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ORIGINAL PAPER

Changes in human skeletal muscle length during stimulated eccentric muscle actions

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Abstract Following eccentric exercise, increases in muscle length alter the length-tension relation of skeletal muscle. However, its unclear if this change occurs during eccentric exercise. Therefore, 70 eccentric actions of the knee extensors of one leg (with superimposed electrical stimulation) were performed at 100°/s, from full extension to full flexion. Angle-specific eccentric force was recorded throughout. Force decreased at all angles although this was non-uniform. At 70°, force decreased by 25%, whereas at 130°, force decreased by 41%. Initial peak force was recorded at 100° (590 ± 232 N); the exercise bout induced a 21% decrease in peak force and a 10° shift in the position of peak force production to 90°. The rightward shift in the muscle length-tension relation thus occurred during eccentric exercise, where greater force loss at short muscle lengths suggested an eccentric-induced over-stretching of sarcomeres.

Keywords Eccentric exercise · Muscle damage · Length tension · Skeletal muscle

Introduction

Unaccustomed eccentric muscle actions may cause damage to skeletal muscle [1, 2]. Initial myofibril disruption following eccentric muscle actions has been attributed to muscle force [3], high tensile stresses [4], or an imbalance in adjacent sarcomere tension [5]. It has been suggested that adjacent sarcomeres may not have an identical force velocity relationship, and at certain lengthening velocities, a potential imbalance between adjacent sarcomere tension may lead to shear forces in an active fibre [5]. During eccentric muscle actions, shear forces between sarcomeres may provide an explanation for the Z disc disruption observed immediately post exercise [5].

Tension generated by a sarcomere is critically dependent on sarcomere length. It has been suggested that due to random variations in the lengths of series sarcomeres, stretches which occur during eccentric muscle actions take place non-uniformly by rapid and uncontrolled lengthening of sarcomeres beyond myofilament overlap [6]. Thus, sarcomeres with a tension-generating capacity that decreased with increasing length (i.e. those on the descending limb of their length-tension curve) would be prone to instabilities during an eccentric action; this may result in 'over-stretched' sarcomeres. Reduced myofilament overlap and therefore reduced tension in sarcomeres on the descending limb of their length-tension relationship could decrease further by higher tensions produced by series sarcomeres on the plateau or ascending limb of their length-tension relationship. Such a random distribution of sarcomere lengths within a myofibril may partly explain the focal nature of contraction-induced injury [5, 6].

Experimentation on muscle fibre segments [7] has demonstrated that the range of sarcomere lengths increased during a maximum tetanus and that regions which contained the longest sarcomere lengths (those on the descending limb of their length-tension relationship) contained the majority of damaged sarcomeres following a single stretch of 40% strain relative to optimal length.

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A consequence of these observations is that there is a shift in the force-length relation of muscle damaged during eccentric muscle actions [8].

Both transient and chronic changes in muscle length have been reported following eccentric muscle actions of mammalian skeletal muscle. For example, following eccentric muscle actions of the human *triceps surae*, a shift in the torque-angle curve consistent with an increase in muscle length was observed [8]. Similarly, a transient change in isometric contraction force consistent with an increased human *biceps brachii* muscle length has also been reported [9], a finding also reported for the human knee extensors [10]. Others have shown a rightward shift in the isometric length-tension curve of eccentrically exercised skeletal muscle, although the magnitude of the shift was dependent on the amount of both damage and fatigue induced by the exercise [11–13]. It has been suggested [14] that eccentric exercise-induced series sarcomerogenesis protects muscle from further eccentric exercise-induced injury [15], and this has the effect of increasing muscle length.

A consistent feature of these previous studies is a lack of eccentric muscle force-length measures reported during the exercise bout. Also, there are limited reports which make use of electrical stimulation superimposed on a maximum voluntary action—this technique has the benefit of minimising the influence of voluntary under-recruitment of motor units during the eccentric exercise bout. Therefore, the aim of the present study was to measure angle-specific eccentric muscle force during a bout of maximum voluntary eccentric muscle actions with superimposed myostimulation, in humans. It was hypothesized that the change in muscle length observed by previous authors develops during the exercise bout, and this would be evidenced by a rightward shift in the joint angle-muscle force relation toward higher relative forces at longer muscle lengths.

Methods

With appropriate ethics committee approval, eight subjects (four male, four female; age range 21–31 years) performed a single bout of 70 eccentric muscle actions using the knee extensors of one leg.

