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Acute changes in motor unit discharge property after concentric versus eccentric contraction exercise in knee extensor

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ABSTRACT

This study aimed to investigate the motor unit firing property immediately after concentric or eccentric contraction exercise. Eighteen healthy men performed repetitive maximal isokinetic knee extension exercises with only concentric or eccentric contraction until they exerted less than 80% of the baseline strength. Before and after the fatiguing exercise, high-density surface electromyography of the vastus lateralis was recorded during submaximal ramp-up isometric contraction and individual motor units were identified. Only motor units that could be tracked before and after exercise were analyzed. Muscle cross-sectional area of the vastus lateralis was measured using ultrasound, and electrically evoked torque was recorded before and after the exercise. Sixty-five and fifty-three motor units were analyzed before and after the concentric and eccentric contractions, respectively. The results showed that motor units with moderate to high recruitment thresholds significantly decreased recruitment thresholds under both conditions, and the motor unit discharge rates significantly increased after concentric contraction compared to eccentric contraction. A greater muscle cross-sectional area was observed with concentric contraction. The evoked torque was significantly decreased under both conditions, but no difference between the conditions. These results suggest that fatiguing exercise with concentric contraction contributes to greater neural input to muscles and metabolic responses than eccentric contraction.

1. Introduction

Resistance exercise is usually conducted to improve muscle strength. Since muscle strength is determined by both muscle morphological and neurophysiological factors, muscle weakness is also contributed by morphological or neural factors. For example, in older adults, muscle weakness is not explained by only muscle atrophy (Delmonico et al., 2009; Manini and Clark, 2012), suggesting that neural factors are main contributors. In another case, patients with chronic ankle instability have ankle strength weakness, but not muscle atrophy (Feger et al., 2016), suggesting that neural factors are impaired. Therefore, we should consider whether to focus on morphological or neurophysiological factors in resistance exercise methods, depending on patients' condition and the purpose of the exercise. Resistance exercise comprises various variables, such as exercise intensity, volume, contraction mode, and rest period. Previous studies (American College of Sports Medicine, 2009; Grgic et al., 2017; Grgic et al., 2018; Schoenfeld et al., 2017) reported that various variables were dependent on improvement of muscle strength or muscle size. Each variable can contribute to morphological or neuromuscular adaptations, but neuromuscular adaptation has not been investigated in detail because of methodological limitations. While it is easier to quantify morphological adaptation by measuring metabolic responses such as muscle swelling or blood sample tests immediately after exercise or muscle hypertrophy after chronic intervention, there is no standard method to quantify neuromuscular activation. Recently, a novel method that can measure central nervous system properties using high-density surface electromyography (HDsEMG) was developed (Holobar and Zazula, 2004, 2008). Grouping motor units by their recruitment threshold and examining the discharge rate during different exerted force levels, we can evaluate the changes in motor unit

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activation properties as neural input from the central nervous system to peripheral muscles in detail (Watanabe et al., 2016; Watanabe et al., 2020). Since this method can track some of the detected motor units and identify the same individual motor unit behavior between different time periods, detailed physiological information on the neuromuscular system is provided.

Different contraction modes, i.e., concentric or eccentric contraction, have varying effects on exerted torque, neuromuscular adaptation, and the metabolic response; therefore, the contraction mode is one of the most important resistance exercise factors. Eccentric contraction can generate stronger tension and mechanical stress than concentric contraction (Hanten and Ramberg, 1988), but inhibits neural drive activation (Duchateau and Baudry, 2014; Gonzalez-Izal et al., 2014). Therefore, eccentric contraction has less metabolic cost, shown by phenomena such as oxygen consumption and lactate accumulation (Gonzalez-Izal et al., 2014; Hoppeler, 2016), and so is associated with a higher performance-cost ratio than concentric contraction (Nishikawa, 2016). A previous study investigating motor unit firing properties during eccentric and concentric contractions reported that the motor unit firing rate was greater during concentric than eccentric contraction (Pasquet et al., 2006). However, there are no reports on the effects of the contraction mode on recruited motor unit types, such as high/low recruitment thresholds. It is well-known that discharge properties of motor units with different recruitment thresholds are not consistent (Monster and Chan, 1977; Watanabe and Holobar, 2021; Watanabe et al., 2016).

Immediately after resistance exercise, muscle strength decreases, what is termed neuromuscular fatigue (Gandevia, 2001). This comprises central and peripheral fatigue (Siegler and Marshall, 2015). When neuromuscular fatigue or pain occurs, central neural activation increases to facilitate exertion of a constant force (Contessa et al., 2009; Martinez-Valdes et al., 2020). Muscle contractions activate adenosine triphosphate (ATP) and promote glycolysis, leading to an increase in intracellular metabolites including ions and reactive oxygen species, resulting in impaired muscle force (Wan et al., 2017). Different muscle contraction modes can promote different metabolites and the afferent pathway (Bottas et al., 2005). For example, when the same exercise volume was performed using concentric and eccentric contractions, the accumulation of metabolites evaluated by measuring muscle swelling was greater after concentric than eccentric contraction (Vieira et al., 2018). Therefore, neural input from the central nervous system such as motor unit discharge rate, which can be affected by those factors, should vary with different muscle contraction modes.

The purpose of this study was to investigate acute changes in motor unit firing properties, muscle contractile properties, and muscle swelling immediately after fatiguing exercises involving concentric or eccentric contraction. Based on different neural activities, mechanical stress, and metabolic costs (Hoppeler, 2016; Nishikawa, 2016), we hypothesized that concentric contraction induces greater increases in the motor unit discharge rate and muscle cross-sectional area immediately after fatiguing exercise when compared with eccentric contraction because eccentric contraction can produce strong tension without neural input to muscle (Hanten and Ramberg, 1988) and concentric contraction requires greater metabolic cost which can require high neural activation (Hoppeler, 2016; Nishikawa, 2016).

