Comparison between maximal lengthening and shortening contractions for biceps brachii muscle oxygenation and hemodynamics

Makii Muthalib,1,4 Hoseong Lee,1 Guillaume Y. Millet,1,2 Marco Ferrari,3 and Kazunori Nosaka1

1School of Exercise, Biomedical and Health Sciences, Edith Cowan University, Joondalup, Western Australia, Australia; 2Université de Lyon, F-42023, and Exercise Physiology Laboratory, Jean Monnet University, Saint-Etienne, France; 3Department of Health Sciences, University of L’Aquila, L’Aquila, Italy; and 4Institute of Health and Biomedical Innovation and School of Human Movement Studies, Queensland University of Technology, Brisbane, Queensland, Australia

Submitted 18 November 2009; accepted in final form 30 June 2010

Muthalib M, Lee H, Millet GY, Ferrari M, Nosaka K. Comparison between maximal lengthening and shortening contractions for biceps brachii muscle oxygenation and hemodynamics. J Appl Physiol 109: 710–720, 2010. First published July 1, 2010; doi:10.1152/japplphysiol.01297.2009.—Eccentric contractions (ECC) require lower systemic oxygen (O2) demand of the exercising muscle is lower during maximal ECC contractions. It is not known whether oxidative metabolic demand of the exercising muscle is lower during maximal ECC contractions compared with maximal CON contractions. Near-infrared spectroscopy (NIRS) is a noninvasive optical technique that allows for the continuous measurements of muscle oxygenation and hemodynamics (14, 15). NIRS has been used to assess local muscle oxidative metabolism during exercise (14, 15, 28). It was thought that NIRS could clarify a difference in oxidative metabolic demand between maximal ECC and CON exercise. No previous study has compared between maximal ECC and CON contractions for changes in biceps brachii muscle oxidative metabolism using NIRS. Therefore, the first aim of the present study was to investigate the changes in biceps brachii muscle oxygenation and hemodynamics during maximal ECC and CON contractions of the elbow flexors using NIRS. We hypothesized that changes in biceps brachii muscle oxygenation and hemodynamics during ECC contractions would be smaller compared with that during CON contractions.

It has been well documented that unaccustomed exercise consisting of ECC contractions induces microtrauma to muscle fibers and/or extracellular matrix, followed by inflammatory responses, which are associated with delayed-onset muscle soreness, prolonged strength loss, and increase in muscle proteins, such as creatine kinase (CK), in the systemic circulation (7, 31). Several animal studies have shown an alteration/dysfunction in the muscle microcirculation after ECC contractions (16, 18, 19). For example, Kano et al. (18) reported a faster rate of decrease in rat muscle microcirculation O2 pressure during 3-min electrically evoked, repeated muscle contractions at 1–3 days after downhill running compared with nondamaged muscle. They suggested that this was due to microcirculation dysfunction reducing muscle O2 supply. In human studies, Davids et al. (9) reported that the rate of decrease in vastus lateralis muscle oxygenation measured using NIRS was significantly slower during a near-maximal intensity cycling task 2 days after squat exercise compared with the preexercise rate and suggested that this was due to an elevation of O2 supply relative to O2 demand because of microcirculation dysfunction. Ahmadi et al. (2) showed significantly smaller biceps brachii muscle oxygenation amplitude com-
pared with the preexercise values during a sustained isometric contraction at 80% maximal voluntary contraction (MVC) intensity 1–3 days after maximal ECC contractions of the elbow flexors. However, the time course of the effects of muscle damage induced by ECC contractions on muscle oxygenation has not been clarified, and no previous studies have compared the postexercise changes in muscle oxygenation and hemodynamics following ECC compared with CON that does not generally result in muscle damage (22).

Thus the second aim of this study was to compare between maximal ECC and CON contractions of the elbow flexors for changes in muscle damage markers and biceps brachii muscle oxygenation and hemodynamics during sustained and repeated MVC tasks following exercise for 3 days. It was hypothesized that biceps brachii muscle oxygenation and hemodynamic amplitude during the sustained and repeated MVC tasks would be smaller following ECC than CON contractions.

MATERIALS AND METHODS

Subjects

Seven men and three women participated in this study, and their mean (±SD) age, height, and body mass were 28.9 ± 6.3 yr, 172.5 ± 8.2 cm, and 70.8 ± 9.0 kg, respectively. The number of subjects was determined by a sample size analysis based on the effect size of 1, α-level of 0.05, and a power (1-β) of 0.80 for an expected difference of 20% in muscle oxygenation amplitude during a sustained MVC task between ECC and CON using our laboratory’s previous NIRS study data (28). All subjects had no known metabolic or neuromuscular disorders, or any upper extremity muscle or joint injuries. None of the subjects had taken part in any resistance training exercise of the elbow flexors for at least 6 mo before starting the study. The subjects were requested to avoid taking any anti-inflammatory medication during the study. The study was approved by the Edith Cowan University Human Research Ethics Committee, and the study was conducted in conformity with the Declaration of Helsinki. A written, informed consent form was signed by each subject.

