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ORIGINAL ARTICLE

H. Degens · S. Salmons · J.C. Jarvis

Intramuscular pressure, force and blood flow in rabbit tibialis anterior muscles during single and repetitive contractions

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Abstract The elevated intramuscular pressure (IMP) associated with sustained muscle contraction can affect blood flow, and could influence the long-term viability of functional skeletal muscle grafts. We therefore examined the relationship between force, peak IMP and blood flow in the tibialis anterior muscle of the anaesthetized rabbit. During isometric contractions, IMP was related linearly to force, and only the slope of the relationship varied between animals. During isotonic contractions, however, the highest values of IMP were found at the lowest force levels, and IMP appeared to be related to the amount and speed of shortening. During repeated isometric contractions, the ratio of IMP to force varied with time, stimulation pattern and subject. Mean blood flow did not differ appreciably between repetitive isometric contractions at duty cycles of 10–40%, and was unrelated to integrated pressure, integrated force, or depth from the surface. We conclude: (1) that IMP is unlikely to affect mean blood flow during cyclic activity that has a duty cycle less than 40%; and (2) that the clinical use of IMP as a predictor of muscle force appears to be justified only for single isometric contractions, and needs to be interpreted cautiously when contractions involve shortening or fatigue.

Key words Blood flow · Intramuscular pressure · Skeletal muscle

H. Degens
Department of Anatomy, MDC Box 6,
College of Medicine, University of South Florida,
12901 Bruce B. Downs Boulevard, Tampa, FL 33612, USA

H. Degens · S. Salmons (✉) · J.C. Jarvis
Department of Human Anatomy and Cell Biology,
University of Liverpool, New Medical School,
Ashton Street, Liverpool L69 3GE, UK

Introduction

During a sustained isometric contraction the oxygen consumption of skeletal muscle increases with increasing force (Colier et al. 1995). At the same time the rise in intramuscular pressure (IMP) during such a contraction (Kirkebø and Wisnes 1982; Sejersted et al. 1984) may impair the blood flow to the muscle and thus contribute to fatigue (Petrofsky and Hendershot 1984; Sadamoto et al. 1983; Sejersted and Hargens 1995; Van Leeuwen and Spoor 1992). It is probably for this reason that an artificial increase in the perfusion pressure delays the onset of fatigue during sustained isometric contractions (Petrofsky and Hendershot 1984).

The pressure within a muscle during such sustained isometric contractions is reported to vary along its length and depth (Kirkebø and Wisnes 1982; Sejersted et al. 1984), and such variations are predicted by numerical models that take account of the shape of the muscle and the disposition of its attachments (Van Leeuwen and Spoor 1992). This may account for regional variations in blood flow (Wisnes and Kirkebø 1976). Model studies suggest that the rise in IMP associated with force production should also be dependent on the instantaneous length of the muscle, because of the change in muscle architecture that accompanies changes in length (Sejersted et al. 1984; Van Leeuwen and Spoor 1992).

During *intermittent* isometric contractions the rhythmical increases in intramuscular pressure may actually assist forward blood flow (Van Leeuwen and Spoor 1992) and mean blood flow has been observed to increase above resting level under these conditions (Hussain and Magder 1991; Vøllestad et al. 1990). However, little is known about the influence of duty cycle on this effect.

Such issues are important in the context of clinical applications of chronic muscle stimulation, in which they could have a profound influence on the long-term viability of the muscle. We therefore undertook a study of the relationship between IMP, force and blood flow in

the rabbit tibialis anterior (TA) muscle during both isometric and isotonic contractions, and during repetitive isometric contractions at various duty cycles. In this study we wanted to address two questions in particular. Firstly, is there a relationship between intramuscular pressure and force that is maintained consistently under all conditions? Secondly, how is mean blood flow related to duty cycle during intermittent contractions? The results of the study contain unexpected complexities which suggest that the clinical use of IMP as a measure of muscle force is valid only under closely prescribed conditions.

