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The force-velocity relation of the rabbit inferior oblique muscle; influence of temperature

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Abstract. The contractile properties of the rabbit inferior oblique muscle (IO) were studied in vitro with direct stimulation at temperatures between 20 and 35°C. Isovelocity releases were used to determine the force/velocity relation. Cooling the muscle from 35°C to 20°C increased contraction and half-relaxation times of single twitches with a temperature coefficient (Q_{10}) of 0.4, but did not affect significantly the twitch tension. The tetanic tension increases with increasing temperature (Q_{10} = 1.32). Cooling decreased the maximum shortening velocity of the IO with a Q_{10} of 1.6 and the maximum mechanical power with a Q_{10} of 2.3. At 35°C, the maximum speed of shortening of the muscle (19 ± 2 muscle lengths/s, mean ± SEM) corresponded to a maximum shortening velocity of the sarcomeres of 57 ± 6 μm/s. This value is similar to data obtained for extraocular muscles (EOM) of smaller rodents (mice and rats). In comparison with mammalian limb muscles the isometric and force-velocity properties of mammalian EOM appear to be virtually independent of the size of the animal. Thus, IO is a fast-twitch muscle endowed with a maximum velocity of shortening higher than that of fast-twitch skeletal muscle, but using a tetanic mechanical power lower than that produced by slow-twitch muscle: the combination of these properties makes it ideally suited to move an ocular globe of low mass at high velocity.

Key words: Extraocular muscle – Inferior oblique muscle – Force-velocity relation – Temperature

Introduction

In many mammalian species [2], extraocular muscles (EOM) are characterized by a much more rapid time course of isometric twitch contractions, a higher fusion frequency, a lower twitch-to-tetanus ratio and a higher fatigue resistance than fast-twitch muscles of the same individual.

There is much less information about the speed of shortening of EOM fibres. In rat [11] and mouse [17] inferior rectus muscles, isometric twitch time-to-peak (t_p) values were half those of rat fast-twitch extensor digitorum longus muscles, whilst the maximum speed of shortening of the sarcomeres, V_{max}, was virtually the same in both muscles. As these experiments were done on small animals, it is of interest to know whether this is also true in larger ones. So we decided to determine the isometric contractile properties and the force-velocity relation of the inferior oblique (IO) muscle of the rabbit. We found that its V_{max} is similar to that of the ocular muscle from mice or rats. Thus ocular V_{max} appears to be independent of animal size, in contrast with the V_{max} of slow or fast muscle, which decreases in larger animals [8]. Moreover the peak tetanic power is low, comparable to that of slow muscle. We also observed that decreasing the temperature changes V_{max} and t_p in the same way as does an increase in body mass, suggesting that the relation between these two variables [8] could depend on controlling the sensitivity of actomyosin ATPase activity to temperature, as a function of body mass.

Materials and methods

Muscle preparation. Grey-brown rabbits (n = 18, gift of Janssen Pharmaceutica), were anaesthetized with a mixture of fluanisone (5 mg/kg body weight) and fentanyl (0.1 mg/kg body weight) and quickly decapitated. The eyeball was exposed by removal of the inferior and superior tarsus. The IO was dissected free from connective tissue and exposed over its whole length. The resting length of the muscle in situ (L_r) was measured with the eyeball in primary position. The diameter of the globe was also determined. In order to avoid muscle damage, a surgical thread was passed close to the insertion of the muscle through four holes in the sclera and sutured. The IO was then separated from the globe by cutting around the patch of sclera, dissected free along its whole length and a small piece of bone on which the muscle has its origin was cut out after attaching a short piece of thread.

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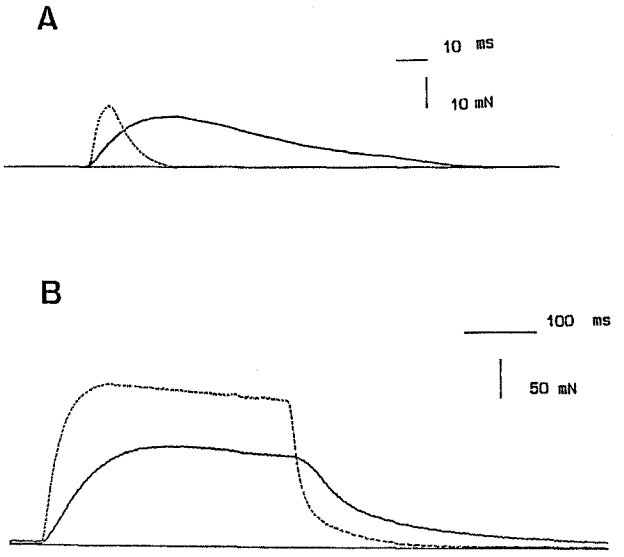

