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Propagation of Contraction Wave in Single Muscle Fibres I. Electrical Stimulation[1)]

With 2 Text-figures and Plate XII

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(*Communicated by* T. YAMAMOTO)

It has long been known that, by stimulation of whole muscle, a contraction (shortening) wave is initiated from the point of stimulation and is propagated along the longitudinal axis of the muscle (e.g., Bethe and Happel 1923). But in single muscle fibres, several investigations concerned with this problem (Asmussen and Lindhard 1935, Brown and Sichel 1936, Ota 1940, Kamada and Kinosita 1943, Matsumoto 1945) have been made in the past with somewhat conflicting results. The present work is concerned with a quantitative analysis of propagated contraction in an isolated single muscle fibre.

MATERIAL AND METHOD

Single muscle fibre was isolated from the biceps femoris and tibialis anticus of the frog (*Rana japonica*) employing the method of Kamada and Kinosita (1943).

A diagram of the experimental arrangement is shown in figure 1. In a glass vessel (V) filled with Ringer's solution the muscle fibre (M) is connected at one tendon with a glass hook (H), and the other tendon is connected with an isotonic lever (I) through a silk fibre (S). The muscle fibre is stimulated by a break induction shock through a capillary electrode (E_1; Ag-AgCl-Ringer type; cathode) and an independent electrode (E_2; anode). Unless otherwise stated, the tip of the capillary electrode (calibre: 40 microns) is placed about 50 microns away from the surface of the muscle fibre near its fixed end. The local movement of the elementary parts of the muscle fibre during contraction is recorded photographically by the "granule method" which is described elsewhere (Kamada and Kinosita 1943).

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Isotonic lever. As is shown in figure 1, a thin steel wire (w) is stretched holizontally under a proper amount of tension. A cantilever made of a thin glass capillary (g) is fixed at right angles at the middle point of w, and the muscle fibre is connected to the other end of the glass lever through a silk fibre at the tendon, which is made as small as possible. In experiments, unless specially stated, muscle fibre was stretched under 10 dynes of tension by winding the wire (w) in the direction of arrows in the figure.

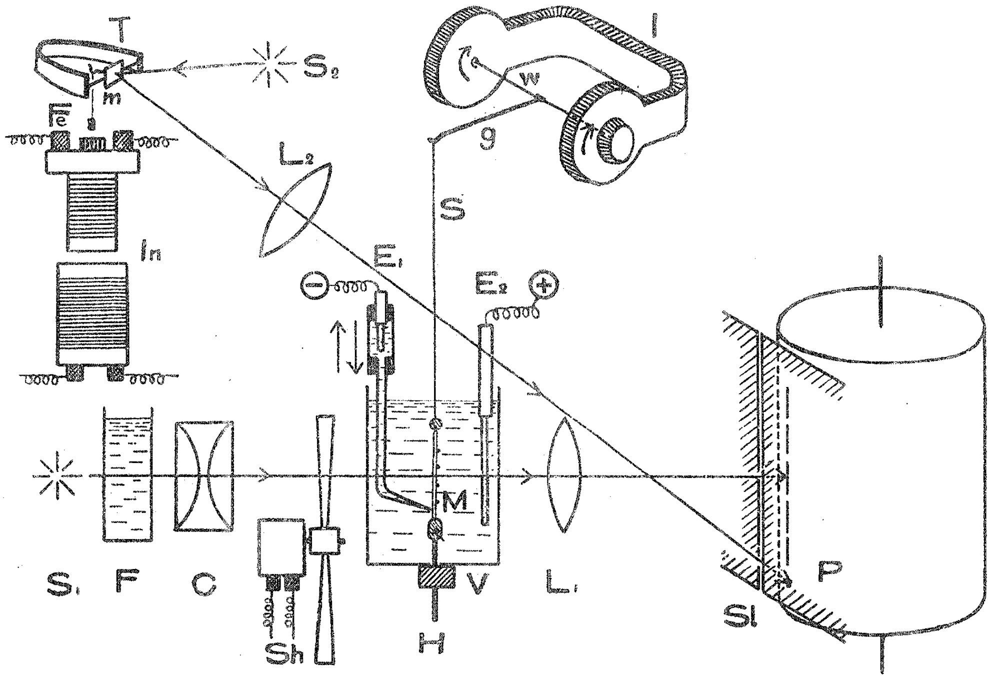

Fig. 1. Diagram of the experimental arrangement.
C: condenser lens.
E_1: capillary electrode.
E_2: independent electrode.
F: light filter.
Fe: piece of iron.
H: glass hook.
I: isotonic lever (g: glass capillary, w: steel wire).
In: inductorium.
L_1, L_2: lens.
M: muscle fibre.
P: photographic paper.
S: silk fibre.
S_1, S_2: light source.
Sh: shutter.
Sl: slit.
T: tension lever (m: mirror).
V: glass vessel filled with Ringer's solution.

