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TENSION DEVELOPMENT IN HIGHLY STRETCHED VERTEBRATE MUSCLE FIBRES

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SUMMARY

1. An apparatus is described by which the length of a selected part of an isolated muscle fibre can be held constant, giving isometric conditions, or alternatively its length can be measured while tension is held constant (isotonic). Control can be switched between length and tension so as to carry out afterloaded contractions with a shortening stop.

2. When a part of a fibre with uniform striation spacing is stretched so far that there is presumably no overlap of filaments, the tension developed during an isometric tetanus with this apparatus is very small (not more than 3–5% of the tension developed at optimum length).

3. If the tendon ends are held stationary, a fibre with the same initial length develops a large amount of tension (order of 30–40% of tension at optimum length) with a slow time course. This additional tension is due to shortening of the end parts of the fibre, where the striation spacing is smaller and overlap of filaments still exists.

4. The resistance to elongation of a part of a fibre where there is no overlap is only slightly increased on stimulation.

5. To a first approximation, the results are in good agreement with expectations based on the sliding filament theory. The development of detectable amounts of tension, and of a slight increase of stiffness, on stimulation, are however not expected on the simplest form of this theory; possible explanations are discussed.

INTRODUCTION

It has long been known that the tension developed by a vertebrate skeletal muscle during an isometric tetanus decreases as the length of the muscle is altered in either direction from an optimum value (Heidenhain,

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1864; Blix, 1895; Beck, 1922). The form of this relation between length and tension acquired a new interest when the sliding filament theory of muscular contraction emerged, because this theory offered a new prospect of interpreting the effects of changes in length. In particular, A. F. Huxley & Niedergerke (1954) suggested that the linear drop of tetanic tension found by Ramsey & Street (1940) with increase of length above the optimum might be explained if tension were proportional to the amount of overlap of the two sets of filaments, as would be expected if a relative force between the two filaments is generated at each of a uniform series of points in the region of overlap in each half-sarcomere. On this basis, the tension should drop to zero at the length where the two sets of filaments just cease to overlap each other. This could not be determined from Ramsey & Street's results because they did not measure the striation spacings in their fibres. A. F. Huxley & Peachey (1961) therefore specifically investigated this point. They found that isometric tetani did not give a clear result, because the fibres did not stretch uniformly. Fibres that were stretched enough so that there was no overlap in the main part of their length were found to have a considerable amount of overlap near to their ends, and during a tetanus in which the tendons were held stationary the ends were found to shorten greatly, stretching the middle part of the fibre and producing substantial amounts of tension. They therefore used isotonic tetani, with a microscope to detect whether a region in the middle of the fibre did or did not shorten. They found that there was no shortening when the striation spacing exceeded a critical value which they estimated as 3.52 μ, agreeing closely with their estimate (3.52–3.54 μ) from electron microscopy of the striation spacing at which overlap ceases. Analogous experiments by Podolsky (1964) on the stripped-fibre preparation of Natori (1954), stimulated by the application of solutions containing calcium, gave a value of about 3.65 μ for the critical length, and a recent determination of filament lengths (Page & H. E. Huxley, 1963), with new precautions against shrinkage during preparation, gave 3.65 μ as the spacing at which overlap ceases. The agreement between all these values is probably as good as can reasonably be expected from such measurements, and indicates that contraction does not occur if there is no overlap between the two sets of filaments.

However, Carlsen, Knappeis & Buchthal (1961) re-determined the isometric tension–length curve, with measurement of striation spacings, and found large tensions at lengths where there is no overlap. Thus, at a spacing of 3.7 μ the tension developed was 30–40% of that developed at the optimum length, and the developed tension did not approach zero until the spacing reached 4.1–4.2 μ or even more. They confirmed that the spacing was less at the ends of the fibre, but estimated that contraction
of the ends would account for only about one-sixth of the tension observed at spacings from 3.5 to 4.4 μ unless the parts of the fibre with no overlap did contract, or at least underwent an increase of stiffness.

The experiments described in this paper were undertaken in the hope of clearing up this discrepancy. The methods are described at some length because they are used also in other series of experiments which will be reported separately. Short accounts of the apparatus (Gordon, Huxley & Julian, 1963) and of the main results (Gordon, Huxley & Julian, 1964) have already appeared.

**METHODS**

*Principle of the method*

A part of the length of an isolated muscle fibre, within which the striation spacing was sufficiently uniform, was defined by two 'markers' (pieces of gold leaf) stuck to the fibre with grease. The length \( L \) of the part between these markers was measured continuously by a photoelectric device (the 'photo-electronic spot follower'). \( L \) could be held constant ('length control') by feeding from the output of this device to a moving-coil apparatus which acted as a servo motor, pulling on the tendon at one end of the fibre; stimulation in this condition produced an isometric contraction of the part of the fibre between the markers, and the tension was recorded by a transducer attached to the other tendon. Alternatively, the tension could be held constant ('tension control') by feeding from the tension signal to the servo motor; the contraction was then isotonic and the shortening of the part between the markers was signalled by the photo-electronic spot follower. A diode circuit allowed tension control to take over when tension reached a pre-set level, and length control to take over again when shortening reached a pre-set value, so as to make the part of the fibre between the markers undergo an afterloaded contraction with shortening stop.

*Dissection*

Twitch fibres, together with pieces of tendon at either end, were dissected from the dorsal part of the semitendinosus muscles of frogs *Rana temporaria* stored before use in a moist environment at about 4° C. The muscle was dissected at room temperature in Ringer's solution containing tubocurarine (10⁻⁴ g/ml.), using knives made from pieces of stainless-steel razor blade. To avoid non-uniformities of striation spacing, special care was taken to remove capillaries and other adherent tissue, and to avoid stretching the fibres heavily. In most experiments the fibres were stored overnight in the usual Ringer solution at 4° C before use the next day (cf. Ramsey & Street, 1940). There were no obvious differences between the results given by fibres used immediately after dissection and by fibres stored overnight. The fibre was transferred from the dissecting chamber to the experimental trough by carefully lifting it up out of the dissection solution adhering to a thin glass rod, which was then submerged in the Ringer's solution filling the experimental trough under microscopic observation. The fibre was separated from the rod by pulling on one tendon while rotating the rod in such a way as to prevent the fibre becoming twisted.

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The composition of the Ringer solution was: NaCl, 115 mM; KCl, 2-5 mM; CaCl₂, 1-8 mM; Na₂HPO₄, 2-15 mM; NaH₂PO₄, 0-85 mM.

Fig. 1. Arrangements for holding the fibre, in vertical section (above) and in plan (below). A, ‘butterfly’, hooked into right-hand tendon; in upper diagram shown both hooked to transducer (right) and in detached position (left). B, slider, hooked into left-hand tendon. C, motor stop. D, fibre. E, markers. F, tension transducer. Ringer solution surrounding the fibre is not shown.

