative elongation of the central zone is a direct function of the applied stretch.

In the frog muscle spindle there is no clear differentiation of the intrafusal muscle fibres into nuclear bag fibres and nuclear chain fibres as in the mammalian spindle. It is therefore likely that in the frog spindle the sensory endings on different fibres are relatively uniformly activated during stretch. In the mammalian spindle the situation is different because of the structural differences between the two kinds of fibres. It is reasonable to assume that their mechanical properties also are different. The hypothesis of a mechanical origin for the differentiation of the response (cf. Matthews, 1964) may therefore be valid for the mammalian spindle.

In addition to the possible mechanical factors mentioned above, the electrical properties of the sensory membrane could also be related to the adaptive fall of the response. The dynamic decay could reflect passive properties of the membrane or be related to specific conductance changes and associated movements of ions. Finally, the accommodation properties of the afferent nerve fibre may be important (cf. Gray & Matthews, 1951; Fuortes & Poggio, 1962; Nakajima, 1964). Consideration of these non-mechanical factors raises the possibility that the dynamic overshoot and the decay to a steady static level reflect basic response properties of the sensory membrane of slowly adapting receptors in general; in particular receptors the response may be modified by specific characteristics of the transmitting structures, as in the Pacinian corpuscle (Hubbard, 1958; Loewenstein & Mendelson, 1965), or by the properties of the afferent nerve fibre.

The observations in the present study suggest that the spindle lengthens more or less like a purely elastic element. The effect of the viscous properties appears not to be reflected in any gross differential length changes. The viscosity of the spindle may, nevertheless, be an important factor with respect to the adaptive fall of the response as evidenced by tension measurements (I. Husmark & D. Ottoson, to be published). During maintained stretch tension falls with a time course closely similar to that of the receptor potential. It seems likely that this fall reflects the effect of viscosity and is accompanied by length changes at the ultrastructural level. However, the fall in tension is always relatively less than the fall of the receptor

potential from its dynamic peak to the static level. It would thus appear that the adaptation of the spindle cannot be purely of mechanical origin. This view is also supported by the fact that adaptation is a feature of the response of the decapsulated spindle, as well as of most other slowly adapting receptors. This would lead to the conclusion that the early adaptation in the spindle is partly of mechanical origin and partly of some other origin and most likely attributable to the electrical properties of the sensory membrane.

An interesting finding in the present study was that the spindle returns rapidly to its resting length after stretch provided the stretch is brief and not too strong. This is another evidence of the preponderance and importance of the elastic properties of the spindle. The rapid return of the spindle seems to have functionally important implications. The return of the spindle *in situ* to its resting state is determined by the relaxation of the extrafusal muscle fibres. Due to its elastic properties the spindle will always keep up with the return of the whole muscle and will therefore be ready to respond to a second stretch.

The rapid return following release of stretch is in contrast to the slow fall of the receptor potential. This raises the question why the sensory endings remain depolarized for a considerable period though the spindle has returned to its resting position. One explanation may be that the decay reflects the return of the transducer in the sensory membrane back to resting position or to static level. In this case the time course would be determined by the mechanical properties in and around the sensory endings and could be explained for instance by assuming opening and closing of pores. Another explanation is that the mechanical return at the membrane level is immediately indicated by the gross length changes and the decay therefore is related to the electrical capacity of the membrane of the fine myelinated sensory endings. This is in line with the above explanation of the receptor potential as reflecting the general properties of slowly adapting end organs.

The authors are greatly indebted to Professor B. Katz and Dr P. B. C. Matthews for valuable discussions during the preparation of this manuscript. We wish to thank Miss Olga Popoff for technical assistance.

This work has been supported by the Air Force Office of Scientific Research through the European Office of Aerospace Research, OAR, US Air Force.

