©Journal of Sports Science and Medicine (2014) **13,** 836-845
http://www.jssm.org

Research article

Effect of Differing Intensities of Fatiguing Dynamic Contractions on Contralateral Homologous Muscle Performance

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Abstract
The purpose of this study was to investigate different intensities of unilateral fatiguing dynamic quadriceps contractions on non-exercised, contralateral quadriceps performance. In a randomized crossover study design with 12 recreationally trained male (1.78 ± 0.05 m, 84.5 ± 7.6 kg, 30.0 ± 8.5 yrs) participants, maximal voluntary contraction (MVC) force, force developed in the first 100 ms (F100), and electromyography of the non-exercised contralateral knee extensors were measured before and after fatiguing protocols performed by ipsilateral knee extensors. Non-exercised knee extensors' endurance was also measured post-intervention. The fatigue protocols consisted of four sets of dynamic knee extensions each to task failure with 40% and 70% MVC on separate days. Both the 40% (p = 0.009, Effect Size [ES] = 0.72) and 70% (p = 0.001, ES = 2.03) conditions exhibited 23.7% and 34.6% decreases in F100 respectively with the non-exercised contralateral knee extensors. A significant time effect (p = 0.002) demonstrated that both the 40% (and 70% (conditions exhibited 4.4% (ES = 0.29) and 7.1% (ES = 0.53) force decreases from pre- to post-intervention, respectively. However, the condition * time interaction only showed a trend (p = 0.09) with moderate (40%: ES = 0.62) to large (70%: ES = 0.82) effect sizes for decreased contralateral limb force compared with control session. The 40% (p = 0.09, ES = 0.65) and 70% (p = 0.07, ES = 0.79) protocols had a tendency to induce greater contralateral force variation during sustained submaximal isometric contraction compared with control. In conclusion, this study highlighted that unilateral lower limb fatigue induced by low intensity as well as high intensity dynamic knee extensions provided some evidence of crossover fatigue with the contralateral non-exercised limb.

Key words: Central fatigue; peripheral fatigue; maximal voluntary contraction; dynamic contractions, electromyography.

Introduction

Fatigue induced at a specific muscle can contribute to the development of central (neural) fatigue and result in a non-local response (crossover fatigue)(Martin and Rattey, 2007; Rattey et al., 2006). Crossover fatigue is fatigue of a non-exercised muscle following fatiguing contractions of a disparate muscle. Research exploring crossover fatigue appears to be equivocal. Several studies have not shown significant crossover fatigue effects between homologous (Elmer et al., 2013; Grabiner and Owings, 1999; Regueme et al., 2007; Todd et al., 2003; Zijdewind et al., 1998) and heterologous muscles (Decorte et al., 2012; Humphry et al., 2004; Millet and Lepers, 2003; Place et al., 2004; Ross et al., 2007; 2010). In contrast, significant crossover fatigue effects have been found in contralateral homologous (Doix et al., 2013; Martin and Rattey, 2007; Rattey et al., 2006; Triscott et al., 2008) and heterologous muscle groups (Kennedy et al., 2013; Takahashi et al., 2011) following isolated muscular fatigue. Moreover, crossover fatigue can affect single leg landing strategies (McLean and Samorezov, 2009) and postural control (Paillard et al., 2010). Recent research by Amann and colleagues (2013) found that constant load single leg knee-extensor exercise performed to exhaustion resulted in a reduction of endurance time to exhaustion in the consecutively exercised, non-fatigued contralateral leg by ~49%; however, no significant changes were seen in potentiated twitch, maximum voluntary contraction (MVC) force and voluntary muscle activation. Evidently, there is a conflict in the literature regarding the crossover fatigue phenomenon despite studies claiming that subjects were brought to temporary exhaustion. The discrepancy in results may be related to the inconsistency of unilateral fatiguing protocols as several variables differ such as exercise intensities, volumes and types of contraction.

Research examining crossover fatigue following dynamic contractions is sparse. Crossover fatiguing protocols have utilized several contraction types such as isometric, isotonic (dynamic) and isokinetic and varying contraction intensities. Isometric fatiguing protocols have been shown to induce (Doix et al., 2013; Kennedy et al., 2013; Martin and Rattey, 2007; Paillard et al., 2010; Rattey et al., 2006) as well as not induce (Todd et al., 2003; Zijdewind et al. 1998) crossover fatigue. For example, a 100 s knee extensor isometric MVC fatigue protocol reduced voluntary activation of the contralateral non-fatigued knee extensors but did not alter MVC force (Rattey et al., 2006). In contrast, Martin and Rattey (2007) used the same fatiguing protocol and found a reduction in MVC force output from the contralateral non-fatigued homologous muscles, which was accompanied with larger reductions in voluntary activation. Maximal and submaximal bilateral isometric handgrip exercise held until force was reduced to 80% of pre-fatigue values resulted in a decrease in ankle plantar flexion MVC and voluntary activation (Kennedy et al., 2013). Interestingly, the maximal fatiguing protocol was more impactful on reducing

Received: 13 June 2014 / Accepted: 13 August 2014 / Published (online): 01 December 2014

ankle plantar flexor MVC and voluntary activation compared to the submaximal fatiguing protocol indicating that central fatigue to an uninvolved lower limb muscle is intensity-specific (Kennedy et al., 2013).

