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# THE MECHANICAL PROPERTIES OF OESOPHAGEAL STRIATED MUSCLE IN THE CAT AND SHEEP

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SUMMARY

1. A study has been made of the mechanical behaviour of isolated strips of cat and sheep oesophageal muscle.

2. At 37° C, time to peak tension in an isometric twitch was about 80 ms in both muscles. Tetanic fusion frequency was 30 $s^{-1}$, twitch : tetanus ratio 0·4–0·47, and maximum velocity of shortening was 3 lengths.$s^{-1}$.

3. The results are compared with the properties of other muscles.

## INTRODUCTION

The mechanical properties of mammalian limb muscles have been widely studied, and appear to support an inverse relationship between isometric twitch contraction time and shortening velocity (reviewed by Close, 1972). More recently Close & Luff (1974) have shown that this relationship does not extend to the inferior rectus muscle of the rat. It seemed to be of interest to investigate a striated muscle which forms part of the alimentary tract, and the present paper describes the results of measurements of the mechanical properties of isolated strips of oesophageal muscle from the cat and sheep.

In the sheep, the muscular wall of the oesophagus is composed of striated muscle from the pharynx to the cardia (Floyd, 1973) and the region selected for the present study was the outer muscle wall near the cardia. In contrast, the oesophageal wall of the cat, like that of man, is composed of a mixture of smooth and striated muscle, and tissue was taken from the pharyngeal region which is composed of striated muscle.

## METHODS

Experiments have been performed on strips of oesophageal muscle from eight cats (1·4–2·6 kg), anaesthetized with fluothane (I.C.I.) in $O_2$ and maintained with sodium pentobarbitone (Nembutal, Abbott Laboratories Limited) and fifteen sheep (adult female or castrated male 'Dalesbred', 21–71 kg) anaesthetized with Nembutal. In the cats, the upper 5 cm of the oesophagus near the pharynx was removed; in the sheep, the lower 10 cm was excised from the region near the cardia. The lengths of oesophagus were slit longitudinally and the muscle wall was dissected free from the mucosa and any superficial fat. The orientation of fibres in the outer muscle wall was determined by electrical stimulation and observation under dark-field illumination, and a strip was dissected parallel to the outer wall muscle fibres. In the sheep, where the muscle wall is about 1·5 mm thick, the inner wall was then dissected away in order to leave a parallel-fibred strip of outer muscle wall about 0·5 mm thick, but in the cat, where the wall thickness is only about 0·5 mm, no attempt was made to separate the inner and outer muscle layers.

In the cat, $l_{Pmax}$ for individual strips (outer and inner wall) ranged from 19 to 29 mm, and the maximum isometric tensions recorded were 57–302 mN. In order to estimate the force developed per unit cross-sectional area it has been assumed that the outer wall fibres composed one half of the weight of the strips which ranged from 20 to 62 mg. In the sheep, $l_{Pmax}$ for individual strips was 27–37 mm, the weight of the strips was 25–84 mg, and the maximum isometric tensions recorded were 71–400 mN.

*Solution.* The muscle strips were kept in a Ringer–Locke solution (NaCl: 137 mM; KCl: 5 mM; $CaCl_2$: 2 mM; $NaH_2PO_4$: 1 mM; $NaHCO_3$: 12 mM; glucose: 11 mM) bubbled continuously with a mixture of 95 % $O_2$ and 5 % $CO_2$. The experiments were made at 36·5–38·2° C or at 29·4–30·3° C. During any experiment, the temperature of the solution did not change by more than 0·5° C.

*Stimulation.* Stimuli, produced by charging and discharging a 0·5 $\mu$F capacitor, were applied via an electrode grid consisting of eight platinum strips lying in the plane of the muscle strip. Except where otherwise stated, the rates of stimulation used were 40 $s^{-1}$ (cat, 37° C), 50 $s^{-1}$ (sheep, 37° C) and 25 $s^{-1}$ (sheep, 30 °C), and the muscle strips were stimulated for not more than 0·5 s in every 3 min. During stimulation, the fluid surrounding the muscle was removed for a period of 1·5–2·5 s by rapid deflation and re-inflation of a balloon located within the muscle bath.

