



The Effect of Concentric and Eccentric Exercise on Muscle Hardness

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Objective: The purpose of this study was to investigate the effect of different contraction types on muscle structures, functions and muscle hardness.

Materials: 6 healthy males (age: 22.8 ± 1.5 years, height: 176.1 ± 4.0 cm, weight: 72.3 ± 11.0 kg) participated in this study.

Methods: Subjects performed concentric contraction (CC) exercise of elbow flexor with one arm, and eccentric contraction (EC) exercise of elbow flexor with the other arm with the same total work. Muscle hardness of the biceps brachii measured by strain ratio, elbow joint angle, and maximal voluntary contraction (MVC) torque of elbow flexors were measured before (PRE), 1 hour (1H), 3 hours (3H) and 24 hours (24H) after the exercise protocol. Muscle soreness was measured at 1H, 3H, and 24H time points.

Results: A significant interactions (time \times type) was found in MVC torque ($p < 0.01$), elbow joint angle ($p < 0.01$), and muscle thickness ($p = 0.013$). Strain ratio, MVC torque significantly decreased at 1H, 3H, and 24H compared to PRE after the EC exercise ($p < 0.05$). Main effect in time was detected in Strain ratio ($p = 0.046$) and upper arm circumference ($p = 0.044$). Main effect in contraction type was detected in muscle soreness ($p < 0.01$) with the greater level after the EC exercise. Elbow joint angle significantly increased at 1H, 3H, and 24H ($p < 0.05$) compared to PRE after the EC exercise, and at 1H, 3H compared to PRE after the CC exercise ($p < 0.05$). Upper arm circumference significantly increased at 1H compared to PRE after the CC exercise ($p < 0.05$).

Conclusions: The disruption of muscle function is greater and longer lasting after the eccentric contraction exercise than the concentric contraction exercise, and the muscle hardness only increased after the eccentric exercise when the exercises are performed with the same total work. The mechanisms of functional disruption following exercises and its effect on the muscle hardness may different according to the type of muscle contraction.

Key words: real-time tissue elastography, muscle damage, elbow flexors

Introduction

It is well known that muscle functions are disrupted after muscle contraction exercises. Unaccustomed eccentric exercise induces muscle damage from high mechanical tension¹⁾, which causes structural changes of muscle, increased creatine kinase, muscle soreness, and functional changes such as decreased muscle strength and joint range of motion (ROM), which could last for four to five days²⁾⁻⁹⁾. These muscle functions are also disrupted

after prolonged concentric or isometric contractions due to muscle fatigue from shortage of fuel, impaired transport of substances within muscles, and accumulation of metabolites¹⁰⁾⁻¹³⁾, nervous fatigue or small muscle damage. This disrupted muscle functions recover within 60–120 minutes, which is faster than the recovery period for unaccustomed eccentric contractions⁶⁾.

Another change that occurs to muscles after muscle contractions is muscle hardness. Muscle hardness is a mechanical property of the muscle

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defined as the resistance offered by the muscle against perpendicular pressure. This is different from muscle stiffness which is the ratio of change in force to change in length along the muscle's longitudinal axis¹⁴⁾ even though these two mechanical properties are related.

Researches show that muscle hardness changes after different types of muscle contraction exercises, such as eccentric contractions and submaximal isometric contractions^{9) 15)-18)}. Murayama *et al.*^{9) 19)} explained that exercise-induced changes of muscle hardness are associated with mechanical pressure from connective tissues surrounding the muscle and increased intramuscular pressure from oedema. There are studies investigating the degree of muscle fatigue from the change of muscle hardness^{15) 17) 20)}; however, the changes of muscle fatigue and muscle hardness after different contraction types are not necessarily consistent.

Although it is well known that muscle hardness changes after a single type of muscle contraction exercise, any study compared muscle hardness changes after exercises with various types of muscle contraction. To reveal the effects of exercise on muscle hardness, it is necessary to clarify the effects of different muscle contraction types on muscle hardness. Also, it is necessary to compare the changes of muscle structural/functional changes and the change of muscle hardness to see if there are any relationship between these parameters. The purpose of this study was to investigate the effect of different contraction types on muscle structures, functions and muscle hardness. We hypothesized that muscle hardness and joint ROM limitation would increase, and muscle strength would decrease after eccentric and concentric contraction exercises, with greater and longer lasting changes after eccentric exercise.

