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ISOMETRIC AND CONCENTRIC PERFORMANCE OF ELECTRICALLY STIMULATED ANKLE PLANTAR FLEXOR MUSCLES IN INTACT RAT

MARK E. T. WILLEMS* AND WILLIAM T. STAUBER*†‡

*Departments of *Physiology and †Neurology, West Virginia University, Morgantown, West Virginia 26506, USA*

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SUMMARY

The relationship between muscle force and ankle position during isometric and pre-loaded slow concentric contractions (angular velocity, 0·52 rad s^{-1}; range of motion, 1·22 rad) and the recovery of isometric force following concentric contractions at different velocities were determined for electrically stimulated plantar flexor muscles in intact rats. Pre-loaded refers to the isometric contraction which immediately precedes the concentric contraction. Ankle position was controlled by a dynamometer and force was recorded under the sole of the foot. The peak isometric force (19·2 N) was nearly constant at all ankle positions (range of motion, 1·57 rad). The muscle length and distal fibre length of gastrocnemius medialis at ankle positions between 0·79 rad and 2·01 rad were increased by 12·6 % and 20·3 %, respectively. During slow concentric contractions, the force progressively decreased (23·1 ± 2·1 %); the force decreased by only 6·3 ± 0·9 % during sustained isometric contractions of similar duration (3400 ms). The recovery of isometric force following concentric contractions with similar stimulation frequencies (80 Hz) was velocity dependent (i.e. more rapid at higher velocities). It is concluded that pre-loaded slow concentric contractions of the plantar flexor muscles in intact rats do not follow the same relationship as that of isometric force and ankle position. Our results in intact rats show that the force output of electrically stimulated ankle plantar flexor muscles measured under the sole of the foot can be used to study the physiological properties of skeletal muscle working *in situ*.

INTRODUCTION

Dynamometry is commonly used to evaluate the effects of training and rehabilitation on skeletal muscle performance. It has been widely applied in humans but rarely in animals. Dynamometry allows the measurement of muscle torque during tests with constant joint positions (isometric contractions) and during controlled joint movements (e.g. concentric contractions). These tests then provide information on certain aspects of the isometric and concentric muscle performance such as the torque–position relationship (Sale *et al*. 1982) and strength during concentric contractions (Thomas *et al*. 1987; Gravel *et al*. 1990).

The torque–position relationship can be evaluated using multipositional isometric contractions and slow concentric contractions. In voluntarily activated, plantar flexor muscles of humans, the maximum torque during isometric and slow concentric contractions (angular velocity, 0·52 rad s^{-1}) was nearly equivalent (Fugl-Meyer *et al*. 1980; Seymour & Bacharach, 1990). The torque–position and thus also the force–position relationship of skeletal muscles in humans should be obtained during relatively slow concentric contractions. However, voluntary contactions often occur without pre-activation which alters the force output in the early part of a dynamic contraction (Gransberg & Knutsson, 1983; Gravel *et al*. 1988) but has not always

‡ Corresponding author: wstauber@wvu.edu

been controlled (Fugl-Meyer *et al*. 1980). Thus, it is not clear whether the force–position relationship for isometric and slow concentric contractions is always similar. To our knowledge, the force–position relationship of electrically stimulated skeletal muscles working *in situ* has not been obtained in animals using pre-loaded concentric contractions at slow angular velocities.

Although these concentric contractions only occur during isokinetic testing, they provide information on the force–position relationship of skeletal muscles working *in situ* and the effects of dynamic movements on subsequent isometric force. For example, following isokinetic shortening in isolated skeletal muscle *in situ*, the recovery of isometric force is velocity dependent in isolated cat (Herzog & Leonard, 1997) and rat (Meijer *et al*. 1997) muscle. If joint motion does not alter the muscle response, similar information should be measured at the sole of the foot.

