

Position sense and reaction angle after eccentric exercise: the repeated bout effect

V. Paschalis · M. G. Nikolaidis · G. Giakas ·
A. Z. Jamurtas · E. O. Owolabi · Y. Koutedakis

Abstract The purpose of the present investigation was to examine the effects of a repeated eccentric exercise on position sense and muscle reaction angle. Fourteen healthy women underwent an isokinetic exercise session on their knee flexors, which was repeated after 4 weeks. Muscle damage indices, position sense and joint reaction angle of the knee were examined before, immediately after, as well as at 1, 2, 3, 4 and 7 days after exercise. The second exercise bout induced significantly lesser effects in all muscle damage indices as well as lesser disturbances in position sense and reaction angle when compared to the first one. The main finding of this study is that position sense and joint reaction angle to release of the lower limbs may adapt in response to a repeated bout of eccentric exercise, leading to less disturbances in position sense and reaction angle after the second bout of exercise.

Keywords Adaptation · Creatine kinase · Delayed-onset muscle soreness · Isometric peak torque

Introduction

Unaccustomed exercise, especially when it involves eccentric actions, leads to muscle damage (Nosaka and Sakamoto 2001). Some of the effects of this uncomfortable situation are loss of muscle force and range of movement (ROM), histologic disturbance of muscle and connective tissue, large increases in concentration of muscle proteins in the blood as well as development of delayed-onset muscle soreness (DOMS) and swelling (Clarkson et al. 1992; Nikolaidis et al. 2007; Nosaka and Newton 2002). These effects—except for loss of muscle force that appears immediately after exercise (Clarkson et al. 1992)—begin approximately 6 h after exercise, peak at 1–3 days and subside 4–7 days after exercise (Armstrong 1990).

Adequate position sense and muscle reaction time are required for capable and safe human movement. It is a common experience that we feel unsteady on our legs and have difficulty in performing common movements after participation in unaccustomed activities such as downhill walking. In a recent investigation from our laboratory, it was found that position sense and muscle reaction angle of the knee extensors are disturbed after eccentric exercise (Paschalis et al. 2007). There are many situations in every day life where individuals have to react to stimuli originating from impulses other than visual or auditory, for example, when a person stumbles. Diminished position sense of the lower limbs after, for instance, downhill walking, may increase the risk for injuries. In our previous investigation, muscle reaction angle was determined through a new test developed in our laboratory using a common isokinetic

V. Paschalis · M. G. Nikolaidis · G. Giakas · A. Z. Jamurtas ·
Y. Koutedakis
Institute of Human Performance and Rehabilitation,
Centre for Research and Technology of Thessaly,
Trikala, Greece

V. Paschalis (✉) · M. G. Nikolaidis · G. Giakas · A. Z. Jamurtas ·
Y. Koutedakis
Department of Physical Education and Sports Sciences,
Thessaly University, Karies, 42 100 Trikala, Greece
e-mail: vpasxal@pe.uth.gr

E. O. Owolabi
Department of Physical Education,
Health and Recreation, University of Botswana,
Gaborone, Botswana

Y. Koutedakis
School of Sport, Performing Arts and Leisure,
Wolverhampton University, Walshall, UK

dynamometer. During this test the subjects had to stop the fall of their limb as soon as it was released from the investigator who holds it passively. In this test, the stimulus originates from the muscle itself, in contrast to other frequently used tests (Ives et al. 1993; Miles et al. 1997), where subjects have to respond to a visual or auditory stimulus.

It is well established that when a bout of eccentric exercise is repeated within several months the muscle damage produced is much less than that produced after the first bout, a phenomenon known as “repeated bout effect” (Nosaka et al. 2001). To our knowledge, no studies have investigated the effect of repeated eccentric exercise on position sense or muscle reaction angle of animals or humans. An important preliminary step in ascertaining the possible involvement of eccentric exercise-induced muscle damage to muscle performance is the determination of the temporal relationship between indices of neuromuscular function and indices of muscle damage. The adaptation to eccentric exercise provides an interesting model to study this relationship because responses to a damaging eccentric exercise (bout 1) can be compared to a relatively non-damaging eccentric exercise (bout 2). Therefore, based on our previous finding of disturbed position sense and reaction angle after a single bout of eccentric exercise, the purpose of the present study was to examine whether a repeated bout of eccentric exercise would disturb less these features. We hypothesized that eccentric exercise would disturb position sense and joint reaction angle to release for days after exercise and that this disturbance would be attenuated after a second exercise bout.

Materials and methods

Subjects

Fourteen healthy women (age 20 ± 1 year, height 165 ± 2 cm, mass 56 ± 2 kg) took part in the study. The subjects had not experienced any eccentric exercise training or other activities with large eccentric component for at least 6 months prior to the study and were not taking anti-inflammatory drugs. They were instructed to abstain from strenuous exercise for 3 days prior to and during data collection. All volunteers were eumenorrhoeic (reporting their menstrual cycle as lasting 24–30 days). The eccentric exercise trials fell within the luteal phase, during which oestrogen concentrations are more stable and higher than during the follicular phase. A written informed consent to participate in the study was provided by all participants after the volunteers were informed of all risks, discomforts and benefits involved in the study. The procedures were in accordance with the Helsinki declaration of 1975, and approval was received from Institutional Review Board.

Measurements

All measurements were performed between 09:00 and 12:00 in the morning. Volunteers performed two isokinetic eccentric exercise bouts, separated by 24–30 days depending on the duration of their menstrual cycle. The exercise protocols were undertaken by all participants in their dominant leg (knee flexors), while the other leg was served as control. Isometric peak torque, range of movement (ROM), DOMS, position sense and joint reaction angle to release were determined in random order before, immediately after as well as at 1, 2, 3, 4, and 7 days after exercise. Serum creatine kinase (CK) activity was determined at the same time-points except for immediately after exercise. These measurements were assessed after both eccentric exercise bouts.

