

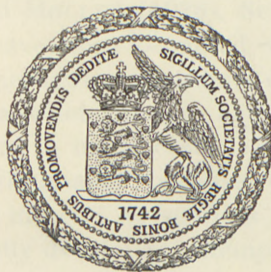
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THE MECHANICAL PROPERTIES OF  
THE SINGLE STRIATED MUSCLE FIBRE  
AT REST AND DURING CONTRACTION  
AND THEIR STRUCTURAL  
INTERPRETATION

BY

FRITZ BUCHTHAL



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## Introduction.

The mechanical properties of the muscle may primarily be expressed by means of length-tension diagrams registered either statically or dynamically. In static experiments, consolidated tension values are registered as a function of stretch. In dynamic experiments, the simultaneous variations of stretch and tension are recorded. The results obtained are a source of valuable information concerning elasticity, viscosity and plasticity of a muscle as a function of length and time.

The first investigations by E. WEBER (1846) deal exclusively with the static properties of the muscle. However, the importance of the dynamic properties was discovered very soon, as may be seen from numerous papers by LUDWIG (1858), VON KRIES (1880), FICK (1882), and BLIX (1895).

After a period of rest of about thirty years, these problems were resumed in 1924 by GASSER and HILL who drew our attention to the quantitative relations of the elastic and the viscous phenomena.

Besides GASSER and HILL, also BECK (1923), STEINHAUSEN (1926), LINDHARD and MØLLER (1926), SULZER (1930), REICHEL (1934), and others have been occupied with the study of the static and dynamic mechanical constants of the muscle. At that time, only work on a whole muscle had been found possible, and these investigations in many cases led to ambiguous or contradictory results, presumably because of the heterogeneous structure of the total muscle. As soon as the technique of preparation was sufficiently developed, attempts were made to study the mechanical properties of fibre bundles or of isolated fibres (SICHEL (1934), BUCHTHAL, KNAPPEIS and LINDHARD (1936), and ASMUSSEN (1936)). The results of these experiments are reported in a summarizing discussion by BUCHTHAL and LINDHARD (1939).

The above mentioned investigations deal exclusively with the static mechanical properties of the fibre, such as length-tension diagrams, and the length of the individual components of the fibre as a function of stretch.

The registration apparatus available at that time did not allow a more complete and precise mechanical analysis of the static and dynamic properties of the muscle fibre. It is, therefore, the aim of the present work to study by means of suitable apparatus the elastic properties of an isolated muscle fibre at rest and during contraction. These properties are investigated by means of length-tension diagrams which represent static stiffness, plasticity, and work-capacity. Furthermore, dynamic stiffness and viscosity are investigated by means of periodic and rapid single length alterations as a function of stretch or loading.

The static experiments are carried out both on the whole fibre and on its anisotropic and isotropic parts, while such a differentiation has not yet been possible in dynamic experiments.

## Method.

**Preparation:** The experiments were carried out on isolated fibres of the frog's m. semitendinosus. Both summer frogs and winter frogs were used (and also the two species *Rana esculenta* and *Rana temporaria*). The m. semitendinosus is especially suited for the present experiments, since all the fibres continue through the total length of the muscle from tendon to tendon and are of uniform cross section in the medial portion of the muscle. A number of comparative experiments were performed on small bundles containing 2 to 8 fibres.

It was found to be of great advantage to kill the frog one day before the muscle is to be used in experiments, since irritability fluctuations which always appear in freshly prepared muscles could be avoided in this way. Preparations showing marked fluctuations of irritability at the beginning of the experiment were discarded so that the irritability of the preparations used in the present experiments was constant throughout the whole period of experimenting. The preparation was made in an ice-cooled Ringer solution with constant  $p_{\text{H}}$  7.2—7.3. In some



of the experiments, the temperature of the Ringer bath containing the muscle during the experiment was kept constant by circulation and was continuously thermoelectrically verified. (12—14° C.)

The hydrogen ion concentration of the Ringer solution was found to be of decisive importance for maintaining constant irritability during a long period of time. Therefore, a stream of a CO<sub>2</sub>—O<sub>2</sub> mixture was passed through the Ringer solution, the CO<sub>2</sub> together with the bicarbonate of the Ringer solution thus guaranteeing a constant p<sub>H</sub> which was checked regularly by means of a glass electrode.

In the first series of experiments, a suitable colloid-osmotic pressure in the Ringer solution was attained by adding dialyzed 6 per cent gum arabic. Since, however, the commercial gum preparations contain varying amounts of K and Ca, and as it is not known how many of the cations can be bound by the gum arabic solution, a dialysis with repeatedly renewed Ringer solution becomes necessary in order to secure the right cation concentration. (Dialysis in cellophane bags, 30 hours, gum concentration 6 per cent, determined refractometrically.) In later experiments, this rather complicated operation was replaced by adding another high molecular substance, chemically well defined, viz. Polyviol Am., 1.35 per cent, osmotic pressure: 110 cm of H<sub>2</sub>O, (Polyvinyl alcohol), a substance which in the doses necessary for these experiments does not noticeably affect the irritability or contractility of the fibre.

**Stimulation:** The stimulation of the preparation was direct or indirect with maximal stimuli and the method of stimulating had no influence on the shape of the length-tension diagrams or the elasticity determinations. The height of the threshold value or application of curarine allows us to differentiate whether the stimulation works directly or through the end plate. As stimulating electrodes, two stainless steel tweezers were applied to hold the tendon ends of the fibre. A few control experiments were carried out with large platinized platinum electrode plates, placed along the fibre (cf. SICHEL and PROSSER (1940)). In the present experiments where the intensity of the stimulation mostly was considerably above the threshold value, no different effects of the various stimulating electrodes could be observed.

A thyatron arrangement was used for the stimulation; the



shape of the stimulating impulses, their duration, strength, and frequency could be varied. The rectangular current impulse of a duration of 2—4 ms was used most frequently. (For a more detailed description of the stimulation device I refer to a later publication.)

By means of repeated controls it was insured that there was no stimulus escape to the registration device.

**Microphotography:** The results of tension- and elasticity measurements may be correlated with the mechanical properties of the different elements of the fibre, if the length and the length alterations of the fibre under various exterior influences and during contraction are known. Therefore, the fibres were microphotographed at rest, during contraction at various extents of stretch and during release from isometric contraction to the same tension as at rest ("release contraction"). In all essential points, a similar technique was applied as described formerly by BUCHTHAL, KNAPPEIS and LINDHARD (1936). As the preparation technique has been further developed since that time, it is now possible to take series of microphotographs of the same preparation at rest and during contraction at a continuously varying stretch.

**Microscope optics:** Objective Apo 70, water immersion, NA. 1.25. Ocular: 10 ×, Zeiss Focu, magnification 350 times. Film: Ilford Pan Hypersensitive. Time of exposure about  $\frac{1}{5}$  sec. In some experiments, a water-cooled Philip's Super High pressure Hg lamp (effective intensity 15000 Lumen) was used as a light source; in most registration experiments, however, a Wolfram arc lamp (5 amps.) was applied.

The photographs during isometric contraction or release were not taken before the fibre had become consolidated in the new state (i. e. about 0.3—0.5 sec. after the beginning of the stimulation). As far as possible, double exposures were taken in all experiments. The negatives were measured by means of a measuring microscope. The measurements included the height of the anisotropic (A) and the isotropic (I) substances and of the total height of compartments (A + I) of 10 to 20 compartments of the microphotogram (magnification of the measurements about 10 times).

**Condenser arrangement for the registration of the tension:** The tendon ends of the muscle fibre were fastened to a pair of micro tweezers each. These micro tweezers (Fig. 1)

were made of phosphor bronze or steel wire, 0.8 mm. in diameter, and their prongs pressed together by moving the ring *a*; the tendon was thus held in the tweezers without danger of displacement.

The micro tweezer (1) (cf. Fig. 2) was in direct contact with the earthed and movable condenser plate (2) whose distance from the other fixed condenser plate (3) was reduced as soon as the fibre was stretched. The tweezer (1) was held by two steel springs (4 and 5), (7.0 mm. broad, 0.11 mm. thick), the stiffness

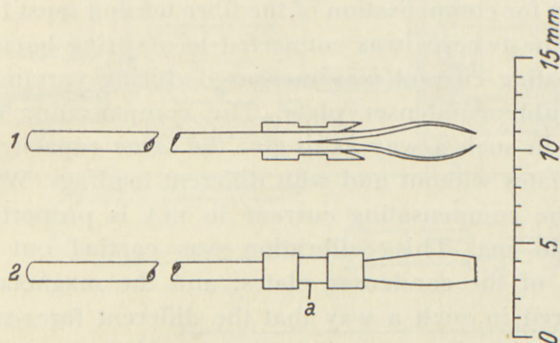


Fig. 1. Micro tweezer to hold the tendon of a muscle fibre. The prongs are pressed together by a movement of (*a*).

(1) side view; (2) viewed from above.

of which may be altered by varying their effective length. These two springs did not only provide the necessary stiffness but they guaranteed furthermore a parallel movement of the tweezer and the condenser plate. The distance between the condenser plates is one of the factors which determine the tension sensitivity of the arrangement and could be varied by moving the slide (6) which served to move forward and backward the micro tweezers, the condenser plate, and the springs. The non-earthed condenser plate was shielded against exterior capacitive disturbances and stimulus escape (7).

During stronger stretching of the fibre, the distance between the condenser plates would be decreased considerably, which might effect the sensitivity of the arrangement. Therefore, it was necessary to maintain a constant distance between the plates by means of a counter-force. The movable condenser plate (2) was provided with a coil (8) (40 windings, wire diameter 0.1 mm.)



which moved in the air gap of a ring-shaped permanent magnet (9) of about 1000 Gauss, the coil and the magnet being arranged similarly to those in a loud-speaker system. By varying the current in the coil, the latter together with the movable condenser plate was drawn with variable force over the centre of the permanent magnet, and in this way we compensated the alterations in the distance between the condenser plates caused by extension or relaxation of the fibre.

As the loading of the fibre was measured in mg., the current necessary for compensation of the fibre tension must be calibrated in mg. The tweezer was connected to a spring balance and the compensating current was measured during varying loading of the movable condenser plate. The compensating current was adjusted in such a way as to give the same capacity of the condenser plates without and with different loadings. Within a wide range, the compensating current in mA is proportional to the loading in mg. This calibration was carried out at different positions of the condenser plates, and the magnetic field must be centered in such a way that the different force-strength constants (in mg/mA) are constant over a wide range (up to 5 mm.). The leads to the coil must be introduced perpendicularly to the direction of the motion as, otherwise, indefinable additional stiffnesses may appear. The magnitude of the compensation current and the impedance of the external circuit did not measurably affect the total stiffness and damping of the system.

The calibration of the spring-balance involved some difficulties, as this should necessarily take place with the spring in the same horizontal position as employed during the loading of the tweezer, without the weight of the spring proper playing any part in the deflection. A calibration by means of a torsion-balance was not feasible, since these instruments can only be used vertically, and a transformation of the loading would introduce essential errors. Therefore, an analytical balance was used for the calibration, the tongue of the balance being connected through a hair with the spring to be calibrated. Under loading of one lever of the balance, the tongue deflects from the equilibrium position and the spring of the spring-balance is spanned until the deflection of the tongue is compensated. The tension of the spring was produced by a side-movement of the



spring-balance which was placed on a movable slide. The position of the spring was read by means of a microscope and an ocular micrometer. In order to calculate the actual loading of the spring  $P_1$ , we must know the loading of one lever of the balance  $P$ ,

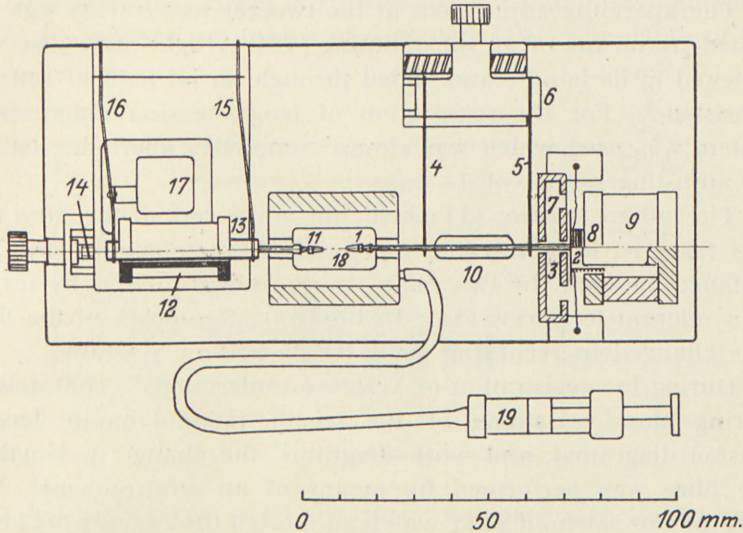


Fig. 2. Apparatus applied to the registration of length-tension diagrams and the measurement of dynamic stiffness.

- (1) micro tweezer;
- (2) movable condenser plate in connection with (1);
- (3) fixed condenser plate connected with the grid of the high frequency circuit;
- (4) and (5) steel springs to keep the tweezer (1) in position;
- (6) cog-wheel mechanism or micrometer screw to vary the distance between the condenser plates (2) and (3);
- (7) screen for the non-earthed condenser plate (3);
- (8) coil firmly attached to condenser plate (2);
- (9) ring shaped permanent magnet;
- (10) variable oil damping for tweezer (1);
- (11) micro tweezer to hold the other tendon end of the muscle fibre;
- (12) and (13) solenoid with iron core;
- (14) micrometer screw to vary the distance between (1) and (11);
- (15) and (16) strong steel springs to hold the iron core (12) in the axis of the solenoid (13);
- (17) oil bath to damp movements of tweezer (11);
- (18) chamber with Ringer solution;
- (19) syringe for changing Ringer solution in (18).

the distance between the point of application of the spring and the point of rotation of the balance ( $a$ ) and the point of application of the weighing pan ( $b$ )  $P_1 = \frac{P \cdot b}{a}$ . The measuring range of the calibrated spring-balance was 1—130 mgm.

Within a small range of loading, a compensation is not necessary, since loading and change in capacity are practically proportional. The stiffness of the system was regulated so that additional contraction tensions could be correctly registered.

The aperiodic adjustment of the tweezer movements was obtained by means of an oil damping (10). A light mica disc was fastened to its handle and slid through an oil bath of suitable consistency. For the registration of length-tension diagrams, a system was used which was almost completely aperiodic, having an adjusting period of 1—2 ms.

The micro tweezer (11) held the other end of the fibre and was fastened to a movable iron core of the solenoid (13). The distance between the two micro tweezers was altered by means of a micrometer screw (14). In this way, the length of the fibre was changed in recording static length-tension diagrams.

During the registration of "release contractions", contractions during slow variations of the length (semi-dynamic length-tension diagrams), and work diagrams, the change in length of the fibre was performed by means of an electromagnet. The core of the solenoid (12) which supported the tweezer (11) consisted of iron from the tweezer to the middle of the solenoid, and the rest of brass. By means of two strong flat springs, the core was kept in the axis of the coil. When the current in the coil (12) was varied, the iron portion of the core was drawn into the middle of the solenoid with a force proportional to the magnitude of the current. This current was calibrated relative to the movements of the tweezer by means of a measuring microscope and hence became a measure of the length alterations. A rheostat served to regulate the movement of the core, and these movements were damped by an oil bath (17). In the present arrangement, the movement of the tweezer was 12 mm. at the most. The length alterations were registered by means of a torsion band oscillograph (Fig. 3).

The original length of the fibre and—in static experiments—the increases in length were measured with a measuring microscope, the tubes of which can be moved horizontally over a range of 20 cm. The accuracy of the measurements is 0.01 mm.

For the measurement of the dynamic stiffness in vibration experiments, practically the same arrangement was used as for



the registration of length-tension diagrams. The springs 4 and 5 were replaced by two very long and soft springs. The period of vibration of the system was further increased by increasing the mass of the registering system.

The chamber (18) was filled with RINGER solution which could easily be renewed by means of a syringe (19). The depth of the

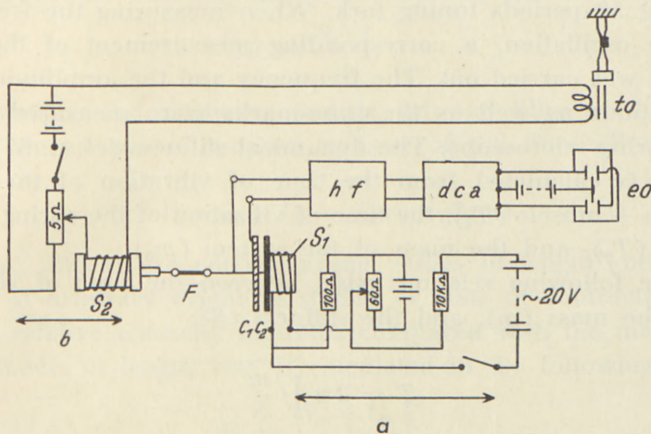


Fig. 3. Schematic diagram of the arrangement for recording tension and length variation.

(a) arrangement to compensate mechanical tension by the current in coil  $S_1$  (= (8) of Fig. 2); the same arrangement is used to give a sudden impulse producing vibrations in dynamic elasticity measurements.

$F$  = muscle fibre;

$C_1$  and  $C_2$  = condenser plates ((2) and (3) of Fig. 2);

$hf$  = high frequency apparatus;

$dca$  = direct current amplifier;

$eo$  = electrostatic oscillograph employed for the measurements of the variations in capacitance between  $C_1$  and  $C_2$ ;

(b) arrangement for varying the fibre length by means of an electromagnetic system ((12) and (13) of Fig. 2).

$S_2$  = solenoid;

$to$  = torsion oscillograph registering the current in  $S_2$ .

chamber was 0.5 cm. and even very markedly relaxed fibres were not in danger of touching the glass on the bottom of the chamber. In vibration experiments, it was found that the friction resistance of the RINGER solution can introduce a considerable error. Therefore, the RINGER solution was removed immediately before the vibration impulse occurred and was replaced later. In order to facilitate the adjustment of the fibre in the tweezers, an object slide was inserted directly beneath the tweezers while preparing took place.



The fibre and the registering arrangement were caused to vibrate by sudden current variations in the solenoid (8) (cf. Fig. 2). The different stretches at rest and during contraction were registered twice with four vibration impulses. The individual values are thus mean values from 8 determinations.

Simultaneously with the vibrations, time-marks were registered from a 50 periods tuning fork. When measuring the frequency of the oscillation, a corresponding measurement of the time-marks was carried out. The frequency and the amplitude of the oscillations as well as the time-marks were measured with a measuring microscope. The dynamical stiffness (cf. p. 67) of the object is calculated from the time of vibration of the spring system + muscle ( $T_1$ ), the time of vibration of the spring system alone ( $T_0$ ), and the mass of the system ( $m_0$ ).

The following relation exists between the time of vibration ( $T$ ), the mass ( $m$ ), and the stiffness ( $S$ ):

$$T = 2\pi \sqrt{\frac{m}{S}}. \quad (1)$$

For the calculation of the muscle stiffness ( $S_1$ ), the stiffness of the spring system ( $S_0$ ) and its mass ( $m_0$ ) must be known. The effective mass of the spring system was determined by measuring its natural time of vibration and the time of vibration ( $T'_0$ ) with a small additional mass ( $m'_0$ ).

On the basis of equation (1), we get the following relations:

$$T_0 = 2\pi \sqrt{\frac{m_0}{S_0}} \quad (2)$$

$$T'_0 = 2\pi \sqrt{\frac{m_0 + m'_0}{S_0}} \quad (3)$$

$$T_1 = 2\pi \sqrt{\frac{m_0}{S_0 + S_1}}. \quad (4)$$

Transposing  $m_0$ ,  $S_0$ , and  $S_1$ , we get

$$m_0 = m'_0 \frac{T_0^2}{T_0'^2 - T_0^2} \quad (5)$$

$$S_0 = 4\pi^2 \cdot m'_0 \frac{1}{T_0'^2 - T_0^2}. \quad (6)$$

The stiffness of the object ( $S_1$ ) is found as the additional stiffness of the system

$$S_1 = 4 \pi^2 \cdot m_0 \frac{1}{T_1^2} - S_0. \quad (7)$$

If the stiffness of the fibre, its length ( $l$ ), and cross section ( $q$ ) are known, the elasticity modulus ( $E$ ) may be calculated as

$$E = \frac{S_1 \cdot l}{q}. \quad (8)$$

Comparing the elasticity modulus of one fibre at different lengths we assume a constant volume of the fibre (Poisson's ratio = 2)

$$q_1 \cdot l_1 = q_m \cdot l_m = \text{fibre volume} \quad (9)$$

where  $q_m$  and  $l_m$  are corresponding values of length and cross section at arbitrary extent of stretch or state of contraction.

The relative elasticity modulus compared with the modulus, for instance, at length 100, is calculated in the following way:

$$E_m = \frac{S_m}{S_{100}} \left( \frac{l_m}{100} \right)^2 \quad (10)$$

where  $l_m$  is the length of the fibre in per cent of the equilibrium length,  $S_m$  the stiffness measured at  $l_m$ ,  $S_{100}$  the stiffness at equilibrium length, and  $E_m$  is the required relative elasticity modulus. Equation (10) gives a correction for length alterations and corresponding changes of the cross section during stretch and release contractions.

In every experiment, we register the vibration frequencies of the spring system + the resting fibre, of the spring system + the tetanically contracted fibre, and of the unloaded and the loaded spring system. It is of great importance that the length alterations imposed on the fibre are small (less than 1 per cent of the length of the fibre) and that they do not give rise to a mechanical stimulation. Furthermore, the stiffness of the system and that of the fibre should be of the same order of magnitude so as to enable the highest possible accuracy of the measurements. Working with springs which are very stiff compared with the muscle—as those used by GASSER and HILL (1924)—considerably reduces the difference in the time of vibration of the system with or without the muscle and, consequently, the accuracy of the measurements.



In the present experiments, the period of vibration of the system amounted to 200—300 ms. and its effective mass was 2—3 gm. If the stiffness is measured during contraction, a constant height of contraction during a longer period of time can only be maintained in a tetanus. It has been possible to register tetanic contractions of a single fibre of a duration longer than 40 sec. at practically constant level. In general, however, the shortest

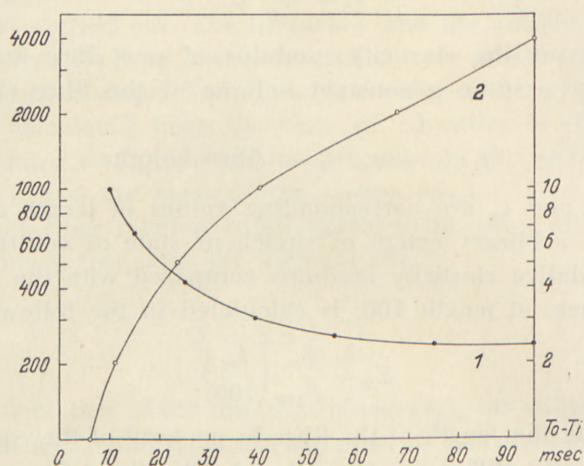


Fig. 4. Curve 1 = standard error in determination of stiffness as a function of oscillation period ( $T_0 - T_1$ ).

Curve 2 = stiffness as a function of variation in the oscillation period.

abscissa = variation of the oscillation period in ms;

ordinate = (to the right belonging to curve 1) percentage error;

(to the left belonging to curve 2) stiffness in dynes  $\text{cm}^{-1}$ .

possible contractions were applied, i. e. of a duration limited by the consolidation of the fibre. For the registration of the stiffness during release contractions, the fibre was brought to vibrate after being adapted to the release length during contraction.

Accuracy of the measurements: As mentioned before, the stiffness of the object was measured by determining the characteristic period of vibration of the system with and without the object. The uncertainty of the determination of the period of vibration or the variation measured of the system + object without exterior influences was found to be 2.5—3 ms when the period of vibration varied between 270—175 ms. The influence of this uncertainty on the calculation of the stiffness is illustrated



in Fig. 4 which shows the standard error of an individual point determined by seven measurements (Curve 1). It may be concluded from this figure that, at a difference of 10 ms. (stiffness 200 dynes  $\text{cm}^{-1}$ ), the standard error of the stiffness determination amounts to 10 per cent, corresponding to 20 dynes  $\text{cm}^{-1}$ . The error in per cent decreases with increasing stiffness and amounts to less than 3 per cent if the measured stiffness is above 1000 dynes  $\text{cm}^{-1}$ . The standard error is then 30 dynes  $\text{cm}^{-1}$ . In the present experiments, stiffnesses between 400–5000 dynes  $\text{cm}^{-1}$  are determined, i. e. the experimental error is between 2.5 and 5 per cent.

High frequency arrangement for the tension-registration: The changes in tension of the muscle fibre were registered as minute changes in length. These length alterations were measured as variations in the capacity of a plate condenser, the one plate of this condenser being connected

with the fibre and, at the same time, electrically connected to earth. The changes in capacity were measured by a high frequency arrangement, the principle of which has been described by ZAKARIÁS (1938) as especially suited for condenser microphones. The scheme of the circuit is given in Fig. 5.

An octode is connected with two tuned circuits. Grid 1 and grid 2 together with the first oscillating circuit which is coupled with the object form an oscillator, the frequency of which is given by the self induction  $L_1$  and the sum of the capacity of the object + the leads and the capacity of the variable condenser  $c_1$ . When this circuit is oscillating, the current flowing through the valve oscillates in time with it. Grid 3 and grid 5 behave like screened grids and, hence, do not take part in the process mentioned. Grid 4, however, is influenced capacitively by the current impulses because of space charge capacities and is affected as if a negative capacity was introduced between grid 1 and grid 4. Grid 4 is connected with a circuit  $L_2c_2$  which is

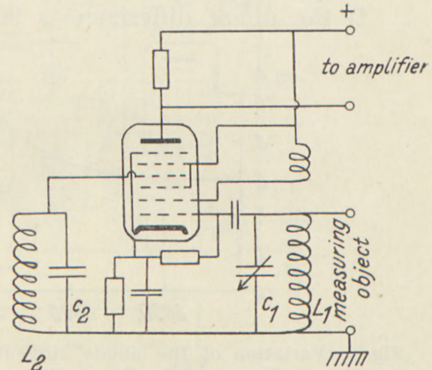


Fig. 5. High frequency circuit for measuring small variations in capacity (explanation, see text, pp. 15–16).

tuned to the same frequency as the oscillator circuit. If the resonance frequency is the same as the oscillator frequency, the circuit  $L_2c_2$  acts as a resistance, the imposed high frequency potential on grid 4 having a phase difference of  $90^\circ$  relative to the potential of the oscillator. The resulting anode current in the valve depends upon the potential of the oscillator grid and grid 4 and, furthermore, on the phase difference between these two potentials.

If the phase difference is  $90^\circ$ , these two grids do not effect

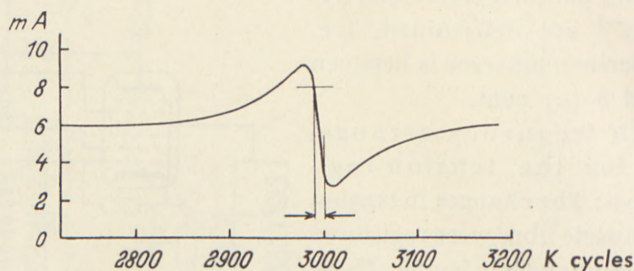


Fig. 6. Variation of the anode current (ordinate in mA) as a function of the frequency in the oscillator (abscissa in frequency/sec.).

the resulting emission of the plate. At a phase difference of  $0^\circ$ , the highest possible emission is attained, and at a phase difference of  $180^\circ$ , the plate emission is at a minimum, the grids counteracting each other. A frequency alteration of the oscillator will cause the circuit  $L_2c_2$  to cease acting as a resistance but as a capacity or an induction and, consequently, the high frequency on grid 4 will be phase-shifted either more or less than  $90^\circ$ , thus resulting in a smaller or greater anode current. The curve of Fig. 6 shows the variation of the anode current as a function of the frequency variation. Hence, the anode current reaches a constant mean value before resonance between the circuits is attained. The very low impedance of the circuit  $L_2c_2$  explains this fact. With the oscillator frequency approaching the resonance frequency of  $L_2c_2$ , the anode current increases, reaches a maximum (at a phase difference of  $135^\circ$ ), decreases again very rapidly, and passes the mean value (at a phase difference of  $90^\circ$ ). The decrease continues to a minimum at a phase difference of  $45^\circ$  and is followed by a slow increase in the anode current to its stationary value. The range between the maximum and the minimum is



especially suited for the measurement of minute changes of capacity, since a frequency variation of about half the resonance range is sufficient for optimum loading of the octode. The accuracy of the measurements with this arrangement is not limited

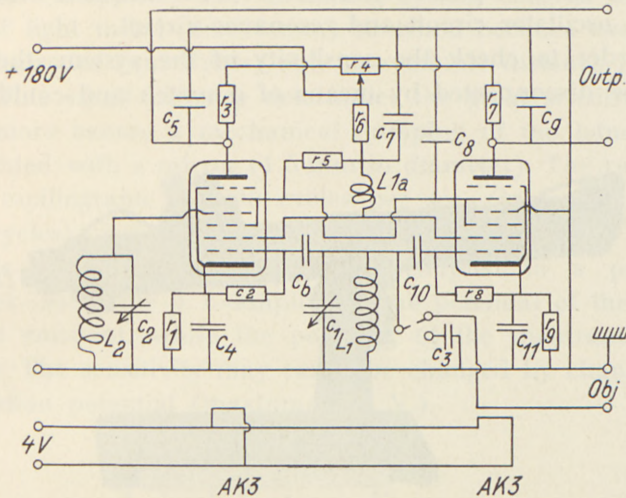


Fig. 7. Balanced high frequency circuit as used in the present investigation.

resistances.	condensers.
$r_1 = 300.$	$c_1 = 100 \mu\mu F.$
$r_2 = 0,2 \text{ meg. Ohm.}$	$c_2 = 50 \mu\mu F.$
$r_3 = 50 \text{ k Ohm.}$	$c_3 = \text{condenser for comparison.}$
$r_4 = 25 \text{ k Ohm (potentiometer).}$	$c_4 = 0.1 \mu F.$
$r_5 = 50 \text{ k Ohm.}$	$c_5 = 1000 \mu\mu F.$
$r_6 = 10 \text{ k Ohm.}$	$c_6 = 100 \mu\mu F.$
$r_7 = 50 \text{ k Ohm.}$	$c_7 = 0.1 \mu F.$
$r_8 = 0.2 \text{ meg. Ohm.}$	$c_8 = 0.1 \mu F.$
$r_9 = 300 \text{ Ohm.}$	$c_9 = 1000 \mu\mu F.$
	$c_{10} = 100 \mu\mu F.$
	$c_{11} = 0.1 \mu F.$

$AK_3 =$  indirectly heated four ray octode.\*

\* In more recent experiments, a directly heated heptode has been used with satisfactory results. In using this tube, a dry battery placed inside the apparatus may serve as a source of the filament current; one of the output terminals can be connected to earth.

by the electrical properties, but by the purely mechanical vibrations of the movable plates of the measuring condenser.

For the present purpose, the system was built in a balanced circuit, with two octodes and the oscillator parts in parallel (Fig. 7). One of the control grids was connected with the resonance circuit, the other control grids were earthed, the potential difference

between the two anodes thus being the desired measuring voltage. The potential difference is independent of temperature variations of the cathode within a wide range, and is furthermore independent of the anode potential and the high frequency potential of the oscillator. It depends exclusively on the frequency difference between oscillator circuit and resonance circuit.

In order to check the sensitivity of the system, the object could be disconnected by means of a switch and could be re-

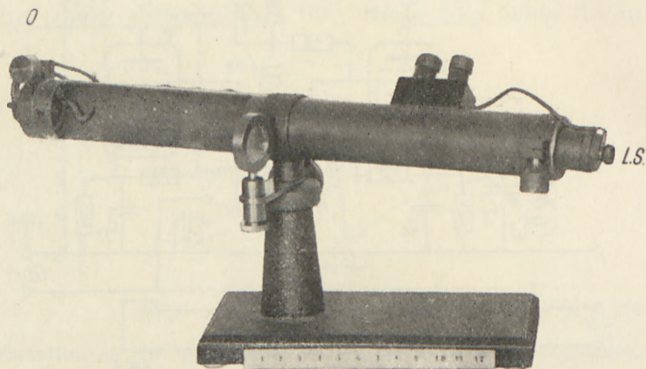


Fig. 8. Electrostatic oscillograph.  
L.S. = light source; O = oscillograph.

placed by a capacity. Since, however, minute capacity variations have to be measured, great stress must be laid upon keeping the capacity of the leads constant. The leads from the measuring condenser to the high frequency arrangement were placed concentrically into a metal tube and supported at numerous points in order to avoid vibrations and, consequently, capacity variations. The output potential of the high frequency system was led through a 1- or 2-stage d. c.-amplifier (BUCHTHAL and NIELSEN, 1936) to the oscillograph described below.

By means of a 1-stage d. c.-amplifier (70 times) the sensitivity can amount to a 1 mm deflection with a condenser movement of  $5 \cdot 10^{-3} \mu$ . (Distance between oscillograph and camera 60 cm.).

The movement of the condenser plate was registered by means of an electrostatic oscillograph. Originally, this oscillograph has been employed in a somewhat different form for sound-film recording according to BEER. The apparatus was adapted for biophysical application according to our suggestions.



Fig. 8 shows the apparatus in its present form with the light source placed in a fixed position on the stand of the oscillograph. The electrostatic oscillograph is a potential-sensitive mirror oscillograph, a type which is of special advantage for the connection to a valve amplifier. The oscillating system consists of a thin band of light metal (0.0015 mm) stretched between two sets of solid electrodes (quadrants) and at a minute distance from the latter. This small distance determines the great sensitivity and furthermore causes a mechanical damping of the band which is provided with a mirror (1.5 mm in diameter). The resonance of the oscillograph is 3000 cycles per sec. (increasable up to 5000 cycles), its sensitivity at a 60 cm registration distance amounts to 0.5—1 mm/volt. When coupled to a push-pull amplifier—as in the d. c.-amplifiers—the potential of the torsion band is constant, while the potential of the quadrants varies (Fig. 3). The sensitivity may easily be changed by changing the polarization potential (maximum 90 V.).