Methods

Animals and preparation

Ten New Zealand White rabbits (2.2–4.2 kg) were kept in a 12-h light 12-h dark cycle at 25°C and supplied with food and water ad libitum. The care and experimental use of these animals was strictly in accordance with the United Kingdom Government's Animals (Scientific Procedures) Act 1986. The rabbits were anaesthetized with urethane (250 g l^{-1}; 500 mg kg^{-1}) and pentobarbitone sodium (Sagatal, May and Baker; 30 mg kg^{-1}) administered via the marginal ear vein. Anaesthesia was maintained with supplementary doses of pentobarbitone. The trachea was cannulated and flap electrodes were placed around the left common peroneal nerve for indirect stimulation of the TA and extensor digitorum longus (EDL) muscles (Jarvis 1993).

IMP measurements

Contractile properties were measured as described earlier (Jarvis 1993). The tendons of the TA and EDL muscles on the left side were cut, with the epimysial fascia left intact. The TA tendon was connected to an ergometer system with a natural frequency greater than 100 Hz, the length of free tendon being kept to a minimum. The lower hind limb was clamped rigidly. The TA muscle was stimulated supramaximally via the common peroneal nerve. The muscle was set at its optimal length, defined as the length at which it produced maximum twitch force. A slit catheter (length 150 mm; outer diameter 0.55 mm), made in-house, was connected via a stopcock to a pressure transducer (Gaeltec, Dunvegan, Scotland). This was calibrated before each experiment. The catheter was introduced through a hypodermic needle (outer diameter 1.05 mm) into the middle of the muscle at an angle of ≈20° to the long axis of the muscle over a length of ≈10 mm. The compliance of the pressure measurement system was 0.4 mm^3 per 13.33 kPa. Its response time was sufficient to record changes that did not lag observably on force under isometric conditions (see last contraction in Fig. 1) or length under isotonic conditions (see first four contractions in Fig. 1). Each series of measurements was made without disturbing the position of the probe. If the catheter had to be repositioned, the measurements were repeated.

Isometric contractions of 250 ms duration were elicited at frequencies of 10, 20, 40, 70, 100 and 200 Hz. Each contraction was followed by 30 s of rest. The muscle was then stimulated for 250 ms at 200 Hz to contract isotonically against servo-controlled constant loads of 2, 4, 6, 8, 12, 16, 20, 22, 24, 26 and 30 N. Contractions were separated by 1-min rest intervals. In most experiments the isometric and isotonic series were repeated, and the data plotted in Figs. 2 and 3 therefore represent the pooled measurements from isometric series that alternated with isotonic series of contractions. For any given muscle there is good agreement between results derived from different series, and this attests to the reproducibility of the measurement procedure.

In four animals, measurements were repeated with and without the skin around the muscles, care being taken to leave the catheter undisturbed. These measurements confirmed that peak IMP values were not influenced by the presence or absence of the skin.

For each contraction, IMP, force and length records were captured on-line on a 486 IBM-compatible PC.

Determination of blood flow

The use of microspheres to measure blood flow is based on a comparison between the number of systemically injected microspheres that are trapped in the tissue of interest and the number that appear in a blood sample withdrawn at a known rate. Coloured polystyrene microspheres [15 (0.1) μm diameter, mean (SD); red, yellow, blue and violet spheres; Triton Technology, "Dye-Track", San Diego, USA] were injected into the left ventricle via the left carotid artery, and blood was withdrawn at a rate of 2.4 ml min^{-1} from the right carotid artery, as described previously (Degens et al. 1996). Flow was determined in the left TA and EDL muscles during isometric contractile activity elicited by supramaximal stimulation at 70 Hz or 200 Hz; the right TA and EDL muscles were not stimulated. In these experiments, the duration of the stimulus train was maintained at 100 ms and the duty cycle was varied between 10% and 40% by changing the intervals between trains. Measurements of IMP and force were captured on-line. In six rabbits, haemodynamic stability was monitored closely: blood pressure was recorded continuously via a pressure transducer (Gaeltec) connected to the cannula in the right carotid artery, and heart rate and oxygen saturation of the blood were monitored by pulse oximetry (Ohmeda Biox 3700e Pulse Oximeter).

