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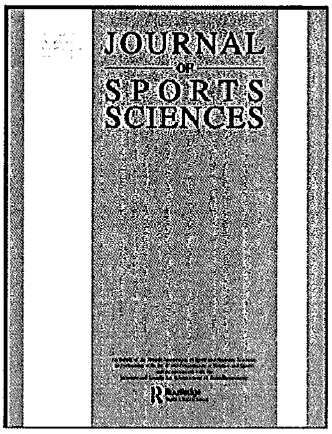

Journal of Sports Sciences
Publication details, including instructions for authors and subscription information:
http://www.informaworld.com/smpp/title~content=t713721847

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Online Publication Date: 01 March 2009

To cite this Article Yasuda, Tomohiro, Brechue, William F., Fujita, Taku, Shirakawa, Jun, Sato, Yoshiaki and Abe, Takashi(2009)'Muscle activation during low-intensity muscle contractions with restricted blood flow',Journal of Sports Sciences,27:5,479 — 489

To link to this Article: DOI: 10.1080/02640410802626567

URL: http://dx.doi.org/10.1080/02640410802626567

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Journal of Sports Sciences, March 2009; 27(5): 479–489

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Muscle activation during low-intensity muscle contractions with restricted blood flow

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(Accepted 14 November 2008)

Abstract

We examined muscle activation during low-intensity muscle contractions with a moderate restriction of blood flow and complete occlusion of blood flow. Unilateral elbow flexion muscle contractions (20% of 1-RM) were performed in Experiment 1 (30 contractions), Experiment 2 (3 sets × 10 contractions), and Experiment 3 (30 repetitive contractions followed by 3 sets × 15 contractions) with moderate restriction, complete occlusion of blood flow or unrestricted blood flow (control). Electromyography (EMG) was recorded from surface electrodes placed on the biceps brachii muscle and the integrated EMG (iEMG) and mean power frequency (MPF) obtained. During Experiments 1 and 2, muscle activation was progressively increased in complete occlusion and moderate restriction of blood flow to levels greater than in the control. The decline in maximal voluntary isometric contraction (MVC) following the bout of contractions was greater with complete occlusion (39–48%) than moderate restriction of blood flow (16–19%); control MVC did not change. In Experiment 3, changes in MVC, iEMG, and MPF were greater with moderate restriction of blood flow than in the control but comparable with complete occlusion of blood flow where less total work was performed. In conclusion, moderate restriction of blood flow results in similar neural manifestations in muscle as complete occlusion of blood flow but without the apparent contractile/metabolic impairment observed with complete occlusion. Thus, low-intensity muscle contractions, with moderate restriction of blood flow, leads to more intense activation of the muscle relative to the external load.

Keywords: *Moderate restriction of blood flow, complete occlusion of blood flow, electromyography, neuromuscular function, 20% 1-RM*

Introduction

Blood flow is an important component of oxygen transport to muscle during exercise (Andersen & Saltin, 1985). To sustain submaximal exercise, it is necessary to increase and maintain blood flow to supply sufficient oxygen and substrates to, and remove by-products and waste from, active muscle (Fukunaga, Matsuo, Hyodo, Yata, & Ryushi, 1986; Wernbom, Augustsson, & Thomee, 2006). However, increased intramuscular pressure associated with muscle contractions (muscular force $>20\%$ maximal voluntary isometric contraction; Humphreys & Lind, 1963) results in significant vessel compression and has been shown to impede arterial inflow to, and venous outflow from, muscle during exercise (Bonde-Petersen, Mork, & Nielsen, 1975). This vessel compression and altered blood flow has been shown to alter the metabolic response of muscle isolated *in situ* during repetitive contractions (Ameredes, Brechue, & Stainsby, 1994; Brechue, Barclay, O'Drobinak, & Stainsby, 1993) and whole body exercise *in vivo* (Abe, Kearns, & Sato, 2006; Sundberg, 1994). However, occluded blood flow secondary to vessel compression during high-load resistance exercise training figures prominently in the adaptive processes of muscle, muscle hypertrophy, and strength gains (Campos et al., 2002; McDonagh & Davies, 1984).

Thus it appears that insufficient blood flow is a necessary condition for adaptation following resistance exercise training. This hypothesis is supported

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ISSN 0264-0414 print/ISSN 1466-447X online © 2009 Taylor & Francis
DOI: 10.1080/02640410802626567

by recent studies showing that volitional occlusion of blood flow (by external compression of vessels) during low-load resistance exercise training leads to adaptations comparable to those observed during high-load resistance exercise training; including muscle hypertrophy, strength gains, and increased muscle work capacity (Abe et al., 2006; Burgomaster et al., 2003; Sinohara, Kouzaki, Yoshihisa, & Fukunaga, 1998; Sundberg, 1994; Takarada et al., 2000b; Takarada, Sato, & Ishii, 2002; Takarada, Tsuruta, & Ishii, 2004; Yasuda et al., 2005). The mechanism by which occluded blood flow potentiates the training effect of low-load resistance training remains obscure but appears to be related to an increased muscle activation (increased integrated electromyographic activity) associated with complete blood flow occlusion (Moritani, Sherman, Shibata, Matsumoto, & Shinohara, 1992; Sundberg, 1994; Takarada et al., 2000a). Accordingly, an important issue that remains to be investigated is the relationship between occluded blood flow and increased integrated EMG (iEMG) activity. Thus, the purpose of the present study was to compare muscle activation (EMG activity, etc.) during bouts of low-intensity muscle contractions with a moderate restriction and complete occlusion of blood flow. We hypothesized that muscle activation (iEMG) would increase with a reduction in blood flow (moderate restriction vs. complete occlusion of blood flow). However, this increased activation should not sustain muscle function during complete occlusion of blood flow, as fatigue will be greater and recovery of contractile function slower.

