Effects of Unilateral, Isometric Resistance Training on Strength Development and the Hoffmann-Reflex Response in the Trained and Untrained Limb

By

Olle Lagerquist
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ABSTRACT

The purpose of this study was to determine the effects of a 5-week unilateral, isometric strength-training program on presynaptic inhibition (PSI) and alterations in the H-reflex in both the trained and untrained limbs. Thirteen subjects, aged 23-42 years old were assigned to either a control group (n=6) or an exercise group (n=7). Both groups were tested at the beginning and end of a 5-week interval on both limbs for maximal voluntary isometric contractions (MVIC) of the plantar flexors as well as three different conditioning protocols of the Soleus Hoffmann (H) reflex. Experimental group participants significantly increased MVIC in both legs following training ($p<0.05$) while control group participants showed no increase for either leg. Experimental subjects displayed increased normalized H-reflex values at M=5% (H_A) ($p<0.05$) in the trained leg only. Adaptations in H_A for the trained limb in the presence of a substantial strength increase suggests that spinal mechanisms may partly explain the increase in strength, possibly due to increased α-motoneuronal excitability. However, the lack of H_A increase in contralateral limb in the presence of a substantial strength increase, points to different neural mechanisms responsible for the cross education effect.

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Acknowledgments

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Till

Hela min familj, men specielt till Farfar

EFFECTS OF CROSS EDUCATION ON THE HOFFMANN REFLEX

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Introduction

In response to resistance training, changes within skeletal muscle are an important adaptation for the development of strength (Sale, 1988). However, strength is determined not only by the quantity and quality of the involved musculature but also by the degree to which the muscle mass has been activated. It has been suggested that resistance training induces change within the nervous system that allows better activation of all relevant muscles causing a greater net force (Moritani & deVries, 1979). However, neural adaptations induced by unilateral resistance training have also been shown to affect the non-exercised homologous muscles of the contralateral limb (Zhou, 2000).

Numerous studies have reported that chronic unilateral motor activity can affect performance of the homologous muscles in the contralateral limb. This phenomenon, known as cross education, occurs during improvements in strength and the learning of motor skills, and displays specificity to the training of the opposite limb (Hortobagyi, Scott, Lambert, Hamilton, & Tracy, 1999). Structural and functional adaptations due to resistance training are specific to the exercised musculature and the greatest training effect is found when testing procedures match the training protocol (Sale, 1988). However, cross education of the contralateral limb shows evidence of neuromuscular adaptations despite not being involved in the tasks performed during training. Both supraspinal (supraspinal) and spinal mechanisms have been proposed to contribute to the cross education (refer to appendix B), however, to date no consensus has been reached as to the major cause of adaptation.

In an attempt to elucidate neural adaptations to strength training and chronic physical activity, exercise studies have examined reflex pathways by using electromyography in conjunction with muscle and nerve stimulation. The Hoffmann (H) reflex is possibly the most widely studied reflex due to the ease with which it can be elicited in various muscles. The H-reflex is considered the electrical equivalent of a stretch reflex and is predominantly characterized by the monosynaptic projections of group Ia afferents onto homonomous motoneurons (Zehr, 2002; Misiaszek, 2003). Evoking the H-reflex involves percutaneously stimulating both motor and sensory axons of peripheral nerves. Increasing the intensity of stimulation causes the larger diameter Ia afferent sensory fibers to be recruited before the smaller diameter motor fibers. The H-reflex is recorded when the electrical stimulation causes enough neurotransmitter release via depolarization of the afferent terminals leading to a depolarization of alpha motoneurons. Consequent neurotransmitter release at the neuromuscular junction leads to depolarization and muscular contraction, which is recorded as the H-reflex (Zehr, 2002).

Many exercise studies have examined the H-reflex with various hypotheses as to why it may be potentiated or attenuated due to chronic physical activity. However, no exercise studies utilizing the H-reflex have accounted for the strong effects of presynaptic inhibition (PSI) in modulating the H-reflex, thus severely limiting the interpretation of existing literature. The influence of a strength-training program on PSI and its relevance to cross education has yet to be established (see appendix C). It is possible that unilateral strength training alters

PSI in the trained and untrained homologous limb, thereby affecting the efficacy of alpha-motoneuron pool excitability and influencing force production capabilities. Exercise and cross education studies utilizing the H-reflex in conjunction with measures of PSI are needed in order to elucidate how reflex mechanisms may be affected by chronic physical activity such as programs designed to increase strength.

Statement of the Problem and Purpose

Presently, there is a lack of understanding in regards to the neural loci of adaptations due to strength training as well as cross education. Past experiments investigating changes to the H-reflex due to training have been excluding the strong effects of PSI, and to date no cross education study has utilized the H-reflex as a tool. While there is ample reason to believe that the H-reflex is modulated with chronic physical activity, a better understanding of the influence of PSI in this process will help to clarify the mechanisms involved in neural adaptations to movement. A better understanding of the mechanisms affecting human neural circuitry has widespread application to the many fields of neurophysiology that use the H-reflex as a tool, from the investigation of functional organizations of neural circuitry to the study of adaptive plasticity in healthy and diseased states.

The purpose of this study was to examine the effects of a 5-week unilateral, isometric strength-training program on levels of PSI and alterations in the H-reflex in both the trained and untrained limbs. A similar 5 week protocol has previously been used (Cannon & Cafarelli, 1987) to induce strength gains and a significant cross education effect in the adductor pollicis muscle of the hand. In addition, Shima et al. (2002) have demonstrated a significant increase in isometric plantar flexion following a 6 week unilateral strength training program.

Research questions

1. Does chronic strength training alter the H-reflex response in the trained muscle?
2. Does chronic strength training alter the H-reflex response in the homologous, contralateral, untrained muscle?
3. If strength training alters the H-reflex response in both the trained and untrained limb, is there a relationship in the magnitude of difference across subjects?
4. Does chronic strength training alter the PSI in the trained muscle?
5. Does chronic strength training alter the PSI in the homologous, contralateral, untrained muscle?
6. If strength training alters PSI in both the trained and untrained limb, is there a relationship in the magnitude of difference across subjects?

Hypotheses

1. Chronic strength training will significantly increase strength in the trained muscle and untrained homologous, contralateral muscle.
2. Chronic strength training will alter the H-reflex response in the trained and homologous, contralateral, untrained muscle.
3. The trained and homologous, contralateral, untrained muscle will display reduced PSI after chronic strength training.

Operational definitions

1. Untrained subjects: Individuals that have not engaged in regular lower body resistance training, or power training for one year prior to the beginning of the study.
2. Maximal voluntary isometric contraction (MVIC): The greatest force that an individual is able to generate with no movement about the joint.
3. Radiating threshold: The threshold of stimulation where a clear radiating parasthaesia in the cutaneous field is elicited.
4. Motor threshold: the weakest stimulation that produces a measurable muscle twitch.

Delimitations

1. Participants will be male and female
2. Participants will be untrained
3. Participants will be between 22-42 years of age.

Limitations

1. Training status, physical fitness and other individual differences of participants may result in different adaptations.

Assumptions

1. All subjects will provide maximal effort during MVIC.
2. All subjects will refrain from additional resistance, or endurance training of the lower body for the duration of the study.

Methodology

Participants

15 untrained university-aged participants were invited to participate in the study. G power analysis using power=.8, effect size=1.6, and alpha= .05 revealed N=12 for a cross education effect due to strength training. Thus N=15 was chosen to account for possible attrition of participants. The alpha level was set at $p<0.05$ for significance. Participants had no known neurological or orthopaedic pathologies and were free from lower leg injury at the time of data collection. Dominant lower extremity was determined by asking participants which leg they preferred to use when kicking a ball. Written consent explaining the purpose and possible risks associated with the study was obtained from all participants prior to participation, following approval from the University of Victoria Human Ethics Committee.

