J. Physiol. (1974), **236**, *pp.* 259–270
With 4 *text-figures*
Printed in Great Britain

DYNAMIC PROPERTIES OF INFERIOR RECTUS MUSCLE OF THE RAT

BY R. I. CLOSE AND A. R. LUFF

From the Department of Physiology, John Curtin School of Medical Research, Australian National University, Canberra, Australia

(*Received 18 January 1973*)

SUMMARY

1. Isometric responses of rat inferior rectus muscle to indirect and direct stimulation were compared, and conditions were found for selective direct stimulation of twitch fibres *in vitro*.

2. Most of the twitch fibres were qualitatively 'fast'.

3. The influence of length on isometric contractions and the relation between relative load and speed of sarcomere shortening of fast-twitch fibres were determined.

4. The isometric twitch contraction and half-relaxation times of fast-twitch inferior rectus fibres were only about one half of those of rat extensor digitorum longus fibres in the same conditions, whereas the force: velocity properties of these two fibre groups were virtually the same. These results show that the relation between intrinsic speed of shortening and duration of the active state of the contractile material is not the same for rat extraocular and hind-limb muscles.

INTRODUCTION

The time course of isometric twitch contractions of extraocular muscles of mammals is much more rapid than that of the fastest limb muscles (Cooper & Eccles, 1930; Brown & Harvey, 1941; Matyushkin, 1964; Bach-y-Rita & Ito, 1966; Steinacker & Bach-y-Rita, 1968; Barmack, Bell & Rence, 1971; Fuchs & Luschei, 1971), but the factors that cause this difference were not determined in earlier work. In the present investigation some of the dynamic properties of rat inferior rectus muscle have been determined and are compared with those of extensor digitorum longus muscle of the hind limb. The main finding is that the relation between relative force and speed of sarcomere shortening is virtually the same for the two muscles and that differences in their isometric twitch contraction times are not attributable to differences in the intrinsic speed of shortening of the contractile material.

METHODS

Inferior rectus muscles were taken from female Wistar rats 2–3 months old and weighing 148–221 g. All contractions were recorded *in vitro* at about 35° C (35·04° C ± 0·17° C S.D.) with one end of the muscle connected to a transducer and the other end held by a clamp on the presphenoid bone. The muscle was bathed in Ringer solution (NaCl, 137 mM; KCl, 5 mM; $CaCl_2$, 2 mM; $MgCl_2$, 1 mM; NaH_2PO_4, 1 mM; $NaHCO_3$, 2 g/l.; glucose 2 g/l.) that was bubbled continuously with 95% O_2 and 5% CO_2.

Oculomotor nerve-muscle preparations were stimulated indirectly by 50 μsec pulses through platinum wire electrodes; the amplitude of the pulse for twitch and tetanic contractions was usually about four times the threshold of the least excitable twitch-fibre motor units, but trains of pulses up to fifty times this threshold were used to elicit responses from a small slow-relaxing component of the muscle (Fig. 1*C*, *E*). Direct excitation of twitch fibres was by 'massive' stimulation (Mostofsky & Sandow, 1951) through bright platinum electrodes with 20 $V.cm^{-1}$, 0·3 msec pulses in the presence of 2×10^{-5} g tubocurarine chloride/ml. Ringer solution. The frequency of repetitive stimulation was 500 c/s for isometric tetani and 600 c/s for isotonic tetanic contractions.

Inferior rectus muscles remained in good condition during measurements; the mean ratio of final value to initial value was 0·97 (± 0·03 S.D.) for both P_0 (defined below) and the speed of isotonic shortening against the load equivalent to 0·1 P_0.

Signals from transducers were displayed on a Tektronix 565 oscilloscope with 3A3 vertical amplifier and photographed. The accuracy of time mark calibrations was ± 0·01%. Isometric contractions were recorded with several different transducers; the compliances were 1–13 μm/g, the linearities of voltage output were 0·5–2·0% and the natural frequencies were 1200–2000 c/s. After loaded isotonic contractions were recorded with a photo-electric displacement transducer with the muscle and load connected through a lever. A stainless steel connexion between muscle and lever was less than 10 mg weight. The lever ratio was 25·6:1, the equivalent mass was 12 mg and the displacement transducer was linear within 1% of the maximum signal. The break-away torque of the lever bearings was less than $1{\cdot}52 \times 10^{-3}$ g.cm, and this was equivalent to about 0·3 mg at the point of muscle attachment.