Methods

Participants

Ten healthy male students (mean age 24.1 years, $s = 3.2$; height 1.76 m, $s = 0.04$; body mass 69.7 kg, $s = 6.7$) volunteered for the study. Although all students participated in regular aerobic-type exercise (2–3 times per week), none had engaged in resistance exercise training for at least 6 months prior to inclusion in the study. All participants received a verbal and written description of the study and provided written informed consent before taking part in the experiments. The study was approved by the Ethics Committee for Human Experiments of Tokyo Metropolitan University.

Protocol

To evaluate muscle activation during low-load bouts of muscle contractions with moderate restriction and complete occlusion of blood flow, three experiments were performed:

- *Experiment 1*: repetitive contractions – this bout of exercise consisted of a total of 30 muscle contractions.
- *Experiment 2*: intermittent contractions – this bout of exercise consisted of 3 sets of 10 muscle contractions.
- *Experiment 3*: combination bout – this bout of exercise consisted of 30 repetitive muscle contractions followed by 3 sets of 15 muscle contractions.

In all experiments, participants performed unilateral elbow flexion (biceps curls) contractions, with sets separated by 30 s of rest. One week before the experiments, participants performed a one-repetition maximum (1-RM) biceps curl test and were familiarized with the muscle contractions and restricted blood flow conditions. A schematic illustration of the experimental protocol is given in Figure 1.

To begin each experiment, a maximal voluntary isometric contraction (MVC) biceps curl was performed with elbow flexed at 90°. To impede blood flow, the pressure cuff, placed around the most proximal portion of the test arm, was inflated to the

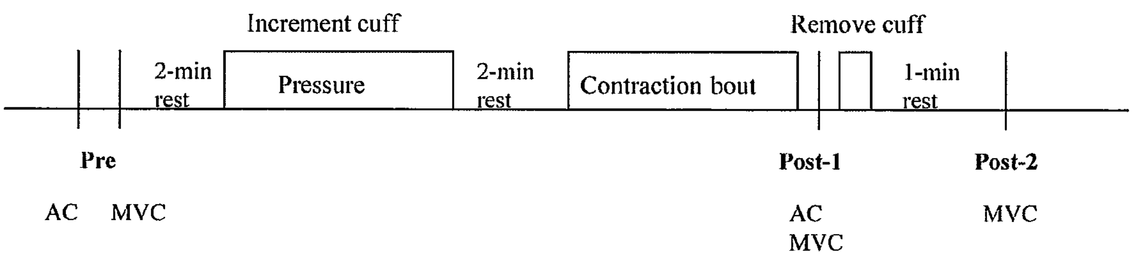

Figure 1. Schematic representation of the experimental protocol. Basic format for all experiments. "Pre" is resting data collected 30 min before the start of the experiment, "Post-1" is immediately after the bout of contractions, and "Post-2" is 1 min after removal of the cuff. Increment cuff: moderate restriction of blood flow, cuff pressure 160 mmHg; complete occlusion of blood flow, cuff pressure 300 mmHg. Contraction bout = various experiments, AC = arm circumference, MVC = maximal voluntary isometric contraction.

desired pressure (160 mmHg as a moderate restriction or 300 mmHg for complete occlusion of blood flow). A 2-min rest period was given before and after cuff inflation. Once the cuff was inflated, it remained so for the entire bout of contractions including rest periods. Immediately after the contractions (Post-1), MVC was determined and the pressure cuff was quickly removed. The MVC was again determined 1 min after cuff removal (Post-2). Heart rate was measured throughout the bout of contractions (heart rate monitor CE0537, Polar Electro Oy, Finland). Arm circumference (tape measure) was determined at baseline (Pre) and Post-1, measured at 60% of the distance between the lateral epicondyle of the humerus and the acromial process of the radius by the same experienced examiner. Coefficients of variation for arm circumference measurements (all experiments at baseline) were approximately 0.09.

For Experiments 1 and 2, participants performed two bouts of contractions each day with a minimum of 4 h between bouts and 3–4 days' rest between trials. Order of contraction bout and blood flow perturbation was randomized. In a preliminary study of Experiment 3, participants were unable to complete the contraction bout with complete occlusion of blood flow. Therefore, only moderate restriction of blood flow and a control were performed in Experiment 3, with both trials performed on the same day with a minimum of 4 h between bouts, with the control trial performed first and the moderate restriction of blood flow trial performed second. The order of experiments (Experiment 1, 2, and 3) was randomized.