Eccentric exercise bout

Subjects performed the eccentric exercise bout lying prone on an isokinetic dynamometer (Kin-Com, Chattecx, TN, USA). Fixation straps were placed across the pelvic area and across the upper leg of both exercising and non-exercising limbs. Throughout the bout, subject fixation was regularly checked, and the approximate centre of rotation of the knee of the exercising limb was always kept in line with the dynamometer arm centre of rotation. Each eccentric action was performed at 100°/s, through a range of near full extension (170°) to near full flexion (50°), where full flexion corresponded to a 'long' knee extensor muscle length and full extension corresponded to a 'short' muscle length. The sampling frequency of the dynamometer load cell was 200 Hz. For a contraction range of motion from 170° to 50°, at 100°/s, the dynamometer force was sampled 250 times. Therefore, 250 data points for each 1.2 s contraction allowed the peak force to be identified with reasonable accuracy, with at least two values of force measured for each 1° joint angle.

Immediately before each eccentric muscle action, subjects were required to generate a maximum effort isometric contraction of the knee extensors, and after approximately 2 s, the maximum effort eccentric action was initiated. Approximately 1.5 s into the isometric contraction and throughout the eccentric action, percutaneous electrical myostimulation (PES) at 100 Hz was applied via two copper plate electrodes (dimensions 150 × 100 × 2 mm) contained in moistened felt pouches. Electrodes were superficially fixed over the proximal and distal regions of the active knee extensors, approximately 5 cm proximal to the superior border of the patella with the knee fully extended, with an inter-electrode distance of 2–3 cm. A stimulator (Bioscience Type 200, Sheerness, Kent, UK) applied an unidirectional square wave electrical potential (pulse width 0.5 ms) at a voltage sufficient to elicit at least 30% of the knee extensor maximum isometric contraction force at an angle of 110°. During initial preliminary testing with myostimulation, all subjects included in this study tolerated PES at a high enough voltage (at 100 Hz) to generate at least 30% of their voluntary isometric strength; potential subjects who could not tolerate PES at a sufficient voltage to elicit 30% of the maximum knee extensor muscle force were excluded from the study. The isometric 'pre-load' allowed intramuscular force to increase prior to eccentric activity. The experimenter was provided with a continuous visual feedback of force levels applied to the dynamometer load cell so that forces could be closely monitored throughout the bout. Appropriate verbal encouragement directed at the subject and the use of PES contributed to subject motivation and helped ensure activation of the muscle throughout the duration of the exercise bout. Throughout the exercise bout, angle specific force was recorded by the dynamometer for repetitions 1, 10, 20, 30, 40, 50, 60 and 70. One repetition was defined as the isometric activation and eccentric muscle action (maximum voluntary effort with superimposed myostimulation) throughout the full range of motion. Subjects performed a single bout of 70 repetitions, with an approximate 10 s recovery period between each repetition. During the recovery period, the exercising limb was fully relaxed and returned to the 170° start position by the experimenter.

Prior to exercise (‘pre-’), and again 5 min after exercise (‘post’), maximum isometric contraction force of the exercised knee extensors was measured. Subjects were seated on the isokinetic dynamometer with the knee positioned at an angle of 110° knee flexion. Subjects were instructed to maximally contract the knee extensors isometrically for 3 s. Duplicate measures were recorded.

Statistical analysis

Pre-isometric and post isometric contraction force data were compared using a paired Student’s *t* test. The mean repetition force measurements were analysed using analysis of variance (ANOVA) with one within factor (repetition number). Where significant (i.e. $P < 0.05$), a post-hoc Duncan multiple range test was used to identify differences between individual data points. Angle-specific force data were analysed using a repeated measures analysis of variance (ANOVA) with two within factors (repetition number and knee joint angle). Where a significant difference was found (i.e. $P < 0.05$), a post-hoc Student’s paired *t* test (Bonferroni adjusted alpha, where $P < 0.015$) was used to identify differences between individual data points. Continuous force-joint angle curves were constructed from original data using quadratic fitting techniques, and in all cases, $R^2 > 0.8$. The position at which the force maxima occurred was computed, and data were analysed using ANOVA with one within factor (repetition number).

Results

An example of ‘raw data’ is shown in Fig. 1. In this figure, the eccentric force recorded throughout the range of motion is shown, with two sequential contractions displayed in each panel. The eccentric exercise bout induced a decrease in maximum isometric knee contraction force, measured at 110° knee flexion, from 259 ± 55 N pre-exercise to 131 ± 42 N post exercise ($P > 0.001$). Since the seated position knee angle of 110° corresponded to the prone position knee angle of 110°, initial eccentric force at this angle (559 ± 218 N) was approximately 100% greater than peak isometric force. The final eccentric force measured at 110° (373 ± 142 N) was approximately 180% greater than the post exercise maximum isometric contraction force. Mean eccentric force decreased by 140 N during the eccentric exercise bout ($P > 0.05$; see Table 1). The decrease in mean eccentric force was most pronounced between the initial and tenth repetition, amounting to 64% of the total force loss ($P > 0.01$).

