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SKELETAL MUSCLE

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Low-frequency fatigue is fibre type related and most pronounced after eccentric activity in rat medial gastrocnemius muscle

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Abstract Effects of fibre type composition and type of contraction on low-frequency fatigue (LFF) were investigated in isolated rat medial gastrocnemius (GM) muscle. Fast oxidative or fast glycolytic GM muscle parts of anaesthetised male Wistar rats (n=18) were activated selectively by maximal electrical stimulation of the nerve after selective cutting of sub-branches. LFF was induced by a series of 40 isometric, concentric or eccentric contractions. Post exercise (55 min), the force–frequency curves differed significantly from the pre-exercise curves. Decreased forces were exerted mainly at the lower frequencies. This effect was significantly greater for glycolytic than oxidative muscle parts and following eccentric compared to isometric and concentric exercise. Seventy minutes following eccentric exercise, the relative values of the 60:200 Hz force ratios for the oxidative compared to the glycolytic parts were 65.6±2.2% and 43.6 ±4.6% (mean±SE) of the pre-fatigue values (=100%), respectively. In conclusion, for conditions of identical activation, eccentric exercise led to significantly more LFF than isometric and concentric exercise. In addition, and independent of the exercise type, fast glycolytic muscle parts were more susceptible to LFF than fast oxidative muscle parts.

Keywords Concentric · Force–frequency characteristics · Isometric · Muscle fatigue

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Introduction

Muscular fatigue consists of short and longer-lasting components. Short-term fatigue is generally related to metabolic changes within the muscle (e.g. [9]) and recovers relatively quickly. Low-frequency fatigue (LFF) is a long-lasting form of fatigue that appears after intense muscle activity and is characterized by reduced tetanic force at low frequencies of stimulation while force is not or less reduced at high frequencies [10, 37]. The most likely cause of LFF is a disturbance of the excitation-contraction (E-C) coupling [10, 21, 37]. In vivo during locomotion, motoneurones predominantly fire at relatively low rates; high firing rates are only observed during maximal dynamic activities [13]. Therefore, LFF is expected to have important consequences for in vivo muscle function, particularly because recovery of LFF can take up to 24 h [10].

LFF is observed after several types of exercise [10]. However, the extent of LFF depends on the type of exercise performed; for instance, LFF is more pronounced after sustained compared to intermittent contractions [3] or after long-lasting compared to short-lasting contractions during repetitive isometric exercise [31]. It has been suggested that LFF induced by isometric exercise is different from LFF induced by eccentric exercise [31]. Edwards et al. [11] and Newham et al. [26] showed that LFF was greater after eccentric compared to concentric exercise but this may be related to differences in activation parameters rather than to the concentric and eccentric nature of the exercise per se. In the latter studies, the subjects performed a voluntary step test, which makes it unlikely that the knee extensor muscles had been activated to a similar extent during concentric and eccentric exercise. Moreover, recruitment patterns may have been different between the conditions [24]. These factors can be controlled in isolated muscle preparations. However, to our knowledge a systematic comparison between LFF after isometric, concentric and eccentric exercise has not been made. Therefore, the first aim of the present study

was to compare LFF induced by isometric, concentric and eccentric exercise under similar activation conditions.

Muscle damage or mechanical disturbances of muscle, which would interfere with normal E-C coupling, have been indicated as cause of LFF [11, 19]. Muscle damage after eccentric exercise is thought to be fibre type specific. For rabbit tibialis anterior muscle, Lieber and Friden [22] demonstrated that, after eccentric exercise, fast glycolytic fibres were damaged selectively over fast oxidative and slow oxidative fibres. Moreover, changes in E-C coupling during fatigue are thought to be fibre type specific as well [34]. Consequently, LFF may differ for different fibre types. Although LFF has been found to appear in both fast- and slow-twitch animal muscles [21], fast fatigue-resistant single motor units have been found to be less susceptible to LFF compared to fast fatigue-intermediate and fast fatigable motor units in cat flexor digitorum muscle [29] and cat peroneus tertius muscle [18]. Therefore, an effect of fibre type composition on LFF can be expected. However, these studies on single motor units investigated the effects of isometric exercise on LFF whereas the effects of concentric and eccentric exercise in relation to LFF have not been studied before. Consequently, the second aim of the present study was to investigate the influence of fibre type composition on LFF induced by different types of exercise.