Isokinetic exercise protocol

The isokinetic dynamometer Cybex Norm (Ronkonkoma, NY) was calibrated weekly according to the manufacturer’s instructions. Subjects lay prone on the dynamometer and their position was recorded for the follow-up measurements. Their lateral femoral condyle was aligned to the axis of rotation of the dynamometer while the ankle cuff was attached proximally to the lateral malleolus. Each subject’s functional range of motion was set electronically between 0° (full knee extension) and 90° of knee flexion to prevent hyperextension and hyperflexion. Gravitational corrections were made to account for the effect of limb weight on torque measurements. Feedback of the intensity and duration of eccentric exercise was provided automatically by the dynamometer.

In each of the two eccentric exercise sessions, volunteers had to accomplish 5 sets of 15 eccentric maximal voluntary contractions of knee flexors at an angular velocity of 60° s^{-1} in the prone position as previously described (Prou et al. 1999). A 2-min rest interval was incorporated between sets. Prior to each exercise session, subjects performed a warm-up consisting of 8-min cycling on a Monark cycle ergometer (Vansbro, Sweden) at 70 rpm and 50 W followed by 5-min ordinary stretching exercises of the major muscle groups of the lower limbs. The stretching exercises were performed at low intensity with specific instructions and supervision by the investigator. Specifically, the subjects performed stretching exercises for the quadriceps, hamstrings and triceps surae. For each muscle group, four stretches were performed without pain, lasting 7–10 s each.

Muscle damage indices

The isokinetic dynamometer was also used for the measurement of isometric knee flexors peak torque at 90° knee

flexion (Paddon-Jones and Abernethy 2001; Paschalis et al. 2005a; Paschalis et al. 2005b). The best of three maximal voluntary contractions were recorded. There was 1-min rest between isometric efforts. Prior to the maximal voluntary contractions all subjects familiarized with the experimental procedure.

The assessment of ROM was performed manually on the isokinetic dynamometer. The investigator moved the calf at a very low angular velocity from 130° knee flexion to the position where the subject felt discomfort. The angle was recorded to indicate the end of the pain-free ROM. All participants were pain-free at 130° flexion.

Volunteers subjectively assessed DOMS by palpating their belly muscle and the distal region of the biceps femoris in a seated position with the muscles relaxed. The assessment of soreness of the exercised lower limb was also performed during walking. Perceived soreness for both conditions was rated on a scale ranging from 1 (normal) to 10 (very sore) as previously suggested (Jamurtas et al. 2000).

Blood samples were drawn from an antecubital vein into plain evacuated test tubes. The blood was allowed to clot at room temperature for 30 min and centrifuged at $1,500\times g$ for 10 min. The serum layer was removed and frozen at -30°C until analyzed. Serum CK activity was determined spectrophotometrically (Milton Roy, Spectronic 401, Rochester, NY) in duplicates using commercially available kit (Spinreact, Sant Esteve, Spain). The reference range of serum CK activity for women according to this method is up to 170 U L^{-1} at 37°C .

Position sense at the knee

Subjects lay prone on the isokinetic dynamometer and all assessments were applied to both lower limbs in random order. The angles were automatically recorded by the dynamometer. The investigator positioned the lower limb in a random order, at 30° , 45° and 60° knee flexion and maintained it for 10 s (Fig. 1). The movement for the placement

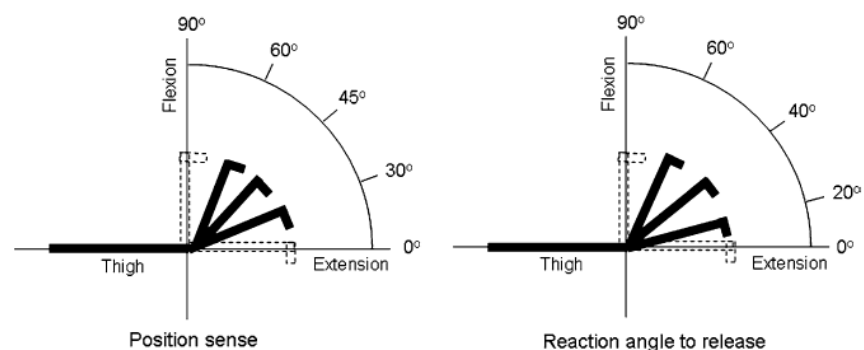
of the limb was done manually but the position was fixed or controlled or blocked by the dynamometer. This means that the appropriate angle was chosen by the dynamometer in order to be sure that the limb was positioned in exactly the same angle within and between subjects and so it is difficult to dissociate changes in limb position from the limb movement. The subjects were asked to recall the reference position after the limb had been placed in that position. The subjects actively moved concentrically their limb to the target angle and when they were satisfied with the angle they had selected they held it for about 2 s. The direction and degrees deviating from the reference angle were recorded. It should be noted that some of the errors in position sense would be due to differences in subjects' ability to recall, although the intraclass correlation coefficient for this test is 0.96 (Paschalis et al. 2007). Four trials were recorded at each angle and the mean value of them was used for the statistical analysis. The leg moved from 0° to 90° to the target position and then back to 0° prior to each of the four efforts.

Two types of angles were computed in order to assess subject's ability to match the reference angle: the "absolute angle" and the "signed angle". The absolute or unsigned angle was calculated as the difference (degrees in absolute values) between the angle chosen by the subject and the reference angle and represents an index of the magnitude of matching error. The signed angle was calculated as the difference (degrees in signed values) between the chosen position and the reference angle and indicates whether the subjects placed the knee joint in a flexed or an extended position relative to the reference angle (Willems et al. 2002). The test-retest reliability of the position sense in absolute values was 0.92 (see "Statistical analysis" for how it was calculated).