2. Methods

2.1. Participants

Eighteen healthy young men participated in the present study (age: 24.9 ± 5.3 years, height: 170.8 ± 5.6 cm, body mass: 67.2 ± 11.4 kg). They had no history of neuromuscular disorders or surgery involving their lower limbs. Participants with physical problems such as vestibular disease, neurological dysfunctions, and musculoskeletal lesions, and receiving treatments that may affect the assessments were excluded. The purpose and procedures were explained to the participants before they provided informed written consent to participate in the present study. This study was conducted in accordance with the Declaration of Helsinki and approved by the Research Ethics Committee of Chukyo University (2021-049).

A priori analysis of sample size for the present study was conducted using G*Power software (version 3.1, Heinrich Hein University, Dusseldorf, Germany). Referring to our pilot data of 17 motor units from four participants, power analysis with an alpha error of 0.05, a power of 0.80 and partial eta squares of 0.075, revealed that a total of the required sample size was 76 motor units. We prospected three or four detected tracked motor units through the all measurements per participants in each condition, therefore 18 participants were recruited in the present study.

2.2. Procedure

The participants visited a laboratory on two separate days. They performed concentric or eccentric contraction fatiguing exercises in random order. The interval between the two conditions was 7 days. All measurements and exercise were performed using their right leg.

Before exercise (PRE), the participants lay on a bed and the muscle cross-sectional area of the vastus lateralis was measured. Then, the knee extensor maximal isometric voluntary contraction strength was measured. HDsEMG was assessed during submaximal contraction, and electrically evoked torque was also measured. After these measurements, they performed concentric or eccentric contraction fatiguing exercise following a warm-up. Maximum isometric voluntary torque was evaluated immediately before starting (baseline) and between every set. When the maximum torque was lower than 80% of the baseline torque in two consecutive sets, the exercise was stopped. Immediately after the exercise (POST), HDsEMG during submaximal contractions, electrically evoked torque, and the muscle cross- sectional area were measured again. The procedure is illustrated in Fig. 1.

2.3. Muscle cross-sectional area

The participants lay on a bed and their lower legs were placed on another bed so that the measured site of the thigh did not contact the beds, in order to measure the vastus lateralis size including the posterior surface of the thigh using an ultrasound device (LOGIQ e Premium, GE Healthcare) with a 10-MHz linear array probe. The muscle cross-sectional area of the vastus lateralis was determined from extended-field-of-view ultrasound images, following previous studies (Scott et al., 2017). Transversal images were taken at three sites: 30, 50, and 70% of the distance from the greater trochanter to lateral condyle of the femur, determined as proximal, middle, and distal sites, respectively (Hirono et al., 2022). The cross-sectional area was determined as the area surrounded by the fascia on the image. Images were taken twice each at PRE and POST. The mean value of two images, obtained for each PRE and POST, was used for further analyses. Averaged values among three locations were used as the results at PRE or POST.

Prior to the present study, the reliability of the muscle cross-sectional area measurements was assessed in the other five men (age: 25.7 ± 6.6 years, height: 174.4 ± 6.2 cm, body mass: 75.4 ± 15.7 kg) who did not perform any exercise. The intraclass correlation coefficient (1, 1) was 0.997, revealing good reliability.

3. Maximum isometric voluntary contraction and recording of high-density surface electromyography during submaximal contraction

The participants were seated in a custom-made dynamometer (Takei Scientific Instruments Co., Ltd.) fixed to a force transducer (LU-100KSE; Kyowa Electronic Instruments). The hip was flexed at 90 degrees and the knee was flexed at 90 degrees. They performed maximum voluntary

Fig. 1. Experimental protocol PRE: before fatiguing exercise, POST: after fatiguing exercise, MVC: maximal voluntary contraction.

isometric contraction involving knee extension twice. The peak force during the contraction was recorded and the greater value of the two measurements was determined as the maximum voluntary contraction (MVC) force. The MVC torque was calculated by multiplying the MVC force and an arm length, determined as the distance between the knee joint axis and force transducer.

After measuring MVC, the participants performed submaximal ramp-up contraction. Ramp contraction consisted of a 17-sec increasing phase to 50% of the MVC force level and 10-sec sustained phase at 50% of the MVC force level. The sustained phase was not analyzed and was used only to ensure reliable motor unit identification. The exerted and target forces were shown on a monitor in real time as visual feedback. During the submaximal ramp-up contraction, HDsEMG signals were recorded from the vastus lateralis using a semi-disposable adhesive grid of 64 electrodes and a 1-mm diameter and 8-mm inter-electrode distance, with one missing electrode in the upper left corner (GR08MM1305, OT Bioelectronica, Torino, Italy). The electrode was attached to the skin with a bi-adhesive sheet (KITAD064, OT Bioelettronica) after applying conductive paste (Elefix Z-181BE, NIHONKOHDEN, Japan). The participants' thigh hair was removed, the skin was cleaned with alcohol, and electrodes were attached at the midpoint of the line between the head of the greater trochanter and inferior lateral edge of the patella, used as the center of the electrode grid, and the line was also used to determine the direction of electrode grids, whereby columns of electrodes were aligned along it. A reference electrode was attached on the tibial tuberosity. Monopolar surface EMG signals were filtered with a bandpass filter from 10 to 500 Hz, and amplified by a factor of 150, sampled at 2,048 Hz, and converted to digital form by a 16-bit analog-to-digital converter (Quattrocento, OT Bioelectronica, Torino, Italy). The signal from the force transducer was synchronized with HDsEMG signals on this analog-to-digital converter.