The animals were killed without recovery from anaesthesia by injecting 5 ml of saturated KCl into the left ventricle. The TA and EDL muscles were excised and divided either longitudinally into three parts (superficial, TAS, and EDLS; middle, TAM, and EDLM; and deep, TAD, and EDLD), or transversely into five parts (numbered 1–5 from proximal to distal) each of 0.5–1.0 g. In all ten animals the cortex of both kidneys opposite the hilus was sampled to confirm that the microspheres had been distributed uniformly in the systemic circulation.

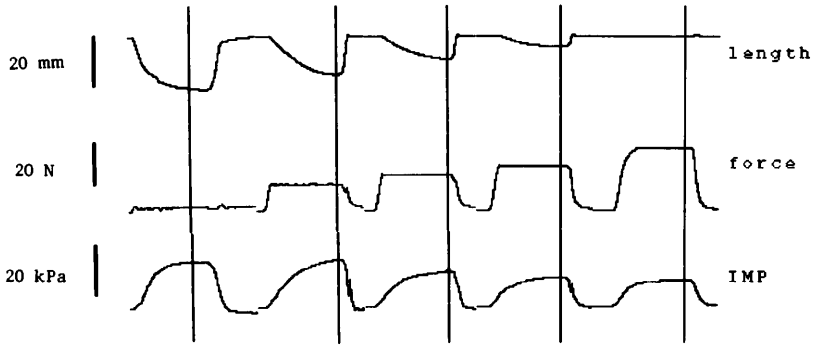


Fig. 1 Length, force and intramuscular pressure (*IMP*) tracings during isotonic contractions at 2, 12, 16, 20 N and an isometric contraction. *Vertical lines* coincide with the moments of peak IMP. The duration of each contraction is 250 ms. *Scale bars* in the *left-hand margin* calibrate the amplitude range of each trace

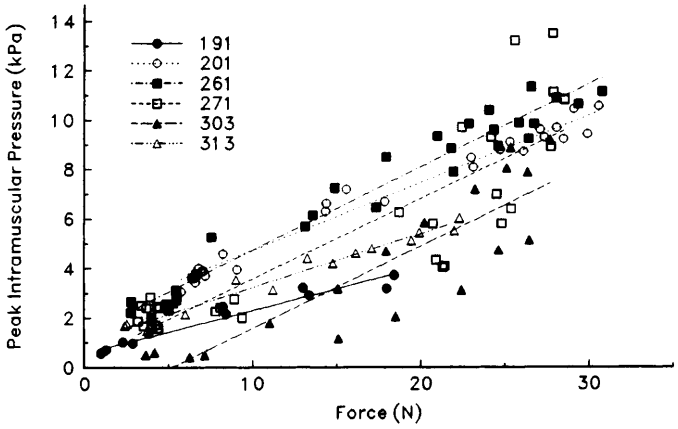


Fig. 2 Relationship between peak intramuscular pressure (*IMP*) and force for individual rabbit tibialis anterior muscles during isometric contractions. To avoid undue compression of the *y*-axis, IMP values for rabbit 303 have been scaled downwards by a factor of 5 in this figure