Fig. 1. Records of isometric single twitches (**A**) and tetanic contractions (**B**) of an isolated rabbit inferior oblique (IO) muscle at 20°C (*full line*) and 35°C (*dotted line*)

Mechanical recordings. The bony end of the muscle was attached to a fixed frame, and the muscle was inserted between two parallel rows of eight platinum electrodes, 2 mm apart. The global end of the muscle was connected to the force transducer of an electromagnetic puller [18]. Force and length signals were sampled at a rate of 1 kHz, digitized through an A/D conversion card (RTI-815), displayed on an AT computer and analysed using a QuickBASIC program. The velocity of the movement was adjustable in both directions from 0.2 up to 72.2 mm/s. Differentiation of the signal from the displacement transducer showed that the final speed was reached in less than 2 ms and that it did not vary by more than 1% during the movement, within a range of 4.4 mm. There was negligible phase shift for sinusoidal movements up to 180 Hz. The compliance of the system was 2 μm/N.

The preparation was kept vertically in a Krebs solution (mM: NaCl 118; KCl 5; $CaCl_2$ 2.5; $MgSO_4$ 1; KH_2PO_4 1; $NaHCO_3$ 25; glucose 5) oxygenated with a gas mixture of 95% O_2 and 5% CO_2, the pH was adjusted to 7.4. The assembly was placed in a thermostatic bath (maximum fluctuation 0.3°C). The length of the muscle was adjusted to give a maximum twitch tension (optimum length L_o). When stretched from L_r to L_r + 2 mm (= L_o, approximately 110% of L_r), the resting force was about 8 mN. The muscle was stimulated by square waves of alternate polarity (duration 0.25 ms, output impedance 100 Ω). Twitches were evoked at a frequency of 1 Hz. After the initial staircase effect, the twitches were similar and the tenth twitch was recorded and analysed (Fig. 1 A). For tetanic contractions (Fig. 1 B), the preparation was stimulated either for 350 ms (20 and 25°C) or for 300 ms (30 and 35°C). The stimulus frequency was 330 Hz at all temperatures. It has been reported earlier that 330 Hz is the fusion frequency of EOM at 35°C and that tetanic force did not change for higher frequency of stimulation [2]. We assumed that this is also true at lower temperatures.

The force-velocity relation of the muscle was obtained by the method of isovelocity releases [18]. Briefly (Fig. 2 A), the muscle, stretched to L_o was tetanically stimulated and released at a time when the tension reached a plateau (i. e. maximum isometric tetanic stress, S_o, 150 ms after the onset of the stimulation), from L_o to L_r at a constant velocity. The release started with a short (150 μm) release at high velocity (300 mm/s), in order to help discharge the series elastic elements. The contribution of the series elastic elements could not be completely eliminated, since the force still fell rapidly during the following slow release. For this reason, we had to release the muscle until a plateau was reached.