Experimental arrangements

The experimental trough was mounted on the mechanical stage of a conventional microscope, which also carried the servo motor and tension transducer (RCA 5734) on adjustable brackets. Cooling water circulated below the glass bottom of the trough, and below this again was a sealed air space to prevent condensation. The temperature of the Ringer’s solution around the fibre was a few degrees above that of the thermostatically controlled tank of cooling fluid; the difference was checked periodically with a thermocouple. Two strips of 1 mm glass cemented parallel to one another on the bottom of the trough formed a channel to guide the ‘slider’ to which the left-hand tendon of the fibre was attached (see Fig. 1). The right-hand tendon was hooked on to a device made from platinum wire (A, Fig. 1, weight 5-4 mg, referred to as the ‘butterfly’) which could in turn be hooked to the tension transducer but could be detached from it and left in the position shown in Fig. 1 simply by moving the transducer to the left: this was done in order to take all load off the transducer when a base line corresponding to zero tension was to be recorded. The sloping surfaces at the right-hand end of Fig. 1 ensured that the ‘butterfly’ would slide up to the position shown when the transducer was moved along. The slider (B, Fig. 1; 18 mg) was made from stainless-steel wire. Its upright member fitted into a clip on the arm of the servo motor, and therefore moved in an arc of a circle. The movement of the muscle fibre was, however, in a straight line since the C-shaped piece at the other end of the slider fitted into the channel formed by the glass strips and the hook which held the left-hand tendon was attached to the slider near the centre of the C-shaped piece.

When the motor was not under feed-back control, its position could be adjusted by the ‘motor stop’ C (Fig. 1) which was carried on a screw movement with vernier scale, parallel to the long axis of the fibre. In this condition, a steady current was passed through the motor to force its arm into contact with the stop.
Procedure

The fibre was transferred to the trough, and the ‘butterfly’ and the slider were hooked into its tendons, under a binocular dissecting microscope. The motor and the transducer were attached to the stage and the slider and butterfly were connected to them respectively. The water immersion objective was attached to the microscope tube; the fibre was examined under a magnification of 1000× and extended to the desired length by moving the ‘motor stop’. Positions for the markers were selected by the criteria described under ‘Results’ (p. 154) and identified by readings of the lateral vernier of the stage. The markers were pieces of gold foil 2-5 μ thick cut as rectangles 1-0 × 0-7 mm (mass 34 μg). A strip 0-1 mm wide was folded under along each of the long sides in order to prevent sharp edges from damaging the fibre; the final width of each marker was thus 0-5 mm. They were smeared on top with tap grease and brought up underneath the fibre with a micro-manipulator. A thread of tap grease was stuck down to the marker on one side of the fibre, looped over the fibre and stuck down on the marker on the other side, thus fastening the fibre to the marker. The marker was then released from the manipulator, which was removed. These operations were carried out at room temperature as the grease was too stiff at the temperatures used in the experiments. The markers stuck very tenaciously to the fibres, but appeared not to damage them as fibres carrying markers survived as well (up to 2 days) as ordinary isolated fibres.

Further details of the procedure are given in the Results section.

Microscopy

Measurements of striation spacing and fibre diameter were made with a 4 mm water immersion objective, N.A. 0-75. The metal surround of the front lens was coated with grease to prevent contamination of the Ringer solution. Visual measurements were made with a 25× eyepiece with no lenses below the graticule; for photography no eyepiece was used (to avoid distortion) and the magnification on the film (35 mm) was ×78. In each case, magnification was determined with a stage micrometer. A tungsten lamp with green filter was used, and the N.A. of the illuminating cone was about 0-23.

Striation spacings were measured in the photographs by projecting the film on to a sheet of paper on which eleven dots were marked, spaced accurately at intervals of 1-5 mm. The magnification was adjusted until the spacing of the striation pattern matched that of the dots, and was then estimated by measuring the distance between the images of the two edges of the film. Repeat measurements at the same position in the image rarely differed by more than 0-5%. On each frame, readings were taken at six widely spaced positions.

The cross-sectional area was found by the method mentioned by Blinks (1965, p. 48) and shown by him to give a fair approximation when tested with actual outlines of cross-sections of frog muscle fibres.

Stimulation

The trough was divided into two compartments by means of glass strips and petroleum jelly, and a platinum black electrode, about 6 × 15 mm, was introduced below the Ringer’s solution in each compartment. Alternating condenser discharges (time constant 4–6 msec) were fed to these electrodes through a transformer from an electronic stimulator which delivered a series of shocks at adjustable frequency throughout the duration of a signal from a master pulse generator. The partitions were arranged so that each odd-numbered shock stimulated the fibre at two points near the markers, but between them, while each even-numbered shock stimulated the fibre near to each of its ends. The amplitude was set to about 1-5 times the twitch threshold for the odd shocks, which was a little higher than for the even ones. A frequency of 20/sec was used for fibres at 3–5°C; tetani were usually of 1 or 2 sec duration and were given at intervals of either 2 or 3 min.
Measurement of tension

An RCA 5734 mechano-electronic transducer was used, with grid connected to cathode; it was mounted in a brass block for thermal stability with the case (anode) earthed. A 90 V battery was used with half the drop across the tube and half across the (adjustable) cathode load; a 45 V coupling battery from the cathode raised the output to near earth potential. Lead accumulators provided 6 V for the heater.

The hook which connected to the 'butterfly' (p. 146) was held on a rigid arm, length 3-0 cm, fixed to the anode pin, and consisting of a thin glass tube 15 mm long cemented to the pin and a stainless-steel wire tripod attached to the tube with shellac. The frequency of the oscillations when this arm was suddenly released from a deflected position was 500 c/s.

The transducer was calibrated in each experiment by recording the output when a standard force, produced by deflecting a spring wire to a measured extent, was removed from the tip of the arm. The wire itself was calibrated by holding it horizontal and hanging a weight on its tip. The sensitivity was about 1 V/g, and hardly varied during the course of this work.

The chief limitation of the system was drift, of the order of 0-5 mV/min. This necessitated the arrangement described on p. 146 by which the transducer arm could be unhooked from the 'butterfly' and fibre when a base line was needed; this could be done with the length regulator on (p. 151) so that the length of the fibre was kept constant.