## Length-tension diagrams.

### Static length-tension diagrams.

#### 1) Rest.

The curve begins at a point corresponding to the equilibrium length of the fibre (length 100, Fig. 9a), i. e. the length where the fibre is just developing tension as a consequence of increased length. The increase in tension ( $t$ ) following the increase in length ( $l$ ) ( $\frac{\Delta t}{\Delta l}$  = static stiffness) increases with the extent of stretch over the whole range of the curve until the fibre is disintegrated. A stretching of the fibre up to a length of 200—220 per cent of the equilibrium length has been observed.

The stiffness measured in the beginning varies and depends—to some extent—on the sensitivity of the registering system, i. e. a more sensitive system would register a somewhat shorter equilibrium length, because an increase in tension would be noticed at an earlier stage. However, the uncertainty originating from this fact does not exceed 5 per cent of the “true” length of the fibre.

The slight incline of the curve in the beginning, at a stretch from about equilibrium length to length 130, must be interpreted as originating partly from a length-orientation of minute structure elements (micellae). This accords with BUCHTHAL and KNAPPERS' (1939) optical experiments which show an adjustment of the elements up to a stretch of 30 per cent. From that point an

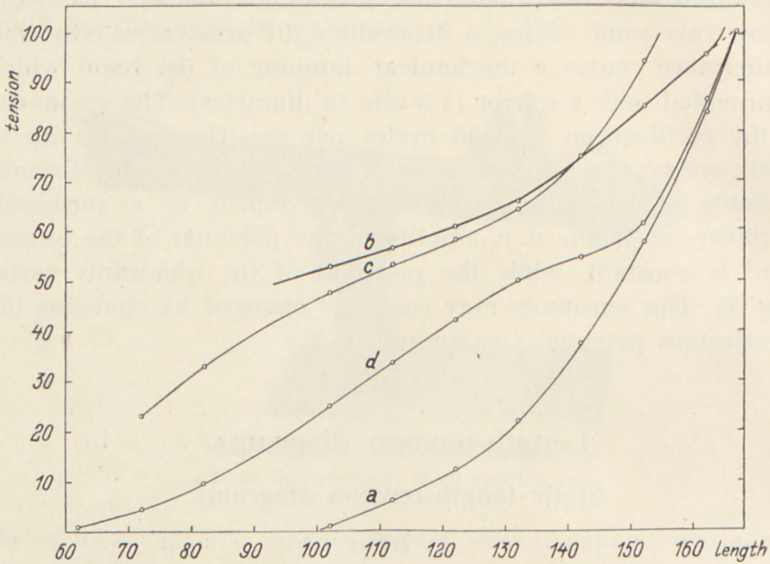


Fig. 9. Length tension diagram of the isolated striated muscle fibre.

(a) rest; (b) tetanic isometric contraction (fibre stretched at rest); (c) tetanic isometric contraction (fibre stretched during contraction); (d) release contraction (release to the same tension as at rest).

abscissa = length of the fibre (equilibrium length = 100);  
ordinate = tension in relative units.

obvious gradient increase appears, the micellae are adjusted and they cannot contribute further to the elasticity because of complete orientation. After this stretch, the curve represents the "true" qualities of the elements of the fibre. In agreement with ASMUSSEN'S (1936) experiments, stretching up to a length of 150 was found to be reversible. At higher extent of stretch, the increase in length was partly irreversible (plasticity).

## 2) Isometric tetanic contraction.

The isometrically contracted fibre develops a tension in equilibrium length (length 100) approximately corresponding to the



tension of a resting fibre at length 150 (Fig. 9*b*). With increasing length, the tension of the contracted fibre increases and generally the tension difference between contraction and rest is constant up to a length of about 140. At further stretch, the contraction tension is relatively reduced; rest and contraction curves approach each other and they meet at the length 160—200.

At a length above 160, the isometric length-tension curve exhibits a somewhat irregular course; the total tension changes its rising tendency rather suddenly, becomes constant, and may even be reduced in a range of about 10 per cent of stretch. Later,

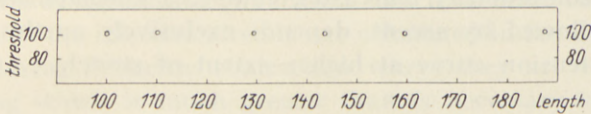


Fig. 10. Irritability of the directly stimulated fibre as a function of stretch. abscissa = length of the fibre (equilibrium length = 100); ordinate = threshold value in relative units (threshold of the non-extended fibre = 100).

the curve inclines rapidly. This deviation from the continuous course may be of different origin. A change in irritability of the fibre has been suggested as the cause (ASMUSSEN 1936). In a number of experiments the threshold value was constant up to lengths of 180—200. This observation proved to be true for directly (in some experiments curarized) as well as indirectly stimulated fibres (Fig. 10). As an indicator of the threshold value, the contraction of the single fibre visible under the microscope or sometimes the tension developed has been applied. The decrease in extra-tension at high extensions can therefore not be due to a change in irritability, as an increase in stimulation intensity, which was maximal at moderate stretch, does not inhibit the decrease in extra-tension during contraction at high extensions. When registering the length-tension diagram, stimuli being considerably above the threshold value were chosen.

The decrease in tension already described by BLIX (1892) is scarcely caused by fatigue. As supposed by BLIX, it may rather originate from reduced contractility during heavy loading or from reduced stiffness. In the case of the I substance, a reduced stiffness following the contraction could be observed, since under the same loading I is elongated during contraction when a certain

stretch is reached (cf. length-tension diagrams of the I substance, where the rest-curve and the contraction curve have a point of intersection at higher stretch; comp. Fig. 28.).

However, this small change of the length can scarcely explain the disappearance of tension (extra-tension) during contraction. The main cause of the reduced extra-tension must be found in a diminished contractility. A structural interpretation of this behaviour is given in a later section.

The total contraction tension during isometric contraction is = tension at rest + extra tension. Whether the contraction curve shows a continuously increasing course, a constant level, or a decline followed by ascent, depends exclusively on the slope of the extra-tension curve at higher extent of stretch.

### 3) Stretch of a tetanically contracted fibre.

During stretch of a tetanically contracted fibre, the curve corresponds up to length 160—in all our experiments—to the length-tension diagram of a fibre which is stretched at rest, and contracted isometrically (Fig. 9c). In this case, it is furthermore possible to register at a length below the equilibrium length, i. e. at length 80, a tension corresponding to the resting fibre at length 140 can be registered. Of course, the tension 0 must correspond to the shortest contraction length of the fibre.

In BECK'S (1923), SULZER'S (1930) and ASMUSSEN'S (1936) experiments, the muscle or small fibre bundles, respectively, show—when they are stretched during contraction to a length 125—a marked increase in tension, compared with that during isometric contraction at the same length. This difference increases with increasing stretch. In the present experiments, up to a length 150, it has not been possible to observe a difference between these two curves beyond the limits of the uncertainty of the measurements.

ASMUSSEN interprets the deviation as expressing an incomplete consolidation. In our experiments with single fibres, however, the adaptation must have been sufficiently accomplished.

The length-tension diagrams in which the increase in length occurs during the contraction itself do not indicate the above mentioned decrease in tension at higher extent of stretch, as



found in the isometric length-tension diagrams. If the already contracted fibre is stretched, the contractile elements adjust themselves to the maximum extent of contraction in the non-extended state, and they develop the highest possible tension when they are stretched.

For both types of length-tension diagrams during isometric contraction it must be emphasized that the curves are uniform, where the gradient variation is most marked in the curve of the resting fibre, thus indicating an orientation of the elements. This fact is in agreement with the optical experiments on muscle fibres already mentioned (BUCHTHAL and KNAPPEIS, 1939) which proved that the micellae already are orientated in the equilibrium length during isometric contraction where they are exposed to a loading which is much greater than is necessary to orientate the micellae at rest.

Therefore the change in direction of the curve (9c) at a length 140—150 cannot originate from a micellar adjustment. The relation between these phenomena and the minute structure will be discussed in a later paragraph (cf. p. 119).

#### 4) Release of the tetanically contracted fibre to the same tension as at rest.

During extension of the contracted fibre, a length-tension diagram is found which corresponds rather well to the length-tension diagrams during isometric contraction of a fibre stretched at rest. After release during contraction, however, quite different corresponding values of length and tension are observed (Fig. 9d). The tension developed in the release diagrams is much less than the tension at the same length during isometric contraction and in the stretched contracted fibre. Nevertheless, the tension is always higher than the tension at rest.

In a series of experiments, the length-tension diagram was registered in such a way that the fibre was released during tetanic contraction to the same consolidated tension as at rest. Obviously, this length is of special interest, since it offers the best possibilities of comparing the state of the fibre at rest and during contraction. The exterior mechanical conditions are the same and there is some reason to assume that the interior mechanical

situation of the fibre can best be compared with that of the resting fibre.

By means of the "compensation method" (cf. p. 8), it has been possible to register the shortest length of the fibre during contraction (contraction equilibrium length).

After release from isometric contraction at equilibrium length (rest) to the tension 0 during contraction, the single fibre was found to be shortened on average by 30 per cent. However, this is not the shortest length of the fibre during contraction since, during tensionless contraction, an average shortening of 45 per cent (limits 35—55 per cent) could be measured. This phenomenon has been investigated in greater detail in a special series of experiments in which the fibre was released from isometric contraction to the tension 0, then contracted in completely released state (in order to attain a tensionless contraction) and, finally, stretched until the beginning development of tension. These two lengths—at release contraction, where the tension ceases, and at tensionless contraction, where the developing tension begins—have been determined up to six times on the same fibre in different experiments. The difference is in full agreement with the material available which, at whatever extent of stretch above 100, showed less tension at the same length during release contraction than in any other "type of contraction". The difference may be explained by an "elastic locking" of the fibre at the maximum of the isometric contraction, an effect which will be analyzed more thoroughly in a later paragraph.

In some preliminary experiments on single contractions no similar phenomena could be observed. Also in these experiments, the fibre was released from the equilibrium length to that length where the peak-tension disappears; the completely released fibre was then stimulated and stretched until tension begins to develop. During release contraction a shortening of 33 per cent was found, during tensionless contraction the shortening amounted to 35 per cent. The explanation of the lack of any difference in the case of single contractions must be found in an interruption of the mentioned "locking" in between every stimulation.

Comparative experiments with fibre bundles (20—30 fibres) did not lead to unambiguous results as regards the difference in the shortening during release contraction and tensionless con-



traction. Here, the shortest length was 45—50 per cent of the original equilibrium length. However, the equilibrium length which was checked in between every experiment showed considerable variations—in contrast to the experiments with single fibres. These variations are presumably caused by deformation of the fibre originating from the connective tissue.

Especially in the older literature, we find some notes on the shortening of the total muscle of up to 85—90 per cent of the length at rest (WEBER 1846). These remarkable shortenings are certainly due to an incorrect definition of the initial length of the muscle. However, it is not improbable that the values found on total muscles can exceed the maximum shortenings found on the single fibre. It is well-known that the muscles most frequently used in physiological investigations contain fibres of considerably differing lengths (cf. LINDHARD'S (1926) measurements on *m. gastrocnemius* with length variations from 1.8 to 5 mm and on *m. sartorius* varying from 5 to 24 mm). From these facts it can be concluded that the muscle at an arbitrary stretch may contain fibres with far different degrees of stretch. Even at the length 100, it can be assumed that fibres may exist which are held in a stretched position by the supporting tissue of the muscle: e. g. a muscle bundle, 13 mm long, consists, for example, of fibres of an equilibrium length of 10, 13, and 16 mm, respectively. The shortening of the single fibre may amount to 30 per cent, which means that the single fibres are shortened to 7, 9, or 11 mm, respectively. The shortest fibre causes a curling of the others and, consequently, the total muscle is shortened to a length of 7 mm = 46 per cent.

During isotonic contraction with relatively small loading only part of the fibre material (the most stretched fibres) is able to work. Even when contracted, the rest will follow passively the length alterations of the muscle, as these fibres curl as soon as they have reached their shortest contraction length (cf. WEBER, 1846, and the author's own observations). During a higher extent of stretch, however, those fibres which are least stretched have to perform the greatest work, since the extra-tension of the most stretched ones has passed the maximum. In agreement herewith, the extensibility of the total muscle is considerably smaller than the extensibility of a single fibre. This phenomenon is not

only due to the reduced extensibility of the connective tissue but, first of all, to the inhomogeneous state of stretch of the single fibres.

In the first part of the curve (Fig. 9*d*), the shape of the length-tension diagram during release to the same tension as at rest corresponds accurately to the length-tension diagram at rest, apart from a length difference of 30 per cent. At stretch above 150 per cent, the contraction tension approaches the curve at rest (in agreement with the results from isometric curves) and runs parallel with it. At high extent of stretch, this curve and that at rest coincide.

The diagram of release contraction (tension under contraction = tension at rest) cannot be considered reversible, which means that every individual point can only be reached by producing continuous tetanic contraction and then releasing the fibre to the desired length. When the fibre is stretched in this state, the tension will rise above the curve, and on release, the tension will decline to lower values. This indicates: from every point of the isometric length-tension curve proceeds a special length-tension diagram connecting this isometric point with the corresponding release point. Hence, the curves of the isometric maxima and those of the release contractions (release to the same tension as at rest) differ essentially and are not reversible.

The phenomenon here described may be called an elastic "locking" of the fibre. In this state, the fibre follows only one among all possible length-tension diagrams at different release or stretch until the locking is broken off, for instance on account of a further stretch or interruption of the stimulation.

For further illustration of these length-tension diagrams, a number of experiments were carried out in which the tension was measured during isometric contraction, for instance at the length  $a$ , then at a length of  $(a + 1)$  mm. and released during contraction to the length  $a$ . The stimulation was then interrupted for a short time and—as a check measurement—the fibre was restimulated at the length  $a$ . The experiments were carried out at various extents of stretch. The release contraction reveals essentially less tension than the isometric contraction at the same length. The control contraction shows thereafter the same length as the contraction in the beginning.



In some cases, the control does not regain the original value, which presumably may be ascribed to fatigue of the fibre. These experiments seem to indicate that release contractions fatigue the fibre more rapidly than ordinary isometric contractions of the same duration.

Thus, the contraction process depends not only upon the stimulation but also on the external conditions under which the contraction occurs. This has already been stated by VON KRIES (1880); later, SEEMANN (1905) came to corresponding conclusions on the basis of experiments with length alterations during contraction.

At sudden release during contraction of the whole muscle, GASSER and HILL (1924) found that the resulting tension after consolidation is only a function of the instantaneous length and independent of the preceding length or of alterations of the loading. The curve of the isometric maxima should then be reversible which, however, is in disagreement with our experiments with release contractions on single fibres where the final tension—in spite of complete consolidation—does not reach the isometric maximum corresponding to this length. The first part of the tension decrease during “quick release” is, of course, caused by “viscosity”. However, the viscosity effect cannot explain the continuously lower tension during contraction in relation to the corresponding isometric maximum. Our differing observations on single fibres as compared with those of GASSER and HILL on total muscle might be due to a discontinuous activity of the individual fibre in the muscle. (A fatigued muscle fibre will cease to contract and will after restitution begin again with its isometric maximum). The rapidity of the tension development after release was found to be considerably less in SULZER'S (1930) and in our own experiments than found by GASSER and HILL, a fact which might indicate that the majority of fibres were in an unstimulated state in these experiments.

In experiments on total muscle, SULZER (1930) found a reversibility of the length- and tension alterations as long as a certain low loading was not exceeded. According to our interpretation, this observation is due to a tension too low to produce the locking (cf. p. 24); stop-contractions and support-contractions, as described by REICHEL (1934) in his experiments on total muscles, show a length-tension function which indicates clearly that the curve of the isometric maxima is not reversible. However, REICHEL'S correlation between the resting curve, the

curve for isotonic maxima, and the curve for isometric maxima is not correct, since it is based on experiments which show rather low extra-tension during contraction; furthermore, REICHEL assumes a linear dependence between isotonic shortening and initial length.

The locking after release from isometric contraction is not identical with the "catch mechanism" which appears in smooth muscle. It has often been attempted to transfer the observations on smooth muscles to cross-striated muscles. BECK (1923), for instance, thought he had demonstrated such a mechanism in cross-striated muscles. It is, however, not admissible to interpret the difference between the curves for the isometric maxima at long-lasting tetanic stimulation and the length-tension diagrams of the stretch of a tetanized muscle at short-lasting (0.1 sec.) tetani as a "catch mechanism" in the tetanic contraction. A tetanus lasting 0.1 sec. does not cause a full development of tension, it must rather be compared with a single contraction, the tension of which may amount to  $\frac{1}{3}$  of the tension during isometric contraction (cf. p. 33).

In contrast to the "catch mechanism", a "locking" can only be observed during release of a tetanized muscle fibre by a steeper partial length-tension diagram than the curve of the isometric maximum. Certainly, this steep diagram may continue above the curve of the isometric maximum, but only to about 5 per cent of the extra stretch; then, the curve bends sharply—the locking is broken—and the curve proceeds parallel with or overlapping the curve of the isometric maxima. While, in physiological respect, the "catch mechanism" would be a very economical procedure, this is not the case in the above described locking (cf. work diagrams with and without locking, p. 43).

On the basis of these release-length-tension diagrams, it becomes possible to draw some conclusions as regards the largest possible amount of work which a stretched muscle is able to perform during length reduction.

If the length reduction occurs during continuous stimulation, the work performed is but a fraction of the area between the resting curve and the curve of the isometric maxima of the muscle. If, however, the reduction of length occurs during repeated interruption of the stimulation, an isometric maximum



is reached at the start of the stimulation. The tension is then somewhat reduced, the stimulation is interrupted, and a new stimulation begins. In this way, the average tension of the fibre is held on a much higher level in spite of—or rather just because of—the interruptions of the stimulation.

The quantitative conditions are investigated more thoroughly in the registration of work-diagrams (cf. p. 43).

### Length-tension diagrams from single contractions.

#### 1) Single contractions at long time intervals.

The diagram of Fig. 11 represents the resting tension, the contraction extra-tension, and the resting tension + extra tension

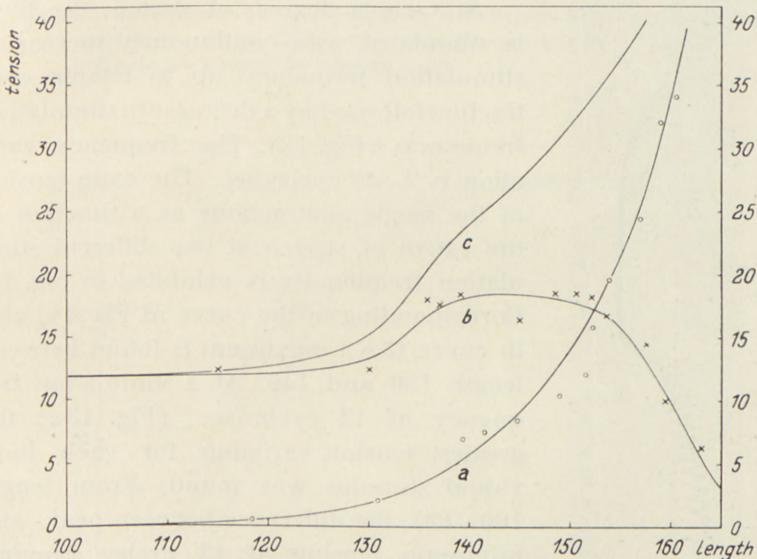
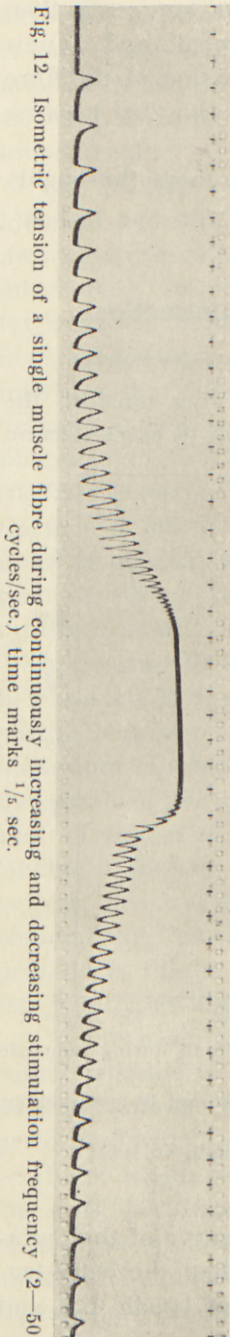


Fig. 11. Length-tension diagram of a single fibre at rest and during isometric contraction (single contractions).

(a) length-tension diagram at rest; (b) extra-tension produced by contraction; (c) initial tension + extra-tension.

abscissa = length of the fibre (equilibrium length = 100);  
 ordinate = tension in mgm.

(peak tension) as a function of length. The curve of the extra-tension is horizontal from length 100—130, then the extra-tension increases, reaches a maximum at about length 140 and



decreases again approximating 0 with increasing stretch. The maximum of the extra-tension indicates that in a single contraction the fibre has the greatest mechanical reaction at moderate stretch. The increase in extra-tension occurs in the same range of stretch where we must assume that the orientation of the elements of the fibre occurs and, thus, greater tension is transmitted to the tendon.

## 2) Single contractions at varying time intervals.

At various degrees of stretch, the fibre is stimulated with continuously increasing stimulation frequency up to tetanic contraction followed by a decrease in stimulation frequency. (Fig. 12). The frequency variation is 2—50 cycles/sec. The extra-tension of the single contractions as a function of the extent of stretch at two different stimulation frequencies is exhibited in Fig. 13. Corresponding to the curve of Fig. 11, also in curve 13*b* a maximum is found between length 130 and 140. At a stimulation frequency of 12 cycles/sec. (Fig. 13*a*) the greatest tension variation for each individual stimulus was found. From length 100—125, the difference between peak- and minimum tension at 12 cycles amounts to about twice the "pure" single contractions (Fig. 13*b*) with long time intervals. Fig. 14 shows the course of tension of a fibre in equilibrium length as a function of the stimulation frequency. The height of the single contractions (curve *a*) in the first range is equal to peak-tension minus rest tension. Gradually as the stimulating impulses follow more frequently, the fibre



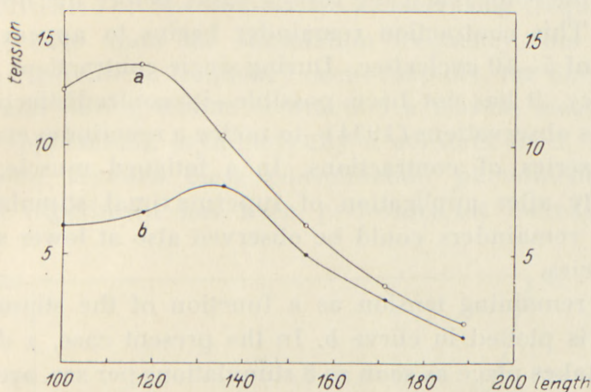


Fig. 13. Extra-tension (peak-tension) produced by single contractions of the isolated fibre as a function of stretch.

(a) stimulation frequency 12 cycles/sec.; (b) stimulation frequency 2 cycles/sec.  
 abscissa = length of the fibre (equilibrium length = 100);  
 ordinate = tension in relative units.

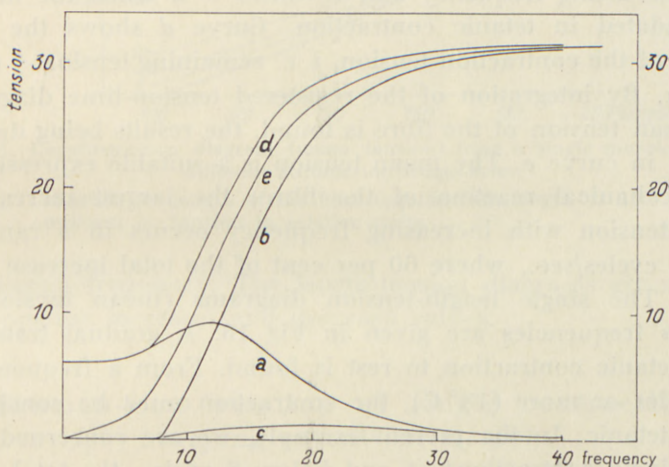


Fig. 14. Tension produced by a single non-extended fibre (length = 100) as a function of the stimulation frequency.

(a) height of the single contractions; (b) contraction remainder; (c) increase in contraction remainder per stimulus; (d) peak values of tension during contraction (contraction remainder + extra-tension); (e) mean tension.

abscissa = stimulation frequency, cycles/sec.;  
 ordinate = tension in relative units.

tension does not reach the resting value before the new stimulus begins. This contraction remainder begins to appear at a frequency of 5—10 cycles/sec. During single contractions at a lower frequency, it has not been possible—in contradistinction to ASMUSSEN'S observations (1934)—to notice a remainder even in long-lasting series of contractions. In a fatigued muscle, however, especially after application of supermaximal stimulation, contraction remainders could be observed also at lower stimulation frequencies.

The remaining tension as a function of the stimulation frequency is plotted in curve *b*. In the present case, a direct summation takes place as soon as 8 stimulations per sec. are exceeded. The increase of the remainder per stimulus as a function of frequency is shown in curve *c*. As is to be expected, the curve inclines up to 20 cycles, since the relaxation time is shorter at smaller stimulation intervals. However, this increase can only continue up to a certain limit, because the extra-tension is reduced with increasing frequency and becomes = 0 when the fibre is consolidated in tetanic contraction. Curve *d* shows the peak values of the contraction tension, i. e. remaining tension + extra-tension. By integration of the registered tension-time diagrams, the mean tension of the fibre is found, the results being demonstrated in curve *e*. The mean tension is a suitable expression of the mechanical reaction of the fibre; the largest increase in mean tension with increasing frequency occurs in a range of 10—20 cycles/sec., where 60 per cent of the total increase takes place. The single length-tension diagrams (mean tension) at various frequencies are given in Fig. 15. A gradual transition from tetanic contraction to rest is found. From a frequency of 30 cycles or more (18° C), the contraction must be considered to be tetanic. In the present example, we are concerned with pure single contractions at and below 8 cycles, the total mean tension being so low that the yield of work cannot be positive because of viscous loss. The principal variation range is between 10 and 30 cycles. At 8 cycles, where the intervals between the single contractions are so long that the rest tension may just be reached before the following stimulation begins (remainder = 0), the mean extra-tension amounts to  $\frac{1}{5}$  of the tension in tetanic contraction.



Consolidation: The summation at increasing frequency depends not only upon the stimulation frequency, but also on time. If the increase in frequency occurs rapidly, the fibre cannot "follow" and during tetanic contraction a tension may thus be observed approaching asymptotically a constant level. In order to take into account these consolidation phenomena, every individual experiment has been performed at increasing and

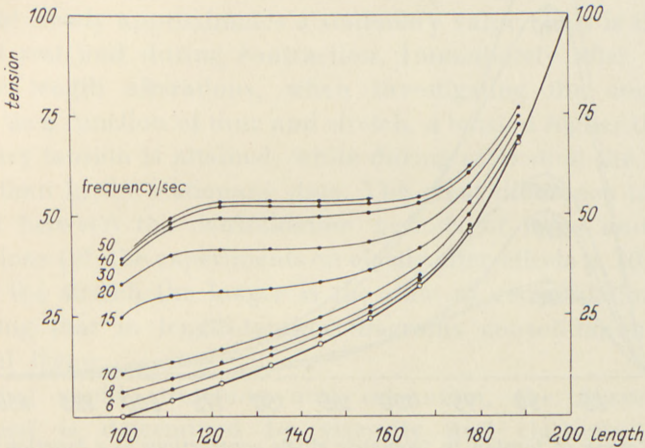


Fig. 15. Length-tension diagram (mean tension) from a single muscle fibre at different stimulation frequencies.

abscissa = length of the fibre (equilibrium length = 100);  
 ordinate = tension in relative units.

decreasing frequency. The length-tension diagrams given lie in between the increase- and decrease values.

3) Tension-time relation of single contractions at varying extents of stretch.

Fig. 16 shows the tension during isometric single contraction as a function of time. The peak extra-tension developed is reached 40 ms. after the first noticeable development of tension (temp. 18° C). The duration of the development of tension is not influenced by the extent of stretch as long as the fibre is not fatigued. The course of tension is considerably prolonged in tired fibres. The peak extra-tension is not highest at the equilibrium length (cf. length-tension diagram, Fig. 11), but increases

with increasing extent of stretch reaching a maximum at a length of 120—130.

At length 100, the duration of the relaxation from the peak extra-tension to half of its value lies around 30 ms and increases continuously to 50 ms at a length of 170—180. Correspon-

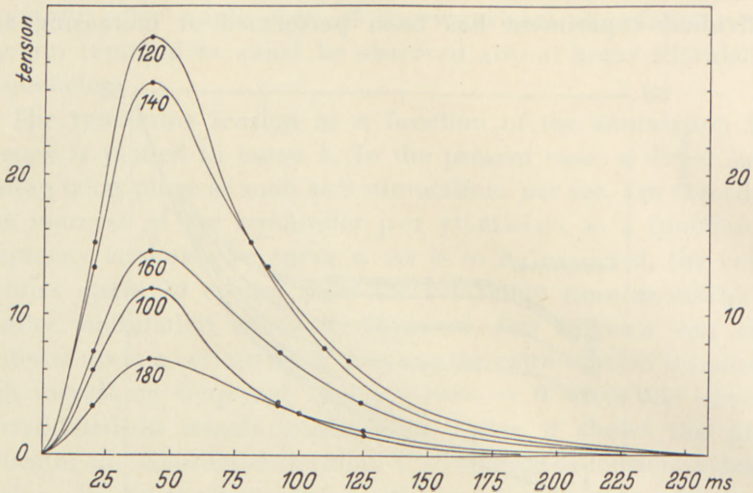


Fig. 16. Course of tension in isometric single contractions as a function of time; different extents of stretch (the figures below the curves indicate the length of the fibre).

abscissa = time in msec.  
ordinate = tension in relative units.

dingly, the distance from the peak extra-tension to  $\frac{1}{4}$  of its value increases from 55 to 80 ms.

### Semi-dynamic length-tension diagrams.

In static length-tension diagrams, the elastic properties of the fibre mainly determine the slope of the curves. It must, however, be emphasized that also other physical properties of the fibre are changed proportionally to the stretch and its duration. This may be proved by comparing the equilibrium length of the fibre before and after the experiment. The equilibrium length is generally increased by 10 per cent after stretch above a length 130—150. This change can be partially restored by allowing the



fibre to remain for some time in an unloaded state, but full restoration of the original length is not attained above length 150, which may be ascribed to an irreversible alteration (plasticity).

Hence, the static length-tension diagram does not give full information about the elastic properties of the fibre. By registering the fibre-tension developed simultaneously with the stretch, it was found that the tension does not immediately reach a constant level but slowly approximates a stationary value. This is the case both at rest and during contraction. Immediately after the respective length alterations, when investigating the course of tension as a function of time and stretch, a tension higher than the stationary tension is attained, while during relaxation the tension is less than in the stationary state. The great difference becomes evident between the consolidation periods of large and small elongations (cf. the experiments on elastic after-effects p. 102). The greater the stretch the longer is the time of consolidation, thus indicating that in length-tension diagrams consolidation is an essential factor.

During rapid stretching and relaxation, the fibre-tension developed is determined by viscosity and elasticity of the fibre, while the tension in static length-tension diagrams is given by elasticity and plasticity of the fibre. Hence, the most comprehensive information is derived from static curves combined with length-tension diagrams at varying rates (static, semi-dynamic, and dynamic experiments).

In static length-tension diagrams, the duration of an experiment is about 30 min. In semi-dynamic experiments, the time of duration of stretch for a total length-tension diagram varies from 10 to 1 sec, and in purely dynamic experiments, the duration of a small stretch amounts to 0.1—0.05 sec. On account of the considerably shorter experimental period, the semi-dynamic and dynamic experiments have the advantage of reducing fatigue or other drawbacks conditioned by the duration of the experiment.

Semi-dynamic length-tension diagrams of the whole muscle were investigated by BLIX (1892), FICK (1892), and SULZER (1930). In agreement with the majority of the subsequent investigators, BLIX found even in the resting muscle a difference between the

curves at stretch and those during relaxation, this difference increasing with the rate of stretch. He assumed the curve to be reversible, provided that the length alterations occur sufficiently slowly. Employing BLIX' method, FICK investigated the contracted muscle and he found also here a difference between the curve at stretch and the curve during release. In this case, the difference is so remarkable that it cannot be explained by the effect of viscosity alone; FICK, therefore, assumed an increase of irritability occurring during stretch and, consequently, an increase of tension. At stretch followed by release of a muscle during stimulation, SULZER—in agreement with FICK—does not notice any reversibility.

As already mentioned in the description of the experimental method, length and tension of the fibre were registered simultaneously by means of an electrical transmission (p. 10). The experiments may be classified in two groups: one series in which the fibre is stretched about 50—60 per cent in the beginning, is then released, and thereupon stretched again. In some experiments, stretch and release are repeated several times, beginning with small length alterations and continuing with increasing length alterations starting from the same original length. In other experiments, slight stretch and release are performed at different arbitrary lengths of the fibre.