In the present study, a custom-built dynamometer was used to determine the performance of electrically stimulated plantar flexor muscles working *in situ* in the intact rat during multipositional isometric and pre-loaded concentric contractions. The present study had two objectives: (1) to determine the force–position relationship during isometric and slow concentric contractions (angular velocity, 0·52 rad s^{-1}), and (2) to determine the recovery of isometric force following concentric contractions for plantar flexor muscles using multiple angular velocity movements of the ankle joint. All dynamic movements were preceded by a maximal isometric contraction to eliminate the effect of activation time on force measurement. We hypothesize that the force–position relationship of ankle plantar flexor muscles in intact rats during pre-loaded slow concentric contractions would be equivalent to the force–position relationship during isometric contractions.

Part of this study was presented at the North American Congress of Biomechanics (Willems & Stauber, 1998).

METHODS

Animal care and preparation

Caged sedentary, female Sprague–Dawley rats (3–4 months) were used. The use and care of rats in this study were approved by and followed the guidelines of the West Virginia University Animal Care and Use Committee (WVU-ACUC no. 9511-05). The use of animals in this study complied with Animal Welfare Act P.L. 91-579 and DHHS Guidelines governing the care and use of laboratory animals.

Experiments were performed on electrically stimulated ankle plantar flexor muscles working *in situ* in intact rats to determine: (1) the force–position relationship during isometric contractions and slow concentric contractions ($n = 6$, body mass: 267·8 ± 5·6 g, mean ± S.E.M.), and (2) recovery of isometric force following multivelocity isokinetic concentric contractions ($n = 6$, body mass: 258·2 ± 5·2 g). The animals were anaesthetized with sodium pentobarbital (75 mg kg^{-1} I.P.) and supplementary doses administered as required. The trachea was cannulated using polyethylene tubing (PE 240, Becton Dickinson, MD, USA) to facilitate breathing and the animal was positioned on a heating pad to maintain body temperature.

A mid-line incision was made in the posterior aspect of the hindlimb. Blunt dissection through the popliteal fossa exposed the tibial nerve. Connective tissue and adipose tissue surrounding the nerve were carefully removed and the common peroneal and sural nerves were cut. A bipolar cuff electrode (1·67 mm inner diameter, 2·41 mm outer diameter made of Silastic tubing, (Dow Corning, Midland, MI, USA)) was positioned around the tibial nerve. Nylon sutures were tied around the cuff to secure its position and care was taken not to compress the tibial nerve. The distance between the steel wires (Cooner wire AS632, Chatsworth, CO, USA) in the cuff was approximately 1·5 mm. The wires of the cuff extended through the popliteal fossa and skin, and the skin was closed using nylon sutures. The free ends of the electrodes were connected to the nerve stimulator (Grass SD9 stimulator, Grass Medical Instruments, Quincy, MA, USA).

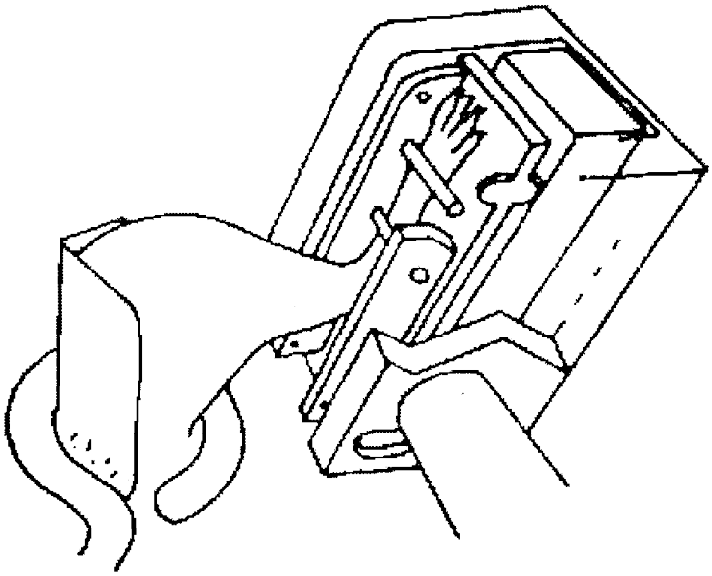

Fig. 1. Position of the rat's foot in load cell fixture and knee holder (reprinted with permission from Cutlip *et al.* 1997).

