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ORIGINAL ARTICLE

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Changes in the angle-force curve of human elbow flexors following eccentric and isometric exercise

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Abstract The aim of this study was to explore and compare the magnitude and time-course of the shift in the angle-force curves obtained from maximal voluntary contractions of the elbow flexors, both before and 4 consecutive days after eccentric and isometric exercise. The maximal isometric force of the elbow flexors of fourteen young male volunteers was measured at five different elbow angles between 50° and 160°. Subjects were then divided into two groups: the eccentric group (ECC, $n=7$) and the isometric group (ISO, $n=7$). Subjects in the ECC group performed 50 maximal voluntary eccentric contractions of the elbow flexors on an isokinetic dynamometer ($30^{\circ}\cdot s^{-1}$), while subjects in the ISO group performed 50 maximal voluntary isometric muscle contractions with the elbow flexors at a lengthened position. Following the ECC and ISO exercise protocols, maximal isometric force at the five angles, muscle soreness, and the relaxed (RANG) and flexed (FANG) elbow angles were measured at 24 h intervals for 4 days. All results were presented as the mean and standard error, and a quadratic curve was used to model the maximal isometric force data obtained at the five elbow angles. This approach not only allowed us to mathematically describe the angle-force curves and estimate the peak force and optimum angle for peak force generation, but also enabled us to statistically compare the shift of the angle-force curves between and within groups. A large and persistent shift of the angle-force curve towards longer muscle lengths was observed 1 day after eccentric exercise ($P<0.01$). This resulted in a ~16° shift of the optimum angle for force generation, which remained unchanged for the whole observation period. A smaller but also persistent shift of the angle-force curve was seen after isometric exercise at long muscle length ($P<0.05$; shift in optimum angle ~5°). ECC exercise caused more muscle damage than ISO exercise, as indicated by the greater changes in RANG and ratings of muscle soreness ($P<0.05$). It was suggested that the shift in the angle-force curve was proportional to the degree of muscle damage and may be explained by the presence of overstretched sarcomeres that increased in series compliance of the muscle.

Keywords Muscle damage · Force-length relationship · Contractile function · Long muscle length

Introduction

Vigorous and unaccustomed exercise may lead to muscle soreness due to structural disruption of myofibrils and damage to the excitation–contraction coupling system (Friden and Lieber 1998; Proske and Morgan 2001). Many studies have shown that the highest degree of muscle damage occurs after eccentric exercise, where the muscles are being lengthened while generating active tension (Hunter and Faulkner 1997; Morgan and Allen 1999). Although the extent of the damage can be quantified histologically (Friden and Lieber 1998), this is not always practicable and, therefore, changes in the mechanical properties of the muscle are commonly used to assess damage. One widely used indirect measure of muscle damage is the decrease in maximal voluntary isometric force (MIF) which remains depressed for several days following eccentric exercise (Clarkson et al. 1992; Cleak and Eston 1992).

In most of the studies that have examined the decline in MIF after eccentric exercise, force was measured at a single muscle length (Ingalls et al. 1998) or a single joint angle (Jones et al. 1989; Clarkson et al. 1992; Nosaka and Sakamoto 2001). However, there is evidence from

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both in vitro and in vivo studies that strength loss is greater when force is measured at short versus optimal or long muscle lengths (Wood et al. 1993; Saxton and Donnelly 1996; Byrne et al. 2001; Proske and Morgan 2001). According to the "popping" sarcomere hypothesis proposed by Morgan (1990), lengthening of active muscle does not occur by uniform lengthening of all sarcomeres, but by a non-uniform distribution of sarcomere length change, causing some weak sarcomeres to over-extend ("pop") beyond filament overlap. This would increase the series compliance of the muscle, leading to a shift of the length-tension (or angle-force) curve to the right, i.e. towards longer muscle lengths, following eccentric exercise (Morgan and Allen 1999; Proske and Morgan 2001).

