



## Research report

# A comparison of the effects of concentric versus eccentric exercise on force and position sense at the human elbow joint

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**Abstract**

It is generally accepted that our sense of limb position and movement is provided, in part, by signals from muscle spindles, while the sense of muscle force derives from signals in tendon organs. Experiments are described here, using human subjects, in which the effects of eccentric and concentric exercise of elbow flexor muscles are compared on the sense of forearm position and the sense of tension in elbow flexors. Subjects were required to compress a preloaded spring with one arm, carrying out a concentric contraction in elbow flexors, then flexors of the other arm released the spring from compression and thereby carried out an eccentric contraction. The force of the spring was adjusted to be 20% maximum voluntary contraction (MVC), and each subject carried out a minimum of 120 contractions. Position sense was measured in blindfolded subjects by placing one forearm at a set angle and asking subjects to match it by positioning the other arm. Over 4 days postexercise, subjects placed the eccentrically exercised arms in a more extended position than the concentrically exercised arm suggesting that they thought the muscle was shorter than it actually was. In a force-matching task, subjects systematically undershot the target 10% MVC with their eccentrically exercised arm. Since it is known that eccentric exercise is associated with damage to muscle fibres, it is postulated that this leads to a disturbance of muscle receptors, the muscle spindles and tendon organs. © 1997 Elsevier Science B.V.

*Keywords:* Eccentric exercise; Muscle damage; Muscle spindle; Tendon organ; Proprioception; Fatigue; Soreness; Voluntary contraction

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**1. Introduction**

It is a common experience to feel clumsy and awkward after a period of intense exercise. This paper describes experiments which compare proprioceptive acuity after concentric and eccentric exercise. The two senses studied are the sense of muscle force and the sense of limb position.

The sense of force is complicated in that it actually incorporates two senses, a peripherally derived sense of force and a centrally derived sense of effort [13]. In a situation where a muscle is fatiguing while being required to maintain a certain level of force, centrally driven activation rates of motoneurons increase to maintain the level of force, and in doing so lead to a perceived increase in effort. Any drop in force-generating capacity due to fatigue should therefore be perceived as a proportional increase in

effort. If the level of force is able to be maintained, this will be reported by a peripherally derived sense of force, presumably coming from tendon organs [12].

The sense of limb position, it is generally agreed, is provided by signals from skin, joint and muscle receptors. The muscle receptors responsible include the primary and secondary endings of muscle spindles, primary endings being concerned with signalling position and movement, secondary endings largely signalling position (for a review see [6]). Position sense would not normally be expected to be disturbed by a fatiguing contraction.

Here we have not addressed the broader question of the effects of exercise on proprioception, but targeted one specific aspect of exercise, whether it is concentric or eccentric exercise. During an eccentric contraction the contracting muscle is forcibly lengthened. This compares with the more common, concentric contraction where the contracting muscle shortens. Eccentric exercise is a major component in downhill walking, skiing and horse riding. Activities which largely involve concentric contractions are cycling, swimming and rowing.

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Eccentric exercise is particularly interesting because it is associated with delayed onset muscle soreness (DOMS). The current view is that the soreness arises from damage to muscle fibres produced by the lengthening contractions (for a review see [1]). One of us [15] has put forward a theory to account for many of the previously unexplained mechanical changes in muscle produced by a period of eccentric exercise. Here we have posed the question, does the damage of eccentric exercise implicate muscle receptors?

An important aspect of the design of our experiments has been to try to distinguish between the short-term effects of exercise, such as fatigue and the accumulation of metabolites, and the longer lasting effects, associated presumably with muscle damage, which are likely to be specific to eccentric exercise. Apparatus has been constructed which allows elbow flexors of one arm to perform a concentric contraction and flexors of the other arm to undergo an eccentric contraction. Proprioceptive acuity is then measured in both arms and any difference that persists for more than a few hours can be attributed to the damaging effects of the eccentric exercise.

A preliminary account of this work has been published in abstract form [3].