Maximal voluntary isometric contraction (MVC)

The MVC was measured (Biodex System 3 dynamometer; Sakai Medical Instrument, Tokyo, Japan) and used as an indicator of force-generating capacity to evaluate the impact of repeated muscle contractions on contractile function. Fatigue is defined here as a decrease in MVC. The participants were seated comfortably on a chair with the arm positioned on a firm and stable table at chest level with an elbow joint angle of 90° (0° at full extension). The upper arm was maintained in the horizontal plane (at 90°) and the hand grasped the Biodex lever in the pronated position, while a diagonal strap was secured over the elbow to maintain a stationary position during the MVC. Participants performed a total of four MVCs, two at baseline separated by a 60-s rest, and one each at Post-1 and Post-2. Participants were instructed to attain a maximal contraction and maintain it for 5 s. The recorded value for MVC was taken as the highest and most stable 3 s of the 5-s contraction. The greater of the two MVCs determined at baseline was used for data analysis.

Contraction bouts

All bouts consisted of unilateral elbow flexion (biceps curls) contractions. During each experiment, participants sat on the arm curl bench, with the arm positioned in front of the body supporting the shoulder at 45° of flexion. Elbow range of joint motion during exercise was completed from full extension to full flexion. Contraction intensity was 20% of 1-RM. Contraction duration was 2.4 s with a 1.2 s/1.2 s shortening – lengthening contraction duty cycle controlled by a metronome (50 beats · min^{-1}). All experiments were performed on the same arm of each participant, but because hand dominance may affect motor unit fibre composition and recruitment strategies during force generation (Adam, De Luca, & Erim, 1998), participants were randomly assigned to the dominant ($n = 5$) or non-dominant ($n = 5$) arm. Before the first MVC, each participant performed a standardized warm-up that included five light stretches of the upper arm (2 s duration each) followed by three individual, low-intensity (<20% MVC) isometric contractions (2 s duration, 10 s rest between contractions).

Occlusion of blood flow

A method for inducing the moderate occlusion of blood flow has been previously reported and is termed *KAATSU* in Japan (Abe et al., 2005b, 2006). A specially designed elastic cuff belt (30 mm wide for the arm; Kaatsu Master, Sato Sports Plaza, Tokyo, Japan) was selected. Complete occlusion of blood flow was verified by an inability to detect blood pressure or pulse saturation (pulse oximeter, Model 9500, Nonin Medical Inc., USA) signals in the occluded arm.

Electromyography

The EMG signals were recorded from surface electrodes. The skin was shaved, abraded with skin preparation gel (Skinpure, Nihon Kohden, Japan), and cleaned with alcohol wipes. During all experiments, skin impedance was less than 2 kΩ. The ground electrode was positioned on the lateral epicondyle. Bipolar electrodes (1 cm diameter, Vitrode F, Ag-AgCl, Nihon Kohden, Tokyo, Japan) were placed over the muscle belly with a constant inter-electrode distance of 20 mm. The electrodes were connected to a pre-amplifier and a differential amplifier with a bandwidth of 0 Hz to 500 kHz (AB 6216, Nihon Kohden, Tokyo, Japan). The EMG signals were collected continuously from the biceps brachii with a sampling rate of 1024 Hz using a 12-bit analog-to-digital converter (Macintosh, Power PC 750, Apple, Japan). Signal analysis was performed during the concentric phase (constant at 1.2 s) of each muscle contraction (Power Lab Chart 4 software, AD Instruments, Japan) since there is a larger effect on EMG amplitude and mean power frequency during the concentric phase (Potvin, 1997). To determine iEMG, signals were fully rectified and integrated. Mean power frequency of the signal amplitude was analysed with the data pad window function and 1024 point Fast-Fourier Transform to obtain the power spectrum.

Ratings of perceived exertion

Ratings of perceived exertion were measured using the Borg scale (Borg, 1973) every 10 contractions in Experiments 1 and 3 and at the time of final repetition of each set of contractions in Experiments 2 and 3.

Statistics

Results are expressed as means and standard deviations (s) for all variables. Statistical analyses were performed by two-way analysis of variance with repeated measures in one domain; all experiments were group × time. *Post hoc* tests were performed by simple main effects where appropriate. *A priori* alpha was set at 0.05 and corrected for multiple comparisons using the Bonferroni technique. The sample size ($n = 10$) was estimated to detect differences in EMG data for the interventions planned. Statistical power was calculated and was greater than 0.80 for all comparisons reported.

Results

There were no differences in MVC, iEMG, level of fatigue or recovery of MVC based on arm dominance in any of the experiments, thus the data were collapsed and are presented as a single group.

Figure 2 shows representative EMG traces from each of the three experiments and each of the blood flow conditions. There were no significant differences between moderate restriction, complete occlusion of blood flow, and control conditions for baseline MVC, iEMG, and MPF (Figure 3). There was a significant decrease in MVC during Experiments 1 and 2 with moderate restriction (16 and 19%, respectively) and complete occlusion of blood flow (39 and 48%, respectively). The decline in MVC was associated with significant decreases in iEMG (Figure 3B) and MPF (Figure 3C), with complete occlusion showing greater declines than moderate restriction of blood flow. No such changes were observed in the control conditions for MVC, iEMG, and MPF in Experiments 1 and 2.