Experimental Design

The experiment consisted of two groups (experimental N=7 and control N=6) and utilized randomized groups with repeated measures design (pre-test, post-test). Participants were required to participate in two familiarization sessions. A third familiarization session was conducted if a greater than 5% difference was detected between pre-training MVIC. After satisfactory completion of the familiarization sessions, participants in the experimental group completed an isometric resistance training protocol three days per week, with a minimum of 2 days rest between training days, for the following five weeks.

avoidant attachment styles than women from intact families. Similarly we have recently reported on results based on a sample of 350 college students which indicated that parental divorce was related to attachment insecurity for females only (Ehrenberg, Bush, Luedemann, & Pringle, 2003). In fact, the majority of females who experienced divorce during childhood reported a fearful attachment style, which is consistent with Sprecher et al.'s (1998) results.

To conclude, empirical evidence suggests a relationship between parental divorce and attachment insecurity in young adulthood. It is likely, however, that parental divorce, per se, may not be the reason for insecure attachment styles, but that specific family mechanisms, which occur more frequently in divorced households than in intact households, may increase the vulnerability for insecure attachment representations in young adulthood, particularly among young women.

Family Systems Theory in the Context of Divorce

Family systems theory suggests that each family consist of several subsystems. The three primary subsystems in a family are the marital, the parent-child, and the sibling subsystem (Goldenberg & Goldenberg, 1995). Difficulties in one family subsystem are hypothesized to result in potential difficulties in another family subsystem (Minuchin, 1988). For example, if the marital subsystem is experiencing problems, then this will likely also have an impact on the parent-child subsystem. All subsystems within a family are interdependent. In the context of divorce, the marital subsystem is disrupted. Thus, family systems theorists would argue that parent-child relationships are vulnerable to difficulties as well and merit consideration.

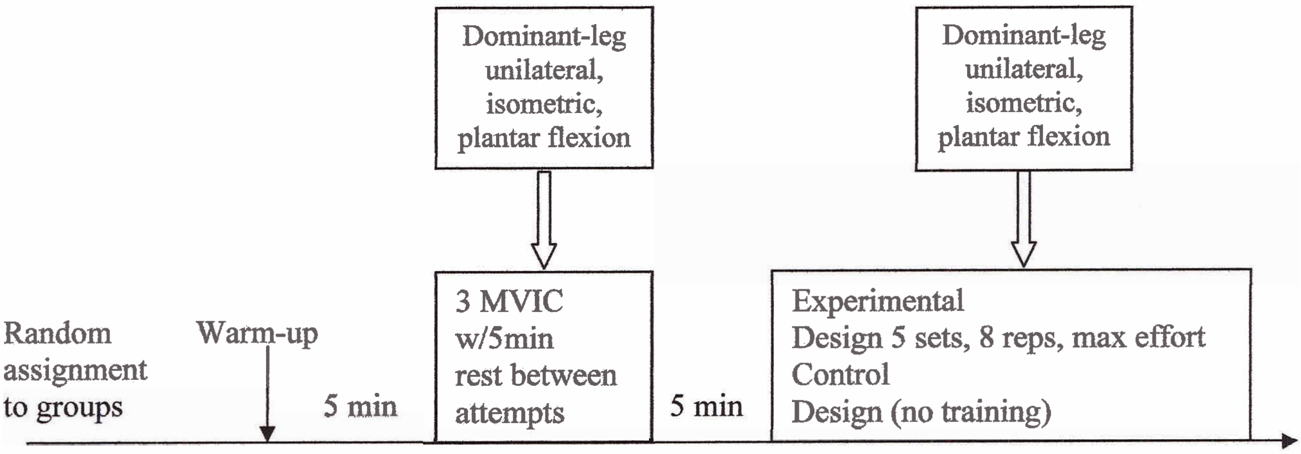

Figure 1. Timeline of the familiarization session.

Protocol

For training and testing sessions participants were seated in a chair with their backs supported. Hip, knee, and ankle angles were set at approximately 90°, 150 °, and 90°, respectively (see figure 2). Restraints were placed around the foot to minimize movement. The behaviour state as well as the posture of the participants was taken into account in order to control for task dependency of reflex modulation. The temperature, noise, and lighting were held as constant as possible between sessions.

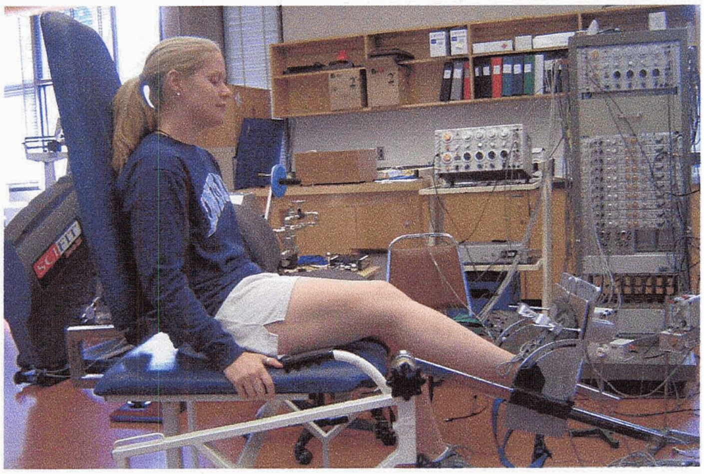

Figure 2. Experimental setup during isometric plantar flexion.

Recordings of MVIC's

Torque values were established via strain gauge (Omegadyne Ltd. Model 101-500, range 0-226.7 kg) and amplified by a custom made high gain amplifier system. The force was displayed using custom built continuous acquisition software utilizing LABVIEW. Torque was calculated after MVIC by converting voltage output into kg (1.00V = 45.3 kg). Plantar flexion force was consistently applied with a moment arm length of 0.15m (measured from the adjustable heel block to the center of the strain gauge).

Soleus H-reflex

The tibial nerve was stimulated with single 1ms square-wave pulses delivered over the popliteal fossa. M-wave and H-reflex recruitment curves were constructed during common peroneal nerve stimulation, sural nerve stimulation and unconditioned data acquisition. The M-waves and H-reflexes of each participant were normalized to the corresponding M-max to reduce inter-subject variability. Two variation of H-reflex data were utilized in this experiment. H_{max} indicates the maximal obtainable H-reflex amplitude while H_A reflects H-reflex values on the ascending limb corresponding to normalized M values of 5%. Mean normalized H_{max} values were calculated from the three largest responses in the unconditioned, CP and sural conditioned trials. Ten normalized H-reflex values were used to calculate the mean H response at a corresponding normalized M value of 5%.

Nerve stimulation

Prior to beginning the training program and after completion, reflexes were evoked by delivering nerve stimulation in both the trained and untrained limb in three ways (as described in Frigon, Collins, & Zehr, 2004):

1) tibial nerve stimulation to evoke an H-reflex response in soleus;
2) sural nerve + tibial nerve to reduce PSI of the H-reflex;
3) Common peroneal + tibial nerve stimulation to increase the PSI of the H-reflex.

To evaluate postsynaptic effects of the conditioning stimulus on the soleus sural and common peroneal nerve, stimulations were delivered alone. For each trial, participants maintained a consistent low-level tonic contraction (~20% EMG) of their dominant soleus muscle (Described in Zehr, 2002). Each type of nerve stimulation was delivered in a separate order randomized across subjects. Participants were re-tested for reflex responses and MVIC 3 days after the completion of the training program.

All nerves were stimulated with bipolar surface electrodes. Stimulation was delivered randomly, not more frequently than with a 3 s repeat to avoid post-activation depression (Zehr, 2002).

Sural nerve and common peroneal nerve

The sural nerve was stimulated at the ankle, immediately below the lateral malleolus using a train of 5 x 1 ms pulses delivered at 300 Hz at two times the radiating threshold (Frigon et al. 2004). The conditioning test interval between the sural nerve conditioning and the test H-reflex was 80ms.