## 2. Materials and methods

A total of 13 healthy young adults, 6 male, 7 female took part in the study (aged 17–29 years). Five subjects carried out both the position- and force-matching tasks, 4 others did the position-matching task only and 4 others the force-matching task only. This meant that 9 subjects could be compared for position matching, and 9 for force matching, but for MVC, resting elbow angles and muscle tenderness comparisons, data from all 13 subjects was available.

The experiments were approved by the local Human Ethics Committee.

### 2.1. Position sense

Blindfolded subjects were seated with their forearms strapped in the supinated position to padded boards (Fig. 1). The boards were hinged along a horizontal axis of rotation coincident with the elbow joint. Potentiometers attached to the hinges gave voltage signals proportional to elbow angle. Differences in elbow angle were read from a digital voltmeter. Position sense was measured with the forearm held at each of three degrees of flexion, 30°, 60° and 90° to the horizontal. One arm, the reference arm, was placed at one of these angles and subjects were asked to carry out a brief isometric contraction of elbow flexors in that arm, to control for muscle history effects [7]. After the contraction, the subject was asked to relax the arm and then position the other, indicator arm to match the position of the reference arm. Once subjects were satisfied that they had made an accurate match, a digital voltmeter readout

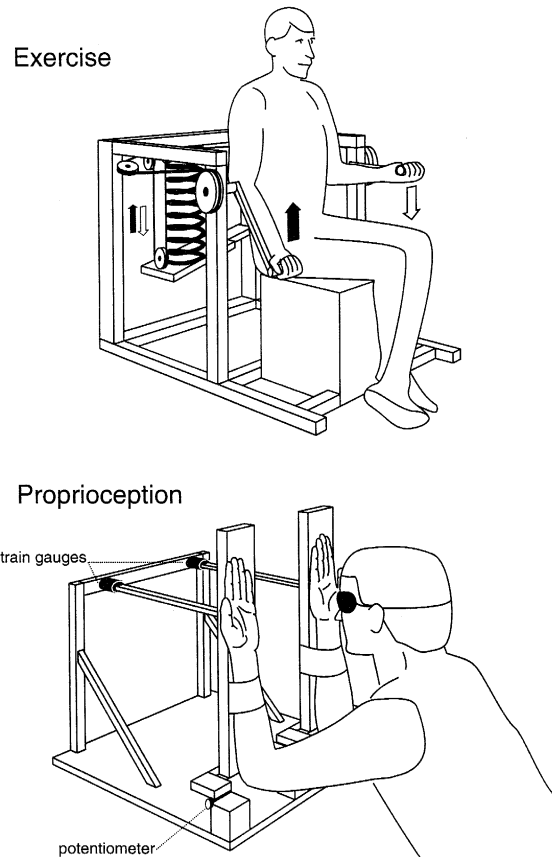


Fig. 1. Upper panel: the arm-curl machine. Two handles were connected to winding drums, each attached to the end of a cable. The cable was connected via a system of pulleys to a preloaded compression spring. Elbow flexors of one arm carried out a concentric contraction which compressed the spring by flexing the arm (filled arrows). Flexors of the other arm had to slowly release the spring from compression and thereby carry out an eccentric contraction against the same force (open arrows). Lower panel: equipment for proprioception measurements. Position sense: blindfolded subjects were seated with their forearms strapped to padded boards. The boards were hinged horizontally, along their axis of rotation, coincident with the elbow joint. Potentiometers attached to the hinges gave voltage outputs proportional to elbow angle. Force sense: the same padded boards were used, but they were locked in the vertical position by a pair of aluminium shafts which were each attached to a strain gauge. Force output during isometric elbow flexor contractions was monitored on the screen of an oscilloscope.

was recorded. After a period of rest, the process was repeated, three times for each elbow angle and with each arm acting as the reference, giving a total of 18 trials. Differences were defined as positive when the eccentrically exercised arm (EA) adopted a more flexed position than the concentrically exercised arm (CA).