The animal was placed supine on an *X–Y* positioning table attached to the dynamometer. Skin temperature of the left hindlimb was maintained at between 30 and 35 °C using an infrared lamp and a surface temperature probe. The knee was secured in flexion (1·57 rad) in a knee holder. The left foot was compressed on an aluminum plate with the ankle axis, assumed to lie on a line between the medial and lateral malleoli, approximately 1 cm from the axis of rotation of the aluminum plate. Figure 1 shows the position of the rat's foot on aluminum plate and knee holder. The aluminum plate was connected to a custom-built dynamometer (Cutlip *et al.* 1997). In short, the dynamometer consists of a DC permanent magnet servomotor (Model 1410C) and a Unidex 1 single axis motion controller (Aerotech Inc., Pittsburgh, PA, USA). The force applied on the aluminum plate at the sole of the foot was translated into a purely vertical movement relative to a Z-11/5 kg load cell (HBM Inc., Marlboro, MA, USA). Consequently, the force measured is independent of foot position on the aluminum plate but only on position of knee and ankle. The fixture of aluminum plate and load cell will be referred to as the force-plate. Note that force of the plantar flexor muscles was measured under the sole of the foot of the rat.

During isometric and concentric testing, the foot was kept firmly positioned (compression force: 12–20 N) using two cross-bars. Between tests, the cross-bars were released to minimize swelling of the foot due to compression. Movement of the force-plate and timing of stimulation were controlled by the computer.

The joint position of the ankle (e.g. 1·57 rad) is defined as the angle between the tibia and the plantar surface of the foot. The angular position of the force-plate corresponds approximately to the ankle angle. The functional range of ankle motion tested (range, 0·61–2·18 rad) covered the range of motion that occurs during rat locomotion (Gruner *et al.* 1980). With the force-plate at 2·09 rad, six to eight isometric contractions were performed to establish the stimulus parameters for maximal activation of the plantar flexor muscles by electrical stimulation of the tibial nerve (200 μs pulse duration, 80 Hz, $6{\cdot}2 \pm 0{\cdot}5$ V). These stimulation parameters were used throughout the testing protocols. At the end of the experiments, the rats were killed by an intracardial injection of sodium pentobarbital.

Experimental procedure

Study 1: *Force–position relationship during isometric and slow concentric contractions*. Since the duration of the experiments was typically 3–4 h, reference isometric force values were determined at three time points: (1) within the first hour before any testing (Ref 1), (2) after the protocol for the

isometric force–position relationship (Ref 2), and (3) after the protocol with sustained isometric actions (Ref 3). The reference isometric forces were determined for three isometric contractions of 600 ms at a force-plate position of 1·57 rad and averaged. Data of six rats producing isometric force values (Ref 2 and Ref 3) ⩾ 90 % of Ref 1 values were analysed.

Slow concentric contractions were performed three times each before and after the protocol for the isometric force–position relationship (see below) and averaged. For concentric contractions, the force-plate was moved from 2·09 to 0·7 rad with an angular velocity of 0·52 rad s^{-1} with relaxed muscles (passive movement). After 100 ms pause, the plantar flexor muscles were maximally activated (isometric pre-load) and 600 ms later the force-plate was returned to 2·09 rad at an angular velocity of 0·52 rad s^{-1} (concentric contraction). Total stimulation time was 3400 ms. The decline in force output during sustained isometric contractions of 3400 ms was tested twice, and averaged at various force-plate positions (1·05, 1·40, 1·74 and 2·09 rad).

To determine the isometric force–position relationship, two isometric contractions of 600 ms were performed at selected force-plate positions (range, 0·61–2·18 rad, with increments of 0·09 rad) and averaged at each position. Rest periods were 2–3 min for contractions of 600 ms and 4–5 min for those of 3400 ms.