The coloured microspheres were quantitated by extracting the dye into a standard volume of dimethylformamide (DMF) and by making use of the linear relationship between the absorption of the dye solution and the number of spheres (Kowallik et al. 1991). Tissue and blood samples were processed essentially as described previously (Degens et al. 1996; Kowallik et al. 1991). Both blood and tissue samples were digested in 4 M KOH 2% Tween 80 at 60 °C for at least 48 h. The digested samples were vacuum filtered (10 μm diameter pore filter; Poretics, Livermore, USA). The filter was allowed to dry for at least 1 min, folded carefully and placed in a 1.5-ml Eppendorf vial to which 200 μl of DMF was added. The samples were then centrifuged for 3 min at 11,600 *g* in a microcentrifuge to minimize scatter from floating particulate matter during spectrophotometry. Samples of the DMF-dye solutions were transferred to a microcuvette, and spectra were obtained with an Ultrospec III spectrophotometer (Pharmacia KB) driven by the Wavescan package (Pharmacia KB) installed on a 486 IBM-compatible PC. The flows were calculated with a Matrix Inversion Software package (MISS, Triton Technology).

Blood flow in the muscles (ml min^{-1} g^{-1}) was calculated as the weighted mean of the flow in the parts. The relative flow in each part was then calculated by dividing its flow by the mean flow for the whole muscle. For each series of measurements the relationship was examined between muscle blood flow and integrated force and pressure, integration taking place over a period of 1 min starting with the onset of contractions. Some of the blood flow data have been reported elsewhere (Degens et al. 1996).

Statistics

Analysis of IMP was based on peak values in single contractions. All values have been presented as mean (SEM) unless otherwise stated. The coefficient of variation was calculated as (SD/mean) × 100%. Significance levels were tested by ANOVA, and where appropriate by repeated-measures ANOVA, and differences were considered significant when the two-tailed probability was less than 5%.

Results

The force-frequency and force-velocity relationships of the muscles in this study were similar to published curves and remained stable during the experiments.

Figure 2 illustrates, for each muscle, the positive correlation between IMP and force when contraction took place isometrically [$R = 0.95$ (0.02) for the pooled group of six muscles]. This positive correlation was lost when contraction took place under isotonic conditions; in fact the highest values of IMP were consistently recorded at the lowest force levels (Figs. 1 and 3). Figure 4 suggests that under these conditions IMP was related more closely to shortening velocity than to force, at least for velocities less than 100–150 mm s^{-1}. There was also a significant correlation between peak IMP and the extent of isotonic shortening [Fig. 5; $R = 0.94$ (0.02); $n = 5$].

When isometric contractions were repeated over a period of several minutes, the changes in IMP and force were not related in the simple, linear manner seen for single contractions from the same (optimal) length (compare Figs. 2 and 6A). Moreover, the responses were subject to considerable variability between animals. Clearly force fatigue was not the sole determinant of

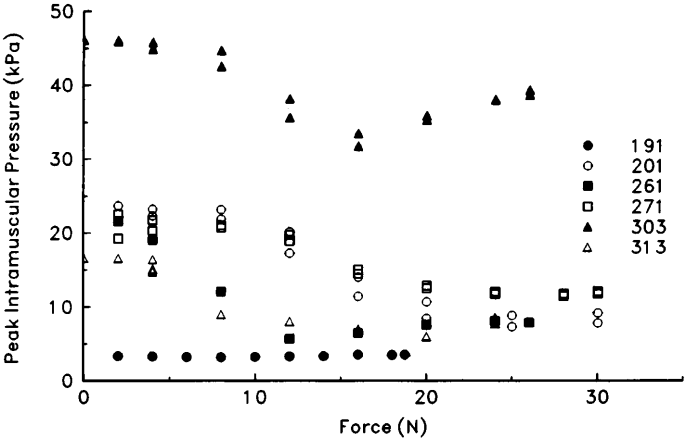


Fig. 3 Relationship between peak intramuscular pressure and force for individual rabbit tibialis anterior muscles during isotonic contractions