There is a growing body of evidence that the shift in the angle-force curve is a more sensitive and more reliable indicator of muscle damage, as compared to force measurement at a single muscle length or joint angle (Talbot and Morgan 1998; Brockett et al. 2001). This is because the shift in the angle-force curve is not confounded by fatigue and it also avoids the problem of uncertainty over the optimum length for a contraction which occurs when force is measured at the same joint angle before and after damaging exercise (Proske and Morgan 2001). Furthermore, the magnitude of the shift seems to be proportional to the degree of muscle damage (Wood et al. 1993; Jones et al. 1997; Morgan and Allen 1999).

Although the phenomenon of the shift in the angle-force curve towards longer muscle lengths following muscle-damaging exercise is well established in single fibres and motor units from animal muscle (Wood et al. 1993; Lynn and Morgan 1994; Lynn et al. 1998; Talbot and Morgan 1998; Brockett et al. 2002), very few studies have quantified this shift in humans (Jones et al. 1997; Whitehead et al. 1998; Brockett et al. 2001). With the exception of the study by Brockett et al. (2001), who used intense, but not maximal, eccentric contractions of the hamstrings (12 sets of 6 repetitions of "hamstring lowers", i.e. lowering the upper body from a kneeling position), all the other human studies have used much lower exercise intensities to cause muscle damage (i.e. walking backwards down an inclined treadmill for 1–2 h; Jones et al. 1997; Whitehead et al. 1998). Therefore, the first aim of the present study was to provide information about the magnitude and the time-course of the possible shift in the angle-force curve of human elbow flexors when the eccentric contractions are performed with maximal voluntary effort. The second purpose of this study was based on findings of a recent study by our group (Philippou et al. 2003), where maximal isometric exercise of the elbow flexors from a long muscle length caused a large and sustained decrease in maximum isometric force which was more pronounced at the more acute elbow angles, indicating a possible shift of the angle-force curve. Our protocol caused significantly more muscle damage compared with isometric protocols reported in previous studies, as indicated by the much larger drop in force and by the several-fold greater changes in indirect markers of muscle damage, such as creatine kinase and relaxed and flexed elbow angle (e.g. Jones et al. 1989; Nosaka et al. 2002). Therefore, the second aim of the present study was to examine if these pronounced changes in contractile function caused by maximal isometric exercise at long muscle length are accompanied by a shift of the angle-force curve, and to compare the magnitude and duration of this shift with that caused by maximal eccentric exercise.

Methods

Subjects

Fourteen male volunteers [age 26.4 (1.6) years, height 175.5 (1.1) cm, mass 77.1 (2.8) kg] gave their informed consent and participated in this study, which was approved by the Athens University Ethics Committee. The subjects were free of musculoskeletal disorders and had not been involved in any type of resistance training for at least 6 months before the study. Subjects were not allowed to perform any vigorous physical activities during the experimental period.

Preliminary measurements

The subjects were familiarized with the procedures of the isometric force measurements of the elbow flexors during at least two visits to the laboratory. All measurements and testing protocols were performed with the elbow flexors of the non-dominant arm. During the preliminary measurements (day 0), muscle shortening ability and spontaneous muscle shortening were evaluated first by measuring flexed (FANG) and relaxed (RANG) elbow angle, respectively (Clarkson et al. 1992). Anatomical reference points were marked with semi-permanent ink on the acromion, the epicondylus lateralis of the humerus, the processi styloidei of the radius and the point halfway between the processi styloidei of the radius and ulna. A hand-held electronic goniometer (Guymon, Lafayette Instruments, Ind., USA) was fixed on the arm using the anatomical reference points. FANG was defined as the elbow angle when the subject tried to fully flex the forearm, with the humerus held on the side and the palm at the supine position. RANG was defined as the elbow angle when the subject kept his arm relaxed on the side.

Following these measurements, subjects were seated upright on a Kin-Com isokinetic dynamometer (Chattanooga, Tenn., USA) switched to the isometric mode. The trunk was immobilized by straps, the shoulder joint was stabilized at the neutral position (with the humerus parallel to the trunk), the forearm was at the supine position and the wrist was placed against the lever arm. The MIF of the elbow flexors was measured at five different elbow angles, i.e. 50°, 70°, 90°, 140° and 160° in random order (180° represents full elbow extension). The elbow angles used for MIF testing were set using the Kin-Com visual display unit after entering a reference datum elbow angle of 90°. This reference angle was measured with a goniometer. Each subject performed two maximal voluntary isometric contractions of 3 s duration at each angle, and the best trial was taken as the MIF of the angle. A resting period between 45 s and 60 s was allowed between repetitions. Strong verbal encouragement was given to the subjects during all trials.