Similarly, fatigue protocols using dynamic contractions also have varying crossover fatigue effects. Isokinetic knee flexion/extension contractions had no effect on the contralateral hamstrings but actually enhanced contralateral quadriceps MVC force (Strang et al., 2009). Dynamic free weight lower body exercise induced crossover fatigue in female athletes (Mclean and Samorezov, 2009). Furthermore, three 5-minute sets of bilateral leg presses performed with 50% of a dynamic MVC was found to depress motor evoked potentials (MEPs) and short interval intracortical inhibition (SICI) in non-exercised upper limb muscles (Takahashi et al., 2011). As the majority of crossover fatigue studies employ isometric contractions, the dearth of literature employing dynamic resistive exercise effects should provide an impetus for further investigations in this area.

It appears that the fatiguing protocol volume is an important factor in the development of crossover fatigue (Doix et al., 2013; Humphry et al., 2004). Performing only one 100-seconds MVC with the knee extensors was insufficient volume to produce crossover fatigue to the contralateral limb while two bouts of 100-seconds MVC was successful (Doix et al., 2013). Additionally, unilateral biceps curls performed with 3.5 kg performed to exhaustion resulted in crossover fatigue effects to the contralateral homologous muscles but failed to do so when only 25% of the volume was performed (Humphry et al., 2004). From the limited research, it appears that fatiguing protocols of higher intensity and larger volumes have greater crossover fatigue effects compared to lower intensity and lower volume protocols.

The objective of the present study was to determine if varying intensities of unilateral dynamic fatiguing resistive exercise would elicit strength and endurance impairments on the contralateral homologous muscle group. Based on the related literature it was hypothesized that a higher intensity of unilateral dynamic exercise would lead to greater crossover fatigue effects, demonstrated by detriments in muscle strength and endurance (time to maintain 70% MVC).

Methods

Subjects

Twelve recreationally trained (at least 2 training sessions a week for the past 6 months) male (height 1.78 ± 0.05 cm, body mass 84.5 ± 7.5 kg, age 30.0 ± 8.5 yrs.) participants were recruited for this study. Eleven of the participants were determined to be right-leg dominant, while one participant was left-leg dominant as assessed with the Edinburgh inventory (Oldfield, 1971) and the leg used to kick a soccer ball. Prior to testing and after a brief explanation of the procedures of the experiment, each participant completed the Physical Activity Readiness Questionnaire-Plus (Canadian Society for Exercise Physiology, 2011) and read and signed a letter of informed consent. Volunteers who reported neurological complications, surgery or injury to knee structures or cardiovascular conditions such as high blood pressure were not allowed to participate in the experiment. To eliminate confounding variables, participants were instructed not to engage in strenuous physical activity and to abstain from alcohol consumption, caffeine or nicotine for the 24-hour period prior to participation. Testing was performed at similar times during the day to avoid diurnal variations. The Health Research Ethics Authority of the Memorial University of Newfoundland approved this research protocol.

Experimental overview

A randomized cross over study design was used to examine the acute effects of localized unilateral knee extensor muscle fatigue on the performance of the contralateral homologous muscle (Figure 1). The participants were required to attend the lab on three separate occasions (separated by at least 48 hours) during which muscle performance (force and electromyography (EMG)) data were collected from both dominant and non-dominant knee extensors. Experimental sessions consisted of three testing sessions including control (no intervention), 40% (dominant leg fatigued by a dynamic knee extension protocol using a load equal to 40% of pretest MVC) and 70% (dominant leg fatigued by a dynamic knee extension protocol using a load equal to 70% of pretest MVC). The three experimental protocols were randomly selected for each experimental session. A series of submaximal and maximal isometric knee extensions were performed with the non-dominant and dominant-limb (fatigued limb) before and after the intervention protocols.

General procedures

Participants were seated in the knee extension machine (Modular Leg Extension, Cybex International, Medway, MA, USA) with the hip and knee were fixed at 90° and 83° respectively. The knee angle was measured with a goniometer and was not equal to 90° because of the angle of the seat pan could not be adjusted. To eliminate upper body involvement, a strap was placed around the waist and participants were instructed to cross their hands across their chest. The dominant - and the non-dominant ankle were then inserted into padded ankle cuffs that were attached to strain gauges (Omega engineering Inc., LCCA 250, Don Mills, Ontario) via taut non-extensible straps. The strain gauge and the straps were secured to the isotonic leg extension machine via a custom-built apparatus (Technical Services Memorial University of Newfoundland) and were adjusted to form a 90^0 angle with the subject's lower shin (Figure 2). Differential voltage from the strain gauge, which was sampled at a rate of 2,000-Hz, was amplified (1000X), digitally converted (Biopac Systems Inc. DA 100 and analog to digital converter MP100WSW; Holliston, MA) and monitored on a computer. A commercial software program (AcqKnowledge III, Biopac Systems Inc., Holliston, MA) was used to analyze the digitally converted analog data.