Recorded monopolar surface EMG signals were transferred to analysis software (MATLAB R2019a, MathWorks GK, Tokyo, Japan), and individual motor units were identified by the Convolution Kernel Compensation (CKC) technique using DEMUSE software (ver. 5.0.1; The University of Maribor, Slovenia) (Farina et al., 2010; Holobar et al., 2009). Any physiologically irregular motor unit discharge (<4 and over 50 Hz) (Adam and De Luca, 2005; Kamen and Knight, 2004; Kirk et al.,

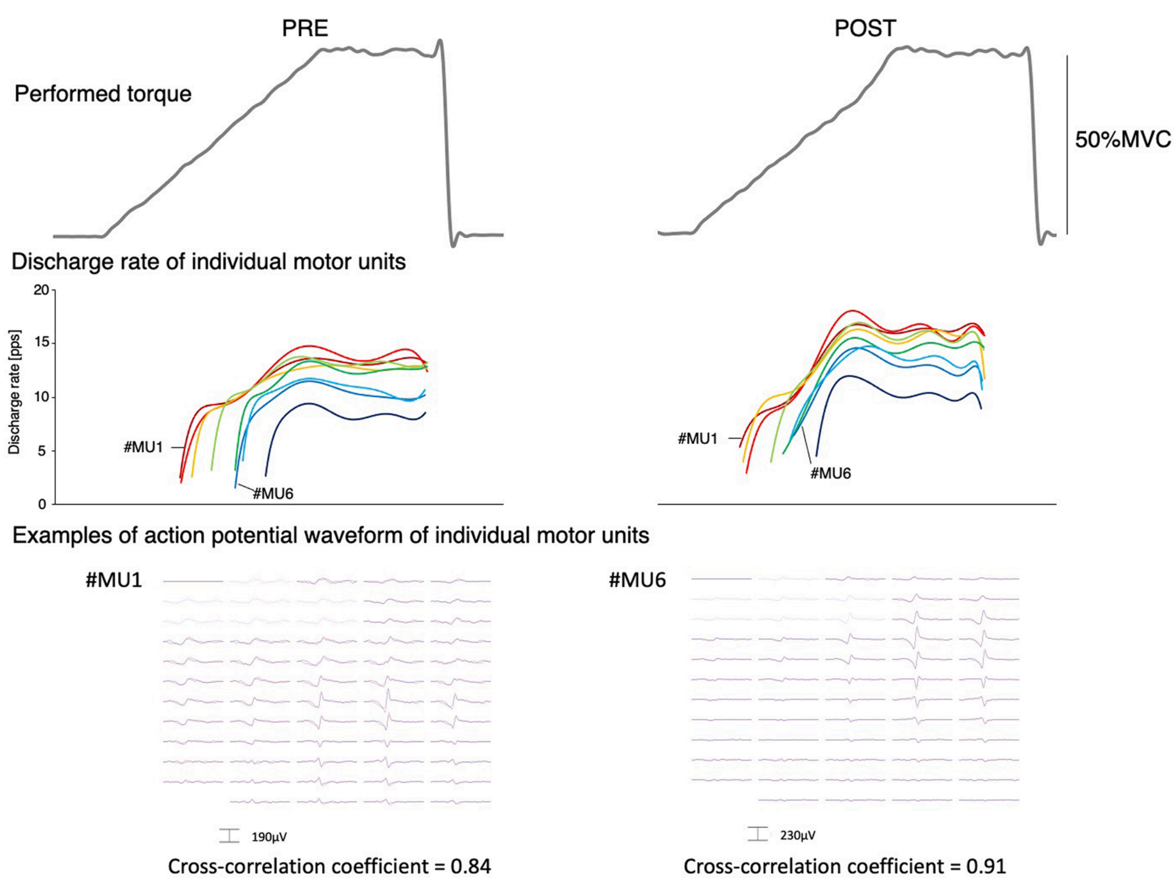

Fig. 2. Example data of performed torque, discharge rate of individual motor units, and action potential waveform of individual motor units. The graph of discharge rate was processed by smoothing. Individual motor unit was tracked between before exercise (PRE) and after exercise (POST). Cross-correlation coefficients of example tracked motor unit action potential waveforms was calculated.

2021; Welsh et al., 2007) and individual motor unit with firing rates showing a coefficient of variation of over 30% were discarded (Fuglevand et al., 1993). In addition, detected motor units were tracked between PRE and POST using the CKC technique in DEMUSE software to calculate the motor unit filters which were estimated at PRE and the same filters were transferred at POST (Francic and Holobar, 2021), and the accuracy of this transfer of the filters were evaluated by cross-correlation analysis of motor unit action potential waveforms between PRE and POST. Fatiguing can change motor unit action potential waveforms (Enoka et al., 1992), but DEMUSE tool can track the gradual changes in motor unit action potentials. Example data were represented in Fig. 2.

Discharge rates of individual motor units were calculated from the interspike interval. Mean discharge rates of individual motor units were calculated from instantaneous discharge rates for the ranges of 0–25% of MVC, 25–40% of MVC, and 40–50% of MVC during ramp-up contraction. Additionally, detected motor units were divided into three groups by the recruitment threshold at PRE. Recruitment thresholds of motor units were determined from the force level when the motor unit discharges first. A relatively low recruitment threshold group consisted of motor units recruited at<25% of MVC (MU0-25), another group consisted of motor units recruited at more than 25% and less than 40% of MVC (MU25-40), and a relatively high recruitment threshold group consisted of motor units recruited at more than 40% of MVC (MU40-50). The group limits were determined empirically after analyzing the number and distribution of the detected motor units.