During the contraction bout in Experiment 1, iEMG increased progressively in all three groups. Mean power frequency did not change in the control or moderate restriction groups, but was significantly reduced during complete occlusion of blood flow at the 30th contraction (Figure 4B). During the contractions in Experiment 2, there was a progressive increase in iEMG with moderate restriction and complete occlusion of blood flow such that complete occlusion was significantly greater than moderate restriction of blood flow and the control condition (Figure 4A). Mean power frequency decreased significantly during the third set of contractions with complete occlusion of blood flow; otherwise, there were no differences among the groups (Figure 4B). After 1 min of recovery, MVC had recovered to greater than 90% of baseline values in the moderate restriction and complete occlusion of blood flow conditions with similar iEMG activity (Figure 3A and B). However, MPF associated with MVC remained depressed following complete occlusion of blood flow in both Experiments 1 and 2 (Figure 3C).

In Experiment 3, participants were unable to complete the contraction bout with complete occlusion of blood flow and thus no data are shown; the comparison was between moderate restriction of blood flow and controls. Baseline MVC, iEMG, and MPF were similar between moderate restriction of blood flow and the control (Figure 3). iEMG increased progressively during the bout of contractions in both groups, with moderate restriction of blood flow showing higher values towards the end of the second set of 15 contractions. Mean power frequency did not change in controls, but decreased significantly with moderate restriction of blood flow after the second set of 15 contractions (Figure 4B). Following the contractions, MVC (37%) and the associated iEMG and MPF decreased with moderate restriction of blood flow but not the control (Figure 3).

During the contraction bouts in Experiments 1 and 2, heart rate increased progressively in all groups and was significantly greater than control with complete occlusion of blood flow (Table I). In Experiment 3, heart rate was significantly higher with moderate restriction of blood flow than the control during the last set of contractions (Table I). Ratings of perceived exertion were progressively increased in all groups and significantly greater than the control for both moderate restriction and complete occlusion of blood flow at various times throughout each experiment (Table I). Following the contractions, arm circumference increased in all groups (Table II). Arm circumference increased significantly immediately after the contractions (Experiment 1 and 2) with moderate restriction