After positioning on the knee extension machine, subjects performed a warm-up including two sets of 10 dynamic bilateral knee extensions with a load equivalent to approximately 30% subject`s body mass. In addition,

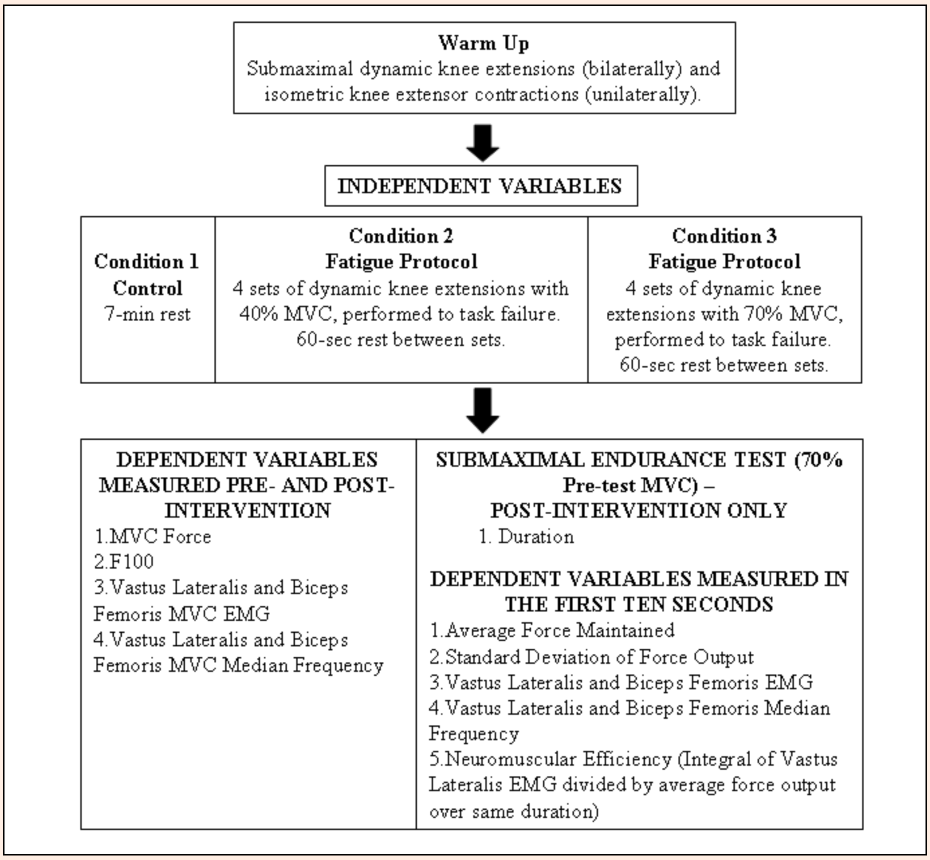

Figure 1. **Experimental design.**

both the left and right legs performed five submaximal unilateral isometric knee extension contractions. Subjects were instructed to contract for five seconds at a force equal to 6-8/10 on a scale of one to ten, where 10/10 equaled maximal effort.

Figure 2. **Leg extension custom apparatus.**

Next, in a randomized order, participants performed two unilateral isometric knee extension MVCs with the non-dominant and dominant limb. Each MVC was performed for 5 s and 2 min rest was given between MVCs. If the difference between the two MVCs was more than 5%, a third MVC was performed. Subjects were instructed to initiate each MVC by contracting their involved muscles as hard and as fast as possible. Subsequently, the intervention protocol (a 7-minute rest period for control session, or the 40% or 70% fatigue protocol) was performed (detail described below). An indication of the extent of dominant limb fatigue was provided with a MVC testing between the third and fourth sets. The last set of the fatigue protocol was then performed after 60-seconds rest. Immediately after (within 10 s) the completion of the dominant leg fatigue protocol, subjects were asked to perform a MVC (five seconds) followed by a submaximal endurance test at 70% pretest MVC (knee at 83^0; 0^0 being full extension) with their non-dominant limb for as long as possible. The knee extension force production was monitored on the screen and participants were instructed to reach the 70% MVC line marked on the screen. However, subjects were not able to view the elapsed time.

Fatigue intervention protocol

The two fatigue protocols used in this study consisted of 4 sets of voluntary dynamic knee extensions (83° to 0° and return with 0° being full knee extension) with each set performed to task failure at loads equal to 40% or 70% of the greatest dominant leg pretest MVC measured at the beginning each testing session. Dynamic knee extensions were performed at a 1-Hz tempo (1s concentric and 1s eccentric contractions), which was dictated by a metronome. One-minute recovery was allotted between sets. Schmidtbleicher (1985) reported that isometric MVC force is approximately 20% higher compared to concentric muscle contractions and 20% lower compared to eccentric contractions. Therefore, the isometric MVC was multiplied by a factor of 0.8 before the 40% and 70% loads were calculated. To determine the appropriate loads for each of the two fatiguing protocols, the average force produced during the entire range of motion in one isotonic knee extension repetition was measured. The knee extension machine was plate loaded (4.55-kg plate increments) and adjusted by changing the location of a pin. One-kilogram weights were used to allow for more precise adjustments in the load. To ensure full range of motion was obtained for each repetition, the distal portion of the shin (tibia) had to contact a piece of nylon tape that was positioned at a height equal to full knee extension. Fatigue was defined as the inability to extend the knee and contact the nylon tape at the prescribed tempo.

Immediately following the third set of the fatigue protocol, an isometric MVC was performed with the dominant knee extensors to determine the extent of dominant knee extensor fatigue. Total repetitions per set were recorded while incomplete repetitions were discounted. The EMG activity was monitored and subjects were instructed to ensure the non-dominant (reference or non-exercised) limb was relaxed during the dominant (fatigued) limb contractions.