### 2.2. Force sense

For this, the same padded boards were used, but they were locked in the vertical position by a pair of horizontal aluminium shafts which were each attached to a proving ring with strain gauges cemented on the inside and outside and connected in a full-bridge configuration (Fig. 1). Sub-

jects were asked to develop a level of tension, 10% maximum voluntary contraction (MVC), with one arm, the reference arm, and were given a visual display of the target tension to help them achieve that level. They would then be asked to match the tension with the other, indicator arm. During the initial learning trials, subjects were provided with visual feedback for both arms to help them achieve a correct match. For the actual tests, visual feedback was provided for the reference arm, but not the indicator arm. Subjects had to achieve control matches with errors of less than 10% of the target force for them to be accepted for the study. Most subjects easily achieved that level of accuracy. Subjects were given no further practice sessions, but a series of 10 control trials was carried out with each arm acting as the reference.

### 2.3. The exercise

The exercise was carried out with subjects seated in a specially constructed arm-curl machine (Fig. 1). The machine consisted of a supporting frame and two handles of adjustable length. The handles were connected to winding drums each attached to the ends of a cable. The cable was connected via a system of pulleys to a preloaded compression spring. The spring was adjusted for each subject so that compression represented 20% MVC. Elbow flexors of one arm carried out a concentric contraction which compressed the spring by flexing the arm. Flexors of the other arm had to develop sufficient force in the flexed position to support the load exerted by the compressed spring and were then allowed to slowly release the spring from compression and thereby carry out an eccentric contraction against the same force. Seat height was adjusted so that the axis of rotation of the subject's elbow was aligned with the axis of rotation of the handle. For each subject, one arm was randomly assigned to exercise eccentrically, the other to exercise concentrically. Each cycle of exercise took about 7 s and was followed by 3 s of rest. Subjects exercised for a minimum of 120 contractions with each arm which took about 20 min. Subjects were encouraged to continue exercising until they were tired. The longest exercise period was 35 min.

### 2.4. Maximum voluntary contraction

MVC was measured for each subject by locking the handles of the arm-curl machine in the horizontal position. Subjects were asked to produce a maximum contraction without using back or shoulder muscles. Three MVCs of 5 s duration were carried out by each arm. The applied torque was measured by strain gauges in the handles.

### 2.5. Relaxed elbow angle

Subjects were asked to stand and let their arms hang by their sides, completely relaxed. The arms of a goniometer

were aligned with the humerus and ulna, the axis of rotation in line with the lateral epicondyle. A drop in the angle measured represented a more flexed elbow.

### 2.6. Muscle tenderness

The term tenderness is preferred to pain or soreness because of the chosen method of measurement. A compression gauge with a 5-mm-diameter disc plunger was applied to different parts of biceps, including the tendons of origin and insertion, the proximal and distal myotendinous regions and the muscle belly. In practice, there was no change in tenderness at the tendons and proximal myotendinous region after the exercise, so that measurements all derived from the muscle belly and distal myotendinous region. Values from both regions were combined and averaged. Subjects were asked to report as soon as they felt any discomfort during application of the gauge. The force of application was read from the dial of the gauge. If a force of 3 kg was applied without any reported discomfort, the score assigned was zero. If at 2 kg subjects reported tenderness, the score was one, at 1 kg it was 2 and so on up to a maximum value of 3 where subjects reported soreness without the muscle being touched at all.

### 2.7. Experimental protocol

After the pre-exercise measurements had been made, subjects were exercised on the arm-curl machine and immediately afterwards a set of position- or force-matching trials was carried out together with measurements of resting elbow angle, MVC and muscle tenderness. Measurements were repeated at 2, 24, 48, 72 and 96 h postexercise. Where the same subject was used for both position- and force-matching tasks, these were carried out sequentially, within half an hour of one another.