Materials and Methods

1. Participants

Six healthy young men (age: 22.8 ± 1.5 years, height: 176.1 ± 4.0 cm, weight: 72.3 ± 11.0 kg) who only participate in recreational activity and do not regularly train or exercise participated in this study. Subjects were excluded if they have any upper extremity injuries or muscle soreness due to previous training or any kind of physical activities. The subjects were asked and reminded to refrain

from unaccustomed exercise and any treatments of the exercised muscle (e.g. massage, stretching, icing) during the study. The subjects were informed regarding the nature, purposes, and possible risks associated with the experimental procedure, and consent was obtained from all participants. The study was conducted in accordance with the 1964 Declaration of Helsinki and was approved by the Ethical Committee of Juntendo University (approved #27-3).

2. Procedure

All subjects performed eccentric elbow joint exercise with a randomly assigned arm (EC), and concentric elbow joint exercise with the other arm (CC). BIODEX system 3 (BIODEX medical, Shirley, NY, USA) isokinetic dynamometer was used for the exercise protocol. Subjects maintained a seated position on a chair (Figure-1). Subjects executed eccentric and concentric exercises from 5° to 125° elbow joint (full extension= 0°) at 60 deg/sec. The eccentric exercise consisted of five sets of six maximal eccentric contractions of the elbow flexors with 120 second rests between sets, uniform with the precedence research^{8) 21)}. The resistance setting was set at 555 N·m which is the maximum resistance setting of the machine. The total eccentric exercise work (J) was recorded and divided by 5 to determine the target work of the

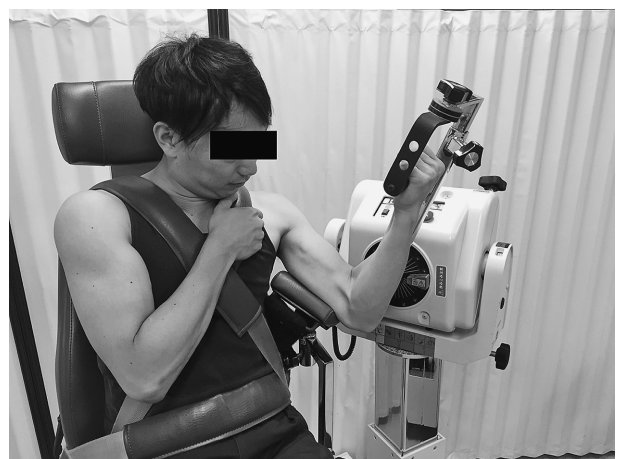


Figure-1 BIODEX setting

MVC torque measurement, EC and CC exercises were performed with BIODEX system 3 isokinetic dynamometer. Subjects' shoulders and pelvis were properly secured by straps, while in a seated position. MVC torque was measured at 90° of elbow joint (full extension = 0°). Both EC and CC exercises were executed from 5° to 125° elbow joint at 60 deg/sec.

concentric exercise. The concentric exercise consisted of five sets of maximal concentric contractions of the elbow flexors with 120 second rests between sets. Instead of fixing the number of repetitions, subjects executed concentric contractions until they achieved the targeted work in each set, determined from the eccentric exercise. The mean total works in this study were $2,291.1 \pm 619.3$ J in the EC arm and $2,282.7 \pm 632.2$ J in the CC arm without a significant difference between the contraction types ($p=0.880$).

Dependent variables consisted of Strain ratio measurements of the long head of the biceps brachii, maximal voluntary contraction (MVC) torque of the elbow flexors, elbow joint angle, soreness of the elbow flexors, thickness of the biceps brachii, and the upper arm circumference.

Measurement time points were: before (PRE), 1 hour (1H), 3 hours (3H), and 24 hours (24H) after the exercise protocol. Strain ratio, MVC torque, thickness of the biceps brachii, the upper arm circumference, and elbow joint angle were measured at PRE, 1H, 3H, and 24H. Muscle soreness was measured at 1H, 3H, and 24H. Muscle hardness, muscle thickness and the upper arm circumference are measured at 50% on the line between the acromion process and the radial tuberosity the with

subjects relaxed in supine position, 30° abducted shoulder joint, and 20° flexed elbow joint¹⁸⁾.