Knee joint reaction angle to release

The isokinetic dynamometer was also used for the evaluation of reaction angle of the lower limb. The subjects lay

Fig. 1 Position of the leg in the dynamometer and the angular range over which position sense (*left panel*) and knee joint reaction angle to release (*right panel*) were performed



prone (180° hip angle) and all assessments were performed on both the lower limbs with the non-dominant limb serving as the control limb. The angles were automatically recorded by the dynamometer. The lower limb was passively positioned by the investigator at one of the three different angles (20°, 40°, and 60°) in random order (Fig. 1). When the knee flexors relaxed at the predetermined angle the investigator, without warning, let the limb to fall. Lack of an EMG recorder in our laboratory enforced us to control the relaxation of knee flexors through palpation of the muscle belly by the investigator. The instruction given to the subjects was to stop the fall of the limb as soon as it was perceived as being released. The angle through which the leg moved before the subjects managed to stop the motion was recorded and considered the knee joint reaction angle to release. Four efforts were performed at each angle and the mean of the two closest to the reference angle were recorded and used for the statistical analysis. The test-retest reliability of the knee joint reaction angle to release was 0.94 (see “Statistical analysis” for how it was calculated).

Statistical analysis

The distribution of all dependent variables was examined by Shapiro–Wilk test and was found not to differ significantly from normal, except for serum CK values. Three-way ANOVA (bout \times limb \times time) with repeated measurements on time were used to analyse muscle damage indices. Four-way ANOVA (bout \times limb \times angle \times time) with repeated measurements on time were used to analyse position sense and reaction angle. Serum CK activity was analysed non-parametrically by Friedman’s test. If a significant interaction was obtained, then pairwise comparisons were performed through contrast analysis. The effect size was calculated as the difference between bout 1 and bout 2 values at the point where the maximum exercise effect appeared divided by the pooled standard deviation of bout 1 and bout 2 at the same time-point. According to a modified Cohen scale (<http://newstats.org>), effect sizes of 0.2, 0.6, 1.2, 2.0, and 4.0 were considered small, moderate, large, very large, and nearly perfect, respectively. For comparison, the values of the original Cohen scale are 0.2 for small, 0.5 for moderate, and 0.8 for large effects. The intra-class correlation coefficient was calculated through a random-effect two-way analysis of variance (ANOVA) model from the values obtained from the five consecutive days in four subjects. Data are presented as mean \pm SEM. The test-retest reliability of position sense and joint reaction angle to release was determined by performing the intraclass reliability test. The level of significance was set at $\alpha = 0.05$. The SPSS version 13.0 was used for all analyses (SPSS Inc., Chicago, Illinois).

Results

Muscle damage indices

The main effects of bout ($P < 0.001$), limb ($P < 0.001$) and time ($P = 0.018$), the two-way interactions bout \times limb ($P = 0.022$), bout \times time ($P = 0.011$), limb \times time ($P = 0.012$), as well as the three-way interaction bout \times limb \times time ($P = 0.033$) were significant. Repeated bout effect after eccentric exercise was evident from the changes in muscle damage indices (Fig. 2). Isometric peak torque (a), ROM (b), DOMS either with palpation (c) or movement (d), and serum CK (e) activity were affected significantly after both eccentric exercise sessions. However, judging from the less significant differences after the second bout of exercise compared to the first one and the several significant differences at each time-point between the two bouts, the second bout produced lower and smaller alterations in all muscle damage indices compared to the initial one.

Position sense at the knee in absolute values

The main effects of bout ($P = 0.014$), limb ($P < 0.001$) and time ($P = 0.023$), the two-way interactions bout \times limb ($P = 0.009$), bout \times time ($P = 0.032$), limb \times time ($P = 0.01$), as well as the three-way interaction bout \times limb \times time ($P = 0.038$) were significant. There was no main effect or interaction with any independent variable of the knee angle. Deterioration of position sense, expressed as the absolute deviation from the reference position, was observed after both eccentric exercise sessions of the knee joint angle at 30°, 45° and 60° (Fig. 3). Disturbances of position sense after the second exercise session were smaller compared to the first session (judging from the less significant differences after the second bout of exercise compared to the first one and the several significant differences at each time-point between the two bouts). The effect sizes of position sense in absolute values were 2.00, 1.43 and 2.71 for 30°, 45° and 60°, respectively. Position sense in absolute values was restored after the initial bout prior to the repeated bout since there were no significant differences between pre exercise and at 7 days post exercise.

Position sense at the knee in signed values

The main effects of bout ($P = 0.012$), limb ($P < 0.001$) and time ($P = 0.009$), the two-way interactions bout \times limb ($P = 0.021$), bout \times time ($P = 0.038$), limb \times time ($P = 0.018$), as well as the three-way interaction bout \times limb \times time ($P = 0.032$) were significant. There was no main effect or interaction with any independent variable of the knee angle. Eccentric exercise also disturbed position sense at the knee joint angle at 30°, 45° and 60° when this was