### 2.8. Statistical analysis

Data were stored on a Macintosh computer and analysed using the program Igor Pro (WaveMetrics, Lake Oswego, OR). The statistical analysis program used was Data Desk (Data Description, Ithaca, NY). For each test, means and standard errors were calculated across all subjects. For force and position matches, the values for the concentric arm were subtracted from those for the eccentric arm to eliminate the effects of fatigue and the accumulation of metabolites, which should have occurred in the muscles of both arms. Tenderness, relaxed elbow angle and MVC were, of course, carried out on each arm separately. Because values for MVC differed widely between subjects these were normalised relative to control values which were assigned a value of one. Analysis of variance was carried out to test for differences between data sets measured at different points in time and multiple linear

regressions were calculated to show up any significant relationships between variables.

### 3. Results

While the exercise carried out by subjects had been relatively mild, representing force levels of only 20% MVC, it did, nevertheless, leave persistent effects that could be measured over the 4-day postexercise period, effects which were interpreted as evidence of muscle damage.

#### 3.1. Muscle tenderness

Subjects reported a mild tenderness of both elbow flexors immediately after the exercise and this intensified in EA over the next 24 h while it gradually faded in CA. The mean tenderness rating in EA reached a peak of 0.94 on day 1 and then gradually fell, returning to near control values by day 4 (Fig. 2). In CA, the mean value rose immediately after the exercise to peak at 0.68 at 2 h postexercise. Tenderness then fell over the rest of the period of measurement. The change in tenderness was significant for EA (one-way ANOVA;  $P < 0.05$ ), but not for CA.

#### 3.2. Relaxed elbow angle

A second indicator of a persistent change in elbow flexors after the exercise was a decrease in relaxed elbow angle. That is, subjects stood with the relaxed arm at their side maintaining a more flexed resting position than before the exercise. This was apparent in EA for 11 of the 12 subjects and in CA in 8 of 12 subjects. The immediate change in elbow angle was much more pronounced in EA, which showed an average decrease by  $4.5^\circ$ . By compari-

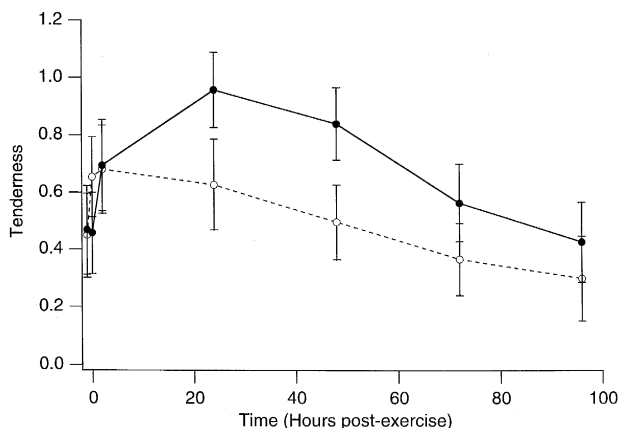


Fig. 2. Mean ( $\pm$ S.E.M.) tenderness ratings of elbow flexor muscles in EA (eccentrically exercised arm, solid line) and in CA (concentrically exercised arm, dashed line) for 13 subjects, before and at various times over 4 days after the exercise. The exercise was carried out at time = 0.

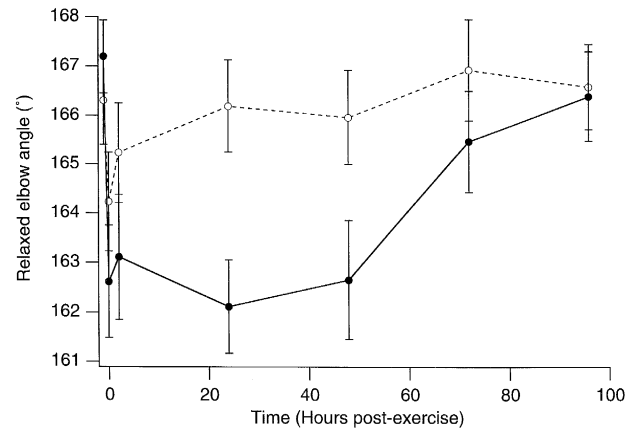


Fig. 3. Mean ( $\pm$ S.E.M.) resting elbow angle, with the arm hanging relaxed at the subject's side, in EA (solid line) and CA (dashed line) for 13 subjects before and after the exercise.

son, CA showed an average decrease of only  $2.1^\circ$ . There was some return towards normal angles by 2 h postexercise, but in EA, there was a further decrease by a mean of  $5.1^\circ$  over the following 24 h. Elbow angle then gradually returned to normal over the next 3 days (Fig. 3). In CA, angles had returned to control values on the first day. For EA, the decrease in elbow angle was significant (one-way ANOVA;  $P < 0.01$  up to 24 h after the exercise). The decrease in elbow angle for CA was not significant.