1) Muscle hardness

Real-time tissue elastography application loaded on Noblus (Hitachi Aloka Medical Ltd., Mitaka, Tokyo, Japan) diagnostic ultrasound imaging system was used to measure Strain ratio of the long head of the biceps brachii. In this method, Strain of a targeted tissue created from pressure applied by a probe is detected. The application then calculates the Strain ratio of the targeted tissue and an acoustic coupler, which has definite hardness, installed on the probe. Strain ratio of the targeted tissue can be measured semi-quantitatively by using an acoustic coupler. In this study, the Strain of the targeted tissue (B) was divided by the Strain of the acoustic coupler (A), and the resulted value (B/A) was used as Strain ratio (Figure-2). Consequently, the smaller the Strain ratio, the harder the targeted tissue. The Strain ratio was measured at the muscle belly of the long head of the biceps brachii. The probe was positioned longitudinally at 50% on the line between the acromion process and the radial tuberosity, and it was ensured that a clear line of humerus bone was depicted behind the muscle belly on B-mode image.

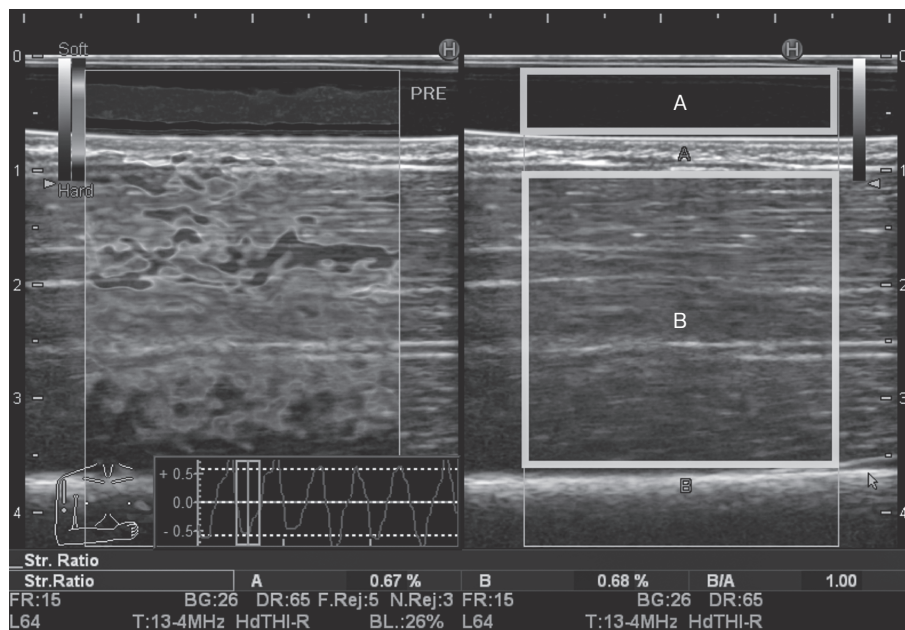


Figure-2 Real-time tissue elastography

In a B-mode image of biceps brachii in longitudinal direction, the area labeled (A) is an acoustic coupler and the area labeled (B) is a targeted tissue. SR is shown as B/A on bottom right of the image.

We took three measurements, and the average value was used for statistical analysis. The average intrarater coefficient of variation of all measurements was 11.8%.

2) Maximal voluntary contraction torque

MVC torque was measured by the BIODEX system 3 (BIODEX medical, Shirley, NY, USA) isokinetic dynamometer. Subjects performed three sets of five-second maximal isometric voluntary elbow flexion at the elbow angle of 90° (1-minute rest between sets). Subjects were vigorously encouraged to produce the greatest torque during each contraction. The average peak torque (N·m) of the three trials was used for statistical analysis.

3) Elbow joint angle

Elbow joint angle was measured by a goniometer in 1°-scale following the measurement method recommended by the Japanese Orthopaedic Association. During the measurement, subjects stood and relaxed at the anatomical position⁹⁾. The examiner put one arm of the goniometer along the long axis of the humerus, and the other arm along the long axis of the radius (Figure-3). The measurement was used to evaluate the limitation of elbow extension.



Figure-3 Measurement of elbow joint angle

Elbow joint angle was measured by a goniometer in 1°-scale following the measurement method recommended by the Japanese Orthopaedic Association. During the measurement, subjects stood and relaxed at the anatomical position. The examiner put one arm of the goniometer along the long axis of the humerus, and the other arm along the long axis of the radius.

4) Muscle soreness

Visual analog scale (VAS) with 100 mm straight line was used to evaluate the muscle soreness of the elbow flexors after each exercise. Subjects evaluated the subjective soreness by marking on the VAS with 0 mm as “no pain” and 100 mm as “intolerable pain” while subjects performing elbow joint and extension several times with standing. The examiner measured the marked position in 1 mm increments and used the results as the evaluation of muscle soreness.