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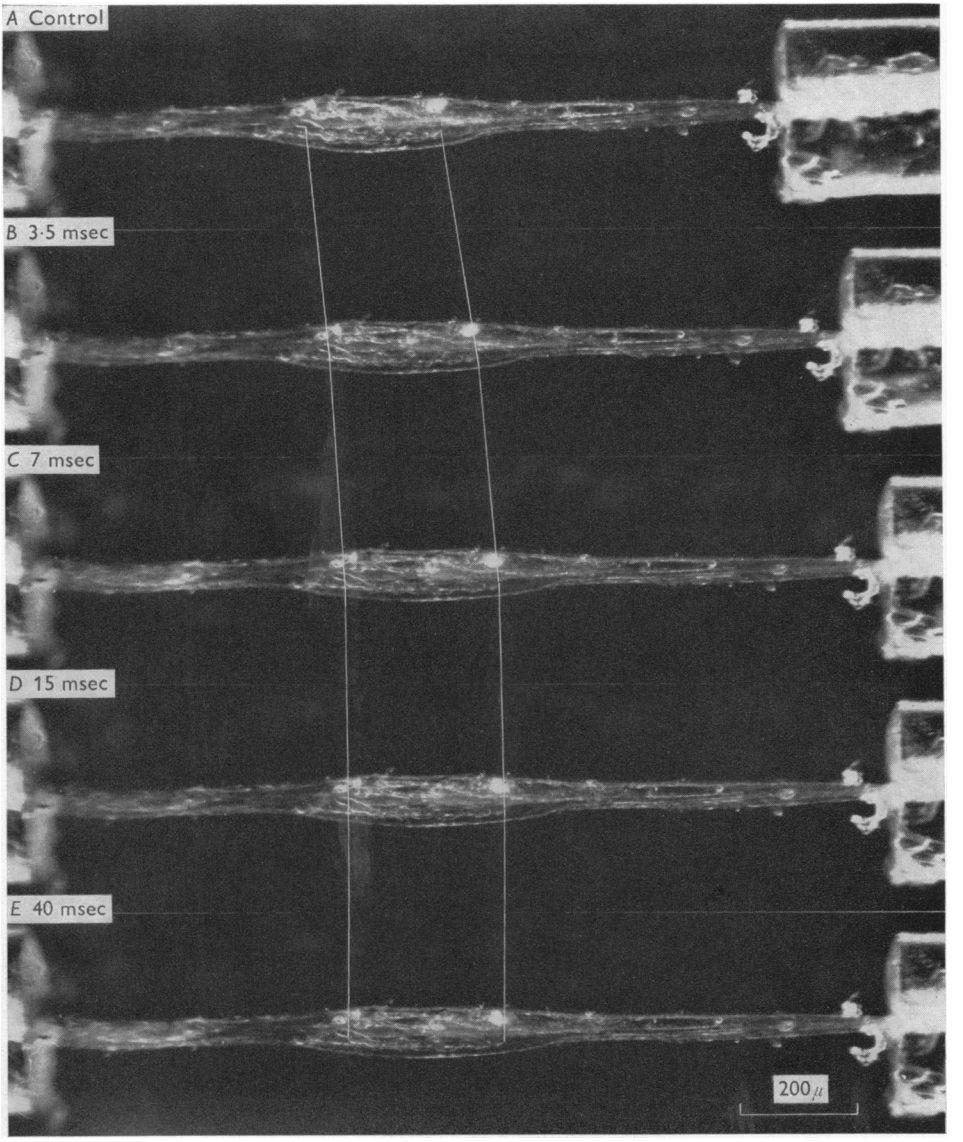