Angle-specific force decreased during the bout ($P < 0.05$). During the initial repetition, a peak force of 590 ± 232 N was recorded at 100°, whereas during the final repetition, a peak force of 466 ± 255 N was recorded at 90°. The decline in force during the bout was not consistent for all knee joint angles, as shown in Fig. 2. A 25% force loss was recorded at a knee joint angle of 70°, whereas a 39% decrease in force was recorded at a knee joint angle of 130° (see Table 2). The relative changes (percent change with respect to initial) at the 130° angle were significantly greater than those at the 70° ($P = 0.013$).

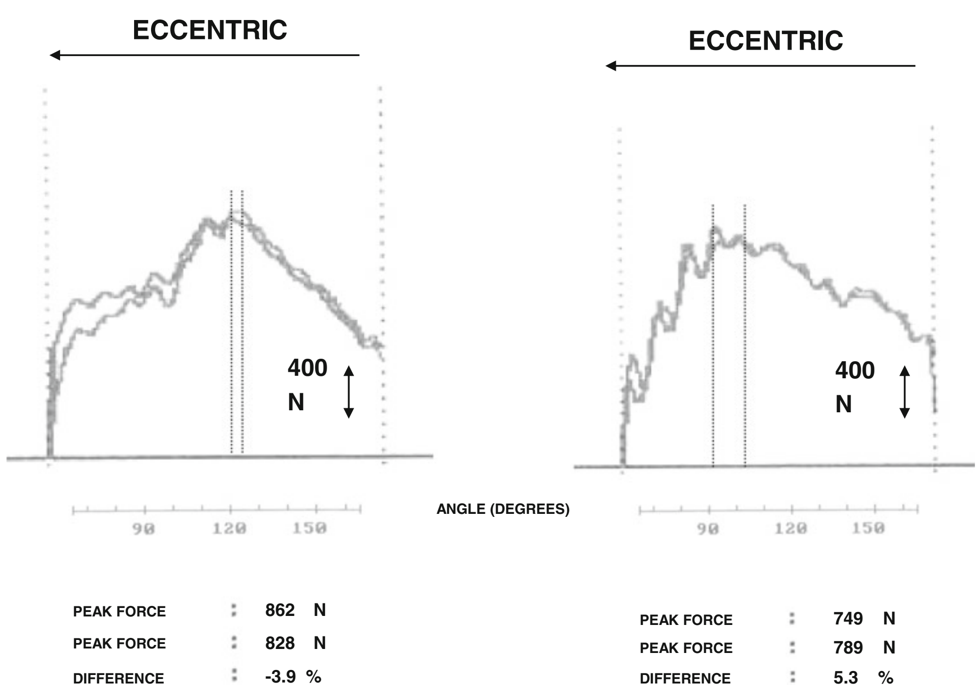

Fig. 1 Representative example of isokinetic dynamometer output for a single subject. Data on the *left panel* show two sequential eccentric repetitions at the start of the bout, and data on the *right panel* show two sequential eccentric repetitions at the end of the bout. Peak forces for each repetition were obtained using the Kin-Com software (data are shown below each force-angle curve, and the difference in peak force between each sequential repetition has been calculated)

Discussion

This investigation measured the knee extensor eccentric force-knee joint angle relation during a single bout of maximum voluntary eccentric muscle actions with superimposed electrical myostimulation to identify any immediate changes in effective muscle length. Both a decrease in knee extensor mean eccentric force and muscle peak eccentric force were recorded during the bout, although these decreases were not consistent throughout the range of movement. Therefore, the present study uniquely offers evidence of a shift in the knee extensor eccentric force-knee joint angle relation toward a greater relative force at longer muscle lengths, and the shift is occurring during the performance of the bout. This study is also unique in that the length-tension curves are derived from the eccentric force measured during the bout and not from measures of isometric forces obtained at different joint angles.

Force generated by lengthening an active muscle is typically higher than the isometric force of the same active muscle, thus the immediate effect of an eccentric contraction following an isometric contraction is an increase in force. However, the decrease in eccentric peak force during the bout of eccentric muscle actions performed by human muscle, as reported in the present study, is consistent with previous work on human skeletal muscle [3, 16, 17]. The decline in force throughout the bout is probably a function of both fatigue and injury [13, 18], although in the present study the method allowed for a recovery period between repetitions.