*Length and tension recording.* Length and tension were recorded electrically with a strain gauge lever (Jewell, Kretzschmar & Woledge, 1967) to which the muscle strip was connected by a thin glass rod; another short glass rod connected the muscle to the base of the electrode assembly. The compliance of the lever was $6{\cdot}3 \times 10^{-5}$ mm. $mN^{-1}$ and the compliance of two typical glass rods tied together with wet cotton thread was less than $5 \times 10^{-4}$ mm.$mN^{-1}$; thus the recording system was stretched by less than 0·15 mm by a force of 250 mN. Length and tension were recorded simultaneously on a Devices pen recorder and displayed on a Tektronix storage oscilloscope.

*Force–velocity curves.* The values of the constants in A. V. Hill's equation were obtained from the observed shortening velocities under various loads by 'fitting' the experimental results with a curve drawn from the equation. This was done by a computer programme of the type described by Woledge (1968).

*Procedure.* The muscle strips were set up at a slack length and their length increased in 1 mm steps until tension development in an isometric tetanus was maximal. A force–velocity relation was then obtained from a number of after-loaded isotonic contractions under different loads, usually arranged in a series and return so that two observations were made with each load. Shortening was limited to 15–25 % of the length ($l_{Pmax}$) at which maximum isometric tension ($P_{max}$) was obtained. Finally, a series of isometric tetani was recorded at 1 or 2 mm intervals of muscle length both below and above $l_{Pmax}$.

Three preliminary experiments on sheep were made with only isometric contractions, and in a number of other experiments additional observations were made of isometric twitches and tetanic fusion frequencies at $l_{Pmax}$.

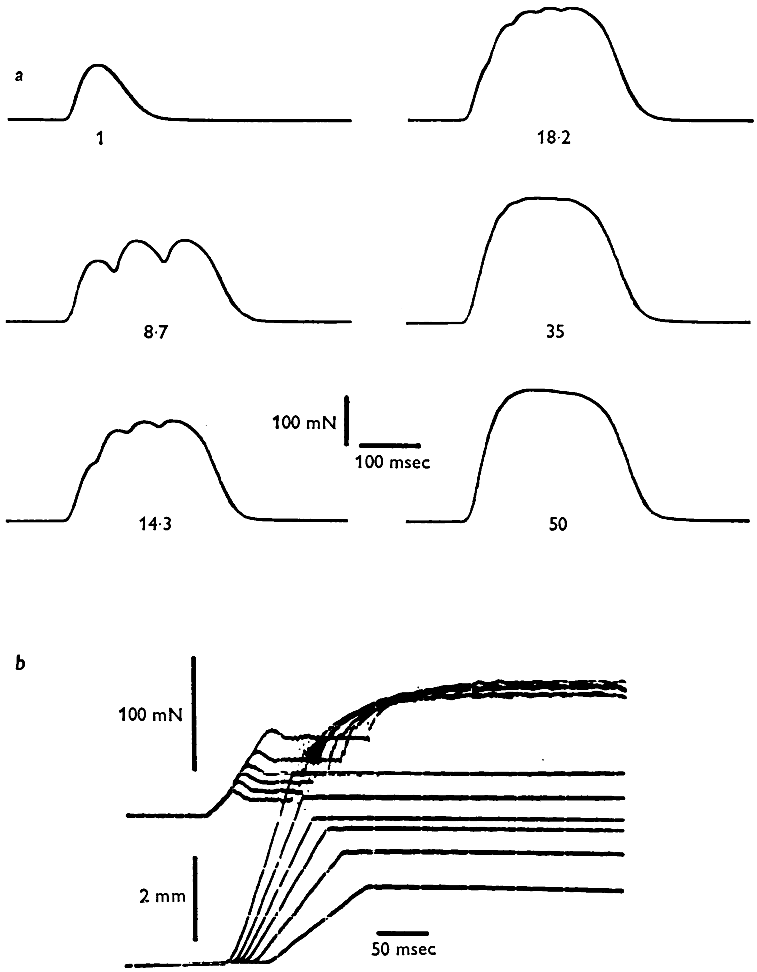


Fig. 1. *a*, original records of isometric tension during repetitive stimulation at various rates, shown below each trace ($s^{-1}$), of an isolated strip of sheep oesophageal muscle at 37° C.