#### 1) Semi-dynamic length-tension diagram of alternating stretch and relaxation at rest.

During stretch (Fig. 17), the tension of the fibre increases with increasing differential quotient. In the beginning, the release curves show a somewhat steeper slope than the stretch curves, a fact which must be ascribed to the viscous resistance of the fibre to length alterations. Completely relaxed fibres exhibit an equilibrium length which is a little greater than that before stretching. This change is reversible, and after a lapse of some time, the fibre will regain its initial length. However, in the present experiments, the intervals are not very long, a new stretch and release following almost immediately. The difference between corresponding stretch- and relaxation-curves and, on the other hand, between the different curves of stretch and relaxation,



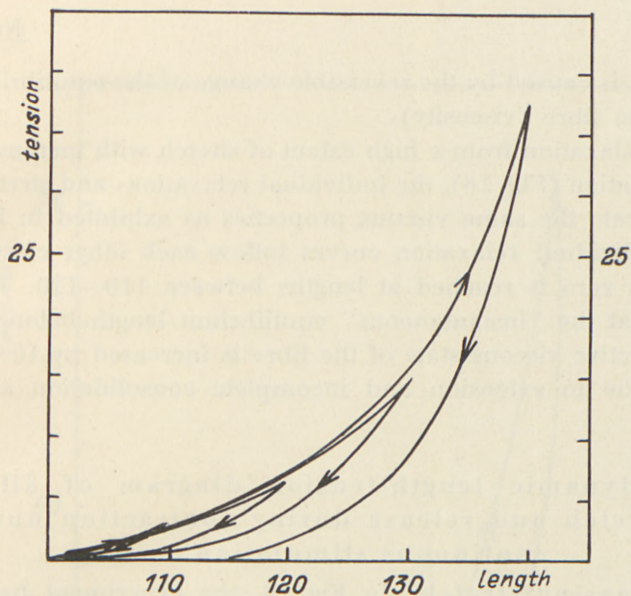


Fig. 17. Semi-dynamic length-tension diagram of the resting fibre; extension with following relaxation starting from length 100.  
 abscissa = length of the fibre (equilibrium length = 100);  
 ordinate = tension in relative units.

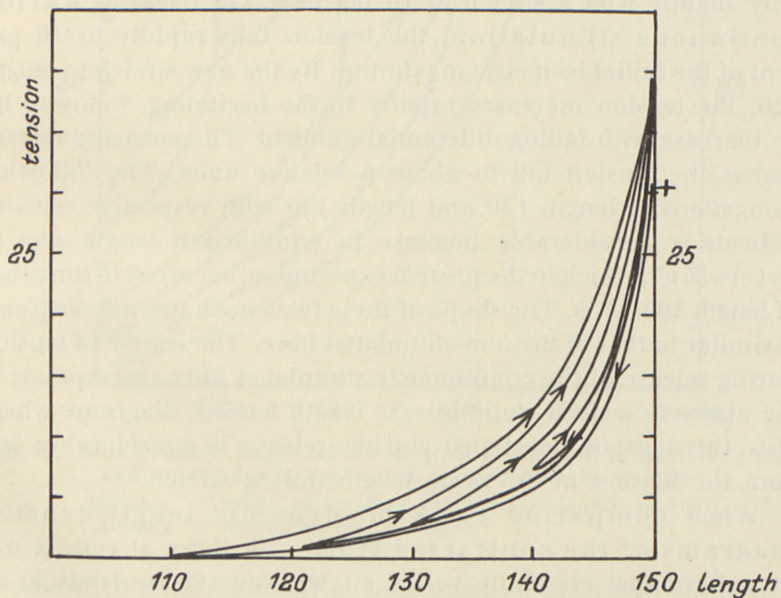


Fig. 18. Semi-dynamic length-tension diagram of the resting fibre; relaxation and extension starting from length 160.  
 abscissa = length of the fibre (equilibrium length = 100);  
 ordinate = tension in relative units.

respectively, is caused by the reversible change of the equilibrium length of the fibre (viscosity).

During relaxation from a high extent of stretch with increasing rate of relaxation (Fig. 18), the individual relaxation- and stretch-curves indicate the same viscous properties as exhibited in Fig. 17. The individual relaxation curves follow each other closely. The tension zero is reached at lengths between 110—120. This indicates that the "instantaneous" equilibrium length belonging to the respective viscous state of the fibre is increased by 10—20 per cent due to extension and incomplete consolidation after relaxation.

## 2) Semi-dynamic length-tension diagram of alternating stretch and release during contraction under continuous stimulation.

a) Increasing stretch: In Fig. 19, the experiment began from length 100 with a stretch of 10 per cent. The curve is markedly different from that representing stretch of the resting fibre. The tension in isometric contraction amounts to 33 units and increases only slightly with a stretch of 10 per cent. On releasing during continuous stimulation, the tension falls rapidly to 40 per cent of the initial isometric maximum. By the new stretch to length 120, the tension increases rapidly in the beginning, followed by an increase with falling differential quotient. The ensuing release makes the tension fall to about 6 relative units. The following elongations to length 130 and length 140 with respective releases indicate a considerable increase in equilibrium length due to "yielding", which in the present experiment, occurred in the range of length 100—130. The shape of these two length tension diagrams is similar to that of the non-stimulated fibre. The course of tension during release of the continuously stimulated fibre corresponds to the above described static release length-tension diagrams where also the tension developed during release is considerably less than the tension at the same length during stretch.

When comparing the semi-dynamic length-tension diagrams of the contracted fibre with those at rest, it will be noticed that gradually varied stretch and release leads to an essentially different course than do similar conditions at rest. During stretch after release from length 110—115 a steep ascent



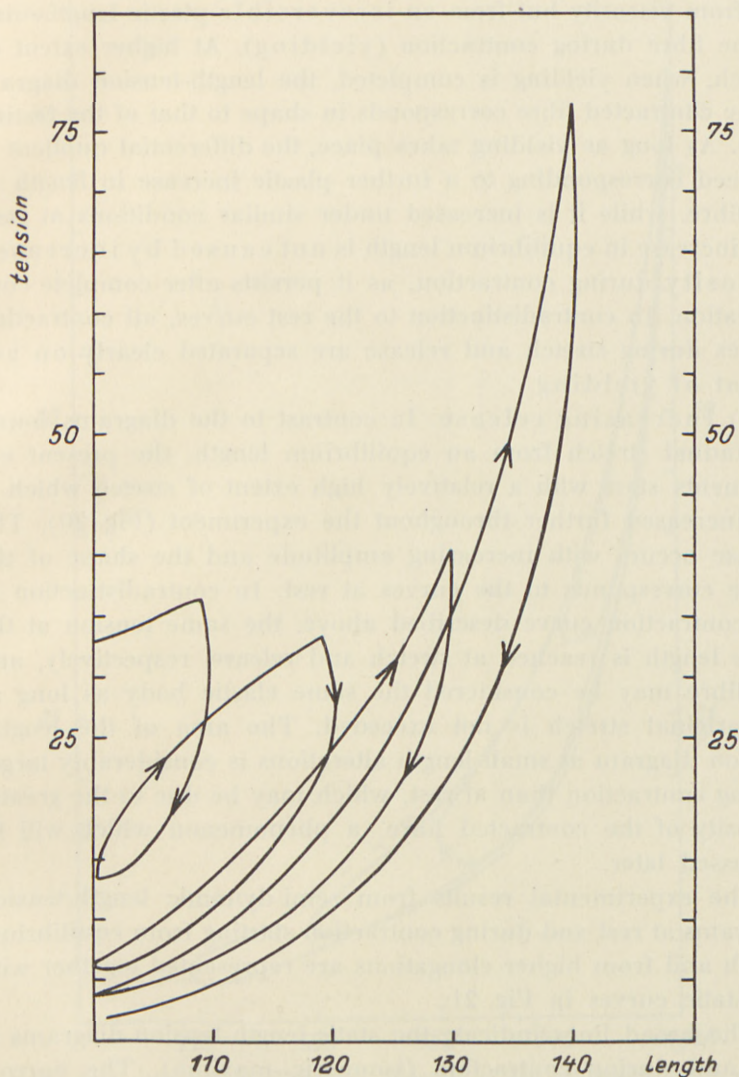


Fig. 19. Semi-dynamic length-tension diagram of the contracted fibre; stretch and release during contraction starting from length 100.  
 abscissa = length of the fibre (equilibrium length = 100);  
 ordinate = tension in relative units.

is found in the beginning, indicating an increased stiffness of the fibre. With further elongation, a reduction of the steepness is observed, in spite of the same rate of extension, originating

not from viscosity but from an irreversible plastic lengthening of the fibre during contraction (yielding). At higher extent of stretch, when yielding is completed, the length-tension diagram of the contracted fibre corresponds in shape to that of the resting fibre. As long as yielding takes place, the differential quotient is reduced corresponding to a further plastic increase in length of the fibre, while it is increased under similar conditions at rest. The increase in equilibrium length is not caused by increased viscosity during contraction, as it persists after complete consolidation. In contradistinction to the rest curves, all contraction curves during stretch and release are separated clearly on account of yielding.

b) Increasing release. In contrast to the diagrams found at gradual stretch from an equilibrium length, the present experiments start with a relatively high extent of stretch which is not increased further throughout the experiment (Fig. 20). The release occurs with increasing amplitude and the shape of the curve corresponds to the curves at rest. In contradistinction to the contraction curve described above, the same tension at the same length is reached at stretch and release, respectively, and the fibre may be considered the same elastic body as long as the original stretch is not exceeded. The area of the length-tension diagram at small length alterations is considerably larger during contraction than at rest, which may be due to the greater viscosity of the contracted fibre, a phenomenon which will be discussed later.

The experimental results from semi-dynamic length-tension diagrams at rest and during contraction starting from equilibrium length and from higher elongations are represented together with the static curves in Fig. 21.

The broad lines indicate the static length-tension diagrams at rest and during contraction (isometric maxima). The narrow lines around the lowest curve show a semi-dynamic length-tension diagram at rest, and the narrow lines of the upper system represent the semi-dynamic curves from a contracted fibre gradually stretched and released at continuously increasing stretch. The arrows denote whether the experiments are carried out starting from equilibrium length or from greater stretch. It is apparent that the release curves during contraction are of a



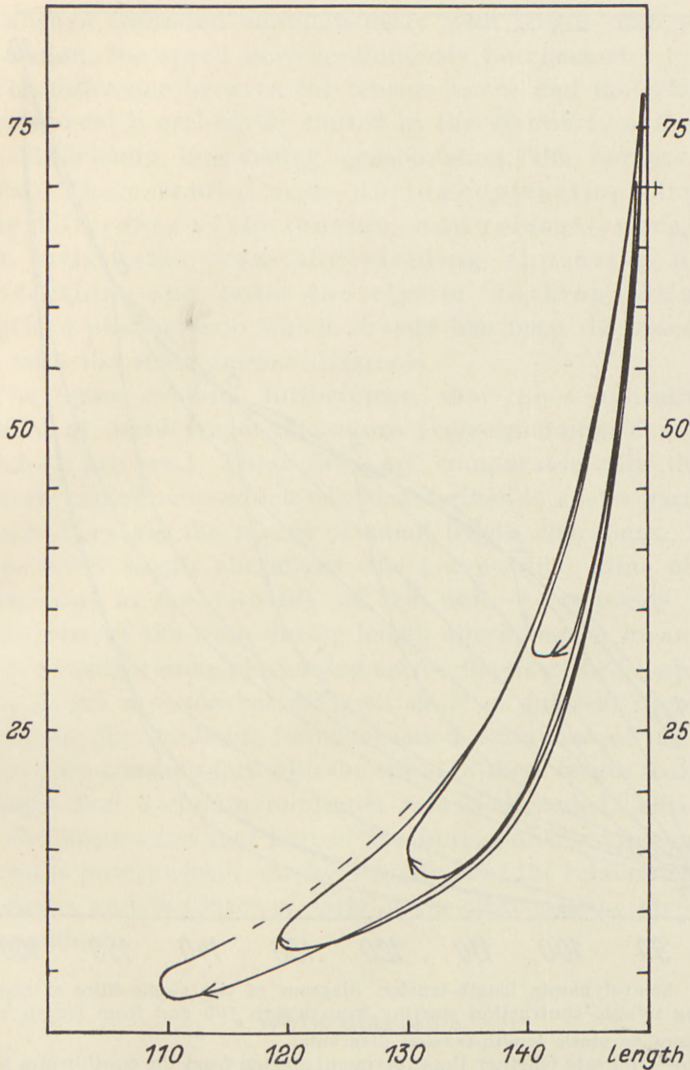


Fig. 20. Semi-dynamic length-tension diagram of the contracted fibre; release and stretch starting from length 150.

abscissa = length of the fibre (equilibrium length = 100);

ordinate = tension in relative units.

+ = starting point of the curve.

uniform type, running parallel, their gradient reminding of length-tension diagrams at rest. The curves indicate a considerably lower tension than at a corresponding length during stretch.

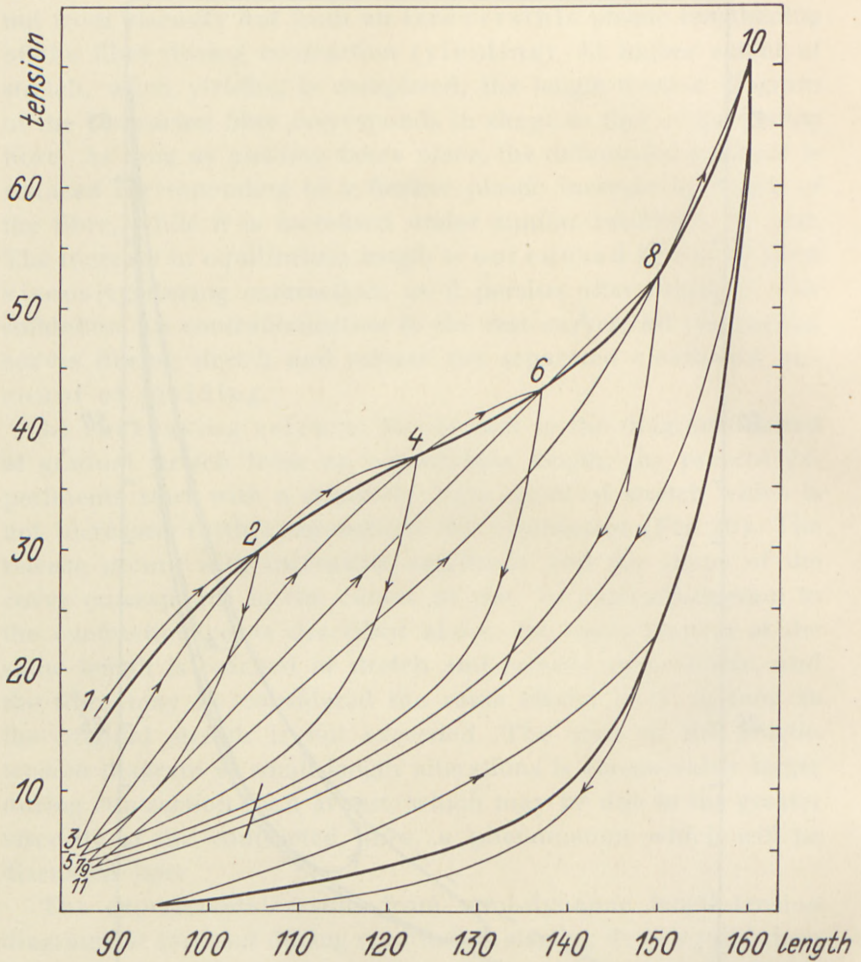


Fig. 21. Semi-dynamic length-tension diagram of the single fibre at rest and during tetanic contraction starting from length 100 and from length 160.

broad lines = static length-tension diagrams;

the arrows indicate whether the experiment started from the equilibrium length or from greater elongations;

the figures on the curves indicate the succession of extensions and releases.

abscissa = length of the fibre (equilibrium length = 100);

ordinate = tension in relative units.

In the semi-dynamic diagrams, the shape of the curves depends greatly on the rate of the length alterations. In the present mean diagram, only such curves are given which are registered at the same rate and which, therefore, are comparable. Since time marks



are always registered simultaneously with length- and tension registration, the speed may continuously be checked.

The difference between the tension curve and the relaxation curve at rest is exclusively caused by the viscosity of the fibre; with sufficiently long-lasting consolidation, the curves would overlap. The essential and—during contraction—irreversible difference of the tension- and release-curve, however, originates from the yielding appearing during contraction, and from the elastic "locking" at a new length, a phenomenon which already has been discussed together with the static release diagrams.

The figure exhibits, furthermore, short lines indicating the gradient of rapid length alterations (corresponding to a period of 0.2—1 per sec.). These lines are comparable with the true dynamic experiments which will be described in a later paragraph (p. 67). They are the results of small length alterations. During rapid small length alterations, the curve will outline an area which—due to the viscosity of the fibre—corresponds to the energy loss of the fibre during length alterations. A mean curve which we might imagine running across the described loop of the curve shows a somewhat different slope at different stretchings.

Finally, the gradients found at small variations of the length do not vary considerably with the speed of these length variations, provided that a certain minimum rate is exceeded. This might give the impression that part of the fibre, only, is viscous while the rest is purely elastic. A closer analysis of the relation between the elastic and the viscous parts of the fibre will be given in a later section.

### Work diagrams.

#### 1) Tetanic contractions.

Using the same experimental procedure as applied to the registration of the above described semi-dynamic length-tension diagrams, work diagrams of isolated single fibres were studied in order to determine the amount of work performed at stretch and following contraction (cf. indicator diagram of, for instance, a steam engine). The fibre was stretched at rest, a process, where energy is externally supplied (compression in the steam engine);

then, it was stimulated tetanically and, finally, allowed to contract and to perform work (expansion). The net work performed (i. e. the amount of work available for exterior purposes) is the difference between contraction work and stretch work. In the length-tension diagram, this magnitude corresponds to the difference in the areas of the contraction curve and the rest curve. All work diagrams were registered with single fibres of known weight (after removal of the tendon tissue which served to fasten the fibre in the tweezers). The work performed is expressed in erg/gm of the fibre substance.

During stretch from length 100 to length 150 and following release, the resulting work performed in a tetanic contraction was almost constant. In all experiments, the stretch- and contraction-period lasted 4 seconds, each. In the case of a non-fatigued fibre, the mean work performed was 10 000 erg/gm of fibre substance.

The difference in the course of the curves of isometric maxima and those of release contractions has been discussed in a former section (p. 23). As a result of this discussion, one might expect a greater energy yield by interrupting the stimulation for a short time during release; on renewed stimulation the curve starts from a new isometric maximum. The influence of an interruption in stimulation is represented in Figs. 22 a and b. Fig. 22 a exhibits a work diagram without interruption of the stimulation. In the present case, the net work performed by the fibre amounts to 10 erg, the stretch being 40 per cent. Fig. 22 b shows a work diagram of the same fibre, indicating the same course at rest and during the first part of release to length 125. The stimulation is then interrupted for a short period (ca. 0.1 sec.) and, when begun anew, a tension is obtained about 2.5 times higher than before the interruption. The tension is then reduced at release during stimulation in the same way as before, but it remains constantly higher than the previous tension. The net work is now 17.7 erg indicating that the interruption of the stimulation brings about a gain of energy of about 80 per cent. The increase in work obtained cannot be interpreted as a consequence of restitution of the fibre during the short period of rest. This could be shown by means of control experiments with long-lasting stimulations and intermittent interruptions without changing the length of the fibre. In general, the short restitution



period within the time of experiment applied here has no discernible influence. As might be expected, the working power of the

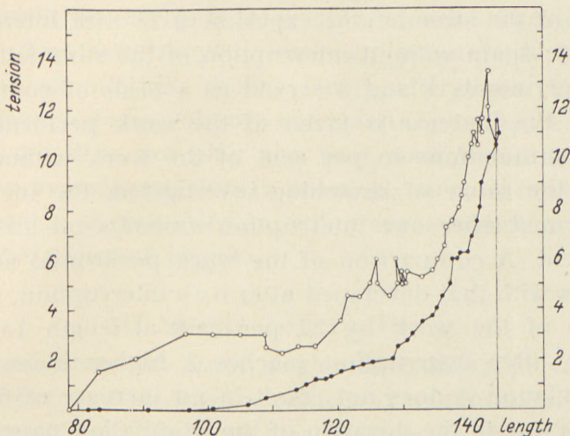


Fig. 22 a. Work diagram of a single fibre. stretch of the resting fibre (lower curve) and release during tetanic contraction (upper curve).

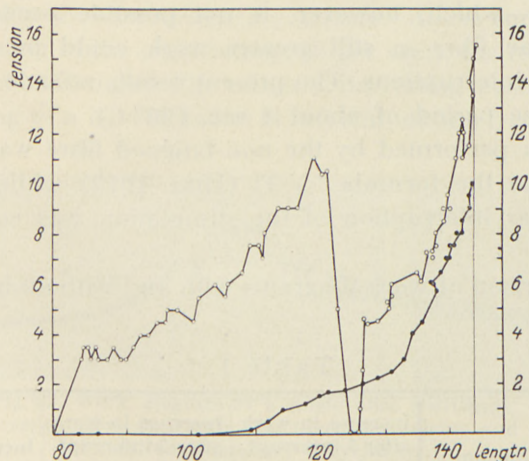


Fig. 22 b. Work diagram of the same fibre as in Fig. 22 a. stretch of the resting fibre (lower curve) and release during tetanic contraction with short stop in stimulation (upper curve); abscissa = length of the fibre (equilibrium length = 100); ordinate = tension in mgm.

fibre changes from one work experiment to another and, therefore, in every experiment for the determination of the difference

between work with interruption and work without interruption at least three work diagrams were recorded. In most cases, the following procedure was employed: Experiment 1: without interruption of the stimulation; experiment 2: with interruption; experiment 3: again without interruption of the stimulation. The mean of experiments 1 and 3 served as a basis of comparison. In Table 1, the increase is given of the work performed with interrupted stimulations in per cent of the work without interruption. In the range of stretching investigated, the increase in work performed after one interruption amounts on an average to 45 per cent. A comparison of the work performed after two interruptions with that developed after one interruption, revealed a reduction of the work by 22 per cent at length 150. Even if the fibre after interruption reaches a higher mean tension during stimulation it does not result in an increase of the work area. This is due to the duration of the stimulation pause. There is, indeed, not sufficient time for two interruption periods. Only at a higher stretch may further work be obtained after two or more interruptions. If the release could be carried out even more slowly—which, however, is not possible because of the fatigue of the fibre—a still greater work could be performed after several interruptions. The present results refer to a duration of the release period of about 4 sec. (20° C).

The work performed by the non-fatigued fibre was found to correspond to the formula  $\frac{1}{6} Tl$  (HILL 1913) while the work obtained after interruption of the stimulation was considerably larger.

A comparison of work diagrams with and without interruption

Table 1.

length (equilibrium length = 100)	Increase in work after 1 interruption in per cent of the work without interruption	Increase in work after 2 interruptions in per cent of the work after 1 interruption	Increase between second and third interruption
140 .....	+ 46	..	..
150 .....	+ 52	- 22	..
155 .....	+ 42	- 9	..
165 .....	+ 39	+ 25	+ 6



is of interest also from a practical aspect, as all dynamic work in muscle is accompanied by a length alteration. If the stimulation during dynamic work was continuously tetanic, the tractive force of the muscle would be considerably reduced during contraction. This does not happen, however, presumably due to the intermittent stimulations during length alterations. The stimulation frequency does probably not reach the tetanic level so that the "locking" does not play any part, and higher tensions are attained. In experiments now in progress, we shall try to compare the frequency of impulses in voluntary contraction with and without alterations of length.

## 2) Single contractions.

The work diagrams from single contractions at various frequencies were registered in the same way as the diagrams during tetanic contractions. The fibre was stretched to about length 140; then, the single stimulations began while the fibre was released from length 140 to its equilibrium length. Fig. 23 exhibits a fibre stretched to length 135. As soon as the increase in length ceases, the fibre tension shows a decreasing tendency due to consolidation. In the beginning of the stimulations (8 per sec.), the length of the fibre is at first unchanged. The values of the resting tension increase corresponding to a consolidation at this stimulation frequency (re-

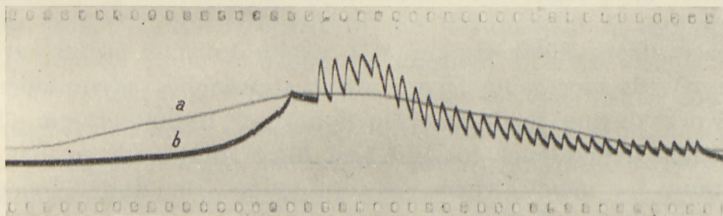


Fig. 23. Work diagram of a single fibre (twitches). Stretch of the resting fibre to length 135, thereafter release and simultaneous stimulation (frequency 8 cycles/sec.).

Work performed = 15.4 erg = 6420 erg/gm fibre.

(a) length recording; (b) tension recording.

mainder). Before the final consolidation tension is reached, the relaxation and, consequently, the decrease in tension begins. The mean tension is found by integration of the registered curve.

The area between the length-tension diagram from resting muscle and the contraction diagram of the mean tension is a direct expression of the work performed by the fibre. In the present case, it amounted to 15.4 erg corresponding to 6400 erg per gm fibre. Fig. 24 represents the work performed by the same fibre at different stimulation frequencies. The actual work

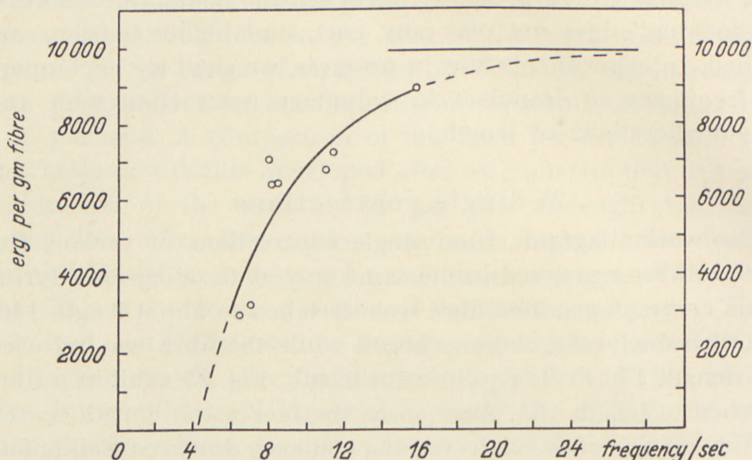


Fig. 24. Work done at different stimulation frequencies of the same fibre. The line at 10 000 ergs indicates the work performed in complete tetanus (frequency 30—50 cycles/sec.); release from length 140 to tension 0.

abscissa = frequency in cycles/sec.;  
ordinate = erg/gm fibre.

increases from 3000 erg/gm at 6 cycles to 9000 erg/gm at 16 cycles. With increasing frequency it approaches asymptotically the work during tetanic contraction, i. e. 10 000 erg/gm. The frequency dependence for different fibres may vary so that the minimum frequency, where the contraction "remainder" occurs, lies between 5 and 10 cycles.

### Length-tension diagrams of the anisotropic (A) and the isotropic (I) substance at rest and during contraction.

Length-tension diagrams of the individual substances (A and I) may be obtained from the tension of A + I as a function of the extension and from the length ratio A : I at different stretchings.



1) The length of A and I at rest as a function of stretch.

When different fibres are examined, a variation is observed of approximately 5 per cent in the ratio A : I, and of approximately 10 per cent in the height of compartments. For our purposes, the height of compartments at rest and at equilibrium length were put at 100, and the mean values of the lengths A and I were calculated relative to  $A + I$ . In addition to the earlier material available (BUCHTHAL, KNAPPEIS and LINDHARD, 1936), new experiments with continuous stretching of the same fibre served as a basis for these calculations.

At equilibrium length at rest, the mean values of A and of I were found to be 61 per cent and 39 per cent, respectively, of the height of compartments. The fibres were photographed at lengths 70—160 and the lengths of A and I were plotted in a coordinate system (Fig. 25), where the abscissa represents the length  $A + I$  in per cent of the equilibrium length, and the ordinate indicates the length of the individual substances in arbitrary units (the height of compartments at equilibrium length is 100 units =  $2.2 \mu$ ). The mean error of the rest curve is approximately 1 per cent. The curves of A and I at rest are practically linear. The increase in length of A is about twice that of I; that is, A is contributing twice as much to the resulting extensibility as I. However, taking into consideration the greater length of A compared with that of I, the elasticity of the A substance is found to be only slightly different from the elasticity of I (c. 20 per cent).

The dotted line represents the ratio A : I at rest as found in earlier experiments (BUCHTHAL, KNAPPEIS and LINDHARD, 1936), not obtained during continuous stretch. In these experiments, the difference of the elasticity moduli of the two substances was greater than in recent experiments, the tendency, however, being the same in both series.

2) The length of A and I during isometric contraction as a function of stretch.

Also at maximum stimulation, different preparations show quantitatively different reactions with respect to changes in the length of the substances at the same stretch. However, it was

observed that changes in length of A and I as a function of stretch vary uniformly and, therefore, it is possible to draw parallel

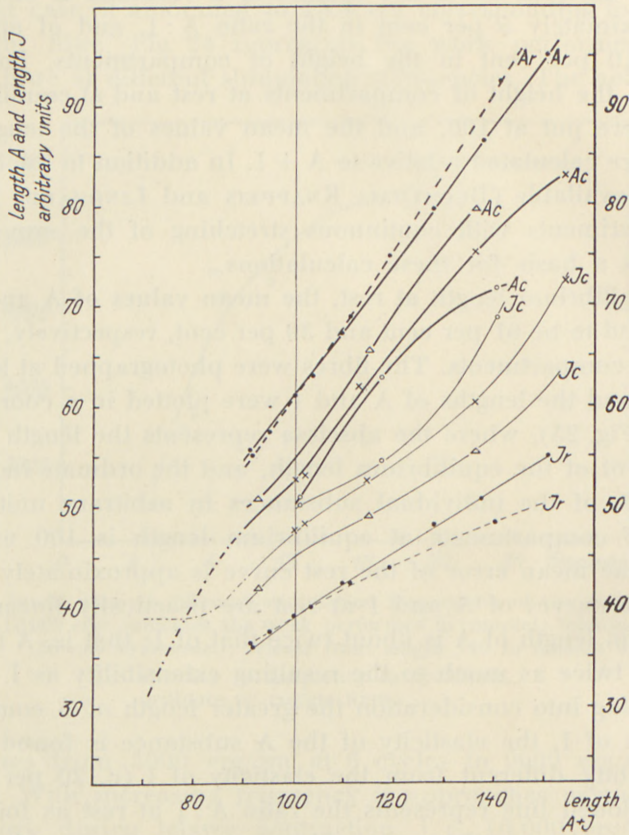


Fig. 25. Length of A and of I substance at rest ( $A_r$ ,  $I_r$ ) and during contraction ( $A_c$ ,  $I_c$ ) as a function of the height of compartment ( $A + I$ ).

- = resting fibre, new material;
- = resting fibre, material BUCHTHAL, KNAPPEIS & LINDHARD (1936);
- +—+— } = fibre groups with different ratio A/I.
- } = fibre groups with different ratio A/I.
- △—△— } = fibre groups with different ratio A/I.

abscissa =  $A + I$  (equilibrium length = 100);

ordinate = length of the individual substances in arbitrary units (100 units = height of compartment in the non-extended fibre =  $2.2 \mu$ ).

curves corresponding to the different ratio A/I (isometric contraction, equilibrium length) (Fig. 25). These curves cover corresponding points of the different preparations in a satisfactory



way. A comparison of different preparations with approximately the same ratio A/I (isometric contraction, equilibrium length) indicates that the mean scattering in these experiments is not very different from that in the rest curves. The experimental material is classified in three groups according to the extent of contraction during maximum stimulation. The error is largest in experiments below the equilibrium length due to the tendency of the fibre to curl up, and to the displacement of the fibrils in the various planes of the fibre.

The dotted part of the curves below length 90 (Fig. 25) refers not only to the above described continuous measurements but, moreover, to a special series of experiments in which it was found that I preserves its length unchanged during tensionless contraction.

During isometric contraction, A always becomes shorter and, consequently, I becomes longer than when at rest, the length of A and I being almost identical at equilibrium length during isometric contraction. At a stretch of 25 per cent, the difference in length between A and I is somewhat greater while, with augmented stretch, the lengths of the two substances again approach each other. During contraction below the equilibrium length, I comes very near to its resting length<sup>1</sup>.

### 3) Length-tension diagram of A and I at rest and during contraction.

The curves described above show the lengths of A and I relative to the height of compartments at equilibrium length. In order to procure a length-tension diagram of A and I separately, the length-tension diagram of the whole fibre must be known, and it must furthermore be assumed that A and I are arranged as links in a long chain so that each is exposed to the same load. Different extensibilities of A and I at constant fibre volume are only possible if a transfer of fluid takes place between A and I regions. This transport of fluid must occur unhindered in order

<sup>1</sup> RAMSAY and STREET (1940) describe a histological investigation of fibre shortenings up to 70 per cent of the equilibrium length. These great shortenings, however, are only to some extent due to shortenings of the working substance, part of them being a coarse, mechanical curling up. The microphoto-

to attain uniform loading of A and I. It is finally implied that no other elements of the fibre are exposed to any considerable tension. With regard to the length-tension diagram, it must be

graph of an extremely shortened fibre, reproduced in RAMSAY and STREET'S paper, proved to correspond to a resting, possibly slightly stretched fibre. The table given below contains our measurements carried out at four different regions of RAMSAY and STREET'S microphotograph, Fig. 10. The last file shows the mean values of a resting living frog muscle fibre determined by BUCHTHAL, KNAPPEIS and LINDHARD (1936) on more than 80 preparations.

Table 2.  
Length of A and I, and of A + I, at different points of  
the microphotogram of an "extremely shortened" fibre,  
according to RAMSAY and STREET.

	A	I	A + I	Point
In per cent. of A + I	1.29 57	0.98 45	2.27	I
In per cent. of A + I	1.50 59.5	1.01 40.5	2.51	II
In per cent. of A + I	0.40 48	0.43 52.1	0.83	III
In per cent. of A + I	1.17 51.5	1.11 48.5	2.28	IV
In per cent. of A + I	1.37 63	0.81 37	2.18	(± 0.01) mean value of resting fibre (BUCHTHAL, KNAPPEIS and LINDHARD (1936)).

Fig. 26. Correlation between the length-tension diagram of the single fibre and the individual length of A and I as a function of stretch. Mean curves.