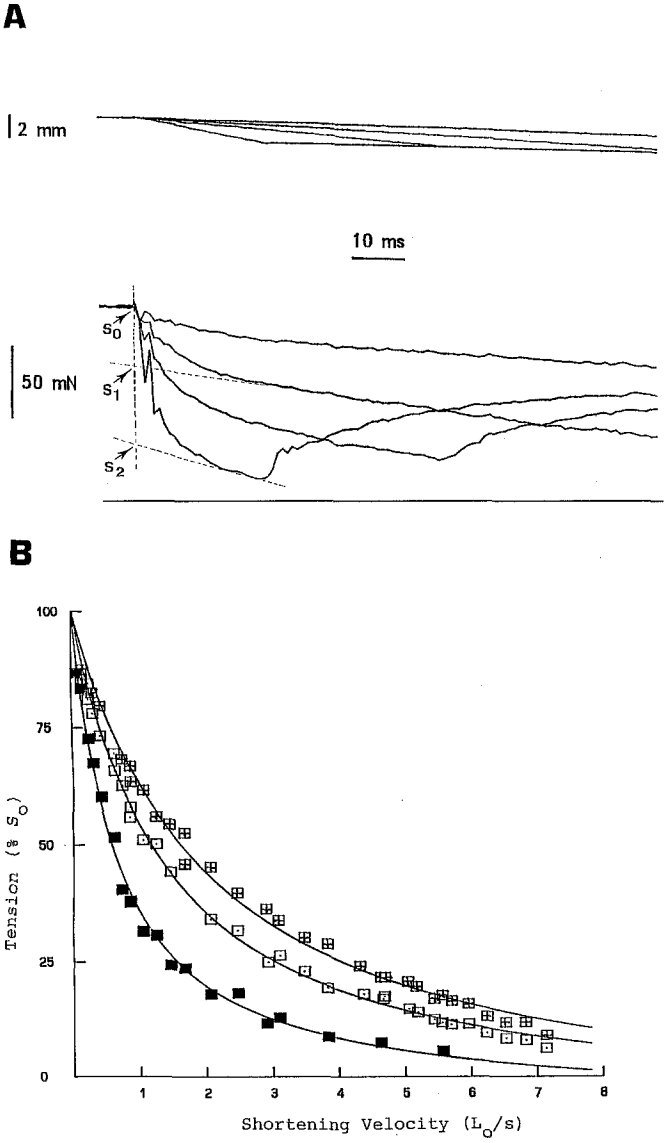

Fig. 2. A Four isovelocity releases of a rabbit IO muscle. The muscle has been isometrically tetanized for 150 ms when these records began. *Upper traces* depict length; *lower traces* depict tension. The velocities of the releases shown were: 5.57, 3.85, 2.08, and 1.06 muscle length/s. S_o shows the point at which the isometric tension was measured. S_1 and S_2 show two examples of the method of extrapolation used to estimate the tension maintained at the starting length of the release. **B** Force-velocity relation of the rabbit IO muscle at 20°C (*black squares*), 30°C (*open squares*) and at 35°C (*crossed squares*). The Hill's hyperbolas were computed by a least squares method. The velocity constants b were respectively: 2.06, 1.42 and 0.68 L_o/s (where L_o is the optimum length), the force constants a/S_o: 0.13, 0.10 and 0.07. The muscle length L_o was 26.5 mm and its weight was 129 mg. The rabbit body weight was 2.8 kg

But even then the force drifted slowly down, because S_o declines at the shorter lengths. In order to estimate the force-velocity data at the initial muscle length, the force maintained during the release was extrapolated to the onset of the release (S_1, S_2, Fig. 2 A). The ratios S_n/S_o (where "n" is the number of the tetanus) paired with the corresponding velocity of release were fitted to the Hill's hyperbolic relation, using a non-linear least squares procedure:

$$S/S_o = (b - a/S_o \times V)/(b + V) \quad (1)$$

yielding values for b, the velocity constant in $mm \cdot s^{-1} \cdot mm^{-1}$

Table 1. Isometric contractions of rabbit IO muscle

Parameter	Temperature				
	20°C	25°C	30°C	35°C	Q_{10}
n	11	6	12	9	
S_{ot} (kN m^{-2})	3.4 ±0.5	3.3 ±0.6	3.2 ±0.2	3.3 ±0.5	1.00
t_p (ms)	20.0 ±1.9	13.7 ±1.0	8.5 ±0.6	7.0 ±0.4	0.47
$t_{r1/2}$ (ms)	29.5 ±3.6	16.2 ±1.6	9.7 ±0.6	7.6 ±1.3	0.41
S_o (kN m^{-2})	28.0 ±2.6	32.9 ±3.2	39.6 ±3.7	38.6 ±4.5	1.32
S_{ot} S_o^{-1}	0.12±0.02	0.10±0.02	0.08±0.02	0.09±0.02	0.80

S_{ot}, Maximum isometric twitch stress in units per cross-section; t_p, twitch time-to-peak; $t_{r1/2}$, twitch half-relaxation time; S_o, maximum isometric tetanic stress; n, number of experiments. Means ± SEM