In the present study, effects of fibre type composition in relation to LFF in response to different exercise types were studied. This was done by making use of the natural regionalization of fibre types in rat medial gastrocnemius (GM) muscle, which makes it possible to selectively activate either the fast oxidative, proximal (10% type I, 10% IIA, 45% IIX, 35% IIB fibres) or the fast glycolytic, distal (20% IIX, 80% IIB fibres) part of this muscle [7]. This model has the additional advantage that morphological and mechanical differences between fibre type populations at different locations within the muscle are smaller than for a comparison of results for two different muscles with different fibre type compositions.

In this study, the effects of fibre type composition and type of exercise (isometric, concentric and eccentric) on LFF were examined in rat GM muscles with either fast oxidative or fast glycolytic muscle parts active exclusively. Since eccentric exercise usually causes more damage than isometric or concentric exercise, we hypothesized that most LFF occurs after eccentric exercise. In addition, we hypothesized most LFF to occur in GM muscles with active fast glycolytic parts because fast glycolytic fibres are known to be more susceptible to damage and fatigue in general.

Materials and methods

In situ experiments were performed on medial gastrocnemius (GM) muscle-tendon complexes of 18 male Wistar rats (body mass 242–276 g). The rats were anaesthetised with 1.5 $g \cdot kg^{-1}$ body mass urethane (administered intraperitoneally). Supplemental injections of 0.63 $g \cdot kg^{-1}$ body mass were given if necessary. Experiments were approved by the Committee on Animal Experimentation, Vrije Universiteit Amsterdam and are in compliance with Dutch law.

Muscle preparation and experimental set-up

During surgery as well as during the experiment, the animal was placed prone on a heated pad of 35°C to prevent hypothermia. The GM muscle-tendon complexes of both legs were dissected free of surrounding tissues. This means that most, if not all, effects of extra- and intramuscular force transmissions (e.g. [17, 25]) were excluded. The blood supply remained intact. The sciatic nerve was cut as proximally as possible within the upper leg. All distal branches of this nerve were cut except the branch to the GM.

The primary nerve branches within the GM muscle were exposed by blunt dissection of the natural nerve hilus. In order to activate selectively fast oxidative (n=18) or fast glycolytic (n=18) muscle parts, either the primary proximal nerve branches or the distal nerve branches of the GM nerve were left intact, respectively. Other branches were cut. For clarity, we will refer to the properties of the rat GM muscle with proximal or distal muscle parts active as the properties of the fast oxidative or fast glycolytic muscle part, respectively.

The femur was clamped in a vertical position, whereas the muscle was positioned horizontally. The distal tendon with a piece of the calcaneal bone was connected to a force transducer. Muscle temperature was controlled by water-saturated airflow around the muscle of approximately 33°C. The sciatic nerve was placed on a bipolar stimulating electrode and used for stimulation. For a more detailed description of the experimental set-up see De Haan et al. [5].

The force transducer used was part of an isovelocity measuring system. The transducer was mounted on a servomotor. Acceleration, velocity, start length, onset of movement and stimulation, stimulation frequency and duration of the muscle contractions were computer controlled. Stimulation current was 1 mA with a pulse width of 0.05 ms for maximal stimulation of all fibres. The data (force, length and stimulation pattern) were AD converted with a sample frequency of 1000 Hz and stored on disc. After the experiments, the rats were killed by cervical dislocation.

Experimental muscle length

All experiments were performed at the GM tetanic optimum length specific for the selected active muscle part. For determination of those optimum lengths, tetani of 100 ms with a stimulation frequency of 200 Hz were used. It is known that optimum length differs for rat GM muscles with different parts active. Because muscle fibres in the distal part contain slightly more sarcomeres in series than fibres in the proximal part [14], the optimum length for GM muscle with an active fast glycolytic part is about 1.5 mm higher than one with a fast oxidative part active [7]. The maximal isometric force generated by the active part reflects the size of the stimulated muscle part.

Pre-exercise force–frequency characteristics and the 60:200 Hz force ratio

Following determination of optimum length, data for the force–frequency relation were obtained by imposing tetani with frequencies of 20, 40, 60, 80, 120 and 200 Hz. The duration of each contraction was 200 ms. Time between contractions was 2 min. With the measurements at stimulation frequencies 60 Hz and 200 Hz, the 60:200 Hz force ratio was calculated. After 10 min of rest, the 60:200 Hz force ratio was determined again. The mean value of the two 60:200 Hz force ratios was used as the pre-exercise value to which subsequent measurements of this ratio were normalised. The 60 Hz contraction was always performed after

the 200 Hz measurement to maintain the same level of potentiation throughout the experiment.