The common peroneal nerve was stimulated immediately distal to the head of the fibula at 1.5 times motor threshold (Frigon et al. 2003). The conditioning-test interval was set at 100 ms.

Electromyography

Electromyography (EMG) was recorded with bipolar surface recording electrodes. EMG signals were pre-amplified and band pass filtered at 30-300 Hz.

Data acquisition

Data was sampled at 2000 Hz with a 12 bit A/D converter controlled by the Lab View program. All trials used 75 sweeps of data collection with a 20 ms pre stimulus window.

Statistics

Repeated analyses of variance tests (2X2 ANOVAs) were used to examine the effects of isometric resistance training on MVIC and H-reflex amplitudes during non-conditioned, CP conditioned and sural conditioned trials across and within groups. Dependent variables were collected from both limbs for control and experimental groups. Fisher's LSD post-hoc test was used to analyze main effects.

Results

Change in MVIC

Control and experimental groups did not significantly differ in pre-test MVIC's measures for either leg across groups. However, significant ($p < 0.05$) interactions were detected for MVIC's across groups in the post-test. The experimental group significantly increased MVIC scores by 17.27% ($p = 0.038$)

and 21.56% ($p = 0.007$) between pre-test and post test measures for the trained right leg and untrained left leg respectively (see table 2 and figure 4). The control group showed no significant change ($p = .127$) in MVIC strength of the left leg ($p=.127$), however, the right leg MVIC decreased by 6.3% ($p = 0.05$, see table 1).

EMG amplitude

There were no significant differences ($p> 0.05$) in pre-stimulus background EMG amplitude for soleus or tibialis anterior between testing sessions for either group. Likewise, the amplitudes of M-max for soleus were not significantly different between or within groups, pre-test to post-test. Subjects held a tonic, isometric plantar flexion contraction of ~20% MVIC during all H-reflex recordings which did not significantly differ between testing sessions ($P > 0.05$).

Response of the soleus H-reflex to CP and sural nerve stimulation

Neither CP nor sural nerve stimulation evoked significant changes in H-max or equivalent normalized H_A values for either group pre-test or post-test ($p > 0.05$). Individual subject data for CP and sural nerve response has been summarized in tables 3-4 and 5-6, respectively. The effects of CP and sural nerve conditioning on the soleus H-reflex for one subject are displayed in figure 2.

Effects of isometric training on the unconditioned soleus H-reflex

Control group subjects showed no significant difference in unconditioned H_{max} or H_A between testing sessions for either leg (see table 1). Similarly the experimental group did not display significant difference in H-max values for either leg, however, H_A values increased significantly ($p = 0.021$) in the trained right leg only (see table 2 and figure 4). This increase caused a left shift and increased slope of the ascending limb in the normalized H/M recruitment curve for experimental subjects (see figure 3).

Soleus/TA EMG ratio

The soleus/TA EMG ratio did not significantly differ between groups or between legs for either pre-test or post-test. When within group comparisons were made, it was found that the experimental group significantly increased their soleus/TA EMG ratio more than 300% from 1.03 to 3.40 in the trained leg and from 1.03 to 3.15 in the untrained leg ($p = 0.0007$ and $p = 0.002$ respectively). This change was not significantly different between legs ($p = 0.86$). The control group did not significantly change their soleus/TA ratio (right, $p = 0.29$; left $p = 0.20$) from pre-test to post-test.

Table 1. Control group data (N=6) of left and right leg for maximal voluntary plantar flexions (MVIC), H_{max} unconditioned (H_{max}), H_{max} with CP nerve stimulation (H_{max} CP), H_{max} with sural nerve stimulation (H_{max} sural), unconditioned H-waveforms at 5% M-max (H_A), H-waveforms at 5% M_{max} with CP nerve stimulation (H_A CP) and H-waveforms at 5% M_{max} with sural nerve stimulation (H_A sural). Asterisks (*) indicate significance at the $p < .05$ level. All H-reflex values expressed as a % of M_{max}.

Control	Left leg pre-test	Left leg post-test	P	F	d	Right leg pre-test	Right leg post-test	P	F	d
MVIC (λ)										
Mean	202.56	208.41	0.12	3.34	0.16	192.87	180.74	0.049*	6.73	0.34
St. Dev.	35.21	35.82				36.61	34.93			
H_{max}										
Mean	57.99	64.66	0.38	0.92	0.33	54.86	48.141	0.22	1.99	0.43
St. Dev.	17.98	22.05				16.67	14.847			
H_{max} CP										
Mean	57.54	55.60	0.76	0.09	0.08	48.05	42.21	0.32	1.21	0.34
St. Dev.	19.95	26.83				18.16	16.36			
H_{max} sural										
Mean	56.22	53.69	0.47	0.58	0.16	52.08	47.38	0.44	0.70	0.23
St. Dev.	17.16	13.89				20.893	20.893			
H_A										
Mean	41.18	47.63	0.46	0.61	0.32	42.06	36.56	0.22	1.96	0.34
St. Dev.	24.42	14.53				16.46	15.47			
H_A CP										
Mean	39.95	37.92	0.57	0.36	0.10	37.34	31.55	0.20	2.23	0.30
St. Dev.	23.82	17.15				20.27	18.82			
H_A sural										
Mean	42.03	39.58	0.49	0.53	0.13	41.24	36.84	0.49	0.56	0.21
St. Dev.	22.17	15.35				26.35	13.30			

Legend

P - probability level
F - distance between individual distributions
d - Cohen's effect size d
λ- torque N/m

Table 2. Experimental group (N=7) data of left and right leg for maximal voluntary plantar flexions (MVIC), H_{max} unconditioned (H_{max}), H_{max} with CP nerve stimulation (H_{max} CP), H_{max} with sural nerve stimulation (H_{max} sural), unconditioned H-waveforms at 5% M-max (H_A), H-waveforms at 5% M_{max} with CP nerve stimulation (H_A CP) and H-waveforms at 5% M_{max} with sural nerve stimulation (H_A sural). Asterisks (*) indicate significance at the $p < .05$ level. All H-reflex values expressed as a % of M_{max}.

Experimental	Left leg pre-test	Left leg post-test	P value	F	d	Right leg pre-test	Right leg post-test	P value	F	d
MVIC (λ)										
Mean	164.66	200.16	0.007*	16.09	1.01	160.34	188.04	0.04*	7.07	0.75
St. Dev.	39.09	31.02				38.25	35.74			
H_{max}										
Mean	67.44	62.51	0.29	1.33	0.26	54.23	63.14	0.24	1.71	0.65
St. Dev.	20.10	16.97				15.17	12.06			
H_{max} CP										
Mean	60.66	52.55	0.30	1.28	0.45	57.68	55.08	0.73	0.13	0.16
St. Dev.	20.04	16.00				20.41	12.21			
H_{max} sural										
Mean	63.11	58.42	0.32	1.17	0.32	58.85	57.14	0.85	0.04	0.09
St. Dev.	16.30	13.08				20.50	16.84			
H_A										
Mean	41.56	45.42	0.63	0.25	0.21	33.95	46.46	0.02*	9.63	1.40
St. Dev.	17.11	19.79				8.55	9.31			
H_A CP										
Mean	30.20	33.36	0.65	0.22	0.21	26.85	35.39	0.42	0.74	0.55
St. Dev.	15.47	14.22				18.16	12.11			
H_A sural										
Mean	37.79	39.95	0.78	0.09	0.12	32.86	39.22	0.42	0.74	0.48
St. Dev.	20.18	16.79				13.13	13.67			

Legend

P - probability level
F - distance between individual distributions
d - Cohen's effect size d
λ- torque, N/m

Table 3. Effect of CP conditioning on normalized H-max values for individual control and experimental subjects. Arrows (↓*,↑*) indicate the presence of a significant ($p < .05$) decreases or increases respectively when compared to the unconditioned H-max values. Equal sign (=) indicates no significant difference.