Electromyography (EMG)

Prior to electrode placement, the skin was shaved and abraded to remove dead skin with sandpaper and cleansed with an isopropyl alcohol swab to decrease skin resistance. Self-adhesive Ag/AgCl electrodes (MeditraceTM 130 ECG conductive adhesive electrodes) were located parallel to the direction of the vastus lateralis (VL) and biceps femoris (BF) muscle fibres. The electrodes were placed at the mid-point of the anterior superior iliac spine to the patella for the VL and the gluteal fold and popliteal space for the BF. The inter-electrode distance was 2 cm (centre to centre) and electrode locations were recorded to ensure consistent placement for all sessions (Paddock and Behm, 2009). The ground electrode was placed on the lateral femoral epicondyle. An inter-electrode impedance of < 5 kOhms was obtained prior to recording to ensure an adequate signal-to-noise ratio. EMG activity was digitally filtered with a linear phase Blackman -61 dB band-pass filter between 10-500 Hz, amplified (bi-polar differential amplifier, input impedance = 2MΩ, common mode rejection ratio > 110 dB min (50/60 Hz), gain x 1000, noise > 5 μV), and analog-to-digitally converted (12 bit). All EMG signals were recorded (Biopac System Inc., DA 100: analog-digital converter MP150WSW; Holliston, Massachusetts) with sampling rate of 2000 Hz using a commercially designed software program (AcqKnowledge III, Biopac System Inc.).

Measurements and data analysis

Isometric MVC and submaximal voluntary contraction (at 70% pretest MVC). Peak force production and instantaneous force output (force developed in the first 100 ms of the MVC) were calculated from the MVC trials (Hearn et al., 2009). In addition, to determine if there were any fatigue-related changes in the ability to maintain 70% isometric MVC during the endurance test (i.e. motor control; co-ordination, synchronization), the average force output and the standard deviation of the force output were measured during the first 10-seconds. That start of the submaximal contraction was considered the point at which the force output exceeded the 70% value of the isometric MVC. The test endurance test was terminated when after two warnings from the researchers, the subject could not consistently maintain the prescribed force output.

EMG. The EMG activity of the VL and BF was quantified during pre- and post-test knee extension MVCs before and after the interventions. A finite infinite response high pass filter was used (frequency cutoff fixed at 20 Hz) on all EMG data. The root mean square of the EMG (average of 50 data points) of each muscle was calculated across 1-second window that included the peak force output (0.5 s before and 0.5 s after peak force). In addition, power spectral analysis was conducted to compute the median frequency with an epoch equal 3-second window that included the peak force output.

For the submaximal endurance test (70% MVC) the root mean square of the EMG signal was measured during the first 10-seconds to determine the EMG output. The first 10-seconds was selected because it was the minimum period of time that all participants were able to hold 70% MVC following various intervention conditions. A power spectrum analysis was then conducted to determine the median frequency. Neuromuscular efficiency during the first 10-seconds of the submaximal contraction was calculated by dividing the integral of the EMG signal by the average force.

Table 1. Intraclass Correlation Coefficients (ICC) for each leg.

Leg	Variable	ICC Cronbach's Alpha
Dominant	MVC Force	.952
Dominant	F100	.647
Dominant	EMG VL	.949
Dominant	EMG BF	.887
Non-Dominant	MVC Force	.977
Non-Dominant	F100	.878
Non-Dominant	EMG VL	.908
Non-Dominant	EMG BF	.791

MVC, maximum voluntary contraction; F100, force in the first 100 milliseonds; EMG, electromyography; VL, vastus lateralis; BF, biceps femoris.

Statistical analysis

Statistical analyses were calculated using SPSS software (Version 16.0, SPSS, Inc, Chicago, IL). As a measure of reliability, intraclass correlation coefficients (ICC) were calculated for MVC force, F100, EMG VL and EMG BF in both dominant and nondominant leg (Table 1). Normality (Kolmogorov-Smirnov) and assumption of Sphericity tests were conducted for all dependent variables. As normality and sphericity were met, the effect of three exercise protocols (control, 40% and 70% of MVC) on pre- and post-test measurements, was performed with a two way analysis of variance (ANOVA) with repeated measure (3 conditions × 2 times) for each variable (e.g. MVC or EMG measures) with the fatigued and non-fatigued leg. If significant main effects or interactions were observed, Bonferroni correction post-hoc tests were used to compare different conditions and times. Significance was defined as $p < 0.05$. In addition, to determine the effect of three exercise protocols (control, 40% and 70% of MVC) on endurance test (submaximal isometric knee extension at 70% MVC) measures, a one way analysis of variance (AVOVA) with repeated measure (3 conditions) was performed followed by a series of paired t-tests to compare different conditions if the ANOVA showed any significant main effect. Significance was defined as $p < 0.05$. Cohen effect size (ES) statistics were conducted to evaluate the magnitude of the changes following various exercise protocols to the criterion of >0.70 large; 0.40-0.70 medium and <0.40 small (Cohen, 1988).

Results

Fatigue intervention protocol

The average number of repetitions performed to task failure was approximately 6 ± 2 (~12 s of work; 70% MVC) and 13 ± 5 (~26 s of work; 40% MVC) per set.