#### 3.3. Change in MVC

Values for MVC showed a drop of 10% in EA and 14% in CA immediately after the exercise (Fig. 4). But this had recovered back to control values by the first day. The drop in MVC was not significant for either arm (one-way ANOVA). This confirmed that the exercise regime chosen had been relatively mild. It is not clear why there was a small increase in MVC above control values from 48 h onwards. Perhaps it was a training effect, or perhaps

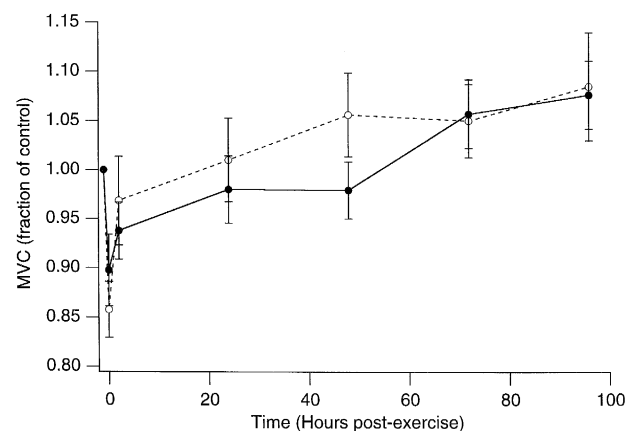


Fig. 4. Mean ( $\pm$ S.E.M.) values for maximum voluntary contraction (MVC) for 13 subjects for EA (solid line) and CA (dashed line), before and after the exercise.

subjects were simply concentrating more on reaching maximal forces as they became more familiar with the equipment.

### 3.4. Position sense

All 9 subjects experienced changes in forearm position sense after the exercise. In control matches, the mean difference between the two arms was  $0.7^\circ$ . By 24-h postexercise, subjects were declaring as accurately matched, elbow angles with differences between them of nearly  $5^\circ$ . EA was always in the more extended position compared to CA, regardless of which arm acted as the reference. That is, in a match where EA adopted the reference angle, CA matched it in a more flexed position while, when CA was the reference, EA adopted a more extended position. Values recorded were the differences in position of the two arms regardless of which was the reference and were scored as negative whenever EA was more extended than CA (Fig. 5). The result suggested that subjects perceived the eccentrically exercised muscles to be shorter than they actually were. There was a gradual recovery of normal position sense over the next 3 days and by 96 h, postexercise errors had returned to pre-exercise values. The changes in position sense after the exercise were significant (one-way ANOVA;  $P < 0.01$ ).

While position errors were consistent in size and direction for all 9 subjects at 24 h, there were some minor differences between subjects at 2 h after the exercise. One subject showed no significant change in errors following exercise while four others matched with their EA more flexed than CA (mean of  $+4.9^\circ$  for the 4 subjects). That is, for these subjects the trend immediately after the exer-