Photo-electronic spot follower

The function of this system was to measure accurately the change, \( \Delta L \), in the length between the right-hand edges of the markers. It works on the principle of a cathode ray tube curve follower. A diagram of its main features is given in Fig. 2. A double-beam cathode ray tube was fixed vertically beneath a hole in the table where the microscope stood. The rest of the oscilloscope components were in a chassis mounted on a separate rack. The microscope mirror could be removed, allowing light (blue, short persistence phosphor) from the tube spots to enter the lens in the substage and then be brought to focus on the marker edges as shown in the diagram. The substage lens was a high quality f/1-9 photographic lens stopped down to f/2-8 to eliminate vignetting and aberrations. Light passing the marker entered a collecting lens whose function was to keep the beams from the two spots separate, and to collect them on the cathodes of two gas-filled photo-cells. The collecting lens and photocell arrangement could be fixed to the microscope tube—in place of the objective lens—and suspended over the top of the fibre. The outputs of the photocells went to cathode followers, whose outputs were adjusted to zero under the condition that one-half of the light from each spot was passing into its photocell. It can be seen in Fig. 2 that there is a feed-back connexion from each cathode follower to the deflexion of the corresponding spot, both of which operate in a negative feed-back sense. A signal from the right-hand photocell deflects both spots equally in the same direction, and, therefore, keeps both spots fixed on the edges of the markers when the markers move in phase. A signal at the output of the length operational amplifier (LOA) coming from the right-hand spot and left-hand photocell gives an additional deflexion to the right-hand spot only, so that the magnitude of this signal is directly proportional to the out-of-phase motion of the left-hand marker compared with the right, i.e. it measures the change in length between the markers. The signal in the 'position' loop gave a nominal 40 mV/mm, and the 'length' signal a nominal 20 V/mm. The length signal was calibrated in each experiment by 'hooking' the right spot to the left marker (with the left spot disconnected), moving the stage laterally in 1 mm steps and recording the \( \Delta L \) output.

Square pulses injected at the points shown in Fig. 2 caused the responses shown in Fig. 3A. The transients are over within 0-2 msec; this is a measure of the time taken by the system to correct for a sudden input disturbance. Drifts were eliminated by checking the separation
Fig. 2. Schematic diagram of photo-electronic spot follower. Explanation in text.
CF, cathode follower. L.O.A., 'length' operational amplifier.

Fig. 3. Responses of spot-follower A and complete servo system B. 11 October 1963; fibre 14-25 mm long, distance between markers 6-9 mm, striation spacing 2-46 μ.

A, response of spot-follower when rectangular pulse, 0-8 msec duration, is injected simultaneously into both points indicated in Fig. 2, with motor on its stop so that both markers are in fact stationary. Upper trace, 'length' signal ΔL (see Figs. 2 and 5), one large division = 0-2 V, equivalent to 9-6 μ or 0-14 % change of marker separation (increase upwards). Lower trace, 'position' signal, one division = 5 mV, equivalent to 0-125 mm displacement of right-hand marker (to right, upwards).

B, operation of complete servo in 'length control' when rectangular pulse, duration 30 msec, is injected at point marked 'length step' in Fig. 5. Upper trace, ΔL, one large division = 0-5 V, equivalent to 24 μ or 0-39 % change of marker separation. Lower trace, output of main amplifier, one division = 2 V.

Figures for sensitivity and time base speed refer to one large grid square.
of the spots on the tube face with a travelling microscope at intervals during the experiment; this measurement was accurate within 0.1 mm, corresponding to 0.03 mm at the fibre, or 0.5 % of the shortest distance between the markers in the experiments reported here.

The performance of the system was limited by (a) residual non-linearities in the amplifiers and deflection systems of the cathode-ray tube, and (b) irregularities in the phosphor. Both of these factors were checked in each experiment by moving the stage laterally, thus moving both markers equally, and recording an X–Y plot (Fig. 4) of the length signal (horizontal) against the position signal (vertical). Ideally, the trace should be a vertical straight line. A slope one way or the other could be corrected by adjusting the gain in the second stage of the amplifier in the position loop. Consistent small scale irregularities developed slowly through ‘burning’ of the phosphor; when they became troublesome the microscope was shifted so as to use a new track on the tube face. Blue filters in front of the photocells made it possible to keep the room illuminated with orange light while working.

Fig. 4. X–Y plots of length signal (horizontal) and position signal (vertical) as fibre is displaced bodily to right (A, spot moving upwards) and to left (B, spot moving downwards), without real change in separation of markers.

Scales: one large division = 20 mV (0.5 mm) vertically for position and 0.5 V (0.025 mm) horizontally for length. Extreme deviations in length signal are about ±5 μ. Experiment of 6 August 1963.

The output of the system is proportional to ΔL, the difference between the actual separation of the markers and a value L₀ which depends on the two ‘Y’ shifts and the input marked ‘Resting length’ in Fig. 2. The latter is the voltage from a ten-turn potentiometer through which is passed a constant current whose value is set at the beginning of each experiment. After the measurement of striation spacing, this current is switched off and the ‘Y’ shift knobs are adjusted to make the two spots coincident with their image falling on the right-hand edge of the left marker. The potentiometer (full scale, 0–10) is set at a reading equal to twice the value in microns of the striation spacing, which has already been measured, and the current is switched on and adjusted so as to bring the image of the left spot on to the right-hand edge of the right marker. The feed-back loops of both spots are now closed; the output signal ΔL is small and is brought exactly to zero by further adjustment of the current through the potentiometer. The potentiometer setting can now
be changed, and the zero of the $\Delta L$ output will correspond to the length at which the striation spacing in microns is half the potentiometer reading; any desired spacing can therefore be set directly on the dial, and the fibre, if passive and under ‘length control’, will be stretched to the corresponding length by the ‘regulator’ (see next section), which operates so as to bring $\Delta L$ to zero.

Fig. 5. Block diagram of servo system. ‘Spot follower’ shown in Fig. 2; ‘Diode switching network’ shown in Fig. 6; other elements explained in text. Feed-back loop used in length control indicated by thicker arrows. The values for sensitivity, gain, etc., in the blocks are representative values for steady-state conditions.

Regulator and servo system

By means of a negative feed-back, proportional control loop, our system acts to keep either the length between the markers, or the tension in the fibre, at some pre-set value (regulator action); also, it can force one or other of these controlled variables to follow an input command signal (servo action). The experiments described in the present paper used only length control, but the other features will be described here as well.

The elements of the system are shown in block form in Fig. 5. The blocks labelled ‘spot follower’ and ‘5734’ have already been dealt with. The block ‘amplifier’ is a differential, d.c., battery-operated amplifier (Palmer & Read, 1962), gain 6–12 in different experiments. A command pulse could be applied to the second input in order to produce step changes of tension while the fibre was under tension control.

The output of the block ‘Diode switching network’ was either $\Delta L$ or tension, plus or minus a pre-set constant quantity, and the remaining elements in Fig. 5 operated so as to keep this output at zero. Thus, either length or tension was held at the desired constant value. The ‘Diode switching network’ will be described on p. 152. The remaining elements will be described in order, going backwards round the loop from the fibre.