During contraction, tension of the muscle fibre is not kept strictly constant. This may be due (1) to the inertia of the lever system (ΔT_1), (2) to the mechanical resistance (ΔT_2) of Ringer's solution to the moving tendon and (3) to the change in torsion (ΔT_3) of the steel wire (w) by the deflection of the arm (g).

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ΔT_1 is calculated from angular acceleration and moment of inertia of lever system. ΔT_2 may be measured directly with a micro-isometric lever by supporting the tendon fragment in Ringer's solution flowing with various velocities. ΔT_3 is calculated from the deflection of the lever (g) during contraction and the coefficient of torsion of the wire (w). As a result of the algebraical summation of ΔT_1, ΔT_2 and ΔT_3, deviation of tension (ΔT) is estimated to be within ± 0.5 dyne during isotonic twitch.

On the other hand, ΔT may be measured directly in the following way: the muscle fibre is connected at its lower end with a micro-isometric lever and at the other with the isotonic lever. As a result, it was realized that the value ΔT was not more than ± 0.5 dyne.

From the results of these two kinds of determinations, it may by said that the contraction (twitch) is practically "isotonic" within ± 5 per cent of deviation.

RESULTS

Propagation of contraction wave. Contraction curves of the elementary parts are constructed by measuring the time change of each length. An example of the results is shown in plate-figure B. It will be clear

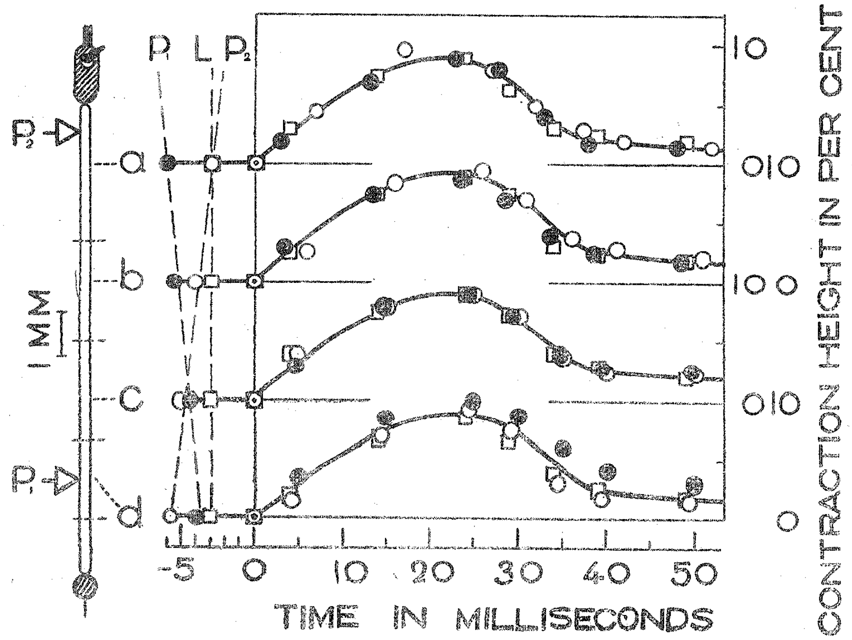

Fig. 2. Contraction curves of elementary parts of the muscle fibre plotted from photographic records obtained from one fibre.

black circles: the fibre is stimulated through a capillary electrode placed at P_1. hollow circles: the fibre is stmulated through a capillary electrode placed at P_2. squares: the fibre is stimulated by transverse current through a pair of large parallel electrodes.

As the original point of the time scale the moment of beginning of contraction is adopted. Broken lines P_1, P_2 and L indicate the moment of stimulation. Biceps muscle. Temp.: 24.5°C.