Study Design

The study used a crossover design where one arm performed exercise of the elbow flexors consisting of ECC contractions, while the contralateral arm performed the elbow flexor exercise consisting of CON contractions in a counterbalanced order, separated by 2–3 wk, to provide enough recovery time from the previous bout (Fig. 1). The use of the dominant and nondominant arm was counterbalanced among subjects, such that six subjects used their dominant arm for ECC, and four subjects used their nondominant arm for ECC in the first bout. The experimental period for each exercise session included a familiarization session was provided, since our laboratory’s previous study (23) and pilot work have indicated that even performing sub-maximal isometric contractions can induce some protective effect on muscle damage. However, before the first testing session, each subject was familiarized with the experimental procedures. The dependent variables for the first aim of the study included torque, muscle oxygenation, and hemodynamics during the maximal ECC and CON contractions. For the second aim of the study, the dependent variables consisted of MVC, muscle soreness, and plasma CK activity as muscle damage markers, and torque and muscle oxygenation and hemodynamic amplitude during a sustained (10-s) and a 30-repeated (1-s contraction, 1-s relaxation) MVC task. As shown in Fig. 1, these dependent variables were measured immediately before and after (except muscle soreness and plasma CK activity), and 1–3 days following ECC and CON exercise. Muscle soreness and plasma CK activity were measured before and 1–3 days following the exercise. These dependent variables have been used in previous studies (28–30), and the ECC exercise has been shown to induce appreciable muscle damage to the biceps brachii muscles (29, 30).

Experimental Setup

Each subject was seated on a preacher arm curl bench, which secured the upper arm at 45° shoulder flexion. The elbow joint was aligned with the axis of rotation of an isokinetic dynamometer (Cybex6000, Lumex, Ronkonkoma, NY) operated by HUMAC-2004 software (Computer Sports Medicine, Stoughton, MA), and the lever arm of the dynamometer was attached to the subject’s wrist in a supinated position with an elbow joint angle of 90°. Torque signals were collected onto a data acquisition system (PowerLab16/30 with Chart 5.5.5 software, AD Instruments, Bella Vista, NSW, Australia) at a sampling rate of 200 Hz.

NIRS. NIRS directly measures the O2 dependent absorption of hemoglobin (Hb) in the microcirculation blood vessels (i.e., arterioles, capillaries, and venules) and myoglobin in the muscle cytoplasm, but the contribution of myoglobin deoxygenation to the NIRS signal during dynamic exercise is still debated and estimated to be <20% (14). This study used a NIRO-200 oximeter (Hamamatsu Photonics K.K., Hamamatsu, Japan), which measures concentration changes in oxygenated-Hb (HbO2), deoxygenated-Hb (HHb), and total Hb volume ([Hb] = HbO2 + HHb), expressed in micromoles times centimeter, and an absolute measure of HbO2 saturation represented as tissue oxygenation index (TOI = HbO2/Hb × 100), expressed in percent, using spatially resolved spectroscopy methods (35). TOI reflects the dynamic balance of O2 supply by the muscle microcirculation and O2 consumption/demand by the muscle (15, 26), and the changes in TOI can be considered an indirect measure of changes in local muscle blood flow/O2 supply (14).

The NIRO-200 optical probe unit consists of one emitter (with three laser-emitting diodes of 775, 810, and 850 nm) and one detector (with two silicon photodiodes separated by a 6-mm center-to-center distance), separated by a center-to-center distance of 4 cm. The optical probe unit was supported by a black rubber shell and was firmly attached to the skin at the medial side over the midbelly of the biceps brachii muscle, parallel to the major axis of the arm by a double-sided adhesive tape, which ensured no sliding of the probe on the skin. The rubber shell was covered by a soft black cloth, and all wires were taped down to minimize movement during exercise. The position of

### Dependent variables

<table>
<thead>
<tr>
<th>Variable</th>
<th>Pre</th>
<th>Exercise</th>
<th>Post 1-d</th>
<th>Post 2-d</th>
<th>Post 3-d</th>
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<tr>
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<td>Arm 1 (CON or ECC 2-3 wk)</td>
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<td>X</td>
<td>X</td>
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<tr>
<td><strong>VAS</strong></td>
<td>X</td>
<td>Arm 2 (ECC or CON)</td>
<td>X</td>
<td>X</td>
<td>X</td>
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<tr>
<td><strong>MVC (3-s)</strong></td>
<td>X</td>
<td>(Torque, TOI, tHb)</td>
<td>X</td>
<td>X</td>
<td>X</td>
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<tr>
<td><strong>10-s sustained MVC</strong></td>
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<td>(Torque, TOI, tHb)</td>
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<td><strong>30-repeated MVC</strong></td>
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<td>(Torque, TOI, tHb)</td>
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Fig. 1. Study protocol. During exercise [eccentric (ECC) or concentric (CON)], torque and near-infrared spectroscopy (NIRS) parameters [tissue oxygenation index (TOI) and total hemoglobin volume ([Hb]) were continuously measured. Before (Pre), immediately after (Post), and 1, 2, and 3 days following exercise, plasma creatine kinase (CK) activity (no measurement at Post), muscle soreness by visual analog scale (VAS) (no measurement at Post), maximal voluntary isometric contraction (MVC) strength, and 10-s sustained MVC and 30-repeated (1-s contraction, 1-s relaxation) MVCs were measured, in this order.
the NIRS probe was marked on the skin with a semipermanent ink marker to obtain consistent measures over subsequent testing sessions. The placement of the probe was similar for the arm used for ECC and CON contractions.

Subcutaneous adipose tissue thickness has been reported to affect NIRS measurement sensitivity (26); therefore, a B-mode ultrasound apparatus fitted with a 7.5-MHz linear probe (SSD-1000, Aloka, Tokyo, Japan) was used to measure the subcutaneous fat layer thickness of the area over which the NIRS optical probe unit was placed. No significant difference in the adipose tissue thickness between the ECC (2.7 ± 0.6 mm) and CON (2.7 ± 0.5 mm) arms was found, and no changes in the thickness were observed 1–3 days following exercise. Considering that the adipose tissue thickness was relatively low, and the penetration depth of the NIRS signal is approximately one-half of the emitter-detector separation (4 cm), the changes in TOI and tHb can be considered to reflect mainly the biceps brachii muscle metabolic and hemodynamic changes, respectively (13).