5) Muscle thickness

Muscle thickness of the biceps brachii was measured by the ultrasound imaging system at the same site of muscle hardness measurement whereas the muscle thickness was measured without any pressure on the muscle. Three B-mode images of the biceps brachii was saved, and the distance between the bone where the brachialis origins and the border of muscle and fat was measured from each image (Figure-4). The average distance of the three measurements was used for statistical analysis.

6) Upper arm circumference

The upper arm circumference was also measured using a Gulik tape measure while the subject was

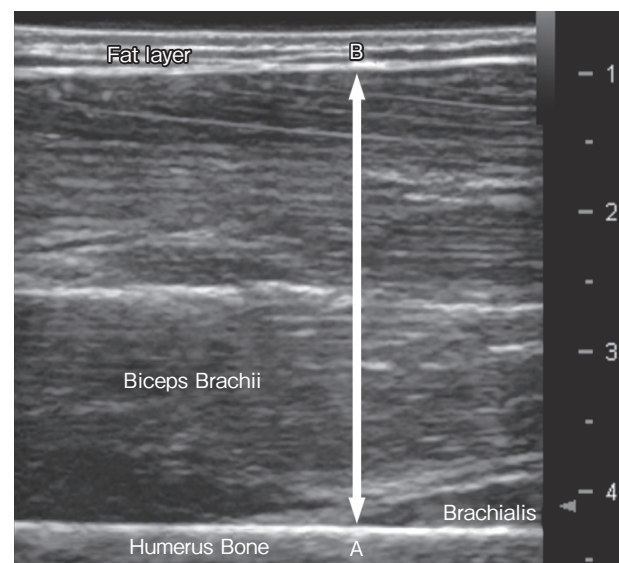


Figure-4 Measurement of muscle thickness on B-mode image

The distance between the bone surface (A) where the brachialis origins and the border of muscle and fat layer (B) was measured as the muscle thickness of the biceps brachii.

relaxing. The perimeter distance of the upper arm perpendicular to the long axis of the humerus was measured.

3. Statistical Analysis

A t-test was used to compare the baseline (PRE) measurement values between the EC and CC arms to see if there was any difference in the baseline values between the arms. A two-way analysis of variance (ANOVA) for repeated measurements [time (PRE, 1H, 3H, 24H) × type (eccentric, concentric)] was used to assess the change in all measurement variables. When the sphericity assumption in repeated measures ANOVA was violated by Mauchly's test, a Greenhouse-Geisser correlation was used. When differences were observed, Dunnett's post-hoc test was conducted for comparison of the measurement time-points. All statistical procedures were completed using the statistical package for Social Science (IBM SPSS, version 22.0; IBM Corp. Armonk, NY, USA). Statistical significance was set at $p < 0.05$. Values are reported as mean ± standard deviation (SD).

Results

The baseline (PRE) measurement values of dependent variables except for muscle soreness are summarized in Table-1. There was no significant difference detected in the baseline values between the EC and EC arms.

A two-way ANOVA for repeated measurements revealed significant interactions (time × type) in MVC torque ($p < 0.01$), elbow joint angle ($p < 0.01$), and muscle thickness ($p = 0.013$) (Figure-5B, C, F). Main effect in time was detected in Strain ratio ($p = 0.046$) and upper arm circumference ($p = 0.044$)

(Figure-5A, E). Main effect in contraction type was detected in muscle soreness ($p < 0.01$) (Figure-5D).

From the post hoc test, Strain ratio significantly decreased at 1H (3.3 ± 1.5 , $p = 0.015$), 3H (3.2 ± 1.5 , $p = 0.012$), and 24H (3.5 ± 1.9 , $p = 0.02$) compared to PRE (7.4 ± 5.4) after the EC exercise, but there was no significant change after the CC exercise (PRE: 7.8 ± 4.9 , 1H: 6.3 ± 5.2 , 3H: 6.7 ± 3.5 , 24H: 6.9 ± 3.9). MVC torque significantly decreased at 1H (33.6 ± 14.4 N·m, $p < 0.01$), 3H (32.9 ± 2.9 N·m, $p < 0.01$), and 24H (38.1 ± 4.2 N·m, $p < 0.01$) compared to PRE (68.6 ± 3.4 N·m) after the EC exercise, and at 1H (61.2 ± 10.7 N·m, $p = 0.029$), 3H (60.7 ± 11.9 N·m, $p = 0.022$) compared to PRE (70.3 ± 12.8 N·m) after the CC exercise. Elbow joint angle significantly increased at 1H ($28.0 \pm 6.5^\circ$, $p < 0.01$), 3H ($32.7 \pm 11.1^\circ$, $p < 0.01$), and 24H ($29.0 \pm 5.9^\circ$, $p < 0.01$) compared to PRE ($7.8 \pm 6.5^\circ$) after the EC exercise, and at 1H ($14.7 \pm 6.1^\circ$, $p = 0.025$), 3H ($14.7 \pm 4.7^\circ$, $p = 0.025$) compared to PRE ($9.8 \pm 7.3^\circ$) after the CC exercise. There was no significant time course change in muscle soreness neither after the EC and CC exercises. Upper arm circumference significantly increased at 1H (33.3 ± 4.5 mm, $p = 0.034$) compared to PRE (32.9 ± 4.8 mm) after the CC exercise.