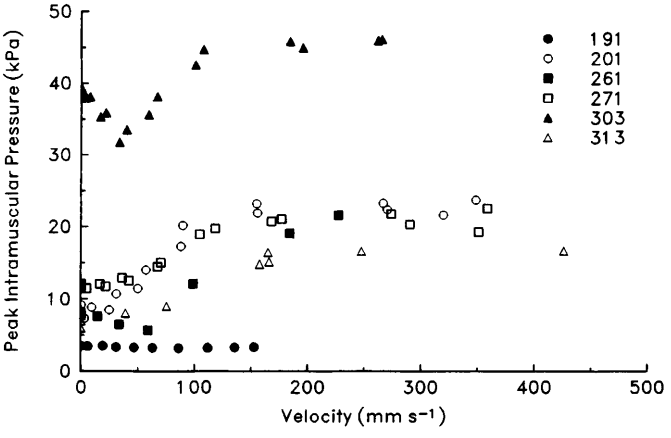


Fig. 4 Relationship between peak intramuscular pressure and contraction velocity for individual rabbit tibialis anterior muscles during isotonic contractions

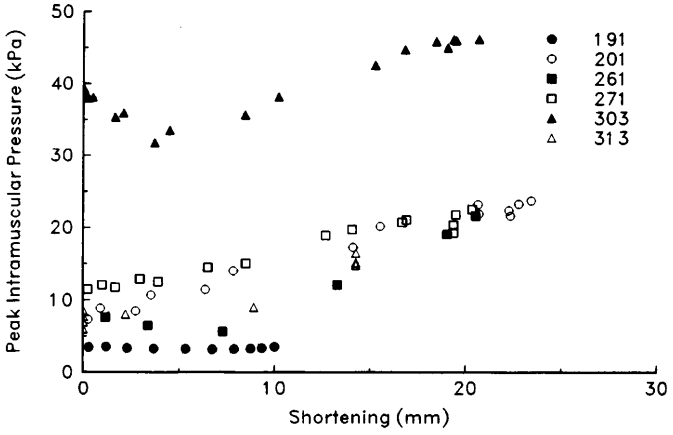


Fig. 5 Relationship between peak intramuscular pressure and the maximum extent of shortening for individual rabbit tibialis anterior muscles during isotonic contraction

IMP under these conditions. Changes in the IMP:force ratio with time are shown in Fig. 6B. In this figure the ratio has been corrected for baseline changes in pressure and force during the test period and expressed relative to its value at $t = 0$; despite these measures, designed to eliminate some of the differences between individual animals, significant variations remained. The results illustrated are for contractions with a duty cycle of 15%; there was considerable variation between duty cycles but this followed no consistent pattern. At every duty cycle there was a good deal of interanimal variation.

To assess the effect of duty cycle on blood flow, stimulus trains with various duty cycles were delivered in random order. This precaution was needed to avoid systematic errors arising from deterioration in the condition of the experimental animal during the sequence of microsphere injections (Degens et al. 1996). The mean flow did not differ significantly between different duty cycles or between TA and EDL muscles (Fig. 7). There was no evidence of any decline in blood flow at higher duty cycles, at least within the range examined. Mean blood flow was not significantly related to integrated pressure ($R = 0.06$; $n = 22$; $P > 0.7$) nor to integrated force ($R = 0.30$; $n = 25$; $P > 0.1$).

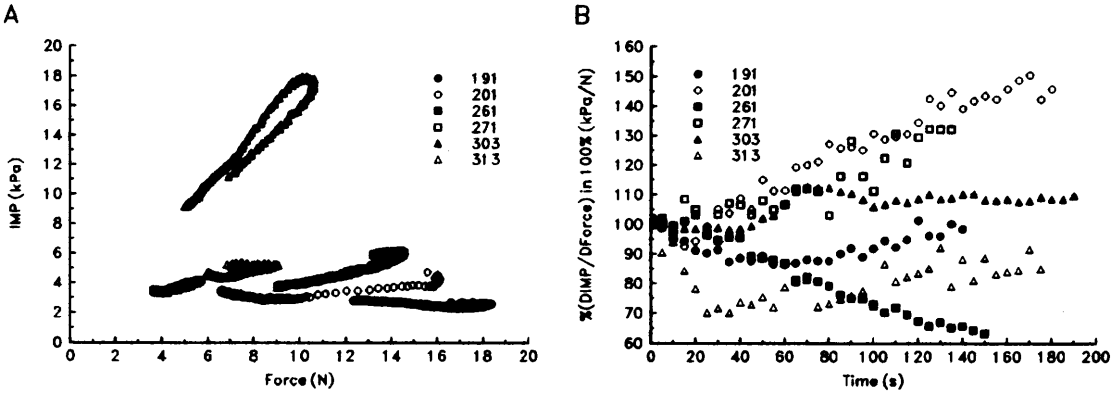
We observed considerable spatial heterogeneity in the blood flow measured during repetitive isometric contractions, and this was similar in extent for the two muscles and for the various duty cycles. However, analysis of blood flow data from individual parts of the muscle revealed no significant variation with depth (Table 1) or length (Table 2) in either the TA or the EDL muscles, so the spatial heterogeneity could not be explained in terms of a consistent regional dependence.