Before each testing session, an initialization procedure on the NIRO-200 was carried out, which set each laser power automatically to establish the optimum measurement conditions. The zero set procedure was also adopted to return the tHb to the zero value. This procedure does not affect the TOI values, since TOI is measured as absolute values instead of a change with respect to the arbitrary initial zero value. NIRS signals were sampled at 6 Hz by the NIRO-200 and were collected simultaneously with torque data onto the PowerLab system and stored on the computer for later analysis.

**ECC and CON Exercise**

ECC exercise consisted of 10 sets of 6 maximal voluntary lengthening contractions of the elbow flexors at a constant velocity of 90°/s. In each contraction, the elbow joint was forcibly extended by the lever arm of the isokinetic dynamometer from a flexed position (90°) to a fully extended position (180°) in 1 s, while the subject was verbally encouraged to maximally resist through the range of motion. The isokinetic dynamometer returned the arm to the flexed position at a constant velocity of 30°/s after each contraction, creating a 3-s passive recovery between contractions, and the rest period between sets was 2 min. For CON exercise, subjects were required to maximally contract the elbow flexors from the fully extended (180°) to the flexed (90°) elbow joint angle. The lever arm of the isokinetic dynamometer moved at a constant velocity of 90°/s for 10 sets of 6 repetitions, with the same rest period between contractions and sets as those of the ECC exercise protocol. This protocol was adopted from the ECC exercise protocol.

**Dependent Variables During Exercise**

Figure 2 shows typical torque, change (Δ) in TOI and ΔtHb changes during a set consisting of six contractions for the ECC and CON sessions. The average torque integral of the six contractions was calculated for each set and used for analysis. The baseline of ΔTOI and ΔtHb was determined as the mean value over 6 s before the onset of the first contraction of the set, which was then offset to zero. TOI

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**Fig. 2.** Typical changes in elbow flexor torque, biceps brachii TOI (ΔTOI), and tHb (ΔtHb) over 6 maximal ECC and CON contractions of a set (4th set). ΔTOI_{min}, minimum ΔTOI amplitude; ΔtHb_{mean} and ΔtHb_{max}, average of minimum and maximum ΔtHb amplitude (bottom and top solid gray line), respectively. Baseline of ΔTOI and ΔtHb was determined as the mean value over 6 s before the onset of the first contraction of the set, which was then offset to zero.
and tHb measurements for each set are presented as the magnitude of change from the respective baseline. Minimum ΔTOI desaturation amplitude (ΔTOI_{min}) was determined as the difference between the minimum TOI value reached during the six contraction phases and TOI baseline before the first contraction. Average decrease of the tHb amplitude (ΔHb_{mean}) was calculated from the average of the differences between the minimum tHb amplitude reached during the six contraction phases and the corresponding baseline value before the first contraction. Average increase of the tHb amplitude (ΔHb_{max}) was the average of the differences between the maximum tHb amplitude reached during the six relaxation phases and the corresponding baseline value before the first contraction.

**Dependent Variables Following ECC and CON Exercise**

**MVC.** MVC was determined on the same apparatus and positioning as that used for the exercise session. Each subject performed two 3-s MVCs at 90° elbow angle with a 45-s rest between contractions, and the peak torque of the two contractions was used as the MVC. The test-retest reliability (coefficient of variation) of the MVC was ~5%, based on our laboratory’s previous study (28).

**Muscle soreness.** Muscle soreness was assessed using a 100-mm visual analog scale, where 0 mm indicates “no pain”, while 100 mm was an indication of “worst pain”. Subjects were instructed to place a mark on the 100-mm line, while the investigator palpated the midbelly of the biceps at a region 9 cm from the elbow crease. Palpation was performed by the same investigator for all subjects using the distal portions of the index and forefingers in a circular motion over the site.

**Plasma CK activity.** Approximately 5 ml of blood were drawn by a standard venipuncture technique from an antecubital vein. Approximately 30 μl of blood were pipetted onto a test strip and assayed in duplicate by a spectrophotometer (Reflotron, Boehringer-Manheim, Pode, Czech Republic) for CK activity. Before each testing session, quality control (calibration) measurements were undertaken, according to the manufacturer recommendations. The “normal” reference range for CK activity, as provided by the manufacturer using this method, is 24–195 IU/L.

**Sustained and repeated MVC tasks.** It has been reported that, during sustained isometric contractions above 30% MVC, muscle O2 supply is impeded due to increased intramuscular pressure compressing the small blood vessels within the muscle microcirculation (11). Therefore, during a sustained isometric task at MVC intensity, changes in muscle oxygenation would primarily represent muscle O2 consumption, which is also considered a measure of energy consumption for muscle force production (10, 13, 20). In contrast, during repeated isometric contractions (1-s contraction, 1-s relaxation), where reoxygenation is permitted during the relaxation phases, the dynamics of O2 supply and O2 demand are both represented (36). Therefore, during a sustained MVC task, the changes in ΔTOI and ΔHb primarily provide information on muscle O2 demand, while, during repeated isometric contractions, the changes in ΔTOI and ΔHb provide additional information on the regulation of O2 supply to meet the muscle metabolic demand for O2. The present study utilized the following sustained and repeated MVC tasks to assess changes in biceps brachii ΔTOI and ΔHb before and following ECC and CON.

After a 3-min rest period from the MVC measure, each subject performed a sustained (10-s) maximal isometric contraction task followed by a 30-repeated (1-s contraction, 1-s relaxation) maximal isometric contraction task at the elbow joint angle of 90° with 10-min rest between the tasks. The torque output was indicated visually on a computer screen as feedback, and the tone from the computer indicated the timing of the contraction and relaxation for the repeated contractions.