Discussion

The present study compared the effect of EC and CC exercises on muscle functions and structures and their time course changes. The hypothesis was that muscle structures and functions would be disrupted after eccentric and concentric exercises accompanied with the increase of muscle hardness, with greater and longer lasting changes after eccentric exercise. The decrease in MVC torque and joint ROM was greater and longer lasting accompanied with increased muscle hardness after the EC exercise, and the level of muscle soreness was greater after the EC exercise than after the CC exercise. This result was consistent with the results of previous researches^{(10) (13) (18) (22)}, and proved our hypothesis. On the other hand, there was no significant change in muscle hardness after the CC exercise, which was different from what we expected. Also, changes in upper arm circumference and muscle thickness were limited.

Table-1 Baseline measurement values of Strain ratio, MVC torque, elbow joint angle, upper arm circumference, and muscle thickness of the EC and CC arms

	EC	CC
Strain Ratio	7.4 ± 5.4	7.8 ± 4.9
MVC torque (N·m)	68.6 ± 3.4	70.3 ± 12.8
Elbow joint angle	7.8 ± 6.5	9.8 ± 7.3
Upper arm circumference (mm)	33.2 ± 4.0	32.9 ± 4.8
Muscle thickness (mm)	27.8 ± 3.7	27.6 ± 3.7

The mean ± SD of the measurement variables are shown. EC: Eccentric Contraction; CC: Concentric Contraction