Eccentric and isometric exercise protocols

Three days after the preliminary measurements, the subjects were randomly divided into two groups [the eccentric exercise group (ECC, $n=7$), and the isometric exercise group (ISO, $n=7$)]. Subjects in the ECC group performed 50 maximal voluntary eccentric contractions of the elbow flexors of the non-dominant arm on the isokinetic dynamometer at an angular velocity of $30°.s^{-1}$ (2 sets of 25 eccentric muscle actions with a 5 min break between sets). This slow angular velocity was chosen in order to maximally load the muscles involved from the start of the range of motion. The body position was standardized as described above (shoulder at neutral position) and the range of elbow joint motion was 120° (from an elbow angle of 50° to 170°). Each muscle action lasted 4 s and a 15-s rest was allowed between repetitions.

Subjects in the ISO group also performed 50 maximal voluntary isometric muscle contractions of the elbow flexors of the non-dominant arm on the isokinetic dynamometer switched to the isometric mode (2 sets of 25 isometric muscle actions with a 5-min break between sets). The body position was standardized as described above but the shoulder was held at 45° extension from the neutral position (i.e. humerus behind the perpendicular level of the torso) and the elbow joint at 140°. This position was chosen to make the elbow flexors contract from a lengthened position during the isometric exercise protocol (Jones et al. 1989). Each maximal isometric contraction was performed for 10 s, with 20 s of intervening rest.

Post-exercise measurements

Following the ECC and ISO exercise protocols subjects visited the laboratory at 24-h intervals for 4 days (days 1–4). Muscle soreness was evaluated by a visual analogue scale that had a continuous line of 100 mm with "no pain" on one end and "extremely sore" on the other. Instructions had been given to the subjects to rate soreness levels during one repetition of flexing and extending the elbow joint throughout the entire range of motion and upon light palpation of the elbow flexors area with the arm at rest (Nosaka and Clarkson 1996). The average of these two values for each subject was used as the criterion score of the day. FANG and RANG were then evaluated. FANG, RANG and ratings of muscle soreness were used as indirect markers of muscle damage (Clarkson et al. 1992). Finally, maximal isometric force of the elbow flexors was measured as described above at the five different elbow angles in random order.

Statistical methods

The angle-MIF profiles of the ECC and ISO groups were analysed separately using two one-way analyses of covariance (ANCOVAs) with repeated measures. Each analysis incorporated 'days' (the baseline day plus the 4 recovery days post-exercise) as a within-subject factor and 'angle' and 'angle^2' as two covariates. The effect of angle was entered as a quadratic polynomial (Force = $a+bA+cA^2$, where a, b and c are the fitted polynomial parameters and A is elbow angle) to accommodate the likelihood that isometric force will peak somewhere between 50° and 160°, according to the angle-force relationship. The parameters 'b' and 'c' of the polynomial correspond to the covariate terms 'angle' and 'angle^2', while 'a' is the constant term of the polynomial. Both covariate terms were also allowed to vary by day (by incorporating a day-by-angle and a day-by-angle^2 interaction term). These interactions were introduced to assess whether these quadratic polynomial curves varied significantly during the recovery days, providing evidence that a shift in the entire angle-force curve had occurred.

In order to confirm that the angle-MIF profiles of the two groups were similar at baseline (day 0), a one way ANCOVA with replications (i.e. at 50°, 70°, 90°, 140° and 160°) was performed. The analysis incorporated a between subjects factor 'group' (ECC versus ISO group) and, as before, adopted 'angle' and 'angle^2' as two covariates. Both covariate terms were also allowed to vary by group (by incorporating a group-by-angle and a group-by-angle^2 interaction term). Similarly, differences between the angle-MIF profiles of the two groups on each recovery day (day 1 to day 4) were examined using this type of analysis.