Figure 3A shows typical changes in torque, ΔTOI, and ΔHb during the 10-s sustained MVC task. The torque integral was determined as the area under the torque traces over the contraction duration. The baseline of TOI and tHb was determined as the mean value over 30-s before the onset of contraction. Since the baseline was stable, the TOI and tHb baseline was offset to zero, and TOI and tHb are presented as the magnitude of change from the respective baseline. ΔTOI_{max} was determined as the difference between the minimum TOI value reached during the contraction phase and the TOI baseline. ΔHb_{mean} was determined as the difference between the average tHb value during the contraction phase and the corresponding tHb baseline.

Figure 3B shows typical changes in torque, ΔTOI, and ΔHb during the 30-repeated MVC task. The torque integral was determined as sum of the area under the torque traces during each of the 30 contractions. ΔTOI_{min} was determined as the difference between the minimum TOI value reached during the 30 contractions and the TOI baseline. ΔHb_{mean} was determined as the difference between average of the minimum tHb amplitude reached during the 30 contractions and the tHb baseline.

The within-day (3 h difference between tests) and between-day (2 days between tests) reliability determined by coefficient of variation for TOI baseline and ΔTOI_{min} during both sustained and repeated MVC tasks were 4 and 7%, respectively (28).

**Statistical Analyses**

All variables were checked for normality using a Shapiro-Wilk test, and muscle soreness and CK were found to be not normally distributed. Changes in torque integral and NIRS parameters (ΔTOI_{min}, ΔHb_{mean}, and ΔHb_{max}) over the 10 sets were compared between ECC and CON sessions by a two-way repeated-measures ANOVA. If a significant main effect for session or interaction effect was found, post hoc multiple pairwise comparisons using Student t-tests with Bonferroni correction were performed. The preexercise values of each measure were compared between ECC and CON sessions by a Student t-test. Changes in MVC, TOI baseline, and torque integral, ΔTOI_{ass}, and ΔHb_{mean} (percentage of the respective preexercise value) during the sustained and repeated MVC tasks were compared between ECC and CON sessions over time using a two-way repeated-measures ANOVA with Bonferroni corrected post hoc tests. When the ANOVA returned a significant main effect for time, separate one-way repeated-measures ANOVAs with Bonferroni corrected post hoc tests were applied to locate any significant differences from the preexercise. Changes in muscle soreness and plasma CK activity following exercise were compared between ECC and CON sessions using nonparametric methods (Friedman, Mann-Whitney, and Wilcoxon tests). Statistical computations were performed using SPSS software (version 15, SPSS Lead Technologies, Chicago, IL). Significance was set at P < 0.05. Data are presented as means ± SE.

**RESULTS**

**Comparison Between ECC and CON During Exercise**

Figure 2 shows torque, ΔTOI, and ΔHb changes over six contractions during a set for the ECC and CON sessions of one subject who showed typical changes in these variables. All subjects and all sets showed a similar pattern to that shown in the figure. The torque increased at the onset of each contraction and returned to baseline at the end of each contraction, but the peak torque was greater for ECC than CON. For CON, ΔTOI decreased from baseline during the contraction phases and increased toward baseline during relaxation phases and reached minimum values at the end of the six contractions. This was also the case for ECC; however, the magnitude of the decreases were smaller than for CON, and minimum ΔTOI amplitude was always higher for ECC than CON. ΔHb decreased from the baseline soon after the onset of contraction and reached similar minimum levels in both ECC and CON. ΔHb quickly recovered toward baseline after the end of the contraction phase and reached
the maximum levels during the relaxation phase, but ΔHb exceeded the baseline value in the relaxation phase for CON, and ΔHb maximum levels were greater for CON than ECC. It should be noted that the timing of the contraction and relaxation phases are slightly different between ECC and CON, but this does not influence the amplitude changes in ΔTOI and ΔHb.

Mean changes in torque integral, ΔTOI_{min}, ΔHb_{mean}, and ΔHb_{max} of 6 contractions over the 10 sets for the ECC and CON sessions are shown in Fig. 4. The torque integral over the 10 sets for ECC was greater (P < 0.05) by 30% compared with CON, and decreased (P < 0.001) progressively over the 10 sets for both ECC and CON. The percent decrease in torque integral from the 1st to the 10th set was not significantly different between ECC (24.1 ± 5.8%) and CON (21.8 ± 3.2%). Over the 10 sets, ΔTOI_{min} during ECC was higher (P < 0.01) by 50% compared with CON. Although ΔTOI_{min} during the 1st set was not significantly different between ECC and CON, ΔTOI_{min} was higher for ECC than CON from the 2nd (P < 0.01) to the 10th set (P < 0.001). There was no significant difference in the changes in ΔHb_{mean} between ECC and CON, but ΔHb_{max} was smaller (P < 0.05) for ECC than CON. Both ΔHb_{mean} and ΔHb_{max} were maintained at similar levels over the 10 sets for both ECC and CON.

Comparison Between ECC and CON Following Exercise

MVC, muscle soreness, and plasma CK activity. Changes in MVC, muscle soreness, and plasma CK activity before and after ECC and CON are shown in Table 1. There were no significant differences between ECC and CON for any of the preexercise values. MVC decrement immediately after the exercise was greater (P < 0.001) for ECC (54.6 ± 3.4%) than CON (20.1 ± 2.5%). MVC was smaller by 35–45% than the preexercise value 1–3 days after ECC (P < 0.05); however, this was not the case after CON. Muscle soreness increased (P < 0.01) from preexercise values 1–3 days only after ECC. Plasma CK activity increased (P < 0.01) from preexercise values 1–3 days after ECC, but only at 1 day after CON (P < 0.05). Increases in CK were greater for ECC than CON at 2 (P < 0.01) and 3 days (P < 0.05).