*b*, original records of changes in tension and length recorded simultaneously during six successive afterloaded isotonic contractions against various loads between 0·118 and 0·50 $P_{max}$. The preparation, an isolated strip of cat oesophageal muscle at 37° C, was stimulated repetitively at 40 $s^{-1}$ for 0·4s every 3 min.

Measurements were made also of the half-contraction and half-relaxation times in fused tetani at $l_{Pmax}$. Because the muscle is in a steady state with respect to force development, such estimates of the rates at which the muscles approach and relax from $P_{max}$ may be of more interest than the commonly quoted parameters of the isometric twitch. In any event, the time parameters during tetanus of a twitch muscle are of value for comparison with the properties of slow muscle fibres.

TABLE 1. Summary of properties of isolated strips of oesophageal muscle from the cat (37° C) and sheep (37 and 30° C). Values refer to the mean ± S.E. of mean (number of preparations)

| | cat (37° C) | sheep (37° C) | sheep (30° C) |
|---|---|---|---|
| Time to peak twitch tension (ms) | 78 ± 2 (8) | 79 ± 6 (6) | 137 ± 8 (5) |
| Half-relaxation time (twitch) (ms) | 73 ± 4 (8) | 85 ± 10 (6) | 145 ± 12 (5) |
| Time to 50 % of peak tetanic tension (ms) | 60 ± 4 (8) | 48 ± 2 (9) | 66 ± 6 (5) |
| Half-relaxation time (tetanus) (ms) | 89 ± 5 (8) | 103 ± 3 (9) | 147 ± 3 (5) |
| Twitch: tetanus ratio | 0·40 ± 0·05 (8) | 0·47 ± 0·06 (6) | 0·55 ± 0·05 (5) |
| Tetanic fusion frequency ($s^{-1}$) | 28 ± 2 (7) | 34 ± 3 (4) | 19 ± 1 (5) |
| Force per unit area ($mN.mm^{-2}$) | 142 ± 24 (8) | 124 ± 18 (4) | 174 ± 15 (5) |
| Maximum shortening velocity ($l_{P_{max}}\,s^{-1}$) | 3·08 ± 0·68 (8) | 3·05 ± 0·42 (7) | 2·27 ± 0·25 (5) |
| $a/P_{max}$ (from force–velocity curve) | 0·29 ± 0·03 (8) | 0·44 ± 0·05 (7) | 0·45 ± 0·03 (5) |

## RESULTS

The results of the experiments on cat and sheep oesophageal muscle appear to be similar in many respects and will therefore be presented together. Fig. 1*a* shows typical records of isometric tension developed during repetitive stimulation at various rates. The time to peak tension in an isometric twitch (37° C) was about 80 ms, similar to that reported for cat soleus muscle (Buller & Lewis, 1965*b*; Luff, 1974). The half-relaxation time following an isometric twitch, the rates of stimulation to produce a fused tetanus ('apparent' fusion frequency, Buller & Lewis, 1965*a*), twitch: tetanus ratios, and the half-contraction and half-relaxation times in fused tetani are compared in Table 1.

The similarity of the contraction and half-relaxation times respectively in isometric twitches of cat and sheep at 37° C contrasts with the differences in the half-contraction and half-relaxation times during tetani. The development of isometric tension in the oesophageal strips was faster in sheep than in the cat, while relaxation was slower in sheep than in the cat (unpaired *t* tests; $P < 0·05$). The differences between the rates of repetitive stimulation for fused tetani, and the twitch: tetanus ratios were not significant. The sheep oesophageal strips at 30° C were slower to develop tension and to relax than at 37° C and required lower rates of repetitive stimulation to produce fused tetani, but the twitch: tetanus ratio was not significantly different from that obtained at 37 °C.