Fatiguing contractions

After an additional 10 min rest, a fatiguing series of 40 isometric (n=6), concentric (n=6) or eccentric (n=6) contractions was performed with 280 ms rest in between contractions. Each contraction lasted 70 ms and was induced by ten stimulation pulses applied with a frequency of 150 Hz. A stimulation frequency of 150 Hz was sufficient to obtain maximal activation. With higher frequencies, the chance of inducing high-frequency fatigue may increase. Figure 1 shows typical examples of force and length traces of isometric, concentric and eccentric force signals as performed in the fatiguing protocols. During concentric or eccentric contractions, the stimulation started simultaneously with shortening or lengthening of the muscle, i.e. without any prior isometric phase. In these dynamic conditions, the range of movement was between +0.5 and −3.5 mm, where 0 mm indicates the specific optimum muscle length for the activated muscle part. By avoiding stretching to non-physiological high muscle lengths we aimed to prevent severe force loss due to the eccentric exercise.

Short-term fatigue and recovery

Immediately after the series of fatiguing contractions, an isometric contraction (200 ms, 200 Hz) was performed to quantify short-term fatigue. To observe the fast component of the recovery process as a function of time, additional contractions were performed (200-ms tetani with 200 Hz stimulation frequency) at t=0.5, 1.5, 3, 6 and 9 min, where t=0 indicates the end of the fatiguing series of contractions.

Post-exercise force–frequency characteristics and the 60:200 force ratio

Because of possible changes of optimum length and their effects on the 60:200 Hz force ratio, the optimum length for tetanic force production of the muscle part was determined again (at t=50 min) with a few isometric contractions at a stimulation frequency of 200 Hz. If the optimum length had changed due to the fatiguing series of contractions, the muscle length was set at the new (i.e. 0.5–1.0 mm higher) length. To estimate LFF, the complete force–frequency curve as well as the 60:200 Hz force ratio was determined. Starting at t=55 min, data for the force–frequency relation were obtained. Following 5 min of additional rest (t=70 min), the 60:200 Hz force ratio was determined. We measured LFF at approximately 1 h after the cessation of fatiguing exercise because muscle metabolites causing short-term fatigue were expected to have returned to their pre-exercise values [6] and LFF was expected to be fully developed by that time (e.g. [18]).

Statistics

All values are described as mean±standard error (SE). Significance was accepted at a level of 0.05. An unpaired t-test was performed to compare the pre-exercise 60:200 Hz force ratios of fast oxidative and fast glycolytic muscle parts. Two-way (muscle part and type of exercise) analyses of variance were used to determine differences in pre-exercise isometric forces and in levels of short-term fatigue directly after exercise. Analyses of variance with two between-subject factors (muscle part and type of exercise) and one within-subject factor (time) were used to test for significant differences in the recovery of the isometric force after exercise and in 60:200 Hz force ratios before and after exercise. Differences in the force–frequency relationship before and after fatigue between the muscle parts and exercise types were determined with analysis of variance with repeated measures on two factors (time and frequency). Data of force–frequency curves in the unfatigued state were tested statistically with analysis of variance with repeated measures on one factor (frequency). If significant main effects or interaction effects were observed, Bonferroni post-hoc tests were performed.