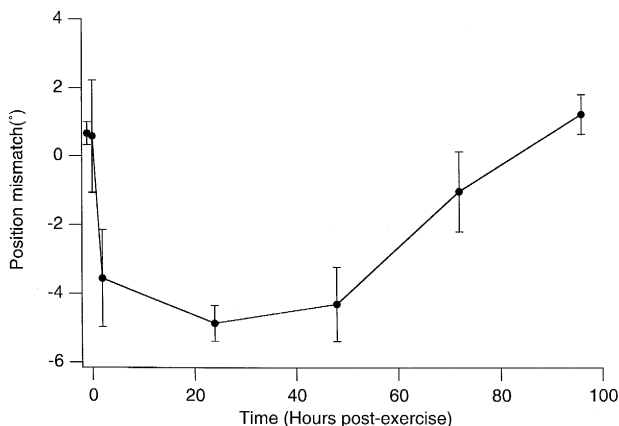


Fig. 5. Mean position-matching error ( $\pm$ S.E.M.) in degrees of flexion at the elbow joint for 9 subjects, before and at various times after a period of eccentric exercise with one arm and concentric exercise with the other. Blindfolded subjects adopted an elbow angle with one arm and were required to match it with the other, indicator arm. Values are given as the difference in positions for the two arms regardless of which was the reference. A negative value means that EA adopted a more extended position, that is, the arm was less flexed, than CA. Results here were combined for data from three different elbow angles ( $30^\circ$ ,  $60^\circ$  and  $90^\circ$ ).

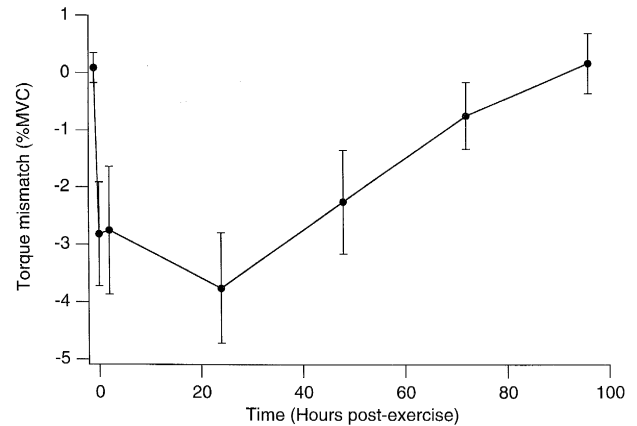


Fig. 6. Mean torque mismatch ( $\pm$ S.E.M.) for 9 subjects before, and at various times after the exercise. The matching task required subjects to produce an isometric contraction at 10% MVC, with visual feedback, with one arm, and, without feedback, match it with the other. The mismatch expressed in % MVC is the difference in force generated between the two arms regardless of which was acting as the reference. Values were scored as negative when EA underestimated the force generated by CA, or conversely when CA overestimated the force generated by EA.

cise was in a direction opposite to that adopted subsequently. The remaining four subjects matched with EA more extended ( $-3.8^\circ$ ). Values for all 9 subjects converged on a mean of  $-4.9^\circ$  at 24 h.

### 3.5. Force sense

All 9 subjects showed disturbance of their force-matching ability immediately after the exercise and over the next 3 days. Errors reached their peak after 1 day and then matching accuracy gradually returned over the following 3 days (Fig. 6). Invariably, EA produced less tension than it should have to achieve an accurate match. For example, with EA as the reference, CA overshot the 10% MVC. Alternatively with CA as the reference, EA undershot the target. Matching errors were declared as the difference in force generated between EA and CA regardless of which was acting as the reference. Values were scored as negative when the force in EA was less than in CA (Fig. 6). Mean control errors were  $+0.1\%$  of MVC. This fell to  $-2.9\%$  immediately after the exercise, recovered slightly to  $-2.8\%$  at 2 h and fell further to the minimum of  $-3.8\%$  at 24 h. From then on, errors decreased and by day 4 were no longer significantly different from control values. The change in force-matching error after the exercise was significant (one-way ANOVA;  $P < 0.001$ ).

## 4. Discussion

The aim of the experiments reported in this study was not to determine the effects of exercise as such on proprioception, but to test whether eccentric exercise produced

effects different from those accompanying concentric exercise. The ultimate aim was to try to link the known changes in mechanical properties of muscles specifically associated with eccentric exercise with any changes in proprioception. Since a feature of the effects of eccentric exercise on mechanical properties was the long time course of recovery, particular attention was paid to longer lasting effects on proprioception. So it was found that after eccentric exercise there were significant changes in subjects' ability to judge low levels of force and different elbow angles, changes which persisted for several days, suggesting that here short-term effects, such as fatigue and accumulation of metabolites, were unlikely to be responsible.