Heterogeneity in sarcomere length has been reported to be a factor contributing to contraction-induced muscle injury [6], and the activation of skeletal muscle can lead to further disparities in sarcomere lengths [19]. In the present study, the isometric contraction immediately preceding the eccentric muscle action may have induced greater sarcomere length heterogeneity within active fibres. If this increase in the range of sarcomere lengths has occurred, more sarcomeres may be placed on the descending limb of their length-tension curve, thereby introducing instability within the muscle. Using a similar exercise protocol, Saxton and Donnelly [9] proposed that a greater relative decline in isometric force at short muscle lengths (or acute elbow joint angles) was attributable to the cumulative effects of regions of lengthened sarcomeres and/or deformed series elastic elements (e.g. myo-tendinous structures). Extended sarcomeres with 'streaming' Z-discs have been observed in skeletal muscle following eccentric muscle actions [20], although these authors reported that ultra-structural damage actually worsened 24–48 h post exercise. A longer muscle length could simultaneously appear to be in a shortened state due to palliative shortening of connective tissue structures [9], and evidence of eccentric exercise-induced connective tissue disruption has

Table 1 Mean (SD) human knee extensor eccentric muscle force and decrease relative to initial mean force during performance of 70 maximum voluntary eccentric muscle actions with superimposed myostimulation

	Repetition number							
	Initial	10	20	30	40	50	60	Final
Mean force	487	397	395	380	354	359	357	347
SD	117	135	112	151	144	155	135	143
Percent decrease		18.5	18.9	22.0	27.3	26.3	26.7	28.7

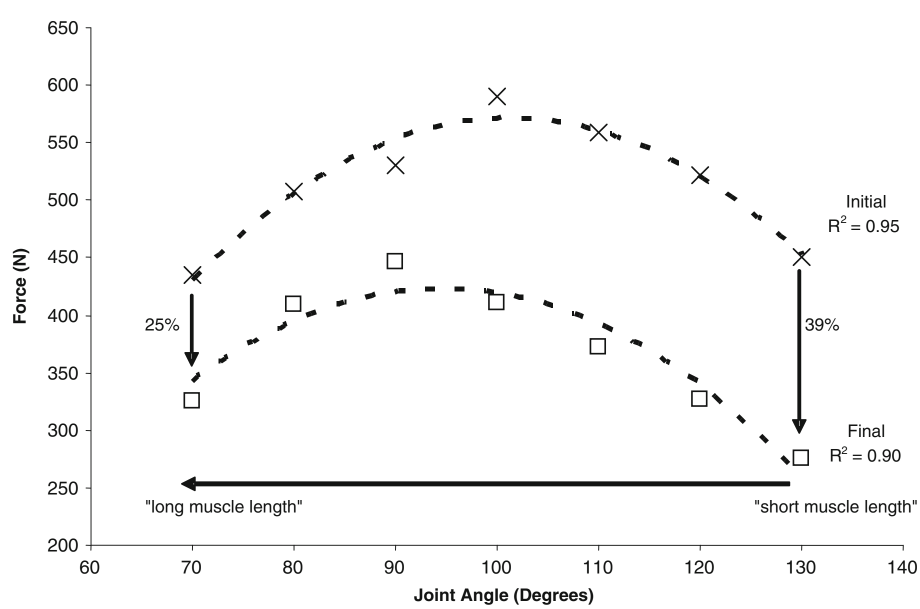

Fig. 2 Mean ($n = 8$) joint angle-specific human knee extensor eccentric muscle force at the start (*Initial*) and the end (*Final*) of a single bout of 70 maximum voluntary eccentric muscle actions with superimposed myostimulation. Standard deviations are omitted for clarity. Quadratic curve fitting with coefficient of determination (R^2) and relative declines in force at the limits of measurement are shown

Table 2 Joint angle-specific measures of human knee extensor eccentric muscle force throughout a single bout of 70 maximum voluntary eccentric muscle actions with superimposed myostimulation

	Joint angle (°)						
	70	80	90	100	110	120	130
Initial contraction	435	507	531	590	559	522	450
10	361	442	485	476	415	377	349
20	396	443	496	503	430	378	329
30	356	462	529	502	429	301	306
40	351	427	487	463	392	329	275
50	340	451	483	448	396	345	284
60	325	392	444	436	405	356	293
Final contraction	325	410	446	411	373	327	276
Percent decrease	25.3	19.1	16.0	30.3	33.3	37.4	38.7

also been reported [21], although the majority of the changes were observed 48 h post exercise.