Study 2: *Depression of isometric force following multivelocity isokinetic concentric contractions*. Reference isometric force values were determined from three isometric contractions of 600 ms at a force-plate position of 1·57 rad before (Ref 1) and after (Ref 2) each sequence of concentric contractions. Each dynamic test was preceded by a movement of the same magnitude with non-contracting muscles (passive movement). For concentric contractions, the position of the force-plate was moved from 1·57 to 0·7 rad with an angular velocity of 0·52 rad s^{-1}. After a pause of 100 ms, the plantar flexor muscles were activated for 600 ms (isometric pre-load) and the force-plate was returned to 1·57 rad with multiple angular velocities, and held for at least 500 ms. Angular velocities tested (0·87, 1·74, 2·62, 3·49, 4·36, 5·23, 6·10, 6·98, 7·85, 8·72, 9·60 and 10·47 rad s^{-1}) were performed twice, and averaged. Rest periods for isometric testing of 600 ms duration were 2–3 min and 3–4 min for all dynamic contractions. Data of six rats producing Ref 2 isometric force values ⩾ 90 % of Ref 1 values were analysed.

Data collection and analysis

Force-plate position and force were sampled at 264 Hz. Force-plate position was converted to ankle position by repeated measurements ($n = 3$) of the ankle angle (i.e. angle between a line from the lateral epicondyle of the tibia and the plantar surface of the foot) using goniometry at force-plate positions between 0·87 and 2·18 rad with steps of 0·09 rad. The mean of the standard deviation of ankle angle, measured for each animal at each force-plate position, was 0·009 rad. Angular positions of the force-plate were fitted with a one degree polynomial with respect to ankle position ($r^2 = 0{\cdot}998 \pm 0{\cdot}001$). Ankle positions at force-plate positions less than 0·87 rad were extrapolated from the curves. Active force values were calculated as the difference between the total force during dynamic contractions and the passive force recorded during movements with no muscle activation.

For isometric contractions of 600 ms, the active force was calculated by subtracting the average force 100 ms before stimulation from the average total force between 500 and 600 ms after stimulation (i.e. on the tetanic plateau). Analysis of variance was used to select the polynomial of best fit between force-plate position and force during isometric contractions ($r^2 = 0{\cdot}583 \pm 0{\cdot}221$), and slow concentric contractions ($r^2 = 0{\cdot}999 \pm 0{\cdot}001$). The force–position relationships during isometric actions and slow concentric actions at the ankle were calculated for selected angles. For slow concentric actions, the force values were calculated at selected ankle angles between 0·79 and 2·01 rad (i.e. during the concentric contraction) omitting the acceleration and deceleration periods at the beginning and the end of the movement.

At the end of the experiment the length of the gastrocnemius medialis muscle (GM) (i.e. distance between the proximal end of the proximal aponeurosis and the distal end of the most distal fibre bundle) and the length of the distal fibre of GM (distance between the distal end of the proximal aponeurosis and the distal end of the distal fibre) were measured with the knee in flexion (1·57 rad) and ankle angles at 0·79, 1·05, 1·57 and 2·01 rad using a pair of dividers and a ruler with a resolution of 0·5 mm.

Statistics

One-way analysis of variance (ANOVA) was used to test the effect of ankle position on active force during either isometric and slow concentric actions. Two-way ANOVA was performed to test (1) for ankle position and isometric and slow concentric contraction, and (2) the effect of velocity on the

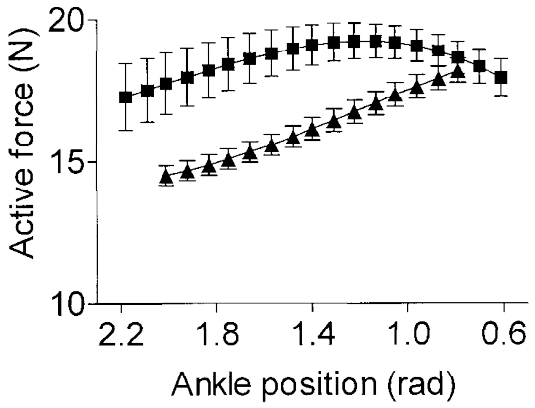

Fig. 2. Active force of the rat plantar flexor muscles as a function of ankle position during isometric (■) and pre-loaded slow concentric (▲) contractions (velocity, 0·52 rad s^{-1}). Data are presented as means ± S.E.M. for six animals.

recovery of isometric force following multivelocity isokinetic concentric contractions. When a significant F ratio was found, *post hoc* testing was done with a Tukey test (e.g. Winer, 1962) to determine where specific differences had occurred. Significance was accepted at $P < 0{\cdot}05$.