- (1) length-tension diagram of the resting fibre;
- (2) curve of isometric maxima;
- $d$  = direction of release length-tension diagrams;
- ordinate (short  $y$  axis) tension in relative units;
- (3) length of I at rest as a function of the height of compartment;
- (4) length of I during contraction as a function of the height of compartment;
- (5) length of A during contraction as a function of the height of compartment;
- (6) length of A at rest as a function of the height of compartment;
- = release contraction-curves for A and I, resp., starting from the curve of isometric maxima;
- ×—×— = stretch during contraction;
- abscissa (common for the length-tension diagram and for the diagram of relative lengths of A and I) height of compartment ( $A + I = 100 =$  equilibrium length);
- ordinate (long  $y$  axis) length of A and of I in arbitrary units (100 units = height of compartment of the fibre at its equilibrium length =  $2.2 \mu$ ).



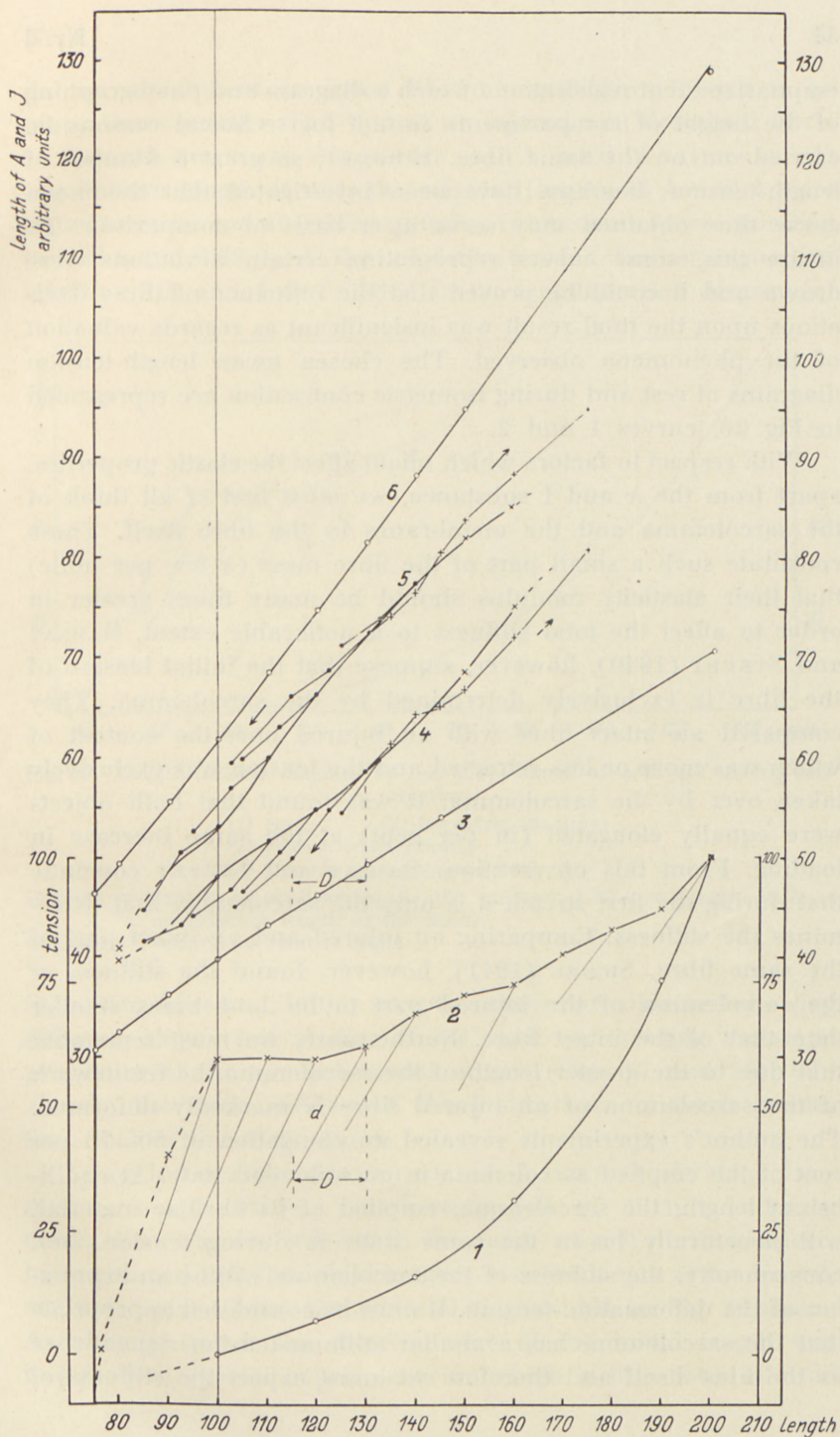


Fig. 26. For explanation, cf. p. 52.

emphasized that registration of such a diagram and photographing of the height of compartments cannot for technical reasons be carried out on the same fibre. However, so great a number of length-tension diagrams have been investigated that the mean curve thus obtained may serve as a basis of comparison. To insure this, some curves representing certain deviations were drawn and it could be proved that the influence of these deviations upon the final result was insignificant as regards valuation of the phenomena observed. The chosen mean length-tension diagrams at rest and during isometric contraction are represented in Fig. 26, curves 1 and 2.

With respect to factors which might affect the elastic properties, apart from the A and I substance, we must first of all think of the sarcolemma and the membranes in the fibre itself. These constitute such a small part of the fibre mass (a few per mille) that their elasticity modulus should be many times greater in order to affect the total stiffness to a noticeable extent. RAMSAY and STREET (1940), however, suppose that the initial tension of the fibre is exclusively determined by the sarcolemma. They compared an intact fibre with an injured one, the content of which was more or less retracted and the tension was exclusively taken over by the sarcolemma. It was found that both objects were equally elongated (in per cent) at the same increase in loading. From this observation, RAMSAY and STREET conclude that during the first stretch it is only the sarcolemma that determines the stiffness. Comparing an injured and an intact part of the same fibre, SICHEL (1941), however, found the stiffness of the sarcolemma of the injured part to be 1—4 times smaller than that of the intact fibre. Furthermore, we must remember that due to the greater length of the sarcolemma the framework of the sarcolemma of an injured fibre is markedly deformed. The author's experiments revealed an elongation of 50—70 per cent of the emptied sarcolemma in an unloaded state. At equilibrium length, the sarcolemma, emptied of its fibrillar material, will structurally be in the same state as during tension and, consequently, the stiffness of the sarcolemma will be an expression of the deformation-tension. It must be considered appropriate that the sarcolemma has a similar stiffness-tension dependence as the fibre itself and therefore we must expect the stiffness of



the sarcolemma of an intact fibre at equilibrium length to be many times smaller than that of an injured and deformed fibre.

Length-tension diagrams of A and I at rest. At equilibrium length at rest, the original lengths of A and I were found to be 60 and 40 arbitrary units, respectively (corresponding to  $1.38 \mu$  and  $0.88 \mu$ ). At the respective tension, the corresponding lengths of A and I are plotted in the length-tension diagram of

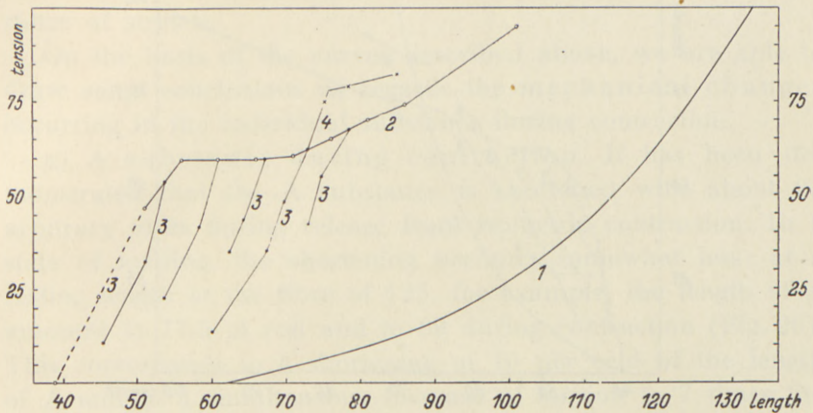


Fig. 27. Length-tension diagram of the A substance at rest and during contraction.

- (1) rest; (2) isometric maxima;  
 (3) release contractions;  
 (4) stretch during contraction;

abscissa = length in arbitrary units (60 units =  $1.32 \mu$  = length of A at equilibrium length of the fibre);  
 ordinate = tension in relative units.

the resting fibre and, in this way, two curves are obtained showing different slopes but similar shape, and representing the static properties of the two substances at rest (Figs. 27 and 28). Obviously, the static stiffness of the I substance is much greater than that of the A substance.

Length-tension diagrams of A and I during isometric contraction. The investigation of A and I during contraction was carried out in the same way; it must, however, be mentioned that the initial lengths, i. e. the length at the load 0, are not derived from the material represented in Fig. 26 alone. As already stated, the determination of the initial length was based upon special experiments in which a fibre was allowed

to shorten without tension. The shortening of the whole fibre, and as far as possible the lengths of the single substances, were measured photographically. During tensionless contraction, it was observed that the I substance did not change in length and, consequently, the shortening of the fibre must, be ascribed to the A substance. If the length of the I substance is assumed to amount to 40 and that of the A substance to 60 arbitrary units,

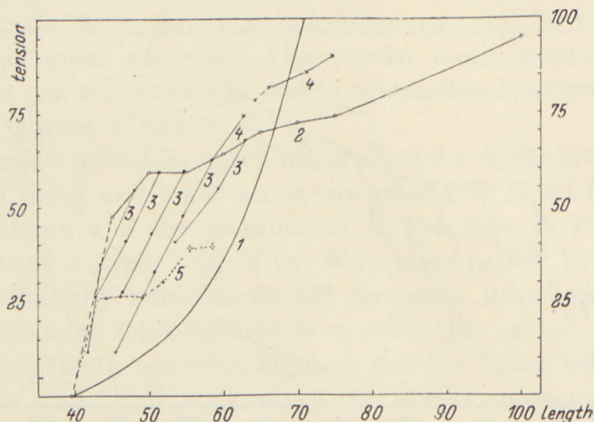


Fig. 28. Length-tension diagram of the I substance at rest and during contraction.

- (1) rest;                   (2) isometric maxima;
- (3) release contractions;
- (4) stretch during contraction;
- (5) "corrected" isometric maxima;

abscissa = length in arbitrary units (40 units =  $0.88 \mu$  = length of I at the equilibrium length of the fibre);

ordinate = tension in relative units.

and if the contraction constitutes 30 per cent, A must contract from length 60 to 30. The other points of the curve were obtained in the same way as the length-tension diagram at rest. The ranges below 45 in the case of I and below 50 in the case of A are dotted, as the length during isometric contraction considerably below the equilibrium length is unknown. The dotted line (3) does not represent the isometric maxima but a length-tension diagram of the release of the fibre from isometric contraction to the tension 0 (cf. p. 60).

It is characteristic for both curves that the initial gradient is considerably steeper than when at rest, and that a decrease in slope occurs with increased loading. This reduction of the steep-



ness is usually ended as soon as the tension of isometric contraction at equilibrium length is reached. In the case of the A substance, the curve shows a horizontal region which is followed by a slight ascent, and in the case of the I substance the curve is slightly ascending and approximately linear.

After the first steep part of the length-tension diagram, an irreversible length alteration (yielding) occurs during contraction which limits the tension attainable within a given range of stretch.

On the basis of the curves described above, we are able to draw some conclusions as regards the mechanical changes occurring in the individual substance during contraction.

a) A substance during contraction. It has been demonstrated that the A substance is shortened with about 25 arbitrary units during release from isometric contraction. In a state of loading, the shortening becomes somewhat less; at a resting length of the fibre of 125, for example, the length of A amounts to 77.5 at rest and to 69 during contraction (Fig. 26). This corresponds to a shortening of 10 per cent of the length of A and to a simultaneous increase of tension to 7 times the original value. Also at other stretchings, the mean shortening of A constitutes 10 per cent of the corresponding length at rest. On the basis of a direct comparison of the length of the A substance at rest and during contraction at the same loading (Fig. 27), one might conclude that A has been shortened corresponding to the difference between the lengths of the substances. At a loading 50, for example, the ratio between the lengths at rest and during contraction is equal to 2. Considering the course of the curves it must, however, be taken into account that the length of A during contraction depends not only on the stretch but also on the length alterations which are imposed during contraction (see page 60).

b) I substance during contraction. The course of the I curve is described above (Fig. 28). At rest, I deviates from A, the rest curve and contraction curve having two common points, viz. the starting point at the tension 0 and a point of intersection at the tension 70 (height of compartments 140). When comparing at the same tension, I was found to be shorter during contraction than at rest until a certain loading is reached. At a higher loading,

I becomes longer than at rest for the same tension. The first part of the curve indicates a certain contractility of the I substance. Even if I undergoes an increase in length due to a contraction tension originating from A, this cannot explain the very high tension of the I substance during contraction, relative to the same rest length. At equilibrium length (tension 0), the length of the I substance is 40. During contraction, I is elongated to 50, which causes an increase in tension amounting to 12. In reality, I is loaded with a tension of 60, i. e. the ratio between rest- and contraction tension is 1 : 5.

The length-tension diagram of I—in contrast to that of the whole fibre—cannot be interpreted as a length-tension diagram of isometric contraction, since the I substance is not only stimulated but, furthermore, increased in length. However, we may correct for this increase in length by means of release-contraction diagrams and, hence, an “isometric” length-tension diagram is constructed the points of which lie probably lower than those obtained in true isometric contractions (cf. other release-contractions). Curve 5, Fig. 28, shows the constructed length-tension diagram which is known from length 40 to 52; above this length, this diagram is extrapolated and constructed on the assumption that the gradient of the release diagram is directed towards the starting point of the curve.

This curve indicates that no increase in tension at the length 40 is registered, as this corresponds to the equilibrium length of the I substance which is unchanged. Length 42 to 47 is the range of the maximum working ability of the I substance, the extra-tension being approximately 20, calculated from a rest tension of only 3 to 8. The extra-tension then decreases and presumably becomes 0 before the point of intersection between the rest curve and the contraction curve is reached.

From the constructed “isometric” length-tension diagram of I it is evident that I is able to perform work which exceeds that supplied by the stretch. In the case of the A substance, a stretch is unnecessary for the performance of work because A changes its equilibrium length during stimulation.

During contraction of fibres up to a length of 150 (length of I at rest = 55, and of I during contraction = 68), also an extra-tension of I could be obtained due to the increasing stiffness



Table 3.

Length of A and of I during isometric contractions and during release contractions at various elongations.

Pre- paration	Isometric contraction			Length (100 = length of equi- librium)	Release contraction			Extent of release in arbitrary units (length of equilibrium = 100 = 2.20 $\mu$ )	$\Delta A$ $\mu$	$\Delta I$ $\mu$	$\frac{\Delta A}{\Delta I}$
	A $\mu$	I $\mu$	A+I $\mu$		A $\mu$	I $\mu$	A+I $\mu$				
166 EIII	1.08	0.97	2.05	93	1.07	0.92	1.99	2.0	0.01	0.05	0.20
166 FIV	1.22	1.10	2.32	105	1.01	0.91	1.92	18.0	0.21	0.19	1.11
220 AIII	1.23	1.02	2.25	102	1.06	0.90	1.96	13.0	0.17	0.12	1.41
207 AI	1.25	1.08	2.13	106	1.16	0.97	2.13	9.0	0.09	0.11	0.82
217 AI	1.34	1.16	2.50	114	1.27	0.96	2.23	13.0	0.07	0.14	0.50
218 AI	1.36	1.18	2.54	115	1.30	1.10	2.40	6.0	0.06	0.08	0.75
217 BI	1.40	1.15	2.55	116	1.32	1.07	2.39	7.0	0.08	0.08	1.00
202 CIII	1.35	1.21	2.56	116	1.09	0.98	2.07	22.0	0.26	0.23	1.13
207 CI	1.37	1.21	2.58	117	1.34	1.12	2.46	5.0	0.03	0.09	0.33
220 BII	1.38	1.21	2.59	118	1.31	1.11	2.42	8.0	0.07	0.10	0.70
166 AI	1.42	1.32	2.74	124	1.33	1.16	2.49	11.0	0.09	0.16	0.56
218 CI	1.47	1.25	2.72	124	1.32	1.14	2.46	12.0	0.15	0.11	1.36
220 BI	1.46	1.28	2.74	125	1.22	1.01	2.23	23.0	0.24	0.27	0.89
220 AII	1.48	1.28	2.76	125	1.45	1.15	2.60	7.0	0.03	6.13	0.23
169 CII	1.49	1.31	2.80	127	1.51	1.27	2.76	2.5	0.02	0.04	0.50
201 CII	1.48	1.34	2.82	128	1.24	0.98	2.22	27.0	0.24	0.36	0.67
159 AI	1.58	1.38	2.96	134	1.43	1.17	2.60	16.0	0.15	0.21	0.72
190 FIII	1.56	1.43	2.99	136	1.45	1.29	2.74	11.0	0.11	0.14	0.79
166 CII	1.61	1.42	3.03	138	1.51	1.35	2.86	8.0	0.10	0.07	1.43
202 IIV	1.62	1.46	3.08	140	1.13	1.07	2.20	40.0	0.49	0.39	1.26
202 DII	1.65	1.50	3.15	143	1.45	1.24	2.69	21.0	0.20	0.36	0.77
218 CII	1.73	1.46	3.19	145	1.64	1.19	2.83	16.0	0.09	0.27	0.33
201 EIII	1.73	1.53	3.26	148	1.45	1.32	2.77	22.0	0.28	0.21	1.33

during contraction. Above 150, I contributes negatively to the contraction. This fact can partly explain the decreasing extra-tension during contraction at high stretchings, which is therefore due partly to a yielding of the I substance (cf. p. 22).

Comparing A and I during contraction, we find that the tension increase in the case of I is due to an alteration of the stiffness; in the case of A it is due not only to a change in stiffness but, furthermore, to a change in equilibrium length.

c) A and I during release contractions. The description of release length-tension diagrams and semi-dynamic length-tension diagrams indicates that the mechanical properties of a fibre contracted at a certain length and then released to a somewhat shorter length are different from those of a fibre which contracts isometrically at a corresponding length. In connection with the elucidation of the properties of A and I during isometric contraction, it was desirable to investigate the corresponding changes of the internal structures during release contraction.

The experiments were carried out in the following way. The fibre was brought to an isometric contraction at a known length and was microphotographed at rest as well as during isometric tetanic contraction. The fibre was then re-stimulated and, immediately after development of tension, released from 4 to 30 per cent of the original length and was photographed during continuous stimulation. The photograph of the release contraction did not require a longer stimulation period than was necessary for the pure isometric contraction.

The material from these experiments which were carried out in cooperation with Mr. G. KNAPPEIS is collected in Table 3 (p. 59). The table contains the lengths of A and I during isometric contraction and during release contraction at various elongations; furthermore, the difference between the length of A—*isometric contraction*—and A—*release contraction*—( $\Delta A$ ), and the corresponding values of I ( $\Delta I$ ). The quotient  $\frac{\Delta A}{\Delta I}$  represents the ratio between the static softness<sup>1</sup> of A and I during release. The softness of A is expressed by  $\frac{\Delta A}{\Delta P}$  and that of I by  $\frac{\Delta I}{\Delta P}$ , where P is the change in load due to length variations, a factor which cancels out when comparing the two softnesses. The ratio  $\frac{\Delta A}{\Delta I}$  is dependent on the initial length and on the extent of release. The results from 25 different experiments, arranged according to the extent of release, are given in Table 4. Each value in the table was determined by 3 to 6 measurements and the mean error for the ratio  $\frac{\Delta A}{\Delta I}$  is  $\pm 0.2$ . The table contains A and I as functions of the length of the fibre and of the extent of release.

<sup>1</sup> Here and in the following, softness =  $\frac{1}{\text{stiffness (dyne cm}^{-1}\text{)}}$ .



Table 4.

Extent of release in length units					
7.5	99.5	116	123	134	length of the fibre during isometric contraction.
...	0.51	0.82	0.62	0.91	$\frac{\Delta A}{\Delta l}$
15	107*	...	141	...	length of the fibre during isometric contraction.
...	1.00	...	0.60	...	$\frac{\Delta A}{\Delta l}$
26	133	...	...	...	length of the fibre during isometric contraction.
...	0.77	...	...	...	$\frac{\Delta A}{\Delta l}$

\* The point marked \* shows a relatively large variation in the length of A. This is due to a compression of I which only can decrease in length down to its equilibrium length.

The figures given in Table 4 were evaluated graphically. In this way, the value of  $\frac{\Delta A}{\Delta l}$  as a function of the extent of release at the lengths 100, 110, 120, 130, and 140 were obtained (Table 5).

Table 5.

Extent of release in length units	Length of fibre					
	100	110	120	130	140	
7.5	0.50	0.60	0.72	0.85	...	$\frac{\Delta A}{\Delta l}$
15	...	0.90	0.74	0.65	0.60	$\frac{\Delta A}{\Delta l}$
26	...	...	...	1.00	...	$\frac{\Delta A}{\Delta l}$

On the basis of these results (Table 5 and Fig. 26), the individual length-tension diagrams may be calculated, starting from the curve of the isometric maxima in the length-tension

diagram of A and I (Figs. 27 and 28).  $\Delta A + \Delta I = D =$  extent of release;  $\frac{\Delta A}{\Delta I}$  is obtained from Table 5 and  $\Delta A$  and  $\Delta I$  are thus calculated for the respective lengths.

The new lengths of A and I were found by subtracting  $\Delta A$  and  $\Delta I$ , respectively, from the original lengths, the mean values of which during isometric contraction are plotted in curves 4 and 5 (Fig. 26).

For example, at the length 130, the release may amount to 15 units.  $\frac{\Delta A}{\Delta I}$  is found from the table to be 0.65. Consequently,

$$\Delta I = \frac{15}{1.65} = 9.1.$$

The length of I during release contraction is thus  $58.5 - 9.1 = 49.4$ , (where 58.5 is the length of I during isometric contraction read from the curve at the length 130, and 9.1 is  $\Delta I$ ). The tension of I during isometric contraction (Fig. 26, curve 2) at the length 130 is found to be 60.8, and the tension of I during release contraction (Fig. 26, curve 2d) from the length 130 to the length 115 is approximately 35. In this way, we get two corresponding values of length and tension from the release length-tension diagram of I starting from a fibre length 130. In a similar way, the release length-tension diagrams of A and I represented in Figs. 27 and 28 were procured.

d) Partial release length-tension diagram of A. In the range investigated, the release diagrams of A are of a uniform type (Fig. 27, 3). The shortening during release contraction from an isometrically obtained tension extrapolated to the equilibrium length of the contracted A amounts to 15–20 units, or 25–30 per cent of the length of A. The gradients of the release diagrams decrease somewhat with the extent of release.

e) Partial release length-tension diagrams of I. The initial steepness of the release diagrams is less in the case of I than of A. In contrast to the diagrams of A, those of I are not parallel but are presumably directed towards the equilibrium length of I (Fig. 28, 3). Also this fact indicates that I has the same equilibrium length at rest and during contraction, while the equilibrium length of A changes. The change in steepness of the partial diagrams, furthermore, expresses a decreasing stiffness of I with increasing stretch.

The release lengths of A and I are plotted in Fig. 26, starting



from the contraction curves 4 and 5. During release from the equilibrium length (abscissa 100), the lengths of A and I coincide with the length alterations obtained during isometric contraction. Hence, the curve is reversible in this range. At higher stretch (length 110—130), the course of the curve during contraction is irreversible, corresponding to a yielding followed by a new locking of the fibre. This is evident in the clear distinction between the length of A during isometric contraction and during release contraction when referring to equal lengths of the fibre. The difference between  $A_{ic}$  (isometric contraction) and  $A_{rc}$  (release contraction) increases continuously in proportion to the extent of release until the equilibrium length is approached.  $\frac{\Delta A}{\Delta I}$  is in the mean  $0.8 \pm 0.1$  (cf. Table 3). During release contraction, A is thus on average 20 per cent stiffer than I, in agreement with the fact that the major part of the length variation during release must be ascribed to I.

Each release diagram represents a new elastic body determined by the stretch at the moment of contraction. The deviation of the individual length-tension diagram from the curve of the isometric maxima may be explained as an elastic locking of the A and I substances. This locking is the true cause of the irreversibility of the length-tension curves of isometric maxima.

#### 4) Stretching of the fibre during contraction.

a) The length of A and I at stretch during contraction. A number of experiments were carried out with fibres stretched during contraction. The experimental technique was the same as in all earlier experiments. In the region investigated, the ratio  $\frac{\Delta A}{\Delta I}$  was found to be a function of stretch, increasing from 0.25 at a stretch of 7.5 per cent to 1.5 at 20 per cent of elongation; the ratio then decreases and amounts to 1.25 at 45 per cent of stretch. Judging from the material available, the initial length is without any influence on the ratio  $\frac{\Delta A}{\Delta I}$ . The stretch diagrams of A and I as a function of the length of the fibre were constructed in the same way as the release diagrams

and plotted in the same curve (Fig. 26). Up to 10 per cent elongations, the points fall on the continuation of the release diagram. The curve then bends, intersects the isometric curve, and continues parallel with the latter. The inflection point is an expression of the yielding of the A substance, since the length of the I substance does not vary much at that point.

b) Length-tension diagram of A and I stretched during contraction. Length-tension diagrams from isometric contraction and length-tension diagrams of stretch during contraction indicated that stretch diagrams and release diagrams join each other and show the same gradient in the tension range of the isometric contraction. In the partial length-tension diagrams of the A substance, the same interdependence between length increase and tension increase was found in the beginning (Fig. 27, 4). In the given example, the A substance was able to endure a stretch of 3 per cent during contraction before a yielding occurred. This corresponds to an increase in tension of 15. The gradually decreasing differential quotient of the length-tension diagrams of the I substance (Fig. 28, 4) indicates that a yielding also appears in this case, however later and to a less pronounced extent than in the A substance.

### Elasticity measurements.

In experiments on single muscle fibres both static and dynamic stiffness have been investigated (method, p. 11). An ideal elastic body will display the same static and dynamic stiffness if only temperature alterations due to deformation are taken into account. Since the deformation energy of this system is small compared with its heat capacity, the adiabatic temperature alterations may be disregarded in this connection.

As well-known, a muscle fibre is no ideal elastic body. Apart from elasticity, we must reckon with viscosity which presumably is not uniformly distributed over the elastic elements of the fibre. Dealing with muscle substance, an agreement between static and dynamic measurements can therefore not be expected. A discussion of the relationship between these properties will be given in a later section (p. 87).



While static measurements are an expression of the total stiffness, dynamic measurements express only part of the stiffness, primarily the stiffness of those elements the length alterations of which are only slightly retarded by viscosity. Static stiffness (criterion: gradient of the curve) is difficult to evaluate due partly to the time of consolidation demanding long-lasting experiments, and partly to fatigue and plastic yielding which require short experiments. On the other hand, dynamic stiffness (criterion: vibration frequency and amplitude) can be investigated under well-defined conditions.

On whole muscle, there exist static as well as dynamic elasticity measurements, the main problem investigated being the changes of elasticity during contraction.

WEBER (1846) found the contracted fibre to be statically softer than the resting fibre under the erroneous assumption, however, that static length-tension diagrams of isometric maxima were reversible. These experiments and their interpretation were soon criticized, among others by WUNDT (1858) and ENKO (1880) who emphasized, further, that the connective tissue was a considerable source of error in WEBER's calculation of the elastic constants of muscle substance. WEBER's experiments did not contain the first part of the length-tension diagram where there is reversibility, presumably because of a too high initial load. In the first part of the length-tension diagram, BLIX (1892-95) observed a greater stiffness of the contracted than of the resting fibre and, in agreement with other investigators, he stated that he had never observed an elongation of the muscle during stimulation at heavy loading (WEBER's paradox). At a greater stretch (above 120), SCHENCK (1899, 1900) and BLIX found a higher extensibility during contraction than at rest. On the basis of constructed partial length-tension diagrams, REICHEL (1934) concluded that the elastic properties are identical at rest and during contraction and, consequently, he rejected the theory of muscle as a new elastic body during contraction.

Semi-dynamic and dynamic elasticity have been investigated both by means of torsion oscillations (WEBER 1846, WUNDT 1858, SCHENCK 1900, KAISER 1899, LINDHARD and MØLLER 1926 and 1928) and by oscillations longitudinal to the axis of the fibre (GASSER and HILL 1924, STEINHAUSEN 1926, RICHTER 1928).

In spite of the constant volume, no relation between torsion elasticity and longitudinal elasticity can be expected in muscle due to its anisotropic structure. In this connection, it may be recalled that a simple crystal has numerous independent elasticity moduli (VOIGT 1909). Hence, the torsion elasticity is independent of the elastic properties derived from the length-tension diagram, but may nevertheless express structural peculiarities which are not accessible when longitudinal oscillations are employed.

GASSER and HILL (1924) were the first to introduce a mechanical, periodically vibrating system, the frequency and damping of which were affected by the total stiffness and viscosity of the muscle. Measurements were carried out during practically isometric contraction where the stiffness was found to be many (11) times greater than when at rest. However, the tension developed during contraction was not taken into account in these experiments, although it caused the predominant part of the registered stiffness, as already pointed out by WEBER. STEINHAUSEN (1924—26), and later RICHTER (1928) performed elasticity measurements by means of impulse-period determinations and introduced tension compensation. They found an increase as well as a decrease in stiffness during contraction. Even for the whole muscle, a systematic investigation of the dynamic stiffness at rest and during contraction over a wide range of load does not exist.

Moreover, all experiments on whole muscle involve essential errors. A change in form and a displacement of the fibres take place even during isometric contraction and, further, inhomogeneous states of stretch and contraction in various parts of the muscle and the connective tissue must exercise an uncontrollable influence upon the results.

Static and dynamic measurements of the elasticity of the single muscle fibre at different loading should therefore be of great significance for the elucidation of the elastic and viscous properties of the muscle fibre.



### A. Dynamic stiffness.

Comparison of the elastic properties of the fibre at rest and during contraction.

The stiffness, i. e.  $\frac{\Delta \text{force}}{\Delta \text{length}}$  expressed as dyne/cm, is accessible to direct measurement in vibration experiments. In the case of a homogeneous body, this magnitude will generally be expressed as the elasticity modulus, viz.

$$\frac{\Delta \text{force} \times \text{length}}{\Delta \text{length} \times \text{cross section}};$$

in a highly elastic body, however, great changes in the existing length and cross section may occur. The elasticity modulus based upon an arbitrary stretch and a corresponding cross section is less suited for the elucidation of the required properties of the respective substance than is the measured stiffness, especially in the case of anisotropic substances. Stiffness-tension variations must primarily be regarded as determined by structural changes in the molecular or micellar constitution of the fibre and, to a minor extent, as dependent on the inversely proportional changes in length and cross section.

In the evaluation of the measurements, primarily the ratio  $\frac{\Delta \text{force}}{\Delta \text{length}} = \text{stiffness}$  furnished a basis of comparison. Measurements of stiffness at rest and during contraction were performed according to the following aspects.

Method I. Stiffness comparison at the same length of the fibre. This would seem to be the most natural procedure, as it corresponds to a comparison of the moduli at constant cross section area.

Method II. Stiffness at the same tension.

- a) At rest and during isometric contraction. On the basis of corresponding values of stiffness and tension, the ratio

$$\frac{\text{Stiffness (contraction)}}{\text{Stiffness (rest)}}$$

is found for equal tension, i. e. we compare fibres the single elements of which are exposed to the same tension but are of different length.

- b) The stiffness is compared at rest and during contraction at the same tension obtained by release from isometric contraction to the same tension as at rest. Also in this case, the length of the resting and the contracted fibre is different.

The elasticity moduli may be calculated on the basis of results obtained from these stiffness experiments. Comparing the stiffness at rest and during contraction as found by method I, we arrive at the elasticity constant referring to the same length of the fibre. The difference between these two measured elasticity moduli is due to contraction. During contraction, an increase in tension occurs which is produced by some kind of change in the fibre substance. In a not "highly elastic" substance, the increase in tension would not influence the elasticity modulus to a considerable degree; in a highly elastic body, however, the tension controls decisively the magnitude of the modulus.

The interesting point in stiffness measurements is more the change of the material constant during the contractile process than the change of the elasticity modulus due to tension. A differentiation of these two magnitudes is essential, as the structural changes accompanying contraction are the most interesting problem, while the tension—which may be regulated externally—is of minor interest. Formerly, it was assumed that the increase in stiffness during contraction should be ascribed mainly to the contraction process itself (GASSER and HILL 1924), while the increase in tension was disregarded. The present material, however, makes it quite clear that the increase in stiffness actually due to contraction is very small and may even be negative and, further, that the very marked increase in stiffness formerly observed by GASSER and HILL is mainly due to tension (i. e. structural changes which will appear in the same way at rest under the influence of exterior forces).

When fibres are compared at the same length (method I), a distorted picture is given of the influence of contraction upon the material.



It must, furthermore, be taken into consideration that the individual substances of the fibre change their lengths also during isometric contraction (shortening of A and elongation of I). An isometric contraction of the fibre is thus not synonymous with isometric conditions of the single elements of the fibre.

The true elasticity constant of the total fibre substance is found by a stiffness comparison of fibres at the same tension at rest and during contraction (method II, a and b) corrected for different lengths and cross sections.

A differentiation of the stiffness and elasticity moduli of the total fibre with respect to the individual substances is given in a later section (p. 90).

### Elasticity measurements at rest and during contraction.

#### 1) Treatment of the material.

The results from the individual experiments are arranged as stiffness at rest and during contraction and corresponding tension as a function of stretch. The extent of stretch proved not to be the most suitable basis of comparison of elastic properties, since it was found that different fibres were able to endure greatly differing elongations. Some fibres may, for example, be stretched to a length 150, others up to 220, before the extra-tension during contraction becomes zero. In the individual length-stiffness and length-tension diagrams, however, it was observed that a variation of the loading generally led to a corresponding variation in stiffness. This variation of the load need not necessarily be externally caused by a length alteration, but it might originate from a change in contractility of the fibre or by fibre yielding. On plotting the stiffness in the different experiments as a function of the load, the material became practically uniform.

In the present investigation, we have been mostly interested in the interdependence of loading, stiffness, and length at rest and during contraction. Absolute values of elasticity moduli have been determined in a special series of experiments where in addition to the length of the fibre its diameter was measured.