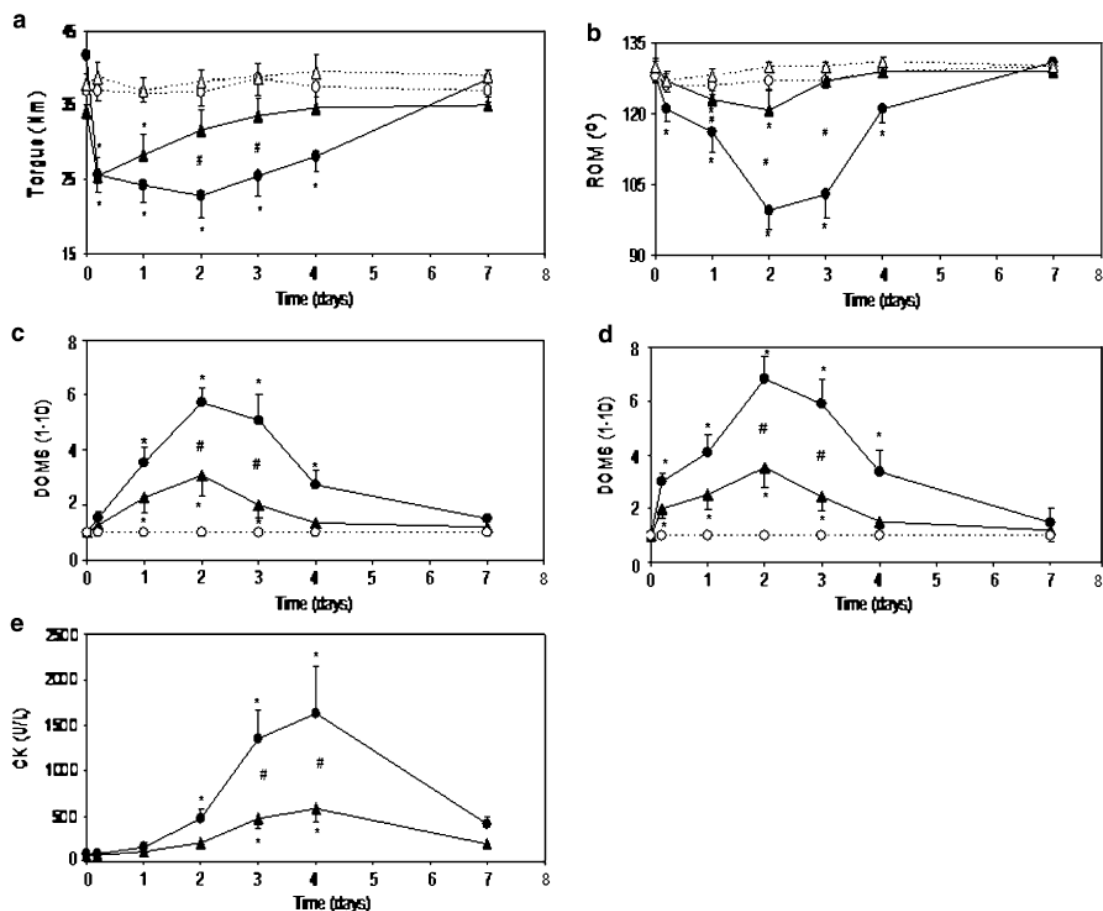


Fig. 2 Isometric peak torque (a), ROM (b), DOMS during palpation (c), DOMS during movement (d) in the test limb and serum CK activity (e) after the first (solid curve and filled circle) and after the second bout (solid curve and filled triangle) of eccentric exercise, as well as in the control limb after the first (dashed curve and open circle) and after

the second bout (dashed curve and open triangle) of eccentric exercise (mean \pm SEM). * Significantly different from the pre-exercise value ($P < 0.05$). # Significantly different between the two eccentric exercise sessions at the same time point ($P < 0.05$). CK creatine kinase, DOMS delayed onset muscle soreness, ROM range of movement

expressed in signed degree values (Fig. 4). In all trials subjects placed their limbs in a more extended position (i.e. produced negative degree values). The disturbance of position sense in the second exercise session was significantly smaller compared to the initial one (judging from the less significant differences after the second bout of exercise compared to the first one and the several significant differences at each time-point between the two bouts), where the subjects placed their limbs at a less extended position. The effect sizes of position sense in signed values were -0.61 , -0.67 and -0.57 for 30° , 45° and 60° , respectively. Position sense in signed values was restored after the initial bout prior to the repeated bout since there were no significant differences between pre exercise and at 7 days post exercise.

Knee joint reaction angle to release

The main effects of bout ($P < 0.001$), limb ($P < 0.001$) and time ($P = 0.011$), the two-way interactions bout \times limb ($P = 0.012$), bout \times time ($P = 0.008$), limb \times time ($P = 0.018$), as well as the three-way interaction bout \times limb \times time ($P = 0.015$) were significant. There was no main effect or interaction with any independent variable of the knee angle. Knee joint reaction angle to release from 20° , 40° , and 60° increased after both eccentric exercise sessions. The disturbances in knee joint reaction angle were significantly lower compared to the first one, judging from the less significant differences after the second bout of exercise compared to the first one and the several significant differences at each time-point between the two bouts (Fig. 5). The effect sizes