Changes in RANG, FANG and muscle soreness were assessed using two-way analyses of variance with repeated measures, with the two modes of exercise 'group' being the between-subject factor and the change over time, 'days' being the within-subject factor. Where significant F ratios were found for main effects or interaction ($P<0.05$), the means were compared using Tukey's post hoc tests. Results are presented as the mean and standard error (SE).

Results

The ANCOVA with replications was unable to detect any differences in the angle-MIF quadratic curves between the ISO and ECC group at baseline (day 0), i.e. the interaction terms group-by-angle^2 and group-by-angle were not significant, and no difference was detected between the two groups' fitted constants (all >0.05). Thus the two groups had similar angle-force curves on day 0 (Table 1).

The ANCOVA comparing the daily changes in angle-force curves within the ECC group identified significant day-by-angle and a day-by-angle^2 interaction terms. The fitted quadratic polynomial parameters and the calculated optimum angle and peak force by day for the ECC group are given in Table 1. The quadratic polynomial angle-force curves of all 4 recovery days were significantly different from day 0 ($P < 0.01$ to 0.05).

In contrast, the ANCOVA comparing the daily changes in angle-force curves within the ISO group identified no significant day-by-angle and a day-by-angle^2 interaction terms. However, by observing the similarity between the fitted angle-force curves (i.e. the constant, angle and angle^2 parameters) for days 2, 3 and 4, the data from these three days were combined to take the same 'day' indicator level for a subsequent re-analysis. The resulting ANCOVA now identified a significant day-by-angle interaction term ($P < 0.05$, see Table 1). Although not as dramatic as the ECC group, this finding confirms that the quadratic polynomial curves for day 1 and days 2, 3 and 4 combined (day 234) changed significantly from the baseline measurement (day 0).

The magnitude of changes of the angle-force curves was greater for the ECC group compared to the ISO group on each of the 4 recovery days ($P < 0.01$). This is evident in Fig. 1 and it is also reflected in the calculated parameters of peak isometric force and optimum angle. Figure 2 shows the percent changes in peak isometric force and the shift of the optimum angle towards greater elbow angles that is greater in the ECC group. The interaction terms group-by-angle^2 and group-by-angle were not significantly different between the post-exercise days (days 1–4) in each of the two groups, indicating that the shape of the angle-MIF curve remained unchanged for all recovery days in both groups and thus the shift persisted.

The changes in relaxed elbow angle were significantly larger for the ECC group compared with the ISO group ($P < 0.05$, Fig. 3). On the other hand, changes in flexed elbow angle were not significantly different between the two groups (no main effect for group, Fig. 3), but the group by day interaction marginally failed to be statistically significant ($P = 0.07$). When examining the absolute values compared to the baseline, RANG and FANG in the ISO group returned to their baseline values by day 3, whereas in the ECC group both RANG and FANG remained depressed for the whole of the recovery period ($P < 0.01$). Ratings of muscle soreness peaked on day 2 in both conditions [53 (10) for ECC and 28 (7) for ISO] and were significantly higher for the ECC compared with the ISO group (main effect for group, $P < 0.05$).

Discussion

The aim of the present study was to examine and compare the time-course of the shift in the angle-force curve of the elbow flexors after two types of maximal voluntary contractions: eccentric and isometric from a long muscle length. This was accomplished by employing a specialized curve fitting procedure for the angle-force data of the elbow joint which not only allowed the calculation of peak force and optimum angle for each day, but also enabled the statistical comparison of the angle-force curves between and within groups. To our knowledge, the studies that have examined the shift in optimum angle in animal (Wood et al. 1993; Lynn and Morgan 1994; Lynn et al. 1998; Talbot and Morgan 1998; Brockett et al. 2002) and human muscle (Jones et al. 1997; Whitehead et al. 1998; Brockett et al. 2001) have all fitted Gaussian curves to the force values close to the optimum (above 75%–90% of the peak tension). The approach used in the present study has the advantage of describing not only the shift of the optimum angle but the changes of the entire angle-tension curve

Table 1 The fitted quadratic polynomial parameters, calculated optimum angle and peak force by day in the ECC and ISO groups (constant, angle and angle^2 correspond to the parameters 'a', 'b' and 'c' of the fitted polynomial model: Force $= a + bA + cA^2$, where A refers to elbow angle). r^2×100 (%) Coefficient of determination for the fitted polynomial equations