Discussion

Pressure in a tissue is a combination of solid and fluid pressures. Pressure measured by balloon catheters is considered to represent total pressure; wick catheters and needles are believed to measure fluid pressure (Guyton et al. 1971). We abandoned the use of needles after preliminary experiments (not reported here) in which the probe registered negative pressures during muscular contraction; this has been attributed to a ball-valve effect at the tip of the needle (Guyton et al. 1971). The slit catheter is similar in accuracy to the wick catheter but has a higher frequency response (Fronek et al. 1987 Sejersted et al. 1984) and does not require continuous infusion of fluid (Sejersted et al. 1984). This was therefore the method of choice for the present study.

A linear correlation between IMP and force in single isometric contractions has been reported previously (Kirkebø and Wisnes 1982; Sadamoto et al. 1983) and was confirmed in this study. In common with earlier observers (Hussain and Magder 1991; Sejersted et al. 1984), we found considerable variation between animals in the actual slope of this relationship. Part of this variation may be due to catheter location, as we found that repositioning the catheter sometimes gave different values of IMP for the same contractile force (data not shown). For this reason we took every precaution to maintain the same catheter position throughout any measurement series.

Fig. 6A, B The relationship between peak intramuscular pressure (*IMP*) and force during tetanic isometric contractions at a duty cycle of 15%. **A** IMP vs force; **B** changes in the IMP:force ratio with time. The ratio has been corrected for changes in baseline pressure and force, and expressed relative to its value at $t = 0$



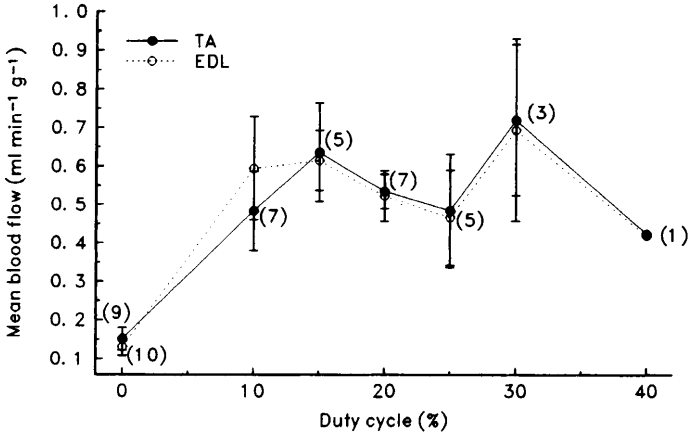


Fig. 7 The relationship between mean blood flow and the duty cycle of repetitive tetanic isometric contractions in the rabbit tibialis anterior and extensor digitorum longus muslces. The number of measurements contributing to each data point is given in *parentheses*