RESULTS

The force–position relationship of electrically stimulated ankle plantar flexor muscles working in situ *during isometric and slow concentric contractions in intact rats*

During isometric contractions, the force of the muscles was not significantly different (one-way ANOVA) between different ankle positions (Fig. 2). The force values at ankle positions of 0·61 and 2·18 rad were 93 % and 90 %, respectively, of the peak value (19·2 N) at the ankle position of 1·18 rad. The force–position relationship of the muscles obtained during multi-positional isometric and slow concentric contractions (angular velocity, 0·52 rad s^{-1}) were notably different (Fig. 2) (two-way ANOVA, $P < 0{\cdot}5$) with the greatest difference at larger ankle angles (e.g. 2·0 rad).

Typical force–time traces for a pre-loaded slow concentric contraction (angular velocity of 0·52 rad s^{-1}) and an isometric contraction held for the same length of time at an ankle joint position of 1·40 rad (in the mid-range of motion for the slow concentric action) are illustrated in Fig. 3. During sustained isometric contractions, force decreased by 6·3 ± 0·9 % compared with 23·1 ± 2·1 % for the slow concentric contraction. Sustained isometric contractions at other ankle joint positions (1·05, 1·74 and 2·09 rad) showed slightly different force decreases but never exceeded 7·9 ± 0·4 %.

Force depression following concentric contractions

The force–time traces for concentric contractions at angular velocities of 0·87 and 10·47 rad s^{-1} are illustrated in Fig. 4. All concentric contractions were preceded by 600 ms of nerve stimulation to fully activate the muscles before initiation of the movement. Stimulation continued for at least 500 ms after the movement stopped to allow recovery of isometric force. The force decreased almost linearly with muscle shortening except for the acceleration and

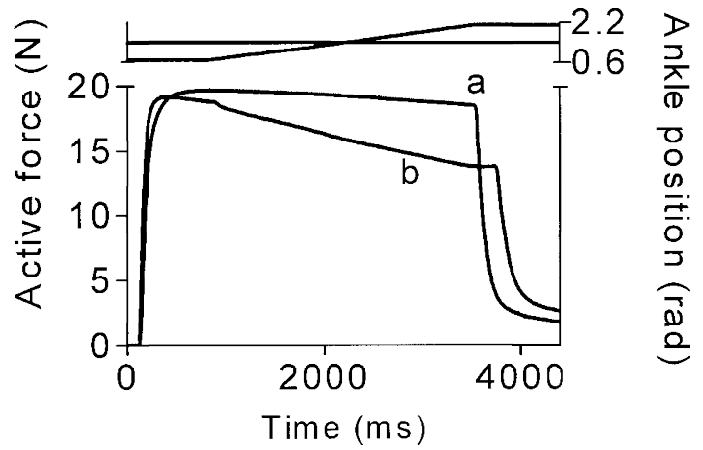

Fig. 3. Active force of the rat plantar flexor muscles as a function of time during a sustained isometric (a) and pre-loaded concentric (b) contraction. Upper traces are recordings of the position of the force-plate (i.e. ankle position) of the dynamometer as a function of time.