ECC group						
Day	Constant**	Angle**	Angle^2**	Optimum angle (°)	Peak force (N)	r^2×100
0	−173 (45)	8.2 (0.9)	−0.036 (0.005)	113.8	292.3 (11.2)	81.8%
1	−48 (35)	3.1 (0.8)	−0.012 (0.004)	129.9	153.5 (8.6)	80.3%
2	−83 (30)	4.0 (0.6)	−0.015 (0.003)	131.7	181.5 (7.4)	89.1%
3	−50 (44)	3.7 (0.9)	−0.014 (0.004)	131.3	190.4 (10.7)	83.5%
4	−96 (43)	5.0 (0.9)	−0.020 (0.004)	126.1	218.9 (10.7)	86.7%
ISO group						
Day	Constant**	Angle*	Angle^2	Optimum angle (°)	Peak force (N)	r^2×100
0	−206 (53)	8.6 (1.1)	−0.038 (0.005)	111.7	272.4 (13.0)	74.7%
1	−298 (48)	8.9 (1.0)	−0.038 (0.005)	116.5	222.7 (11.9)	78.7%
234	−281 (24)	9.0 (0.5)	−0.038 (0.002)	116.9	243.7 (10.1)	83.8%

*$P < 0.05$,
**$P < 0.01$ for day-by-parameter interaction

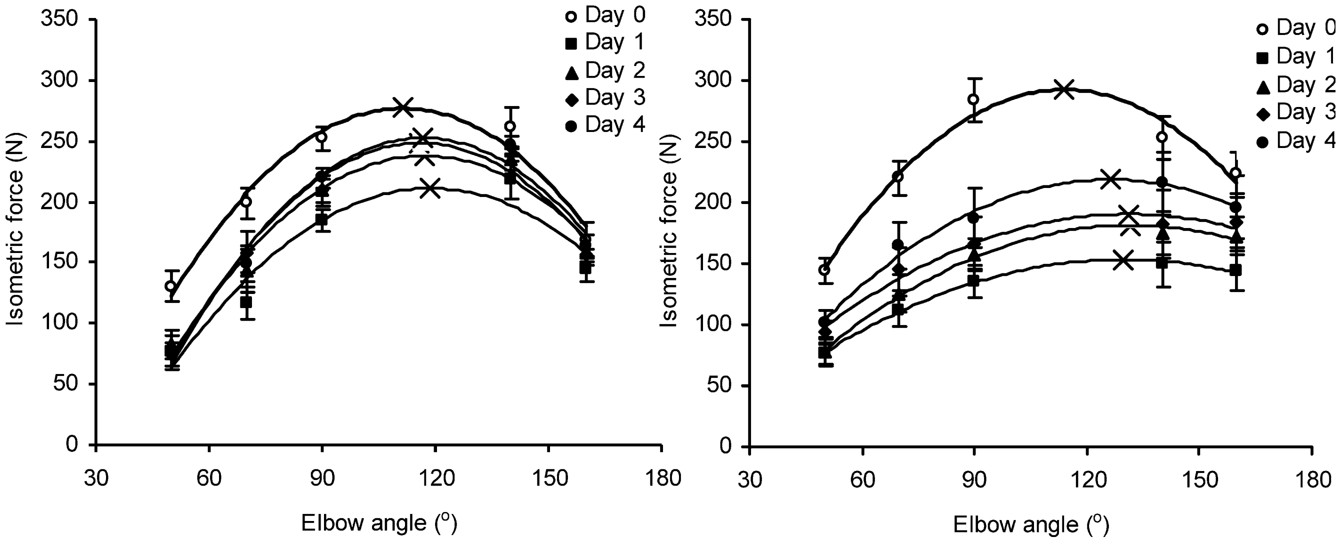

Fig. 1 Angle-force curves reconstructed using the fitted quadratic polynomial parameters for each day for the ISO and ECC groups. *Crosses* indicate the optimum angle for each curve. Standard errors for the reconstructed force data were calculated from the residual mean-square error term from the corresponding ANCOVAs

across the functional range of motion of the joint, by examining the changes in the quadratic polynomial parameters.