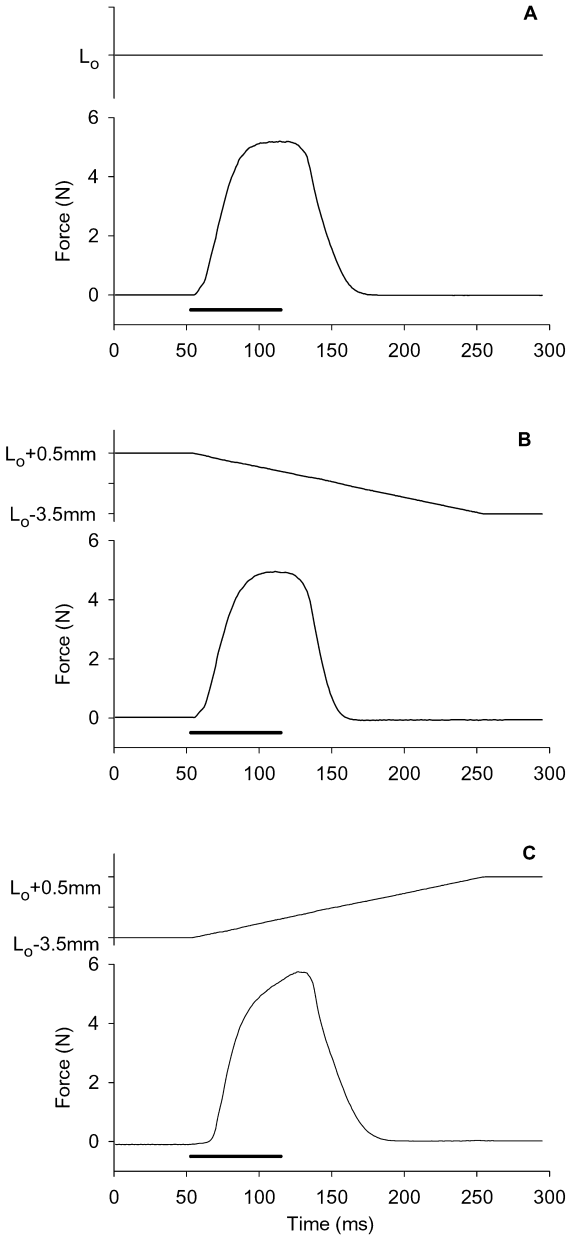

Fig. 1A–C Typical examples of length and force traces prior to fatigue. Length (*top panels*) and force (*bottom panels*) traces during isometric (**A**), concentric (**B**) and eccentric (**C**) contractions of a medial gastrocnemius (*GM*) muscle with a fast glycolytic muscle part active. The first contractions of the isometric, concentric and eccentric fatiguing protocols are shown. The length of the muscle–tendon complex is expressed relative to the isometric optimum length (L_o) of the active muscle part. Stimulation is indicated by the *bold lines* below the force traces

Results

Pre-exercise forces

Isometric force generated by GM muscles was lower for fast oxidative muscle parts compared to fast glycolytic muscle parts (3.9±0.3 N vs. 5.3±0.3 N, respectively, $P<0.05$, $n=18$) indicating larger sizes of the fast glycolytic muscle parts. Prior to the fatiguing exercise, maximal isometric force was not significantly different for the different experimental groups (i.e. groups that were subjected to series of isometric, concentric or eccentric contractions). The peak concentric and eccentric forces at the start of the fatiguing exercise protocol were 79.8±1.7% and 110.6±2.6% of isometric values, respectively.

Short-term fatigue and recovery

Immediately after the fatiguing series of contractions, isometric force (200 Hz) was reduced significantly (Fig. 2, measurement at $t=0$). Isometric force at $t=0$ ranged from 60.9±2.5% (for fast glycolytic parts after concentric-induced fatigue) to 80.1±2.0% (for fast oxidative parts after eccentric-induced fatigue) of the initial isometric force. Following all three types of exercise, the reduction in maximal isometric force was significantly greater for fast glycolytic compared to fast oxidative muscle parts. For fast oxidative as well as for fast glycolytic muscle parts, the series of concentric contractions resulted in significantly greater fatigue than isometric and eccentric series.

After all three types of exercise, fast oxidative muscle parts recovered significantly faster and to a greater extent than fast glycolytic ones (Fig. 2). Recovery after a series of eccentric contractions was significantly less than after an isometric protocol (Fig. 2). After eccentric exercise, force recovered to 98% within 1.5 min in fast oxidative muscle parts (Fig. 2C). However, force decreased after this initial recovery. In fast glycolytic muscle parts, force recovery was not complete after eccentric exercise (<90%). Recovery after a concentric protocol was not different from recovery after an isometric or eccentric protocol (Fig. 2, $P>0.05$). There was no significant interaction effect between muscle part and type of exercise, which means that the differences in recovery were similar for both fast oxidative and fast glycolytic muscle parts.