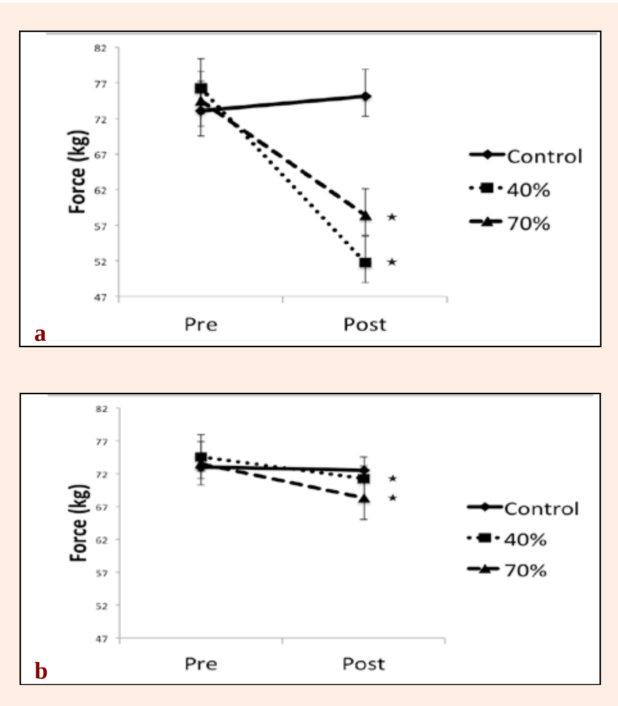

Figure 3. MVC force pre-post intervention. Representation of force in the dominant, fatigued leg (a) and non-dominant, non-exercised leg (b), pre- and post-intervention. Variation in data indicated by standard error. Significance was set at $p < 0.05$. * indicates significant pre-post intervention differences. Whereas there were significant differences between all 3 conditions with the dominant fatigued leg post-intervention, there were no significant differences between the 40% and 70% conditions for the contralateral non-exercised limb post-intervention.

MVC Force

Statistical analysis revealed a significant main effect for time ($p < 0.0001$), condition ($p < 0.0001$) and interaction of time * condition ($p < 0.0001$) for MVC force production by the fatigued leg. MVC forces decreased significantly from pre- to post-test by 32.1% and 21.6% in the 40% ($p < 0.0001$, ES = 2.13) and 70% conditions ($p < 0.0001$, ES = 1.27), respectively. No significant change was observed in the control condition (Figure 3a).

There was a significant time effect ($p = 0.002$) for MVC force production by the non-exercised leg. Bonferroni post hoc test demonstrated smaller MVC for post-test compared with pretest value ($p = 0.01$). Further analysis revealed that both the 40% and 70% conditions exhibited 4.4% (ES = 0.29) and 7.1% (ES = 0.53) force decreases from pre- to post-intervention, respectively. However, the condition * time interaction only showed a trend (p=0.09) with moderate (40%: ES = 0.62) to large (70%: ES = 0.82) ES for decreased contralateral limb force relative to magnitude of change with control session. There was no significant main effect for condition (Figure 3b).

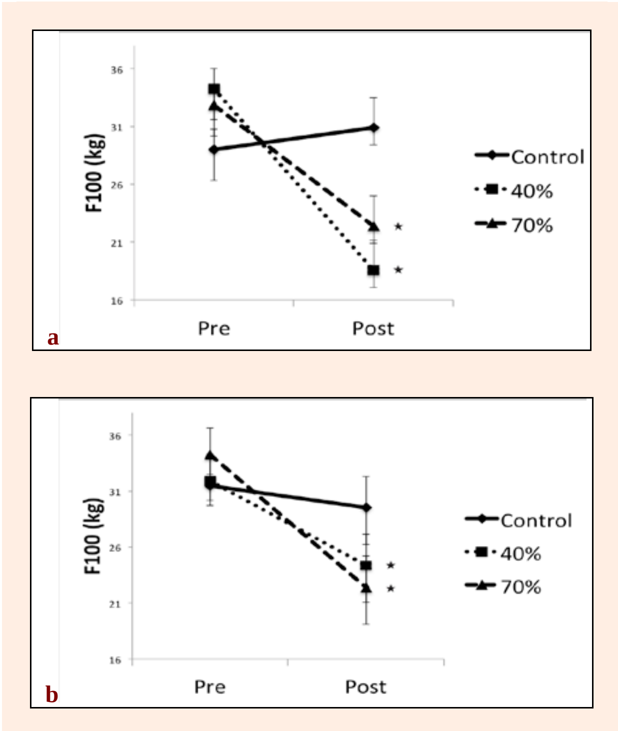

Figure 4. F100 pre-post intervention. Representation of F100 in the dominant, fatigued-leg (a) and non-dominant, non-exercised leg (b), pre- and post-intervention. Variation in data indicated by standard error. Significance was set at $p < 0.05$. * indicates significant pre-post intervention differences.

F100

There was a significant time effect ($p < 0.0001$) and interaction of time * condition ($p = 0.002$) for the fatigued leg for F100. Both the 40% ($p = 0.000$, ES = 2.13) and 70% ($p < 0.0001$, ES = 1.19) conditions showed 45.9% and 31.9% reductions in F100 from pre- to post-intervention, respectively (Figure 4a).