Control	Left leg pre-test CP conditioned	Left leg post-test CP conditioned	Right leg pre-test CP conditioned	Right leg post-test CP conditioned
1	↓*	↓*	↓*	↓*
2	↓*	=	↓*	=
3	↓*	↑*	↑*	=
4	↓*	=	=	=
5	↓*	=	↓*	↓*
6	↑*	↓*	=	=
Experimental				
1	=	↓*	↑*	=
2	↓*	↓*	=	=
3	↓*	↓*	=	↓*
4	↓*	=	=	=
5	↑*	↑*	=	=
6	=	=	=	=
7	↓*	=	=	↓*

Table 4. Effect of sural conditioning on normalized H-max values for individual control and experimental subjects. Arrows (↓*,↑*) indicate the presence of a significant ($p < .05$) decreases or increases respectively when compared to the unconditioned H-max values. Equal sign (=) indicates no significant difference.

Control	Left leg pre-test sural conditioned	Left leg post-test sural conditioned	Right leg pre-test sural conditioned	Right leg post-test sural conditioned
1	↓*	↓*	↓*	=
2	↑*	↓*	↓*	↓*
3	↓*	↑*	↑*	=
4	=	↑*	=	↑*
5	=	↓*	↓*	↓*
6	↑*	=	=	=
Experimental				
1	=	↓*	↑*	=
2	↓*	↓*	=	=
3	↓*	=	=	=
4	=	=	=	=
5	↑*	↑*	=	↓*
6	=	=	=	=
7	↓*	=	↑*	↓*

Table 5. Effect of CP conditioning on ten normalized H-waveforms at M=5% for individual control and experimental subjects. Arrows (↓*,↑*) indicate the presence of a significant (p < .05) decreases or increases respectively when compared to unconditioned values. Equal sign (=) indicates no significant difference.

Control	Left leg pre-test CP conditioned	Left leg post-test CP conditioned	Right leg pre-test CP conditioned	Right leg post-test CP conditioned
1	=	↓*	↓*	↓*
2	↓*	↓*	↓*	↓*
3	=	=	=	=
4	↓*	=	=	=
5	=	↓*	↓*	=
6	=	↓*	=	=
Experimental				
1	↓*	↓*	↓*	=
2	↓*	↓*	=	↓*
3	↓*	↓*	↓*	↑*
4	↓*	↓*	↓*	=
5	=	=	↑*	↓*
6	↓*	↓*	=	=
7	=	=	↓*	↓*

Table 6. Effect of sural conditioning on ten normalized H-waveforms at M=5% for individual control and experimental subjects. Arrows (↓*,↑*) indicate the presence of a significant (p < .05) decreases or increases respectively when compared to unconditioned values. Equal sign (=) indicates no significant difference.

Control	Left leg pre-test sural conditioned	Left leg post-test sural conditioned	Right leg pre-test sural conditioned	Right leg post-test sural conditioned
1	=	↓*	↓*	=
2	=	=	↓*	↓*
3	↓*	=	↑*	=
4	=	=	↑*	=
5	=	=	↓*	=
6	↑*	↓*	=	=
Experimental				
1	↓*	↓*	↓*	↑*
2	↓*	↓*	=	=
3	↓*	=	=	=
4	=	↑*	=	↓*
5	↑*	=	=	↓*
6	=	=	=	=
7	↑*	=	=	↓*

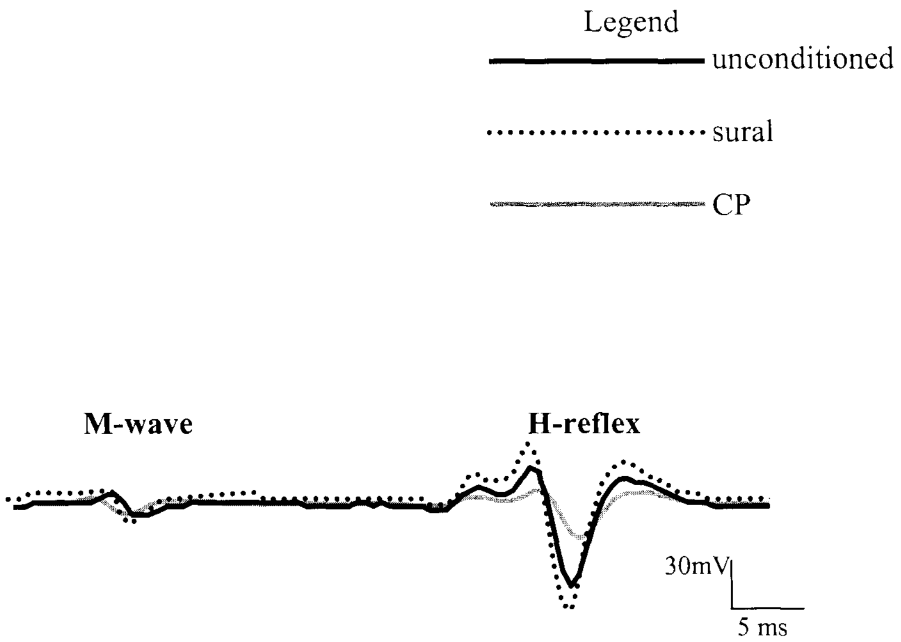

Figure 3. Effect of sural (dotted line) and CP (gray line) conditioning on the soleus H-reflex as compared to unconditioned control trial (black line) for a single pre-test control subject. Lines are an average of 10 sweeps.

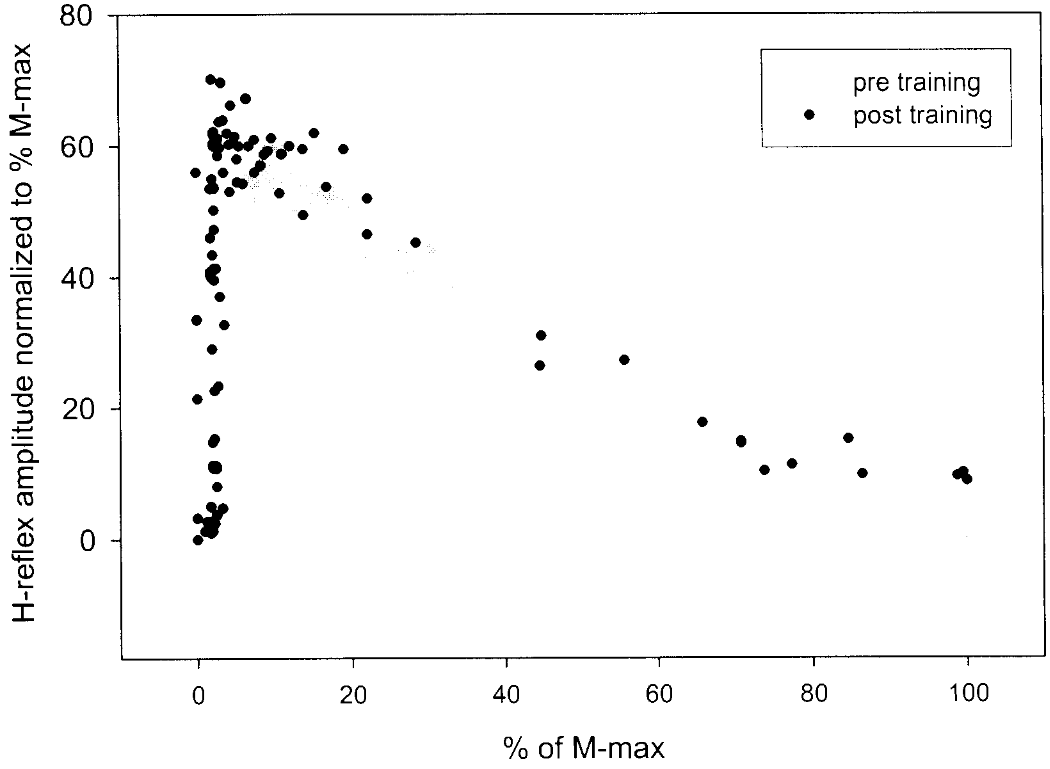

Figure 4. H/M recruitment curves of pre-training data (gray triangles) and post-training data (black circles) from the right leg of one experimental subject. H-reflex data has been normalized to M-max.