Previous work in this laboratory has focused on the changes in mechanical properties of muscle following eccentric exercise [9,16,20]. The experiments were based on a theory proposed by one of us [15] which provides an explanation for many of the effects of eccentric exercise. The theory postulates that the lengthening of a muscle during an eccentric contraction is distributed non-uniformly so that some, weaker sarcomeres within the contracting muscle fibres take up a large fraction of the length change and in the process become overextended. If sarcomere disruption following overextension is not too severe, reinterdigitation and normal recovery of function is possible [9]. Some sarcomeres, however, are unable to recover their normal banding pattern and, especially after repeated eccentric contractions, areas of irreversible damage develop which spread as the exercise continues. A point may be reached where fibre membranes are torn, uncontrolled movements of  $\text{Ca}^{2+}$  occur and a contraction clot develops. Some fibres may ultimately die. Our interpretation of the longer time for tension recovery after eccentric exercise compared with concentric exercise is therefore that not only do the effects of fatigue need to be reversed, but muscle fibres may need to be repaired or replaced.

We have interpreted the increase in tenderness and the smaller relaxed elbow angle observed in this study as evidence of muscle fibre damage in EA [4,10]. The breakdown products of tissue damage and products released by invading macrophages sensitise Group III and IV nerve endings leading to muscle tenderness [14]. A reduction in resting elbow angle, we propose, is the result of tone generated in the muscle by damaged muscle fibres which have gone into contracture. It is known that the change in resting elbow angle is not accompanied by sustained electrical activity in flexor muscles [10]. It was speculated by these authors that non-contractile elements were involved in the change in elbow angle and that possibly swelling within the connective tissue network led to shortening of the muscles. In the light of the recent structural and mechanical data showing damage in muscle fibres after eccentric contractions (see, for example, [9]), we prefer the explanation that damage to fibres leads to loss of  $\text{Ca}^{2+}$  homeostasis and subsequent development of a contracture

clot. The contracture tension produces shortening of the resting muscle and a reduction in elbow angle.

The specific question we have posed here is, does the damage involve, directly or indirectly, the muscle sense organs, the muscle spindle and tendon organ?

#### 4.1. Position sense

It is generally agreed that signals from muscle spindles contribute to the senses of position and movement of our limbs. In the interpretation of our results, we assume that elbow angle is signalled by the maintained level of resting discharge coming from spindles. There is little information in the literature about any dysfunction of muscle spindles after fatiguing contractions. The rise in resting discharge reported by Nelson and Hutton [17] would be expected to lead to errors in position sense in a direction opposite to that found here, but their findings are difficult to interpret since muscle history effects had not been strictly controlled for [18]. It has been proposed that at least one contributing factor to the decline in motor unit discharge during a fatiguing contraction is reduced feedback from muscle receptors [8]. The mechanism for the reduction in spindle discharge has been proposed to involve a reflex inhibition of fusimotor neurones by small muscle afferents excited by the metabolic products of the exercise. According to this hypothesis we should have obtained similar effects in both arms, and therefore the errors should have been small unless eccentric and concentric exercise lead to large differences in the accumulation of metabolites. In any case, this mechanism does not explain the persistence of these errors over several days, at a time when all metabolites would have been removed.

We have considered two mechanisms to explain our findings. It is possible that the damage of eccentric exercise is not restricted to the ordinary muscle fibres, but may involve the intrafusal fibres of spindles as well. During voluntary muscle contraction it is likely that there is co-activation of  $\alpha$ - and  $\gamma$ -motoneurons (for a review see [2]). It means that both extrafusal and intrafusal fibres undergo eccentric contractions, although the compliant connections may reduce the amount of stretch of intrafusal fibres. Nevertheless, damage to intrafusal fibres remains a possibility. If the damaged fibres actually died or were ruptured, spindle discharge levels would fall significantly, which is consistent with the direction of the difference in the observed errors. Subjects perceived EA to be shorter than it actually was.