3.1. Electrically evoked muscle contraction

Contraction torques of knee extensor muscles during twitch stimulation were measured to estimate muscle contraction properties using a constant current stimulator (DS7AH, Digitimer, Ltd., Hertfordshire, UK). Two electrodes (4.5 × 28 cm) were attached at proximal and distal sites of the quadriceps femoris. According to previous studies (Tomita et al., 2020; Watanabe and Holobar, 2021), electrodes were located at the center to lateral position to cover proximal regions of the rectus femoris and vastus lateralis for the proximal site and at the center to medial position to cover distal regions of the rectus femoris and vastus medialis for distal sites. Electrical stimulation was applied via these electrodes with a 200-μs pulse width. The current intensity was increased by 100 mA until evoked knee extension torque reached a plateau to evaluate the maximal twitch torque. The current intensity at PRE was also used at POST. At both PRE and POST, the evoked torque was measured twice, and the mean value was used for analysis.

3.2. Fatiguing exercise

Followed measurements at PRE, participants were seated in a dynamometer (CON-TREX; CMV AG, Dübendorf, Switzerland). After warm-up, they performed MVC twice using isometric mode at a knee joint angle of 90 degrees, and the highest value was determined as the baseline value. They performed maximum voluntary isokinetic contraction from 90 to 20-degree knee flexion (full extension is 0 degrees) using an isokinetic mode. For concentric contraction, they performed maximum voluntary concentric contraction at a speed of 30 degrees per second and they relaxed during flexion at a speed of 60 degrees per second. Conversely, in the eccentric contraction task, they performed maximum voluntary eccentric contraction at a speed of 30 degrees per second and relaxed during extension at a speed of 60 degrees per second. Under both conditions, one set consisted of ten contractions. Immediately after every set, they performed maximum voluntary isometric knee extension at a knee joint angle of 90 degrees, and the torque was recorded for assessing the fatiguing condition. Interval rest periods were 60 s between sets and they recorded their subjective fatigue using a visual analog scale (VAS). If the maximum isometric torque at the intervals was lower than 80% of the baseline torque in two consecutive sets, the exercise was stopped. The number of completed sets and VAS value after the last set were used in subsequent analyses.

3.3. Statistical analyses

All data are presented as the mean ± standard deviation. SPSS (version 25; IBM Corp., Japan) was used for statistical analyses. The Wilcoxon sighed rank test and paired *t*-test were used to compare the number of completed sets and VAS values between concentric and eccentric contraction tasks, respectively. Repeated two-way analyses of variance (ANOVAs) using two factors [contraction mode condition (concentric vs. eccentric contraction) and test time (PRE vs. POST)] were used to analyze the interaction and main effect of muscle cross-sectional area and electrically evoked torque. To analyze the motor unit discharge rate until 25% of MVC, split-plot ANOVA for the between factor of contraction mode condition (concentric vs. eccentric contraction) and within factor of test time (PRE vs. POST) was used. To analyze motor unit discharge rates for ranges of 25–40% of MVC and 40–50% of MVC and motor unit recruitment threshold, split-plot ANOVAs for the between factors of motor unit groups (MU0-25 vs. MU25-40 vs. MU40-50) and contraction mode condition (concentric vs. eccentric contraction), and the within factor of test time (PRE vs. POST) were used. When a significant interaction was found, split-plot two-way ANOVA or Tukey's corrected post-hoc tests were conducted using calculated changes in the motor unit discharge rate between PRE and POST. The significance was set at 0.05.

4. Results

There were no significant differences between concentric and eccentric conditions in the number of completed sets ($p = 0.307$) or VAS of the last set ($p = 0.493$) (Fig. 3).

Table 1 shows numbers and recruitment threshold of identified motor units. Sixty-five motor units for concentric condition and fifty-three motor units for eccentric condition were identified and tracked for data processing. The number of motor unit detected from individuals ranged of 0–12 and 0–17 in concentric and eccentric conditions, respectively. The pulse-to-noise ratios, which suggests the accuracy in motor unit identify (Holobar et al., 2014), were 28.9 ± 3.2 dB and 25.7 ± 3.3 dB at PRE and POST, respectively. The cross-correlation coefficients of waveforms between PRE and POST were 0.81 ± 0.11 (Fig. 2).

For the recruitment threshold of the detected motor units, 3-way ANOVA revealed the main effect of time, indicating that the recruitment threshold was significantly decreased after the exercises, and also revealed a 2-way interaction for the within factor of time and between factor of contraction mode, indicating that the decrease in the recruitment threshold after eccentric exercise was significantly greater than that after concentric exercise. The ANOVA revealed a 2-way interaction for the within factor of time and between factor of motor unit groups and post-hoc test revealed that recruitment thresholds of MU25-40 and M40-50 were significantly decreased after exercise, but not MU0-25.