The absolute values of the different experiments vary con-

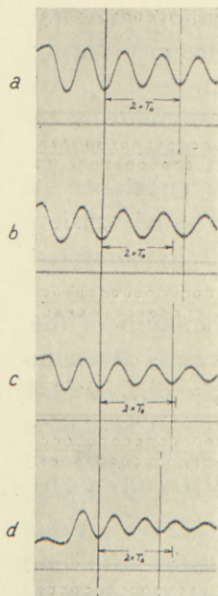


Fig. 29. Determination of dynamic stiffness in vibration experiments.

- (a) oscillations of the vibrating system without muscle fibre ( $T_0$ );  
 (b) oscillations of the system loaded with 0.5 gm (determination of the effective mass of the system);  
 (c) oscillations of the system + resting fibre;  
 (d) oscillations of the system + contracted fibre (release contraction to the same tension as present in the resting fibre).

Time marks = 20 msec.

siderably and it was, therefore, necessary to find a common measure of stiffness and tension for the different fibres. All tension measurements refer to the tension existing in the fibre when the extra-tension during contraction becomes zero due to the stretch. This is a well-defined point on the length-tension diagram and, using it as a basis, the measuring system enables an adequate conformity between the different elastic properties of the fibre.

As a measure of the stretch, the length of the fibre is put = 200, where the extra-tension during contraction becomes zero. This length—twice that at rest—corresponds very closely to the mean value from all experiments with isometric contraction. In a series of experiments on release contractions, however, the measure of length is put = 150, as this is the mean stretch where the extra-tension during contraction is zero. In these latter experiments, the respective fibres showed a maximum extensibility amounting to about half that measured in the first series of experiments with isometric contractions.

The measure of the loading is the same as in the series of experiments during isometric contraction.

As a measure of the stiffness, the stiffness at rest is put = 100 at a stretch where the extra-tension during contraction ceases.

Series I includes measurements of tension and stiffness at rest. Isometric contraction of the fibre followed by release until the contracted fibre shows the same tension as before when at rest (Fig. 29, method IIb, p. 67). Registration of the



corresponding length and stiffness. These measurements were performed at different elongations.

Series II includes determinations of tension and stiffness at rest. Measurements of tension and stiffness at the same length during isometric contraction and, finally, measurements of tension and stiffness during release from isometric contraction to an arbitrary length (and not, as in series I, to the same tension as when the fibre is at rest). The measurements were performed at different elongations.

On the basis of length-stiffness and length-tension diagrams, the respective values of tension and stiffness were corrected to the above described units. From the diagram of the resting fibre, the isometrically contracted fibre and

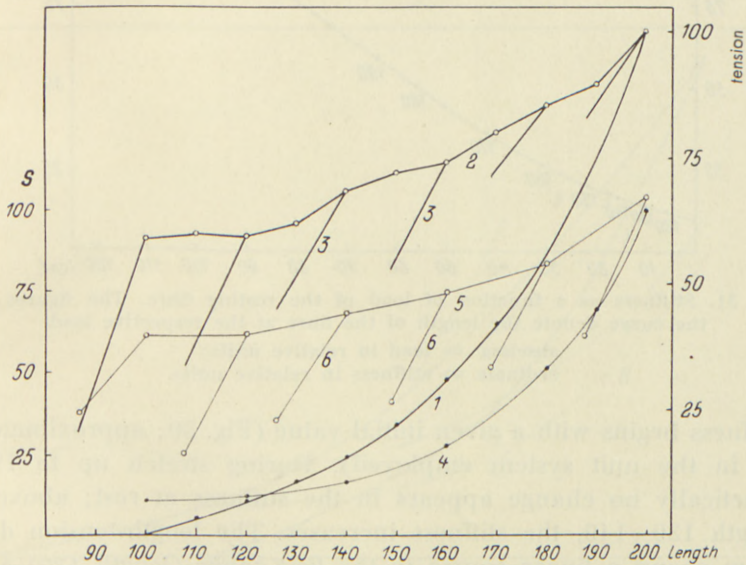


Fig. 30. Length-tension and length-stiffness diagram of the single muscle fibre at rest and during contraction. Mean curve.

- (1) length-tension diagram of the resting fibre;
  - (2) length-tension diagram of isometric maxima;
  - (3) direction of release contractions, when releasing from the isometric maximum;
  - (4) length-stiffness diagram of the resting fibre;
  - (5) length-stiffness diagram of the isometrically contracted fibre;
  - (6) variation of stiffness in release contractions, when releasing from the isometric maximum;
- abscissa = length of the fibre (equilibrium length = 100);  
 ordinate = (left) stiffness in relative units;  
 (right) tension in relative units.

the fibre with release contractions, the ratio  $\frac{S_c}{S_r}$  (with uniform load) was determined for every experiment as a function of the load and the extent of stretch.

## 2) Stiffness at rest.

Length-stiffness diagram. As the fibre has a certain stiffness also at its equilibrium length, the diagram of the dynamic

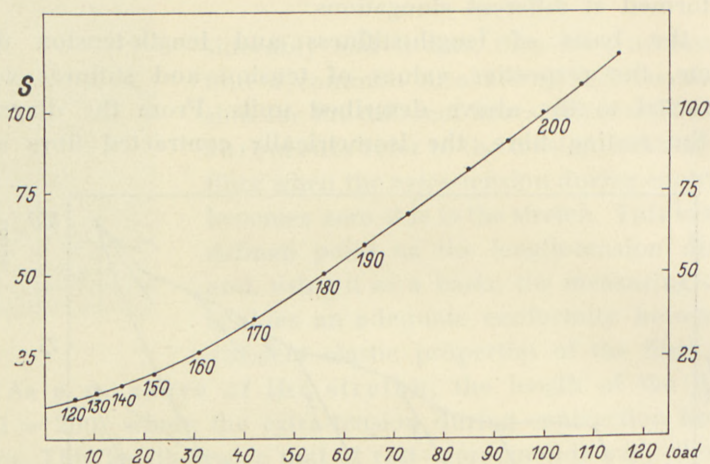


Fig. 31. Stiffness as a function of load of the resting fibre. The figures on the curve denote the length of the fibre at the respective load.

abscissa = load in relative units;  
ordinate = stiffness in relative units.

stiffness begins with a given initial value (Fig. 30; approximately 10 in the unit system employed). During stretch up to 120, practically no change appears in the stiffness at rest; above a length 130—140, the stiffness increases. The length-tension diagram shows a linear course in the first range (length 120) and starts bending between length 130—140, then continuing with increasing differential quotient.

Load-stiffness diagram. This diagram naturally begins at the same value as at length 100, since here the load is 0. Apart from a concave bend towards the  $x$  axis at a load 15, the stiffness increases proportional to the loading. In the mean diagram, the transition between these two ranges (Fig. 31) is slightly smoothed. Actually, the difference in slope is more pronounced



in the case of the individual fibres (Fig. 34). The interpretation of this characteristic straight course of the curve will be given in a later section (p. 116).

### 3) Stiffness during contraction.

Release contractions (release to the same tension as when at rest; method II b).

Length-stiffness diagram. The stiffness of the contracted fibre begins at the load 0 (length 75) with a value of about 30, and remains constant up to length 120 (Fig. 32). From length 100—140, it amounts to approximately 15 units above the resting value when comparing fibres of identical lengths. At greater lengths, the stiffness at rest and during contraction approach each other.

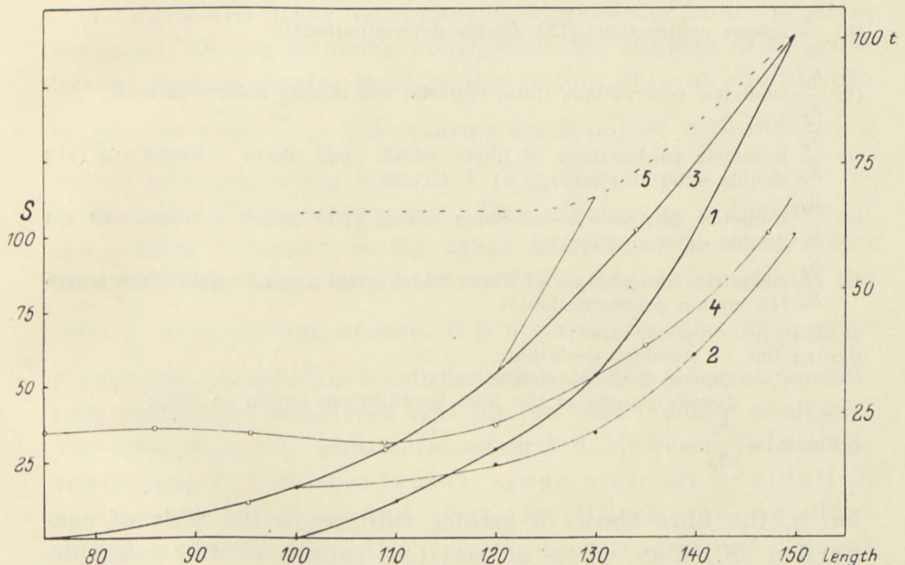
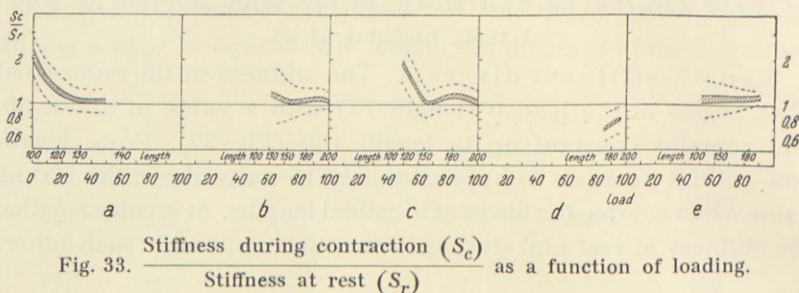


Fig. 32. Length-tension and length-stiffness diagram of fibres at rest and during release contraction.

- (1) length-tension diagram of the resting fibre;
  - (2) length-stiffness diagram of the resting fibre;
  - (3) length-tension diagram of release contractions (release to the same tension as at rest);
  - (4) length-stiffness diagram of release contractions;
  - (5) curve of isometric maxima with partial release diagram;
- abscissa = length of the fibre (equilibrium length = 100);  
 ordinate = (right) tension in relative units;  
 (left) stiffness in relative units.

Load-stiffness diagram. In order to elucidate the variation in stiffness when a fibre is contracting, the ratio contraction stiffness/rest stiffness at the same load is employed (Fig. 33a), as we are mainly interested in a distinction between stiffness during contraction and at rest. After release to the tens-



- (a)  $\frac{S_c}{S_r}$  release contractions (131 double determinations);
- (b)  $\frac{S_c}{S_r}$  isometric contractions (total material 242 double determinations);
- (c)  $\frac{S_c}{S_r}$  isometric contractions of fibres which yield above a length 100 (112 double determinations);
- (d)  $\frac{S_c}{S_r}$  isometric contractions of fibres which yield below a length 100 (84 double determinations);
- (e)  $\frac{S_c}{S_r}$  isometric contractions of fibres which yield around equilibrium length (46 double determinations);

shaded area = mean error;

dashed line = standard deviation;

abscissa = (lower) load in relative units;

(upper) length of the fibre (equilibrium length = 100);

ordinate =  $\frac{S_c}{S_r}$ .

ion 0, the fibre shows a greater stiffness in the state of contraction ( $S_c$ ) than when at rest ( $S_r$ ) (approximately twice the resting value). With increasing load, the ratio  $\frac{S_{\text{release contraction}}}{S_{\text{rest}}}$

decreases converging towards 1. Already at a load of 30 (length 130), the ratio has almost reached the value 1. As the standard deviation is not distributed symmetrically about the mean value, partly because the stiffness cannot attain negative values, the material is unsuited for a graphical representation in linear coordinates. In a logarithmic coordinate system, however,



the individual measurements fall symmetrically around the mean value. For this reason, the ratio  $\frac{S_c}{S_r}$  is plotted in a logarithmic system and the mean curve as well as the standard deviations and the mean errors are represented in this coordinate system.

The shaded part of the curve marks the standard error which amounts to approximately 3 per cent. The dashed line above and below the mean curve, respectively, denotes the standard deviation. The mean error at load 0 is 3.5 per cent of the measured difference between the stiffness at rest and during contraction, and up to a load of 20 units (length approx. 120), the difference must be regarded as real.

#### 4) Isometric contractions (method II a).

Length-stiffness diagram (mean curve from the total material). During isometric contraction, the stiffness of the contracted fibre is greater than in the resting fibre at equilibrium length, the ratio  $\frac{S_c}{S_r} = 5$  decreasing continuously with increasing stretch and converging towards 1 (Fig. 30).

Load-stiffness diagram. The stiffness as a function of the loading is known in the range from isometric contraction at equilibrium length to a stretch of 200. Fig. 33*b* indicates the ratio  $\frac{S_c}{S_r}$  as a function of load. It is apparent that the mean error around the equilibrium length is large, and the difference in stiffness cannot be considered real for the total material available. The error decreases with increased stretch. However, this large scattering is not accidental, since a closer evaluation of the material proved that the fibres can be classified according to the position of a critical "point of yielding" on the tension-stiffness diagram of the contracted fibre. The course of the loading-stiffness diagram of the individual series of experiments is given in the examples of Fig. 34*a*. Fig. 34*b* represents an ideal diagram. The initial stiffness during contraction is somewhat higher than when at rest and increases rapidly with augmented loading. The stiffness shows here a very sharp maximum (the point of yielding) and then decreases rapidly with increased load. At greater loads, the contraction

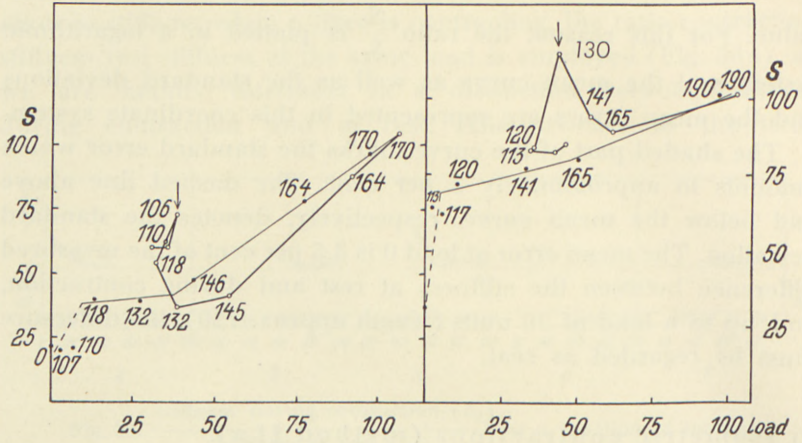


Fig. 34a. Stiffness-load diagram of individual fibres showing yielding at different points of the stretch diagram.

—●—●— = resting fibre;  
 —○—○— = isometrically contracted fibre.

The figures on the curve denote the fibre length at the resp. loading; the arrows indicate the point of yielding.

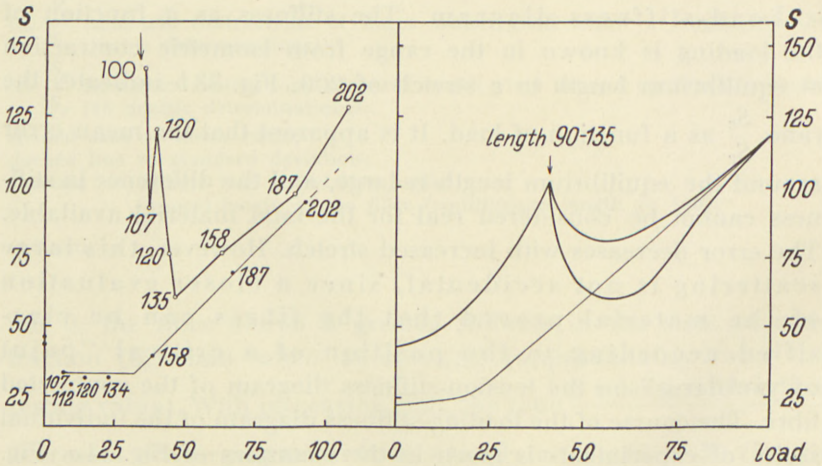


Fig. 34 a.

Fig. 34b. Schematic diagram of stiffness as a function of load at rest and during contraction.

abscissa = load in relative units;  
 ordinate = stiffness in relative units.



curve can fall below the curve of the resting fibre. At maximal elongations,  $S_c$  approaches  $S_r$ . The point of yielding is situated from below equilibrium length up to length 135.

In all cases, the stiffness during contraction is considerably greater than at rest, as long as the yielding point is not exceeded.

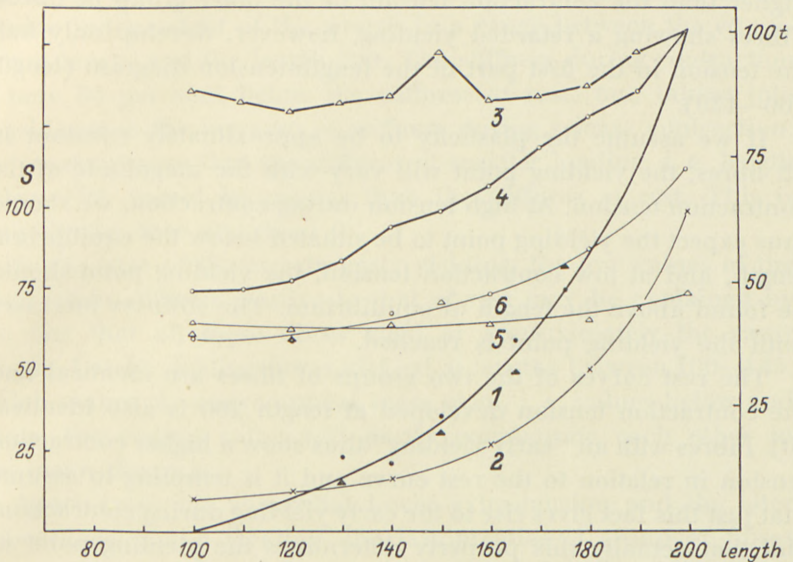


Fig. 35. Length-tension and length-stiffness diagrams of fibres with a yielding below and above length 100, respectively.

- (1) common length-tension diagram of the resting fibre;
  - (2) common length-stiffness diagram of the resting fibre;
  - (3) length-tension diagram, isometric contraction, yielding below length 100;
  - (4) length-tension diagram, isometric contraction, yielding above length 100;
  - (5) length-stiffness diagram, isometric contraction, yielding below length 100;
  - (6) length-stiffness diagram, isometric contraction, yielding above length 100;
- abscissa = length of the fibre (equilibrium length = 100);  
 ordinate = (left) stiffness in relative units;  
 (right) tension in relative units.

Then, the contraction stiffness approaches that of the resting fibre. A uniform treatment of the material is rendered difficult because of the great variation of the yielding point from fibre to fibre. Therefore, we differentiate between fibres having the yielding point below the equilibrium length ("early yielding") and fibres with the yielding point above the length of equilibrium ("late yielding") (Figs. 33c and d). Between these two groups, all transitory types may naturally be found

(Fig. 33e), but when these two characteristic groups are considered separately, the mean length-tension diagrams also reveal typical differences (Fig. 35). Fibres with a yielding point below the equilibrium length develop a contraction tension which is almost constant over the entire range of stretch, and which is much higher than the contraction tension of the other group of fibres. Fibres showing a retarded yielding, however, develop only half the tension in the first part of the length-tension diagram (length 100—130).

If we assume the plasticity to be approximately constant in all fibres, the yielding point will vary with the magnitude of the contraction tension. At high tension during contraction, we should thus expect the yielding point to be situated below the equilibrium length, and at low contraction tension, the yielding point should be found above the length of equilibrium. The stiffness increases until the yielding point is reached.

The rest curves of the two groups of fibres are identical and the contraction tension developed at length 200 is also identical (0). Fibres with an "early yielding" thus show a higher contraction tension in relation to the rest curve and it is tempting to assume that just this fact gives rise to the early yielding during contraction, and that actually this property determines the yielding point of the fibre.

The mean curve of stiffness as a function of load in the late yielding group of fibres indicates the following. (cf. Fig. 33c).

At a load 50 (length 100), the stiffness of the contracted fibres is about 80 per cent above the stiffness at rest at the same loading. It must, however, be taken into consideration that the fibres compared are of different lengths (cf. elasticity moduli, p. 80). In the range between the equilibrium length (load 50) and the shortest length during contraction (load 0), the load-stiffness diagram is not known (only a few single observations are available). From the above described determinations during release contractions it is known that the contraction stiffness at load 0 is about twice that at rest. At stretch from load 50 to 65, the mean stiffness approaches that at rest. The slight deviation from the resting value at a load 75—90 cannot be considered real. The fibres which could endure a stretch exceeding a load 100 indicate that stiffness at rest and during contraction at this



elongation are still approximately identical. The yielding load of the fibres described here is presumably on the average 50 units.

On the mean curve of fibres with an early yielding (Fig. 33*d*), the stiffness as a function of the loading indicates the following results. A curve cannot be drawn from the measurements of this group, since the fibre develops almost constant tension independent of the stretch in a range between the equilibrium length and the length 200. The stiffness during contraction is here 30 per cent below the stiffness at rest; but, taking into consideration the increase in stiffness during release contraction, we must suppose that the stiffness at smaller loading, i. e. length below 100, would be greater than the stiffness at rest. This is actually the case at a load 0.

In the case of fibres with early yielding, the low values of the contraction stiffness relative to that at rest may be explained by the fact that all these fibres yield at approximately the same length. Lately yielding fibres yielded at lengths between 100—135, which makes the curve appear more even, i. e. values below and above the resting value will partly compensate each other in the mean diagram.

Apart from the somewhat lower extra-tension and the later appearance of the yielding, the last mentioned group of fibres does not show any indication of reduced functional qualities. Their irritability, stiffness variation, the character of the release diagram, and the endurance of the fibre are not different from fibres with early yielding.

##### 5) Partial release from isometric contraction.

Length-tension diagram. In the case of partial release (Fig. 30, 3), no difference could be found between the above discussed groups of fibres. When a fibre is brought into isometric contraction and then released, the release curve does not follow the curve of the isometric maxima but shows a much steeper course, a phenomenon which has already been described in connection with the semi-dynamic length-tension diagrams (p. 43). The gradient is similar to that at rest with the load 100. The gradient apparently decreases at higher stretch from length 170—200. At these elongations, the curve of isometric maxima and that of release contraction approach each other. Theoretically,

there is no difference between the releases discussed here and the above mentioned semi-dynamic experiments. The semi-dynamic curves show loops due to viscosity (Fig. 20), while linear curves are obtained by the technique employed here. The present release length-tension diagrams must be considered a "mean line" of the loops in semi-dynamic curves.

**Length-stiffness diagram.** The length-stiffness diagrams of release contractions (Fig. 30, 6) are of the same type as the release length-tension diagrams. It must, however, be emphasized that the stiffness—in contrast to the tension—does not converge towards 0 but towards a given initial value.

**Release stiffness relative to rest stiffness.** As previously mentioned, the stiffness at rest varies over a wide range (loads 25–100, length 130–200) proportional to the load,  $\frac{\Delta S}{\Delta P} = k$ . The same was the case in release contractions for the corresponding extensions, since connecting lines between the coordinates of stiffness and tension of isometric contraction and the corresponding coordinates of release contraction are parallel with the rest curve. Consequently,  $\frac{\Delta S}{\Delta P}$  (isom.) and  $\frac{\Delta S}{\Delta P}$  (release) are approximately equal.

#### 6) Elasticity moduli at rest and during contraction.

On the basis of the measured stiffness  $\left(\frac{\Delta \text{force}}{\Delta \text{length}}\right)$  and the relative lengths, the relative elasticity moduli could be calculated. It is a supposition of this calculation that the fibre volume remains constant during stretch and isometric contraction. Measuring the fibre at different extensions by means of a Fedoroff microscope stage, where the fibre diameter can be determined in different planes, BUCHTHAL and KNAPPEIS<sup>1</sup> found the fibre volume to be constant within the limits of microscope accuracy. Volume changes found in total muscle by ERNST (1925) and by MEYERHOF and collaborators (1933) are considerably smaller than those which are detectable microscopically.

Elasticity modulus =  $\frac{\text{stiffness } (S)}{\text{cross section } (q)} \times \text{length } (l)$ . For the same fibre at various elongations, the modulus is proportional

<sup>1</sup> Unpublished experiments.



to the product  $S \times l^2$ , since the cross section is inversely proportional to the length, if the volume is constant (cf. p. 13).

Apart from the modulus as a function of stretch, Fig. 36 exhibits a length-tension diagram where the tension is calculated as

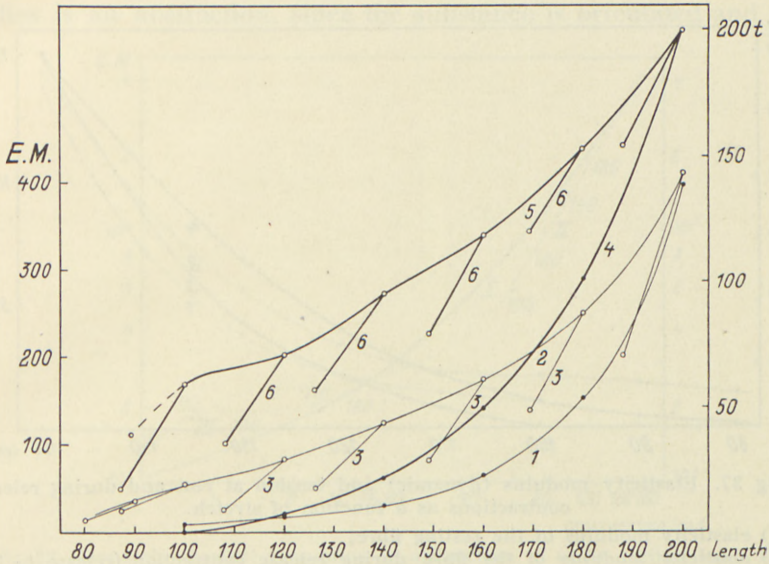


Fig. 36. Elasticity modulus (dynamic) and tension of the single fibre at rest, during isometric contraction, and during release contraction as a function of stretch.

- (1) elasticity modulus of the resting fibre;
  - (2) elasticity modulus of the isometrically contracted fibre;
  - (3) elasticity modulus of the fibre during partial release contractions;
  - (4) length-tension diagram of the resting fibre;
  - (5) length-tension diagram of the isometrically contracted fibre;
  - (6) length-tension diagram of the fibre during partial release contractions;
- abscissa = length of the fibre (equilibrium length = 100);  
 ordinate = (left) dynamically determined elasticity modulus in relative units;  
 (right) cross section loading in relative units.

tension per cross section unit, i. e. the figures of the ordinates (right side of the figure) are proportional to the cross section loading.

When calculating the elasticity modulus, the stiffness values are based on those of a "unit body". It is, therefore, reasonable to base the corresponding loadings upon a unit cross section. Figs. 36 and 37 show the elasticity modulus and the cross section loading at rest, during isometric contraction, and during release contraction as a function of the length of the fibre. These curves

do not reveal any fundamental deviation from the above described length-tension and length-stiffness diagrams. In the last region of stretch, however, they show a relatively steeper slope, as the length directly enters the calculation of the cross section loading as  $l^1$  and of the modulus as  $l^2$ .

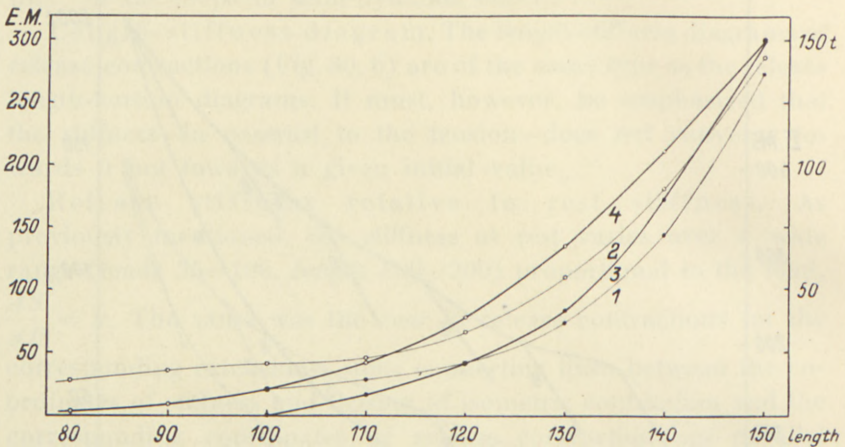


Fig. 37. Elasticity modulus (dynamic) and tension at rest and during release contractions as a function of stretch.

- (1) elasticity modulus of the resting fibre;
- (2) elasticity modulus of the fibre during release contraction (release to the same tension as at rest);
- (3) length-tension diagram, rest;
- (4) length-tension diagram, release contractions;

abscissa = length of the fibre (equilibrium length = 100);

ordinate = (left) dynamically determined elasticity modulus in relative units;  
(right) cross section load in relative units.

The elasticity modulus as a function of the cross section loading is represented in Fig. 38. The difference between the moduli at rest, during isometric contraction, and during release contraction reduced to the same loading is very small. At loads 0—7, the modulus of the contracted fibre (release contraction) is higher than the modulus at rest. At a loading 0—3, the difference amounts to about 30 per cent. In the range 30, the elasticity modulus of the contracted fibre (isometric contraction) is about 25 per cent below the value at rest. The difference decreases at higher loading and becomes zero at the load 100. The measurements of stiffness indicate that scattering in the range 0—3 is relatively low and, in this range, the difference between the elasticity moduli at rest and during contraction



is beyond the limit of error. In the range 30 and at higher load, the scattering is considerable, due to the different position of the yielding point; the latter deviation from rest on the mean curve cannot with certainty be considered real.

As previously emphasized, the modulus of highly elastic bodies is an abstraction, since the substance is orientated and the

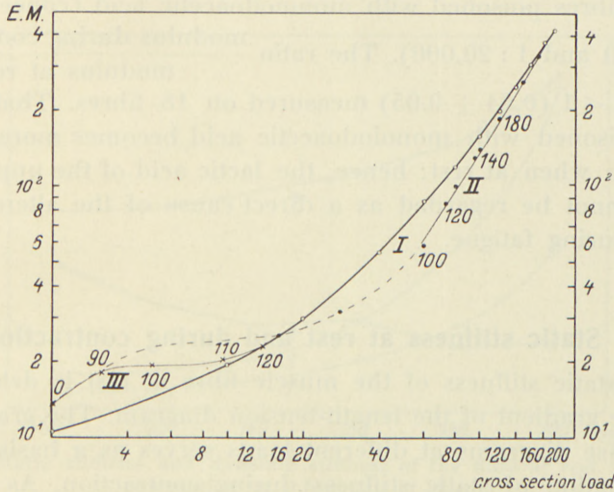


Fig. 38. Dynamic elasticity modulus as a function of cross section load. Mean curve.

- I. resting fibre;
- II. isometric contraction;
- III. release contraction (release to the same tension as at rest).

The figures on the curve denote the length of the fibre at the respective load.  
 abscissa = cross section load in relative units, log scale;  
 ordinate = elasticity modulus in relative units, log scale.

degree of orientation becomes greater at higher stretch. Therefore, the elasticity modulus is less suited to characterize the mechanical composition of the substance than the directly measured stiffness.

7) Elasticity modulus during contraction of a fatigued fibre.

The elasticity modulus of a non-fatigued fibre during release contraction from equilibrium length to the tension 0 is considerably larger than that of the resting fibre. The ratio

$$\frac{\text{modulus during contraction}}{\text{modulus at rest}} = 1.97 \pm 0.13$$

(measured on 19 single fibres). In a fibre fatigued by numerous

preceding contractions (up to 50 contractions), the stiffness during contraction increases much less, and the coefficient is  $1.13 \pm 0.06$  (measured on 15 fibres).

In order to investigate whether this change of stiffness is connected with the production of lactic acid in a fibre fatigued by long-lasting series of contractions, the moduli were studied on fatigued muscle fibres poisoned with monoiodoacetic acid (concentration 1 : 10,000 and 1 : 20,000). The ratio  $\frac{\text{modulus during contraction}}{\text{modulus at rest}}$  becomes  $< 1$  ( $0.84 \pm 0.05$ ) measured on 18 fibres. That is, the fibre poisoned with monoiodoacetic acid becomes more extensible than when at rest; hence, the lactic acid of the unpoisoned fibre cannot be regarded as a direct cause of the altered coefficient during fatigue.

## B. Static stiffness at rest and during contraction.

The static stiffness of the muscle fibre at rest is determined from the gradient of the length-tension diagram. The gradient of the release diagrams at different loads serves as a basis for the determination of static stiffness during contraction. As already discussed, the curve of the isometric maxima is irreversible and therefore unsuited for a calculation of stiffness.

In the following sections, the material from measurements of the statically determined stiffness and of the elasticity modulus is treated in the same way as the dynamically determined material.

### 1) Static stiffness as a function of stretch.

In analogy to dynamic stiffness, static stiffness at rest increases with increasing elongation and amounts to about half the dynamic stiffness (Fig. 39, 1). During contraction, however, the static stiffness deviates essentially from the dynamic measurements, as static stiffness decreases with increasing stretch.

During contraction at equilibrium length,  $S_c$  lies about 10 times above the stiffness at rest (Fig. 39, 2). At length 180, the stiffness at rest is equal to that during contraction, and at length 200, the stiffness during contraction, is only about 50 per cent of the stiffness at rest.

Compared with the shortening in equilibrium length, the change in stiffness during contraction has not been considered an impor-



tant factor for the amount of tension developed by the muscle. However up to length 150 the increase in tension during isometric contraction is predominantly due to the increase in stiffness, as shown by the following example.