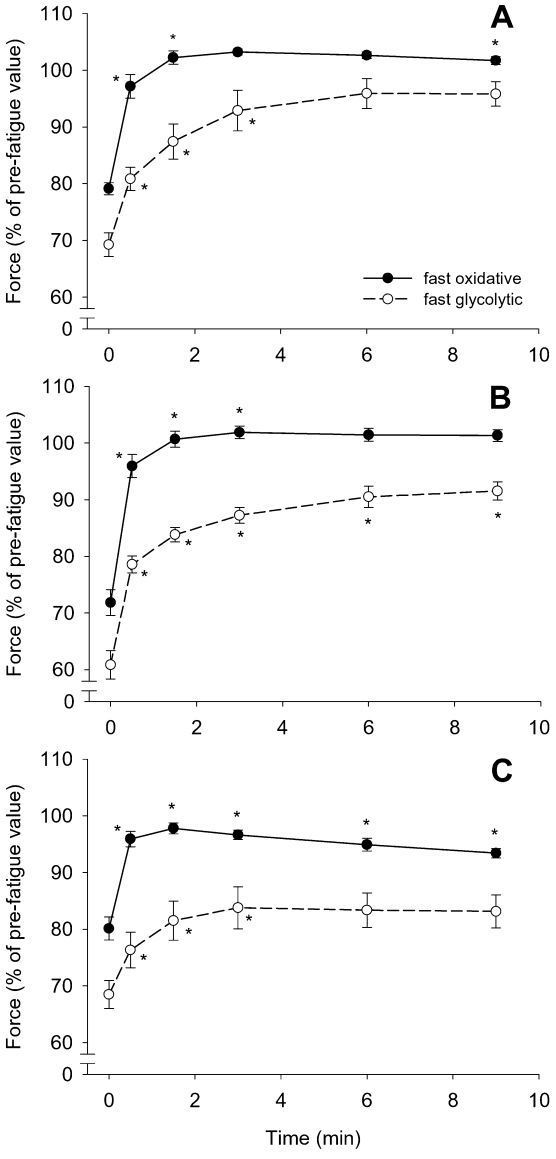

Fig. 2A–C Recovery of isometric muscle force of fast oxidative (*closed symbols*) and fast glycolytic (*open symbols*) rat GM muscle parts after an isometric (**A**), concentric (**B**) or eccentric (**C**) fatiguing series of contractions. $t=0$ indicates the end of the fatiguing series of contractions. After the fatiguing series, 200-ms tetani (200 Hz) were applied to estimate isometric force recovery. The first measurement (at $t=0$ min) was performed immediately after the fatiguing series of contractions and represents the fatigue level. Force is expressed as a percentage of the pre-fatigue value. Values are means±SE. The fast oxidative muscle part recovered significantly faster and to a greater extent than the fast glycolytic part ($P<0.05$). Recovery after an eccentric series of contractions was significantly less than after an isometric protocol ($P<0.05$). *Significant difference from the preceding measurement

Force–frequency characteristics

The force–frequency curves in the pre-fatigue state were not significantly different for fast oxidative or fast glycolytic muscle parts. However, 55 min following exercise, the force–frequency curves had altered significantly (Fig. 3). Lower forces were exerted than in the pre-fatigue state. This reduction was greatest at lower frequencies, which is an indication for LFF. For each of the three types of exercise, the change of the force–frequency curve was significantly more pronounced for fast glycolytic than for fast oxidative muscle parts (Fig. 3). No significant interaction effect between muscle part and type of exercise was present. For fast oxidative as well as fast glycolytic muscle parts, eccentric exercise caused significantly greater changes of force–frequency curves than isometric or concentric exercise (Fig. 3). Isometri-