The average number of sarcomeres in fibres from the global side of the inferior rectus muscle was determined by counting (Close, 1964). Some measurements were made on bundles of fibres from extensor digitorum longus muscles and the number of sarcomeres in these fibres was estimated from the average sarcomere length (determined by optical diffraction) and the fibre length.

RESULTS

Comparison of isometric responses to indirect and direct stimulation

Records of isometric contractions were obtained from six inferior rectus muscles that were first stimulated indirectly, then curarized and stimulated directly. The mean isometric twitch contraction time was 5·27 msec (± 0·3 msec S.D.) for indirect stimulation whereas it was 4·53 msec (± 0·3 msec S.D.) for direct stimulation, and the difference between these means is significant ($P < 0{\cdot}001$). In contrast, the responses to the two kinds of stimulation did not differ significantly in isometric twitch half-relaxation time ($P > 0{\cdot}9$) and maximum isometric tetanic tension ($P > 0{\cdot}3$); the mean half-relaxation times were 5·62 msec (±0·31 msec S.D.) for indirect stimulation and 5·61 msec (±0·26 msec S.D.) for direct stimulation. Fig. 1*A*, *B* show tension:time and rate of change of tension:time curves for the twitch responses of one muscle to indirect and direct stimulation. The longer contraction time of the response to indirect stimulation is probably attributable mainly to the time required for conduction of the muscle action potential and the effects of asynchronous activation of different parts of the fibre. In order to obtain a good estimate of the time course of the twitch response of sarcomeres of this muscle it is essential to use some form of 'all-over' stimulation.

The isometric tetanic response to indirect stimulation showed a slow phase of relaxation that is not present in records of contraction elicited by direct stimulation; this difference is illustrated in Fig. 1*C*, *D*, *E*. The slow response was not elicited by direct stimulation in the conditions used for determining the length:tension and force:velocity relations described below.

Motor units

Records of twitch contractions of single motor units, similar to the one in Fig. 2*A*, *c* were obtained from seven muscles by threshold stimulation of small filaments of the oculomotor nerve. The twitch tension:time curves of twelve other motor units were determined by analysing increments in records of the summed responses of up to five units which had relatively constant differences in threshold (Fig. 2*A* *a*, *b*, *c*). There were no significant differences between the characteristics of the two groups of motor units, and the results for the nineteen units were 5·11 msec (±0·86 msec S.D.) for contraction time, 6·28 msec (±1·06 msec S.D.) for half-relaxation time and 0·84 mg (±0·45 mg S.D., range 0·3–1·76 mg) for peak twitch tension. These temporal characteristics of the twitch of motor units are not significantly different from those obtained for indirectly stimulated whole muscles (text above). Furthermore, the ranges of the contraction and half-relaxation times were small, and slow-twitch motor unit responses comparable to those described by Bach-y-Rita & Ito (1966) were never observed.

The composition of inferior rectus muscles was investigated further by recording the twitch responses to a series of indirect stimuli that covered the whole range of axon thresholds. The relations between relative peak tension and time course of twitches of eight muscles are shown graphically in Fig. 2*B*, *C*; similar results were obtained by Barmack *et al.* (1971) for cat lateral rectus muscle. There are significant correlations ($P < 0{\cdot}001$) between the three variables in Fig. 2*B*, *C*.