When the resting fibre is stretched 30 units (from 100—130), the tension developed amounts to only 15 tension-units. During

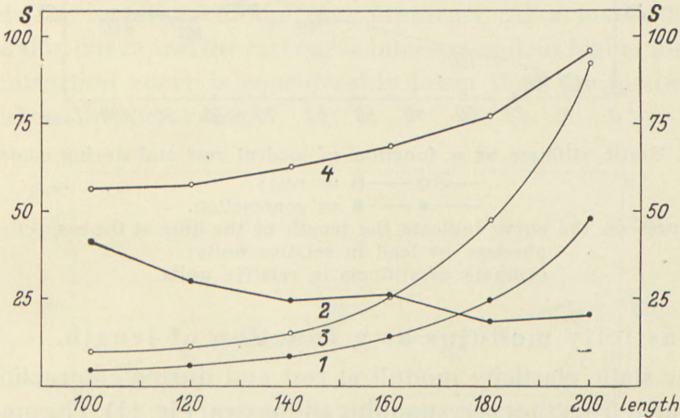


Fig. 39. Static stiffness and dynamic stiffness of the fibre at rest and during contraction as a function of stretch.

- (1) static stiffness, rest;
  - (2) static stiffness, contraction;
  - (3) dynamic stiffness, rest;
  - (4) dynamic stiffness, contraction;
- abscissa = length of the fibre (equilibrium length = 100);  
ordinate = stiffness in relative units.

isometric contraction at length 100, on the other hand, the equilibrium length shortens 30 units to length 70 (cf. release diagram) while the tension amounts here to four times that of the resting fibre, (60 tension-units).

2) Static stiffness as a function of loading.

Static stiffness at rest shows an approximately linear course as a function of load. During contraction, we find corresponding relations, as already described when discussing stiffness-length diagrams (Fig. 40); the stiffness decreases with increasing length and, consequently, also with increasing loading. At a load 60, the stiffness is twice that at rest; at a load 72, the

rest curve and contraction curve intersect and then the contraction stiffness decreases to about half that at rest.

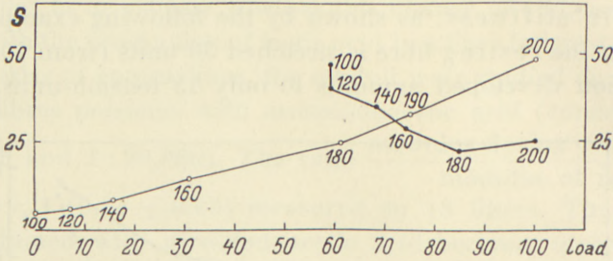


Fig. 40. Static stiffness as a function of load at rest and during contraction.

—○—○ = rest;  
—●—● = contraction.

The figures on the curve indicate the length of the fibre at the respective load.  
abscissa = load in relative units;  
ordinate = stiffness in relative units.

### 3) Elasticity modulus as a function of length.

The static elasticity moduli at rest and during contraction are calculated from the corresponding stiffnesses (Fig. 41). The modulus

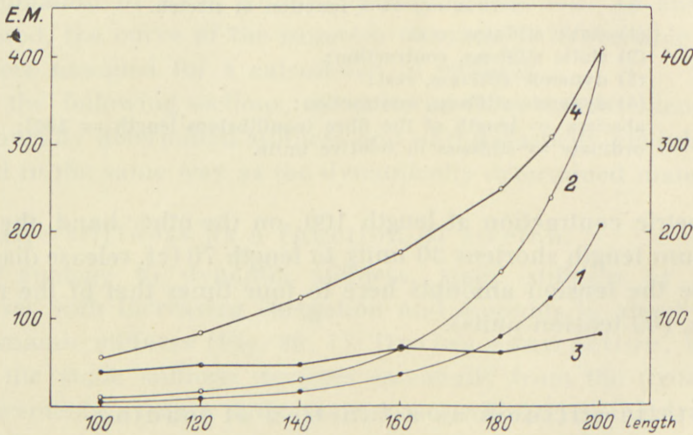


Fig. 41. Static and dynamic elasticity moduli of the fibre at rest and during contraction as a function of stretch.

(1) static elasticity modulus, rest;  
(2) dynamic elasticity modulus, rest;  
(3) static elasticity modulus, contraction;  
(4) dynamic elasticity modulus, contraction;  
abscissa = length of the fibre (equilibrium length = 100);  
ordinate = elasticity modulus in relative units.



during contraction exceeds the modulus at rest up to a length 175, where the curves intersect each other.

4) Elasticity modulus as a function of cross section load.

With a cross section load 60—80, the static modulus during contraction is somewhat higher than the modulus at rest (Fig. 42) when referred to the same load; however, the difference scarcely exceeds the accuracy of the measurements. At a load 100, the contraction curve and the rest curve intersect and, at higher loading, the contraction curve is considerably lower than the modulus at rest (about 50 per cent).

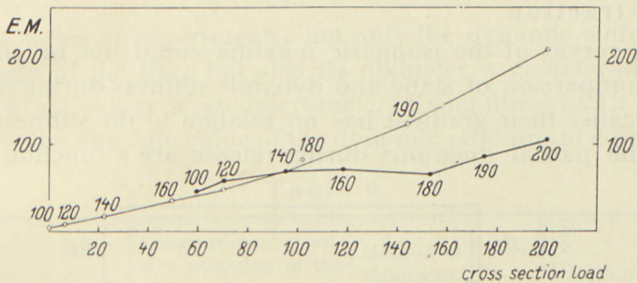


Fig. 42. Static elasticity modulus at rest and during contraction as a function of cross section loading.

—○—○ = rest;  
 —●—● = contraction.

The figures on the curve indicate the length of the fibre at the respective loading.

abscissa = cross section load in relative units;  
 ordinate = elasticity modulus in relative units.

C. Comparison of static and dynamic stiffness.

1) Resting fibre.

A comparison of the gradient of the single length-tension diagrams in dynes/cm with the measured dynamic stiffness in dynes/cm reveals that the dynamic stiffness measured in vibration experiments is about twice the static stiffness. The ratio  $\frac{S_{static}}{S_{dynamic}}$  varies only slightly with stretch and amounts on an average to 0.5 (variation between 0.45 and 0.6; Fig. 43). This means that only approximately half of the extensible material participates in the rapid length alterations produced by vibrations.

Hence, the viscosity is not uniformly distributed over the extensible elements of the fibre and part of this is not hindered by viscosity. (For a more detailed discussion of the viscosity and elasticity distribution see p. 105.)

In a new series of experiments (carried out at another time of the year and on different frogs), we found the ratio  $\frac{S_{\text{static}}}{S_{\text{dynamic}}} = 0.7$  (variation between 0.6 and 0.8). The deviation from the above described experiments was not surprising, as the first mentioned material showed other elastic properties, especially an inferior extensibility.

## 2) Contraction.

The curves of the isometric maxima could not be employed for a comparison of static and dynamic stiffness during contraction, because their gradient has no relation to the stiffness. However, the partial diagrams during release are a function of stiff-

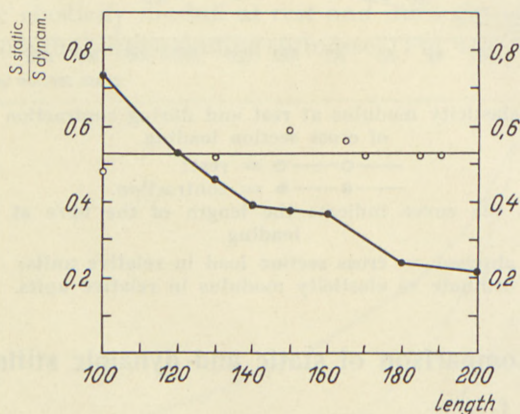


Fig. 43. Relation between static stiffness and dynamic stiffness as a function of stretch, at rest and during contraction.

—○—○ = rest;  
 —●—● = contraction;  
 abscissa = length of the fibre (equilibrium length = 100);  
 ordinate =  $\frac{\text{static stiffness}}{\text{dynamic stiffness}}$ .

ness, since they are reversible to the same extent as the rest curves.

$\frac{S_{\text{static}}}{S_{\text{dynamic}}}$  during contraction varies considerably with the stretch (Fig. 43). At equilibrium length, the ratio between static



and dynamic stiffness is highest (0.75), decreasing until the value 0.2 is reached at the length 200. It would be reasonable from this fact to conclude that below the equilibrium length the ratio will approach unity, so that the total elastic mass is uniformly involved in the elastic deformations. At higher stretch, smaller and smaller parts of the fibre participate in the rapid elastic length alterations; at a stretch around 180—200, for example, only  $\frac{1}{5}$  of the total elasticity of the fibre is at the disposal of the rapid vibrations (5 per sec.) here applied; the rest is blocked by viscosity.

#### D. Absolute values of the elasticity modulus of the striated muscle fibre.

In a series of experiments, not only the dynamic stiffness and the length of the fibre but also its diameter were determined, by means of an ocular screw micrometer. Using fibres of 12 different muscles, the absolute value of the dynamic modulus at equilibrium

Table 6.

Preparation	Longitudinal elasticity modulus of the resting frog muscle in dynes $\times$ cm <sup>-2</sup> *	Method of determination	Author
Total muscle . . . . .	$0.6 \times 10^6$	static	E. WEBER (1846)
» . . . . .	$0.94 \times 10^6$	static	WUNDT (1858)
» . . . . .	$(0.01 - 1.0) \times 10^6$	static	TRIEPEL (1902)
» . . . . .	$(2.7 - 3.9) \times 10^{6**}$	static	BOUCKAERT a. o. (1930)
» . . . . .	$(0.09 - 0.17) \times 10^6$	static	WÖHLISCH a. o. (1930)
» . . . . .	$(0.01 - 0.15) \times 10^6$	static	WÖHLISCH and CLAMANN (1936)
» . . . . .	$0.15 \times 10^6$	dynamic	STEINHAUSEN (1926)
0.5 mm part of single fibre . . . . .	$(0.7 - 2.8) \times 10^6$	static	SICHEL (1934)
non-injured single fibre . . . . .	$0.5 \times 10^6$	static	BUCHTHAL (1942)
» . . . . .	$(0.81 \pm 0.11) \times 10^6$	dynamic	BUCHTHAL (1942)
Slightly vulcanized caoutchouc . . . . .	$10 \times 10^6$	static	K. H. MEYER (1940)
Caoutchouc, not specified . . . . .	$0.5 \times 10^6$	static	WÖHLISCH (1940)
Myosin thread . . . . .	$2.0 \times 10^6$	static	H. H. WEBER

\* For the transformation of an elasticity modulus given in kgm/mm<sup>2</sup> into the c.g.s.-system, the first mentioned is multiplied by  $1.02 \times 10^7$ .

\*\* Temperature: 0° C.

length is on an average  $(0.81 \pm 0.11) \times 10^6$  dynes  $\times$  cm<sup>-2</sup>. The static modulus is between 75 and 50 per cent of the dynamic modulus and amounts on the average to  $0.5 \times 10^6$  dynes  $\times$  cm<sup>-2</sup>.

Table 6 shows measurements of elasticity moduli available from total muscles and single fibres at rest. Most of the determinations were carried out at equilibrium length or at a slight initial tension.

### E. Static stiffness of A and I at rest and during contraction.

The stiffness at rest is obtained from the curve of the total static softness ( $\frac{1}{S} = \frac{1}{S}A + \frac{1}{S}I$ ) which is taken from the curve of static stiffness (Fig. 39, 1) and from the ratio  $\frac{\text{softness of A}}{\text{softness of I}}$ ; the latter is identical with the ratio between the increase in length of the two substances at a small elongation of the whole fibre. At rest, the length of A and I as a function of stretch is used to determine the ratio  $\frac{\Delta A}{\Delta I}$  (Fig. 26). During contraction, however, the gradient of the curve of isometric contraction is unsuitable for stiffness determinations because of its irreversibility. The ratio  $\frac{\Delta A}{\Delta I}$  may be found, however, from release- and stretch contractions. As previously discussed, these curves represent a reversible length-tension alteration. From the ratio  $\frac{\Delta A}{\Delta I}$  and the sum of softness A and softness I, the softnesses of both substances may be derived.

#### 1) Static softness of A and I at rest as a function of stretch.

The upper curve of Fig. 44 represents the softness of the whole fibre (A + I), and the distance from the x-axis to the lower curve (Fig. 44, 2) is an expression of the softness of I. The distance between both curves is a measure of the softness of the A substance. The softness of both substances decreases uniformly with increasing stretch. The softness of A is the greater, mainly due to its greater length (cf. the moduli, p. 95). The ratio  $\frac{S_A}{S_I}$  (Fig. 45, 1) indicates that the softness of A at equilibrium length is about twice that of I, a ratio which increases to about 2.5 at length 200.



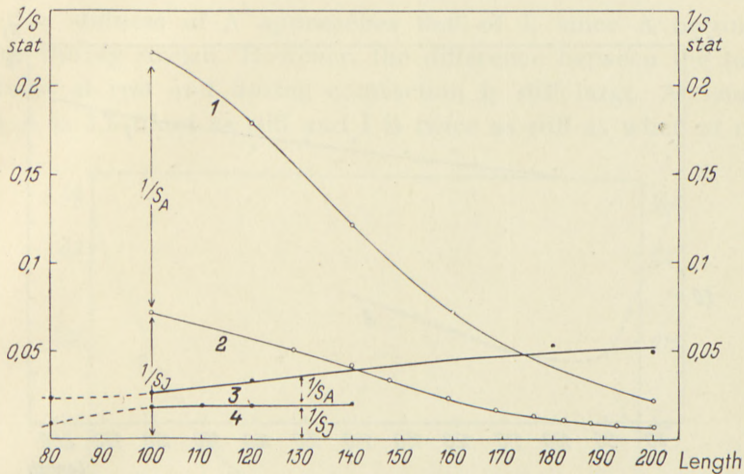


Fig. 44. Static softness ( $\frac{1}{S}$ ) of A and I at rest and during contraction as a function of stretch.

(1)  $\frac{1}{S}$  of A + I at rest;

(2)  $\frac{1}{S}$  of I at rest.

The difference between curve (1) and curve (2) corresponds to  $\frac{1}{S}$  of the A substance at rest.

(3)  $\frac{1}{S}$  of A + I during contraction;

(4)  $\frac{1}{S}$  of I during contraction.

The difference between curve (3) and curve (4) corresponds to  $\frac{1}{S}$  of the A substance during contraction.

abscissa = length of the fibre (equilibrium length = 100);

ordinate =  $\frac{1}{S}$  (static) in relative units.

2) Static softness of A and I during contraction as a function of stretch.

The ratio  $\frac{\Delta A}{\Delta I}$  (release contraction Fig. 45, 2) is known in the range of length 100—140 and, furthermore, at lengths 80—100 from interpolation (determination of the gradients in the length-tension diagram of the single substances, Figs. 27 and 28). The remarkable increase in stiffness during contraction, referring to the same length as when at rest (Fig. 44), originates from a change in stiffness of both substances. At equilibrium length, A becomes 7 times stiffer and I becomes 4 times stiffer than when at rest (Fig. 46). At stretch above equilibrium length, the con-

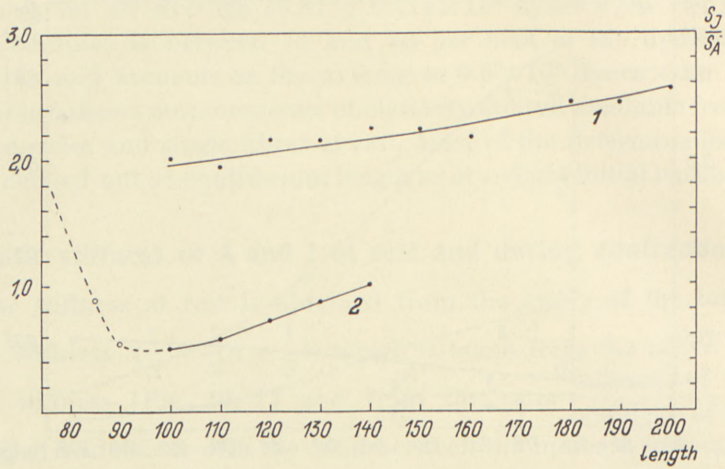


Fig. 45.  $\frac{\text{Softness of A}}{\text{Softness of I}}$  at rest and during contraction as a function of stretch.

- (1)  $\frac{\text{softness A}}{\text{softness I}}$  at rest;
- (2)  $\frac{\text{softness A}}{\text{softness I}}$  during contraction;

abscissa = length of the fibre (equilibrium length = 100);

ordinate =  $\frac{\text{softness A}}{\text{softness I}} = \frac{S_I}{S_A}$ .

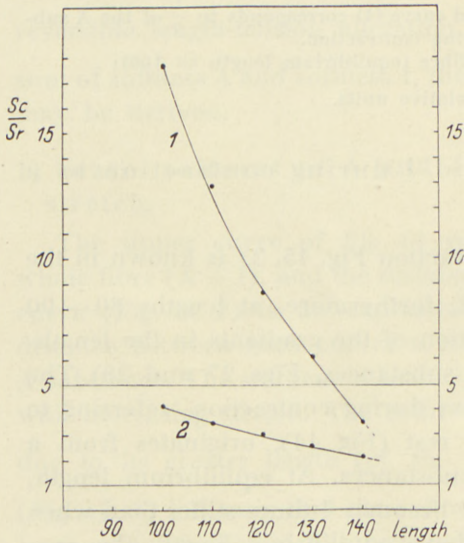


Fig. 46.  $\frac{\text{Stiffness during contraction}}{\text{Stiffness at rest}}$  of the A and I substance as a function of stretch of the fibre.

- (1)  $\frac{S_c}{S_r}$  A substance;
- (2)  $\frac{S_c}{S_r}$  I substance;

abscissa = length of the fibre (equilibrium length = 100);

ordinate =  $\frac{S_c}{S_r}$ .



traction stiffness of A approaches that of I, since A becomes softer during stretch. However, the difference between the total stiffness at rest and during contraction is still large. At length 140, A is 3.5 times as stiff and I is twice as stiff as when at rest

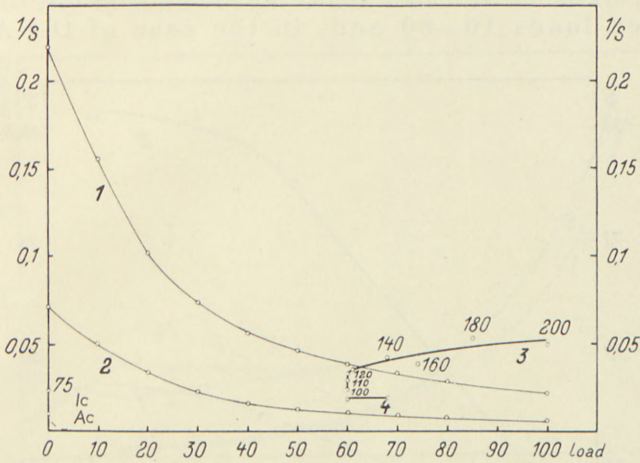


Fig. 47. Static softness  $\frac{1}{S}$  of A and I at rest and during contraction as a function of loading.

(1)  $\frac{1}{S}$  of A and I at rest;

(2)  $\frac{1}{S}$  of I at rest.

The difference between curve (1) and curve (2) corresponds to  $\frac{1}{S}$  of A at rest.

(3)  $\frac{1}{S}$  of A + I during contraction;

(4)  $\frac{1}{S}$  of I during contraction.

The difference between curve (3) and curve (4) corresponds to  $\frac{1}{S}$  of A during contraction. The figures on the curve denote the length of the fibre at the respective load.

abscissa = load in relative units;

ordinate = softness  $\frac{1}{S}$  in relative units.

(Fig. 46). At lengths below 100, the stiffness of A and I shows a peculiar course, the total stiffness being almost constant; the distribution between A and I, however, being changed (Fig. 44). At length 100, A is almost twice as stiff as I, and at length 80, I is about twice as stiff as A. The large increase in stiffness found from rest to contraction at low loading must first of all be ascribed to the I substance.

## 3) Static softness of A and I as a function of load.

Resting fibre. The static softness of A and I at rest as a function of load decreases continuously with increasing load (Fig. 47). The curve of stiffness (Fig. 48) as a function of load shows for the I substance a straight course between loads 10—60 and, in the case of the A sub-

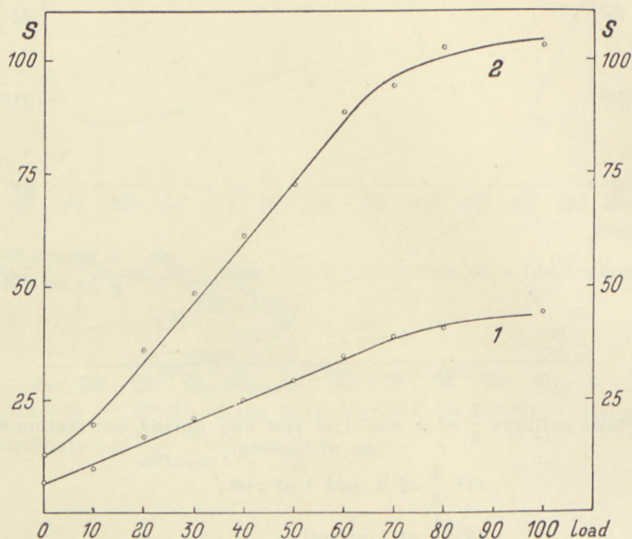


Fig. 48. Static stiffness of A and I at rest as a function of loading

- (1) Stiffness of the A substance;  
 (2) stiffness of the I substance;  
 abscissa = loading in relative units;  
 ordinate = stiffness in relative units.

stance, the curve is linear between loads 0—70. This corresponds to the linear interdependence of loading and dynamic stiffness (Fig. 30). The structural interpretation of this course of the curve will be given in a later section.

Contracted fibre. The static softness of the single substances is known from length 100—140, corresponding to a load 60—70 and, further, at a load 0 (Fig. 47). At load 0, I is about twice as stiff as A, and the total stiffness is approximately the same as up to load 60. At load 60, the stiffness of A decreases suddenly (yielding) and then continuously, while the stiffness of I remains constant.



F. Elasticity moduli of A and I.

1) Elasticity moduli of A and I as a function of stretch.

Resting fibre. The moduli of A and I at rest are not markedly different referring to the same fibre length (Fig. 49). On an average, the elasticity modulus of the A substance is about 20 per cent

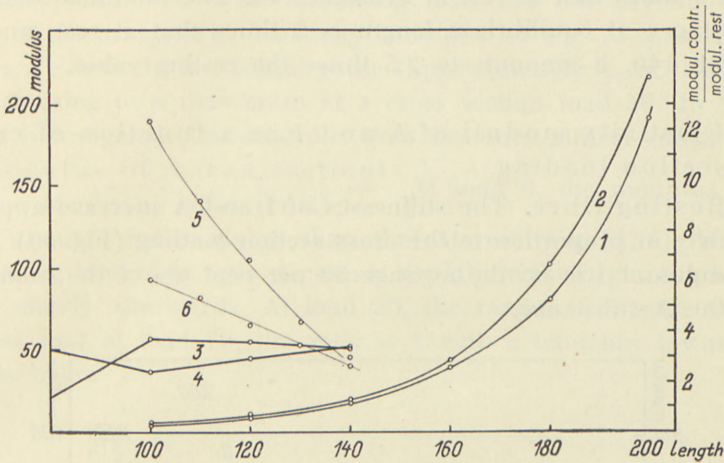


Fig. 49. Static elasticity modulus (EM) of A and I at rest and during contraction as a function of stretch.

- (1) EM of the A substance at rest;
- (2) EM of the I substance at rest;
- (3) EM of the A substance during contraction;
- (4) EM of the I substance during contraction;
- (5)  $\frac{\text{modulus A contraction}}{\text{modulus A rest}}$ ;
- (6)  $\frac{\text{static modulus I contraction}}{\text{static modulus I rest}}$ ;

abscissa = length of the fibre (equilibrium length = 100);

ordinate = (left) static elasticity modulus in relative units;

(right)  $\frac{\text{modulus contraction}}{\text{modulus rest}}$ .

below that of I. The moduli increase uniformly with increasing length and at a length 200, they are about 35 times higher than at equilibrium length.

Contracted fibre. At equilibrium length, the elasticity modulus of A is about 50 per cent higher than that of I. The modulus of A decreases with increasing stretch while that of I increases, the moduli becoming equal at a length 140. In the range below the equilibrium length, the ratio  $\frac{\text{modulus A}}{\text{modulus I}}$  is

reversed in analogy to the stiffness of the substances; the modulus of the I substance is about 2.5 times that of A. Compared with those at rest, the moduli of both substances are considerably higher (Fig. 49, 5, 6). At equilibrium length, the modulus of the A substance is thus 14 times higher than when at rest, decreasing to 2.5 times that at rest at a length 140. The modulus of the I substance at equilibrium length is 6 times that at rest, and at length 140, it amounts to 2.5 times the resting value.

## 2) Elasticity moduli of A and I as a function of cross section loading.

Resting fibre. The stiffnesses of I and A increase approximately in proportion to the cross section loading (Fig. 50). The modulus of I is on the average 30 per cent above the modulus of the A substance.

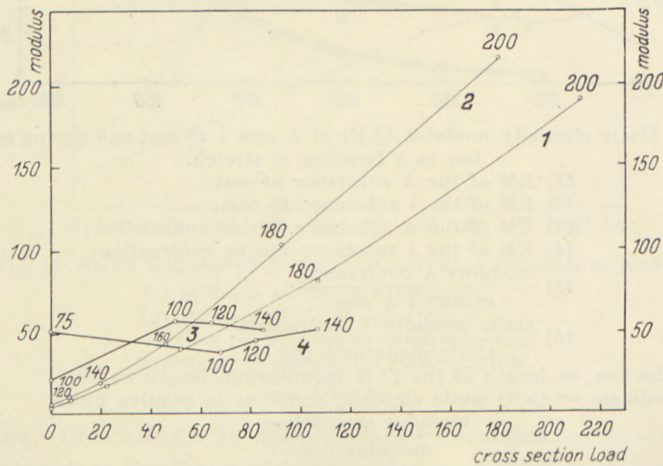


Fig. 50. Static elasticity modulus of A and I at rest and during contraction as a function of cross section loading.

- (1) EM of the A substance at rest;
- (2) EM of the I substance at rest;
- (3) EM of the A substance during contraction;
- (4) EM of the I substance during contraction.

The figures on the curve denote the length of the fibre at the respective load.  
abscissa = cross section load in relative units

(load 100 = cross section load 200 = mean length 200);  
ordinate = elasticity modulus in relative units.

Contracted fibre. When studying the elasticity moduli at rest and during contraction, the modulus



as a function of the cross section loading represents an elasticity constant which is best suited for comparison.

The modulus of the I substance does not vary considerably and at the load 0, it is 2.5 times above the modulus of A. The variations observed with increasing load are not beyond the limit of accuracy. The elasticity modulus of the A substance shows a relatively low initial value (approximately  $\frac{1}{3}$  of that of I) increasing to a maximum at a cross section load 50. In the range investigated, the modulus then becomes almost constant.

Modulus of A (contraction)  
Modulus of A (rest). At load 0, the modulus of A is about 5 times higher than that at rest (Fig. 51, 1). With increasing load, this ratio decreases rapidly in the beginning and more slowly afterwards. At load 30, the modulus is twice that at rest and at load 70, the ratio is 1 with a tendency towards values below 1.

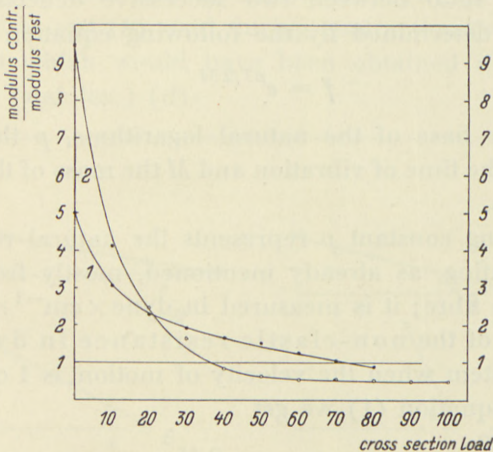


Fig. 51.  $\frac{\text{Modulus contraction}}{\text{Modulus rest}}$  as a function of cross section load.

(1)  $\frac{\text{Modulus contraction}}{\text{Modulus rest}}$  of the A substance;

(2)  $\frac{\text{Modulus contraction}}{\text{Modulus rest}}$  of the I substance;

abscissa = cross section load in relative units;

ordinate =  $\frac{\text{modulus contraction}}{\text{modulus rest}}$ .

$\frac{\text{Modulus of I (contraction)}}{\text{Modulus of I (rest)}}$ . At load 0 (Fig. 51, 2), the ratio is 10, decreasing rapidly with increasing load. At load 35, the ratio is 1, and at load 60–100, the ratio is 0.5.

### Determination of the damping constant (viscosity) of the single muscle fibre.

A preceding section (p. 67) dealt with vibration experiments in which the dynamic stiffness was determined from a change in the period of vibration. The same experiments served, further, for the measurement of the vibration amplitude which was found to decrease exponentially with time. Hence, we are here concerned with periodic, damped oscillations. The decrease in vibration energy originates mainly from the muscle fibre itself and is an expression of its viscosity. In a vibrating system, the damping rate, i. e. the ratio between two successive deflections to the same side, is determined by the following equation

$$f = e^{pT/2M} \quad (1)$$

where  $e$  is the base of the natural logarithms,  $p$  the damping constant,  $T$  is the time of vibration and  $M$  the mass of the vibrating system in gms.

The damping constant  $p$  represents the natural resistance to motion originating, as already mentioned, mostly from internal friction in the fibre; it is measured in  $\text{dyne} \times \text{cm}^{-1} \times \text{sec}$  and is an expression of the non-elastic resistance in dynes which retards the system when the velocity of motion is 1 cm per sec.

From the equation (1) we get

$$p = \ln f \frac{2M}{T}. \quad (2)$$

$p$  is independent of the absolute amplitude values of vibration, but depends on the ratio of successive amplitudes and is, thus, proportional to the natural logarithm of this ratio (the logarithmic decrement) and inversely proportional to the period of vibration.

In the previously mentioned vibration experiments, the period of vibration and the single amplitudes were measured. The



amplitudes were plotted as ordinates in a semi-logarithmic coordinate system, the period of vibration being represented as a constant distance on the abscissa. The gradient of these curves is then proportional to the logarithmic decrement. The expression (2) can therefore be written as follows

$$p = \frac{\tan \alpha}{\tan \alpha_e} \times \frac{2M}{T} \tag{3}$$

where  $\tan \alpha$  is the gradient of the curve between the values of the amplitudes and  $\tan \alpha_e$  the slope of a line corresponding to the damping rate  $e$ . The logarithmic graph of the individual deflections indicates that the damping at rest and during contraction is an exponential function. The value of  $p$  found in the single experiments expresses the total damping. In order to find the damping of the fibre, that of the measuring system itself must be subtracted.

Fig. 52 exhibits an example of the course of the amplitude of the vibrating system without muscle fibre (a), of the system + muscle fibre at rest (b), and during contraction (c) and, finally, the gradient which would have been obtained if the damping rate were  $e$  (nat. log.) (d).

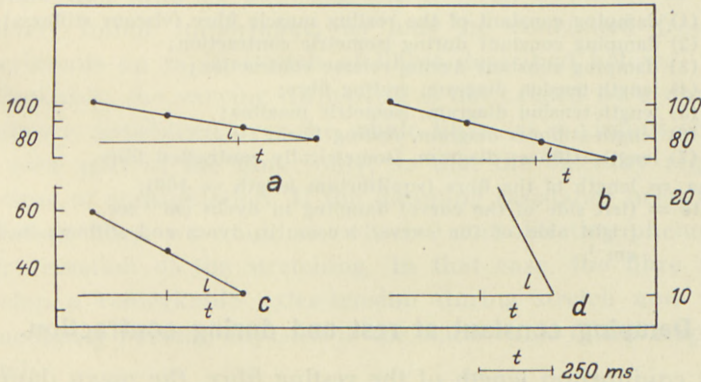


Fig. 52. Amplitude of damped oscillation of

- (a) vibrating system without muscle fibre;
- (b) vibrating system with muscle fibre at rest;
- (c) vibrating system with muscle fibre during isometric contraction;
- (d) gradient of  $f = e$ .

The difference in  $\tan \alpha$  of curves (b) and (c) is a direct expression of the increase in damping during isometric contraction.

abscissa = time,  $t = 250$  msec;

ordinate = log of successive amplitudes.

All damping constants available from curves of this kind are represented in Fig. 53 as a function of stretch. Besides the damping constant at rest and during contraction, the length-tension diagram is plotted in the same figure.

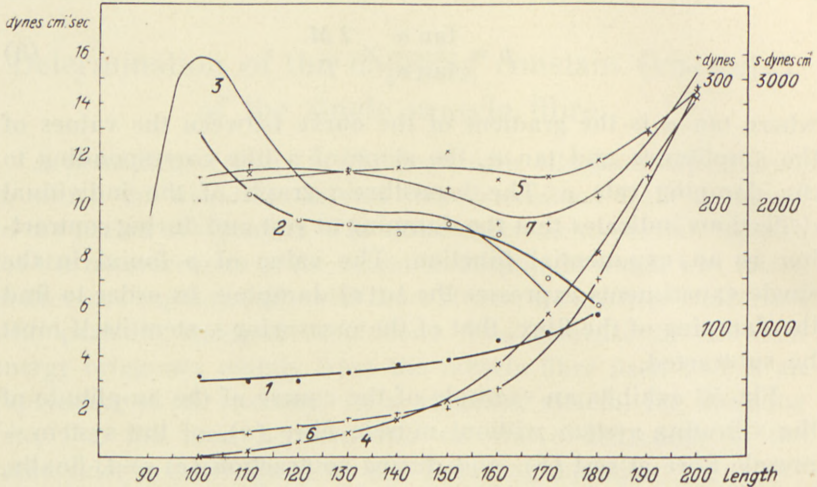


Fig. 53. Mean curve of the damping constant at rest and during contraction as a function of stretch; length-tension and length-stiffness diagrams of the same material.

- (1) damping constant of the resting muscle fibre (viscous stiffness);
- (2) damping constant during isometric contraction;
- (3) damping constant during release contraction;
- (4) length-tension diagram, resting fibre;
- (5) length-tension diagram, isometric maxima;
- (6) length-stiffness diagram, resting fibre;
- (7) length-stiffness diagram, isometrically contracted fibre.

abscissa = length of the fibre (equilibrium length = 100);

ordinate = (left side of the curve) damping in  $\text{dynes cm}^{-1} \text{ sec}$ .