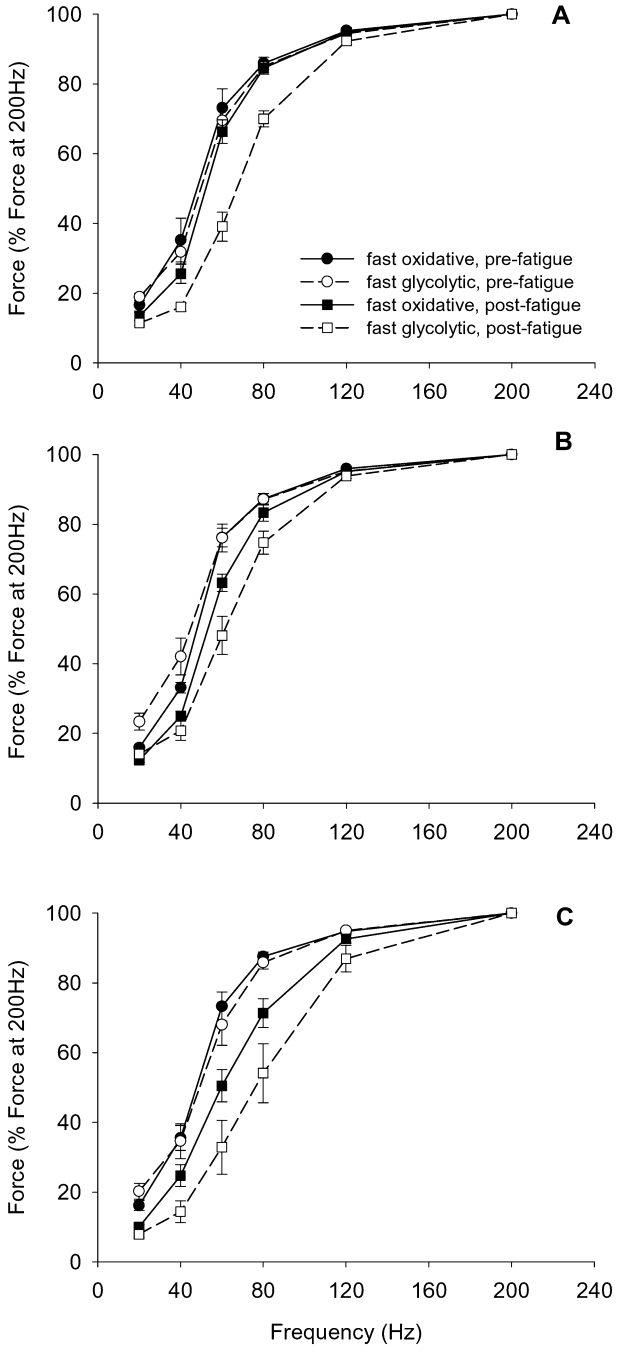

Fig. 3A–C Effects of fibre type composition and type of exercise on force–frequency curves. Normalised force–frequency relations for fast oxidative (*closed symbols*) and fast glycolytic (*open symbols*) GM muscle parts before (*circles*) and 55 min after (*squares*) isometric (**A**), concentric (**B**) or eccentric (**C**) exercise are shown. Pre- and post-measurements were made at the initial and corrected GM optimum length for force production of the active muscle part, respectively. Force is expressed as a percentage of force at 200 Hz. Values are means±SE. After each of the three types of exercise, the change of the force–frequency curve was greater for the fast glycolytic than the fast oxidative muscle part ($P<0.05$). The changes of the curves were more pronounced after eccentric exercise than after isometric and concentric exercise ($P<0.05$) for both muscle parts

cally- and concentrically induced fatigue caused similar changes of the force–frequency curves ($P>0.05$).

The 60:200 Hz force ratio

Prior to the fatiguing series, the mean 60:200 Hz force ratio was 0.75±0.02 for fast oxidative muscle parts and 0.69±0.03 ($n=18$) for fast glycolytic parts ($P>0.05$). Figure 4 shows the 60:200 Hz force ratio 70 min after exercise expressed as a percentage of the pre-exercise value. At this time, the 60:200 Hz force ratios were significantly lower compared to the pre-exercise value. Moreover, the 60:200 Hz force ratios of the fast glycolytic muscle parts were significantly more depressed than the ratio of the fast oxidative muscle parts. This indicates more LFF in fast glycolytic muscle parts than in the fast oxidative ones. Furthermore, an eccentric series of contractions caused significantly more LFF than an isometric or concentric series ($P<0.05$). No significant interaction effect occurred between muscle part and type of exercise. Consequently, at t=70 min, in both the fast oxidative parts and the fast glycolytic muscle parts the 60:200 Hz force ratio had declined to significantly lower values following eccentric (65.6±2.2% and 43.6±4.6%, respectively) exercise than following isometric (89.2 ±3.4%, 65.1±3.7, respectively) and concentric (85.1 ±2.6% and 73.2±8.5%, respectively) exercise (Fig. 4). LFF was comparable after isometric and concentric exercise in both muscle parts ($P>0.05$).

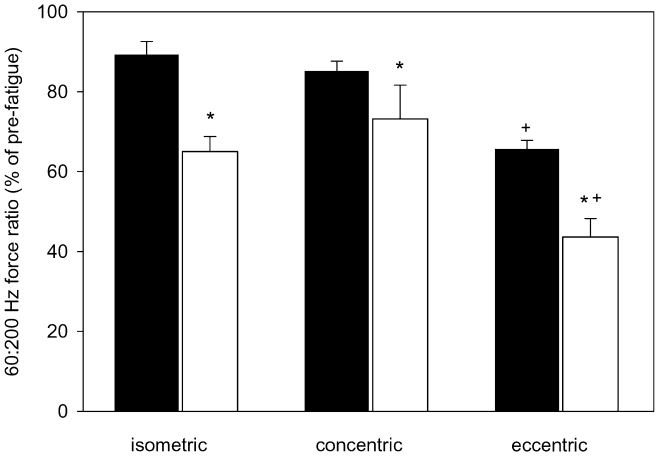

Fig. 4 Effects of type of exercise on low-frequency fatigue for different fibre type compositions. Normalised ratios of tetanic force (60:200 Hz) for fast oxidative (*black bars*) and fast glycolytic (*white bars*) rat GM muscle parts at 70 min after isometric, concentric and eccentric exercise are presented. Ratios are expressed as a percentage of pre-fatigue values (=100%). Values are means±SE. Measurements were performed at the corrected GM optimum length for force production of the active muscle part. *Significant difference from values of fast oxidative muscle parts; +significant difference from values after isometric and concentric exercise