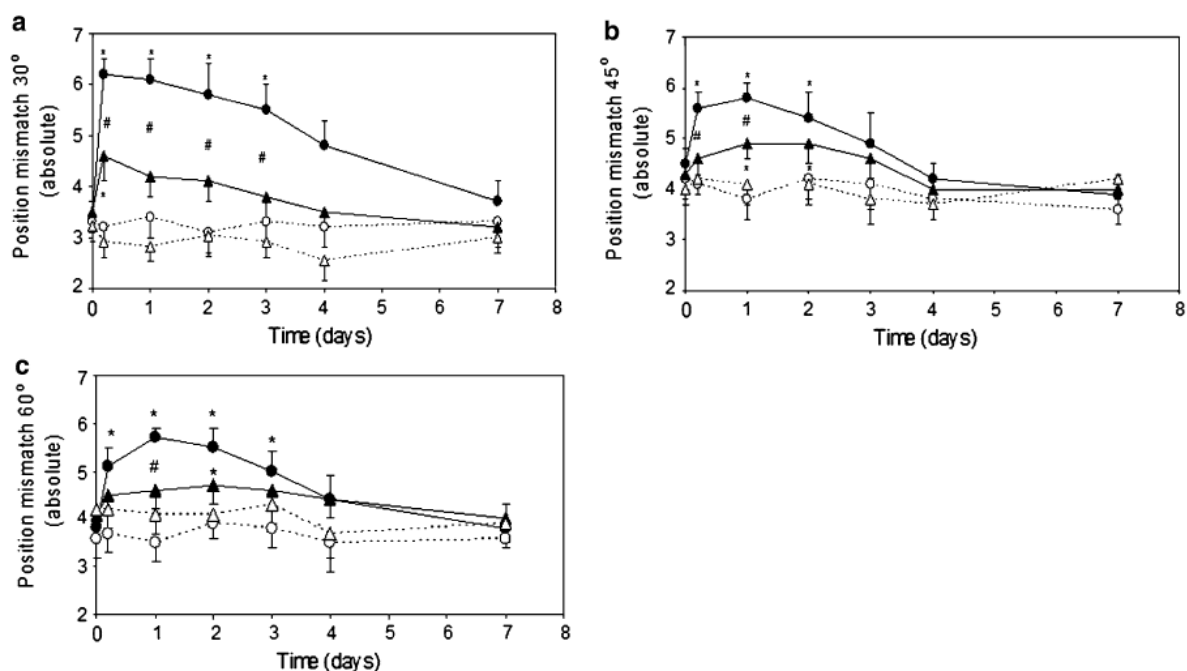


Fig. 3 Position error of the knee joint at 30° (a), 45° (b) and 60° (c) knee flexion in absolute values in the test limb after the first (solid curve and filled circle) and after the second bout (solid curve and filled triangle) of eccentric exercise, as well as in the control limb after the first (dashed curve and open circle) as well as after the second bout

(dashed curve and open triangle) of eccentric exercise (mean \pm SEM). * Significantly different from the pre-exercise value ($P < 0.05$). # Significantly different between the two eccentric exercise sessions at the same time point ($P < 0.05$)

of knee joint reaction angle to release were 0.44, 0.55 and 0.65 for 20°, 40° and 60°, respectively. Knee joint reaction angle was restored after the initial bout prior to the repeated bout since there were no significant differences between pre exercise and at 7 days post exercise.

Discussion

To our knowledge, this is the first report on the repeated bout effect of eccentric exercise on position sense and reaction angle to release of the lower limbs. Additionally, in the present investigation, we employed three angles to measure position sense instead of one angle measured in our previous investigation (Paschalis et al. 2007). This was done in order to explore the possible effect of muscle length on position sense, since muscle length has been found to affect several properties of muscle function [e.g. the shift in length-torque relationship after exercise (Chen et al. 2007)].

Muscle function and damage during recovery from eccentric exercise

Even though all muscle damage indices were affected significantly after both eccentric exercise sessions, the changes

after bout 2 were smaller compared to those produced after bout 1. Numerous studies have demonstrated the repeated bout effect (Chen 2003; Lynn and Morgan 1994; Lynn et al. 1998; Newham et al. 1987; Nosaka et al. 2001); however, there is little consensus as to the actual mechanism that induces it (McHugh et al. 1999). In general, the phenomenon has been attributed to neural, connective tissue or cellular adaptations, while other possible mechanisms such as alterations in excitation-contraction coupling or in the inflammatory response have been proposed (McHugh et al. 1999). The "neural theory" suggests that after a repeated bout of eccentric exercise there is an increase in motor unit activation and/or a shift from fast-twitch to slow-twitch fibre (which are more resistant to damage) activation, which distributes the contractile stress over a larger number of active fibres. The "connective tissue theory" suggests that remodelling of the damaged intermediate filaments and/or increased intramuscular connective tissue is responsible for the repeated bout effect. The "cellular theory" suggests that an increase in the number of sarcomeres connected in series, following an initial bout, reduces sarcomere strain during a repeated bout and limits the subsequent damage. It is unlikely that one "theory" alone can explain the repeated bout effect found; instead, it is possible that the repeated bout effects occur through interaction of

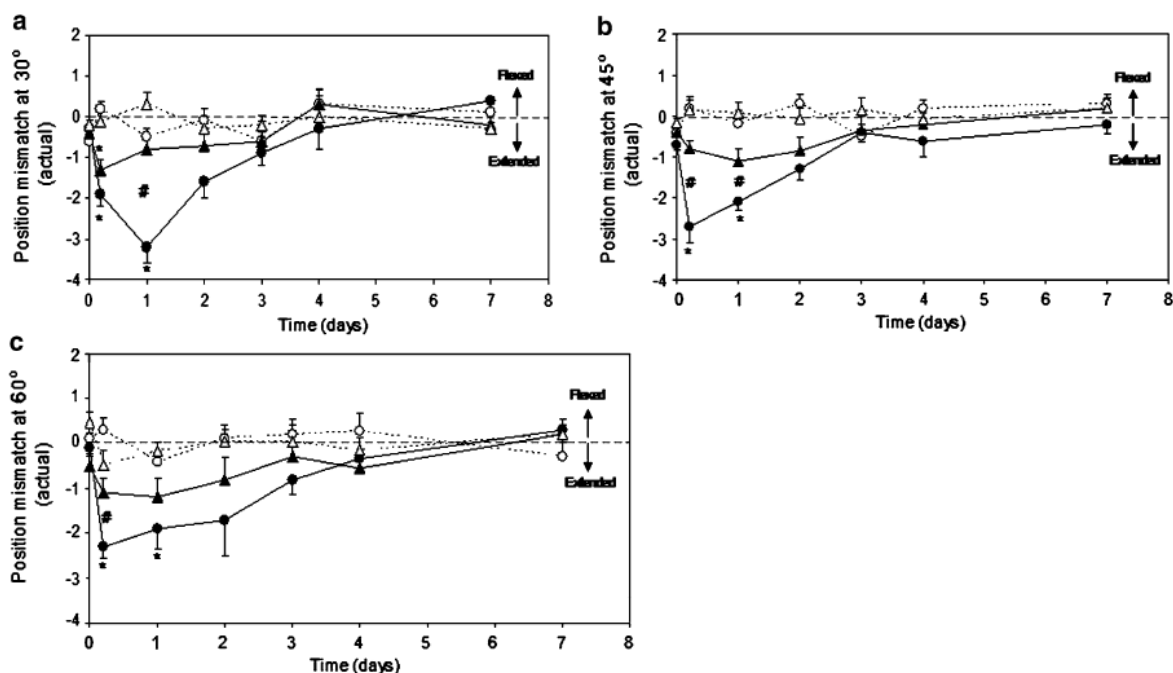


Fig. 4 Position error of the knee joint at 30° (a), 45° (b), 60° (c) knee flexion in signed values in the test limb after the first (solid curve and filled circle) and after the second bout (solid curve and filled triangle) of eccentric exercise as well as in the control limb after the first (dashed curve and open circle) as well as after the second bout (dashed curve

and open triangle) of eccentric exercise (mean \pm SEM). * Significantly different from the pre-exercise value ($P < 0.05$). # Significantly different between the two eccentric exercise sessions at the same time point ($P < 0.05$)

various neural, connective tissue and cellular factors (McHugh et al. 1999).