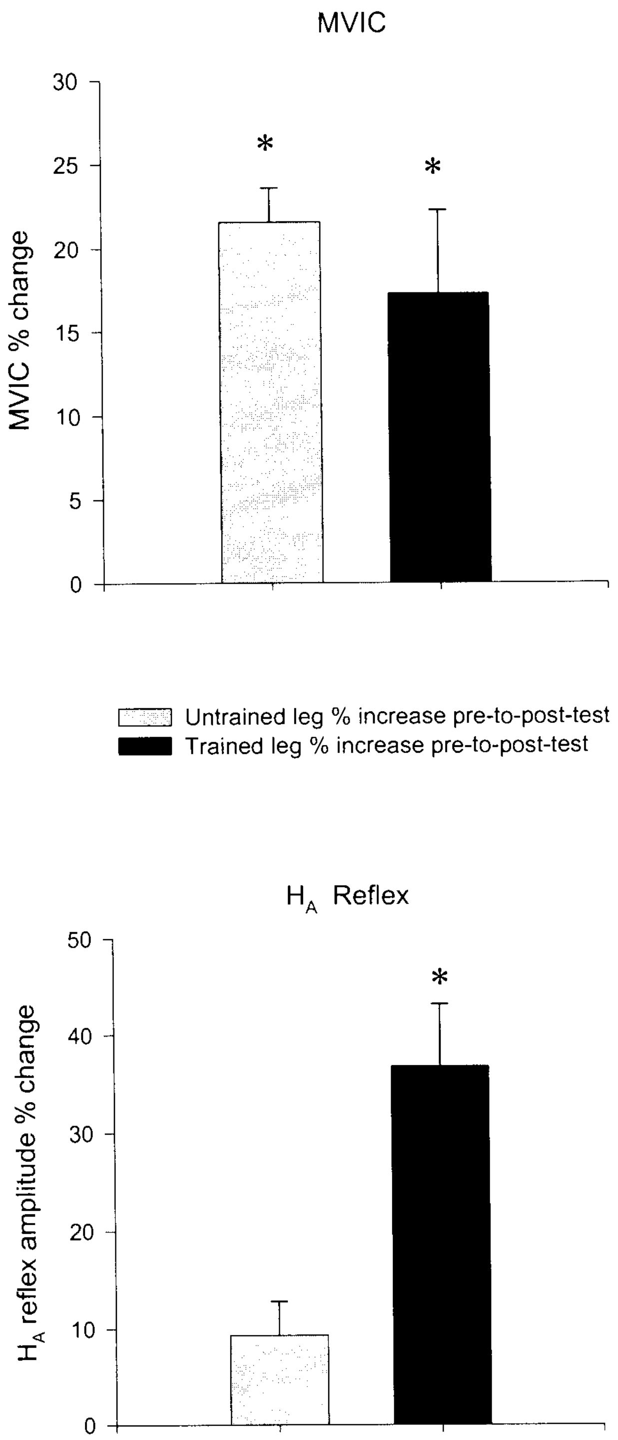

Figure 5. Percentage increase between pre-test and post-test measures of left (grey) and right (black) legs with respect to MVIC (top graph) and H_A reflex amplitude (bottom graph) for experimental participants. Asterisks (*) indicates significant differences between pre-test and post-test scores at the $p<0.05$ level.

Discussion

There are two main findings to this experiment. First, our five week isometric training program significantly increased strength in both the trained and untrained limb of the experimental group. Second, H_A values significantly increased in the trained leg of the experimental group only. Since there was a significant cross education effect without a change in H_A value for the untrained leg, increased spinal reflex excitability did not appear to influence the cross education effect in this experiment. The modulation of H_A values for the trained limb may be due to increased somatosensory stimulation, whereas supraspinal mechanism might be responsible for the cross education effect. This suggests that a five week program designed to increase strength is sufficient to induce spinal cord plasticity affecting the trained but not the untrained limb.

Change in MVIC's and the cross education effect

Experimental subjects significantly increased their force production capacity in both the trained and untrained limb and thus displayed a large cross education effect (see table 2). The experimental group significantly increased isometric plantar flexion strength by 17.27% ($p = 0.04$) in the trained right limb and 21.56% ($p = 0.007$) in the untrained left limb. The 21.6% increase in force production by the untrained limb was larger than expected considering that the trained limb increased 17.3%. However, this difference in strength increase between the trained and untrained leg was not significant ($p =.24$). If a longer training period had been followed it is possible that the right trained limb would have continued to increase in strength, while the cross education effect may be taking place in the preliminary stages of learning the task. The time course of the cross education effect due to strength training has not been examined. In addition, this is the first experiment to utilize isometric plantar flexion as the training method, thus direct comparisons from previous literature is not possible. Previous cross education studies have reported increases of 5-35% in force production for the untrained limb during concentric and isometric contractions using training periods of 8-10 weeks (Zhou, 2000). Eccentric contractions have been found to induce greater cross education effects when compared to isometric and concentric contractions. For example, Hortobagyi et al., 1999 found cross education effects as large as104% during eccentric, isokinetic knee extension training. To date no other study has examined the effect of a unilateral isometric plantar flexion training program on the cross education effect. Our findings suggest that the response of isometric plantar flexion to strength training and the cross education effect is similar to that reported in other muscle using concentric and isometric contractions but not as great as that imposed by eccentric training (see appendix B for more information regarding the specificity of cross education and different modes of training).

Control subjects did not significantly alter their force production capacity in the left leg although the right leg decreased significantly in strength during the 5 weeks between pre-test and post-test (see table 2). This decrease was not expected. However, considering that two to three familiarization sessions were employed it is possible that a learning effect was present which deteriorated in the following five weeks of rest. In addition, the probability level of this finding is borderline ($p = 0.049$) with a small corresponding effect size ($d = 0.34$), and thus may be a spurious finding.

Training induced changes in H_A response

As hypothesized, control group subjects did not display significant changes in H-reflex amplitude for either leg between pre-test and post-test measures. However, the experimental group experienced a 36.83% increase ($p = 0.02$) in H_A amplitude values in the trained leg. This increase in H_A amplitude of the trained leg may reflect adaptations in the Ia spinal reflex pathway, causing increased reflex excitability, allowing for greater motor unit recruitment and force generating capabilities. However, the lack of increased H-reflex amplitude in the experimental groups' untrained limb, with an accompanied increase in force production suggests that two loci of control may be present. Supraspinal mechanisms may play a larger part in influencing the cross education effect of the contralateral limb, while spinal mechanisms may affect only the trained limb. This lack of change in H_A amplitude in the untrained left leg, despite the presence of a substantial strength increase, may indicate different neurological adaptations in the trained and untrained limb. Alternatively, the H-reflex may be modulated due to some other mechanism not related to an increase in strength, although this seems unlikely. The increased soleus/TA EMG ratio in the experimental group is likely due to the effects of increased reciprocal inhibition to the TA. However, this effect does not account for the increased H_A values of the trained leg. The soleus/TA EMG ratio increased in both legs of the experimental group with no significant difference between legs ($p = 0.86$) while only the trained leg displayed increased H_A values. While ANOVA's did not reveal a significant ($p<0.05$) group by time by leg interaction, significant group by time interactions were detected for MVIC's and unconditioned H_A.