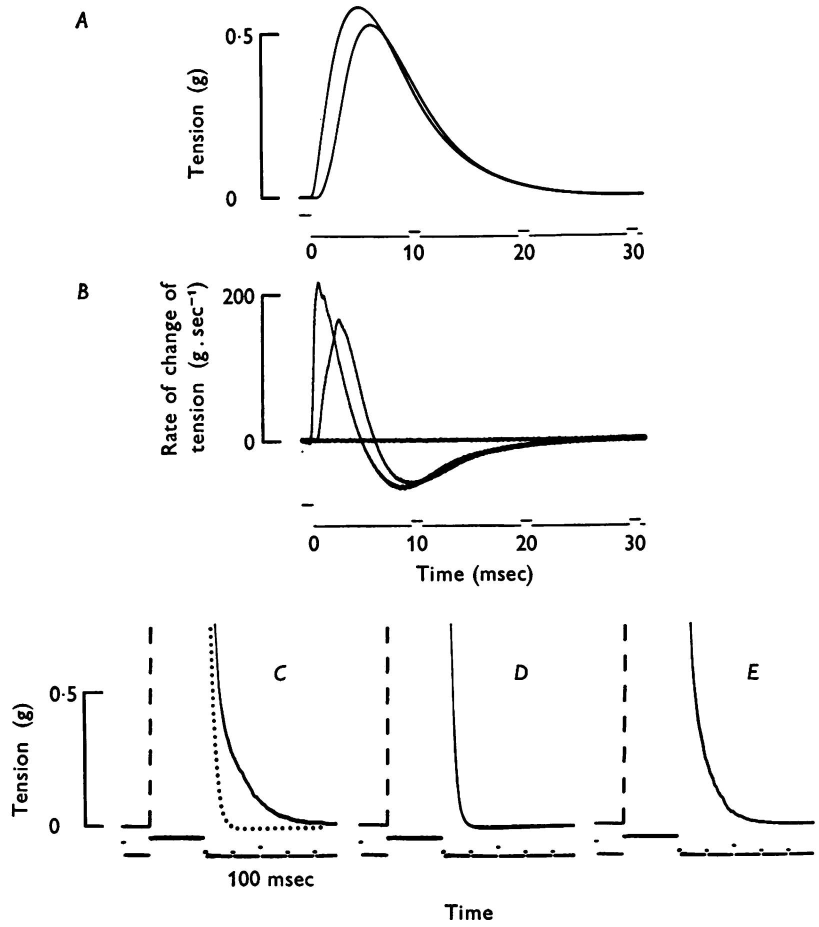

Fig. 1. Time course of isometric twitch tension (*A*) and the rate of change of tension (*B*) following indirect and direct stimulation of one inferior rectus muscle. In *A* and *B* the curve with the shorter latency represents the response of the curarized muscle to direct stimulation. The stimulus occurred at the beginning of the sweep. The undeflected sweep in *B* is the base line at zero rate of change of tension. The muscle weighed 4·9 mg and the temperature was 35° C.

Time courses of the final stages of relaxation from isometric tetanic contractions are shown in *C*, *D* and *E*. The muscle was first stimulated indirectly (*C*), then stimulated directly (*D*) in the presence of $2{\cdot}5 \times 10^{-6}$ g tubocurarine chloride/ml. Ringer, and finally stimulated indirectly again after washing out the curare (*E*). The tension : time curve *D* has been plotted as a dotted curve in *C*. Maximum isometric tetanic tension (P_0) was 4·3 g. The frequency of stimulation was 500 c/s in the period 100–300 msec after the beginning of the sweep. The interval between time marks was 100 msec. The muscle weighed 4·55 mg and the temperature varied between 34·8 and 35·3° C.