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that the contraction curves of the elementary parts of the fibre look almost alike, and the closer to the cathode the part is, the earlier its contraction begins. The same relation is observed when the position of the electrode is altered as is shown in figure 2; namely, a contraction wave is initiated from the part nearest the electrode and is propagated in both directions along the length of the fibre. Therefore it may be concluded that the propagated contraction may arise at any point of the fibre, and is not related to some special structure such as a motor end plate.

The propagation velocity of the contraction wave may be determined from the difference in reaction time of each part. It is shown that the wave of contraction is transmitted with an average velocity of 1~3 m/sec, (temp.: 10°~17° C); a value nearly identical with the data obtained in the sartorius muscle of the frog leg (e.g., Bethe and Happel 1923). The latent period of the muscle fibre at the point of stimulation is about 5 milliseconds (10°~17° C).

The results described above indicate that muscle fibre responds to the single shock with a typical twitch just as does a whole muscle. Inconsistent results have been obtained with regard to the response of an excised muscle fibre (e.g., Asmussen and Lindhard 1935, Brown and Sichel 1936, Ota 1940 and Matsumoto 1945). These are probably "cathodic shortenings" (Ramsey and Street 1938) or mixed responses of cathodic shortening and propagated contraction.

All-or-none principle in propagated contraction. The all-or-none principle is found to be valid in the case of propagated response. In a few cases, a local, small contraction,—so small that it is hardly detectable from the photographic record,—is observed near the electrode when the stimulation intensity is just below the threshold for propagated response. Such local contractions have already reported by many investigators (e.g., Hashida 1929).

Transverse stimulation through a pair of large plate electrodes. Supermaximal induction current is applied to the fibre in a transverse direction through a pair of large plate electrodes (Ag-AgCl type) lying parallel to each other and to the longitudinal axis of the fibre. A representative result is shown in figure 2 (squares). It will be clear from the figure that all parts of the fibre begin to contract almost simultaneously. Moreover it is clearly shown in the figure that the contraction curve of the elementary part of the fibre is quite identical whether the contraction is initiated from that part or the response is a conducted one. Therefore it may be concluded that "contraction waves are propagated without decrement".

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Responses vs. applied tension. Isotonic response is analysed in one fibre when the tension applied is altered in the following way: 3→5→10→20→40→20→10→5→3 dynes. It is found that contraction is propagated without decrement independently of the tension applied, although an increase of tension causes a decrease in contraction height in the elementary parts of the fibre.

Anodal stimulation. A muscle fibre is stimulated by an induction shock of threshold strength through a capillary electrode as anode and an independent electrode as cathode. A contraction wave starts from the part of the fibre near the anode, and is propagated along the whole length of the fibre. The form of the contraction wave is identical with that in the case of cathodal stimulation.

Time change in response of muscle fibres. As is mentioned elsewhere (Tamasige 1947), the response of single muscle fibre to electrical stimulation changes with the advance of time. It is shown, however, that the change is not gradual, but somewhat abrupt. For an hour or two after the isolation of the single muscle fibre, both threshold and form of contraction remain nearly constant. Then, quite suddenly, the threshold shows an abrupt increase, and at the same time the contraction becomes localized at the part of the fibre nearest the tip of the capillary electrode, and no propagated contraction (twitch) is obtainable even with increase in the stimulating current. This local contraction resembles in appearance Hashida's small contraction mentioned above. When such a fibre is stimulated with a very strong electrical shock, a slow contraction occurs at the point of stimulation. This contraction is not of an all-or-none type, and the response of each part gradually decreases with increase in distance from the point of stimulation.

Summary and Conclusions

Isotonic contraction of elementary parts of single frog muscle fibre was recorded by the "granule method" of Kamada and Kinosita (1943). In consequence, the following results were obtained:

1. When a part of the muscle fibre is stimulated by a single electrical shock, a contraction wave is initiated from the point of stimulation and is propagated without decrement along the entire length of the fibre with a velocity of 1~3 m/sec.

2. The propagated contraction (twitch) obeys the all-or-none principle.

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3. With the lapse of time after isolation, the muscle fibre undergoes a sudden change of excitability and responsiveness. The all-or-none principle becomes invalid, and the contraction spreads over the fibre with decrement.

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EXPLANATION OF PLATE

Figure A: Example of photographic record taken by the "granule method". White tracings indicate movement of carmine granules adhering on the surface of the muscle fibre. Black tracing is stimulation signal. Site of capillary electrode is shown on the left-hand side of the figure. By the scale on the right-hand side of the figure, the distances between granules can be measured in an absolute unit. Vertical lines show time intervals of 5 milliseconds. The lowest line shows time course of stimulating current recorded by electromagnetic oscillograph (break induction shock).