Two-way ANOVA for the discharge rate at MU0-25 (Fig. 4A) and 3-way ANOVA for the discharge rate at MU25-40 (Fig. 4B) showed no interaction but did show the main effect of time ($F = 17.16$; $p < 0.001$, $F = 210.30$; $p < 0.001$, respectively), indicating that the discharge rate significantly decreased after exercise with both contraction modes. However, 3-way ANOVA for the discharge rate at MU40-50 showed significant 2-way interactions (time × contraction mode; $F = 4.63$; $p = 0.034$, time × motor unit group; $F = 3.98$; $p = 0.021$, Fig. 4C-a). The 2-way interaction of time × contraction mode indicated that concentric contraction fatigue induced a significantly greater increase in the discharge rate than eccentric contraction (Fig. 4C-b). Post-hoc tests for the interaction of time × motor unit group revealed that the discharge rate at MU40-50 increased significantly greater than the other groups (compared with MU0-25; $p < 0.001$, compared with MU25-40; $p <$

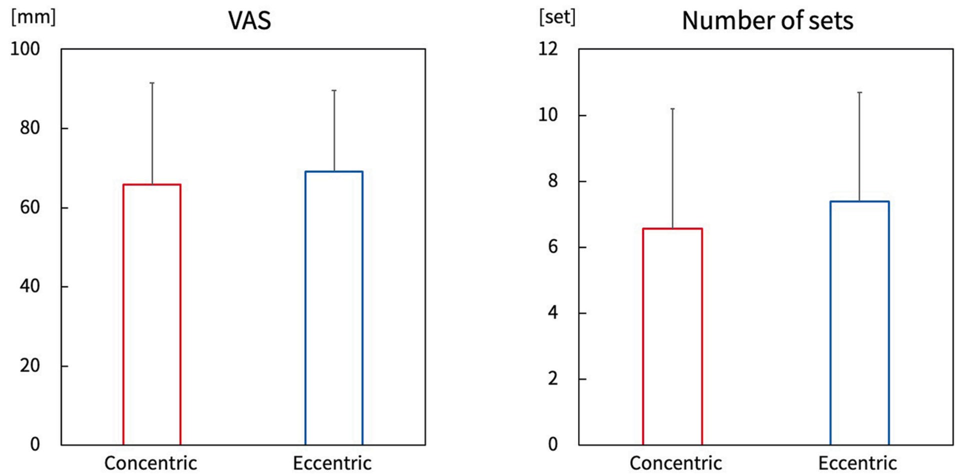

Fig. 3. Subjective fatigue evaluated by visual analog scale (VA) after completed exercise (left) and the number of completed sets (right). Mean values are shown as columns, and standard deviations are error bars.

Table 1
Analyzed number of detected motor units and recruitment threshold.

	Condition	Detected number	Recruitment threshold at PRE (%MVC)	Recruitment threshold at POST (%MVC)	3-way ANOVA	2-way ANOVA (time × contraction mode)	2-way ANOVA (time × motor unit group)	Main effect (time)
MU0-25	Concentric	22	18.8 ± 4.3	18.5 ± 4.3	F = 0.13		F = 25.30	F = 145.75
	Eccentric	12	19.0 ± 4.3	17.6 ± 5.4	P = 0.882		P < 0.001	P < 0.001
	Both	34	18.9 ± 4.3	18.2 ± 4.7				
MU25-40	Concentric	25	33.7 ± 4.2	29.9 ± 4.5				
	Eccentric	29	33.8 ± 4.2	28.2 ± 4.7				
	Both	54	33.8 ± 4.2	29.0 ± 4.6 *				
MU40-50	Concentric	18	43.8 ± 3.0	37.1 ± 4.5				
	Eccentric	12	43.4 ± 3.2	34.8 ± 3.9				
	Both	30	43.6 ± 3.0	36.2 ± 4.4 *				
Total	Concentric	65	31.5 ± 10.7	28.0 ± 8.7 *		F = 4.50		
	Eccentric	53	32.6 ± 9.3	27.3 ± 7.5 *		P = 0.036		

The values show the mean ± standard deviation.
PRE: before fatiguing exercise, POST: after fatiguing exercise.
MU0-25: motor unit group recruited until 25% of MVC, MU25-40: motor unit group recruited at 25 – 40% of MVC, MU40-50: motor unit group recruited at 40 – 50% of MVC.
* $p < 0.05$ compared with PRE.

0.001, Fig. 4C-c, -d).

For the muscle cross-sectional area, 2-way ANOVA revealed a significant interaction ($F = 16.81$; $p = 0.001$) and main effect of time ($F = 83.34$; $p < 0.001$, Fig. 5). In both concentric and eccentric contraction fatiguing exercises, the cross-sectional area significantly increased, but concentric exercise induced a significantly greater increase in the cross-sectional area than eccentric exercise.

For electrically evoked torque, 2-way ANOVA revealed the main effect of time ($F = 90.46$; $p < 0.001$), but no interaction ($F = 2.87$; $p = 0.110$), indicating that there was no difference in contraction properties between contraction modes (Fig. 6). The relative values based on MVC decreased from 27.0 ± 8.8 and 28.2 ± 7.6 %MVC at PRE to 16.7 ± 8.8 and 18.8 ± 7.0 %MVC at POST in concentric and eccentric condition, respectively.

5. Discussion

The present study investigated the effects of fatiguing exercises with different contraction modes on neural input from the central nervous system estimated by motor unit firing properties using HDsEMG, muscle contraction properties evaluated by electrically evoked torque, and metabolic responses by measuring the muscle cross-sectional area. The results showed that concentric contraction fatiguing exercise induced greater increases in the motor unit discharge rate and a greater acute increase in metabolic responses than eccentric contraction, even if both contraction-mode exercises caused the same decreases of MVC and electrically evoked torques. This is the first study to investigate acute changes in motor unit firing properties and muscle properties when the similar decline of maximum voluntary strength of isometric contraction was caused by concentric and eccentric contraction exercises. Additionally, there was no decrease in mCSA or maximal strength at PRE between first visit and second visit ($p = 0.920$, 0.310, respectively), suggesting that interval duration of 7 days could be sufficient for recover muscle conditions.