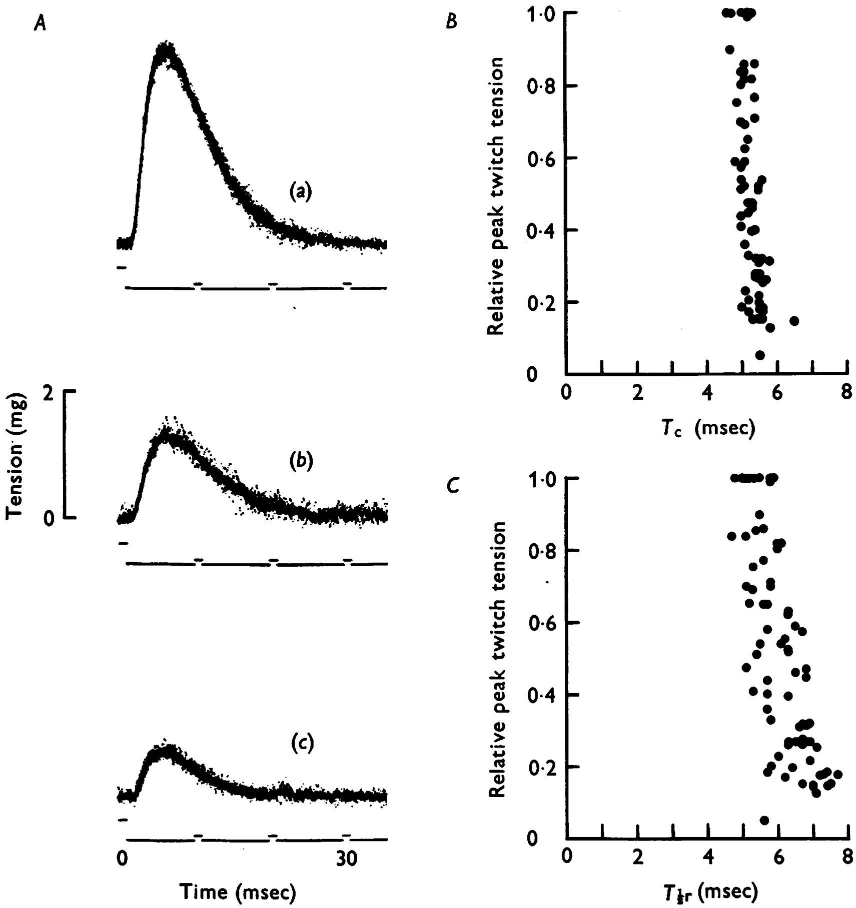

Fig. 2. The tension:time curves in *A* are records of isometric twitch responses of one or more motor units of inferior rectus muscle. The records *a*, *b* and *c* from one nerve filament-muscle preparation are the responses of three units, two units and one unit respectively. Records of responses were averaged photographically by superimposing 21–29 sweeps. The temperature was 35° C. The scatter diagrams in *B* and *C* show the relations between relative peak twitch tension (maximum response = 1·0), the contraction time (T_c) and the half-relaxation time ($T_{\frac{1}{2}r}$) for submaximum and maximum responses of eight oculomotor nerve-inferior rectus muscle preparations. The size of the response was varied by altering the amplitude of the stimulus pulse that was applied to the nerve. The mean peak tension for the maximum response was 0·50 g ± 0·08 g S.D. The temperature was 35° C.

Influence of length on isometric contractions

Fig. 3 shows the relations between length change, the maximum isometric tetanic tension, peak twitch tension and isometric twitch contraction time for a directly stimulated inferior rectus muscle *in vitro.*

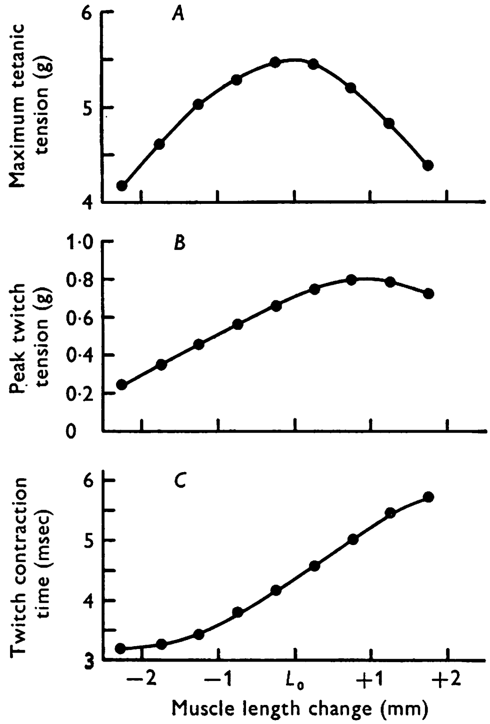

Fig. 3. Relations between length change and maximum isometric tetanic tension, peak twitch tension and isometric twitch contraction time. The length of fibres on the global side of the muscle was about 9 mm at the optimum length (L_0) for tetanic contractions. The muscle weighed 4·65 mg and the temperature was 35° C.

The abbreviation P_0 (below) defines the maximum isometric tetanic tension at the optimum length (L_0) for tetanic contractions; the magnitude of each of these variables was estimated by interpolation where necessary (e.g. Fig. 3). The mean difference between the optimum lengths for twitch and tetanus was 1·0 mm ± 0·27 mm S.D. ($n = 5$). The results obtained from five inferior rectus muscles are summarized in Table 1. The maximum isometric tetanic tension per unit cross-sectional area of muscle was about 1·0 kg.cm^{-2}.

Measurements on eight muscles at optimum length showed that the peak twitch tension at 21–22° C was about 1·85 times greater than it was at 35° C. Furthermore, directly stimulated, curarized inferior rectus muscles show post-tetanic potentiation of peak twitch tension at optimum length and 35° C. These two important properties were not studied in detail but sufficient information was obtained for the purpose of identifying the principal twitch-fibre component as being qualitatively 'fast' (cf. Close & Hoh, 1968*a*, *b*; Close, 1972).