Discussion

A novel aspect of the present study is the systematic investigation of the influence of fibre type composition on LFF induced by isometric, concentric or eccentric exercise. LFF, indicated by a decreased 60:200 Hz force ratio as well as by changes of the force–frequency curve, was present following each type of exercise. Eccentric exercise caused significantly more LFF than isometric and concentric exercise in both muscle parts. In addition, fast glycolytic rat GM muscle parts showed significantly more LFF than fast oxidative parts following all three types of exercise. Since motoneurones usually fire at relatively low (<60 Hz) frequencies during in vivo action [13] and force was approximately halved at those frequencies of stimulation in the present study, LFF after eccentric exercise in particular may have large effects on in vivo performance. To date it is unknown whether, and if so to what extent, the central nervous system can increase muscle activation frequencies during LFF to prevent a loss of force output.

Short-term fatigue and recovery

Directly after a concentric fatiguing series of contractions, maximal isometric force was significantly more reduced than after an isometric or eccentric series. The decline of maximal isometric force after the latter conditions was similar, indicating that severe force loss due to the eccentric exercise was limited. This is what we aimed for in the present study. Peak forces during the eccentric contractions were only slightly higher than isometric force. The type of fatigue present shortly after exercise is known to be related to a reduction in ATP and accumulation of several of metabolites (i.e. lactate, inorganic phosphate, AMP, ADP, IMP) [4]. This type of (short-term) fatigue seems to be linked to peak metabolic fluxes, which are higher during concentric than eccentric exercise, resulting in a higher level of fatigue after concentric exercise.

Fast oxidative muscle parts were less fatigued and recovered faster than fast glycolytic parts, which is in accordance with the greater oxidative capacity of the fast oxidative compared to the fast glycolytic fibre population [7]. However, recovery was significantly less complete after eccentric exercise than after isometric exercise and force recovered to a lesser extent in the fast glycolytic than in the fast oxidative muscle parts. Comparable losses of force have been found by others following eccentric exercise in vivo (e.g. [15, 27]).

LFF after different types of exercise

As expected, LFF became apparent following short-term recovery of maximal isometric force. Our findings of more pronounced LFF following eccentric exercise as compared to isometric and concentric exercise are in agreement with the results of studies on human muscle during voluntary contractions [11, 26]. However, in the present study the muscle parts were activated by electrical stimulation of the nerve. Therefore, we are confident that all fibres were activated in an identical manner regardless of the type of exercise performed. In previous work [11, 26], this was uncertain because of the voluntary exercise protocols. For instance, particularly during eccentric contractions there may be neural inhibition during voluntary effort [8, 36, 38]. This may lead to differences in motor unit recruitment and/or muscle fibre activation when effects of contraction type are studied using voluntary exercise protocols.

It is very important to keep muscle activation identical in each exercise protocol because the extent of LFF depends on the duration of the contractions [31]. An additional important feature of the present study is that measurements were performed at the optimum length of the active muscle part. From previous experiments [7] it is known that the fast oxidative and fast glycolytic muscle parts of the GM muscle have different optimum lengths. Measuring at optimum length of the whole muscle would not be appropriate, since force–frequency relations are length-dependent [32]. Furthermore, different populations of fibres would be relatively shortened or stretched more than others if shortening or lengthening occurred at the optimum length of the whole muscle [23, 30]. In addition, the force and the extent of damage caused by eccentric exercise are dependent on the length range over which contractions are carried out. Obviously it is of great importance to recognize this, especially when fibre-type-dependent effects of eccentric exercise are studied and knowing that many muscles of laboratory animals, including the rat, have a regionalized fibre type composition.

Yet, the different responses between the muscle parts after the eccentric exercise could, in principle, have been a result of different stretch distances and/or velocities of the fibres in the different muscle parts. In the rat GM muscle, the angle of pennation of the fast glycolytic fibres is slightly larger than for the fast oxidative fibres, although this difference is not significant [40]. Relatively larger pennation angles of the fast glycolytic fibres would induce a relatively longer stretch of these fibres. However, the fast glycolytic fibres are slightly longer than the fast oxidative fibres [14], which would lead to relatively less stretched fibres. Overall, we do not expect that there were large differences in stretch between the different fibre populations that could have induced the observed difference in LFF.