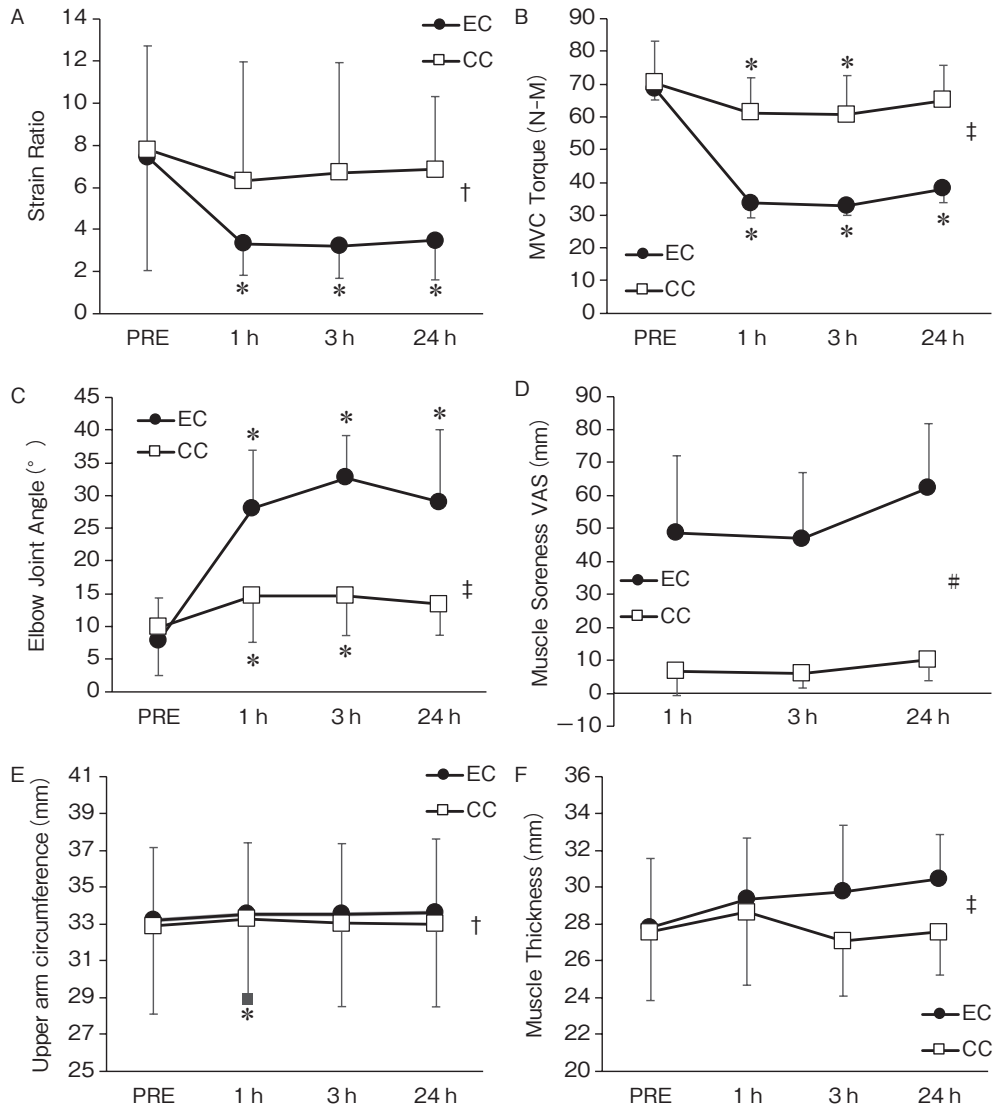


Figure-5

Changes in (A) Strain ratio, (B) MVC torque (N·m), (C) elbow joint angle (°), (D) muscle soreness VAS (mm), (E) upper arm circumference (mm), and (F) muscle thickness (mm) of the EC and CC arms through the time course.

Mean \pm SD values of each arms are shown.

‡ indicates the interaction ($p < 0.05$), † indicates the main effect of time ($p < 0.05$), and # indicates the main effect of type shown by the A two-way ANOVA for repeated measurements. * indicates a significant difference compared with the PRE-value based of the post hoc test except for the muscle soreness ($p < 0.05$).

Decreased MVC torque and joint ROM, and presence of muscle soreness has been reported to be an indirect index of muscle damage following an EC exercise, and the decreased MVC torque is the most valid and reliable index^(6) 23). It is well known that muscle damage causes the increase in intracellular Ca^{2+} level because of damaged sarcolemma⁽²⁴⁾⁻²⁸⁾. Researchers reported that increased Ca^{2+} level after the EC exercise induces cross bridge of actin and myosin causing muscle contracture which can lead to the increase in muscle hardness^(3) 4) 6) 9) 18) 22). Concerning the similar time course changes of

muscle hardness, MVC torque and elbow joint angle, and greater muscle soreness (Figure-5A~D), it is most likely that this phenomenon occurred in the present study causing the long-lasting increase in muscle hardness after the EC exercise.

While there was a significant and long-lasting disruption of muscle functions and muscle soreness after the EC exercise, those after the CC exercise was significant but smaller and shorter lasting. Above all, the CC exercise induced no significant change on muscle hardness. From this result, it is

less likely that a remarkable muscle damage occurred after the CC exercise. As mentioned above, the muscle functions are also disrupted due to muscle fatigue from shortage of fuel, impaired transport of substances within muscles, and accumulation of metabolites¹⁰⁻¹³⁾. In the previous research, it is reported that muscle fatigue is accompanied by decreased MVC torque and decreased ROM^{29) 30)}. These disrupted muscle functions recover within 120 minutes as muscle fatigue recovers³¹⁾. In the present study, the disruption (decreased MVC torque and joint ROM) remained at least 3 hours after the CC exercise, which was longer than the previous study. This difference could be from the different exercise protocol. Subjects performed repeated maximum voluntary contractions in the present study while subjects performed repeated 30% of the isometric MVC in the previous study³¹⁾. If the disruption of muscle functions after the CC exercise was caused by the muscle fatigue, the effect of muscle fatigue on muscle hardness after the CC exercise was not captured in the previous study protocol.