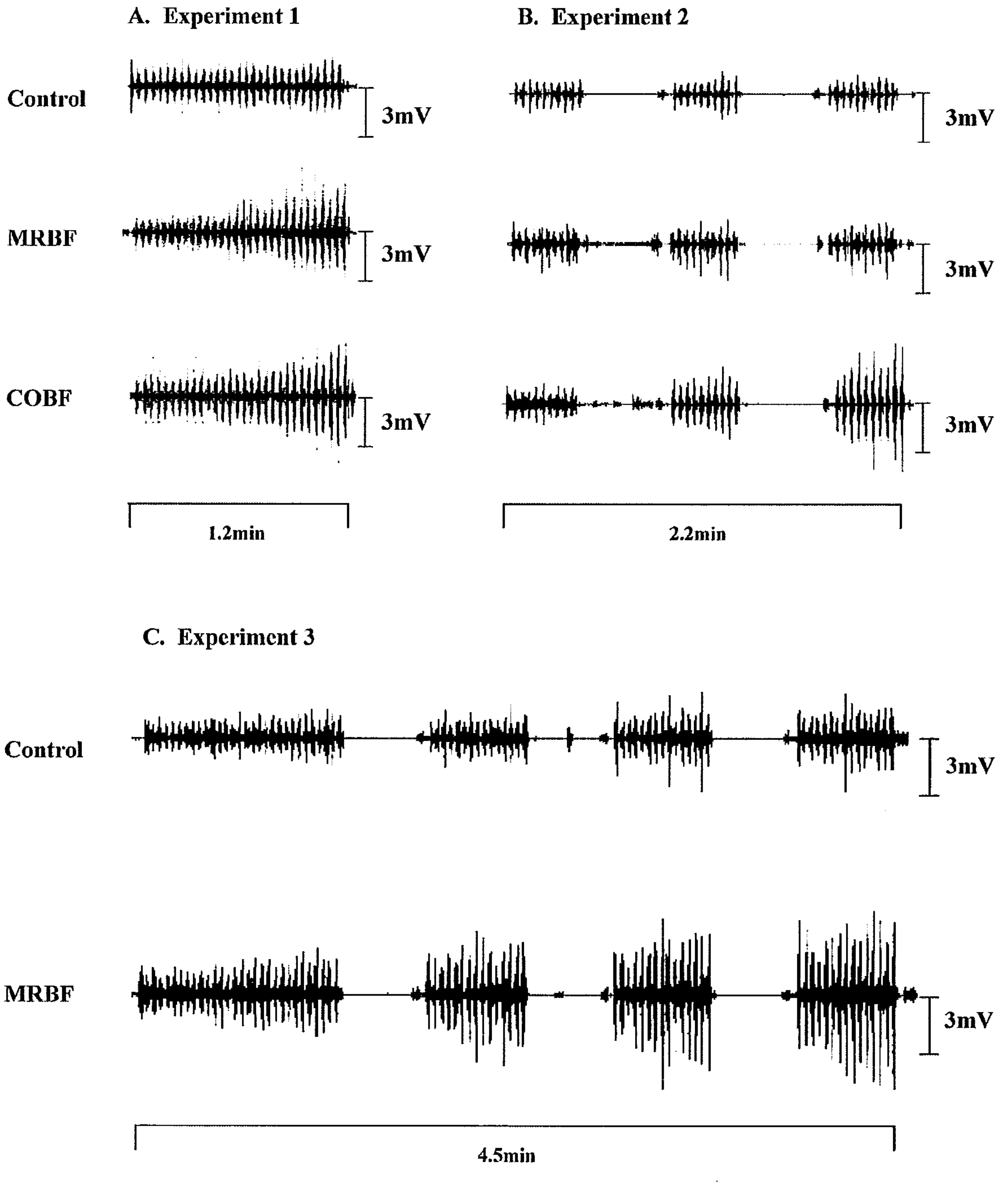

Figure 2. Representative EMG traces from the three experiments. (A) Experiment 1: 30 repetitive contractions; (B) Experiment 2: three sets of 10 repetitions; (C) Experiment 3: 30 repetitive contractions followed by three sets of 15 repetitions. Muscle contractions were biceps curls at 20% of 1RM. MRBF = moderate restriction of blood flow, cuff pressure 160 mmHg; COBF = complete occlusion of blood flow, cuff pressure 300 mmHg.

(5.0 and 6.1%, respectively) and complete occlusion of blood flow (3.2 and 3.2%, respectively), both of which were significantly greater than the control (1.8 and 1.1%, respectively). Similarly, the significant increase in arm circumference after Experiment 3 was greater with moderate restriction of blood flow (6.8%) than the control (1.8%).

Discussion

Critique of methods

Moderate restriction of blood flow has previously been shown to cause complete venous occlusion and partial occlusion of arterial blood flow from the brachial artery as determined by Doppler

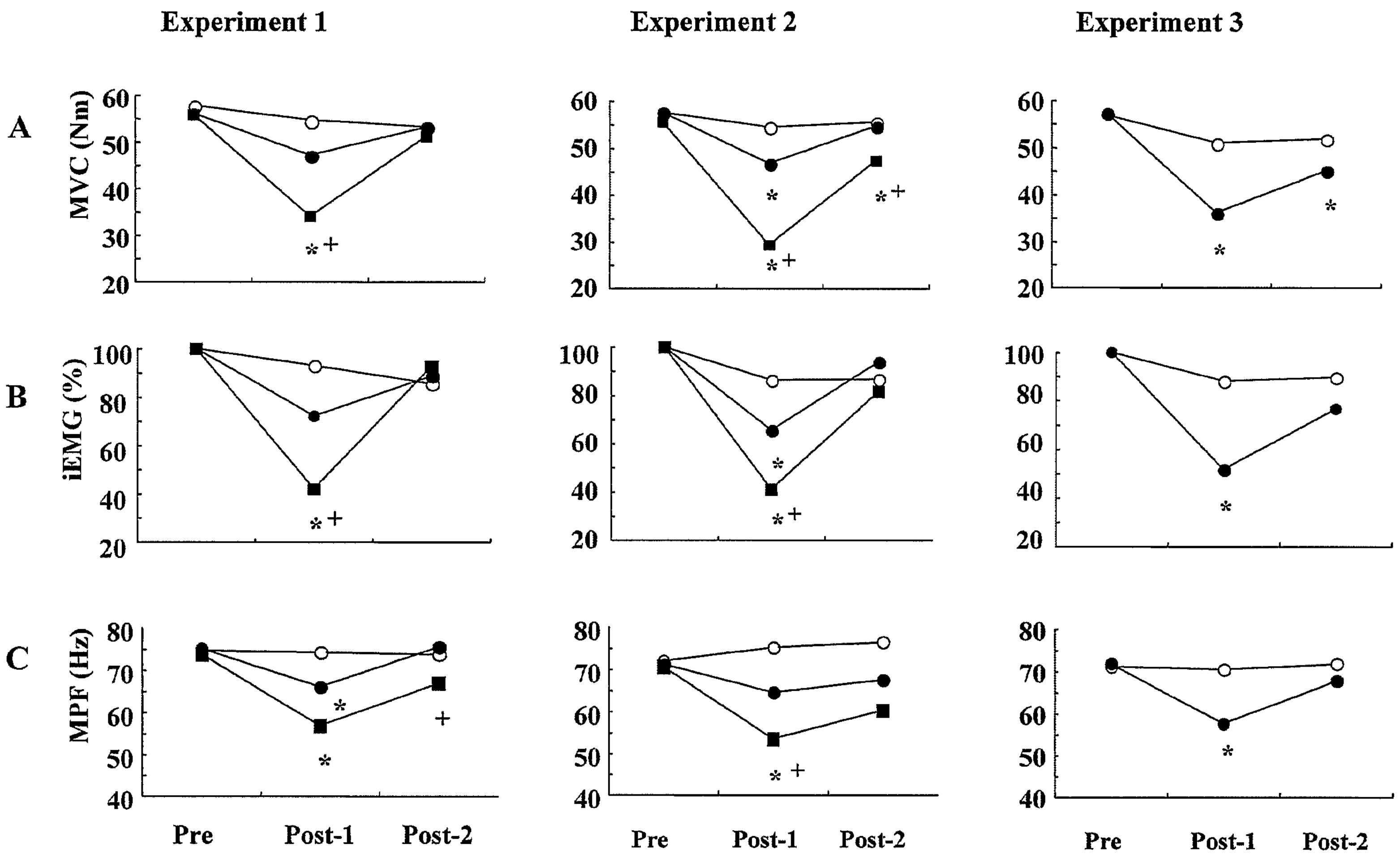

Figure 3. Maximal voluntary isometric contraction (MVC) and EMG parameters at MVC in three experiments ($n = 10$). Data are means but standard deviations (s) are not included for clarity; standard deviation ranges are given in parentheses with the definition of each variable. (A) MVC ($s = 7$–15), (B) integrated EMG data (iEMG; $s = 12$–29), (C) mean power frequency (MPF; $s = 6$–15). ○, control; ●, moderate restriction of blood flow; ■, complete occlusion of blood flow. *Significantly different from control, $P < 0.05$. $^{+}$ Significantly different from moderate restriction of blood flow, $P < 0.05$. Statistical power was 0.87–1.00.