Motor unit behaviors were evaluated during isometric contraction before and after fatiguing exercises. The aim of the present study was to compare the neuromuscular changes due to muscle contraction modes, but we did not conduct an evaluation of motor units during concentric and eccentric contraction, because they had different behaviors (Duchateau and Enoka, 2016). We attempted to compare the effects of fatiguing exercise on neuromuscular properties, and the changes of motor unit discharge properties, which was assessed during isometric contraction, was caused by different fatiguing exercise with different contraction.

During ramp-up contraction until 50% of MVC, the discharge rate significantly increased after both concentric and eccentric contraction fatiguing exercises (Fig. 4). Previous studies (Cowling et al., 2016; Harwood et al., 2012) reported that motor unit discharge rate during fatigue significantly decreased during maximal voluntary contractions. Although the results of the present study may appear to contradict with

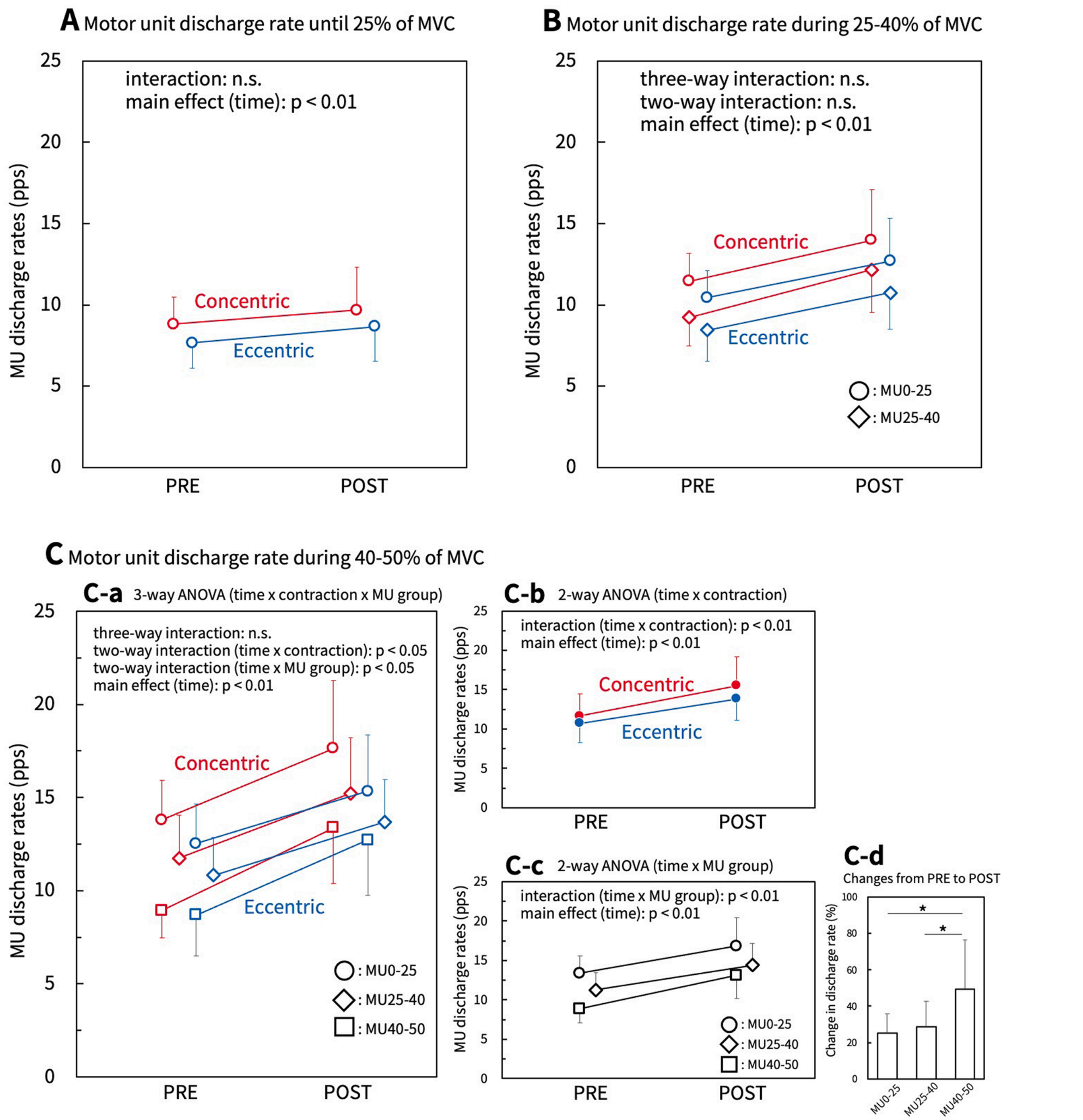

Fig. 4. Acute changes in motor unit discharge rate. (A) Acute changes in motor unit discharge rate during ramp-up contraction until 25% of MVC. Red points and line show concentric contraction fatiguing exercise, and blue points and line show eccentric contraction fatiguing exercise. There is a main effect of time but no interaction. PRE: before exercise, POST: after exercise. (B) Acute changes in motor unit discharge rate during ramp-up contraction from 25 to 40% of MVC. Red points and line show concentric contraction fatiguing exercise, and blue points and line show eccentric contraction fatiguing exercise. Motor unit groups recruited until 25% of MVC (MU0-25) are shown as circles, and motor unit groups recruited from 25 to 40% of MVC (MU25-40) are shown as rhomboids. There is a main effect of time but no 3-way or 2-way interactions. PRE: before exercise, POST: after exercise. (C) Acute changes in motor unit discharge rate during ramp-up contraction from 40 to 50% of MVC. Red points and line show concentric contraction fatiguing exercise, and blue points and line show eccentric contraction fatiguing exercise. Motor unit (MU) groups recruited until 25% of MVC (MU0-25) are shown as circles, and MU groups recruited from 25 to 40% of MVC (MU25-40) are shown as rhomboids. MU groups recruited at over 40% of MVC (MU40-50) are shown as squares. C-a shows the results of 3-way analysis of variance (ANOVA), with a main effect of time and also 2-way interactions (time × contraction mode and time × MU group). After a break down, C-b shows the results of 2-way ANOVA (time × contraction mode), with a main effect of time and an interaction. C-c shows the results of 2-way ANOVA (time × MU group), with a main effect of time and an interaction. C-d shows the results of a post-hoc test comparing changes from PRE to POST in the discharge rate among the three MU groups. The increase in the discharge rate in MU40-50 group was significantly greater than in the other MU groups. PRE: before exercise, POST: after exercise. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

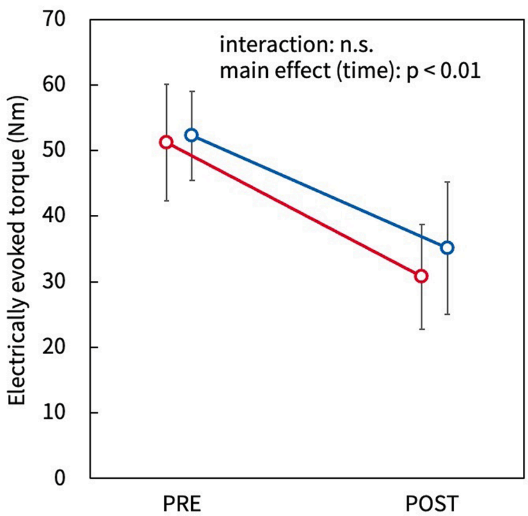