The servo motor. The servo motor was a galvanometer assembly specially modified for us by the Cambridge Instrument Co., Ltd. It was essentially their ‘5 in.’ moving-coil instrument with the following alterations:

1. The normal pointer was replaced by a rigid tripod arm 3-5 cm long made of 0-5 mm aluminium tube.
2. The hairspring was omitted.
3. The coil contained two independent windings.
The stainless-steel clip attached to the arm for holding the slider brought its effective radius to 4-0 cm. The arm was coated with shellac to prevent contact between the aluminium and the Ringer solution in the trough.

The ‘driving coil’ was of 76 turns, 24 Ω resistance; current in it produced a torque of 70 g.cm/A. The purpose of the other winding (‘pick-off coil’, 420 turns, 340 Ω) will be described in the section ‘transient velocity feed-back’. The inductance of the driving coil was so small that it did not detectably delay the rise of current in the coil. The moment of inertia of the rotating parts was about 1 g.cm². The maximum current that could be supplied by the driving amplifier and cathode follower was about ±130 mA, corresponding to an acceleration of about 25,000 cm/sec² at the slider. The performance of this motor was adequate in all respects except that its moving parts and bearings were sufficiently flexible to allow internal oscillations at a frequency of about 500 c/s. This affected the overall speed of response because it limited the amount of forward gain that could be used without the closed-loop response becoming unstable.

Although based on a micro-ammeter movement, the motor performed satisfactorily with currents of the order of 0·1 A provided their duration was short enough to avoid dangerous heating effects. To prevent large currents of long duration from being passed accidentally through the coil, it was protected by a relay operated with a lag from the driving voltage (block labelled ‘Safety circuit’ in Fig. 5).

**Main amplifier and cathode follower.** This was an operational amplifier with output swing of ±100 V, used at a gain of either 100 or 200, feeding a cathode follower with very high power gain. The cathode follower had an independent power supply to avoid feed-back through H.T. lines to input stages. The total output impedance of the cathode follower, including that of the motor circuit, was about 100 Ω, and its voltage gain was about 0·85.

**Transient velocity feed-back.** Rotation of the motor generated an e.m.f. in the ‘pick-off coil’ which was used for stabilizing the closed-loop response. This signal was used in preference to a differentiated error signal because the latter would be subject to additional lags due to compliance in the fibre and to the spot follower.

The e.m.f. was 34 mV per radian/sec, or 8·5 mV per cm/sec at the end of the arm; this was amplified in the ‘main amplifier’ by an amount (usually about 500 x ) which could be adjusted to obtain an optimum response. The two coils in the motor also acted as a transformer so that the output of the pick-off coil contained an unwanted component related to the driving voltage. This was eliminated by putting each winding in series with the corresponding winding of a dummy motor identical with the real motor except that the coil was fixed, the direction of the connections being such that the e.m.f.s due to transformer action in the two ‘pick-off’ windings were opposed to one another.

The velocity signal derived in this way would cause an error in length (or tension) proportional to angular velocity of the motor; this was eliminated for steady-state conditions by coupling the signal to the main amplifier through a series condenser which gave a time constant of 4·4 msec, so that the damping effect was present only during rapid transients.

**Low frequency gain.** This block represents an attenuator with fixed gain of 0·2 at high frequencies but additional gain at low frequencies variable from zero to a maximum which gave 0·5 over-all at d.c. The additional gain, if used, came on exponentially with a time constant of 23 msec. This additional gain improved the steady-state stiffness of the system without introducing the instability which would have been caused by an equal increase of gain at all frequencies.

**Diode switching network.** The circuit represented by this block is shown in Fig. 6. The output is connected through the main amplifier to the motor in such a way that a positive output signal makes the fibre shorter, thus decreasing both the ΔL and the T inputs to the circuit, and hence also the output signal. The system is adjusted so that this regulator action, with its high gain, keeps the output at (or very near) earth potential. Initially the fibre is at rest, with T₁ set at a value between the resting tension and the isometric tetanus.
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tension; an $L_1$ is set; and $\Delta L$ is near zero. In this condition: (a) the voltage at $C$ is positive; hence the voltage at $N_\beta$ is positive and diode 4 is cut off; hence the 10 $\mu$A fed in at the central point of Fig. 6 must flow through diode 3 to $N_\alpha$, while the 20 $\mu$A drawn off at $N_\beta$ is supplied by the $\Delta L$ input (low impedance) through diode 5; and (b) the voltage at $B$ is negative; hence diode 2 is cut off and diode 1 must pass 10 $\mu$A to make up, together with the 10 $\mu$A through diode 3, the 20 $\mu$A drawn off from node $N_\alpha$. Hence diodes 1 and 3 pass equal currents, the voltage drops across them are equal, and the output point is at the same potential as the $\Delta L$ input point. The complete system therefore operates so as to hold $\Delta L$ at zero.

Fig. 6. Diode switching network. ‘$\Delta L$’ and ‘$T$’, length and tension signals from low-impedance points; ‘output’ leads to the main amplifier through a cathode follower. For explanation, see text.

If the fibre is stimulated, its length is thus held constant at first, and the tension rises. As $(T - T_1)$ approaches zero, diode 2 begins to conduct, raising the potential at $N_\alpha$ and therefore also at the output. The servo is actuated, shortening the fibre, so that the $\Delta L$ input goes negative, cutting off diode 1. When this switch-over is complete, diodes 2 and 3 pass equal currents (10 $\mu$A each) and the output point is at the potential corresponding to $(T - T_1)$. The complete system still holds the output at zero, so that now $T = T_1$, and the change of length, $\Delta L$, can be recorded.

At later stages in the contraction, similar switch-overs occur (a) from diode 3 to diode 4, and (b) from diode 5 to diode 6. The complete contraction therefore comprises the following four stages:

1. Connexion is through diodes 1 and 3: isometric tension developed at length $L_\beta$ until the tension reaches $T_1$.
2. Connexion is through diodes 2 and 3: isotonic shortening under tension $T_1$ until length reaches $(L_\beta - L_1)$.
3. Connexion is through diodes 5 and 4: isometric tension development at length $(L_\beta - L_1)$ until tension reaches $T_2$ ($T_2 > T_1$).
4. Connexion is through diodes 6 and 4: isotonic shortening under tension $T_1$

Stage four can be eliminated by setting $T_1$ at a value greater than the fibre can develop; the result is then an after-loaded contraction with shortening stop. Similarly, a simple isometric contraction is obtained if $T_1$ is set at a high value.

The diodes are of silicon (Mullard OA 202), which give a slope resistance of about 4000 $\Omega$ with a current of 10 $\mu$A; their back resistance is of the order of 10$^4$ $\Omega$. The $\Delta L$ and $T$ inputs come from cathode followers with output impedance about 1000 $\Omega$; the output feeds to a cathode follower with high input impedance. The voltage $L_1$ is provided by a floating HT battery; $T_1$ and $T_2$ are provided by potentiometer settings on the parallel cathode loads of the tension cathode follower.