Table 2. Force-velocity relation of rabbit IO muscle

Parameter	Temperature				
	20°C	25°C	30°C	35°C	Q_{10}
n	11	6	12	9	
b (L_o s^{-1})	0.82±0.08	1.10±0.15	1.53±0.14	1.72±0.21	1.7
a S_o^{-1}	0.09±0.01	0.09±0.02	0.11±0.02	0.10±0.02	1.2
V_{max} (μm s^{-1})	28.0 ±2.1	38.3 ±3.9	48.8 ±4.7	57.3 ±5.8	1.6
P_{max} (μW mm^{-3})	12.8 ±1.5	18.8 ±3.5	31.9 ±3.9	35.8 ±5.6	2.3

b, Velocity constant (Eq. 1); a S_o^{-1}, force constant (Eq. 1); V_{max}, maximum velocity of shortening of sarcomeres; P_{max}, maximum mechanical power per unit volume; n, number of experiments. Means ± SEM

muscle fibre length, and a/S_o, the force constant, dimensionless. Each experiment consisted in two series of ten twitches (one at L_o and one at L_r), two isometric tetani (one at L_o and one at L_r) and a series of isovelocity releases (19 at 20°C and 25°C or 26 at 30°C and 35°C) in a quasi mirror order. Between each tetanic contraction the muscle was allowed to rest for 3 min. At the end of the experiment the muscle was lightly blotted to remove excess water and its weight recorded. In a pilot series the measurements were done at 25°C. In a newer set of experiments three different temperatures were tested for each muscle (20, 30 and 35°C).

The arrangement of the muscle fibres is extremely complex in EOM [22]. Slow tonic fibres run from tendon to tendon, but these fibres were probably not stimulated by the stimulation procedure used in this work [2]. The fast fibres are arranged in series of 2–4 fibres connected by small myomyous junctions, and therefore, their length is shorter than the muscle length. Since the electrodes were placed every 2 mm along the muscle length, we believe that we stimulated simultaneously all the fast-twitch muscle fibres. Since the muscle is not feathered, we considered the fast-twitch fibres in series, as equivalent to one fibre running from one tendon to the other.

Results

The isometric contraction

Isometric twitches of rabbit IO were studied at four different temperatures (Fig. 1, Table 1). The muscle was stimulated ten times but only the tenth twitch was recorded and analysed. Figure 1 A shows, as a typical example, the tenth twitch from the same muscle at 20°C and at 35°C. The isometric stress of the single twitch (S_{ot}) was not influenced by the temperature (Table 1). In a few experiments, a small potentiation was observed on cooling.

The t_p increases as the temperature decreased. The half-relaxation time ($t_{r1/2}$) also increased with decreasing temperature, but the effect was more pronounced than that on t_p (Table 1). As a consequence the Q_{10} is smaller than 1 for both variables, being, in the case of $t_{r1/2}$, as small as 0.4. Although the effects of temperature seem to be smaller between 30 and 35°C, the experimental errors are too large to ascertain this impression.

Figure 1 B shows typical examples of isometric tetani of the same muscle at 20 and 35°C. Also the time course of the tetanus rise and fall were prolonged by cooling. S_o decreased between 35 and 20°C (Table 1, Fig. 1 B), with a Q_{10} of about 1.3. However, there was no significant effect of temperature on S_o between 30 and 35°C. The twitch to tetanus ratio (S_{ot}/S_o) was rather low (Table 1) and it might slightly increase with diminishing temperature (probability of the regression coefficient: $0.1 < P < 0.05$).

The force-velocity relation

It was obtained by the method of controlled releases. An example is presented in Fig. 2 A: 0.15 s after the onset of the isometric tetanic contraction, the muscle was released at a constant velocity.

The tension (S) was estimated by extrapolation of the tension maintained during the release back to the onset of release and then expressed in units of the isometric tension at that moment. The three curves in Fig. 2 B show how the ratio S/S_o changed as a function of the velocity of shortening for the same preparation investigated at 20, 30 and 35°C. The parameters of the Hill's hyperbolic equation (Eq. 1) were computed from the data points by a non-linear least squares procedure and the corresponding hyperbola was fitted to the points. This procedure was repeated for 6–12 muscles and the results were averaged (Table 2).