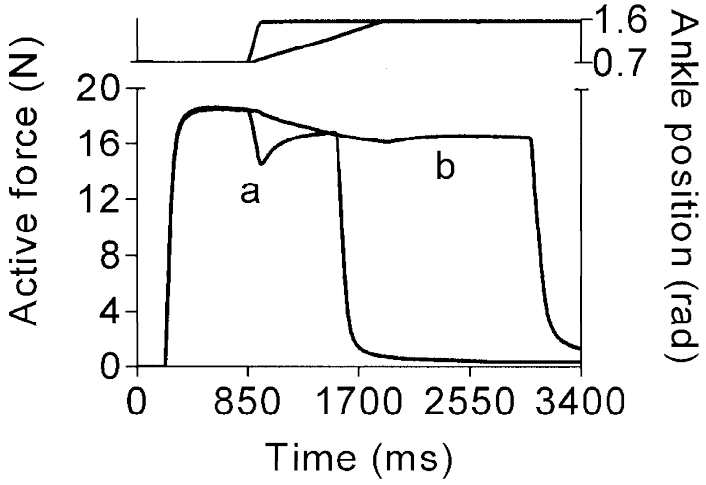

Fig. 4. Active force of the rat plantar flexor muscles as a function of time for pre-loaded concentric contractions with angular velocities of 0·87 (a) and 10·47 (b) rad s^{-1}. Upper traces are recordings of the position of the force-plate (i.e. ankle position) of the dynamometer as a function of time. For clarity of the figure, velocities tested between 0·87 and 10·47 rad s^{-1} are not shown.

deceleration phases at the beginning and the end of the movement (Fig. 4). The lowest force during shortening was smaller for the high compared with the slow velocities of movement.

The response of the muscles after the concentric contraction was a rise in force which was much more rapid for the high velocity movements. The isometric force immediately following shortening was always depressed compared with the isometric force at the same joint position without shortening (Fig. 5).

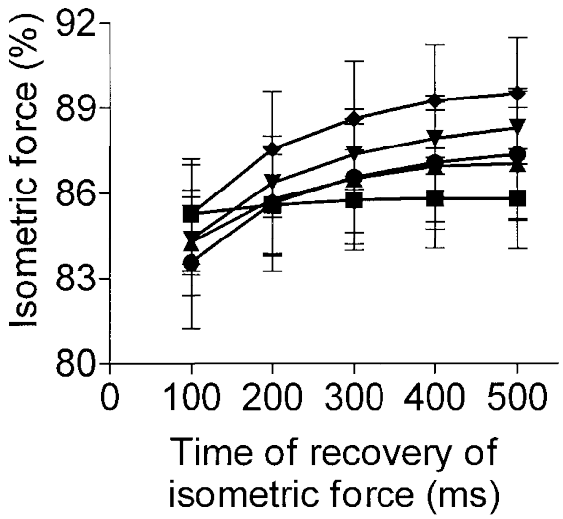

Fig. 5. Recovery of isometric force following multivelocity pre-loaded concentric contractions. The isometric force is expressed as a percentage of the isometric force at an ankle position of 1·57 rad. For clarity of the figure not all velocities tested are shown (concentric velocities (rad s^{-1}): ■, 0·87; ▲, 3·49; ▼, 6·11; ◆, 8·72; ●, 10·47). Continuous lines are for illustrative purposes only. Data are presented as means ± S.E.M. for six animals.

Muscle and fibre length changes of GM

In the range of ankle positions between 0·79 and 2·01 rad, the muscle length of rat GM decreased by 12·6 % from 34·9 ± 0·7 mm to 30·5 ± 1·1 mm. In the same range of motion, the distal fibre length of the GM decreased by 20·3 % from 13·8 ± 0·9 to 10·6 ± 0·6 mm.

DISCUSSION

In this study, the force output under the sole of the foot of an intact rat was measured during nerve stimulation of ankle plantar flexor muscles at controlled ankle positions to test: (1) the isometric force–ankle position relationship, (2) the force–ankle position relationship during slow concentric contractions, and (3) the recovery of isometric force following concentric contractions at different velocities. For several reasons, the study of a muscle group working *in situ* in intact animals permits analysis of force within a physiological range of motion. First, the origin and insertion of plantar flexor muscles were intact as *in vivo*. Second, the force of the plantar flexor muscles was transmitted via tendon and foot as occurs during walking or running. Although control of the ankle movement of the rat by the dynamometer was similar to that used to control joint movements by dynamometry in humans *in vivo*, our approach is unique because the force output of skeletal muscle was measured directly under the sole of the foot. In humans, skeletal muscle force is mostly obtained by dividing torque by the length of the moment arm of the muscles (Leedham & Dowling, 1995).