D. OTTOSON AND G. M. SHEPHERD

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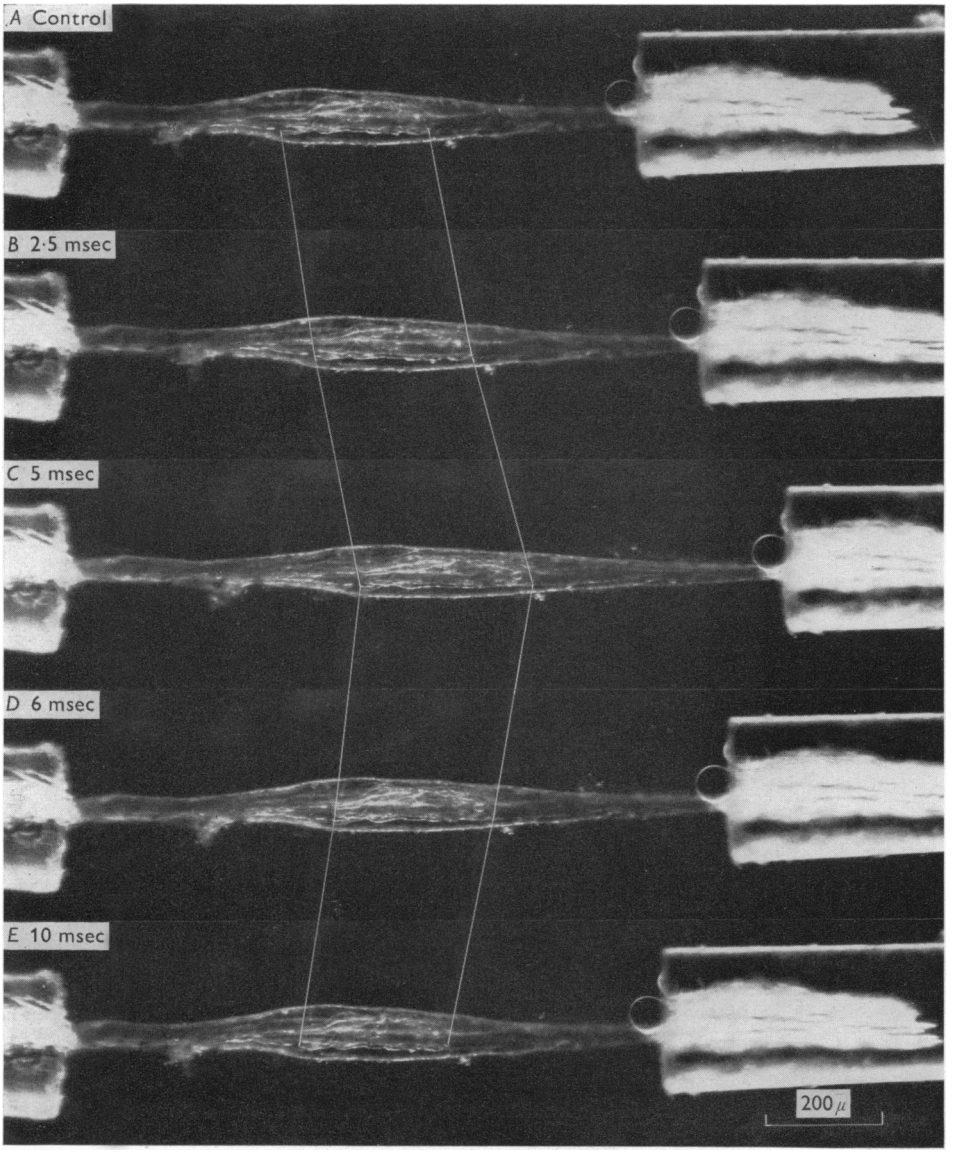