Torque, TOI, and tHb during sustained and repeated MVC tasks. As shown in Fig. 3A, absolute changes in torque, ΔTOI, and ΔHb during the sustained MVC task at 1 day after ECC were smaller compared with preexercise values for a typical subject. Similarly, for the repeated MVC task, absolute changes in torque, ΔTOI, and ΔHb during the contraction phases were smaller at 1 day after ECC com-
pared with those at preexercise, and ΔTOI was maintained near or above baseline levels throughout the repeated MVC task (Fig. 3B).

TOI baseline for the sustained and repeated MVC task was not significantly different between ECC and CON measured at preexercise (55.6 ± 1.8 vs. 54.9 ± 1.9% and 56.6 ± 1.5 vs. 56.5 ± 1.7%, respectively) and 1- to 3-day postexercise testing time points; however, TOI baseline for the sustained MVC task measured immediately postexercise was greater (P < 0.05) than that of preexercise for both ECC (60.3 ± 1.5%) and CON (59.5 ± 1.4%), without significant difference between the two sessions.

Preexercise values in torque integral, TOImin, and tHbmean during the sustained MVC task were not significantly different between ECC (547.7 ± 57.0 Nm, 40.6 ± 2.7%, and 388.2 ± 65.5 μM·cm, respectively) and CON (544.8 ± 60.6 Nm, 38.6 ±

Table 1. Changes in MVC, muscle soreness (VAS), and plasma CK activity measured Pre, Post, and 1–3 days following ECC and CON sessions

<table>
<thead>
<tr>
<th></th>
<th>Pre</th>
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<th>3 Days</th>
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<tr>
<td>ECC</td>
<td>55.1 ± 5.4</td>
<td>24.6 ± 3.0+†</td>
<td>30.6 ± 4.3+†</td>
<td>32.9 ± 5.0†</td>
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<td>CON</td>
<td>56.4 ± 5.7</td>
<td>45.2 ± 5.3†</td>
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<td>VAS, mm</td>
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<tr>
<td>ECC</td>
<td>0.0 ± 0.0</td>
<td>31.9 ± 2.8+†</td>
<td>47.2 ± 4.4+†</td>
<td>42.9 ± 6.4+†</td>
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<tr>
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<tr>
<td>ECC</td>
<td>87.3 ± 11.4</td>
<td>213.5 ± 56.4+†</td>
<td>211.6 ± 37.6+†</td>
<td>493.2 ± 199.0+†</td>
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<tr>
<td>CON</td>
<td>89.8 ± 7.2</td>
<td>122.7 ± 20.2†</td>
<td>114.9 ± 10.9</td>
<td>106.9 ± 8.6</td>
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</table>

Values are means ± SE; N = 10 subjects. Pre, before; Post, immediately after; MVC, maximal voluntary isometric contraction; VAS, visual analog scale; CK, creatine kinase; ECC, eccentric; CON, concentric. *Significantly (P < 0.05) different from the corresponding value of CON. †Significantly (P < 0.05) different from Pre.
2.7%, and −370.2 ± 59.6 μM·cm, respectively) sessions. Figure 5A shows the percent changes in torque integral, ΔTOI<sub>min</sub>, and ΔtHb<sub>mean</sub> from the preexercise value during the sustained MVC task after ECC and CON sessions. Although the decrease in torque integral immediately after exercise was greater (P < 0.001) for ECC than CON, the decrease in ΔTOI<sub>min</sub> and ΔtHb<sub>mean</sub> was not significantly different between ECC and CON immediately after exercise. Figure 5A shows the percent changes in torque integral, ΔTOI<sub>min</sub>, and ΔtHb<sub>mean</sub> from the preexercise value during the sustained MVC task after ECC and CON sessions. Although the decrease in torque integral immediately after exercise was greater (P < 0.001) for ECC than CON, the decrease in ΔTOI<sub>min</sub> and ΔtHb<sub>mean</sub> was not significantly different between ECC and CON immediately after exercise. Torque integral was decreased (P < 0.001) by 40–50% at 1–3 days after ECC; however, no significant changes in torque integral were evident after CON. ΔTOI<sub>min</sub> was decreased by 30–50% at 1 (P < 0.01) to 3 days (P < 0.05) after ECC; however, no significant changes in ΔTOI<sub>min</sub> were evident after CON. ΔTOI<sub>min</sub> was lower from 1 (P < 0.01) to 3 days (P < 0.05) after ECC compared with CON. ΔtHb<sub>mean</sub> decreased from preexercise values by 40–50% at 1 (P < 0.01) and 2 days (P < 0.05) after ECC; however, no significant changes in ΔtHb<sub>mean</sub> were evident after CON.