The velocity constant b (Eq. 1) increased rapidly with temperature with a Q_{10} of 1.7, whilst the force constant a/S_o (Eq. 1) was virtually independent of the temperature in the range explored. V_{max} was computed using the ratio $b/(a/S_o)$, and as shown in Fig. 3, it increased linearly with temperature with a slope of about 0.5 muscle length s^{-1} °C^{-1}. Its average Q_{10} was 1.6; however the relation between temperature and V_{max} fitted much better the linear relation than the log relation used to compute the Q_{10}.

The maximum mechanical power per unit of volume (P_{max}) strongly increased with temperature between 20 and 30°C. There was a further increase in P_{max} between 30 and 35°C but it was not statistically significant.

The relation between the t_p and the V_{max} of sarcomere shortening

It is well known that there is an inverse relation between the speed of shortening of the sarcomeres and the iso-

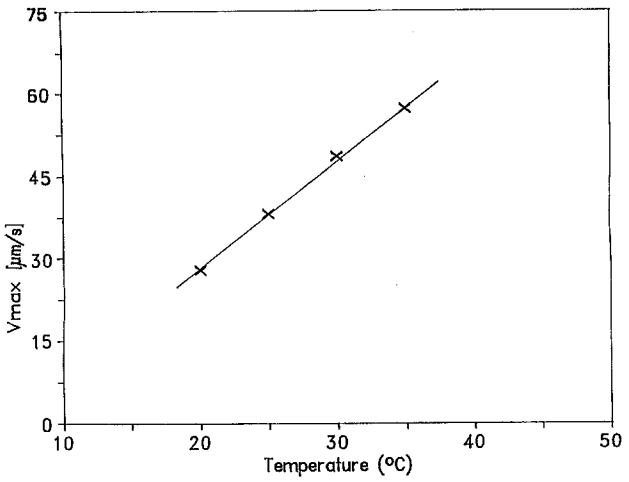

Fig. 3. Influence of temperature on the maximum shortening velocity (V_{max}) of sarcomeres of the rabbit IO muscle

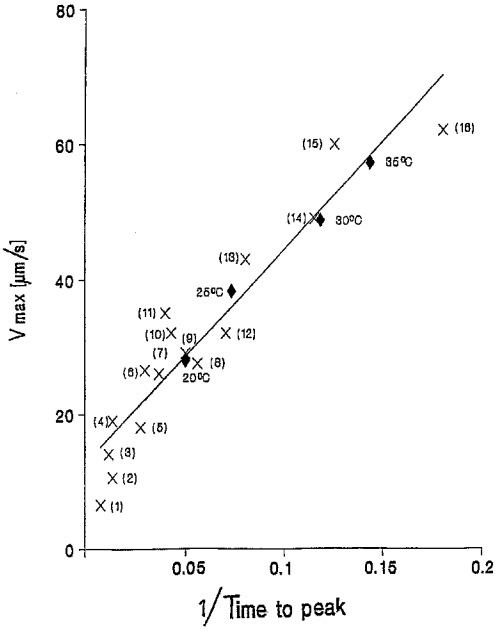

Fig. 4. Relation between reciprocal time-to-peak tension ($1/t_p$) and V_{max} of sarcomeres for limb muscles of various animals (*crosses* at 35–37°C) and for the rabbit IO muscles at different temperatures used in this study (*black diamonds*). The equation describing the relation is $V_{max} = 13 + 317\ t_p^{-1}$ ($r = 0.95$). Data: (*1*) man [8], (*2*) cat soleus [8], (*3*) cat soleus [16], (*4*) cat soleus [15], (*5*) rat soleus [8], (*6*) rabbit digastricus [1], (*7*) rat diaphragm [8], (*8*) cat fast [8], (*9*) cat flexor digitorum longus [13], (*10*) cat extensor digitorum longus [16], (*11*) cat flexor digitorum longus [15], (*12*) mouse soleus [8], (*13*) rat extensor digitorum longus [8], (*14*) rat extensor digitorum longus [11], (*15*) mouse extensor digitorum longus [8], (*16*) rat inferior rectus [11]

metric twitch contraction time [8, 9]. If we neglect the myomyous junctions between the fibres, we could assume that the length of the sarcomeres of the fast muscle fibres of the rabbit EOM is about 2.5 µm, the same as in other fast-twitch muscle fibres of the rabbit, and calculate the V_{max} of the sarcomeres of the IO fibres (Table 2). Figure 4 shows the relation between the inverse of t_p and V_{max} for IO at four different temperatures: this relation is approximately linear; it coincides with the classical relation between these two variables measured on various muscles from a number of mammals (data collected from the literature).