One main finding of this study was the large and persistent shift of the angle-force curve towards a longer muscle length after repeated maximal eccentric contractions. The magnitude of the shift in optimum angle observed in the present study (16–18°) is the highest reported in the literature for human muscles in vivo. The other main finding of our study was that a smaller but long lasting shift of the angle-force curve was also observed after isometric exercise with the elbow flexors contracting from a long muscle length. A possible explanation for the shift of the angle-force curve after both eccentric and isometric exercise at long muscle length is the presence of "overstretched" sarcomeres in the fibres of the muscles involved. The "popping" sarcomere hypothesis has been described in detail (Morgan 1990; Proske and Morgan 2001) and has been supported by a number of studies in both single fibres and human muscles in vivo (Jones et al. 1997; Whitehead et al. 1998). This hypothesis is based on the potential instability of half-sarcomere lengths in a muscle contracting on the descending limb of the angle-force relationship, i.e. beyond the optimum length (Morgan and Allen 1999). Earlier work has shown that the more "disadvantaged" sarcomeres in this respect are located in the middle part of the muscle fibres, because sarcomere spacing is greater compared to that near the ends (Lieber and Baskin 1983; Friden and Lieber 1992). During contraction beyond the optimum muscle length, these sarcomeres may be stretched more than their neighbouring sarcomeres and thus become disrupted or "overstretched". This will increase the series compliance of the muscle, leading to a shift of the angle-force curve to the right (Proske and Morgan 2001). Work on animal muscle fibres by Macpherson et al. (1996) has provided electron micrographs which support this hypothesis by

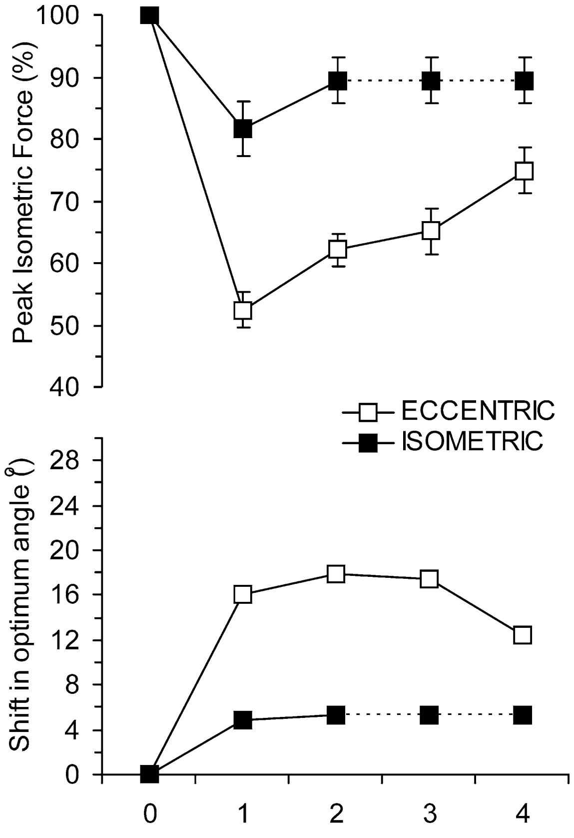

Fig. 2 Percent changes in peak isometric force compared to day 0 (*upper panel*) and shift in optimum elbow angle (*lower panel*), calculated from the fitted quadratic polynomial parameters presented in Table 1. Data for peak force and shift in optimum angle for the combined days 234 in the ISO group are shown as repeated points (*dotted line*). Standard errors for the peak force data were calculated from the residual mean-square error term from the corresponding ANCOVAs