Position sense at the knee

We found that after the first eccentric exercise bout, subjects thought during active positioning that their knee flexors were shorter than they actually were and so they adopted a position representing a longer muscle length, placing the lower limb in a more extended position. Several relevant studies reported disturbances in position sense at the knee joint after an acute bout of non-eccentric exercise (Hiemstra et al. 2001; Lattanzio et al. 1997; Wojtys et al. 1996). In agreement to our findings, several studies have reported that position sense of the upper limb was impaired after eccentric exercise of elbow flexors, where subjects were placing the exercised arm in a more extended position (Brockett et al. 1997; Nardone and Schieppati 1988; Saxton et al. 1995; Walsh et al. 2004; Weerakkody et al. 2003). In contrast, in our previous investigation (Paschalis et al. 2007) in a different muscle group (knee extensors), even though we found that subjects placed their knee joint in a more extended position after eccentric exercise, the adopted position represented a shorter muscle length. It is possible that the different

anatomical characteristics and function of knee flexors and knee extensors explain this discrepancy.

Overall, position sense data after the first exercise bout indicate that the subjects placed their limb in a more extended position relative to the reference angle. Since it is generally agreed that signals from muscle spindles contribute to the sense of position and movement of the limbs (Proske and Allen 2005), it has been proposed that the rise in passive tension after eccentric exercise can mechanically unload muscle spindles (Brockett et al. 1997). Unloading of muscle spindles can lower their passive discharge rates leading subjects to lengthen their muscles more by extending the knee joint (Proske and Morgan 2001). It is worth noting that different mechanisms (i.e. different recruitment pattern of muscle spindles depending on active state of the muscle) might exist during passive positioning of the limb by the investigator and active positioning by the subject. Therefore, it is difficult to exactly predict how muscle spindles contributed to the more extended position of the knee presented in this study. Moreover, Gregory et al. (2004) found no significant changes in spindle firing rates in eccentrically contracted muscles of anesthetized cats. Besides, tendon organs also appear not to be affected by eccentric muscle damage (Gregory et al. 2004). Except for the proprioceptors (such as muscle spindles and tendon

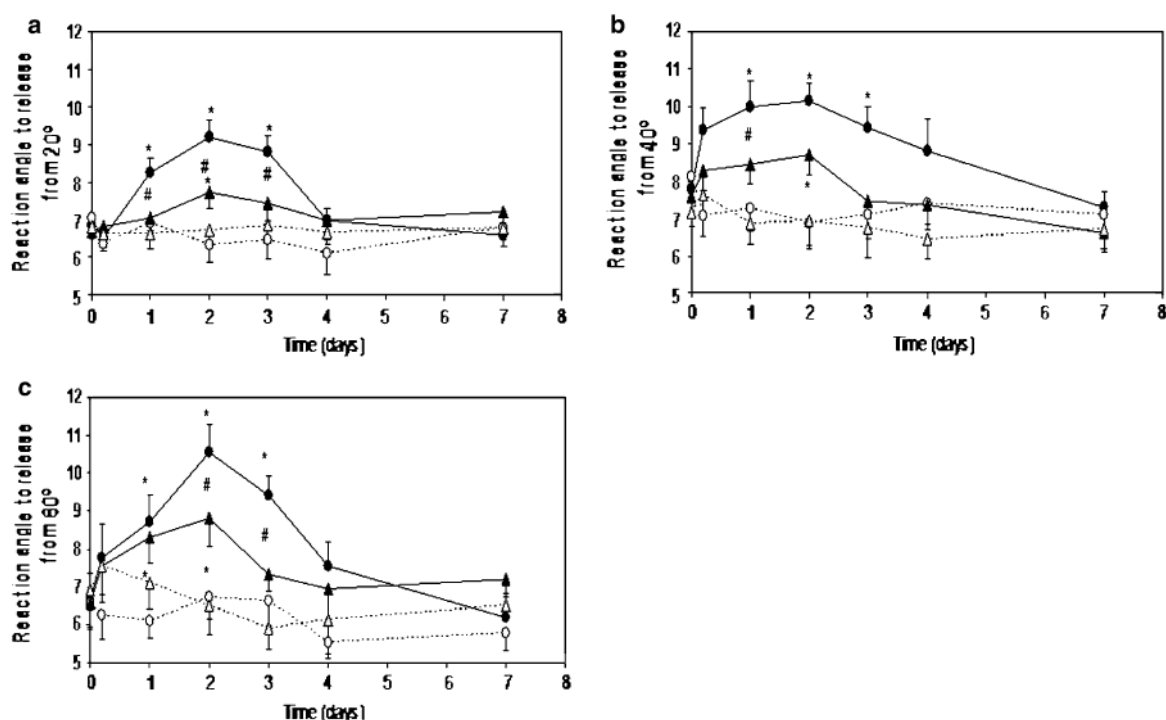


Fig. 5 Knee joint reaction angle to release from 20° (a), 40° (b) and 60° (c) knee flexion in the test limb after the first (solid curve and filled circle) and after the second bout (solid curve and filled triangle) of eccentric exercise as well as in the control limb after the first (dashed curve and open circle) as well as after the second bout (dashed curve

and open triangle) of eccentric exercise (mean \pm SEM). * Significantly different from the pre-exercise value ($P < 0.05$). # Significantly different between the two eccentric exercise sessions at the same time point ($P < 0.05$)

organs) detecting stimuli generated by the muscle itself there are also exteroceptors, which detect external stimuli (such as cutaneous receptors). Such cutaneous receptors are the Ruffini endings, which respond to skin stretch and have been implicated in position and movement sense (Collins et al. 2005). Given the fact that eccentric exercise increases muscle circumference (Nosaka et al. 2001) this may increase the pressure sensed by these mechanoreceptors and may lead the subjects to adopt a more extended position, which produces less pressure on these receptors.