The present study reports the observation of an approximately 10° shift in the position at which peak eccentric force is generated, indicative of an increased muscle length. This is consistent with the findings of others [8]. Using an isometric contraction derived torque-angle curve for the human *triceps surae*, Whitehead et al. [8] reported a mean shift in the position of peak torque of 4.4° toward higher relative forces at longer muscle lengths. Also, Yeung and Yeung [12] reported a 4° shift in the angle at which *quadriceps* peak isometric torque occurred following eccentric exercise, and they also demonstrated that the shift toward longer muscle lengths could occur with minimal muscle damage. The methodological differences in the present study compared to those of others [8, 12, 13] probably account for the difference in magnitude of the observed shift. It should also be noted that the rightward shift in the length-tension curve of skeletal muscle may occur through concentric training [22].

Peak eccentric muscle force is often cited as being approximately 1.8 times peak isometric force [23], although this has been questioned by previous work [24]. In the present study, pre-isometric and post isometric forces were measured with the subject in a seated position, thus potentially affecting the contributions to force production by all the knee extensors (due in part to the length of bi-articular muscles). Therefore, making a single comparison between force produced by the knee extensors when the hip joint is in a different position is questionable. However, in the present study, we were able to make the comparison at the start of the exercise bout and at the end of the exercise bout, thus potentially identifying possible mechanisms by which knee extensor force was developed in eccentric exercise-induced damaged muscle. The final eccentric force of approximately 180% of the post-eccentric isometric force (measured at the same joint angle but in a seated position) possibly reflected the extent of increased muscle recruitment induced by the PES. Isometric forces were determined by voluntary recruitment alone, whereas eccentric actions were a combination of voluntary and electrically stimulated actions. In the present study, PES was used to contribute to activation of the knee extensors during the eccentric muscle actions while in the prone position, and the recording of initial eccentric forces in excess of twice the measured isometric force (e.g. at 100°) may suggest a decreased recruitment of motor units during voluntary eccentric actions. Since the final peak eccentric force (measured in a prone position) was approximately three times greater than the post exercise isometric force (measured in a seated position), this could also suggest that a decreased ability to recruit motor units also occurred during post exercise isometric contractions, as reported in previous investigations [24]. However, it should be noted that the force of knee extension is affected by the hip joint angle. When in a seated position with the hip flexed at approximately 90°, the *rectus femoris* is at a shorter muscle length than when the hip is extended to an approximate internal joint angle of 180°—such as in the prone position adopted for the exercise bout in this study. Therefore, caution should be exercised when comparing values of knee extensor force when the hip joint angle is not the same.

Using an eccentric exercise protocol which induced a 12° rightward shift in the isometric length-tension curve, low frequency fatigue was more pronounced at short muscle lengths [25]—further evidence that recruitment of motor units is impaired following eccentric muscle actions. The force difference between voluntary activation and the voluntary activation with superimposed myostimulation has the potential to indicate an element of central fatigue, whereby the central nervous system's failure to recruit motor units through the normal processes can be overridden. Human muscle performing isometric actions following a bout of damaging eccentric exercise has been shown to produce higher isometric forces (approximately 10%) when PES is superimposed on voluntary activation [24]. In the present study, the electrical stimulation was superimposed throughout each eccentric repetition after a voluntary isometric pre-load. Thus in the present study, the potential increase in force attributable to PES alone could not be determined—this would require a maximum voluntary eccentric action to be performed at selected intervals throughout the bout, immediately followed by a maximum effort eccentric action with superimposed PES. Applying this method would allow the effect of the PES to be quantified at appropriate points during the bout of exercise.

Mechanical factors such as high muscle forces and strain rates, when generated at the start of a bout of eccentric exercise, may initiate muscle damage [5, 10, 26, 27]. When strain magnitude and strain rate were controlled [10], high forces during the initial stages of an eccentric exercise bout appeared to be a major determinant of subsequent damage. In the present study, the greatest proportional force loss occurred in the first 10 repetitions, thus adding some support to the notion that initial high forces contributed significantly to the muscle damage. However, others [28, 29] reported that it was not high force that appeared to cause muscle damage during eccentric contractions, but the magnitude of strain during active lengthening. In the present study, the large range of motion used, the isometric 'pre-load' and the superimposed myostimulation during the maximum voluntary activation all contributed to both high muscle force and strain, thus making it impossible to speculate on which mechanical factor caused the shift in optimum muscle length.

The findings of the present study suggest that a change in effective muscle length may occur during a bout of eccentric exercise, and this adds some insight into the behaviour of human skeletal muscle during eccentric muscle actions. The disproportionate loss of force at shorter muscle lengths during an eccentric exercise bout and the shift toward optimal force production at longer muscle lengths are indirect evidence of an exercise-induced change in effective muscle length, possibly as a result of the over-stretching of sarcomeres.

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