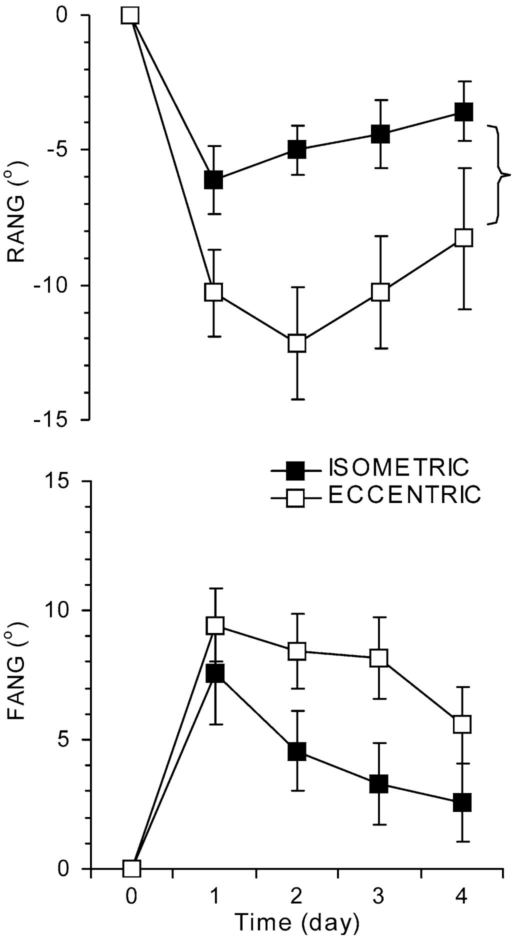

Fig. 3 Changes in relaxed elbow angle (*RANG, upper panel*) and flexed elbow angle (*FANG, lower panel*) compared to baseline day 0 (mean ± SE). $*P < 0.05$ main effect (ISO versus ECC group)

showing that regions of long sarcomere lengths before an active stretch contained the majority of disrupted sarcomeres after the stretch.

An interesting observation when comparing the magnitude of the shift in optimum angle in the present study with the values reported in the other human studies is that it seems to be proportional to the characteristics of the exercise bout which determine muscle damage, namely intensity, amplitude of stretch and initial length of muscle (Talbot and Morgan 1998, Brockett et al. 2001). Thus, exercise protocols that involve low forces and small amplitudes of stretch, such as downhill walking (Jones et al. 1997; Whitehead et al. 1998), result in less damage and a smaller shift of the optimum angle (about 4° that reverses shortly after exercise). On the other hand, exercise protocols that involve higher forces and larger amplitudes of motion result in greater muscle damage and larger shifts in optimum angle, which are proportional to the magnitude of force and stretch amplitude. For example, a 7–8° shift in optimum angle was observed after "hamstring lowers" (Brockett et al. 2001) where the eccentric contractions were intense, but not maximal, and the range of motion was around 30°. In the present study subjects in the ECC group performed 50 maximal eccentric contractions across almost the entire range of motion of the elbow flexors and this resulted in a large shift of the optimum angle (16–18°) that persisted for the whole of the 4-day recovery period. The significant, but not as large, shift in optimum angle in the ISO group in present study (about 5°, see Fig. 2) showed that considerable muscle damage can occur during maximal isometric exercise, provided that the muscle operates on the descending limb of the angle-force curve. In the present study, the significantly higher RANG and ratings of muscle soreness, as well as the tendency for greater changes in FANG (group by day interaction, $P = 0.07$) after eccentric exercise, also provide indirect evidence to support the suggestion that eccentric exercise caused more muscle damage than isometric exercise at long muscle length. However, the changes of these indirect markers as well as the decrease in force after isometric exercise at long muscle length are much greater compared to those reported for "conventional" isometric protocols (McCully and Faulkner 1985; Clarkson et al. 1992; Hesselink et al. 1996; Nosaka et al. 2002). Initial evidence that maximal isometric exercise at long muscle length can cause a significantly greater impairment of contractile function compared with isometric exercise at short muscle length has been published by Jones et al. (1989) and more recently by our group (Philippou et al. 2003). However, the present study is the first to show that in addition to the force drop, a long-lasting shift of the angle-force curve also occurs following this type of exercise. The only studies that have examined the shift of the optimum muscle length after isometric exercise have been performed on isolated animal muscles, and showed small changes that were restored within 4–6 h post-exercise (Wood et al. 1993, Jones et al. 1997). In contrast, the isometric exercise protocol used in the present study with human subjects resulted in a shift of the optimum angle that remained unchanged over the 4-day period of recovery (Fig. 2). This was also accompanied by a long-lasting drop in peak force (Fig. 2) and probably reflects a greater degree of muscle damage compared to the "standard" isometric exercise protocols performed with the muscles contracting at muscle lengths close to the optimum (e.g. Clarkson et al. 1992; Nosaka et al. 2002). An additional factor that may have contributed to the more pronounced functional disturbances of the elbow flexors in the present study was the long duration of each maximal isometric contraction (10 s), which, together with the stretched position of the muscles, may increase the number of damaged or "overstretched" sarcomeres (Hunter and Faulkner 1997). Thus, our results from the comparison between eccentric and isometric exercise provide further support to the suggestion that the magnitude of the shift of the angle-force curve after exercise is proportional to the degree of muscle damage (Talbot and Morgan 1998).