During the repeated MVC task, preexercise values in torque integral, ΔTOI<sub>min</sub>, and ΔtHb<sub>mean</sub> were not significantly different between ECC (1,216.1 ± 117.4 Nm, −27.7 ± 2.4%, and −339.5 ± 61.7 μM·cm, respectively) and CON (1,301.9 ± 144.1 Nm, −23.5 ± 2.7%, and −324.7 ± 55.1 μM·cm, respectively). The percent changes in torque integral and ΔTOI<sub>min</sub> and ΔtHb<sub>mean</sub> from the preexercise value during the repeated MVC task after ECC and CON are shown in Fig. 5B. Although the decrease in torque integral immediately after exercise was greater (P < 0.001) for ECC than CON, the decrease in ΔTOI<sub>min</sub> and ΔtHb<sub>mean</sub> were not significantly different between ECC and CON immediately after exercise. ECC resulted in 40–50% decreases (P < 0.001) in torque integral 1–3 days after exercise; however, no significant changes were observed after CON. ΔTOI<sub>min</sub> decreased from the preexercise value by 40–70% at 1–3 days (P < 0.05) after ECC, but no such changes were seen after CON. ΔTOI<sub>min</sub> was lower 1–3 days (P < 0.05) after ECC compared with CON. ΔtHb<sub>mean</sub> was significantly smaller by 30–40% at 1 (P < 0.01) and 2 days (P < 0.05) after ECC; however, no significant differences in ΔtHb<sub>mean</sub> from the preexercise value were evident after CON.

Fig. 5. Percent changes from preexercise (mean ± SE; N = 10) in elbow flexor torque integral and biceps brachii ΔTOI<sub>min</sub> and ΔtHb<sub>mean</sub> during the sustained (A) and repeated (B) maximal isometric contraction tasks measured Pre, Post, and 1–3 days after the ECC and CON sessions. *Significantly (P < 0.05) different between ECC and CON. #Significantly (P < 0.05) different from Pre.
DISCUSSION

This is the first NIRS study to compare between maximal ECC and CON contractions for changes in biceps brachii muscle oxidative metabolism during exercise and for 3 days postexercise. Despite the torque generated during the exercise being ~30% greater for ECC than CON, ΔTOI_{min} was ~50% higher during ECC than CON, and ΔHb_{max} was ~100% lower for ECC than CON. No significant difference in ΔHb_{mean} was found between sessions. These results support our first hypothesis that ECC contractions would result in smaller changes in biceps brachii muscle oxygenation and hemodynamics compared with CON contractions. In the 1–3 days following ECC, the torque integral, ΔTOI_{min}, and ΔHb_{mean} during the sustained and repeated MVC tasks were smaller than their respective preexercise values; while no significant changes in these variables from preexercise were apparent 1–3 days after CON. Moreover, both torque integral and ΔTOI_{min} were consistently smaller 1–3 days after ECC than CON. These findings support our second hypothesis that biceps brachii muscle oxygenation and hemodynamic amplitude during the sustained and repeated MVC tasks would be smaller following ECC than CON contractions.

Comparison Between ECC and CON During Exercise

Torque integral during the 10 sets were significantly greater by ~30% for ECC than CON, which confirms previous findings on the elbow flexors (24) and knee extensors (4), showing that ECC contractions produce greater torque than CON contractions. Over the 10 sets, torque integral decreased for both ECC and CON, such that the percent decline in ECC and CON torque integral from the 1st to the 10th set was similar. These changes were similar to those shown in a previous study (24).

The magnitude of change in torque, ΔTOI, and ΔHb over the six contractions of a set in ECC and CON, as shown in Fig. 2, are well represented in the mean values shown in Fig. 4. The similar ΔHb_{mean} between ECC and CON would suggest that intramuscular pressure during the 1-s contraction phases was high enough to occlude/displace a similar amount of blood volume (11), which then returned during the subsequent relaxation phases. However, the greater ΔHb_{max} in the relaxation phases for CON than ECC suggests that CON induced a greater vasodilatory stimulus than ECC. Muscle blood flow has been shown to increase in proportion to the metabolic demands of the tissue, such that there is a direct relationship between the increase in muscle blood flow and increased muscle O_{2} consumption (8). Therefore, the greater increase in ΔHb_{max} for CON than ECC may indicate that blood flow/O_{2} supply was increased to a greater extent in the relaxation phases for CON than ECC. Despite a greater blood flow for CON, ΔTOI steadily decreased from baseline over successive contraction phases in CON, while ΔTOI decreased at a much slower rate for ECC, and ΔTOI_{min} values were consistently lower for CON than ECC (Figs. 2 and 4). The results of the present study suggest that the biceps brachii muscle oxygenation, representing blood flow to O_{2} utilization, during maximal ECC contractions was ~50% smaller than that during maximal CON contractions.

Perrey et al. (32) compared pulmonary O_{2} consumption kinetics between near-maximal intensity ECC and CON cycling (6 min) and reported that the steady-state O_{2} consumption during ECC cycling was ~30% of that during CON cycling at the same power output. Since the exercise mode and intensity, muscle group, and measurement technique are different between the present study and the study by Perrey et al., a direct comparison cannot be made. However, it is interesting to note that the smaller systemic O_{2} consumption for ECC than CON (30%) corresponds to the smaller local muscle oxygenation for ECC than CON shown in the present study (50%), although the magnitude of difference between ECC and CON is not necessarily the same between the two parameters. It should be investigated further how much difference in systemic O_{2} consumption exists between maximal ECC and CON contractions of the elbow flexors.

Previous research has shown a lower muscle activation during ECC than CON for a greater or similar force production (3–5, 39). For example, Beltman et al. (4) demonstrated using interpolated twitch technique that knee extensor voluntary activation during 10 (1-s contraction, 1-s relaxation) maximal contractions at a velocity of 60°/s was significantly lower for ECC (~79%) than CON (~92%) contractions, while torque production was ~30% greater for ECC than CON contractions. Needle biopsies collected from the vastus lateralis muscle immediately after the respective contractions indicated a ~55% lower phosphocreatine-to-creatine ratio of grouped muscle fiber populations for ECC than CON contractions. This difference in torque production and phosphocreatine-to-creatine ratio between ECC and CON reported in the Beltman et al. study is similar to the ~30 and ~50% difference in torque and ΔTOI_{min} amplitude, respectively, shown in the present study. This may suggest that the lower biceps brachii muscle metabolic demand for O_{2} during ECC than CON contractions is most likely due to a lower centrally mediated activation for ECC than CON contractions. However, it is also acknowledged that part of the lower metabolic demand for O_{2} could stem from a lower ATP demand at the muscle level for ECC than CON contractions (34). Therefore, the smaller oxidative metabolic demand for a greater torque output for ECC than CON contractions would suggest that muscle metabolic efficiency (i.e., metabolic energy used per unit of mechanical energy output) was greater for ECC than CON contractions.