Figure B: Contraction curves of elementary parts. Curve a, b, c, d and e represent the respective time changes of the lengths a, b, c, d and e in figure A. The original point of time scale indicates the beginning of stimulation. Frog biceps muscle. Temp.: 13.5°C.

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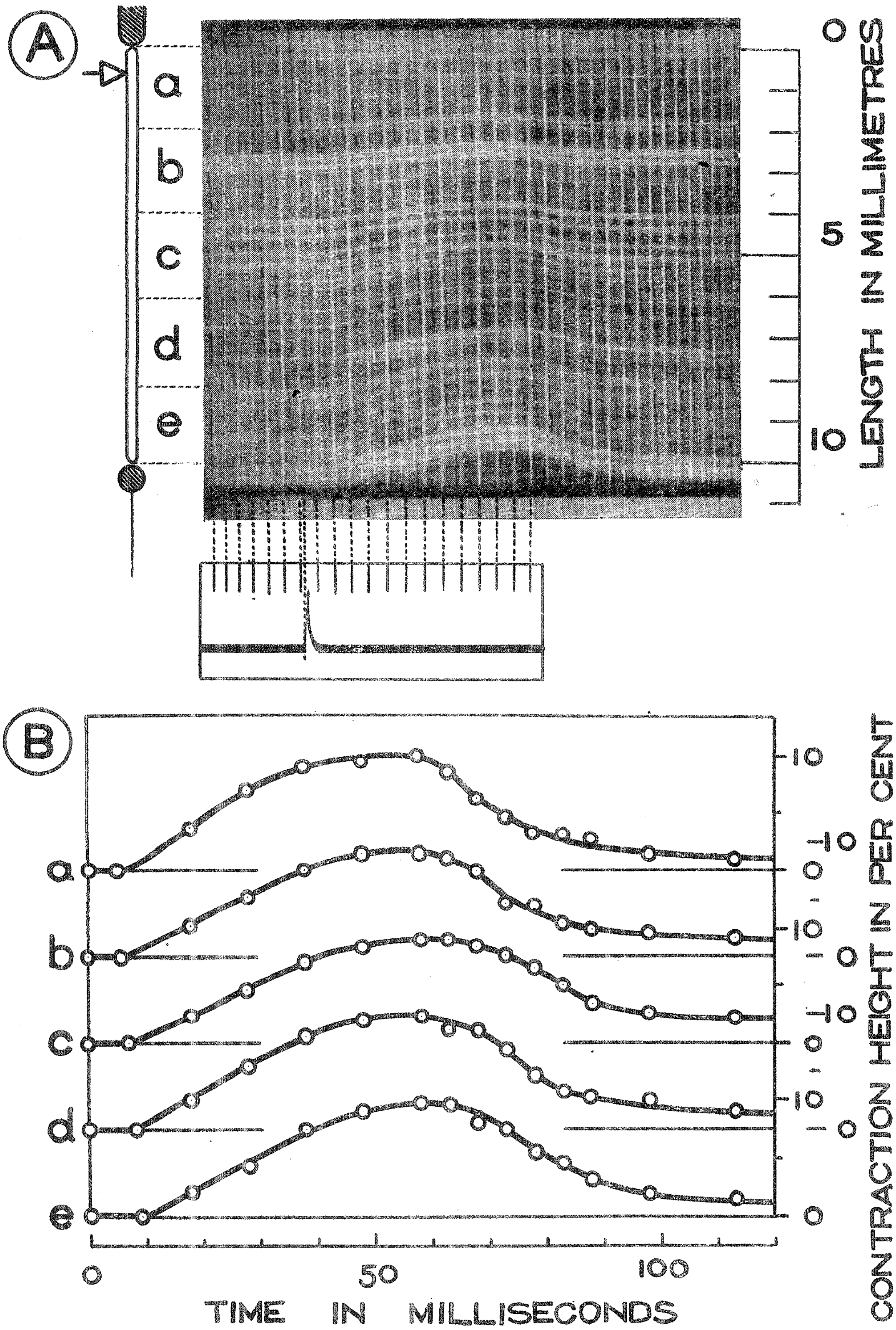

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