Muscle damage caused by an EC exercise also induces increased blood flow and fluid accumulation inside and around the muscle³²⁾, which causes increased intramuscular pressure leading to increase of muscle hardness^{19) 22)}. Murayama *et al.*⁹⁾, however, reported that the effect of swelling (oedema) on the muscle hardness was shown at 4 to 5 days after the EC exercise. Chleboun *et al.*³³⁾ also reported the change of muscle hardness is not associated with swelling within 48 hours after the EC exercise. Howell *et al.*³⁾ found increased upper arm circumference right after the EC exercise, but reported that it was mostly caused by increased subcutaneous fluid accumulation rather than muscle swelling. In the present study, there was no obvious morphological change in upper arm circumference and muscle thickness neither after the EC nor CC exercises except for the momentary increase in upper arm circumference after the CC exercise (Figure-5E), and their time course changes did not match that in muscle hardness. Since the measurement was conducted up to 24 hours after the exercise protocol in the present study, it seems that the change in intramuscular pressure and its effect on the muscle hardness was limited.

There are some limitations regarding the present study. First of all, there is a risk of type II error (false negative) because of the small sample size (n=6). Therefore, it is possible that more statistical significance would appear with a larger sample size. As a nature of the study protocol including the time consuming and vigorous exercise intervention in the present study, recruitment was the biggest issue. Secondly, we did not measure direct indicators of muscle damage and fatigue such as creatine kinase and Ca²⁺ even though we assumed that muscle damage and/or fatigue occurred after the exercise protocol. In the present study, muscle damage and fatigue were evaluated from indirect measurement such as MVC torque, joint ROM, and muscle soreness instead of direct measurements.

In conclusion, the disruption of muscle function was greater and longer lasting after the eccentric contraction exercise than the concentric contraction exercise when the exercises were performed with the same total work, and the muscle hardness only increased after the eccentric exercise without any morphological change up to 24-hours. The mechanisms of functional disruption following exercises and its effect on the muscle hardness may differ according to the type of muscle contraction.

Conflict of interest

The authors declare that they have no conflict of interest related to this study.

Acknowledgment

I appreciate Dr. Yoshio Suzuki's assistance with gathering statistics for the experiment. The results of the present study do not constitute endorsement of any products by the authors or the National Strength and Conditioning Association.

References

- 1) Clarkson PM, Hubal MJ: Exercise-induced muscle damage in humans. *Am J Phys Med Rehabil*, 2002; 81 (11 Suppl): S52-69.
- 2) Clarkson PM, Nosaka K, Braun B: Muscle function after exercise-induced muscle damage and rapid adaptation. *Med Sci Sports Exerc*, 1992; 24: 512-520.
- 3) Howell JN, Chleboun G, Conatser R: Muscle stiffness, strength loss, swelling and soreness following exercise-induced injury in humans. *J Physiol*, 1993; 464: 183-196.
- 4) Proske U, Morgan DL: Muscle damage from eccentric