The large attenuation in change in position sense after bout 2 can be largely attributed to decreased muscle damage after bout 2 compared to bout 1. How does the decreased muscle damage lead to decreased change position sense? Less muscle damage after bout 2 could lead to reduced rise in passive tension after eccentric exercise and, as a result, less mechanical unloading of muscle spindles (Brockett et al. 1997), leading subjects to lengthen their muscles less after bout 2 than bout 1, and finally achieving more accurate matching to the reference angle. Additionally, as suggested by Gregory et al. (2004) and Walsh et al. (2004), less position errors after bout 2 may appear due to

the less effort required to maintain the limb position against the gravity compared to bout 1.

It is worth mentioning that an inherent problem in all tests evaluating limb position is that it is impossible to dissociate changes in limb position from limb movement.

This limitation probably arises because most of the relevant tests move the experimental limb from a resting position to a target position and back to the resting position, that is, employing a specific course that may be memorized by the subject. In addition, determination of an index of consistency of the error in position sense (e.g. variable error) could have given insights into the consistency of the errors. In that case, however, much more trials per subject would be required for reliable calculation of variable error.

Knee joint reaction angle to release

We found increased reaction angle to release after eccentric exercise at all angles assessed. This finding is in line with the results of our previous investigation where we found that eccentrically exercised knee extensors increased the reaction angle to release of knee joint (Paschalis et al.

2007). A relevant study performed in upper limbs has also reported increased reaction angle to a light stimulus after eccentric exercise of the elbow flexors (Miles et al. 1997). Adequate position sense and muscle reaction angle are required for capable and safe human movement.

It has been reported that after a first bout of eccentric exercise the number of functional sarcomeres and whole myofibrils is decreased (Morgan et al. 2004). As a result, the rise rate of force during a voluntary contraction is decreased. Therefore, the eccentrically exercised (i.e. damaged) muscle cannot equal the tension developed by the undamaged muscle in response to lower limb release. In addition, the total series compliance of muscle fibers are expected to be increased due to the presence of disrupted sarcomeres (Morgan et al. 2004), leading to delayed tension rise in response to stretch (Whitehead et al. 2001). If knee flexor compliance had increased after the eccentric exercise, knee flexors may need to be stretched further before spindles signalled the fall of the lower limb. However, it is not clear why increased compliance due to the disrupted sarcomeres should alter the response of muscle spindles to stretch, since the spindles are parallel to the extrafusal muscle fibres and so changes in compliance of these fibres may not necessarily affect the spindle response.

The fact that the subjects erred by placing their limbs in a more extended position (i.e. increased muscle length) seems interesting because it is consistent with the acute rightward shift in the length-tension relationship associated with muscle damage (Chen et al. 2007; Morgan and Proske 2004). The cellular mechanism for this effect may be the disrupted sarcomeres, lying in series with functional sarcomeres, that lead to the increase of the muscle's series compliance, resulting in a shift of optimum length for peak active tension at longer muscle length (Wood et al. 1993). The fact that the proprioceptive feedback error and the length-tension shift moved similarly after exercise may indicate a relationship between muscle feedback mechanisms and muscle length (i.e. increases in muscle length increases spindle firing). However, Walsh et al. (2004) found that concentric exercise, which does not cause a rightward shift in force-length relationship, induced position errors in the same direction to the present study, indicating that another mechanism may also exist.

Conclusion

To our knowledge, this is the first report on the effects of eccentric exercise of knee flexors on reaction angle of the lower limbs. Additionally, this is probably the first report on the effects of repeated eccentric exercise on position sense and muscle reaction angle either in upper or lower limbs. The main finding of this study is that position sense

and joint reaction angle to release of the lower limbs may adapt in response to a repeated bout of eccentric exercise, leading to lesser disturbances in these motor features after the second bout of exercise. These adaptations may have occurred, at least in part, due to an attenuation of the eccentric exercise-induced muscle damage after the second bout.