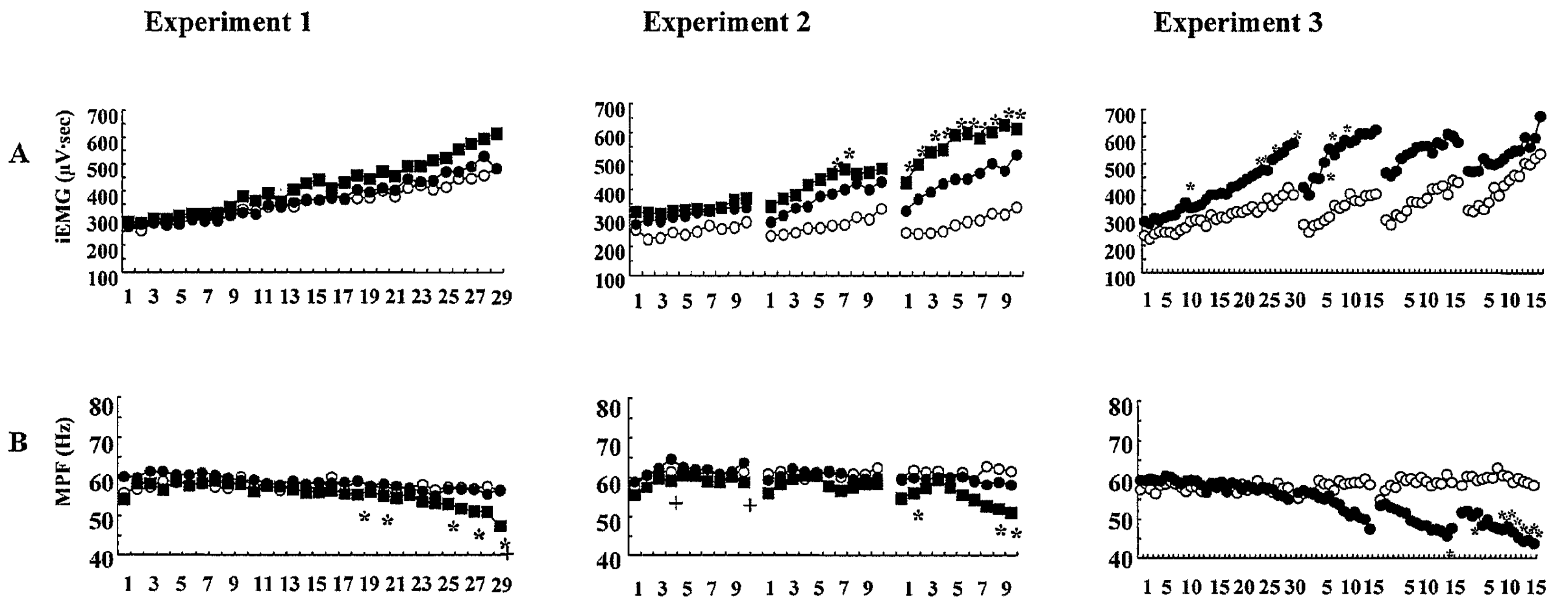

Figure 4. EMG parameters during muscle contractions. For the contraction bout, panel (A) is the iEMG per contraction ($s = 5$–32) and panel (B) is the MPF per contraction ($s = 4$–14). ○, control; ●, moderate restriction of blood flow; ■, complete occlusion of blood flow. *Significantly different from control, $P < 0.05$. $^+$ Significantly different from moderate restriction of blood flow, $P < 0.05$. Statistical power was 0.99–1.00.

Table I. Heart rate and ratings of perceived exertion during Experiments 1, 2, and 3, for muscle contraction of biceps curls performed at 20% of 1-RM.

	Experiment 1				Experiment 2				Experiment 3						
	Pre	C10	C20	C30	Pre	S1-R10	S2-R10	S3-R10	Pre	C10	C20	C30	S1-R15	S2-R15	S3-R15
Heart rate															
Control	66	81	82	82	67	80	81	82	64	80	83	83	83	83	84
	8	9	10	9	9	9	10	9	12	12	12	11	12	11	11
MRBF	64	84	87	88	65	83	85	86	65	85	89	89	89	91	96*
	10	9	10	12	7	7	7	8	10	10	13	14	16	15	15
COBF	68	91*	95*	95*	64	88	90*	93*							
	8	8	12	13	7	7	10	12							
Ratings of perceived exertion															
Control		10	11	13		9	10	11		9	11	12	13	13	14
		2	1	1		2	2	3		2	2	2	2	2	2
MRBF		11	13*	15*		11	13*	15*		11	13	15*	16*	17*	18*
		2	2	2		2	2	3		2	2	1	2	2	2
COBF		12*	14*$^{+}$	18*$^{+}$		11*	14*	17*							
		1	1	2		2	1	2							