Multipositional isometric contractions

The isometric force of plantar flexor muscles working *in situ* in intact rats was comparable to those measured for isolated plantar flexor muscles *in situ*. In our study, the peak isometric

force of plantar flexor muscles was 19·2 N (at an ankle position of 1·17 rad) and 8 % lower than the optimum force of isolated plantar flexor muscles *in situ* (21·0 ± 0·8 N) of female rats of equivalent weight measured by attaching the tendon to a force transducer (Dodd *et al*. 1995). Similar findings were reported for mice using a dynamometer; the isometric force of plantar flexor muscles in intact mice was lower (11 %) than the isometric force measured *in situ* (Ashton-Miller *et al*. 1992). It is concluded that the force output of plantar flexor muscles working *in situ* in intact rats can be accurately measured by recording the force under the sole of the foot.

In general, the force output at any ankle position is the sum of force output by all the individual muscles of the plantar flexor group. As such, force–length characteristics, muscle fibre type and mass of the individual muscles contribute to the force output of the plantar flexor group. This muscle group includes m. soleus (SO), GM, m. gastrocnemius lateralis (GL) and m. plantaris (PL) composed of type I (slow-twitch, SO) and type II (fast-twitch, e.g. GM) muscle fibres (Delp & Duan, 1996). Slow-twitch SO has the slowest rise time to peak tetanic force but reaches plateau levels after 500 ms (Claflin & Faulkner, 1989), whereas GM reaches plateau levels after 200 ms (Roszek *et al*. 1994). In the present study, the isometric force was the average force value between 500 and 600 ms after the onset of stimulation; all muscles would be fully activated. SO, GM and GL, and PL contribute about 6, 78 and 16 %, respectively, to the mass of the rat plantar flexor muscles (Woittiez *et al*. 1985; McDonald *et al*. 1992; Delp & Duan, 1996) indicating a substantial contribution of the gastrocnemius muscle to the force output of the plantar flexor muscles. The force–length characteristics *in situ* and morphological data of isolated rat GM (Zuurbier & Huijing, 1993) and GM length changes measured in our study reveal that the GM has the capability of generating high forces. This observation is in agreement with predictions for force capabilities of GM *in vivo* by Ettema (1997) as GM had muscle lengths *in vivo* close to its optimum muscle length *in situ*. Interestingly, the rat tibialis anterior muscle (dorsiflexor) also generates nearly maximum force values over the normal range of motion (Hawkins & Bey, 1997), but cat plantar flexor muscles seem to operate on the ascending and descending limbs (Herzog *et al*. 1992). Ettema (1997) used a geometrical model to predict the length of the GM from knee and ankle angles and found that GM *in vivo* produces more than 80 % of its optimum force with the knee at 1·57 rad and the ankle between 0·79 and 2·01 rad – the range used in this study. If the characteristics of isolated GM *in situ* resemble those of isolated GL *in situ* and both muscles show similar length changes *in vivo*, the isometric force–position relationship of ankle plantar flexor muscles in intact rats of the present study is consistent with the force–length data of the isolated GM *in situ* (i.e. functional around optimum length). However, video microscopy of rat SO *in vivo* (Ledvina & Segal, 1995) demonstrated that sarcomere lengths are situated well onto the descending limb of the force–length relationship in the range of ankle positions tested in this muscle. Sarcomere lengths of SO increased from 2·22 ± 0·04 μm at maximal plantar flexion (2·97 rad) to 3·17 ± 0·03 μm at maximal dorsiflexion (0·52 rad) (Ledvina & Segal, 1995). However, the SO makes up only 3 % of the mass of the plantar flexor muscles and as such its contribution to the force characteristics of the plantar flexor muscles is small and decreases further at small ankle angles; no information on the properties of rat plantaris muscle *in vivo* is available. Hence, it appears that within the plantar flexor–ankle joint system of the rat, the various muscles probably operate on different parts of their force–length relationship. It is concluded that electrically stimulated plantar flexor muscles of rat can produce high forces over a wide range of functional ankle joint positions and that recording of force under the sole of the foot can be

used for the physiological testing of isometric performance *in situ* in intact rats without alteration by the ankle or foot.