It is possible that the greater force produced for a lower metabolic demand during ECC than CON contractions is related to the difference in cross-bridge behavior (17). Brunello et al. (6) indicated that an ECC contraction promotes the attachment of the second myosin head to actin, which results in greater forces being exerted by individual cross bridges than CON contractions. The neural input and metabolic cost required to produce a greater force output is lower during ECC than CON contractions (12). However, the greater muscle mechanical efficiency (i.e., lower ATP hydrolysis) for ECC than CON contractions is also acknowledged (34). The greater force per activated cross bridge during ECC than CON contractions may well be the cause of damage to the muscle fibers and/or extracellular matrix (7).

Comparison Between ECC and CON Following Exercise

The MVC decrement and increases in muscle soreness and plasma CK activity were significantly greater after ECC than CON, as shown in previous studies (7, 22), suggesting greater muscle damage after ECC than CON (7, 31). Since MVC was
not significantly different from preexercise at 1 day for CON, and the increases in plasma CK activity was minimal following CON, it did not appear that CON resulted in muscle damage. Thus the greater percent decrement in torque integral, $\Delta TOI_{\text{min}}$, and $\Delta tHb_{\text{mean}}$ from the respective preexercise values during the sustained and repeated MVC tasks 1–3 days after ECC compared with CON were most likely due to muscle damage.

It is interesting to note that, although MVC and torque integral decrement were significantly greater for ECC than CON during both sustained and repeated MVC tasks immediately postexercise, no significant differences in $\Delta TOI_{\text{min}}$ and $\Delta tHb_{\text{mean}}$ were apparent between ECC and CON at this time point (Fig. 5). It is possible that the changes in torque integral, $\Delta TOI_{\text{min}}$, and $\Delta tHb_{\text{mean}}$ immediately after exercise were due to not only muscle damage but also muscle fatigue. In fact, MVC and torque integral decreased after CON; therefore, the changes in $\Delta TOI_{\text{min}}$ and $\Delta tHb_{\text{mean}}$ during the sustained and repeated MVC tasks immediately after ECC and CON can be partly explained by lower maximal torque output. Since the decrement in torque integral was significantly greater for ECC than CON, but $\Delta TOI_{\text{min}}$ and $\Delta tHb_{\text{mean}}$ were similar between the two sessions, other factors apart from strength loss would also be influencing the decrease in $\Delta TOI_{\text{min}}$ and $\Delta tHb_{\text{mean}}$ immediately postexercise. Ahmadi et al. (2) have reported that biceps brachii muscle oxygenation, and muscle $O_2$ consumption assessed at rest using NIRS, were significantly increased immediately after a bout of 70 maximal ECC contractions (2 sets of 35 contractions) and suggested that the increased metabolic responses rather than muscle damage were associated with the increase in NIRS parameters. The present study also found a higher resting baseline TOI before the sustained MVC task for both ECC and CON, but the absolute magnitude of the change in resting TOI was greater for the Ahmadi et al. study than the present study (14 vs. 5%). Therefore, the effect of the increased metabolic responses influencing $\Delta TOI_{\text{min}}$ was probably low in the present study. Because of the greater influence of fatigue and metabolic responses at the immediately postexercise time point, the 1–3 days postexercise time points would provide a better discussion on the influence of muscle damage on $\Delta TOI_{\text{min}}$ and $\Delta tHb_{\text{mean}}$.

Ahmadi et al. (2) reported a $\sim 30\%$ reduction in muscle oxygenation amplitude from preexercise values during a sustained task at 80% MVC at 1 day after ECC that resulted in a similar reduction in MVC immediately after ECC ($\sim 50\%$) to that of the present study. The present study also found a 40% decrement in $\Delta TOI_{\text{min}}$ from the preexercise value during a sustained MVC task at 1 day after ECC (Fig. 5A). Ahmadi et al. have proposed that the smaller muscle oxygenation amplitude compared with preexercise after ECC may be a consequence of lower $O_2$ consumption due to mitochondrial disturbance and concomitant increase in anaerobic metabolism, and/or to an increase in $O_2$ supply due to an inflammatory response. However, no significant changes in resting muscle $O_2$ consumption were found at 1–6 days after ECC in their study. Similarly, Walsh et al. (37) found no changes in resting muscle $O_2$ consumption assessed using NIRS or in single muscle fiber mitochondrial oxidative function from biopsies taken immediately after, and 2–4 days after, high-intensity ECC cycling exercise. Furthermore, Laaksonen et al. (21) found no significant changes in $O_2$ extraction fraction during a 12-min dynamic knee extension exercise protocol at 3 days after single leg jump squat exercise compared with preexercise values. Thus mitochondrial disturbances were a less likely candidate to explain the smaller $\Delta TOI_{\text{min}}$ and $\Delta tHb_{\text{mean}}$ after ECC in the present study.