TABLE 1. Characteristics of isometric twitch and tetanic contractions of five inferior rectus muscles at the optimum length (L_0) for tetanic contraction. The muscles were stimulated directly. The characteristics listed are the contraction time (T_c), half-relaxation time ($T_{1/2r}$) and peak tension of isometric twitch (P_t), the maximum isometric tetanic tension (P_0) and the muscle weight (M). The fibre length of the principal fibres on the global side of these muscles was about 9 mm at L_0. Temperature: 35° C

	T_c (msec)	$T_{1/2r}$ (msec)	P_t (g)	P_0 (g)	P_t/P_0	M (mg)
Mean	4·38	4·82	0·66	5·12	0·130	4·6
S.D.	±0·41	±0·48	±0·03	±0·38	±0·01	±0·1
Range	3·8–5·07	4·2–5·45	0·63–0·71	4·42–5·47	0·115–0·146	4·4–4·8

Records of contractions of directly stimulated (20 V.cm^{-1}, 0·3 msec pulse) bundles of extensor digitorum longus (digit V) fibres were obtained for comparison, using the same equipment and conditions that were used for determining the properties of inferior rectus muscles. The isometric twitch contraction time of extensor digitorum longus fibres *in vitro* was 8·7 msec ± 0·8 msec S.D. ($n = 6$) and the twitch:tetanus ratio was 0·199 ± 0·04 S.D.

Force: velocity relation

The speed of shortening of directly stimulated inferior rectus muscle fibres was determined graphically from records of afterloaded isotonic tetanic contractions. Some representative records are shown in Fig. 4*A*. The method used for estimating the speed of shortening of sarcomeres has been described earlier (Close, 1964).

The force: velocity data for the inferior rectus muscles could not be described adequately by Hill's equation (Hill, 1938); this equation could be made to fit the results reasonably well for loads greater than about $0{\cdot}2P_0$, but when this was done the observed velocities for loads less than about $0{\cdot}2P_0$ were considerably higher than the predicted values. The relation between speed of shortening of sarcomeres (V_s) and relative load (P/P_0) has been described by the sum of one linear term and two exponential terms. The general form of the equation was

$$V_s = A\,e^{-\alpha P/P_0} + B\,e^{-\beta P/P_0} + C - \gamma P/P_0, \qquad (1)$$

where P is the isotonic load, P_0 is the maximum isometric tetanic tension, and A, B, C, α, β and γ are constants.

Force: velocity measurements were made on eight inferior rectus muscles and the results are shown in Fig. 4*B*. The data for each muscle were described by eqn. (1). The closeness of fit of the curves was remarkably good