Note: Values are mean with standard deviation below ($n = 10$). C10 = 10th contraction, C20 = 20th contraction, and C30 = 30th contraction. S1-R10 = 10th repetition of the first set, S2-R10 = 10th repetition of the second set, and S3-R10 = 10th repetition of the third set. MRBF = moderate restriction of blood flow; 160 mmHg cuff pressure; COBF = complete occlusion of blood flow; cuff pressure 300 mmHg. Pre = pre-contraction (baseline) bout. *Significantly different from control, $P < 0.05$. $^{+}$Significantly different from MRBF, $P < 0.05$. Statistical power was 0.81–1.00.

Table II. Arm circumference (cm) before and after Experiments 1, 2, and 3, for muscle contractions of biceps curls at 20% of 1-RM.

	Experiment 1			Experiment 2			Experiment 3		
	Pre	Post-1	Difference	Pre	Post-1	Difference	Pre	Post-1	Difference
Control	27.9	28.4	0.5	28.1	28.4	0.3	28.0	28.5	0.5
	2.5	2.4		2.4	2.4		2.4	2.4	
MRBF	28.0	29.4	1.4*	28.0	29.7	1.7*	28.1	30.0	1.9*
	2.4	2.3		2.4	2.4		2.5	2.3	
COBF	28.1	29.0	0.9*	28.1	29.0	0.9			
	2.4	2.6		2.6	2.9				

Note: Values are mean with standard deviation below ($n = 10$). Pre = pre-contraction (baseline) bout, Post-1 = immediately after the bout of contractions before removing the pressure cuff. MRBF = moderate restriction of blood flow; 160 mmHg cuff pressure; COBF = complete occlusion of blood flow; cuff pressure 300 mmHg pressure. *Significantly different from control, $P < 0.05$. Statistical power was 1.00.

ultrasonograms (Takarada et al., 2000b). Furthermore, in the present experiments blood pressure or pulse saturation signals were detectable during contractions with moderate restriction of blood flow, indicating that arterial flow was not completely occluded. In contrast, there was a complete absence of detectable signals during complete occlusion of blood flow, indicating no blood flow.

There were no differences in initial MVC or the iEMG and MPF associated with MVC of any bout, and there were no differences in iEMG and MPF during the initial contractions of any bout or experimental condition (Figure 3). Thus, there appears to be no indication of modifications or fatigue associated with multiple experimental bouts (Experiment 3) or, if there were changes, they were balanced through randomization (Experiment 1 and 2). Furthermore, there were no changes in external load (20% of 1-RM), contraction duty cycle or range of motion during the various bouts of contractions. This indicates that the mechanical characteristics of the muscle contractions performed at 20% of 1-RM external load were similar across groups. This supports our conclusion that differences in neural response of the muscles during and after the contractions noted between complete occlusion, moderate restriction of blood flow, and the control condition are specifically related to experimental perturbations – differences in level of nerve compression and/or blood flow occlusion.

Comparison with other data

As stated above, the initial mechanical and neural responses to contractions were similar among groups and experiments. Yet, there is a progressive nature to muscle activation and fatigue with respect to the level of blood flow perturbation noted among the three experiments. This is indicative of a progression in "apparent" contraction intensity despite the same external load, contraction duty cycle, and range of motion.

The basis for the increased activation and "apparent" contraction intensity may be related to impairment of sensory function, which disturbs central nervous system regulation of muscle force generation secondary to the external compression and/or blood flow perturbation (Leonard et al., 1994). With complete occlusion of blood flow, there was a reduction in reflex inhibition of alpha motoneurons and inappropriate increases in MPF, hence inappropriate motor unit recruitment (Leonard et al., 1994). However, in the present case the inappropriate increase in motor unit recruitment appears to be related to reductions in motor unit discharge rates to maintain force by protecting against conduction failure and by optimizing the input to motor units as their contractile properties change during fatigue (Bigland-Ritchie, Johansson, Lippold, Smith, & Wood, 1983; Jones, 1996; Jones, Bigland-Ritchie, & Edwards, 1979). That a reduction in stimulation frequency matching reduced membrane conduction failure is indicated by the progressive reductions in MPF with increasing iEMG during Experiments 1 and 2 with complete occlusion and Experiment 3 with moderate restriction of blood flow. Thus, the derangement of central nervous system regulation "caused" by the external nerve compression and/or blood flow reduction leads to increased motor unit recruitment at the same external load and muscle force production, hence the greater apparent contraction intensity. The greater contraction intensity at the same external load is supported by higher heart rates and ratings of perceived exertion during the bouts of contraction with reduced blood flow (Table I). Furthermore, moderate restriction of blood flow has been shown to result in greater oxygen uptake during treadmill walking than control conditions with unimpeded blood flow (Abe et al., 2006), suggesting a higher energy demand. The inability of participants to complete the combination contraction bout (Experiment 3) under complete occlusion of blood flow, which is in line with previous observations (Cook, Clark, & Ploutz-Snyder, 2007), indicates an extreme mismatch of energy demand (increasing muscle activation) and energy supply (no blood flow) and clearly shows that increasing motor unit recruitment (increased iEMG) with declining MPF is unable to compensate for changes in energy supply. This results in feelings of maximal exertion (ratings of perceived exertion; Table I) and complete mechanical failure, and thus an inability to complete the contraction bout (as described above in the Methods section).