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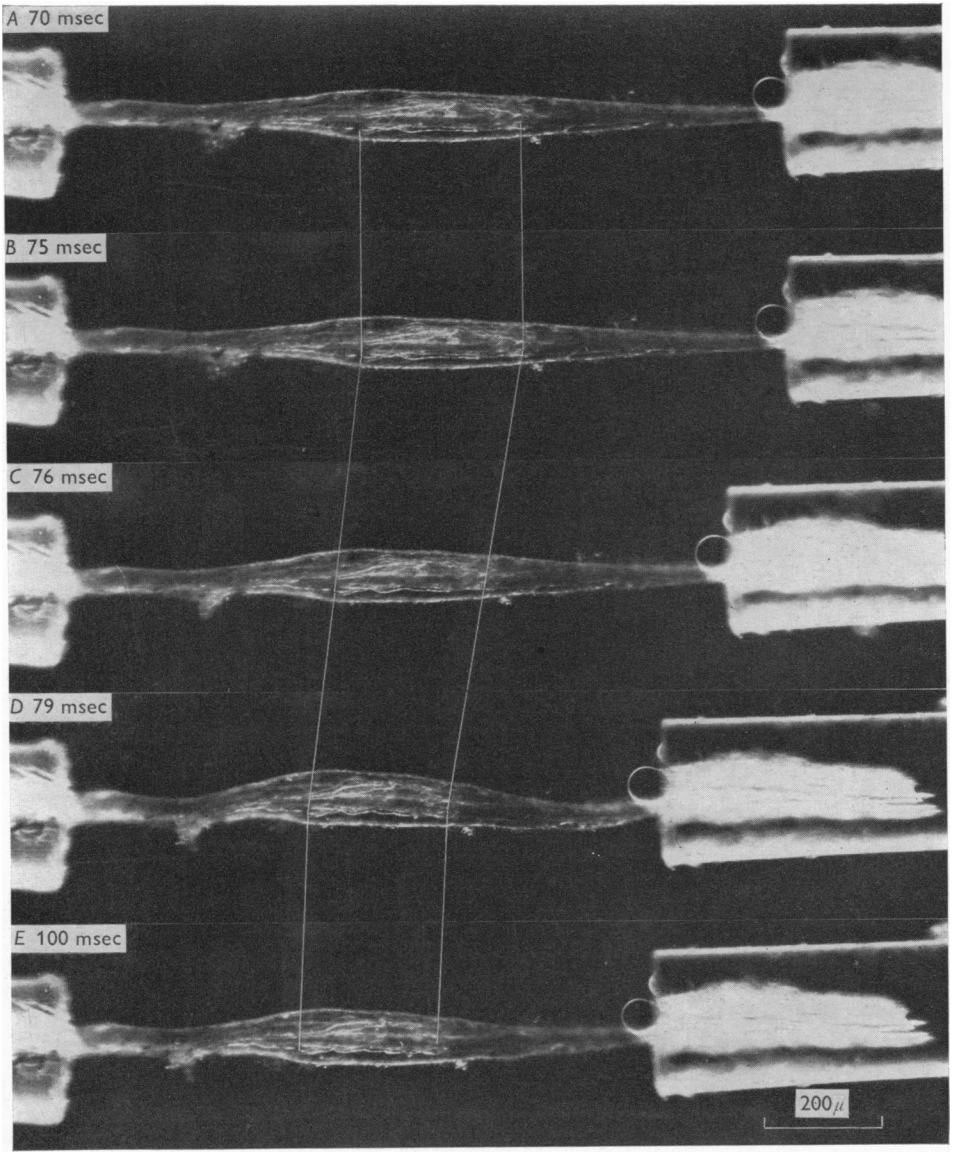
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B 75 msec
C 76 msec
D 79 msec
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EXPLANATION OF PLATES

PLATE 1

Photomicrographs of isolated frog muscle spindle obtained with dark field illumination using brief flashes from stroboscope. Spindle is held between two fine nylon threads (350 μ diameter). Photographs are from a sequence taken during application of a step stretch: note movement of right-hand rod. Timing of photographs during stretch as indicated. White lines indicate movement of two landmarks on either side of the central zone of the spindle. Complete sequence of measurements is plotted in Text-fig. 2*B*.

PLATE 2

Photomicrographs of a different isolated spindle before and during a brief dynamic stretch. Note movement of right-hand rod; timing of stroboscope flashes as indicated. White lines indicate movement of two landmarks on either side of central zone. Diameter of nylon thread 250 μ. Full sequence of measurements is plotted is Text-fig. 3*B*.

PLATE 3

Same spindle as in Plate 2 during and after release of static stretch. Full sequence of measurements is plotted in Text-fig. 3*D*. Note slight curling of spindle at 79 msec (*D*).