**Phase advance.** These blocks are $R$-$C$ networks attenuating a steady signal to one half, and providing an adjustable amount of phase advance (time constant 0–1 msec) to reduce the lag due to motor inertia when the diode circuit switches over, and to improve the stability of the complete system.

**Recording C.R.O.** This was the Tektronix 502 oscilloscope, with a 35 mm recording camera.

**Performance.** Figure 3B shows the change (increase) of length, recorded by the photo-electronic spot follower, when a rectangular pulse was injected at the point marked 'Length Step' in Fig. 5. There is a slight overshoot, whose peak is reached about 3 msec after the start of the pulse. The response at the end of the pulse is less good because the fibre becomes slacker as it is shortened, so that the movement of the motor is transmitted to the markers with a delay.

The overall stiffness of the servo can be obtained by multiplying together the sensitivity or gain factors associated with the elements in the loop. These are given in the preceding paragraphs and summarized in Fig. 5. Using the values in Fig. 5, it is seen that under 'length control' a steady error of 1 $\mu$ in the distance between the markers causes a force of about 70 mg wt. at the tendon attached to the motor arm. This is to be compared with (a) static friction in the slider, etc., amounting to about 30 mg, or (b) the tension developed by the fibre, say 300 mg in a large fibre, or (c) the stiffness of the fibre. This last may be estimated on the basis that the isometric tension drops to zero with about 1% sudden shortening; for a large fibre with 10 mm between the markers this is 300 mg for 100 $\mu$, or 3 mg/$\mu$. The servo is about twenty times stiffer than this in the steady state; at short times it was 2.5 times less stiff, leaving a factor of about eight over the stiffness of the fibre.

**RESULTS**

**Procedure**

The procedure in experiments on highly stretched fibres was repeatedly modified so as to improve the uniformity of striation spacing in the part of the fibre between the markers. The procedure finally adopted was as follows.

1. The fibre was mounted as described under Methods, and its length adjusted by moving the 'motor stop' until the striation spacing, measured visually at one or two places near the middle of the fibre, was about 3.7 $\mu$.

2. The striation spacing was measured visually with great care at intervals of not more than 2 mm along the whole length of the fibre and 1 mm in the part of the fibre that we expected to use. The results were plotted out and positions for the markers were chosen, 6–10 mm apart, in such a way that the variations of striation spacing in the part of the fibre between the markers should be as small as possible.
3. The markers were attached to the fibre and their separation measured exactly by reading the stage vernier when each was in the centre of the field.

4. The height and width of the fibre and the striation spacing were measured visually at intervals of 2 mm along the part of the fibre between the markers.

5. The fibre was photographed by ordinary light microscopy at intervals of either 1 or 2 mm between and just outside the markers for subsequent more precise measurement of striation spacing.

6. Circulation of the cooling water was begun.

7. The photocell assembly was mounted on the microscope, the spots ‘hooked’ on to the markers, and the length signal calibrated, as described under Methods.

8. The servo control of fibre length was turned on.

9. The threshold for twitches was measured; it was sometimes necessary to shorten the fibre a little in order for the twitches to be detectable.

10. Recording of tetani was begun.

The important features of the procedure were (a) that a uniform part of the fibre was selected, (b) that the fibre was not stimulated between making the measurements and turning on the servo, since a contraction might have caused the distance between the markers to change; (c) that the fibre was not stimulated tetanically at moderate lengths before the observations at great length, since such stimulation would be expected to increase the residual non-uniformity of striation spacing (Hill, 1953); and (d) that the fibre was stretched to just beyond the expected critical length before attaching the markers, since the grease on them might have prevented the parts of the fibre in contact with them from stretching like the rest.

**Tension in isometric and fixed-end tetani**

The lower trace of each pair of records in Fig. 7A–D shows the tension developed during a tetanus by a fibre stretched to a length where one would expect there to be no overlap of thick and thin filaments. In Fig. 7C–D, the servo control was switched off and the tendons were held stationary; a considerable amount of tension was developed slowly, in agreement with Ramsey & Street (1940), Huxley & Peachey (1961) and Carlsen et al. (1961). The upward deflexion of the upper traces indicates that the part of the fibre between the markers was being stretched. Fig. 7A and B, however, show the result of tetanic stimulation of the same fibres at the same initial length, under control by the regulator so that the length of the part of the fibre between the markers was held constant. The tension rise was very much smaller than when the tendons were held. The upward deflexion of the upper trace in this case means that
the right-hand marker was moving towards the right. The right-hand tendon was held stationary by its attachment to the tension recorder, so the right-hand end of the fibre between the marker and the tendon must have been shortening. No doubt the left-hand end of the fibre, to the left of the left-hand marker, was also shortening but this could not be recorded.

![Graph](https://example.com/graph.png)

**Fig. 7.** Tetanic stimulation of isolated fibres, with servo control of length (A and B) and with tendons held (C and D); A, C, E, experiment of 28 August 1963, 4°C, average striation spacing between the markers 3.92 μ; B, D, F, experiment of 20 September 1963, 3°C, striation spacing 3.86 μ. A and B (with servo control of a nearly uniform part of the fibre length): lower trace, tension; upper trace, position of right-hand marker (upward deflexion signals movement towards the right-hand tendon). C and D (with tendons held stationary), lower trace, tension; upper trace, change in distance between markers (increase upwards). In C, distance between markers is 6.1 mm, so that one grid square represents 0.39% increase; in D, distance is 7.65 mm, and one grid square represents 0.62% increase. E and F: time of occurrence of stimuli. Note difference of amplification between B and D. Sensitivity and speed figures refer to one grid square.

In Figs. 8 and 9 are reproduced the two sets of records of servo-controlled isometric contractions at varying degrees of stretch from which Fig. 7A and B are taken. The measurements of striation spacing in these same two fibres are shown in Figs. 10 and 11. At the shorter lengths in Fig. 9, and even at extreme degrees of stretch in some other experiments (e.g. Fig. 14), the tension continued to rise slowly throughout the tetanus. The evidence given in the next section makes it probable that this slow rise was due to the residual irregularity of striation spacing, so that overlap existed locally and would increase progressively as these regions shortened. On this basis, the measure of tension appropriate for relating to the striation spacings measured in the resting fibre will be that given by extrapolating the tension record back to the beginning of stimulation. Most of the records
contained a small component detected by this procedure, which developed at a speed similar to that of an isometric tetanus at the slack length of the fibre. The results were plotted against mean striation spacing, and two such graphs derived from the same experiments as Figs. 7–11 are reproduced in Figs. 12 and 13. The resting tensions are also shown in these

Fig. 8. Tetanic responses of a nearly uniform part of the fibre length under servo control. Experiment of 28 August 1963, 4°C. Various striation spacings, as indicated on the figure. A is the same frame as Fig. 7A. Upper trace of each pair, position of right-hand marker; lower trace, tension. Note that amplification of both channels is half as great in D as in A, B, C and E. E, no stimulus, tension recorder moved by hand to the right, and other end of fibre is moved by the servo: note absence of tension change. F, times of stimuli. Sensitivity and speed figures refer to one grid square.