Several mechanisms have been proposed to influence the cross education effect with conflicting evidence suggesting either spinal or supraspinal influences. Kristeva, Cheyene and Deecke (1991) hypothesized that excitation of supraspinal motor points during voluntary contractions of a muscle might produce an effect on the contralateral motor cortex after finding bilateral topography of the premotor readiness field for both unilateral and bilateral movements. Movement related magnetic fields accompanying voluntary movement were studies in both motor cortices during left and right unilateral and bilateral finger flexions. Magnetic fields were similar in both the left and right motor cortex regardless of the nature of the task (bilateral or unilateral). This finding suggested the presence of a bilateral generator and that unilateral voluntary movements involved activation of the contralateral motor cortex. Because 15% of corticospinal fibers cross to the contralateral side (Martini, Timmons, & Tallitsch, 2003), co-activation of homologous muscles may be caused by an overflow of descending signals. Yue and Cole (1992) provided compelling evidence of supraspinal involvement in cross education when they demonstrated an 11% increase in the strength of the homologous, untrained hand muscle due to imagined contractions of the ipsilateral hand. Since descending commands from supraspinal structures can modulate the H-reflex response (Miziaszek. 2003; Zehr, 2002) it is possible that supraspinal adaptations are responsible for the change we observed in H_A

values of the trained leg of the experimental group. The lack of change in H_A values of the untrained leg of the experimental group suggests that if supraspinal adaptations are responsible for the cross education effect, they do not exert an effect on alpha motoneuronal excitability in the contralateral limb. Possibly, the untrained limb is affected more by supraspinal adaptations while the trained limb may incur adaptations that are both supraspinal and spinal.

Evidence for spinal mechanism involvement in cross education has come primarily from experiments using electrical muscle stimulation (EMS). EMS artificially stimulates muscle and consequently eliminates supraspinal control of muscle activity. Hortobagyi (1999) found that EMS-evoked eccentric contractions evoked greater cross education strength in the contralateral limb when tested using EMS-evoked eccentric contractions than compared to voluntary eccentric contractions. It has been hypothesized that since EMS can simultaneously activate sensory afferent fibers and α-motoneurons, a cross education effect may be induced at the spinal level by increasing the excitability of motor neurons and interneurons affecting the contralateral limb (Zhou, 2000). Horobagyi et al. (1990) suggested that a lack of EMG activity from the contralateral muscle during training sessions was a strong indicator that spinal mechanisms were responsible for the cross education effect. It was reasoned that due to the bilateral topography of the motor cortices, any supraspinal influence would have materialized in inadvertent elevated EMG amplitude of the homologous, contralateral muscle. However, because EMG measures only muscle activity and not descending efferent volleys, Hortobagyi's and colleagues' results do not exclude the possibility that descending supraspinal commands may still cause a cross education effect without elevated EMG in the contralateral muscle. Our results do not suggest that spinal mechanisms that alter the excitability of the α- motoneuron pool are responsible for the cross education effects since no change was detected in either the H_{max}-to-M_{max} ratio or H_A in the untrained limb. In contrast the fact that the trained right limb increased H_A values may be due to increased α-motoneuron excitability. While increased H_A values may be due to decreased levels of PSI, our results are inconclusive since CP and sural conditioning of the H-reflex was ineffective. Possibly, the trained limb experienced increased somatosensory feedback during training compared to the untrained. Because somatosensory stimuli can alter the H-reflex response (Zehr, 2002) this may be the mechanisms which differentiate the trained and untrained leg responses. We propose that increased somatosensory stimuli generated by the trained limb, in conjunction with descending supraspinal commands, function synergistically to potentiate Ia spinal reflex pathways, contributing to an increased force generating capacity. Furthermore, the contralateral untrained limb, void of such direct stimuli likely increases force generating capacity through supraspinal mechanisms.

H_{max}-to-M_{max} ratio

Previous studies have examined changes in evoked H-reflex amplitude induced by resistance training (Aagaard et al., 2000, Scaglioni et al., 2002). The H_{max}-to-M_{max} ratio has been shown to display a certain degree of plasticity to regular physical exercise (Casabona Polizzi & Perciavalle, 1990; Nielson, Crone & Hultborn, 1993). However, to our knowledge this is the first experiment to utilize H-reflex measures when examining the cross education effect due to strength training.

In our experiment the H_{max}-to-M_{max} ratio did not change in the experimental or control group for either leg. Available literature on the sensitivity of the H_{max}-to-M_{max} ratio to training is mixed. Casabona et al., (1990) found decreased H_{max}-to-M_{max} ratios in athletes trained for explosive movements. They suggested that intensive training utilizing primarily type II fibers decreased the synaptic strength of type Ia excitatory afferents on small and intermediate motorneurons. This implies that strength training may result in a small to large motoneuron transformation that can be detected via the H-reflex. In conflict with Casabona et al., Perot, Goubel, and Mora, (1991) found decreased H_{max}-to-M_{max} ratios in subjects who undertook 8 weeks of endurance training. Reduced H_{max}-to-M_{max} ratios have also been found following 20 days of bed rest (Yamanaka et al., 1999) and in highly trained ballet dancers (Nielson, Rone & Hultborn, 1992). Since endurance training is unlikely to result in a small to large motoneuron transformation, Casabona's theory appears unlikely. However, these seemingly conflicting findings may be due to different methodologies since H-reflex measures are sensitive to a host of influences such as limb position and muscle activity (Zehr, 2002). Alternatively, it could be theorized that an increased H_{max}-to-M_{max} ratio reflects increased alpha-motoneuron excitability and increased reflex excitability via the Ia pathway, leading to a greater recruitment of motoneurons. Our findings do not support that increases in strength are associated with an altered H_{max}-to-M_{max} ratio since both limbs of the experimental group improved significantly in force production capacity. Possibly, the H_{max}-to-M_{max} ratio is not a sensitive enough measure to detect subtle neurological changes at the level of the motoneuron during initial stages of strength training. Whereas past experiments have utilized the H_{max}-to-M_{max} ratio almost exclusively during exercise studies, analyzing the H-reflex at an M-wave of 5% may give additional insight into neurological adaptations.

Methodological considerations

While this experiment was adequately powered for detecting effects of cross education, it is possible that significant differences in H-reflex data due to CP and sural conditioning were not detectable due to the small sample size. In addition, the effect of holding a systematically higher than expected level of tonic contraction (20% instead of 10%) during the acquisition of H-reflex data are unknown and may decrease the susceptibility of the soleus H-reflex to CP and sural conditioning.

H-reflex conditioning due to CP and sural nerve stimulation

Modulation of H-reflexes recorded at similar contraction levels is primarily due to PSI of the afferent volley (Zehr, 2002). One method used to assess changes in PSI is to condition the H-reflex pathway via stimulation of the CP and sural nerves. Stimulation of the CP nerve at C-T intervals of 100 ms increases PSI of the soleus H-reflex pathway, while stimulation of the sural nerve at CT intervals of 80 ms decreases PSI of this pathway (Frigon et al., 2004). This experiment attempted to test weather a unilateral strength training program influenced the effect of CP and sural conditioning at the level of Ia PSI on the soleus H-reflex. Unexpectedly, neither CP nor sural nerve conditioning significantly altered the H-reflex response in overall group data for either control or experimental subjects. This finding differs from previous studies that have successfully used similar conditioning trials (Frigon et al., 2004; Iles, 1996). However, on an individual basis, some subjects displayed the expected results. Possibly, the N was too small to detect these changes, even though the power of the study was adequate to detect a cross education effect. Previous studies using tonic contractions of the soleus when assessing PSI have held approximately a 10% level of contraction (Frigon et al., 2004). In the present experiment subjects held an approximation of 10% EMG output during all H-reflex testing. However, upon further analysis of the force tracings it was discovered that average levels of contraction were ≈25%.MVIC. The effects of maintaining a 25% level of tonic contraction on CP and sural conditioning of the soleus H-reflex are unknown. However, since increased levels of muscle contraction result in a potentiation of H-reflex values (Aaagaard et al., 2000), it is possible that the ineffectiveness of sural conditioning to increase H-reflex values as hypothesized may be explained by a ceiling effect because it may not be possible to potentiate the H-reflex further through conditioning if intermediate and large motoneurons have depolarized. While the ineffectiveness of sural nerve conditioning to potentiate the H-reflex has a candidate mechanism explanation, the ineffectiveness of CP nerve conditioning to attenuate the soleus H-reflex in this experiment remains unclear.