(right side of the curve) tension in dynes and stiffness in  $\text{dynes cm}^{-1}$ .

### Damping constant at rest and during contraction.

At equilibrium length of the resting fibre, the mean damping is  $3 \text{ dynes cm}^{-1} \text{ sec}$ , increasing with augmented stretch to about  $6 \text{ dynes cm}^{-1} \text{ sec}$  at a length 180.

During isometric contraction, the damping increases at equilibrium length up to 4 times the initial value, and decreases then with increasing stretch approximating the damping at rest. The curve of the damping constant of release contraction does



not differ considerably from the curve of the isometric contraction. At lengths below 100, lower dampings are found than at equilibrium length.

The increased damping during contraction is due partly to the "contractile changes" and partly to tension. In the case of release contractions, the tension in this state can be compared with that at rest. In spite of an identical tension at rest and during contraction, a contraction damping is found, which is 3 times as high as the damping at rest. For isometric contraction, this comparison cannot be made with the material available, as we do not know the damping of the resting fibre at tensions similar to those developed during isometric contraction.

On total muscle, GASSER and HILL (1924) found an increase of damping during contraction of about 16 times that at rest, while the difference found on single fibres amounts to 4—5 times that at rest. The difference measured by GASSER and HILL must be mainly ascribed to the friction between fibres, caused by their different states of contraction and stretch.

GASSER and HILL explain the main part of this difference in "viscosity" between rest and contraction by a transport of fluid. Though this kind of damping exists, it is, however, of quantitatively minor importance, as may be concluded from the experiments on rapid stretch of fibres described below.

Probably, the varying damping is not caused by a damping resistance distributed over the whole fibre—as a viscous shunt—but over part of the fibre, only, so that the viscosity regulates the time of consolidation. If the damping resistance occurred in the whole fibre, we would not observe consolidation phenomena after cessation of the stretching. In that case, the fibre would develop a remarkable extra-tension during stretch and would immediately become adjusted to the static value of the respective stretch.

In some experiments in which the vibration frequency was approximately 4 times higher than 5 cycles/sec (the frequency used in most experiments), the same fibre showed a damping considerably smaller than at lower frequency (Fig. 54). This frequency dependence indicates that the damping effect of the fibre on the vibrating system must be in series with the main part of the

elastic mass of the fibre. For a system with a damping in parallel, the damping constant would be independent of the vibration frequency.

Apart from the damping, the course of consolidation after a change of length or tension is an expression of the viscous properties of the fibre, and the first investigations of the magnitude of viscosity were thus based upon the study of elastic after-effects. v. KRIES (1880) found elastic after-effects both in the

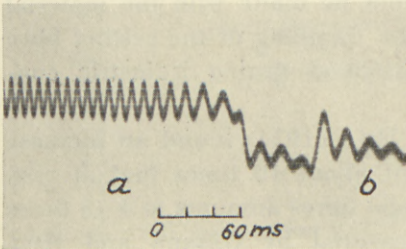


Fig. 54. Vibration experiment at higher frequency of oscillations (Isometric contraction).

At higher frequencies (a) in the range 12—6 cycles/sec, the damping is about  $\frac{1}{4}$  of the damping at 6 cycles (b) per sec.

Time marks = 20 msec.

resting fibre and still more pronounced in the contracted muscle. BLIX (1892) made a precise investigation of the course of consolidation at rest and during contraction and he found that the viscous resistance cannot be distributed uniformly over the muscle substance. GASSER and HILL (1924), however, assumed the viscosity to be arranged as a shunt across the whole muscle and—in contradistinction to v.

KRIES and BLIX, GASSER and

HILL were not able to observe elastic after-effects in the resting muscle. LEVIN and WYMAN (1927) continued GASSER and HILL's experiments and they constructed a mechanical model in agreement with BLIX' interpretation. BOUCKAERT et al. (1930) obtained a purely exponential consolidation curve due to the technique applied which excluded the measurement of rapid variations.

For the purpose of comparison between the elastic after-effects of single fibres and total muscle, the friction between the individual fibres diminishes the applicability of results obtained from total muscle.

### Experiments with rapid stretches.

In order to study the viscosity of the single fibre at rest and during tetanic contraction, a series of experiments were carried out with instantaneous stretches of 1 mm or approximately



10—20 per cent at various elongations. The ratio between the decrease in tension during consolidation and the increase in tension at this sudden increase in length (elastic after-effect) was found to amount to 0.4 at rest at a length 100. This ratio increased to 0.5 at a length 180. During contraction, the elastic after-effect is 0.3 at equilibrium length, increasing to 0.6 at length 170. At further stretch, the contraction values approach the values found at rest. The variation in the elastic after-effects is complementary to the variation of the ratio  $\frac{\text{static stiffness}}{\text{dynamic stiffness}}$  (Fig. 43) which at rest amounts to approximately 0.5. During contraction, the ratio varies between 0.7—0.35 (length 100—160), i. e. an elastic after-effect of 0.3—0.65.

On total muscle, H. H. WEBER (1941) found a very slight elastic after-effect at equilibrium length relative to the increase in tension, while the elastic after-effects at moderate and maximum loading corresponded to those measured in the present experiments. The disagreement in the case of the equilibrium length is presumably due to a coarse mechanical adjustment of individual fibres of the muscle, a process which is not accompanied by essential changes of the structure and, therefore, is of a purely elastic type. The elastic after-effect in the myosin thread (which is about 10 per cent higher than in a resting muscle fibre) corresponds better to the results on single fibres, since myosin threads do not show the great change of the after-effect between equilibrium length and moderate loading.

Measurements of the gradient at different points of the tension curve revealed that this curve represents the sum of at least 3 approximately exponential curves with rather different time constants. In the example exhibited in Fig. 55, the gradient is plotted as a function of time in a semi-logarithmic coordinate system. As a basis of calculation, the course of the curve was interpreted in the following way. After a sudden stretch, the tension increases instantaneously and then decreases rapidly, mainly according to the short time constant  $\tau_1$ . This part of the curve is consolidated very soon, and the following part represents the course of consolidation corresponding to the time constant  $\tau_2$ . When this region is practically consolidated, the last time constant  $\tau_3$  can be observed. Plotted in a logarithmic coordinate system,

a curve of uniform course is found consisting of three almost linear parts. Each of these regions corresponds mainly to the effective range of one time constant, and the magnitude of  $\tau_1$ ,  $\tau_2$ , and  $\tau_3$  may be determined by the gradients of the different parts of the curve.

The lowest time constant  $\tau_1$  at rest and during contraction amounts to approximately 10 ms. The constant  $\tau_2$  is about 25 ms

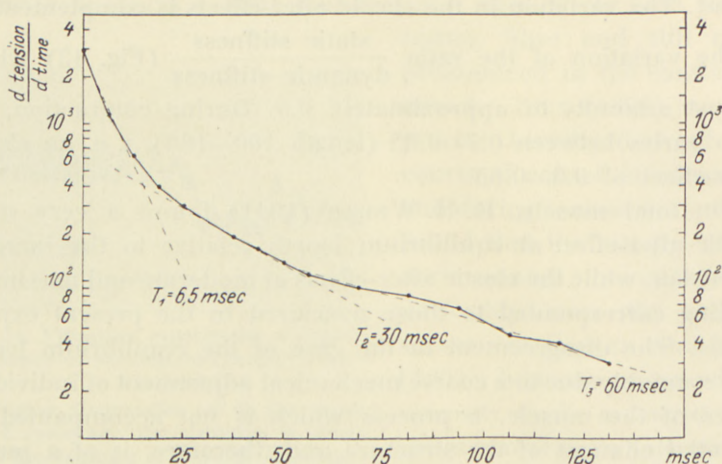


Fig. 55. Logarithm of the rate of change in tension after rapid stretch as a function of time.  
 abscissa = time in msec.  
 ordinate =  $\log \frac{d \text{ tension}}{d \text{ time}}$ .

at rest and 30–35 ms during contraction.  $\tau_1$  and  $\tau_2$  are independent of the extent of stretch.  $\tau_3$  varies with the stretch at rest, from 50 ms at length 100, to 100 ms at length 180. The variation of  $\tau_3$  during contraction is less marked with increasing elongation than at rest.

On total muscle, GASSER and HILL (1924) found the time constant of the tension development after release of the contracted muscle to be 150 ms. According to GASSER and HILL, this time constant is very similar to that of the tension development during isometric contraction. Our observations (cf. p. 26) indicate that this is not the case when dealing with single fibres. The development of tension after release occurs considerably more slowly (time constant 200–250 ms) than that during isometric contraction (time constant 50 ms).



At rapid stretching of the contracted fibre, we could only observe a course of tension corresponding to type B of GASSER and HILL's experiments (p. 412, Fig. 9). One might assume that curves of the type D appear after a mechanical stimulation of the muscle during rapid stretching.

BOUCKAERT et al. (1930) found a time constant of 150 ms at rest after rapid stretch, while we find  $\tau_3 = 50$  ms. This difference may be due to the lower temperature applied ( $0^\circ$ ) or to fibre displacements in the total muscle.

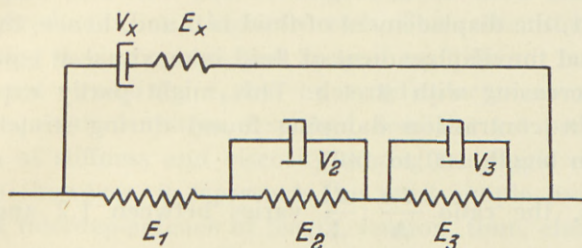


Fig. 56. Equivalent circuit of elasticities ( $E$ ) and viscosities ( $V$ ).  
Explanation see text p. 105.

When testing various combinations of damping and elasticity, the system given in Fig. 56 was derived from all observations available. This system seems to be the best equivalent of the elastic and viscous properties of the fibre, as represented by the three measured time constants.

The mathematical evaluation of elasticity and viscosity was carried out in analogy to the usual treatment of resistance and capacity, respectively, in complex electric systems. The magnitude of the single elasticities of the fibre were obtained by determining the extra-tension due to stretch (difference between initial tension and consolidation tension) in the beginning of the respective parts of the curve. In this way,  $E_2$  and  $E_3$  were found to be equal, while the corresponding viscosities were markedly different (one of them being about 5–10 times greater than the other).

The damping corresponding to  $\tau_1$  which is determined from the stiffnesses  $E_1$  and  $E_2$  and the viscosity  $V_2$  is not noticeable in our dynamic experiments, as the vibrations occur so slowly that the fibre is continuously able to consolidate. The system  $E_2V_2$  must be regarded as purely elastic at 5 cycles.

A small part of the increase in the damping constant during

contraction is presumably caused by the exchange of fluid between the different parts of the compartment which are not stretched and released equally (in per cent) during the vibrating loading. If the change in per cent of A and I was the same during a change of length, no displacement of fluid would be necessary. The maximum displacement of fluid between A and I takes place during contraction. Here, the ratio  $\frac{\Delta A}{A} : \frac{\Delta I}{I}$  varies between 0.45 and 0.8 at lengths of 100 and 140, respectively. At a ratio 1, the displacement of fluid is 0 and, hence, the results indicate that the displacement of fluid is maximal at equilibrium length, decreasing with stretch. This might partly explain the decrease in contraction damping found during stretch of the fibre (from length 100 to 140).

At rest, the ratio  $\frac{\Delta A}{A} : \frac{\Delta I}{I}$  varies between 1.2 and 1.3 at equilibrium length and length 160, respectively. This means that the transport of fluid increases only slightly with the extent of stretch.

The resistance due to fluid displacement between A and I might be placed as a complex shunt across the fibre, consisting of a viscosity  $V_x$  and an elasticity  $E_x$  in series. These components must be assumed to determine the time constant  $\tau_2$ . The total stiffness of this shunt is zero if the stiffness of one component becomes zero.  $E_x$  depends on the disproportion of the elasticity moduli of the A and I substance. During contraction,  $E_x$  amounts to about 10 per cent of the total stiffness of the fibre substance, decreasing with the extent of stretch. At rest,  $E_x$  is about 4 per cent of the fibre stiffness. This means that  $E_x$  can only be noticed during contraction at equilibrium length.

The time constant  $\tau_3$  which is determined by the elasticities  $E_1, E_2, E_3$ , and the viscosity  $V_3$  introduces the maximum damping at such frequencies as employed in the present investigations. If  $\tau_3$  was 40 ms, we would get the same stiffness in the viscous and the elastic components at vibrations of 5 cycles, i. e. the highest possible damping. If  $\tau_3$  is more or less than 40 ms, a smaller damping would be obtained: in the first case, because the main part of the deformation is elastic, in the second case, because the viscosity is reduced.



The damping might be expected to become less at a higher stretch due to an increase of  $\tau_3$ . However, the total stiffness of the fibre increases, and therefore the damping fails to decrease. This phenomenon presumably explains the rather small increase in total damping of the resting fibre during extension (cf. Fig. 53, 1).

The time constant  $\tau_3$  is also essentially determining the course of the damping curve during contraction. In the range of stretch investigated, the stiffness is almost constant and the deviation of  $\tau_3$  from the optimum value must be ascribed to the observed damping reduction at a higher stretch. The rather steep increase in damping during contraction around equilibrium length, however, is not caused by  $\tau_3$  but by  $\tau_2$  (displacement of fluid).

The equivalent system described does not yet permit a distribution of stiffness and viscosity among the single elements of the fibre; however, it represents the most simple model of the observed interdependence of length, tension, time, elasticity, and viscosity. Hence, the difference between static, semi-dynamic, and dynamic stiffness is caused by a different damping in the fibre substances.

### The elastic properties of the fibre in relation to its submicroscopic structure.

The present section attempts to correlate results from investigations of the elastic properties of the fibre with its minute structure.

The main points of these results were as follows.

**Resting fibre.** The elasticity moduli of the A and I substances are only slightly different. The stiffness-loading diagram shows a constant level in the beginning, followed by a linear increase after a short region of transition.

**Contracted fibre.** The length-tension diagram of the contracted fibre cannot be interpreted as a single reversible curve but as a system of curves the single components of which can be regarded as originating from the isometric maximum and directed towards the tension zero (reached by release contraction). The single curves, however, may be considered reversible. The course of the curve indicates an "elastic locking" at the maximum of the isometric, tetanic contraction at the respective fibre length.

On account of the "locking", the fibre remains at a greater length during release than during isometric contraction producing the same tension. The locking is mainly located in the A substance.

During contraction, the fibres yield at a given tension (on the average the tension which corresponds to the extra-tension at equilibrium length). Before the occurrence of a yielding, the fibre is considerably stiffer during contraction than at rest; after the yielding, the fibre becomes softer, sometimes markedly softer than when at rest at the same loading. At further stretch, the stiffness increases again, approaching the values of the stiffness at rest at maximum stretch.

The "locking" which appears at the maximum of the isometric contraction is not an absolute locking. Release of a fibre which has been stretched above the point of yielding reveals a new locking at a greater length. This displacement of the locking, which is caused by a new small yielding as soon as a given tension is reached, is indicated in the length-tension diagram by a reduced increase in tension.

The modern conception of the minute structure of a muscle fibre is based upon investigations and theories by K. H. MEYER (1929), H. H. WEBER (1934), and ASTBURY (1936). Chains of proteins are assumed to be the active elements. As first pointed out by K. H. MEYER, these chain-molecules can be brought into contraction and out of contraction by chemical changes of the surrounding medium. Although ENGELMANN (1875), HERMANN (1879), and v. KRIES (1880) already suggested that molecular changes of the contractile substance occurred during contraction, K. H. MEYER's theory is the basis of further discussions and of our present picture of the minute structure of muscle.

The investigations of the X-ray pattern, the birefringence, and the thermo-elastic properties of the fibre form the fundament of the theory of the submicroscopic structure.

As regards K. H. MEYER's and ASTBURY's X-ray diagrams of the muscle, it must be emphasized that most of them are performed on dead muscles. Apart from that, they do not permit a closer analysis of the type of linkages, and until now they cannot reveal more than do birefringence measurements, viz. the presence of a certain moderate molecular orientation in the muscle. Further-



more, it seems doubtful whether it is admissible from diagrams of smooth muscles to draw general conclusions applicable to the structure of cross-striated muscle.

The existence of movable chain-molecules was made probable by thermo-elastic experiments carried out by WÖHLISCH (1931) and by MEYER and PICKEN (1937). In a resting muscle, these authors found a negative temperature coefficient at a length 100—130, which indicates an increased orientation of structural elements at stretchings within this range. Part of this negative temperature coefficient may, however, be ascribed to a micellar structure, the orientation of which occurs just at lengths 100—130.

In some essential points, however, K. H. MEYER's interpretation (1940) of the viscous properties is not in agreement with our experimental observations on single fibres.

In analogy to the structure of rubber, the molecules of the fibre substance are assumed to be arranged as a framework with freely movable chains. The framework itself represents the true elastic resistance, and the freely movable chains are thought to slide over one another and form the viscous resistance. At a high stretch, the free chains slide away from each other and, thus, come in a certain state of disorder. This state should be noticeable in birefringence<sup>1</sup> measurements which, however, do not show any decrease until the fibre is stretched so violently that its cross-striation is disintegrated (BUCHTHAL and KNAPPEIS 1938). According to K. H. MEYER's model, we must assume that the dynamic stiffness corresponds to the total stiffness of framework and chains, while the static stiffness is that of the framework, only. In the resting muscle, the ratio  $\frac{\text{static stiffness}}{\text{dynamic stiffness}}$  is independent of the extent of stretch and reaches a value considerably below 1 (Fig. 43).

If K. H. MEYER's conception of the framework and the free chains were correct, we should expect a better agreement between static and dynamic stiffness at higher stretchings, since then exclusively the structure of the frame would be involved. Further, we should expect that the viscosity decreases with increasing stretch, as the surface of contact between the free chains is reduced. However, experiments proved that the viscosity increases with

<sup>1</sup> Due to the mutual fibre displacement, changes in birefringence found on total muscle cannot serve as a proof.

increasing stretch, although not quite proportional to the tension developed.

On the basis of his own and ASTBURY'S investigations, H. H. WEBER (1934) considered the myosin threads to be the main components of the contractile substance, and he suggested a "zig-zag" molecular structure similar to that discussed by the author in Fig. 57. The forces between the single arms of the molecules should be mass attraction forces. In agreement with SULZER (1930), WEBER assumed two different lengths at which the molecules can develop the same tension and, further, that they can be brought from one length to the other by thermal forces.

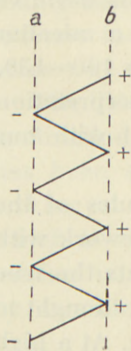


Fig. 57. "Zig-zag" molecule with two series of charges (a and b).

In this way, it should be possible to explain the viscosity and the irreversible behaviour of the myosin threads. However, it seems difficult to understand that a molecule of this kind—i. e. without electrostatic forces and with pure mass forces, only—shows so strong connective forces that the repulsive effects due to thermal movement are counteracted and that a state of disorder can be avoided. The assumption of electrostatic intermolecular forces is certainly necessary in order to maintain a state of the molecule as described by WEBER.

If we assume the presence of electrostatic forces in a molecule of this type with two series of charges, and furthermore, a mobility of the chain elements, then its elements must necessarily be unstable and will straighten out or possibly carry out a helical movement turning into a space system which consists of an odd number of charge series (cf. p. 113).

WÖHLISCH (1940) made an attempt to symbolize the change in the mechanical properties of the fibre during contraction by a rather primitive spring model. The intramolecular forces are represented by a spring which is somewhat compressed at the equilibrium length of the model. A spring which is slightly extended at equilibrium length represents the normal muscle elasticity. When the first mentioned spring is removed, the model will contract, i. e. the contraction mechanism is symbolized in the removal by a simple extending force. As a support of this



view, WÖHLISCH used the length-tension diagram of the muscle at rest and during isometric contraction. At the point of indifference (where the extra-tension during contraction disappears), no extra-tension appears, since here the extended spring has its natural length. However, the length-tension diagram of the model (showing WEBER's paradox) is not in agreement with experimental observations on the single fibre. The contraction curve and the rest curve overlap from the point of indifference and they have no point of intersection, as claimed for the model, when the stiffness of the extended spring is eliminated. The greater stiffness during contraction at small loading of the fibre is, furthermore, incompatible with the spring model which, therefore, does not seem to be a suitable equivalent for the demonstration of the elementary differences between rest and contraction.

On the basis of their experiments on the electrostatic properties of the fibre, BUCHTHAL and LINDHARD (1939) assumed that the electrostatic energy present in the resting muscle is in equilibrium with the elastic forces. According to this theory, the electrostatic energy is transformed into mechanical energy during contraction. On the basis of this hypothesis and of the observations on the mechanical properties of the fibre as described in the preceding chapters, the author has made an attempt to find the simplest molecular structure which might agree with the observed properties.

In molecular systems which one might imagine as mechanical equivalents of the fibre, the following main forces should be present:

- 1) Central forces.
  - a) Electrostatic central forces originating from attraction between charges of opposite sign and from repulsion between charges of the same sign.
  - b) Central forces originating from mass attraction. These are insignificant in comparison with electrostatic central forces and, therefore, not considered in the calculations.
- 2) Angular forces between two neighbouring elements of the molecular chain due to the linkage structure located in the electron orbits.
- 3) Thermal forces in the form of attraction due to "curling"

caused by Brownian movements or as a kind of repulsion caused by collisions between neighbouring chains.

The influence of the respective forces on the equilibrium of the molecule will be discussed in the following.

All calculations were carried out in accordance with the rules of central forces in classical physics. When dealing with molecular magnitudes, the classical interpretation cannot quite satisfactorily describe the phenomena, and quantum mechanical considerations should be applied. Since, however, the present considerations are approximations, only, this omission will not be of essential influence upon the results.

### 1) Electrostatic central forces in the proposed molecular system.

The simplest type of a molecular chain, where the single elements of the molecule lie in the same plane, is represented in Fig. 57 ("zigzag" molecule). If the vertices of the angles carry alternately positive and negative charges, the same side of the molecules will show a charge of the same sign. The forces between neighbouring vertices must consequently be repulsive forces, giving rise to an orientation effect. Forces between  $a$  and  $b$  charges cause an attraction and, hence, a certain curling. The calculation of such forces in a system of this kind reveals that the repulsive forces at any stretch are greater than the attractive forces and, hence, this system will endeavour to straighten out as far as possible. While the internal forces of an almost straightened system are small and cause only a negligible deviation of the molecule out of its plane, a molecule with the type of charge distribution described cannot be in equilibrium as a plane system in a somewhat folded state. Neighbouring charges will repulse each other and thus turn the elements of the chain into a three-dimensional system, as shown in Fig. 58. Here, the neighbouring charges are of opposite sign, attracting each other and, therefore, the molecule must exhibit at least three series of charges ( $a_1, a_2, a_3, a_4, a_5; b_1-b_5; c_1-c_5$ ).

In a molecular chain with four series of charges, the same instability will appear as in system 1, the system either turning into a system with five or with three series of charges. At five



series of charges, we shall again obtain stability against curling. The angular forces discussed on p. 114 determine the number of charge series.

Consequently, the simplest stable system is that with three charge series, and the following calculations are based upon this assumption.

For the calculation of the resulting effect of the electrostatic forces, we consider one single vertex of an angle and the corresponding point of charge  $a_1$  (Fig. 58). This point is affected by all other charged points of the molecular system. We assume the effective charge of the individual points of the molecular system to be equal, but of alternating sign. The point  $a_1$  is thus influenced by potentials originating from the charges of the  $b$  as well as the  $c$  series. For symmetry reasons, the forces—projected on the longitudinal axis of the fibre—are assumed to be equal in both directions and, therefore, we consider only the forces in one direction of the molecule.  $a_1$  is attracted in a longitudinal direction by  $a_2$ , is repulsed by  $a_3$ , attracted by  $a_4$  etc., with a force inversely proportional to the square of the distance. Simultaneously,  $a_1$  is repulsed by the charges of  $c_1$  and  $b_2$ . These forces do not operate parallel to the longitudinal axis of the fibre, but must be projected on the axis, whereby their components are reduced. The forces originating from  $b_4$  and  $c_3$ , however, are attractive forces.

Vertical to the longitudinal axis of the molecule we find the effect of some forces, the resultant of which tends to increase the cross section of the molecule and thus causes a contracting effect.

A calculation of the resulting central forces in a longitudinal direction, which is based upon the rules of central forces brings out a length-tension dependence as follows: At the shortest lengths, the attractive forces are predominant, but they decrease rapidly during stretch; when the molecule is stretched to about

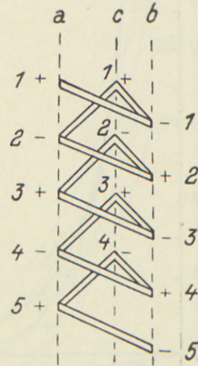


Fig. 58. Molecular chain with three series of charges ( $a$ ,  $b$ , and  $c$ ).

half the maximum length, these forces are practically negligible (Fig. 59, 1). In the present system—in contrast to the “zigzag” system—the electrostatic forces have a contracting effect.

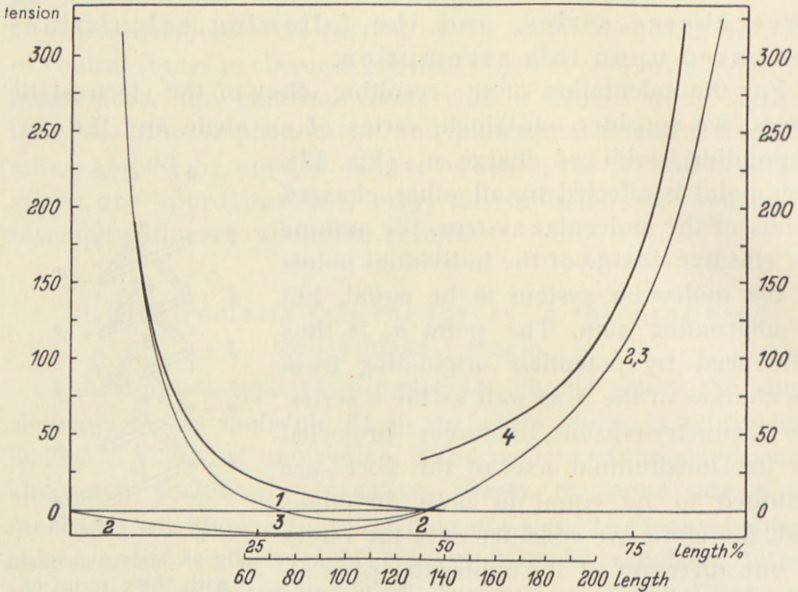


Fig. 59. Intramolecular attractive and repulsive forces as a function of the length of the molecule.

- (1) resulting electrostatic central forces;
- (2) elastic forces, originating from angular forces, natural angle  $80^\circ$ ;
- (3) length-tension diagram obtained by summation of curves (1) and (2);
- (4) length-stiffness diagram of curve 3;

abscissa = (above) length in per cent of the maximum molecular length;  
 (below) length in relation to the muscle fibre, equilibrium length = 100;  
 on account of micellar adjustment, length 100 does not correspond to load 0;  
 ordinate = tension in relative units.

## 2) Angular forces.

The angular forces between neighbouring elements of the molecular chain acting on the lines of the angle have a contracting and extending effect, respectively, dependent on whether the angle is larger or smaller than the natural angle. As the natural angle we denote that which is exclusively determined by the atomic forces between two neighbouring arms. Fig. 60 exhibits the calculated relative course of tension corresponding to natural



angles between  $60^\circ$  and  $90^\circ$ . At an angle of  $60^\circ$ , the angular force in the completely contracted system is 0 and the contractive force increases with increasing length. At natural angles above  $60^\circ$ , the force is 0 in the beginning, attaining negative values, passing 0, and reaching positive, i. e. contracting values. Tension

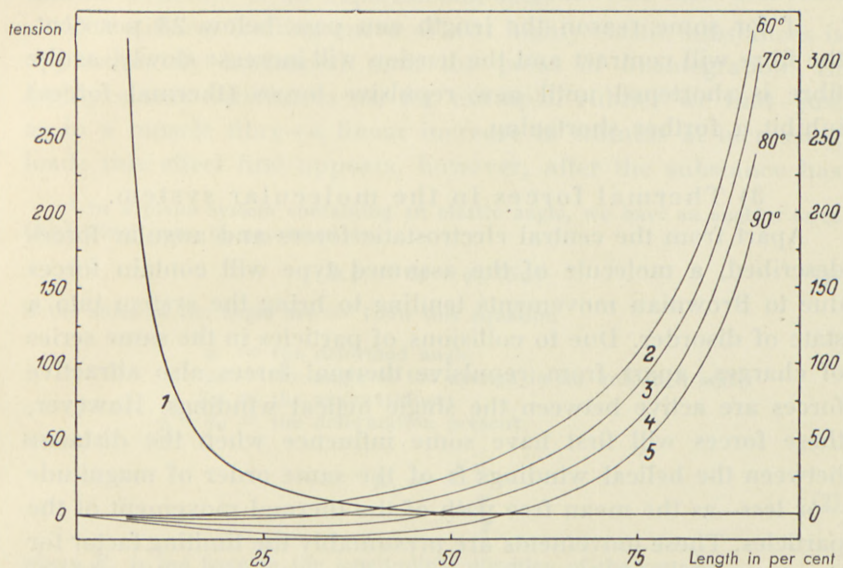


Fig. 60. Length-tension diagram of intramolecular forces of a system with three series of charges.

- (1) electrostatic central forces;
- (2) angular forces at a natural angle of  $60^\circ$ ;
- (3) angular forces at a natural angle of  $70^\circ$ ;
- (4) angular forces at a natural angle of  $80^\circ$ ;
- (5) angular forces at a natural angle of  $90^\circ$ ;

abscissa = length in per cent of the maximum molecular length;  
ordinate = tension in relative units.

0 is obtained at a length where the angle is equal to the natural angle. At an angle of  $70^\circ$ , this tension is reached at 33 per cent of the maximum length. At an angle of  $90^\circ$ , the tension 0 is obtained at 57 per cent of the maximum length.

Natural angles above  $90^\circ$  cannot exist in this system, since they would lead to a five-edge system.

Fig. 59, 2 shows the dependence of the elastic forces on the length at a natural angle of  $80^\circ$ .

Fig. 59, 3 shows a resulting length-tension curve of the central

electrostatic forces and of the angular forces with a natural angle of  $80^\circ$ . It is apparent that the forces are in an unstable equilibrium at a length 28 per cent of the maximum length, and in a stable equilibrium at 47 per cent of the maximum length. From length 47 per cent (stable equilibrium length), the tension increases with increasing stretch.

If for some reason the length can pass below 28 per cent, the fibre will contract and the tension will increase slowly, as the fibre is shortened until new repulsive forces (thermal forces) inhibit a further shortening.

### 3) Thermal forces in the molecular system.

Apart from the central electrostatic forces and angular forces described, a molecule of the assumed type will contain forces due to Brownian movements tending to bring the system into a state of disorder. Due to collisions of particles in the same series of charges, apart from repulsive thermal forces also attractive forces are active between the single helical windings. However, these forces will first have some influence when the distance between the helical windings is of the same order of magnitude—or less—as the mean free path of the thermal movement of the particles. These movements are presumably the limiting factor for the shortest length of contraction. The thermal forces will probably be of secondary influence on the single arms; but the linear tension-temperature dependence found in highly elastic substances indicates that the thermal movements are of great significance for the whole molecule or for molecule aggregates.

Stiffness-loading diagram of the resulting electrostatic and angular forces. From the slopes of the curves of Fig. 59, 3 a stiffness-loading diagram (Fig. 61) of the resulting electrostatic forces and angular forces ( $\frac{\text{tension}}{\text{length}}$  as a function of tension) was obtained. From the length 100 (stable equilibrium length) to the length 200 (corresponding to a length 130—200 of a muscle fibre) the stiffness-tension curves are linear. Their course thus corresponds to the stiffness-tension curve of the muscle fibre after the micellae being adjusted.

The variation of stiffness with loading indicates



that the fibre structure must include single elements between which angular movements occur<sup>1</sup>.

Even if the above considerations on the mutual relation between the internal forces within the molecule are abstractions, the mentioned angular movement between elements of the minute structure is an experimental fact.

The stiffness-loading curve of not highly elastic substances is approximately horizontal until the point of disintegration. In highly elastic substances as, for example, rubber we find—just as in a muscle fibre—a linear increase in stiffness at increasing load; this effect first appears, however, after the substance has

<sup>1</sup> In a plane system containing an elastic angle, we have an angular force ( $K\varphi$ ) which may be expressed as

$$K\varphi = (\varphi - \varphi_0)(S\varphi) \tag{1}$$

if the sides of the angle are = 1. In this equation

- $\varphi$  = the deformed angle
- $\varphi_0$  = the angle of the system in an unloaded state
- $S\varphi$  = the angle stiffness
- $\varphi - \varphi_0$  = the deformation present.

Hence,

$$K_L = \frac{K\varphi}{\cos \frac{\varphi}{2}} \tag{2}$$

where  $K_L$  is the force in the longitudinal direction of the system.

$$L = 2 \sin \frac{\varphi}{2} \tag{3}$$

where  $L$  is the length of the system in the direction of loading.