Possible causes of LFF

In contrast to short-term fatigue, which was greatest after concentric exercise, LFF was most pronounced after eccentric exercise. Therefore, LFF is obviously not related to metabolic fluxes or the work done by the muscle. It is more likely that LFF is the result of an impairment of the process of E-C coupling [10] leading to a reduced Ca^{2+} release from the sarcoplasmic reticulum (SR) per action potential [16, 37]. The exact cause of the reduced Ca^{2+}

release, however, has not yet been unravelled. However, its effect may be interpreted as follows. Low stimulation frequencies correspond to the steep part of the sigmoidal Ca^{2+}–force curve and high frequencies to the horizontal part. Therefore, similar changes in Ca^{2+} concentrations result in larger changes in force production at low stimulation frequencies than at high frequencies [20, 37]. The result is an altered force–frequency curve and a decrease in the ratio of force at low versus high stimulation frequency during LFF.

LFF has also been related to muscle damage. Newham et al. [26] suggested that LFF may be the consequence of some injury or mechanical disturbance of muscle. It is known that, after eccentric contractions, muscle damage is more likely to occur than after other types of exercise (e.g. [2]). Although we aimed to avoid severe muscle damage in the present study, a certain amount of damage could have occurred as a result of the eccentric exercise. This could explain the more pronounced LFF after eccentric compared to isometric or concentric exercise. Muscle damage may include damage of the SR, resulting in decreased Ca^{2+} release [19]. Another possibility is that sarcolemmal damage leads to disruption of Ca^{2+} homeostasis in the injured fibres [1]. It has been suggested [20] that a change of the force–frequency curve may occur independently of changes in Ca^{2+} release and could be accompanied by a shift of the optimum length of the muscle due to damage following eccentric contractions. This theory has been supported by data from, for example, Wood et al. [39]. To avoid the influence of a change in the force-length relation in the present study, muscles were set to their new optimum length before the force–frequency curve following exercise was obtained and a change of the curve to higher frequencies was still observed.

Influence of fibre type on the degree of LFF

Although the exact cause of LFF remains obscure, the present study not only clearly shows that LFF was more pronounced following eccentric exercise, but also demonstrates that LFF was greater in fast glycolytic compared to fast oxidative fibres within the same muscle. It is possible that differences in fatigability between various muscle fibres are linked to fibre-type-specific differences in E-C coupling [34]. Takekura et al. [35] showed a disorder in the membrane systems involved in E-C coupling in rat muscle after eccentric exercise. This disorder was mainly present in the fast fibres and less pronounced in slow fibres. Unfortunately, neither Stephenson et al. [34] nor Takekura et al. [35] explicitly compared fast oxidative and fast glycolytic fibres. Lieber and Friden [22] showed that after eccentric exercise, fast glycolytic fibres were selectively damaged rather than fast oxidative and slow oxidative fibres in rabbit tibialis anterior. Powers and Binder [29] studied LFF in fast motor units. They showed that fast fatigue-resistant motor units are less susceptible to LFF compared to fast intermediate-fatigable and fast fatigable motor units in cat flexor digitorum muscle following repeated isometric contractions. Our results are in agreement with these findings. The present study extends these earlier findings by showing that, besides LFF being greater after eccentric than after isometric and concentric exercise, this contraction-type-related enhancement of LFF was similar for fast oxidative and fast glycolytic fibres. Muscle damage might deteriorate the disturbance in E-C coupling. A disturbance in E-C coupling is seen as the main cause of LFF [10]. The greater susceptibility of fast glycolytic fibres to fatigue and damage might explain the higher level of LFF in fast glycolytic active muscle parts compared to fast oxidative ones.

It is however not clear if increased oxidative capacity of a muscle protects muscle fibres from eccentric contraction-induced damage or from LFF. Evans et al. [12] showed that endurance training of human muscle led to less damage following eccentric contractions while data from Patel et al. [28] showed that, in rat muscles, increased oxidative capacity by electrical stimulation training did not result in less injury after eccentric exercise. Furthermore, Skurvydas et al. [33] stated that endurance training and slow muscle fibre type prevalence does not result in less LFF, and neither does it accelerate the recovery of muscle contraction force following maximal, intermittent stretch-shortening cycle exercise. However, in these studies it is difficult to determine if the different fibre types have been stretched to a similar extent.

Conclusion

In conclusion, LFF was more severe after eccentric than isometric and concentric exercise in isolated rat GM muscle. Following exercise, LFF was greater in the fast glycolytic compared to the fast oxidative part of the muscle and this fibre-type-related effect was similar after all three types of exercise.

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