An increase in vasodilation ($O_2$ supply) due to an inflammatory response (21) and/or microvascular dysfunction (18) is feasible to explain the smaller $\Delta TOI_{\text{min}}$ and $\Delta tHb_{\text{mean}}$ values during the sustained MVC task 1–3 days after ECC. However, since torque integral was 60–70% MVC at 1–3 days after ECC, we considered that $O_2$ supply would still be prevented during the sustained MVC task due to the high intramuscular pressures (i.e., $tHb$ was relatively constant, see Fig. 3A), and this would minimize reoxygenation affecting $\Delta TOI_{\text{min}}$ and $\Delta tHb_{\text{mean}}$ values (11). Consequently, any variation of blood flow/O2 supply due to microvascular dysfunction and/or inflammatory vasodilation influencing $\Delta TOI_{\text{min}}$ and $\Delta tHb_{\text{mean}}$ during the sustained MVC task would be prevented, such that smaller $\Delta TOI_{\text{min}}$ and $\Delta tHb_{\text{mean}}$ values after ECC than CON were primarily mediated by a lower muscle $O_2$ demand. Since there were similar percent decrements in MVC, and torque integral, $\Delta TOI_{\text{min}}$, and $\Delta tHb_{\text{mean}}$ during the sustained MVC task after ECC, this would suggest that MVC, torque integral, $\Delta TOI_{\text{min}}$, and $\Delta tHb_{\text{mean}}$ are associated. Therefore, it seems likely that the smaller $\Delta TOI_{\text{min}}$ and $\Delta tHb_{\text{mean}}$ after ECC were due to a lower maximal muscle mass activated as a consequence of strength loss. Warren et al. (38) have shown that at least 70% of strength loss up to 3 days after ECC is due to alteration/damage to structures involved in excitation-contraction coupling. Therefore, assuming there was no central activation failure later than 1 day after ECC (33), it could be suggested that most of the reductions in the biceps brachii muscle metabolic demand for $O_2$ during the sustained MVC task 1–3 days after ECC can be explained by excitation-contraction coupling failure.

It should be noted that, due to the strength deficit at 1–3 days following ECC, the relative intensity of the MVC tasks was largely different between ECC and CON. One might ask whether the MVC tasks best represent the difference in the changes in muscle oxygenation and hemodynamics between ECC and CON. In our subsequent study (unpublished data), changes in muscle oxygenation after ECC were compared between the first and second bouts separated by 4 wk, and we included a submaximal sustained and repeated task in which the same torque output (30% of preexercise MVC) was undertaken over days after exercise. The results showed that, despite the MVC being reduced 1–3 days after the first ECC bout with a similar magnitude to that of the present study, $\Delta TOI_{\text{min}}$ during the 30% MVC tasks were unchanged from before to 1–3 days postexercise. Thus it seems likely that no significant changes in $\Delta TOI_{\text{min}}$ during submaximal tasks at 30% MVC would have been found in the present study, and MVC tasks well represented the difference in the changes in muscle oxygenation and hemodynamics after exercise between ECC and CON.

The repeated MVC task enabled us to investigate the dynamic regulation of microvascular $O_2$ supply to meet the muscle metabolic demand for $O_2$ during exercise and provided information on the possible influence of inflammatory vasodilation and/or microvascular dysfunction on biceps brachii muscle oxygenation and hemodynamics after ECC. Our novel finding of a smaller $\Delta TOI_{\text{min}}$ and $\Delta tHb_{\text{mean}}$ compared with
preexercise values during the repeated MVC task 1–3 days following ECC suggests an increase in O$_2$ supply relative to O$_2$ demand. These findings are in agreement with Davies et al. (9), who reported a slower HHb mean response time compared with preexercise values during the baseline-to-maximal cycling exercise transition 2 days after ECC. However, we observed ΔTOI$_{\text{min}}$ and ΔHHb$_{\text{mean}}$ amplitude decreased 30–50% from the preexercise values after ECC, whereas Davies et al. found no changes in HHb or Hb amplitude after ECC. Differences in ECC exercise (squat exercise vs. maximal ECC contractions of the elbow flexors), testing tasks (near-maximal cycling vs. repeated MVC task), and MVC decrement (20 vs. 40%) between the Davies et al. study and the present study are the most likely reasons for the discrepant findings. In the present study, the smaller ΔTOI$_{\text{min}}$ and ΔHHb$_{\text{mean}}$ during the repeated MVC task after ECC can also be explained by strength loss and an increase in muscle microcirculation blood flow/O$_2$ supply (i.e., reoxygenation). An elevated exercise hyperemic response during the repeated MVC task after ECC could be due to microcirculatory dysfunction (18), which necessitated an adaptive compensatory mechanism to maintain adequate blood-muscle O$_2$ flux for muscle force production (9) and/or to an inflammatory vasodilatory response due to muscle damage/remodeling (21).

It is concluded that the biceps brachii muscle utilizes a lower amount of O$_2$ relative to O$_2$ supply to produce greater torque outputs during maximal ECC contractions compared with maximal CON contractions, which would most likely be related to the greater inherent force-producing capacity of cross bridges and lower ATP hydrolysis during ECC than CON contractions. In the 3-day postexercise recovery period, percent changes in the biceps brachii ΔTOI$_{\text{min}}$ amplitude during the sustained and repeated MVC task were smaller than the respective preexercise values for ECC than CON sessions. Since MVC and torque integral were also decreased 1–3 days after ECC but not CON session, the smaller ΔTOI$_{\text{min}}$ amplitude would represent lower O$_2$ consumption that could partly be due to a smaller maximal muscle mass activated as a consequence of strength loss; however, the influence of elevated O$_2$ supply due to microcirculation dysfunction and/or inflammatory vasodilatory responses after ECC is also recognized.

DISCUSSIONS

No conflicts of interest, financial or otherwise, are declared by the author(s).

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