Fig. 9. As Fig. 8, but another experiment (20 September 1963, 3°C). Note changes of amplification. A is the same frame as Fig. 7B. Times of stimulating shocks as in Fig. 7F. J: bodily displacement of the whole fibre, as in Fig. 8E. Sensitivity and speed figures refer to one grid square.
figures. It will be seen that the results deviate only slightly from the ideal case of a linear fall up to a striation spacing a little over 3·6 μ, and zero tension at greater degrees of stretch. The corner is somewhat rounded, but the greatest deviation from the ideal result is only about 3–5% of the tension developed by the fibre at its optimum length.

Fig. 10. Measurements of striation spacing in fibre of 28 August 1963. Open circles, visual measurements before markers were attached; filled circles, visual measurements after markers were attached; open rectangles, range of photographic measurements, with horizontal line at mean (twenty-one measurements on each frame between the markers; six on each of the two frames outside the markers). a, at position with much connective tissue adhering to fibre; b, at position of end-plate. The shaded rectangles indicate the positions where the markers were attached, and the vertical lines show the positions of the extreme ends of the fibre. Abscissa: reading of vernier on horizontal movement of mechanical stage.

Fig. 11. As Fig. 10, for fibre of 20 September 1963. Each photograph measured at six positions. a, pair of measurements at position of end-plate.

Origin of slow tension rise

Huxley & Peachey (1961) attributed the slow development of substantial amounts of tension in highly stretched fibres to the shortening of the ends, where the filaments still overlapped, with corresponding stretch of the
TENSION DEVELOPMENT IN STRETCHED MUSCLE

Fig. 12. Graph of tension against striation spacing for fibre of 28 August 1963. Crosses, maximum tension developed in servo-controlled tetani; filled circles, tension in same tetani extrapolated back to start of stimulation as shown in inset of Fig. 13; means from two to four tetani as indicated. Duration of tetanus, 1 sec at 20 shocks/sec. Vertical bars: range of resting tensions, which varied considerably according to sequence of length changes. Tensions related to cross-sectional area at striation spacing of 2.1 μm. Isometric tension at spacing of 2.72 μm was 1.70 kg/cm², which corresponds to about 2.6 kg/cm² at the optimum length.

Fig. 13. As Fig. 12, for experiment of 20 September 1963. Only one measurement of resting tension at each length, shown by open circles. Tetanus, 1 sec at 20 shocks/sec. Tetanic tension at optimum length about 2.8 kg/cm². Inset shows method of extrapolating back to start of tetanus.
middle part of the fibre. This explanation is strongly supported by the observation that the amount of tension developed is reduced to a small fraction when the length of a nearly uniform part of the fibre was held constant. If this is correct, it suggests that the small slow rise of tension that was sometimes found even with the servo arrangement described here (e.g. Fig. 14), in which the effect of shortening of the ends of the fibre is eliminated, may have been due to the residual irregularities of striation spacing within the part of the fibre between the markers. This interpretation is supported by the experiment illustrated in Fig. 14, which shows

![Graph](image)

**Fig. 14.** Servo-controlled tetani at the same length (mean striation spacing $3.83 \mu$), with various procedures in between. Experiment of 6 August 1963; $5^\circ$ C. Lower trace, tension; upper trace, position of right-hand marker except in C where it shows $\Delta L$. A, the first tetanus undergone by this fibre. B, 5 min later, with no stimulation or change of length since A. Between B and C, fibre released to $s = 3.73 \mu$, stretched to 3.93 $\mu$ and released to 3.83 $\mu$, without stimulation. Between C and D, fibre released to $s = 2.8 \mu$ and stretched again to 3.83 $\mu$, three times over, without stimulation. Between D and E, fibres given two tetani at $s = 3.52 \mu$ (note reduced amplification of tension trace in E). F, stimuli on same time scale. Sensitivity and speed figures refer to one grid square.

a series of tetani, all under servo control at the same length, with an average striation spacing of $3.81 \mu$. The treatment of the fibre between these successive tetani is described in the legend, and comparison of the tension records shows that the slow component of tension rise is greater in the second of two tetani with the muscle left alone in between (compare B with A) or with a tetanus at shorter length in between (compare E with D), while the slow rise was decreased if the fibre was passively released and stretched in between (compare C with B, and D with C). The first two procedures would be expected to increase, and the last to diminish, any irregularity of striation spacing.
Resistance to stretching

As mentioned in the Introduction (p. 144), Carlsen et al. (1961) concluded that sarcomeres stretched to a length where there is no overlap must either be capable of developing substantial tensions or else must undergo a large increase (order of fivefold) in their resistance to stretch. The results presented on pp. 155–160 show that only a very small amount of tension is developed so long as the length of the part of the fibre in question is held constant. The possibility of an increase in stiffness on stimulation was examined in experiments of two types.

Manual stretch. In the first, the rise of tension during a tetanus with the tendons held stationary was compared with the rise of tension when the same fibre was stretched, without stimulation, so that the part between the markers was extended by an equal amount. Records obtained in two such experiments are shown in Fig. 15. A and B show the tension developed in fixed-end tetani (lower traces) and the increase in separation of the

![Graph](https://example.com/graph.png)

Fig. 15. Comparison of tension increase during fixed-end tetani (upper frames) and during passive stretch of the same fibre without stimulation (lower frames). Upper trace: change in separation between the markers; lower trace: tension. A, C, E, experiment of 28 August 1963; mean striation spacing between the markers 3.92 μ at beginning of the records; temperature 4°C. Distance between markers 6.1 mm, so that one square of deflexion of the length trace represents 0.39% stretch. B, D, F, experiment of 20 September 1963; initial mean striation spacing 3.86 μ; temperature 3°C. Distance between markers 7.65 mm, so that one square of deflexion of the length trace represents 0.62% stretch. Sensitivity and speed figures refer to one grid square.

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markers (upper traces) due to shortening of the end parts of the fibre. In \( C \) and \( D \), the same fibres are stretched, without stimulation, by moving the 'motor stop' manually, and the same quantities, tension and separation of the markers, are recorded on the two traces. The manual stretch was carried out, as nearly as could be judged visually on the oscilloscope, at the same speed as the elongation during the tetanus.