Discussion

The heterogeneity of EOM

EOM display a complexity ranging from their anatomical organization down to the molecular level (review in [22]). Six different types of muscle fibres have been described, and six different isoforms of myosin have been isolated, one of them being specific to EOM [21]. Therefore studying the mechanical properties of a whole muscle this complex may be questionable. In contrast to the wealth of information published on the anatomical, histological and biochemical aspects of EOM, our knowledge of their mechanical properties is still scarce. We feel therefore that it is worthwhile to examine their mechanical properties, even though we are well aware of the difficulties of interpretation resulting from the complex organization of these muscles. Two facts contribute to lessen the problem somewhat. First, a large minority of EOM fibres are multiply innervated, being similar to the slow tonic fibres: these fibres are most probably not excited by our stimulation protocol [2]. Second, most of the singly innervated fibres that are stimulated are similar to the fast-twitch type fibres: we accept, as a first approximation, that our findings mostly reflect the properties of these fibres.

The twitch time to peak

The t_p (Table 1) is very short in rabbit IO, shorter than the t_p of the fastest limb muscles. However, muscles of smaller animals are faster than the corresponding muscles of larger animals [10]. This is true for slow-twitch as well as for fast-twitch muscles. In contrast, EOM of animals ranging from mouse to sheep have almost similar t_p [6–8, 11, 13, 15–17, 23]. Our result for rabbit IO (at 35°C) is in perfect agreement with these studies. It is clear that the t_p of EOM is nearly independent of body mass.

The maximum velocity of shortening, V_{max}

V_{max} can be computed from the parameters of the force/velocity relation [14], as equal to the ratio $b/(a/S_o)$, or from the time needed to take up the slack after a quick release [12]. The two methods yield the same result only if the muscle is made up of identical muscle fibres, otherwise, the second method measures V_{max} of the fastest fibres, whilst the first one gives an estimate intermediate between the fastest fibres and the slowest ones, being closest to the value characteristic of the most numerous fibres of the same type [3]. Most of the authors

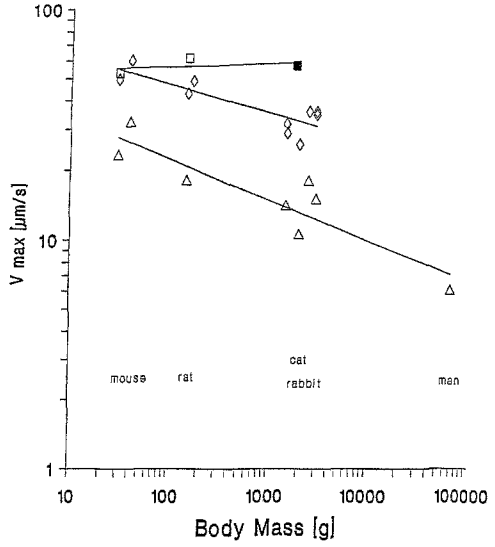

Fig. 5. Scaling of V_{max} of slow-twitch (*triangles*), fast-twitch (*diamonds*) and extraocular muscles (*squares*) with the body mass (BM) on log scales for the different animals shown on the graph. The equations describing the relation are $V_{max} = 47\,BM^{-0.16}$ ($r = 0.87$) for the slow-twitch, $V_{max} = 84\,BM^{-0.12}$ ($r = 0.88$) for the fast-twitch and $V_{max} = 53\,BM^{-0.01}$ ($r = 0.56$) for the extraocular muscles. Slow-twitch muscles: mouse [8]; rat [8]; cat [7, 8, 15, 17]; man [8]. Fast-twitch muscles: mouse [8]; rat [8]; cat [7, 8, 13, 15, 16]. Extraocular muscles: mouse [17]; rat [11]; rabbit this study (*black square*)

who worked on whole muscle (including us in this work) used Hill's method [14].

For slow-twitch as well as for fast-twitch limb muscle, V_{max} decreases when body mass increases (Fig. 5). We found only two reports in the literature giving V_{max} for mouse and rat EOM (Fig. 5): they are similar to that of rabbit EOM (this work, black square in Fig. 5). These results suggest that the intrinsic speed of shortening of EOM of mammals is independent from their size.