Conclusions

Further research using the H-reflex in cross education experiments is needed to validate if a difference in spinal reflex excitability exists due to the cross education effect. Because no measure of supraspinal excitability (such as TMS or TES) were included in this study, it is not possible to conclude that the predominant mechanism behind the cross education effect is supraspinal in nature. However, the lack of change in the H-reflex, suggests that increased α-motoneuronal excitability is not the principal mechanism responsible for the increased strength in the contralateral limb.

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Appendix A

Informed Consent

Effects of Unilateral, Isometric resistance Training on Strength Development and Presynaptic Inhibition in the Trained and Untrained Limb

You are being invited to participate in a study entitled **The effects of unilateral, isometric resistance training on strength development and presynaptic inhibition in the trained and untrained limb** that is being conducted by Olle Lagerquist who is a graduate student in the School of Physical Education at the University of Victoria. You may contact him if you have further questions by either phone (721-2792) or email (olle@uvic.ca). As a graduate student I am required to conduct research as part of the requirements for a degree in Master's of Science. It is being conducted under the supervision of Dr. David Docherty and Dr. Paul Zehr. You may contact Dr. Docherty at 721-8375 or docherty@uvic.ca and Dr. Zehr at 721-8379 or pzehr@uvic.ca.

The purpose of this research project is to examine the effects of a 5-week unilateral, isometric strength training program on levels of presynaptic inhibition and alterations in the H-reflex in both the trained and untrained limbs.

To date no study has examined the contribution of presynaptic inhibition on strength acquisition. By examining the effects of a unilateral strength training program on strength development in both the trained and untrained limb in conjunction with measures of presynaptic inhibition, a better understanding of the neural circuitry will be achieved. A better understanding of the neurological response to chronic, unilateral training will benefit rehabilitative techniques involving stroke victims, as well as persons with unilateral limb damage.

You are invited to participate in this study because you have not participated in chronic strengthening activities involving the plantar flexors for 1 year prior to beginning the study, have no history of neurologic or orthapedic disorders and are free of a lower leg injury.

If you agree to voluntarily participate in this research, your participation will include performance of various exercise protocols and the administration of the Hoffmann reflex in the soleus muscle. The Hoffmann reflex involves electrical stimulus to the tibial nerve, resulting in a mild contraction of the soleus muscle. Use of the Hoffmann reflex in conjunction with stimulation of the common peroneal nerve and sural nerve will be used to determine levels of presynaptic inhibition.

The experiment will consist of one exercise protocol (experimental group) of unilateral isometric plantar flexion designed to strengthen the soleus muscle of the dominant leg. Experimental group participants will be required to participate in a minimum of two familiarization sessions. A third familiarization session will be conducted if there is a greater than 5% difference in the acquired maximal isometric plantar flexion. After satisfactory completion of the familiarization sessions, experimental group participants will perform the exercise protocol on separate days with approximately 48 hrs between training sessions. The H-reflex will be evoked and tested before the 5 week as well as after the completion of the program. Control group participants will be required to participate in a minimum of two familiarization sessions as well as pre and post measures of the Hoffmann reflex. Control group participants will not perform any exercise intervention. For control group participants, the Hoffmann reflex will be evoked again after 5 weeks. Experimental group participants will be required to abstain from any other lower leg conditioning during the study other than the prescribed unilateral isometric training protocol. Control group participants will be required to abstain from beginning any lower body conditioning for the duration of the study.

Participation in this study may cause some inconvenience to you because of the time commitment, approximately 11.75 hours over a period of 6 weeks for the experimental group and 8 hours over a period of 6 weeks for the control group. Although very unlikely, you may also experience some discomfort during the mild electrical stimulus necessary for evoking the Hoffmann reflex

Experimental group participants may experience minor muscle soreness following the training protocol. Gentle stretching of the affected muscles should alleviate the stiffness. If the muscle soreness persists for more than 48 hours or if you experience discomfort greater than normally encountered during a regular training session please inform the investigator (7251-2792) and the test will be terminated. You can either reschedule another appointment to complete the test or withdraw from the study.

Your participation in this research must be completely voluntary. If you do decide to participate, you may withdraw at any time without consequence or explanation. An initial consent will be signed by each participant and at each subsequent testing or training period, I will remind you that you can choose to participate or not, and you can withdraw without consequence. If you do withdraw from the study your data will not be used in the study.

In terms of protecting your anonymity, your data will be stored by assigning a code number to the data sheet rather than a name. Only the principal investigator and the supervising professor will have access to the data.

Your confidentiality and the confidentiality of the data will be protected. All information collected during the study will only be accessible by the principal investigator or supervisor and personal results will not shared without your consent.

Data from this study consisting of raw data and electronic files (recorded onto a CD) will be stored in a personal locked file cabinet for a minimum of 5 years. Upon completion of the retention period, the documents will be shredded and the CD destroyed.

It is anticipated that the results of this study will be shared via a thesis paper and published article.

In addition to being able to contact the researcher at the above phone numbers, you may verify the ethical approval of this study, or raise any concerns you might have, by contacting the Associate Vice-President, Research at the University of Victoria (250-472-4362).

Your signature below indicates that you understand the above conditions of participation in this study and that you have had the opportunity to have your questions answered by the researchers.

Name of Participant	*Signature*	*Date*

A copy of this consent will be left with you, and a copy will be taken by the researcher.

Appendix B

Physiological Indicators of Neural Adaptation in Cross Education

Physiological Markers of Neural Adaptation in Cross Education

Chronic resistance training causes muscular adaptations in the exercised musculature and is suspected of influencing neural adaptations (Carrol, Riek, and Carson, 2002). Likewise, acquisition of motor skills is associated with supraspinal modulations (Classen, Liepert, Wise, Hallet, and Cohen, 1998). Numerous studies have also reported that chronic unilateral motor activity can affect performance of the homologous muscles in the contralateral limb. This phenomenon, known as cross education, results in both improvements in strength and the acquisition of motor skills, and is specific to the prescribed training (Hortobagyi, Scott, lambert, Hamilton, and Tracy, 1999).

A suggested practical application for cross education is in neuromuscular rehabilitation for persons who are incapable of exercising a limb. Stromberg (1986) reported that patients who participated in a contralateral therapy program, after one arm was immobilized due to surgery, experienced increased mobility and hand grip strength compared with unexercised controls. However, the mechanisms underlying cross education and the most efficient intervention program for rehabilitation have not been clearly identified.

Indirect evidence exists for both spinal and supraspinal mechanisms of adaptation in cross education. Unfortunately, most cross education studies fail to use appropriate physiological markers, resulting in paucity of evidence as to the locus of neurological adaptations. This brief review will address the phenomenon of cross education, examine the mechanisms proposed to be responsible for contralateral strength gains, and explore directions for future research.

Occurrence of Cross Education

Cross education has been documented during a variety of training programs including voluntary isometric, concentric, and eccentric contractions, as well as electrically stimulated contractions.