A second possibility is based on our interpretation of a reduced elbow angle in EA after the exercise. If this is due to damaged muscle fibres producing some resting tension in the muscle, spindles adjacent to these damaged fibres may be mechanically unloaded by the contractures leading to a reduced spindle output at a set muscle length. It will require further experiments to test these proposals. For example, if unloading is responsible, tendon jerk reflexes

should be normal, but if spindles are damaged tendon jerks would be expected to be depressed. This test would have to be carried out at a time when the short-term effects of fatigue had passed [5].

In the only other study of position sense after eccentric contractions, Saxton et al. [19] found that the exercised elbow flexors adopted a more flexed position in matching the position of the unexercised reference arm; in other words, the opposite of our finding. We do not have any explanation for this result, but would point to the differences in conditions of the experiments of Saxton et al. [19] and our own. Our subjects carried out a minimum of 120 eccentric contractions of about 20% MVC. We considered 20% sufficient because the evidence suggested that damage from eccentric exercise was not dependent on high levels of tension [4,11]. Saxton et al. [19] required subjects to carry out 50 maximum eccentric contractions. Significantly, these were followed by a 52% drop in MVC immediately after the exercise and 5 days later, force was still only at 80% of control levels. In our experiments, apart from a small, non-significant drop immediately after the exercise, MVC values were, on average, larger than controls. So our exercise was very much less severe. Interestingly, immediately after the exercise, for four of our subjects, errors were in the same direction as reported by Saxton et al. [19]. The direction of these errors suggests a higher than normal output from spindles. Is a rise in spindle discharge indicative of internal damage within the receptor, which is not incurred by mild exercise?

#### 4.2. Force sense

Force errors at their largest were 3.8% of MVC which, given the target was 10% MVC, was approximately 40% of the target force, so that the errors were quite large (see Fig. 6). The direction of the errors was always the same, EA adopting a matching tension below the value generated by CA. Conversely, with CA as the indicator, tension in EA was overestimated. This direction of errors is the same as that observed by Saxton et al. [19], although errors in our study were very much smaller. This is not surprising since our subjects had very much smaller changes in MVC. Saxton et al. [19] found that when they calculated the 35% value of the target tension, taking into account that MVC had fallen by half, the matching tensions were reasonably accurate. From this, they concluded that central mechanisms were likely to be responsible for the mismatch.

For our observations we argue that in the face of no significant drop in MVC, a force-matching error of 40% of the target is not likely to be due to central mechanisms. If there was a small undetected drop contained within our MVC measurements, it seems unlikely that it would be largely contained within the bottom 10% of a voluntary contraction. More likely, if a few fibres had been damaged, they would be scattered amongst motor units of a range of

sizes and then the extra effort required to achieve the 10% target would be insufficient to account for the sizes of errors, unless the relationship between tension deficit and change in effort was highly non-linear [12].

One explanation we have considered for these findings is that contractures in the muscle fibres damaged by the eccentric contractions and responsible for the reduced elbow angle will activate some tendon organs. If the tendon organ output of the muscle rises because of the higher resting tension, this may lead to the perception of a higher level of force in the muscle than was actually generated and that would produce the observed tension mismatch.

In an attempt to obtain support for our explanation, we have made some preliminary observations in an animal experiment (Gregory, Morgan and Proske, unpublished observations). After 100 maximal eccentric contractions of the soleus muscle of the anaesthetised cat, 4 of 5 identified tendon organs showed responses to muscle stretch which were proportionately greater than after a similar number of concentric contractions. However, it will require further experiments to confirm the finding and to extend the observations to active contractions.

In conclusion, we report that both elbow joint position sense and force sense are disturbed over a number of days by eccentric exercise. The direction of the errors suggests that receptors responsible for position sense have become less sensitive. Errors in force estimation suggest subjects perceived the eccentrically exercised muscle to be generating more force than it really was. It is argued that this is not due to central mechanisms and a sensitisation of tendon organs is postulated. The ongoing animal experiments will hopefully resolve this question.

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