Fig. 16. Graphs of tension increase against increase of length between the markers during fixed-end stimulation (crosses and full lines) and during passive stretch (circles and broken lines). \( A \), experiment of 18 March 1963, temperature 6° C, initial striation spacing 3.88 \( \mu \). +, tetanus of 2 sec duration (recorded only up to 0.5 sec); ●, passive stretch; ×, tetanus of 2 sec duration, in that order. \( B \), experiment of 20 September 1963, temperature 3° C, initial striation spacing 3.86 \( \mu \). +, tetanus of 1 sec duration (Fig. 15B); ○, passive stretch, at rather irregular speed; ●, passive stretch repeated (Fig. 15D). Tensions referred to cross-sectional area at 2.1 \( \mu \) striation spacing. Cross on tension axis shows tension in servo-controlled isometric tetanus at same length, extrapolated as in inset of Fig. 12.

In Fig. 16 the rise of tension is plotted against increase of distance between the markers for two experiments of this kind. It is seen that the points from each pair of records fall fairly well on a straight line, the tension dropping below the line as the speed of stretch decreases at the end. The lines referring to passive stretch of resting fibres pass through the origin, while those from fixed-end tetani have a finite intercept on the tension axis which in most cases agrees well with the tension measured at the same length in servo-controlled tetani. The slopes of the lines, which are a measure of the resistance to stretch, are collected in column 8 of Table 1.

In most experiments, the slope from a fixed-end tetanus was about 50% larger than that from passive stretch. This suggests that the resistance
### Table 1. Comparison of apparent stiffness of highly stretched parts of fibres, (a) during tetanic stimulation with tendons held and (b) unstimulated, with manual stretch.

<table>
<thead>
<tr>
<th>Date</th>
<th>Temperature (°C)</th>
<th>Striation spacing (μ)</th>
<th>Separation of markers (mm)</th>
<th>Cross-sectional area (μ²)</th>
<th>Isometric tension at optimum length (mg)</th>
<th>Tetanus duration (sec)</th>
<th>Maximum lengthening between markers</th>
<th>Slope of ( T-L ) plot (mg/mm)</th>
<th>Stiffness (kg/cm²)</th>
<th>Units of ( P_a/L_o ) as defined for table IV, column 2 of Carlson et al. (1961). Calculated as ( [(8 \times 3 \times 2.2)/2 \times (2 \times 5)] ).</th>
</tr>
</thead>
<tbody>
<tr>
<td>5. iii 63</td>
<td>6</td>
<td>3.96</td>
<td>10.8</td>
<td>14680</td>
<td>400 (est.)</td>
<td>2.5</td>
<td>0.3</td>
<td>396</td>
<td>29</td>
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</tr>
<tr>
<td>18. iii 63</td>
<td>6</td>
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<td>8.2</td>
<td>11320</td>
<td>280</td>
<td>2*</td>
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<td>362</td>
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<tr>
<td>29. vii 63</td>
<td>4</td>
<td>3.76</td>
<td>9.3</td>
<td>4670</td>
<td>137</td>
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<td>0.13</td>
<td>300</td>
<td>60</td>
<td>11.9</td>
</tr>
<tr>
<td>6. viii 63</td>
<td>5</td>
<td>3.83</td>
<td>7.7</td>
<td>5500</td>
<td>163</td>
<td>2</td>
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<td>213</td>
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<td>12. viii 63</td>
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<td>7.3</td>
<td>9950</td>
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<td>0.05</td>
<td>196</td>
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<td>7.8</td>
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<td>1</td>
<td>0.035</td>
<td>712</td>
<td>46</td>
<td>9.8</td>
</tr>
</tbody>
</table>

* Only the first 0.5 sec of this tetanus could be analysed, cf. Fig. 16.
of a fibre to stretch is increased in this proportion as a result of stimulation, but three other factors account for much of the difference.

1. In cases where two stimulated records (18 March 1963) or two resting records (20 September 1963) were made on the same fibre, the slope of the line was 10–20% less in the second than the first. In all cases except one the stimulated record was taken before the resting, so that this progressive decline in the slope would make the value for the resting case too low for comparison with the stimulated. In the one experiment (18 March 1963) where a second stimulated record was taken after the resting one, the slope of the resting line was intermediate between the values for the two stimulated ones, being very close to their mean.

2. In some cases (6 August 1963, 28 August 1963) the rate of elongation was appreciably less in the unstimulated stretch than in the fixed-end tetanus.

3. In the experiments of 5 March 1963 and 6 August 1963 there was a considerable slow rise of tension even in a servo-controlled isometric tetanus at the same length, probably due to the fact that the striation spacing showed wide variation even in the part of the fibre between the markers (these experiments were done before the full procedure described on pp. 154–155 had been worked out). If this tension rise is subtracted from that observed in the fixed-end tetanus, the slopes of the stimulated and resting lines become approximately equal.

It is not possible to say with any precision how much of the difference between the stimulated and resting slopes is due to these factors, but it seems unlikely that the resistance to stretch at speeds of this order is increased by more than 20–30% as a result of stimulation, and it is possible that the effect is much smaller.

*Square-pulse stretch.* The second type of experiment consisted in subjecting the fibre to a nearly instantaneous increase of length, through the servo control, and recording the tension, both with the fibre at rest and during a servo-controlled isometric tetanus. Records from three such experiments are shown in Fig. 17. The tension rise is greater during stimulation than at rest; measurements on the records are collected in Table 2. The measure of stiffness tabulated in columns 7 and 8 is directly comparable with that of Table 1, column 9. For each experiment which appears in both tables, the value derived from the manual stretch is repeated in column 9 of Table 2, and it will be seen that it lies between those for the initial rise and the final level of the square pulse stretch in every case except one of the values for the experiment of 20 September 1963, where the pulse duration was less than in the other experiments.

In all cases, the rise of tension is greater when the stretch was applied during stimulation than at rest, and there is a suggestion that the effect was larger as regards the initial rise than for the level at the end of the
pulse, though the figures for the latter are more uncertain because of the necessity for interpolating for the tension change that would have occurred in the absence of the stretch. The increases are about 1.3 times for the end of the pulse and about 1.5 times for the initial rise, except at the striation spacing of 3.77 μ on 20 September 1963, when the increase was 2.5–3 times.