*Length dependence.* The active isometric tensions at various muscle

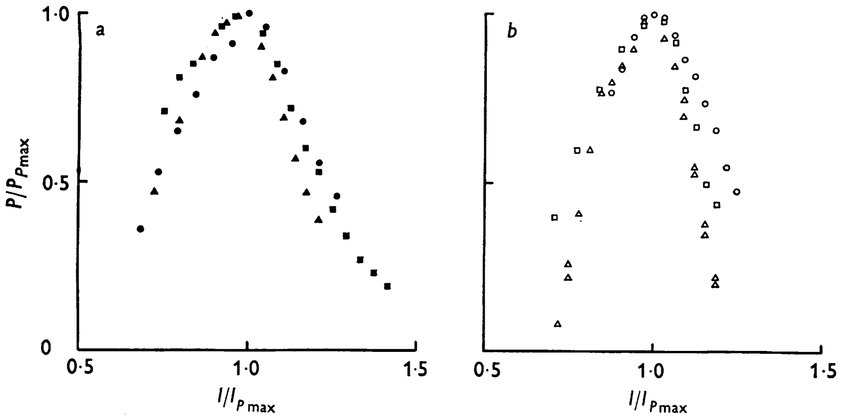


Fig. 2. Variation of active isometric tension, expressed as a fraction of the maximum isometric tension ($P/P_{max}$), with the relative lengths of the isolated strips ($l/l_{Pmax}$) from cat (*a*) and sheep (*b*) oesophageal muscle. The lengths of the muscle strips at which maximum tensions were obtained ($l_{Pmax}$) were 19 mm (●), 24 mm (■), 29 mm (▲), 31 mm (□) and 32 mm (○, △).

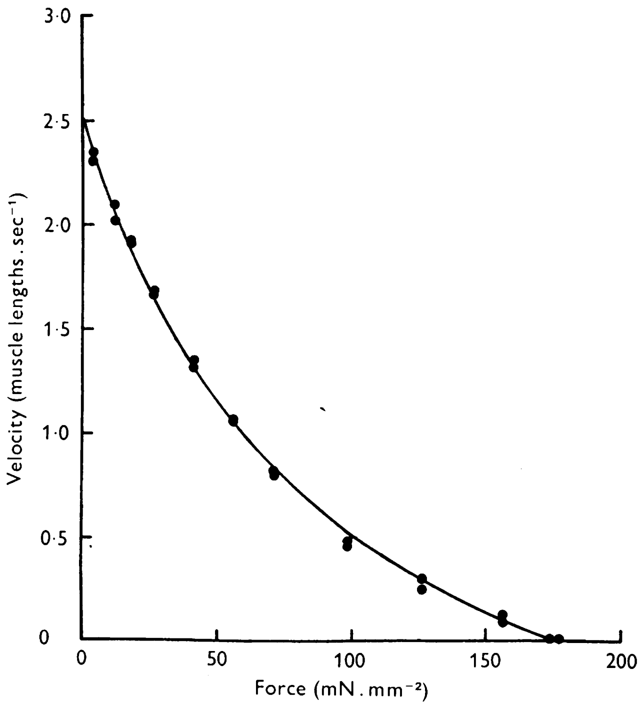


Fig. 3. Force–velocity curve obtained from an isolated strip of sheep oesophageal muscle at 30° C. The line is drawn from A. V. Hill's (1938) equation, $V = b\,(P_{max} - P)/(P + a)$, with $a$ = 137 mN, $V_{max}$ = 77·9 mm. s$^{-1}$, $P_{max}$ = 284 mN, $l_{Pmax}$ = 31 mm, and weight of strip = 49 mg.

lengths in six preparations are shown in Fig. 2. It has not been possible to relate the lengths of the isolated muscle strips to *in situ* muscle fibre lengths, and the strip length at which maximum isometric tension was obtained has been arbitrarily defined as $l_{\mathrm{Pmax}}$. The resting tension at $l_{\mathrm{Pmax}}$ was small, about 10% of the active isometric tension.

The active tension decreased in an approximately linear fashion at lengths greater and less than $l_{\mathrm{Pmax}}$, and the curves were approximately symmetrical over the range of strip lengths investigated. The extrapolated point of zero tension at stretched lengths ranges from about 1·2–1·6 $l_{\mathrm{Pmax}}$.

*Force–velocity curve.* Simultaneous records of tension and length changes during afterloaded isotonic contractions of a strip of cat oesophageal muscle at 37° C are shown in Fig. 1*b*, and a force–velocity curve obtained in an experiment on an isolated strip of sheep oesophageal muscle at 30° C is shown in Fig. 3. The relation between the experimental observations of velocity and load appear to be adequately described by curves drawn from A. V. Hill's equation with mean values of $a/P_{\mathrm{max}} = 0{\cdot}29$ (cat) and 0·44 (sheep). The mean maximum shortening velocity for both cat and sheep muscle strips at 37° C was about 3 lengths. $s^{-1}$. The results are summarized in Table 1.