Fig. 5. Electrically evoked torque There is a main effect of time, but no interaction. Red points and line show concentric contraction fatiguing exercise, and blue points and line show eccentric contraction fatiguing exercise. PRE: before exercise, POST: after exercise. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

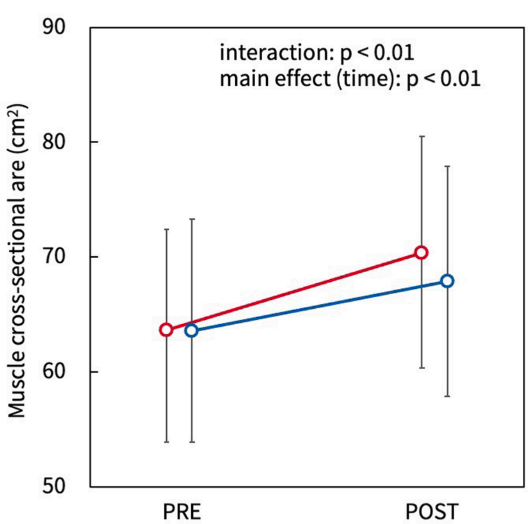

Fig. 6. Acute changes in vastus lateralis muscle cross-sectional area There is a main effect of time, and also an interaction. Red points and line show concentric contraction fatiguing exercise, and blue points and line show eccentric contraction fatiguing exercise. PRE: before exercise, POST: after exercise. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the previous studies (Cowling et al., 2016; Harwood et al., 2012), the intensities where motor unit discharge properties were assessed were different. We conducted to assess the motor unit discharge pattern during submaximal intensity. Focusing on other previous studies investigating the properties during submaximal intensities and after fatiguing exercise (Contessa et al., 2009; Piitulainen et al., 2012), the motor unit discharge rate increases to maintain constant force exertion instead of decreasing muscle contraction properties. In the present study, maximum voluntary contraction torque decreased to under 80% of the baseline, and electrically evoked torque also decreased under both conditions (Fig. 5), suggesting that a functional deficit in the peripheral muscle contraction properties. The evoked torque was not affected by the condition of the central nervous system because the electrically evoked torque was regarded as a peripheral function only. The increase in motor unit discharge rate might be why muscle force production (the electrically evoked torque) was decreased in both condition and neural input to muscle (discharge rate) attempted to compensate for the impaired force production and to maintain the same knee extension torque as PRE, especially during high intensity torque exertion. This compensation of increasing discharge rate of active motor units was found in other previous works (Contessa et al., 2009; Piitulainen et al., 2012). In addition, our data revealed the decrease in recruitment thresholds (Table 1), suggesting that motor unit recruited by relative high threshold was recruited earlier to compensate the decrease of muscle contraction properties. After fatiguing exercise, the increase in neural input to muscle could compensate for the lack of peripheral muscle contraction properties.

Previously some works have reported discharge rate of low-threshold motor unit are greater than that of high-threshold motor unit, which is called as onion skin phenomenon. This is observed during submaximal ramp-up contraction (Erim et al., 1996), but discharge rate of high-threshold motor unit increases greater than that of low-threshold motor unit (Oya et al., 2009). In the present study, since motor unit discharge behaviors were observed until 50% of MVC based at PRE, relatively high-threshold motor units had low discharge rate. After fatiguing, relatively high-threshold motor unit changed significantly increase in discharge rate (Fig. 4C-d), which suggested relatively high-thresholds motor unit can be changeable characteristics to maintain muscle strength when peripheral muscle contraction property would be damaged, because of general high-threshold motor unit behavior to achieve force production across a large range of strength (Grimby et al., 1979).