![Fig. 17. Tension increase on extension of highly stretched fibres at rest (left) or during isometric servo-controlled tetanus at same length (right). Lower trace: tension; upper trace: in A and B, position of right-hand marker, in C, D, E and F, distance between markers. A and B, experiment of 6 August 1963, 5°C C, striation spacing 4.00 μ. C–F, experiment of 20 September 1963, 3°C C and D, striation spacing 3.86 μ; E and F, spacing 3.77 μ. Sensitivity and speed figures refer to one grid square.](image)

**DISCUSSION**

*Origin of tension in fixed-end tetani*

Our results confirm that a tension rise of about the magnitude seen by Carlsen *et al.* (1961) does occur during a tetanus in a fibre held with the ends stationary, even when it is stretched so far that presumably there is no overlap of filaments in the main part of the length of the fibre. We found, however (Fig. 7), that this tension was reduced to a small fraction when we excluded the effects of shortening in the ends of the fibre where substantial overlap of filaments existed, and also (Figs. 15–17, and Tables 1 and 2) that, if stimulation causes an increase in the resistance to stretching, this increase is of a smaller order of magnitude than the five- or sixfold rise suggested by Carlsen *et al.* These results appear to us to show that the large tensions recorded in fixed-end tetani in these highly stretched fibres are...
Table 2. Results of square-pulse stretch experiments on highly stretched fibres (compare Fig. 17)

(3) Time from first stimulus of tetanus to beginning of pulse.
(5) Increase of striation spacing produced by the pulse.
(7), (8) and (9) Stiffness calculated in same way as in column (9) of Table 1.
(7) From initial peak in tension record.
(8) From level of tension record just before end of pulse.
(9) During manual stretch: values from column (9) of Table 1.

Between the two pairs of records on 12 August 1963, the fibre underwent an isometric tetanus at striation spacing 2.9 μ, and was passively stretched and released in the sequence (μ): 3.91–2.9–3.91–2.9–3.91–3.55–3.91–3.55–3.91–3.55–3.91.

After the first pair of records on 20 September 1963 the fibre underwent an isometric tetanus at striation spacing 3.77 μ.

In every case, the ends of the pulse were rounded with a time constant of 5 msec.

<table>
<thead>
<tr>
<th>Date</th>
<th>Temperature (°C)</th>
<th>Striation spacing (μ)</th>
<th>Time of start (sec)</th>
<th>Duration (sec)</th>
<th>Amplitude (μ/sarcomere)</th>
<th>Stimulated or resting</th>
<th>1st peak</th>
<th>Final level</th>
<th>Manual stretch (Table 1)</th>
</tr>
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<td>5. iii. 63</td>
<td>6</td>
<td>3.96</td>
<td>0.65</td>
<td>0.39</td>
<td>0.017</td>
<td>S</td>
<td>34</td>
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<tr>
<td></td>
<td>3.96</td>
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<td>R</td>
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<td>0.0135</td>
<td>S</td>
<td>54</td>
<td>38</td>
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</table>
due to shortening of the ends of the fibres, as suggested by A. F. Huxley & Peachey (1959, 1961) without any large change of properties in regions where there is no overlap of filaments. Objections to the sliding filament theory based on tension development in highly stretched fibres with the tendons held stationary are therefore not valid. Our results do, however, suggest that tension development and stiffness increase of an altogether smaller order of magnitude do occur; these are discussed in the next section.

The point where there is a direct disagreement between our results and those of Carlsen et al. (1961) is that we found that the tension rise in a fixed-end tetanus is almost completely accounted for (within a factor of 1.5 x) by the stretching of parts of the fibre with no overlap, while Carlsen et al. claimed that the tension rise expected from this stretching (assuming no change of properties on stimulation) was only 15–20% of that observed. A large part of this discrepancy is in the values for the resistance to stretch of the unstimulated fibre. Column 10 of our Table 1 is expressed in the same units as column 2 of Carlsen et al.’s table IV; our values for unstimulated fibres (for stretch at about the speed which occurred in the fixed-end tetani) are about five times larger than Carlsen et al.’s for the static stiffness, while the multiplying factor used by Carlsen et al. to convert the static figure to the ‘semidynamic’ conditions in a tetanus was only 2.

The corresponding values for stiffness in the stimulated fibres can be obtained from Carlsen et al.’s table IV by dividing each figure in their column 3 by the product of the figures in the same row in columns 1 and 4; the results are a little larger—averaging about 1.35 times—than those for stimulated fibres in column 10 of our Table 1. This may well be a real difference, since we took extreme precautions to avoid irregularities of striation spacing in the part of the fibre between the markers, and any irregularities sufficient to produce overlap would cause an increase in the apparent stiffness on stimulation.

Residual tension development in fibres at extreme length

Although at spacings above 3.65 μ, where no overlap of filaments is to be expected, the tensions we recorded in servo-controlled isometric tetani were of a smaller order of magnitude than are observed when the tendons are held stationary, we did, nevertheless, record detectable tensions up to striation spacings of 3.8 or 3.9 μ. These records always included a rapid component with roughly the same time course as in a tetanus at the optimum length, and sometimes also a slow component which rose throughout the period of stimulation employed by us. The slow component may reasonably be attributed to the presence of residual irregularities of striation spacing, so that overlap still existed at some points between the markers; such parts
of the fibre would be expected to shorten slowly and cause a corresponding rise of tension as suggested by Hill (1953), the effect being similar to the rise of tension due to shortening of the ends of the fibre in a tetanus with the tendons held stationary, which is likewise slow. Evidence strongly supporting this interpretation was presented on p. 160, and irregular shortening of the kind required for this explanation was observed directly under the microscope by A. F. Huxley & Peachey (1961, p. 157 and Pl. 2). It seems to us, however, that any tension rise due to effects of this kind would necessarily have a slow time course, and that therefore the relatively fast component cannot be explained in this way. Further evidence for the reality of the fast component is provided by graphs such as are shown in Fig. 16, plotting tension increment against increase in separation of the markers. For unstimulated fibres the lines pass satisfactorily through the origin, but for stimulated ones they extrapolate back to an amount of tension about equal to that which appeared in a servo-controlled tetanus at the same length.

Several possible explanations for this fast component suggest themselves and are listed below, but there does not appear to be any evidence at present on which to reach a firm conclusion about its origin.

1. Irregular positioning of filaments within a fibril, or existence of filaments of greater length than normal. The occasional overlap that might exist from these causes would not be expected to increase slowly and progressively if the fibril structure is rigid enough.

2. The thick filaments are tapered at their ends (H. E. Huxley, 1957, 1963). Although it is not evident in the published pictures of H. E. Huxley (1963), it is possible that the number of bridges per unit length may decrease as the filament gets thinner. The tapering appears to extend over about 0.1 μ at each end of the filament; its effects would therefore be likely to spread over about 0.2 μ of striation spacing.

3. There may be a length change in one or other of the filaments, associated with activation, though if this were the explanation it is not clear why the tension rise should disappear at striation spacings above about 3.9 μ.

The small increase of stiffness which is suggested by the observations described on p. 164 may be associated with the same cause as the residual tension increase.

REFERENCES


Tension development in highly stretched vertebrate muscle fibres
A. M. Gordon, A. F. Huxley and F. J. Julian

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