The possibility still remains that V_{max} depends on the size of the orbit or on the diameter of the eyeball. Considering the fact that the eyeball of the rabbit has a diameter of 20 ± 2 mm, and the length of the IO muscle is 22 ± 2 mm (mean ± SEM), the V_{max} at zero load corresponds to an angular rotation velocity of the eyeball of 2400°/s. This value is only of theoretical interest because the resting tension of rabbit EOM in situ is, depending on the position of the eye, between 5 to 20% of S_o ([4] and personal observations) and between 10 and 15% if the eye is in primary position. Assuming a resting load of 10% of S_o, the shortening velocity of the inferior oblique is about 7 muscle lengths/s, which corresponds to an angular rotation velocity of the eyeball of about 850°/s. This value is of the same order of magnitude as that of the fastest saccadic eye movements (600°/s, [20]).

V_{max} increases with temperature with a Q_{10} of 1.6 (Table 1): this figure is comparable with data obtained in rat fast-twitch muscles (1.8 in [19]) and human handgrip muscles (1.2 in [5]). V_{max} at various temperatures is a linear function of $1/t_p$ measured at the corresponding temperatures (black diamonds, Fig. 4). It is remarkable that this relation fits with the general relation between V_{max} and t_p obtained from animals of increasing sizes (line in Fig. 4). These facts suggest that a common mechanism controls the variations of V_{max} and $1/t_p$ as a function of temperature or body mass. A possible mechanism could be that the sensitivity to temperature of actomyosin ATPase activity is differently adjusted according to body mass.

The maximum isometric tension, S_o

The S_o value of the tetanus is low in EOM [2, 11, 17]. In our experiments, the IO produced a tension that is only 20% of that produced by mouse soleus muscle at the same temperature and using the same equipment. Many factors could account for this fact. Only a fraction of the muscle fibres contracted, since our stimulation protocol did not excite the multiply innervated muscle fibres. The extracellular space and the volumes of mitochondria and sarcoplasmic reticulum are large [22], reducing the volume available for the myofibrils. It is also possible that the actomyosin cross-bridges formed by the special extraocular myosin isoform [21] could develop only a weak maximal force, for a reason discussed below.

The twitch-to-tetanus ratio of the IO is lower than that observed in either slow-twitch or fast-twitch muscle. But the influence of temperature on this ratio is similar to its effect on slow-twitch muscle: it does not change significantly with cooling, whilst in fast-twitch skeletal muscles the twitch-to-tetanus ratio rises because the twitch tension is enhanced by cooling and the tetanic tension output decreases [19].

The normalized force-velocity relation

The normalized force-velocity relation is defined by one single parameter, the force constant a/S_o, which controls its curvature and sets the normalized maximal power M^2 [18, 24]. The values of a/S_o, and therefore M^2, are low for IO, being typical of a slow-twitch muscle. They do not change significantly with temperature in the range of 20 to 35°C tested in our experiments whilst cooling decreases a/S_o in slow- and fast-twitch muscles [19].

The maximum mechanical power P_{max}

P_{max} per unit muscle volume is easily computed by appropriately scaling the normalized maximal power [18, 24]:

$$P_{max} = S_o \times V_{max} \times M^2 \qquad (2)$$

Although V_{max} runs into the highest recorded values among muscle, irrespective of body mass (Fig. 5), P_{max} of IO is very low, barely one-third of P_{max} of the slow-twitch mouse soleus measured in exactly the same con-

ditions [18]. The reason for this is that both S_o and M^2 are quite small in EOM.

It appears that the EOM is narrowly specialized for its main function. This muscle must move continuously a small load at high velocities. This requires a large supply of energy, as testified by its large blood flow and high mitochondrial volume. The best efficiency is obtained when the velocity of moving the load equals the "optimal velocity of shortening", itself equal to about one-third V_{max}. At that velocity, the mechanical power is approximately maximal [24]. Equation 1 shows that for a given supply of energy, the production of high velocity of shortening requires a low tension output S_o and a small normalized mechanical power M^2 (equivalent to a small a/S_o). Thus, IO is a fast-twitch muscle endowed with a velocity of shortening higher than that of fast-twitch skeletal muscle but using a tetanic mechanical power lower than that produced by slow-twitch muscle: the combination of these properties makes it ideally suited to move an ocular globe of low mass at high velocity during quick phases and saccades.

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