Multipositional isometric contractions vs. *slow concentric contractions*

The force output of slow concentric contractions was similar to the isometric force at ankle positions between 0·7 and 1·0 rad. However, the concentric contractions did not reproduce the isometric force–position relationship of the plantar flexor muscles at all positions. The decrease in force during a slow concentric contraction in our study was substantial (23 %). Isometric contractions of the same time duration produced only minor decreases in force. Further, since the muscle force remains high (above 80 % of the isometric force), a constant compliance of the series elastic elements would result (Ettema & Huijing, 1989) and possible differences in muscle fibre lengths during isometric and concentric contractions can be excluded. Factors which might have contributed to the observed force decrease during slow concentric contractions include decreased activation, decreased cross-bridge force production, and increased P_i production. First, shortening-induced deactivation could cause a temporary decrease in the affinity of calcium bound to troponin when filament sliding occurs during muscle shortening (Edman, 1996). Second, as high-force cross-bridges are reduced during muscle shortening, the population of low-force cross-bridges increases (Iwamoto, 1995). Third, the metabolic contribution to fatigue is larger during concentric than during isometric contractions (Kushmerick & Davies, 1969). Thus, for complex reasons, slow concentric muscle actions in electrically stimulated plantar flexor muscles working *in situ* result in decreased force output at some ankle positions illustrating that physiological differences exist between isometric and slow concentric muscle actions.

The angular velocity of 0·52 rad s^{-1} during the concentric contraction corresponded to a shortening velocity of 1·89 mm s^{-1} for the GM. Larger force decreases (46 %) during shortening were reported for rat GM *in situ* during slow concentric contractions (1·8 mm s^{-1}) initiated above muscle optimum length ($L_o + 0{\cdot}5$ mm) (Fig. 3 in Huijing & Ettema, 1988–1989). However, differences in stimulation parameters and muscle length may explain the differences in the force decline seen in the two studies. It is concluded that the force output during pre-loaded slow concentric contractions does not match the isometric force–position relationship.

Concentric performance

The force–time relationship of slow concentric contractions obtained in intact rats was similar to the concentric force patterns reported by others for electrically stimulated isolated rat GM *in situ* (Huijing & Ettema, 1988–1989) and the shape of the torque–time relationships of human ankle plantar flexor muscles under voluntary activation (Gravel *et al*. 1988, 1990) and percutaneous stimulation (Thomas *et al*. 1987). Gravel *et al*. (1990) showed an angle dependency on torque measurements with a 66 % decrease in torque throughout a range of ankle motion from –0·17 (10 deg dorsiflexion) to 0·52 (30 deg plantarflexion) rad. In this range of ankle motion, a concentric contraction occurs on the ascending limb of the force–position relationship of human ankle plantar flexor muscles (Sale *et al*. 1982) and thus velocity and length effects determine the magnitude of the torque measured. The decrease in force in our study was substantial (23 %) during a slow concentric contraction. This decrease in force output is a true motion effect as the length effects on force output are negligible in our experimental set-up because the isometric force of the plantar flexor muscles did not change much with position (Fig. 2). Following the concentric contractions, the isometric force increased

with time. The magnitude of the force increase was velocity dependent as was reported for isolated dogfish (Abott & Aubert, 1952), frog sartorius (Maréchal & Plaghki, 1979), rat GM *in situ* (Meijer *et al*. 1997), cat soleus muscle *in situ* (Herzog & Leonard, 1997), and human adductor pollicis muscle (De Ruiter *et al*. 1998). It is concluded that the maximally contracting plantar flexor muscles can be used for physiological testing of concentric performance of skeletal muscle in intact rats.

In summary, this study is the first to describe the isometric and concentric contractions of skeletal muscle working *in situ* in intact rats. The plantar flexor muscles have a high force-producing capability over a wide range of ankle positions. Pre-loaded concentric contractions measured at an angular velocity of 0·52 rad s^{-1} did not duplicate the isometric force–position relationship of plantar flexor muscles working *in situ* except at values close to 1·57 rad. The use of a dynamometer to test in intact rats the isometric and concentric muscle performance will be beneficial in studying longitudinal changes with disease or age.

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