Although IMP was positively correlated with force for single isometric contractions at optimal muscle length, no such relationship was observed for isotonic contractions. Under these conditions IMP was, if anything, inversely related to force at the muscle attachments, and more directly correlated with displacement and contraction velocity. At first sight these results appear to be in conflict with those of Aratow et al. (1993), who reported a positive correlation between IMP and force for human soleus and TA muscles contracting under isokinetic conditions. However, during isokinetic (constant velocity) contractions, the velocity and amount of shortening are held constant, whereas during isotonic (constant force) contractions they vary inversely with force. A positive correlation between IMP and force was also reported by Hussain and Magder (1991) for shortening contractions in strips of dog diaphragm, but there were important methodological differences in their study. These authors varied velocity and displacement by adjusting the degree of recruitment of a muscle working against an inertial load, and velocity and displacement were therefore positively related to force. In our study the load was fixed by a servo-controller and velocity and displacement therefore showed the usual inverse relationship to force. The studies are nevertheless congruent in showing a positive relationship between peak IMP and the amount of shortening.

Steady-state mathematical models of muscle are based on the assumption that there is a static equilibrium between intramuscular forces and restraining forces from the epimysium and muscle attachments. According to these models, IMP should be higher at shorter muscle lengths because the concomitant increase in the curvature of the fibres would tend to direct a larger component of force towards the centre of the muscle and a smaller component of force towards the muscle attachments (Sejersted et al. 1984; Sejersted and Hargens 1995; Van Leeuwen and Spoor 1992). Although such models are supported by measurements of pressure at different points within an isometrically contracting muscle, they have yet to predict in a quantitative way the changes at a given site within a muscle that is shortening. The strength of any dependence of IMP on muscle length would be diluted in the TA muscle, in which the fibres are aligned substantially parallel to the long axis. Moreover, the geometrical tendency for IMP to increase as the muscle length is reduced would be counteracted by the decline in force-generating capacity that results from non-optimal myofilament overlap at short sarcomere lengths. The strong dependence of IMP on shortening velocity observed in the present experiments would therefore seem difficult to account for in terms of geometric considerations alone. We wish to suggest the possibility that IMP is influenced by dynamic, as well as static, equilibrium conditions. Dynamic behaviour could, for example, be the consequence of flow or redistribution of intramuscular material during shortening. Whereas steady-state considerations require that the peak IMP associated with contraction at any given muscle length is unique, the existence of a dynamic

Table 1 Blood flow was measured in the superficial (*S*), middle (*M*), and deep (*D*) parts of the rabbit tibialis anterior (*TA*) and extensor digitorum longus (*EDL*) muscles during tetanic isometric contractions at various duty cycles, and is expressed here relative to the mean flow. Number of animals in *parentheses*

	10%	15%	20%	25%
EDLS	1.08 ± 0.01 (4)	1.02 ± 0.07 (5)	1.00 ± 0.04 (5)	0.91 ± 0.03 (5)
EDLM	0.99 ± 0.06 (4)	0.98 ± 0.03 (5)	1.00 ± 0.04 (5)	1.04 ± 0.05 (5)
EDLD	0.96 ± 0.07 (4)	1.01 ± 0.06 (5)	1.00 ± 0.03 (5)	1.18 ± 0.08 (5)
TAS	1.10 ± 0.07 (4)	1.00 ± 0.07 (5)	1.00 ± 0.04 (5)	0.99 ± 0.03 (5)
TAM	1.00 ± 0.14 (4)	1.02 ± 0.06 (5)	0.95 ± 0.04 (5)	1.06 ± 0.09 (5)
TAD	0.90 ± 0.19 (4)	0.99 ± 0.11 (5)	1.04 ± 0.07 (5)	1.07 ± 0.09 (5)

Table 2 Proximo-distal (1–5) variations in blood flowin the rabbit tibialis anterior (*TA*) and extensor digitorum longus (*EDL*) muscles during tetanic isometric contractions at duty cycles between 10 and 40%, expressed relative to the mean blood flow. Number of measurements in *parentheses*

	1	2	3	4	5
EDL	1.14 ± 0.40 (8)	1.03 ± 0.46 (5)	0.93 ± 0.42 (5)	0.89 ± 0.40 (5)	0.96 ± 0.36 (7)
TA	1.16 ± 0.41 (8)	1.15 ± 0.41 (8)	0.98 ± 0.44 (5)	1.02 ± 0.36 (8)	0.73 ± 0.28 (7)

component implies that IMP is also a function of the speed at which the muscle is shortening as it passes through that length.