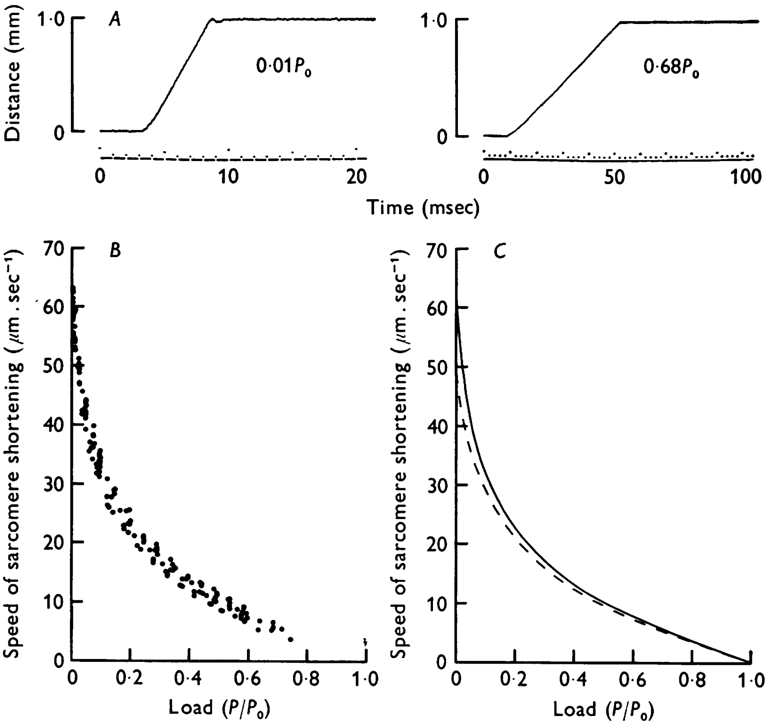

Fig. 4. Distance:time curves for afterloaded isotonic contractions of one inferior rectus muscle (*A*). The load is expressed as a decimal fraction of the maximum isometric tetanic tension (P_0). The average number of sarcomeres in fibres on the global side of the muscle was 3480. The temperature was 35° C. The graph in *B* shows the observed speeds of sarcomere shortening of eight inferior rectus muscles at different relative loads, and the mean force:velocity curve that represents these results is the continuous curve in *C*. The average number of sarcomeres per fibre for the eight inferior rectus muscles was 3680 (range 3480–3856). The interrupted curve in *C* is the standard curve for extensor digitorum longus sarcomeres (see text). The temperature was 35° C.

and the mean ratio of observed velocity to predicted velocity was 0·994 ± 0·036 S.D. (n = 169). Furthermore, the results from six of the eight muscles showed no significant correlation between relative load and the ratio of observed velocity to predicted velocity; the results from the other two muscles gave force: velocity points that were a little below the fitted curve for $P/P_0 > 0{\cdot}5$. Nevertheless, the description of the data by equation (1) was good enough to enable reliable interpolation to be carried out, and this is important in the comparison of force:velocity properties of inferior rectus and extensor digitorum longus muscles given below. The mean force:velocity curve for the inferior rectus muscles is shown in Fig. 4*C* and is described by the equation

$$V_s = 15{\cdot}25\,\mathrm{e}^{-31{\cdot}7P/P_0} + 28{\cdot}44\,\mathrm{e}^{-6{\cdot}15P/P_0} - 18{\cdot}06P/P_0 + 18{\cdot}06. \qquad (2)$$

The intrinsic speed of shortening of sarcomeres was estimated by extrapolating the curve to zero load, and the mean value for the eight inferior rectus muscles was 61·75 μm. sec^{-1} ± 2·53 μm. sec^{-1} S.D.

Records of isotonic contractions of extensor digitorum longus muscles that were obtained earlier (100-day-old rats, see Close, 1964) have been re-measured and the data for individual muscles have been fitted by eqn. (1). The mean curve for these extensor digitorum longus muscles is shown in Fig. 4*C*; this curve is described by

$$V_s = 7{\cdot}4\,\mathrm{e}^{-38{\cdot}9P/P_0} + 25{\cdot}25\,\mathrm{e}^{-5{\cdot}85P/P_0} - 16{\cdot}5P/P_0 + 16{\cdot}5, \qquad (3)$$

and the intrinsic speed of shortening of sarcomeres was 49·15 μm.sec^{-1} ± 3·64 μm.sec^{-1} S.D. ($n = 4$).

The earlier reported intrinsic speed of 42·7 mμ.sec^{-1} (Close, 1964) for extensor digitorum longus of 100-day-old rats was low because an error was made in reading the original photographic record of the displacement calibration.

The main finding of these studies is that the relation between relative force and speed of sarcomere shortening is nearly the same for fast-twitch fibres of inferior rectus and extensor digitorum longus muscles. However, there are small significant differences in speed of sarcomere shortening in these two kinds of fibre at low loads ($P \leqslant 0{\cdot}2P_0$, see Fig. 4*C*); the probability value for the significance of the difference between mean sarcomere velocities was less than 0·001 at $P/P_0 = 0$, and 0·05 at $P/P_0 = 0{\cdot}2$. The same result was obtained with bundles of extensor digitorum longus fibres that were stimulated 'massively' *in vitro*, and it seems likely that small differences in the speeds of shortening of sarcomeres of the two muscles are not attributable to differences in recording conditions.

DISCUSSION

One of the most unexpected results of this investigation is the observation that the contractile response of inferior rectus muscle appears to be quite simple. This muscle, like other extraocular muscles, has a very rapid isometric twitch response. The predominant twitch-fibre component of inferior rectus is 'fast' according to three qualitative criteria that characterize fast-twitch limb muscles (Close, 1972): (1) the myofibrillar material has alkali-stable, acid-labile myosin adenosinetriphosphatase (ATPase) (Yellin, 1969); (2) the peak twitch tension has a negative temperature coefficient (20–35° C) and (3) the fibres show post-tetanic potentiation of peak twitch tension following repetitive direct stimulation.