- exercise: mechanism, mechanical signs, adaptation and clinical applications. *J Physiol*, 2001; 537 (Pt 2): 333-345.
- 5) Chen YW, Hubal MJ, Hoffman EP, Thompson PD, Clarkson PM: Molecular responses of human muscle to eccentric exercise. *J Appl Physiol* (1985), 2003; 95: 2485-2494.
 - 6) Proske U, Allen TJ: Damage to skeletal muscle from eccentric exercise. *Exerc Sport Sci Rev*, 2005; 33: 98-104.
 - 7) Peake J, Nosaka K, Suzuki K: Characterization of inflammatory responses to eccentric exercise in humans. *Exerc Immunol Rev*, 2005; 11: 64-85.
 - 8) Chen TC, Lin KY, Chen HL, Lin MJ, Nosaka K: Comparison in eccentric exercise-induced muscle damage among four limb muscles. *Eur J Appl Physiol*, 2011; 111: 211-223.
 - 9) Murayama M, Nosaka K, Yoneda T, Minamitani K: Changes in hardness of the human elbow flexor muscles after eccentric exercise. *Eur J Appl Physiol*, 2000; 82: 361-367.
 - 10) Sahlin K, Tonkonogi M, Söderlund K: Energy supply and muscle fatigue in humans. *Acta Physiol Scand*, 1998; 162: 261-266.
 - 11) Jones DA, Newham DJ, Torgan C: Mechanical influences on long-lasting human muscle fatigue and delayed-onset pain. *J Physiol*, 1989; 412: 415-427.
 - 12) Sjøgaard G, Savard G, Juel C: Muscle blood flow during isometric activity and its relation to muscle fatigue. *Eur J Appl Physiol Occup Physiol*, 1988; 57: 327-335.
 - 13) Enoka RM, Duchateau J: Muscle fatigue: what, why and how it influences muscle function. *J Physiol*, 2008; 586: 11-23.
 - 14) Inami T, Kawakami Y: Assessment of individual muscle hardness and stiffness using ultrasound elastography. *Journal of Physical Fitness and Sports Medicine*, 2016; 5: 313-317.
 - 15) Nordez A, Guevel A, Casari P, Catheline S, Cornu C: Assessment of muscle hardness changes induced by a submaximal fatiguing isometric contraction. *J Electromyogr Kinesiol*, 2009; 19: 484-491.
 - 16) Yanagisawa O, Niitsu M, Kurihara T, Fukubayashi T: Evaluation of human muscle hardness after dynamic exercise with ultrasound real-time tissue elastography: a feasibility study. *Clin Radiol*, 2011; 66: 815-819.
 - 17) Bouillard K, Jubeau M, Nordez A, Hug F: Effect of vastus lateralis fatigue on load sharing between quadriceps femoris muscles during isometric knee extensions. *J Neurophysiol*, 2014; 111: 768-776.
 - 18) Lacourpaille L, Nordez A, Hug F, Couturier A, Dibie C, Guilhem G: Time-course effect of exercise-induced muscle damage on localized muscle mechanical properties assessed using elastography. *Acta Physiol (Oxf)*, 2014; 211: 135-146.
 - 19) Murayama M, Yoneda T, Kawai S: Muscle tension dynamics of isolated frog muscle with application of perpendicular distortion. *Eur J Appl Physiol*, 2005; 93: 489-495.
 - 20) Witte RS, Kim K, Martin BJ, O'Donnell M: Effect of fatigue on muscle elasticity in the human forearm using ultrasound strain imaging. *Conf Proc IEEE Eng Med Biol Soc*, 2006; 1: 4490-4493.
 - 21) Jamurtas AZ, Theocharis V, Tofas T, *et al*: Comparison between leg and arm eccentric exercises of the same relative intensity on indices of muscle damage. *Eur J Appl Physiol*, 2005; 95: 179-185.
 - 22) Green MA, Sinkus R, Gandevia SC, Herbert RD, Bilston LE: Measuring changes in muscle stiffness after eccentric exercise using elastography. *NMR Biomed*, 2012; 25: 852-858.
 - 23) Warren GL, Lowe DA, Armstrong RB: Measurement tools used in the study of eccentric contraction-induced injury. *Sports Med*, 1999; 27: 43-59.
 - 24) Duncan CJ: Role of calcium in triggering rapid ultrastructural damage in muscle: a study with chemically skinned fibres. *J Cell Sci*, 1987; 87 (Pt 4): 581-594.
 - 25) Duncan CJ, Jackson MJ: Different mechanisms mediate structural changes and intracellular enzyme efflux following damage to skeletal muscle. *J Cell Sci*, 1987; 87 (Pt 1): 183-188.
 - 26) Nosaka K, Clarkson PM, McGuiggin ME, Byrne JM: Time course of muscle adaptation after high force eccentric exercise. *Eur J Appl Physiol Occup Physiol*, 1991; 63: 70-76.
 - 27) Overgaard K, Lindstrøm T, Ingemann-Hansen T, Clausen T: Membrane leakage and increased content of Na⁺-K⁺ pumps and Ca²⁺ in human muscle after a 100-km run. *J Appl Physiol* (1985), 2002; 92: 1891-1898.
 - 28) Snowdowne KW: The effect of stretch on sarcoplasmic free calcium of frog skeletal muscle at rest. *Biochim Biophys Acta*, 1986; 862: 441-444.
 - 29) Cheng AJ, Davidson AW, Rice CL: The influence of muscle length on the fatigue-related reduction in joint range of motion of the human dorsiflexors. *Eur J Appl Physiol*, 2010; 109: 405-415.
 - 30) Cowley JC, Gates DH: Proximal and distal muscle fatigue differentially affect movement coordination. *PLoS One*, 2017; 12: e0172835.
 - 31) Walsh LD, Hesse CW, Morgan DL, Proske U: Human forearm position sense after fatigue of elbow flexor muscles. *J Physiol*, 2004; 558 (Pt 2): 705-715.
 - 32) Ahmadi S, Sinclair PJ, Foroughi N, Davis GM: Monitoring muscle oxygenation after eccentric exercise-induced muscle damage using near-infrared spectroscopy. *Appl Physiol Nutr Metab*, 2008; 33: 743-752.
 - 33) Chleboun GS, Howell JN, Conatser RR, Giesey JJ: Relationship between muscle swelling and stiffness after eccentric exercise. *Med Sci Sports Exerc*, 1998; 30: 529-535.