Discharge rates in MU0-25 and MU25-40 significantly increased following fatiguing contractions with both contraction modes, and the extents of these decreases were not significantly different between concentric and eccentric contraction fatiguing exercises (Fig. 4A, B). On the other hand, the discharge rate at MU40-50 significantly increased under both conditions, and a greater increase in the discharge rate occurred after concentric contraction exercise rather than eccentric contraction exercise (Fig. 4C-a, -b). Focusing on motor unit groups, the increase in the discharge rate became significantly greater after fatiguing exercises in the motor unit group with a relatively high recruitment threshold than the motor unit group with a relatively low recruitment threshold, regardless of the contraction mode (Fig. 4C-c, -d). A previous study investigating concentric contraction of the tibialis anterior reported that the motor unit discharge rate was greater than that during eccentric contraction (Duchateau and Baudry, 2014), because concentric contraction required greater energy expenditure (Pinniger et al., 2000). Considering that the larger energy cost and ATP cost require a high discharge rate of motor units (Christie et al., 2016), concentric contraction may induce a high discharge rate among motor units. Additionally, it was reported that concentric contraction promoted more metabolic stress (Durand et al., 2003; Vieira et al., 2018). Accumulation of metabolites induces an increase in intracellular acidosis after exercise, resulting in an acute increase in the muscle size (Allen et al., 2008; Watson et al., 1993). An acute increase of the muscle size is muscle swelling (Schoenfeld and Contreras, 2014), which is important for muscle growth after an intervention (Hirono et al., 2022; Schoenfeld, 2013). In the present study, the acute increase in the muscle cross-sectional area was also greater after concentric contraction exercise (Fig. 6), suggesting that concentric contraction exercise involved a high ATP cost; therefore, the increase in the motor unit discharge rate was greater when performing high- intensity contractions. The peripheral muscle contraction property evaluated by electronically evoked torque was noy different between two conditions (Fig. 5), therefore, we consider that the nervous system, not muscle component, induce different metabolic and energy productions, which also induced the higher discharge rate after concentric fatiguing exercise.

This study only investigated acute changes in neural input, metabolic responses, and muscle contractile properties. It would be interesting to assess whether concentric contraction training contributes to chronic muscle strength gain due to an increase of neural input from the central nervous system. A previous study reported that eccentric contraction training could lead to greater central nervous activation than concentric contraction training (Maeo et al., 2018). During eccentric contraction, neural activation is inhibited compared with concentric/isometric contractions, whereas after resistance training, such inhibition can be downregulated and abolished (Aagaard et al., 2000). It is not yet clear how motor unit behavior is altered after chronic concentric or eccentric contraction training. A future study should clarify the chronic changes in motor unit firing properties after long-term training.

Because of investigating acute effects, this study could compare two conditions in the same participants with a crossover study design. It was also possible to track the same motor units and evaluate acute changes in the discharge properties of the same motor units because the electrodes were attached at PRE and remained on the muscle until POST. The electrodes were not detached during exercises. However, the electrodes were reattached across concentric and eccentric contraction conditions because two conditions were performed separated days between a week, therefore we did not match motor units across two conditions.

This study has some limitations. One of them is that isokinetic contractions which were used in this study are velocity-invariant and are not like real-life movements that would have varying torque and velocities that must be adjusted for by the nervous system. Future study is needed to investigate the effects of the real-life movements. At second, the evaluation at POST was affected by not only fatiguing exercise with concentric or eccentric contraction but also some maximal voluntary isometric contractions. However, since both conditions included same isometric contraction tasks, the effects of muscle contraction tasks other than the fatiguing exercise would not be a markedly impact on the comparisons between the two conditions. We have another limitation about the contraction mode and intensity which were used for the tasks to record HDsEMG. During fatigue exercise, the participants performed maximal voluntary concentric or eccentric contraction, but during tasks where recording HDsEMG, the participants performed isometric contraction and until 50% of MVC based at PRE. They might perform different motor unit recruit strategies, such as different motor unit pools or different synaptic drive regimes due to contraction modes and intensities. Regarding discharge rate variance, we should consider the interpretation of the present results as a limitation because Tenan et al. (2014) pointed out that individual variance of motor unit discharge rate could affect statistical analyses. We performed analysis of co-variance with discharge rate during 40 – 50 %MVC at PRE as co-variable due to considering the variance, and a significant interaction for the within factor of time and between factor of motor unit groups was found ($p < 0.001$), but no interaction for the within factor of time and between factor of contraction mode was found ($p = 0.103$). In practice, when two-way ANOVA for between factors of contraction mode and motor unit group was performed to compare discharge rate at PRE, significant differences between contraction modes were found ($p = 0.048$). The present results might be interpreted with the baseline differences.

In conclusion, this study investigated acute changes in motor unit discharge, muscle contractile properties, and metabolic responses between before and after concentric or eccentric contraction fatiguing exercises. When maximal voluntary isometric contraction strength decreased to 80% of the baseline after the exercises, electrically evoked torque also decreased under both conditions. During ramp-up contraction until 40% of MVC, the motor unit discharge rate increased under both conditions after fatigue. During ramp-up contraction from 40 to 50% of MVC, the increase in the motor unit discharge rate was greater after concentric contraction fatiguing exercise than eccentric contraction. Muscle metabolic responses evaluated by the acute increase in the muscle cross-sectional area was greater after concentric than eccentric contraction fatiguing exercise. These results suggest that concentric contraction fatiguing exercise contributes to greater increases in neural input to muscle and metabolic stress than eccentric contraction.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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