By differentiation of  $K_L$  and  $L$  with respect to  $\varphi$  we get

$$K'_L = \frac{K'\varphi}{\cos \frac{\varphi}{2}} + \left( \frac{1}{\cos \frac{\varphi}{2}} \right)' K\varphi \tag{4}$$

$$L' = \cos \frac{\varphi}{2}. \tag{5}$$

The required stiffness ( $S_L$ ) in the longitudinal direction of the system becomes

$$S_L = \frac{\frac{dK_L}{d\varphi}}{\frac{dL}{d\varphi}} = \frac{K'_L}{L'} = S\varphi \left( \frac{1}{\cos^2 \frac{\varphi}{2}} + \frac{\sin \frac{\varphi}{2} \times (\varphi - \varphi_0)}{2 \cos^3 \frac{\varphi}{2}} \right). \tag{6}$$

From the equations (2), (3), and (6) we find corresponding values of force, length, and stiffness, respectively; at natural angles from 30° to 90°, the length-tension and the stiffness-load dependence are of the same type as found in the resting muscle fibre.

been sufficiently orientated by elongation (Fig. 63). In the case of a muscle, we find the linear part of the curve already at slight stretch, thus indicating (in agreement with birefringence, diffraction pattern, etc.) that the substance is orientated in the state of equilibrium. In a series of experiments carried out with slightly vulcanized caoutchouc threads, using the same arrangement as employed for the investigations of the muscle fibre, a

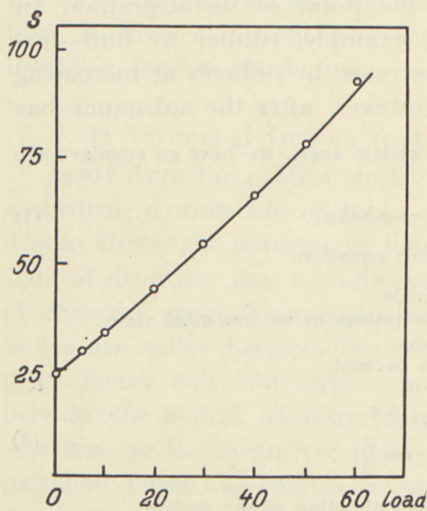


Fig. 61. Stiffness-load diagram of the length-tension diagram Fig. 59, curve 3. abscissa = load in relative units; ordinate = stiffness in relative units.

length-tension diagram was found (Fig. 62) corresponding to that known from the literature. The stiffness-loading diagram of rubber threads shows an approximately linear course after an elongation of about 400 per cent. The length-tension diagram is S-shaped and corresponds after a stretch of 400 per cent to the diagram of the resting muscle fibre.

Assuming the described molecule equivalents (Fig. 58) which do not take into account the mutual effect of different molecules, the contraction might occur in the following

way. By means of an external influence, the distance between  $a_1$  and  $a_2$  is reduced and, hence, the potential difference between  $a_1$  and  $a_2$  decreases, as their charges are constant; the capacity however, increases due to the changed distance.  $a_1$  receives an increase of negative potential and  $a_2$  an increase of positive potential. Part of this charge alteration is transferred to  $b_1$  and  $b_2$ , respectively; the potential difference between these two points is therefore increased. Consequently, the attractive forces are augmented so much that also these two points approach each other. This process is followed by a similar one in the charge series  $c_1$  and  $c_2$ , and the process is continued through the helix until the distance between the not yet contracted parts of the chain is so great that the forces arising are unable to continue the process. The chain will



then consist of contracted and non-contracted elements. If contraction is introduced at small length (tensionless), the whole chain will enter into contraction; if, however, contraction is introduced at greater length (under load), only part of the chain will participate in the contraction until the tension inhibits a further propagation of the process. Contractions from the greatest

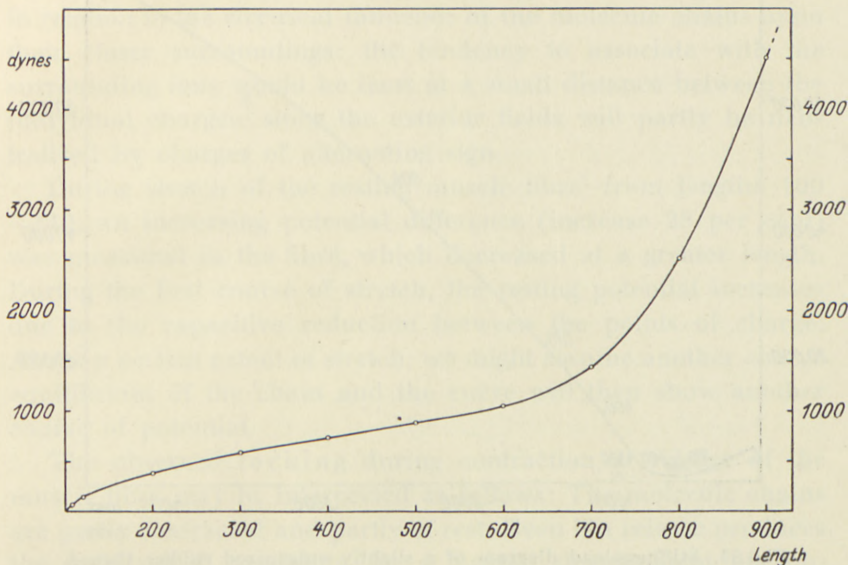


Fig. 62. Length-tension diagram of a slightly vulcanized rubber thread.  
 abscissa = length (equilibrium length = 100);  
 ordinate = load in dynes.

possible length cannot be brought about because the process cannot start. This picture corresponds to the length-tension diagram of the muscle fibre where the extra-tension decreases continuously with increasing stretch after the coarse micellar adjustment of the first part of the curve is finished. Maximum stretch of the contracted fibre produces generally somewhat higher tension than a stretch at rest followed by isometric contraction. In an already contracted molecule, the attractive forces play a greater part—due to smaller distances—than in the case of stimulation of a highly stretched molecule.

In the proposed system, a reduction of the distance between only two neighbouring particles of a chain suffices to produce

contraction. This reduced distance may be obtained in different ways: by addition or neutralization of a charge on one link of the chain by a mechanical, local deformation, or by a violent compression of the whole fibre (pressure contraction, BROWN 1933 and 1936, EBBECKE and HASENBRING 1935). Furthermore,

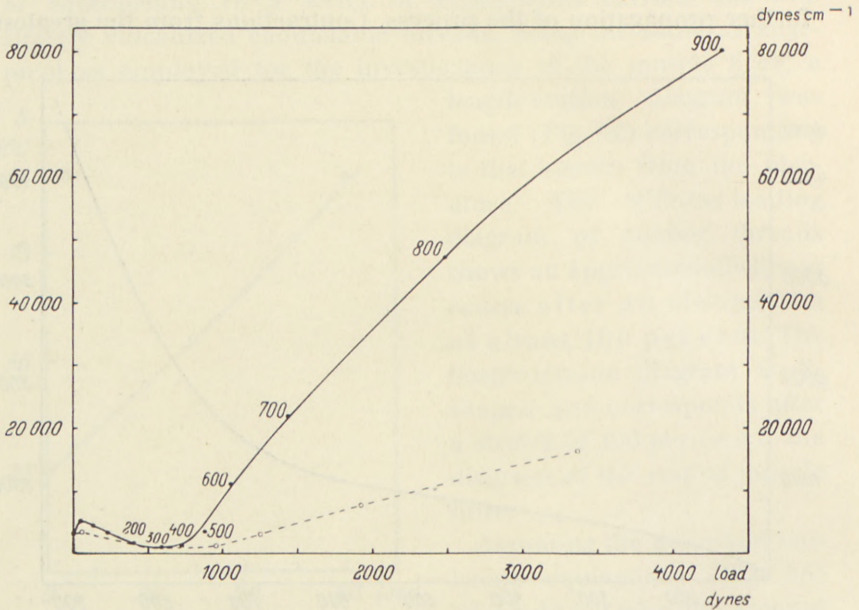


Fig. 63. Stiffness-load diagram of a slightly vulcanized rubber thread.

—●—●—● = dynamic stiffness;

---○---○ = static stiffness.

The figures on the curve denote the length of the thread at the respective load.  
 abscissa = loading in dynes;  
 ordinate = stiffness in dynes  $\text{cm}^{-1}$ .

observations on thermo-elastic properties, where heating causes a shortening due to the increased thermal attractive forces, are in agreement with the given picture.

Yielding, as it appears after stretch of the contracted fibre, might be explained in the following way. We suppose the fibre to be stretched so much that, for example, half of the single molecule chain is contracted while the rest of the molecule chain is passively extended. If the tension of the molecule chain is increased by exterior forces beyond a given point, the forces in the contracted part of the chain are no longer able to maintain equilibrium with the exterior forces and, thus, the links of the



molecules will become straightened successively until the exterior forces are equal to the attracting forces of the contracted links.

When the stimulation ceases, we must necessarily assume the occurrence of neutralization or reduction of charges contracting the chain. These charges must be rebuilt in the period of rest. The increased conductivity during contraction might stand in relation to the electrical influence of the molecule chains upon their closer surroundings: the tendency to associate with the surrounding ions would be least at a small distance between the individual charges, since the exterior fields will partly be neutralized by charges of alternating sign.

During stretch of the resting muscle fibre<sup>1</sup> from lengths 100—140, an increasing potential difference (increase 28 per cent) was measured in the fibre, which decreased at a greater length. During the first course of stretch, the resting potential increases due to the capacitive reduction between the points of charge. Above a certain extent of stretch, we might assume another charge equilibrium of the chain and the curve will then show another course of potential.

The observed locking during contraction at release of the muscle fibre may be interpreted as follows: The molecule chains are partly contracted and partly at rest. Even if a release produces the mechanical possibility for a further development of contraction of the molecule chain, the locking indicates that this does not occur. We might assume that this effect originates in the charge distribution on the boundary between the contracted and the non-contracted parts of the molecule. Before propagation of the contraction wave over the molecule chain, an electric potential increase runs along the points of the charge series which causes the transition from rest to contraction; when the mechanical conditions for the further development of contraction are no longer present, the increase in potential will stop at the first, non-contracted link of the molecule chain. This link will presumably exchange one charge with its surroundings and thus obtain a decreased electric activity. If the mechanical tension of the molecule is reduced, the contraction wave will not continue due to lack of the electrostatic prerequisites,—the fibre is locked.

<sup>1</sup> Unpublished experiments.

Therefore, the fibre must be brought into a new state before the contraction wave is propagated along the fibre.

The properties of the molecule model mainly represent those of the anisotropic substance (increase in tension and stiffness due to contraction, and diminution of the equilibrium length). The resulting properties of the isotropic substance, which does not exhibit a noticeable change in equilibrium length under contraction, are not directly represented by the model. However, there is reason to suppose that the molecules in the I-substance are only slightly orientated compared with those of the A-substance (cf. the difference in birefringence). A parallel orientation of the molecules is the prerequisite for a deformation, i. e. a contraction of the micellae. An increase in tension in the individual molecules will therefore not lead to a noticeable deformation, but only to an increase in stiffness. The difference between the A and the I substance may thus be due to a difference in orientation of the same molecular structure.

The very simple form of the model, as described above, does not include elastic after-effects present in the muscle fibre at rest and during contraction. H. H. WEBER (1934, 1941) explained the elastic after-effects in the myosin thread by assuming that the single link of the molecule chain can only exist either in a contracted or in a stretched state. A certain tension must be exceeded in order that a link is brought from a contracted into a straightened state, and this tension which must be available within a very short time, only, might originate from thermal collisions. If the chain is exposed to a tension just high enough to insure that the molecule can be in equilibrium in a partly unfolded state, but not so high that the molecule can be brought from a folded to a straightened state, WEBER assumed that thermal collisions may produce the resulting tension necessary for the straightening out of the folded elements. If the probability of collision of one single folded element per time unit is the same for all elements, the number of straightened elements per time unit is proportional to the total number of folded elements which can be kept in an unfolded state by the exterior tension available. Hence,  $\Delta L = l \times k$ , where  $L$  is the length of the molecule,  $l$  is the length of the folded elements of the molecule;  $k$  is a proportionality factor determined



by the collision probability per time unit.  $\frac{\Delta L}{\Delta t}$  must be an exponential function of time.

As previously mentioned, WEBER's molecule model cannot satisfy the requirements as revealed by the experimental results. In accordance with WEBER, we assume in the present model that the elastic after-effects must be ascribed to intramolecular linkages which are dependent on the extent of load ("crystallization", WÖHLISCH 1941, H. H. WEBER 1941). The transition from one type of linkage to another (it may be possible that there are two types of linkages, only) lasts some time, and this transition may depend upon ion reactions or purely mechanical, thermal collisions. The velocity with which the substance is transformed from one modification to another must be assumed to be determined by the three time constants previously discussed (cf. p. 103). If the mechanical changes occur very rapidly, the modification of the substance cannot follow, and we must measure a great (dynamic) stiffness with a relatively low damping. At moderate velocities, the stiffness will be reduced relative to that at rapid changes and the damping will play a larger part. In static experiments, the change of linkages is adjusted according to load, and here we find the lowest stiffness.

In this connection, it might be of interest to recall some experiments which indicate an increased chemical activity during stretch (EDDY and DOWNS 1921. In these experiments, care was taken to avoid stimulations during the experiment).

Rubber shows viscous properties similar to those of a muscle fibre, and it is not improbable that the assumption of loaddependent modifications of the linkages may be valid also for this substance. In a range of length, 200—300 (Fig. 63), the static and the dynamic stiffnesses of rubber are equal, showing a minimum value. At greater length, dynamic stiffness increases more markedly than static stiffness, the ratio being finally 4:1. In a range of length 200—300, no change of the linkages occurs—according to our assumption. In the following range of length, viz. 300—900, alterations of the linkages appear which are dependent upon stretch. X-ray diagrams<sup>1</sup> of the rubber thread, the length-tension diagram of which is exhibited in Fig. 62, show rather

<sup>1</sup> The X-ray diagrams were taken by Dr. R. W. ASMUSSEN, Chemical Department A, Royal Technical Institute, Copenhagen.

sudden modifications at length 500 and at length 700—800, respectively, thus indicating a change of orientation in this range.

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## List of definitions and abbreviations.

A substance	anisotropic substance of the cross-striated muscle fibre.
I substance	isotropic substance of the cross-striated muscle fibre.
Equilibrium length	the length at which the fibre just begins to develop tension when it is stretched. In all experiments, the length is given in relative units and the equilibrium length of the resting fibre is put = 100.
Indifference point	denotes an extension, at which the tension developed during isometric contraction just becomes zero and corresponds in the majority of the experiments to twice the equilibrium length = length 200.
Load (= total tension)	in the individual experiments measured in dynes. For comparative purposes, the load at the indifference point is put = 100.
Cross section load	load in relation to a unit cross section, $\frac{\text{load}}{\text{cross section}}$ ; at length 100 the cross section is put = 1.
Extra-tension	tension increase due to contraction (total tension of the contracted fibre minus tension of the resting fibre at the same length).
Isometric maximum	resting tension + extra tension (= total tension) during isometric tetanic contraction under maximal stimulation.
Static length-tension diagram	tension as a function of elongation (stretch). The tension values are measured after complete consolidation, i. e. the elastic after-effects have ceased.

Consolidation	transition to static tension after a variation in length or tension of the fibre.
Semi-dynamic length-tension diagram	simultaneous registration of tension with the variations of length. Duration of stretch 10—1 sec.
Release contraction	the isometrically contracted fibre is allowed to shorten during continuous stimulation, and the new length and tension are registered after consolidation. In a number of experiments, the fibre was released to the same tension as when at rest before stimulation.  In semi-dynamic length-tension experiments, relaxation, in contrast to release denotes the decrease in length resp. tension of the resting fibre.
Partial length-tension diagram	corresponding values of length and consolidated tension, when the fibre is released from the isometric maximum.
Elastic "locking"	a conception introduced to explain the fact that the partial length-tension diagrams of the contracted fibre do not coincide with the curve of isometric maxima, but represent a system of parallel curves running downwards from all points of the curve of isometric maxima. The fibre must be regarded as "locked" to one of these partial diagrams as long as the stimulation continues and the fibre is not stretched above the resp. length in isometric contractions.
Yielding	characterized by a reduction of steepness in the curve of the isometric maxima, and by the critical decrease in stiffness when the yielding tension is reached. By definition yielding is an increase in equilibrium length of the contracted fibre, which is irreversible during contraction, and due to the fibre tension.
Early yielding fibres	fibres with the critical point of yielding at tensions below the equilibrium length at rest.
Late yielding fibres	fibres with the critical point of yielding at tensions above the equilibrium length.
Stiffness ( $S$ )	ratio between corresponding increases in tension and length. $\frac{\Delta \text{tension}}{\Delta \text{length}}$ is measured in dynes $\text{cm}^{-1}$ , and is always expressed in arbitrary units. When characterizing the elastic pro-



- properties of orientated anisotropic substances which display considerable changes in cross section during length alterations, stiffness is preferred to the elasticity modulus.
- Static stiffness consolidated values of  $\frac{\Delta \text{tension}}{\Delta \text{length}}$  derived from static length-tension diagrams.
- Dynamic stiffness  $\frac{\Delta \text{tension}}{\Delta \text{length}}$  as a rule determined by periodic length alterations of the fibre.
- Softness  $\frac{1}{\text{stiffness in dynes cm}^{-1}}$ ; when two or more elastic bodies are connected in series, the total softness = the sum of the individual softnesses; when two or more elastic bodies are connected in parallel, the total stiffness = the sum of the individual stiffnesses.
- Elasticity modulus the force necessary to increase the length of a wire with a cross section of 1 cm<sup>2</sup> to twice its length.  
elasticity modulus  
=  $\frac{\text{stiffness}}{\text{cross section}} \text{ length}$   
= stiffness of a 1 cm cube in dynes cm<sup>-2</sup>.
- Viscosity internal friction in the fibre measured as the decrease in vibration energy:  
$$\frac{\text{friction force}}{\text{velocity of length alteration}}$$
- Damping constant (*p*) expression for the non-elastic resistance in dynes which retards an oscillating system when the velocity of motion = 1 cm per sec; dimension: dyne cm<sup>-1</sup> sec.
- Elastic after-effect ratio between the decrease in tension during consolidation and the increase in tension due to instantaneous stretch.  
BOUCKAERT et al. (1930) express the elastic after-effects as  $\frac{\text{viscous extension}}{\text{total extension}}$ , WEBER (1941) as  $\frac{\text{instantaneous length increase}}{\text{viscous length increase}}$  due to a sudden loading; in WEBER's definition,

the coefficient becomes  $\infty$  when the elastic after-effect = 0.

Time constant ( $\tau$ ) the time necessary to diminish the difference between the instantaneous value (the tension after stretch) and the consolidated value to  $\frac{1}{e}$  ( $e$  = base of the nat. log.) of the initial difference. The time constant is inversely proportional to the consolidation velocity.



## Summary.

(Cf. list of definitions p. 125.)

A new type of myograph is described for the recording of tension developed by a single muscle fibre. The tension arising by stretch or contraction displaces one movable plate of a condenser. The change in capacity is registered by means of a high frequency circuit, an amplifier, and an oscillograph. The same arrangement is employed for measurements of the dynamic stiffness in vibration experiments.

Length-tension diagrams of the single muscle fibre are registered under different conditions.

The tension developed by the resting fibre increases slowly with increasing stretch and then rapidly after an increase in length of 20—30 per cent. The smaller initial gradient of the length-tension diagram is due to a length orientation of micellar elements.

The tension of the isometric maxima (tetanic contraction) increases with increasing length, and the extra-tension (difference between contraction-tension and rest-tension) is constant up to 40 per cent of stretch. With further stretch, the extra-tension developed during contraction decreases, so that the rest curve and the contraction curve overlap at 60—100 per cent of stretch. The decrease in extra-tension originates from a reduced contractility, partly due to the decreasing stiffness of the I-substance during contraction at a higher stretch.

During extension of the isometrically contracted fibre—in contrast to observations on total muscle—we cannot find any deviations from the curve of the isometric maxima up to elongations of 50—60 per cent. At higher extent of stretch, the extra-tension developed during contraction does not decrease to zero. A structural interpretation of the difference in the behaviour of

the extra-tension during stretch of the isometrically contracted fibre, and during isometric contraction of a fibre stretched at rest, is suggested in connection with the description of a molecule model.

Special regard is paid to length-tension diagrams in which fibres at rest and during contraction are compared under the same exterior mechanical conditions (tension). Release of the isometrically contracted fibre to the same tension as when at rest leads to considerably lower values of length and tension than indicated by the corresponding points on the curve of isometric maxima—in spite of a complete consolidation after release. This difference may be explained by an "elastic locking" of the fibre at the maximum of the isometric contraction. Hence, the curve of isometric maxima is irreversible, and every point of the isometric length-tension diagram represents the starting point of a partial diagram which connects the respective isometric point with the corresponding point of the release diagram.

The length - mean tension diagram of single contractions indicates the main increase in tension at a frequency between 10 and 20 stimulations per sec. At 8 stimulations per sec, the mean extra-tension is about  $\frac{1}{5}$  of the tension during complete tetanic contraction (frequency 30 stimulations/sec; temperature  $18^{\circ}$  C). Even in long-lasting experiments, a contraction remainder does not appear as long as the stimulation frequency is below 5 per sec.

The duration of the development of tension in single contractions is only slightly influenced by stretching as long as the fibre is not fatigued.

In semi-dynamic length-tension diagrams, where the time of stretching varies between 10 and 1 sec, length and tension are registered simultaneously. The difference between the static and the semi-dynamic length-tension diagram of the resting fibre is exclusively due to the viscosity of the fibre. During contraction, the difference—apart from viscosity—is due to yielding (irreversible length alteration) and to elastic locking. Increasing stretch causes in the contracted fibre a steeper ascent in the beginning of the curve. At further stretch, the gradient decreases due to the yielding which is irreversible during contraction. Increasing release during contraction of the stretched



fibre leads to considerably lower tensions than stretching of the contracted fibre (elastic locking). As long as the initial extent of stretch is not exceeded, stretch and release during contraction produce the same tension at the same respective lengths and, hence,—apart from viscosity—the curve is reversible.

Work diagrams are recorded with a technique similar to that applied to the registration of semi-dynamic length-tension diagrams. The fibre is extended at rest about 50 per cent, then stimulated tetanically, and released during contraction. The net work obtained is equal to the area of the length-tension diagram during release contraction minus the area of the length-tension diagram of the resting fibre. The mean total net work performed during tetanic contraction is 10,000 erg/gm of the fibre. The net work of a fibre during release contraction is considerably higher (45 per cent) if the stimulation is interrupted for a short time. Control experiments proved that this increase in work is not due to a restitution of the fibre during this short period of rest. After the recommencement of the briefly interrupted stimulation, the fibre starts with an isometric maximum which corresponds to the respective length, the tension being markedly higher than that developed during release contraction.

Work diagrams from single contractions at a stimulation frequency of 6 per sec provide a net work of 3000 erg/gm, increasing with increasing frequency to 9000 erg/gm at a frequency of 16 stimulations per sec.

Length-tension diagrams of the anisotropic (A) and isotropic (I) substance of the single fibre can be determined from the length-tension diagram of the total fibre (A + I) and from the ratio  $\frac{\text{length of A}}{\text{length of I}}$  as a function of A + I. The ratio  $\frac{\text{length of A}}{\text{length of I}}$  is evaluated from microphotograms of the fibre at various states of extension at rest and during contraction.

The gradients in the length-tension diagram of the I curve of the resting fibre are steeper than those of the A curve. During isometric contraction of the fibre, the length-tension diagrams of the A and the I substance show at first a markedly steeper slope than when at rest; the steepness decreases with increasing load. The length-tension diagram of the I substance cannot be regarded

as a diagram obtained under isometric conditions, since I is not only stimulated but also extended due to the shortening of A. We can to some extent correct for this increase in length on the basis of the length-tension diagram of I during release contraction. The corrected "isometric" length-tension diagram of the I substance does not reveal any increase in tension during contraction at equilibrium length. Above the equilibrium length (up to a stretch of the fibre of 30 per cent), however, an extra-tension appears which considerably exceeds the extra-tension produced by a corresponding stretch at rest. The development of tension during contraction of the I substance is caused by an increase in stiffness; in the A substance it is, furthermore, due to a reduction of the equilibrium length.

The length-tension diagram of A and I during stretch- and release contractions deviates essentially from the curve of the isometric maxima. This irreversibility is caused by an "elastic locking" of both substances. The previously mentioned "yielding" obtained during contraction above a certain tension is mainly located in the A substance.

Static and dynamic elasticity are investigated on single fibres. In an ideal elastic body, these magnitudes are identical; the muscle fibre, however, contains viscous elements causing a difference between dynamic and static elasticity. Static measurements give an expression for the total stiffness, while dynamic measurements with short-lasting length alterations (vibrations) represent the elastic properties of those fibre elements the length alterations of which are not markedly retarded by viscosity.

The length-tension diagram serves as a basis for the static determination of elasticity, while the dynamic measurements are performed as vibration experiments. The frequency of the vibrating system applied is 5 vibrations per sec.

In isotropic bodies, the elasticity modulus is generally used as a comparative measure of the elastic properties; in anisotropic, i. e. highly elastic bodies, however, the elasticity modulus is less suited to characterize the structural properties of the substance than the stiffness  $\left(\frac{\Delta \text{length}}{\Delta \text{force}}\right)$  measured directly in dynes  $\text{cm}^{-1}$ .

The stiffness and the elasticity modulus of the single fibre are measured at rest, during isometric contraction, and during



release contraction. The various magnitudes are studied as a function of the extent of stretch and of load.

In the resting fibre, the stiffness increases linearly with increasing load, after the coarse micellar adjustment is accomplished. This behaviour allows us to draw conclusions concerning the structural properties of the fibre.

During isometric contraction, the stiffness is considerably higher than the stiffness of the resting fibre (referring to the same length at rest and during contraction). At equilibrium length, the stiffness during contraction is about 5 times the stiffness at rest. This difference decreases with increasing extent of stretch. However, this increase in stiffness is only partly caused by the contraction itself but by the mechanical tension developed during contraction. The amount of tension developed during isometric contraction at equilibrium length and up to 40 per cent of stretch is predominantly due to the increase in stiffness, while the decrease in equilibrium length is quantitatively of minor importance.

The curve expressing the comparison of stiffness at rest and during contraction at the same load reveals a very typical and elucidative course. At first, the stiffness during contraction is somewhat higher than the stiffness of the resting fibre, increasing rapidly with increasing load until a maximum is reached (point of yielding). After this maximum, the stiffness decreases rapidly with increasing load and may even reach a value below the rest curve. The position of the yielding point varies from fibre to fibre lying sometimes above and sometimes below the equilibrium length. The present material is classified according to the position of the yielding point: one group of fibres yielding at loads above the equilibrium length, and another group yielding below the equilibrium length. Each of these two groups shows a characteristic course of the respective length-tension diagram, and it may be assumed that the extra-tension developed during contraction determines the classification of the fibre with respect to the position of the yielding point.

A comparison at the same load (but different lengths) during release contraction indicates that the stiffness during contraction up to loads of 30 units (length 130) lies above the stiffness of the resting fibre.

In dynamic measurements, the elasticity modulus of the

resting fibre is on the average  $(0.81 \pm 0.11) \times 10^6$  dynes  $\text{cm}^{-2}$ , increasing during contraction, unless we compare rest with contraction at the same tension, i. e. an essential part of the increase is due to the influence of tension. A comparison of the moduli of fibres at rest and during contraction at the same tension makes it clear that in release contractions, the modulus during contraction is up to 30 per cent above the modulus of the resting fibre. During isometric contraction, the difference between rest and contraction depends on whether the comparison is made below or above the point of yielding.

The ratio  $\frac{\text{modulus (contraction)}}{\text{modulus (rest)}}$  of the non-fatigued fibre during release contraction is  $1.97 \pm 0.13$ . In a fatigued fibre, this ratio is considerably less ( $1.13 \pm 0.06$ ). Fibres poisoned with monoiodoacetic acid show the same behaviour, and the lactic acid formed during fatigue cannot be the cause of the change in the elastic properties.

The statically measured modulus of the single fibre is  $0.5 \times 10^6$  dynes  $\text{cm}^{-2}$ . During contraction, the ratio  $\frac{\text{static stiffness}}{\text{dynamic stiffness}}$  decreases with increasing stretch from 0.8 to 0.2. In the range about equilibrium length, the total elastic mass participates uniformly in the elastic deformation; at a stretch of 80 per cent, the dynamic measurements comprise only  $1/5$  of the total elasticity of the fibre.

The static softness  $\left(\frac{1}{\text{stiffness}} = \frac{1}{S}\right)$  of the A and the I substance is determined from the curve of the total softness of the fibre  $\left(\frac{1}{S} = \frac{1}{S}A + \frac{1}{S}I\right)$  and from the ratio  $\frac{AA}{AI}$ . The softness of both substances decreases with increasing length. In the resting fibre, the A substance shows the greater softness—mainly due to its greater length—(i. e.  $A =$  twice the softness of the I substance). During contraction, the softness of both substances decreases markedly if the same lengths at rest and during contraction are compared. A becomes 7 times and I 4 times stiffer than at rest. At lengths below equilibrium length, the increase in stiffness must be mainly ascribed to a change in the I substance.



The load-stiffness diagrams of the A and the I substance of the resting fibre are linear.

A comparison of the static elasticity modulus of A and I in the resting fibre as a function of fibre length reveals only slight differences between the two substances (not more than 20 per cent). The moduli increase with increasing extension. Also during contraction at equilibrium length, the moduli of both substances increase, modulus A being about 50 per cent higher than modulus I. With increasing stretch, modulus A decreases while modulus I increases during contraction.

In the resting fibre, the elasticity moduli as a function of cross section load reveal the modulus of I to be about 30 per cent higher than the modulus of A. During contraction, the modulus of A increases to 5 times the value of I and up to 10 times the corresponding modulus of the resting fibre. The increases become smaller with increasing load.

The damping constant (viscosity) of the fibre at rest and during contraction may be determined from vibration experiments employed for the measurement of the dynamic stiffness. At rest and at equilibrium length, the damping constant is 3 dynes  $\text{cm}^{-1}$  sec (fibre stiffness = 200 dynes  $\text{cm}^{-1}$ ), increasing to 6 dynes  $\text{cm}^{-1}$  sec (fibre stiffness = 1200 dynes  $\text{cm}^{-1}$ ) at 80 per cent of stretch. During isometric contraction, the damping is about 4 times its value at rest. The determination of damping during release contraction proves that the increase in viscosity during contraction is mainly conditioned by the contraction as such and only to a minor extent by the tension developed.

Apart from damping, also elastic after-effects are an expression of the viscosity of the fibre. These elastic after-effects are investigated after sudden small stretchings (10 per cent) at rest and during contraction. Compared with those found on the total muscle, the after-effects in the single fibre are small relative to the increase in tension in the range of moderate elongations. The determinations of elastic after-effects are in good agreement with the variations of the ratio  $\frac{\text{static elasticity}}{\text{dynamic elasticity}}$ .

The consolidation after sudden stretch follows a curve which represents the sum of at least three vastly different exponential curves. In agreement with LEVIN and WYMAN (1927), the course of

consolidation must be considered an expression of the viscosity which is not distributed uniformly over the fibre (like a shunt) but over part of the fibre, only, in series with an elasticity. Determinations of the damping at vibrations of different frequencies, where a lower damping is found at higher frequency, can be interpreted in the same way.

On the basis of the three time constants of the consolidation curve, an equivalent system is calculated which represents the viscous and elastic properties of the fibre. The transport of fluid—by GASSER and HILL regarded as the essential cause of the increasing damping—is quantitatively of minor importance.

On the basis of the experimental results described, an attempt is made to derive the most simple molecular structure which might be regarded as an equivalent of the mechanical-elastic and the electrostatic properties of the muscle fibre. The length-tension and stiffness-load diagrams originating from resulting central forces and angular forces present in such a model are calculated and compared with the mechanical properties of the muscle fibre at rest and during contraction. For the molecule model as well as for the resting muscle fibre, a linear interdependence of stiffness and load is found. The dependence of stiffness on loading indicates the existence of angular movements during the adjustment of minute structure elements. The simplest molecule equivalent is represented by a spiral structure with three series of charges, as a plane system with two series of charges will be unstable. Contraction is interpreted as the propagation of a change in electrostatic charge initiated at one point of the molecule chain. The model may further account for elastic "locking" and yielding. The properties of the model correspond to those of the anisotropic substance, while the properties of the isotropic substance cannot yet be interpreted in a simple way. The difference between the A and I substance may, however, be due mainly to a difference in orientation of the same molecular structure.

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## CONTENTS

	Page
Introduction .....	3
Method .....	4
Length-tension diagrams .....	19
Static length-tension diagram.....	19
1) Rest .....	19
2) Isometric-tetanic contraction .....	20
3) Stretch of a tetanically contracted fibre .....	22
4) Release of the tetanically contracted fibre to the same tension as at rest .....	23
Length-tension diagram from single contractions.....	29
1) Single contractions at long time intervals .....	29
2) Single contractions at varying time intervals .....	30
3) Tension-time dependence of single contractions at varying extents of stretch .....	33
Semi-dynamic length-tension diagrams .....	34
1) Semi-dynamic length-tension diagram of alternating stretch and relaxation at rest .....	36
2) Semi-dynamic length-tension diagram of alternating stretch and release during contraction .....	38
Work diagrams .....	43
1) Tetanic contractions .....	43
2) Single contractions .....	47
Length-tension diagrams of the anisotropic (A) and the iso- tropic (I) substance at rest and during contraction.....	48
1) Length of A and I at rest as a function of stretch .....	49
2) Length of A and I during isometric contraction as a function of stretch .....	49
3) Length-tension diagram of A and I at rest and during contraction	52
4) Stretch of the fibre during contraction .....	63
Elasticity measurements .....	64
A. Dynamic stiffness.....	67
Comparison of the elastic properties of the fibre at rest and during contraction .....	67
Elasticity measurements at rest and during contraction.....	69
1) Treatment of material.....	69
2) Stiffness at rest.....	72
3) Stiffness during release contraction .....	73
4) Stiffness during isometric contraction .....	75
5) Partial release from isometric contraction.....	79
6) Elasticity moduli at rest and during contraction .....	80
7) Elasticity modulus during contraction of a fatigued fibre.....	83

	Page
B. Static stiffness at rest and during contraction .....	84
C. Comparison of static and dynamic stiffness .....	87
D. Absolute values of the elasticity modulus of the striated muscle fibre.....	89
E. Static stiffness of A and I at rest and during contraction	90
F. Elasticity moduli of A and I .....	95
Determination of the damping constant (viscosity) of the single muscle fibre.....	98
Damping constant at rest and during contraction .....	100
Experiments with rapid stretches.....	102
The elastic properties of the fibre in relation to its submi- croscopic structure.....	107
1) Electrostatic central forces in the proposed molecular system ..	112
2) Angular forces in the molecular system .....	114
3) Thermal forces in the molecular system .....	116
List of definitions and abbreviations .....	125
Summary .....	129
References .....	137