Changes in the time course of isometric twitch contractions with recruitment of fibres (Fig. 2*B*, *C*) may be attributable partly to the presence of some slow-twitch units. This interpretation would be consistent with histochemical evidence for the existence of a small component of rat extraocular muscle that is composed of fibres with acid-stable, alkali-labile myosin ATPase (Yellin, 1969). Nevertheless, the results obtained here show quite clearly that the predominant kind of motor unit has twitch time relations that appear to be the same as those for the whole muscle. Consequently, a slow-twitch fibre component, if it exists in rat inferior rectus muscle, must have contributed very little to contractions of the whole muscle preparations *in vitro*.

Slow mechanical components that were evoked by nerve stimulation (Fig. 1*C*, *E*) might have resulted from repetitive spontaneous firing of nerve or muscle fibres after the end of the stimulus train, and this possibility was not excluded. Alternatively, it is possible that the slow component is attributable to slow-graded muscle fibres of the kind described by Hess & Pilar (1963) and Matyushkin (1964). In any event, the slow components contributed very little to the total isometric tension.

The observation that rat inferior rectus muscle behaves as though it were composed largely of fibres with uniform dynamic properties is consistent with the results of histochemical studies which show that most of the total fibre cross-sectional area is occupied by myofibrils having alkali-stable myosin ATPase (Yellin, 1969; Asmussen, Kiessling & Wohlrab, 1971). A high degree of uniformity of contractile response of inferior rectus fibres is not necessarily inconsistent with the heterogeneity described by various investigators who have classified rat extraocular fibres into six categories on other histochemical and structural criteria (e.g. Teräväinen & Huikuri, 1969; Asmussen *et al.* 1971; Mayr, 1971). It is quite possible, for example, that extraocular muscle fibres with identical contractile material may differ in diameter, relative development of oxidative and glycolytic enzyme systems, and so on.

The maximum isometric tetanic tension per unit cross-sectional area of inferior rectus was about one-third to one-half of the values for rat limb muscles (Table 1 and text above; Close, 1969; Bárány & Close, 1971). The explanation for this difference is not known but it could be due to (1) loss of excitability of some inferior rectus fibres *in vitro*, (2) errors in estimating the amount of contractile material in parallel in twitch fibres from measurements of whole muscle weight and fibre length, and (3) differences in activity or properties of actinmyosin cross-bridges during maximum activation in normal physiological conditions. There appears to be no evidence from physiological (above) or histological (Teräväinen, 1968; Mayr, 1971) investigations that the first two possibilities could provide a complete explanation for the low tension output of the inferior rectus muscle. The third possibility seems to be important even though it has no precedent among mammalian twitch muscles. More work should be carried out to clarify this point.

The dynamic properties of inferior rectus muscle are interesting in connexion with the relation between intrinsic speed of sarcomere shortening and the inertia of the structure that is moved by a muscle. Hill wrote an informative paper on this topic in 1950 and suggested that different muscles of a given animal vary widely in intrinsic speed in accordance with their function, those required to move light structures rapidly having higher intrinsic speeds of shortening than those required to move massive structures. This prediction is not supported by the results of the present investigation and further measurements on other heterologous skeletal muscles should be carried out. None of the results obtained up to this time excludes the possibility that there is an inverse relation between intrinsic speed of sarcomere shortening and isometric twitch contraction time of extraocular muscles, or any other homologous muscles, of animal species that have similar body form and different body size.

The most important result of this investigation is the observation that the isometric twitch contraction time of inferior rectus is only about one half that of extensor digitorum longus, whereas the relation between speed of shortening of sarcomeres and relative load is about the same for the two muscles. This shows that the relation between intrinsic speed of shortening and duration of the active state of the contractile material is not the same for fast-twitch fibres of extraocular and hind-limb muscles. Earlier investigations showed that although soleus and extensor digitorum longus muscles differ markedly in speed of contraction, the intrinsic speeds of sarcomere shortening and isometric twitch contraction times are inversely related and the product of these two variables is about the same for the two muscles (Close, 1964, 1965, 1967). There are, therefore, two interesting and contrasting patterns in the relations between characteristics of isometric and isotonic contractions in these three heterologous muscles.