The analysis showed a significant main effect for time for the F100 of the non-dominant leg ($p = 0.01$). In addition, a significant interaction effect (condition * time) was found for this parameter ($p = 0.018$). Both the 40% ($p = 0.009$, ES = 0.72) and 70% ($p = 0.001$, ES = 2.03) conditions exhibited 23.7% and 34.6% decreases in F100 from pre- to post-intervention, respectively (Figure 4b).

Table 2. Absolute values of the dominant Leg. Data are means (±SD).

Variables	Condition	Time	Mean (SD)	p <	ES
VL EMG(mV)	**Control**	Pre	.50 (.19)	.146	.10
		Post	.54 (.22)		
	40%	Pre	.57 (.26)	.005	.61
		Post	.44 (.15)		
	70%	Pre	.51 (.18)	.008	.37
		Post	.45 (.14)		
BF EMG (mV)	**Control**	Pre	.037 (.010)	.504	.06
		Post	.036 (.008)		
	40%	Pre	.035 (.007)	.504	.22
		Post	.030 (.014)		
	70%	Pre	.037 (.012)	.504	.16
		Post	.033 (.013)		
VL MF (Hertz)	**Control**	Pre	35.81 (4.75)	.666	.14
		Post	37.39 (6.47)		
	40%	Pre	35.74 (3.90)	.026	.90
		Post	31.11 (6.09)		
	70%	Pre	37.27 (5.06)	.009	.63
		Post	33.49 (6.69)		
BF MF (Hertz)	**Control**	Pre	37.62 (5.92)	.429	.11
		Post	39.24 (8.79)		
	40%	Pre	39.17 (5.60)	.429	.17
		Post	37.41 (4.52)		
	70%	Pre	40.53 (2.89)	.429	.10
		Post	41.0 (1.28)		

ES, Effect Size; EMG, Electromyography; VL, vastus lateralis; BF, biceps femoris; MF, Median Frequency.

There was no significant decrease with the control condition. There was no significant main effect for condition.

EMG Vastus Lateralis (VL)

A significant main effect for time (p = 0.019) and interaction of condition * time (p = 0.002) was recorded for the dominant fatigued leg for VL EMG. Both the 40% (p = 0.005, ES = 0.61) and 70% (p = 0.008, ES = 0.37) conditions showed 22.8% and 11.7% reductions in VL EMG from pre- to post-intervention, respectively (Table 2). However, no significant results were found regarding VL EMG in the contralateral non-exercised leg (Table 3).

Statistical analysis revealed a significant time effect for the dominant fatigued leg for VL median frequency (p = 0.024). Both the 40% (ES = 0.90) and 70% (ES = 0.63) conditions showed 12.9% and 10.1% reductions in VL median frequency from pre- to post-intervention, respectively. Bonferroni post hoc test demonstrated that post-test was significantly less than pre-test (p = 0.024)(Table 2).

Table 3. Absolute values of the non-dominant Leg. Data are means (±SD).

Variables	Condition	Time	Mean (SD)	p <	ES
VL EMG(mV)	**Control**	Pre	.53 (.22)	.492	.04
		Post	.55 (.26)		
	40%	Pre	.54 (.29)	.492	.00
		Post	.54 (.29)		
	70%	Pre	.52 (.20)	.492	.11
		Post	.50 (.15)		
BF EMG (mV)	**Control**	Pre	.04 (.01)	.408	.00
		Post	.04 (.01)		
	40%	Pre	.06 (.07)	.408	.00
		Post	.06 (.07)		
	70%	Pre	.04 (.02)	.408	.00
		Post	.04 (.02)		
VL MF (Hertz)	**Control**	Pre	34.21 (3.94)	.319	.11
		Post	33.35 (3.92)		
	40%	Pre	33.60 (4.09)	.323	.06
		Post	34.67 (3.84)		
	70%	Pre	32.64 (5.87)	.084	.33
		Post	34.42 (4.92)		
BF MF (Hertz)	**Control**	Pre	36.99 (5.43)	.685	.13
		Post	38.49 (5.85)		
	40%	Pre	37.71 (6.35)	.685	.12
		Post	35.93 (5.91)		
	70%	Pre	35.05 (8.47)	.685	.05
		Post	34.27 (6.98)		

ES, Effect Size; EMG, Electromyography; VL, vastus lateralis; BF, biceps femoris; MF, Median Frequency.

No significant results were found regarding VL median frequency in the contralateral, non-exercised leg (Table 3).

EMG Biceps Femoris (BF)

No significant changes were found regarding BF EMG in both the dominant and non-dominant sides (Table 2 and 3). No significant changes were found regarding BF median frequency in both the dominant and non-dominant sides (Tables 2 and 3).

Submaximal endurance test measures

There was no significant effect of crossover fatigue on the duration of the 70% MVC endurance test (control: 36.21s ± 11.46; 40%: 35.26s ± 10.02; 70%: 33.00s ± 9.49); average force maintained in first 10-seconds, VL and BF EMG, VL and BF median frequency and neuromuscular efficiency. However, the variability of the voluntary force output during the maintenance of 70% MVC of the non-exercised limb exhibited a tendency for a main effect for conditions ($p = 0.07$). Paired sample t-test revealed that 40% ($p = 0.09$, ES = 0.65) and 70% ($p = 0.07$, ES = 0.79) protocols induced greater contralateral force output variation compared with the control condition.