During repetitive contractions, in which isometric conditions were maintained but the force exerted by the muscle was modified by fatigue, IMP and force were not related in a linear, single-valued manner, as might have been predicted from the results of single isometric contractions. Clearly force was only one of the factors influencing IMP under these conditions. The ratio of IMP to force varied with time, and the overall response varied between duty cycles and from one animal to another. There are several possible biological sources of this variability. The force developed by a predominantly fast-twitch muscle during repetitive activation undergoes an initial potentiation and then declines with the onset of fatigue (see, for example, Salmons and Sréter 1976). These changes are accompanied by changes in the dynamics of contraction which are the consequence of changes in both activation and drop-out, through fatigue, of the fastest-contracting fibres. The IMP would be expected to reflect changes in these components, whose time courses could be subject to substantial and independent variation. Finally, fatigue may be associated with changes in tissue compliance and osmotic changes (Sadamoto et al. 1983). Reports of variation in the IMP:force ratio of human muscles during low-level sustained isometric contractions are less relevant to the conditions of the present study, and probably reflect changes in motor unit recruitment (Sadamoto et al. 1983; Sejersted et al. 1984; Sejersted and Hargens 1995).

No significant decrease in mean blood flow could be measured for contraction regimes with duty cycles as high as 40%. This indicates that compensatory flow during the relaxation phase was sufficient to offset any limitation of flow that might have resulted from the elevation of IMP during the contraction phase. Similar observations have been made previously for contractions in which the duty cycle was maintained constant and the force was varied (Hussain and Magder 1991). Flow compensation during the relaxation phase explains why flow does not appear to be related to integrated IMP or force during repetitive isometric contractions. This conclusion is reinforced by measurements of flow in the EDL muscle. Although this muscle performed unloaded contractions at the same time as the TA, the mean blood flow recorded in the two muscles did not differ significantly at any stage.

Wisnes and Kirkebø (1976) have reported differences in blood flow between the inner and outer layers of rat calf muscles during sustained isometric contractions. Such differences could be the consequence of a transverse gradient in IMP. Our data permitted an analysis of relative blood flow in different parts of the TA muscle during repetitive isometric contractions. We found no evidence that flow was related to depth. This would be consistent with the comment, made earlier, that there may be little transverse variation of pressure in a muscle whose fibres are orientated parallel to the long axis. An alternative interpretation is that there is such variation, but compensation of reduced flow during the contraction phase by increased flow during the relaxation phase operates not only at the level of the whole muscle but also at the regional level within the muscle.

In conclusion, the present study confirms that there is a linear relationship between IMP and force during isometric contractions. During repetitive isometric contractions this relationship is replaced by one that varies with time, with activity pattern, and with the experimental subject. During isotonic contractions IMP is related more closely to shortening and shortening velocity than to force, an observation that leads us to suggest the possibility of a dynamic component of IMP. These data indicate that caution is needed if IMP is to be used as a predictor of force other than for single isometric contractions. IMP does not appear to be an important determinant of mean blood flow during repetitive contractions at duty cycles up to 40%, and this study will therefore be reassuring in the context of some clinical uses of functional electrical stimulation. For example, these duty cycles are unlikely to be exceeded in skeletal muscle grafts used to augment cardiac function (El Oakley and Jarvis 1994) or in the functional restoration of muscles paralysed by spinal cord injury (Kralj and Bajd 1989; Elefteriades et al. 1992). The more continuous patterns used for muscle grafts configured as functional neosphincters in the treatment of anorectal pathology or congenital malformations of the distal bowel (Williams et al. 1989) remain a potential source of concern.

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