We thank Mrs Edna Murray for preparing the diagrams.

REFERENCES

Asmussen, G., Kiessling, A. & Wohlrab, F. (1971). Histochemische Charakterisierung der verschiedenen Muskelfasertypen in den äuberen Augenmuskeln von Säugetieren. *Acta anat.* **79**, 526–545.

BACH-Y-RITA, P. & ITO, F. (1966). *In vivo* studies on fast and slow muscle fibers in cat extraocular muscles. *J. gen. Physiol.* **49**, 1177–1198.

BÁRÁNY, M. & CLOSE, R. I. (1971). The transformation of myosin in cross-innervated rat muscles. *J. Physiol.* **213**, 455–474.

BARMACK, N. H., BELL, C. C. & RENCE, B. G. (1971). Tension and rate of tension development during isometric responses of extraocular muscle. *J. Neurophysiol.* **34**, 1072–1079.

BROWN, G. L. & HARVEY, A. M. (1941). Neuro-muscular transmission in the extrinsic muscles of the eye. *J. Physiol.* **99**, 379–399.

CLOSE, R. (1964). Dynamic properties of fast and slow skeletal muscles of the rat during development. *J. Physiol.* **173**, 74–95.

CLOSE, R. (1965). The relation between intrinsic speed of shortening and duration of the active state of muscle. *J. Physiol.* **180**, 542–559.

CLOSE, R. (1967). Dynamic properties of fast and slow skeletal muscles of mammals. In *Exploratory Concepts in Muscular Dystrophy and Related Disorders*, ed. MILHORAT, A. T. Amsterdam: Excerpta Medica Foundation.

CLOSE, R. (1969). Dynamic properties of fast and slow skeletal muscles of the rat rat after nerve cross-union. *J. Physiol.* **204**, 331–346.

CLOSE, R. I. (1972). Dynamic properties of mammalian skeletal muscles. *Physiol. Rev.* **52**, 129–197.

CLOSE, R. & HOH, J. F. Y. (1968*a*). The after-effects of repetitive stimulation on the isometric twitch contraction of rat fast skeletal muscle. *J. Physiol.* **197**, 461–477.

CLOSE, R. & HOH, J. F. Y. (1968*b*). Influence of temperature on isometric contractions of rat skeletal muscles. *Nature, Lond.* **217**, 1179–1180.

COOPER, S. & ECCLES, J. C. (1930). The isometric responses of mammalian muscles. *J. Physiol.* **69**, 377–385.

FUCHS, A. F. & LUSCHEI, E. S. (1971). Development of isometric tension in simian extraocular muscle. *J. Physiol.* **219**, 155–166.

HESS, A. & PILAR, G. (1963). Slow fibres in the extraocular muscles of the cat. *J. Physiol.* **169**, 780–798.

HILL, A. V. (1938). The heat of shortening and dynamic constants of muscle. *Proc. R. Soc.* B **126**, 136–195.

HILL, A. V. (1950). The dimensions of animals and their muscular dynamics. *Sci. Progr.* **38**, 209–230.

MATYUSHKIN, D. P. (1964). Motor systems in the oculomotor apparatus of higher animals. *Fedn Proc.* **23**, T1103–T1106.

MAYR, R. (1971). Structure and distribution of fibre types in the external eye muscles of the rat. *Tissue & Cell* **3**, 433–462.

MOSTOFSKY, D. & SANDOW, A. (1951). High-current dual-purpose physiologic stimulator. *Electronics* **24**, 11–14.

STEINACKER, A. & BACH-Y-RITA, P. (1968). A mechanical study of the cat retractor bulbi muscle. *Experientia* **24**, 1138–1139.

TERÄVÄINEN, H. (1968). Electron microscopic and histochemical observations on different types of nerve endings in the extraocular muscles of the rat. *Z. Zellforsch. mikrosk. Anat.* **90**, 372–388.

TERÄVÄINEN, H. & HUIKURI, K. (1969). Effect of oculomotor and trigeminal nerve section on the ultrastructure of different myoneural junctions in the rat extraocular muscles. *Z. Zellforsch. microsk. Anat.* **102**, 466–482.

YELLIN, H. (1969). Unique intrafusal and extraocular muscle fibres exhibiting dual actomyosin ATPase activity. *Expl Neurol.* **25**, 153–163.