Discussion

The most important finding of the present study was ipsilateral dynamic contractions provided some evidence of crossover fatigue of the non-exercised contralateral leg extensors. Major specific findings were that with the non-exercised contralateral knee extensors 1) both 40% and 70% MVC dynamic fatiguing protocols caused a significant decrease in subsequent F100, 2) there was a statistical tendency ($p = 0.09$) with moderate and large ES for decreased force, and 3) force variability during the initial 10 s of the submaximal endurance test exhibited a statistical tendency ($p = 0.07$) with a moderate magnitude ES to increase in both the 40% and 70% conditions compared with the control condition.

While only F100 provided statistically significant evidence of crossover fatigue, the nearly significant force (with moderate and large ES) and force variability (with moderate ES) results contradicted the lack of change in EMG activity. The frequency of force decrements occurring in the non-dominant, non-exercised leg with 40% and 70% fatiguing protocols in the present study was 10/12 and 11/12 subjects respectively. This mixed evidence for crossover fatigue reflects the conflict in the literature. MVC force decrements have been reported in both the ipsilateral and contralateral lower limbs following a unilateral fatiguing protocol (Amann et al., 2013; Doix et al., 2013; Martin and Rattey, 2007; Takahashi et al., 2011). However not all studies exhibit crossover fatigue. A lack of crossover fatigue impairments was reported with a 100 s duration isometric quadriceps fatiguing protocol (Rattey et al, 2006). Furthermore, Todd et al. (2003) had subjects alternate between two 60-second MVCs performed with the elbow flexors and found that voluntary drive from the motor cortex measured with transcranial magnetic stimulation (TMS) was slightly less able to produce maximal force by the contralateral muscles implying that the crossover fatigue effect is small and has a minor functional effect. Isometric contractions of the smaller upper limb muscles such as the first dorsal interosseous (Zijdewind et al., 1998) and extensor carpi radialis (Samii et al., 1997) have also failed to create crossover fatigue effects. The unique aspect of this study however was that the fatiguing protocol consisted of dynamic leg extensions involving both concentric and eccentric contractions.

There are few studies that demonstrate crossover fatigue performance deficits with dynamic contractions (Amann et al., 2013; Triscott et al., 2008). Amann et al. 2013 found that constant load single leg knee-extensor exercise performed to exhaustion (> 9 min) resulted in a reduction of time to exhaustion in the non-fatigued contralateral leg; however, no significant changes were seen in potentiated twitch, MVC force and voluntary muscle activation. Dynamic biceps curls performed to exhaustion have resulted in reduced biceps curl endurance performance and a reduction in MEPs in the contralateral non-fatigued elbow flexors (Humphry et al., 2004; Triscott et al., 2008). Additionally, bilateral leg presses performed with 50% of a dynamic MVC were found to depress cortical excitability of non-exercised upper limb muscles (Takahashi et al., 2011). H-reflex (afferent excitability of the motoneuron) activity decreases with higher velocity contractions (Duclay et al., 2009) and hence dynamic contractions may induce greater motoneuron inhibition than isometric contractions. Furthermore, crossover fatigue effects following lengthening and shortening (eccentric / concentric) contractions may arise from the greater afferent feedback from the muscle spindle afferents (Ribot-Ciscar et al., 2003) than with isometric or concentric only (isokinetic) contractions. Furthermore, Doix et al. (2013) suggested the body compensates for a fatigued lower limb by reducing the performance of the non-exercised leg to maintain lower limb homeostasis or symmetry. On the contrary, isokinetic exercise consisting of concentric/concentric knee flexion/extension contractions (7 sets of 20 repetitions) had no effect on the contralateral hamstrings but actually enhanced contralateral quadriceps MVC force (Strang et al., 2009). Grabiner and Owings (1999) used unilateral isokinetic concentric- and eccentric-only MVCs (3 sets of 25 repetitions) and found no crossover fatigue effects following the concentric fatigue protocol but found an enhanced eccentric MVC following the eccentric fatigue protocol. Furthermore, both unilateral submaximal plyometric exercise (432 ± 178 rebounds) performed until exhaustion on a sledge ergometer (Regueme et al., 2007) and 10-minutes of maximal unilateral cycling (Elmer et al., 2013) failed to result in crossover fatigue effects.

Differences in volume and intensity are variables that may confound the crossover fatigue evidence. The present study demonstrated that although both contraction intensities resulted in significant and near significant F100 and force decrements respectively, the higher (70%) intensity manifested moderate to large magnitude effects (force and F100 respectively) compared to small to moderate magnitude effects (F100 and force respectively) for the 40% condition (no statistical significant difference between conditions). While not well elucidated in the literature, there is some corroborating evidence for a more substantial crossover fatigue effect with higher intensity contractions. Kennedy et al. (2013) compared maximal and submaximal (30% MVC) bilateral isometric handgrip exercise performed to exhaustion and examined if any fatigue effects would be seen in the ankle plantar flexors. Interestingly, the maximal fatiguing protocol was more impactful on reducing ankle plantar flexor MVC and voluntary activation, compared to the submaximal fatiguing protocol (Kennedy et al., 2013). The average number of repetitions to failure in the present study was approximately 6 (~12 s of work; 70% MVC) and 13 (~26 s of work; 40% MVC). Other lower body crossover fatigue studies have implemented higher volume, lower intensity activities such as 3-7 sets of 20-25 knee extension/flexion repetitions (Grabiner and Owings, 1999; Strang et al., 2009), 432 rebound actions (Regueme et al., 2007), 9-10 minutes of knee extensions (Amann et al., 2013) or cycling (Elmer et al., 2013). Thus higher intensity dynamic contractions may accentuate the crossover fatigue effect.