## DISCUSSION

The maximum isometric tensions recorded in these experiments, 78–282 mN. $mm^{-2}$, are not particularly high, but fall within the range of values reported for other mammalian muscles (Close, 1972). The dissection of the muscle strips will almost inevitably lead to damage to a number of fibres and hence to an underestimate of the force developed per unit cross-sectional area. The tension developed also depends upon the way in which the muscle fibres are packed together (A. F. Huxley, 1957), and there is some evidence to suggest that the fibres in sheep oesophageal muscle are not regularly arranged (Floyd, 1973).

### *Cat oesophagus*

Titchen & Wheeler (1971) reported a tetanic fusion frequency (obtained with oesophageal balloons) of 15 $s^{-1}$ which contrasts with the value of about 30 $s^{-1}$, similar to cat soleus muscle (Cooper & Eccles, 1930; Rosenblueth & Rubio, 1959; Buller & Lewis, 1965*a*), obtained in the present experiments. The time to peak tension in an isometric twitch (about 80 ms) is also similar to that found in soleus, but the mean twitch : tetanus ratio of 0·4 is somewhat higher than any of the reported values for cat muscles (Close, 1972).

The mean maximum shortening velocity of cat oesophageal muscle was three strip lengths. $s^{-1}$. Assuming a sarcomere length of 2·5–3·0 $\mu$m, the maximum speed of shortening per sarcomere ($V_s$; Close, 1965) is 7·5–9·0 $\mu$m.s$^{-1}$, which contrasts with values of 13–14 $\mu$m.s$^{-1}$ for soleus (Close, & Hoh, 1967; Luff, 1974). Thus the present results do not support the relationship between maximum shortening velocity and time to peak twitch tension first proposed by Close (1965). In contrast to the results of Close & Luff (1974) in which rat inferior rectus and extensor digitorum longus had similar maximum velocities but different times to peak tension, oesophagus and soleus have similar times to peak tension but different maximum velocities.

The force–velocity curve tends to be rather flat and has a value $a/P_{max}$ = 0·29. Values in this range are thought to be associated with fast-twitch muscles, while values of 0·15–0·20 are found in slow-twitch muscles (Close, 1972), although Luff (1974) has recently reported a similar value ($a/P_0$ = 0·26) for soleus.

Thus the oesophageal muscle of the cat appears to be a slow-twitch muscle with isometric twitch contraction time and fusion frequency similar to soleus, but with a high twitch:tetanus ratio, and a lower maximum shortening velocity.

*Sheep oesophagus*

The mechanical properties of isolated strips from the outer wall of the sheep oesophagus are similar to those described for the cat. The isometric twitch contraction times, twitch:tetanus ratio, fusion frequencies and mean maximum shortening velocities are almost identical; the rate of rise of tetanic tension is faster than in the cat, relaxation following tetanus is slower, and the force–velocity relation is less curved ($a/P_{max}$ = 0·44).

The rapid contraction in a tetanus, followed by a slow relaxation, is an unusual combination which is made more striking by the differences between sheep and cat oesophageal muscle. It remains to be seen whether the differences in the time parameters of isometric tetani, and the flatness of the force–velocity curve, are accompanied by differences in heat production (cf. Woledge, 1968).

An attempt has also been made to examine the mechanical properties of the oesophagus *in vivo*. Three sheep were anaesthetized with sodium pentobarbitone, the left side of the chest was opened, and the diaphragm was divided to release the terminal oesophagus. Cut distal branches of the vagus were stimulated electrically (5–12 V, 0·5 ms) and pressure recordings were obtained from air filled balloons (frequency response flat to > 50 Hz) inserted via the mouth into the terminal 5 cm of oesophagus. Following a single stimulus to a vagal branch, the time to the peak of the pressure transient was about 60 ms. During repetitive stimulation the apparent fusion frequency was 20–40 s$^{-1}$, and the ratio of maximum pressures following single and repetitive stimuli was 0·36–0·6.

Unfortunately there is little data available for comparison with other muscles of the sheep. A preliminary report by Krnjević & Mitchell (1961) suggested that the time to peak tension in isometric twitches of both fast and slow muscles were about 50 % longer than in the cat (e.g. 120 ms in sheep soleus), and similar differences in the isotonic contraction times of laryngeal muscles have been reported by Martensson & Skoglund (1964).

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