An essential element of our findings was the maintenance of the shift of the angle-force curve and optimum angle throughout the 4-day recovery period after both eccentric and isometric exercise (Figs. 1, 2). The only other study that reported a long-lasting (10-day) shift in optimum angle in humans was performed by Brockett et al. (2001). They suggested that this long-term shift was a training adaptation to eccentric exercise caused by the addition of sarcomeres in series. This suggestion is a corollary of the "overstretched" sarcomeres hypothesis described by Morgan (1990), who argued that the increase in the number of sarcomeres in series would allow muscle fibres to operate at longer lengths in order to avoid the descending limb of the angle-force curve, which is the region of sarcomere length instability and damage. This explanation is supported by evidence from animal studies where 1 week of eccentric training resulted in an addition of sarcomeres (Lynn and Morgan 1994). In a subsequent animal study, the same group showed that after only 5 days of decline running the optimum length of the trained muscles shifted to the right and sarcomere count increased significantly (Lynn et al. 1998). Moreover, after training, the muscles of these rats were more resistant to muscle damage, as indicated by a smaller drop in force and a smaller shift in optimum angle when they performed eccentric exercise. Thus, the fact that the shift of the angle-force curve in our study remained unchanged for 4 days may also indicate a protective adaptation similar to that reported in the above studies. This protective adaptation may have developed as follows: The initial shift of the curve may be due to the presence of "overstretched" sarcomeres. During the recovery period, the shift is expected to partially reverse because some damaged fibres die and therefore no longer contribute to the angle-force curve, while in other less damaged fibres the "overstretched" sarcomeres recover their normal arrangement (Jones et al. 1997, Brockett et al. 2001). However, if the exercise bout is very intense, the possible addition of sarcomeres in series would tend to counteract this reversal of the shift, resulting in the maintenance of the shift over long periods of time. This explanation was put forward by Brockett et al. (2001) and may also explain the prolonged shift observed in the present study.

The shift in angle-force curve could, alternatively, be interpreted as a reduced level of activation caused by excitation-contraction coupling failure (Warren et al. 1993) combined with a change in length-dependent sensitivity of the myofilaments to Ca^{2+} (Endo 1973). According to these hypotheses, a stimulation rate which produced a maximal contraction at all lengths before exercise would produce sub-maximal contractions at short lengths, but more near-maximal contractions at long lengths. However, studies on single fibres and motor units have shown that the length-tension curves determined after muscle damaging exercise cross the pre-contraction curves at long lengths (Morgan et al. 1996; Brockett et al. 2002). This means that higher tension can be generated at long lengths after the muscle damaging exercise, which is incompatible with the theories of reduced activation (Proske and Morgan 2001). In contrast, the hypothesis of "overstretched" sarcomeres has no such constraints because the shift in optimum length depends on the number of disrupted sarcomeres and the increase in series compliance of the muscle (Morgan and Allen 1999; Allen 2001). Interestingly, Fig. 1 shows that the pre- and post-exercise angle-force curves may cross at long muscle lengths (i.e. the right side of each graph) after both isometric and eccentric exercise, lending support to the "overstretched" sarcomeres hypothesis.

In summary, a long-lasting shift in the angle-force curve of the human elbow flexors was observed both after repeated maximal eccentric contractions as well as after repeated maximal isometric exercise with the muscles contracting from a stretched position. The magnitude of the shift in optimum angle after eccentric exercise was the largest reported for humans, while the shift after isometric exercise was smaller but significant. The shift in the angle-force curve seems to be proportional to the degree of muscle damage and may be explained by the presence of overstretched sarcomeres that increased in series compliance of the muscle.

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