However, contrary to Martin and Rattey (2007), the evidence of contralateral F100 deficits in the non-exercised leg of the present study were seen with no significant change in VL EMG activity or median frequency. The frequency of VL EMG decrements occurring in the non-exercised leg with the 40% and 70% fatiguing protocols was 5/11 and 6/12 subjects, respectively. Also, the frequency of VL median frequency increases occurring in the non-exercised leg with the 40% and 70% fatiguing protocols was 6/12 and 8/12 subjects, respectively. Perhaps this non-significant response can be explained by the non-linear force-EMG relationship (Solomonow et al., 1986). The earliest studies on the force-EMG relationship reported a linear relationship (Bigland and Lippold, 1954) however; contemporary studies have illustrated a non-linear or curvilinear force-EMG relationships with the quadriceps during isometric (Alkner et al., 2000) and dynamic (Fujita et al., 2011) contractions. A non-linear force-EMG relationship indicates that the EMG is not sensitive to all changes in force output. As the contralateral force deficits were modest ranging from 4-7%, the non-linear force-EMG relationship may not have portrayed possible changes in activation.

Additionally, force impairments without reductions in EMG activity have also been reported with instability resistance exercise studies (Anderson and Behm, 2004; Behm and Colado, 2012; Behm et al., 2010). Described as a stiffening strategy, the body utilizes a greater component of a muscular contraction to protect the joints in novel, threatening or fatiguing situations, which results in less force available to exert against an external resistance (Behm et al., 2010).

In the present study, there was some evidence for motor control impairment as well. There was a tendency with moderate ES for greater variability in the maintenance of submaximal forces (70% MVC). Other studies have also demonstrated non-local fatigue-induced motor control deficits such as alterations in single leg landing strategies (Mclean and Samorezov, 2009), center of pressure during bilateral stance (Berger et al., 2010) and postural control during single leg stance (Paillard et al., 2010). Muscle fatigue can affect joint position sense by affecting the afferent feedback, therefore affecting proprioceptive and kinesthetic feedback (Gribble and Hertel, 2004). The change in perception and movement execution strategies seen in the contralateral limb have been attributed to altered supraspinal and spinal control pathways, (Mclean and Samorezov, 2009) likely modified via the inhibitory action of the fatigued muscles in the ipsilateral limb (Paillard et al., 2010).

Although not directly measured in the present study, there are a number of mechanisms that could contribute to the crossover fatigue effect. Previous investigations attribute performance decrements in the non-fatigued limb to centrally derived mechanisms (Bonato et al., 1996; Doix et al., 2013; Martin and Rattey, 2007; Rattey et al., 2006) that could occur at both the spinal and supraspinal levels (Gruet et al., 2012; Taylor and Gandevia, 2008). They speculated that following unilateral training, changes in higher order inputs to the primary motor cortex occur bilaterally and can reduce central drive via modulation of ipsilateral primary motor cortex excitability (Carroll et al., 2006). In the present study, F100 provided robust evidence of crossover fatigue; whereas MVC force and force variability exhibited moderate magnitude effects and EMG, representative of central drive showed no effect. Based on these findings, reports of either no change or facilitation of MEP amplitude (Todd et al., 2003; Zhou, 2000) as well as increased muscle activation in non-fatigued limbs (Farthing et al., 2009; Zhou, 2003), it can be hypothesized that non-fatigued limb decrements may not be primarily associated with altered excitability of the primary motor cortex. The greater effect of crossover fatigue on F100 could be attributed to mechanisms upstream of the primary motor cortex such as secondary motor areas including dorsal and ventral premotor cortices and supplementary motor cortex. These areas contribute to the planning and expectation / anticipation of movements. Therefore, impairment in the transfer of signals from these areas to the primary motor cortex due to a global sense of fatigue may inhibit development of instantaneous force output. Since during MVC force production subjects had 5 seconds to build up maximal force output, planning, expectation and anticipation may play a less important role. This hypothesis was not measured in the present study therefore further investigations are required to address this concept.

Conclusion

In conclusion, this study highlighted that unilateral lower limb fatigue induced by low intensity, high volume as well as high intensity, low volume dynamic knee extensions leads to significant deficits in contralateral F100 and moderate to large magnitude non-significant impairments to force and force variability. Further research should investigate the neural mechanism(s) responsible for the affected performance of the contralateral limb.

Acknowledgements

The Natural Science, Engineering and Research Council (NSERC) of Canada supported this study.

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Key points

- There was a pattern of crossover fatigue effects with significant impairments in F100, near significant, moderate to large magnitude decrements in MVC force and moderate magnitude increases in submaximal force variability in the contralateral knee extensors.
- Although both contraction intensities resulted in significant and near significant F100 and force decrements respectively, higher intensity (70%) fatiguing contractions manifested moderate to large magnitude effects (force and F100 respectively) compared to small to moderate magnitude effects (F100 and force respectively) for the lower intensity (40%) fatiguing contractions.

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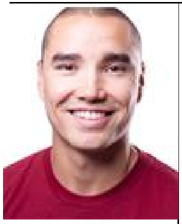

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