Additionally, in three cases there were visible indications of shaking and jerking during completion of the final repetitions during Experiment 2 with complete occlusion ($n = 2$) and Experiment 3 with moderate restriction of blood flow ($n = 1$). Despite this shaking and jerking, the participants maintained the 1.2 s/1.2 s contraction – relaxation duty cycle and contraction range of motion. This apparent decrement in motor control is interpreted as a sign of synchronous rather than asynchronous motor unit recruitment, and is indicative of increased activation and the neural changes concluded above.

Thus, compared with complete occlusion, moderate restriction of blood flow presented a lesser neural derangement and energy demand/energy supply mismatch at the same work (Experiments 1 and 2) or allowed more work to be accomplished (Experiment 3). This is in line with previous work in which fewer repetitions could be completed with complete occlusion than moderate restriction of blood flow (Cook et al., 2007). Compared with the control, moderate restriction of blood flow accomplished the same work output, but at a higher level of muscle activation. Therefore, the external compression of the nerve and blood flow perturbations employed here resulted in progressive changes in the apparent intensity of the contractions as judged by muscle activation and level of decline of MVC (fatigue). Stated another way, neural compression and blood flow impairment altered the energy demand/energy supply relationship during the contractions, resulting in a greater muscle activation and greater energetic demand at the same external load (20% of 1-RM).

Moderate restriction of blood flow and muscle adaptation to training

Previous studies of low-load training with a moderate restriction of blood flow have reported significant increases in muscle enlargement and muscular strength that are comparable to those observed with much higher training loads (Abe et al., 2005b, 2006; Takarada et al., 2004; Yasuda et al., 2005). The basis for these seemingly paradoxical adaptations appears to originate from an increased internal demand (increased muscle activation; reported herein) relative to the external load caused by nerve compression and/or an appropriate reduction in blood flow (moderate restriction vs. complete occlusion of blood flow). Based on the muscle activation and fatigue patterns reported here, there appears to be an appropriate match between the level of the external load adopted and neural impairment (the level of nerve compression and blood flow occlusion) so as to avoid serious impairments in neuromuscular function that would lead to undue fatigue and delayed recovery (e.g. complete occlusion of blood flow and Experiment 3). This would ultimately limit the effectiveness of the low-load muscle contractions to stimulate the training responses reported previously (Abe et al., 2005b, 2006; Cook et al., 2007; Takarada et al., 2004; Yasuda et al., 2005). Consequently, a 20% of 1-RM external load with nerve compression and a moderate restriction of blood flow appears to fulfil this requirement based on the level of muscle activation and fatigue during the bout of contractions and rapid recovery of mechanical function (MVC) following the contractions.

Arm circumference increased following every contraction bout with moderate restriction or complete occlusion of blood flow as anticipated (Abe, 2004). Ploutz-Snyder and colleagues (Ploutz-Snyder, Convertino, & Dudley, 1995) reported that the increase in muscle cross-sectional area immediately after a high-load resistance exercise bout was associated with an absolute loss of plasma volume, reflecting a primary fluid shift from the vascular space into active muscle. There was no such externally measurable fluid movement in the control condition, likely because the load was so light. This apparent fluid shift may play an important role in the hypertrophic response of muscle to training with low loads and moderate restriction of blood flow (e.g. Abe, 2004; Abe, Beekley, Hinata, Koizumi, & Sato, 2005a; Abe et al., 2005b). Recently, it has been noted in humans that cell swelling (i.e. via saline infusion) results in a reduction in proteolysis (Berneis, Ninnis, Haussinger, & Keller, 1999; Keller, Szinnai, Bilz, & Berneis, 2003). This may be due to activation of a signalling mechanism such as h-sgk, which is known to be triggered by cell swelling *in vivo* (Waldegger, Barth, Raber, & Lang, 1997). This, in combination with the increased protein production (activation of mTOR; Fujita et al., 2007), could contribute to increased net protein balance and subsequently an anabolic response of skeletal muscle observed following low-load training with moderate restriction of blood flow.

In conclusion, nerve compression and/or blood flow occlusion with moderate restriction of blood flow results in similar neural manifestations in muscle as observed with complete occlusion of blood flow but without the apparent contractile/metabolic impairment observed with complete occlusion. Furthermore, increased muscle activation associated with low external loads (20% of 1-RM) caused by neural compression and/or occlusion of blood flow appears to result in greater internal activation intensity on the muscle relative to the external load. This appears to be the basis for a greater relative energy demand, and therefore the greater muscle enlargement and muscular strength training effects observed previously (Abe et al., 2005b, 2006; Takarada et al., 2004; Yasuda et al., 2005). Further experimentation is needed to address the relationship between changes in energy demand (increased muscle activation) and sensory feedback with moderate restriction of blood flow and how this impacts muscle adaptation following training.

Acknowledgements

The authors thank the students who participated in this study. This study was supported by Grant-in-aid 15300221 from the Japan Ministry of Education, Culture, Sports, Science, and Technology.

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