References

- Armstrong RB (1990) Initial events in exercise-induced muscular injury. *Med Sci Sports Exerc* 22:429–435
- Brockett C, Warren N, Gregory JE, Morgan DL, Proske U (1997) A comparison of the effects of concentric versus eccentric exercise on force and position sense at the human elbow joint. *Brain Res* 771:251–258
- Chen TC (2003) Effects of a second bout of maximal eccentric exercise on muscle damage and electromyographic activity. *Eur J Appl Physiol* 89:115–121
- Chen TC, Nosaka K, Sacco P (2007) Intensity of eccentric exercise, shift of optimum angle, and the magnitude of repeated-bout effect. *J Appl Physiol* 102:992–999
- Clarkson PM, Nosaka K, Braun B (1992) Muscle function after exercise-induced muscle damage and rapid adaptation. *Med Sci Sports Exerc* 24:512–520
- Collins DF, Refshauge KM, Todd G, Gandevia SC (2005) Cutaneous receptors contribute to kinesthesia at the index finger, elbow, and knee. *J Neurophysiol* 94:1699–1706
- Gregory JE, Morgan DL, Proske U (2004) Responses of muscle spindles following a series of eccentric contractions. *Exp Brain Res* 157:234–240
- Hiemstra LA, Lo IK, Fowler PJ (2001) Effect of fatigue on knee proprioception: implications for dynamic stabilization. *J Orthop Sports Phys Ther* 31:598–605
- Ives JC, Kroll WP, Bultman LL (1993) Rapid movement kinematic and electromyographic control characteristics in males and females. *Res Q Exerc Sport* 64:274–283
- Jamurtas AZ, Fatouros IG, Buckenmeyer P, Kokkinidis E, Taxildaris K, Kambas A, Kyriazis G (2000) Effects of plyometric exercise on muscle damage and plasma creatine kinase levels and its comparison with eccentric and concentric exercise. *J Strength Cond Res* 14:68–74
- Lattanzio PJ, Petrella RJ, Sproule JR, Fowler PJ (1997) Effects of fatigue on knee proprioception. *Clin J Sport Med* 7:22–27
- Lynn R, Morgan DL (1994) Decline running produces more sarcomeres in rat vastus intermedius muscle fibers than does incline running. *J Appl Physiol* 77:1439–1444
- Lynn R, Talbot JA, Morgan DL (1998) Differences in rat skeletal muscles after incline and decline running. *J Appl Physiol* 85:98–104
- McHugh MP, Connolly DA, Eston RG, Gleim GW (1999) Exercise-induced muscle damage and potential mechanisms for the repeated bout effect. *Sports Med* 27:157–170
- Miles MP, Ives JC, Vincent KR (1997) Neuromuscular control following maximal eccentric exercise. *Eur J Appl Physiol Occup Physiol* 76:368–374
- Morgan DL, Proske U (2004) Popping sarcomere hypothesis explains stretch-induced muscle damage. *Clin Exp Pharmacol Physiol* 31:541–545
- Morgan DL, Gregory JE, Proske U (2004) The influence of fatigue on damage from eccentric contractions in the gastrocnemius muscle of the cat. *J Physiol* 561:841–850
- Nardone A, Schieppati M (1988) Shift of activity from slow to fast muscle during voluntary lengthening contractions of the triceps surae muscles in humans. *J Physiol* 395:363–381

- Newham DJ, Jones DA, Clarkson PM (1987) Repeated high-force eccentric exercise: effects on muscle pain and damage. *J Appl Physiol* 63:1381–1386
- Nikolaidis MG, Paschalis V, Giakas G, Fatouros IG, Koutedakis Y, Kouretas D, Jamurtas AZ (2007) Decreased blood oxidative stress after repeated muscle-damaging exercise. *Med Sci Sports Exerc* 39:1080–1089
- Nosaka K, Newton M (2002) Concentric or eccentric training effect on eccentric exercise-induced muscle damage. *Med Sci Sports Exerc* 34:63–69
- Nosaka K, Sakamoto K (2001) Effect of elbow joint angle on the magnitude of muscle damage to the elbow flexors. *Med Sci Sports Exerc* 33:22–29
- Nosaka K, Sakamoto K, Newton M, Sacco P (2001) How long does the protective effect on eccentric exercise-induced muscle damage last? *Med Sci Sports Exerc* 33:1490–1495
- Paddon-Jones D, Abernethy PJ (2001) Acute adaptation to low volume eccentric exercise. *Med Sci Sports Exerc* 33:1213–1219
- Paschalis V, Koutedakis Y, Baltzopoulos V, Mougios V, Jamurtas AZ, Giakas G (2005a) Short vs. long length of rectus femoris during eccentric exercise in relation to muscle damage in healthy males. *Clin Biomech (Bristol, Avon)* 20:617–622
- Paschalis V, Koutedakis Y, Jamurtas AZ, Mougios V, Baltzopoulos V (2005b) Equal volumes of high and low intensity of eccentric exercise in relation to muscle damage and performance. *J Strength Cond Res* 19:184–188
- Paschalis V, Nikolaidis MG, Giakas G, Jamurtas AZ, Pappas A, Koutedakis Y (2007) The effect of eccentric exercise on position sense and joint reaction angle of the lower limbs. *Muscle Nerve* 35:496–503
- Proske U, Allen TJ (2005) Damage to skeletal muscle from eccentric exercise. *Exerc Sport Sci Rev* 33:98–104
- Proske U, Morgan DL (2001) Muscle damage from eccentric exercise: mechanism, mechanical signs, adaptation and clinical applications. *J Physiol* 537:333–345
- Prou E, Guevel A, Benezet P, Marini JF (1999) Exercise-induced muscle damage: absence of adaptive effect after a single session of eccentric isokinetic heavy resistance exercise. *J Sports Med Phys Fitness* 39:226–232
- Saxton JM, Clarkson PM, James R, Miles M, Westerfer M, Clark S, Donnelly AE (1995) Neuromuscular dysfunction following eccentric exercise. *Med Sci Sports Exerc* 27:1185–1193
- Walsh LD, Hesse CW, Morgan DL, Proske U (2004) Human forearm position sense after fatigue of elbow flexor muscles. *J Physiol* 558:705–715
- Weerakkody N, Percival P, Morgan DL, Gregory JE, Proske U (2003) Matching different levels of isometric torque in elbow flexor muscles after eccentric exercise. *Exp Brain Res* 149:141–150
- Whitehead NP, Weerakkody NS, Gregory JE, Morgan DL, Proske U (2001) Changes in passive tension of muscle in humans and animals after eccentric exercise. *J Physiol* 533:593–604
- Willems T, Witvrouw E, Verstuyft J, Vaes P, De Clercq D (2002) Proprioception and muscle strength in subjects with a history of ankle sprains and chronic instability. *J Athl Train* 37:487–493
- Wojtys EM, Wylie BB, Huston LJ (1996) The effects of muscle fatigue on neuromuscular function and anterior tibial translation in healthy knees. *Am J Sports Med* 24:615–621
- Wood SA, Morgan DL, Proske U (1993) Effects of repeated eccentric contractions on structure and mechanical properties of toad sartorius muscle. *Am J Physiol* 265:C792–800