Effect of Muscular Contraction

Several weeks of voluntary isometric or concentric contractions have typically been found to induce strength gains of 5-25% in the contralateral homologous muscle (Zhou, 2000). Eccentric contractions appear to elicit much greater cross education effects as demonstrated by Hortobagyi et al., (1999) who found contralateral strength gains of 77% following isokinetic eccentric knee extension training. The same study found that concentric and isometric training programs elicited contralateral strength gains of 30% and 22% respectively. The reason for greater cross education with eccentric contractions is unknown, however, it has been suggested that eccentric contractions require unique activation strategies by the nervous system (Enoka, 1996).

Experimental evidence supports the concept of a unique strategy of nervous system activation for eccentric contractions. In contrast to concentric or isometric contractions, there is reduced muscle activation during maximal eccentric contractions, altered recruitment order of motor units during submaximal eccentric contractions, and a decrease in the size of the potentials evoked in muscle by transcranial and peripheral nerve stimulation during eccentric contractions (Enoka, 1996). However, it is currently not well understood how these differences in activation strategies could increase cross education. Aagaard et al. (2000) has suggested the existence of a neural regulatory mechanism that limits the recruitment and/or discharge of motor units during maximal voluntary eccentric contractions. Possibly, large increases in eccentric contralateral strength occur due to inhibition of this neural regulatory mechanism. Training with electrical muscle stimulation has been found to induce even greater cross education effects than voluntary contractions, especially for eccentric contractions.

Electrical Muscle Stimulation (EMS)

Hortobagyi et al., (1999) found that six weeks of EMS-evoked eccentric contractions produced strength gains of 104% in the contralateral limb when tested using EMS-evoked eccentric contractions. Comparatively, a 23% strength gain was found after training and testing with voluntary eccentric contractions. Theoretically, the use of EMS bypasses motor cortex involvement due to direct stimulation of the α-motoneurons. However, no studies have examined the effects of EMS training in conjunction with other physiological markers that measure supraspinal activity, such as positron emission topography.

Training Intensity

The overload principle states that an intensity of 60% maximal voluntary contraction (MVIC) is necessary to achieve strength gains. Training that utilizes intensities lower than 60% is likely to increase the endurance of the exercised musculature with little or no increase in absolute strength, while training intensities of 90-100% MVIC will evoke the greatest improvements in MVIC (Heyward, 2002). In contrast, there does not appears to be a similar dose response relationship between training intensity and contralateral strength gains with isometric training. Oakman, Zhou, and Davies (1999) obtained a 21% contralateral strength gain with an isometric training stimulus of 65% MVIC, while Carolan and Cafarelli (1992) noted a 16% contralateral gain in strength following a 100% concentric training stimulus. In a recent review, Zhou (2000) presented data from isometric and concentric cross education experiments *together* in a scatter-plot diagram. This was intended to demonstrate the lack of relationship between intensity of training and magnitude of cross education. However, Zhou did not assess the impact of isometric and concentric training intensity on cross education independently of one another. The data originally amalgamated by Zhou has therefore been split into two separate scatter-plot diagrams. The linear regression equation for a sample of unilateral isometric training studies (figure 1) displays a Y intercept of 15.44 (%initial strength). Possibly, regardless of intensity of unilateral isometric training, one can expect a 15% increase in contralateral strength. However, cross education appears to be more pronounced with increasing training intensities during concentric contractions.

Ploutz et al., (1994) noted a 7% increase in contralateral strength due to a 75% MVIC concentric training program, while Hortobagyi et al., (1997) reported a 22% strength increase following a 100% MVIC concentric training program. The linear regression equation for a sample of unilateral concentric training studies (figure 2) indicates a Y intercept of –28.085 (%initial strength). A negative Y intercept is not expected since we do not anticipate a decrement in contralateral strength regardless of how low the unilateral training intensity. Possibly the small sample size is not representative of the general trend. However, it is interesting that the regression line crosses the X axis at a value of 55 (%MVIC), since this approximates the value of 60% MVIC thought to be essential for any strength improvements dictated by the overload principle.

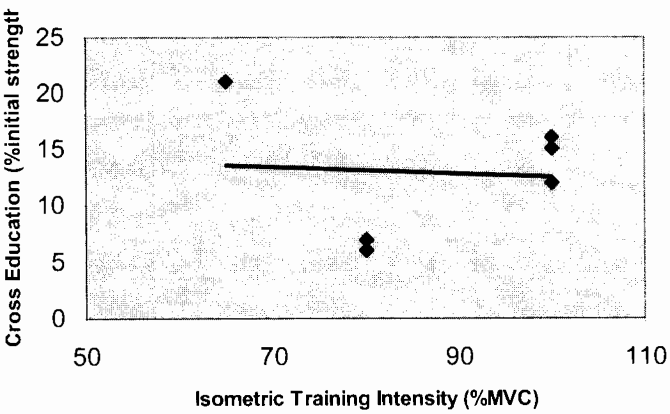

Figure 1 Cross education in relation to isometric training intensity for the knee extensor muscle group. 1, Oakman et al. (1999). *Sci Proc.* 17th ISBS, 401-404; 2, Weir et al., (1995). *Eur. J. Appl. Physiol. Occup. Physiol.* 70:337-343; 3, Jones and Rutherford (1987). *J. Physiol. (Lond.)* 391:1-11; 4, Carolan and Cafarelli, (1992). *J. Appl. Physiol.* 73:911-917; 5, Parker, (1985). *Eur. J. Appl. Physiol.* 54:262-268; 6, Kannus et al., (1992). *Eur. J. Appl. Physiol. Occup. Physiol.* 64:117-126. As cited in Zhou (2000).

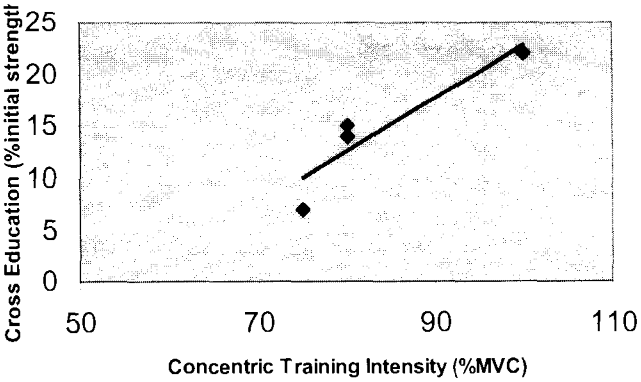

Figure 2 Cross education in relation to concentric training intensity for the knee extensor muscle group. 1, Ploutz et al., (1994). *J. Appl. Physiol.* 76:1675-1681; 2, Weir et al., (1997). *J. Orthop. Sport Phys. Ther.* 25;264-270; 3, Housh et al., (1996). *Int. J. Sports Med.* 17:338-343; 4, Hortobagyi et al., (1997). *Med. Sci. Sports. Exerc.* 29:107-112. As cited in Zhou (2000).

Specificity of Cross Education

Resistance training is known to change skeletal muscle via hypertrophy of muscle fibres as well as increased enzymatic activity. However, strength is determined not only by the quantity and quality of muscle mass but also by the degree of muscular activation. It has been postulated that strength training causes neuromuscular adaptations that allow more activation of prime movers, as well as improving coordination of relevant musculature, thereby resulting in greater net force (Sale, 1988). Neuromuscular adaptations to strength training demonstrates specificity. Structural and functional adaptations are specific to the exercised musculature and greatest training effect is seen when the testing procedure matches the training protocol (Sale, 1988). Seemingly in conflict with the principle of specificity, cross education of the contralateral limb displays evidence of neuromuscular adaptations *despite* never being involved in the tasks that are performed during training. However, experimental evidence has demonstrated that the responses and adaptations in the contralateral limb *are* specific, but are specific with respect to the training imposed on the exercised limb.

Strength gains in cross education appear to be confined to the homologous musculature of the contralateral limb. Hortobagyi et al., (1999) found no change in hand grip strength after 6 weeks of unilateral knee extension training although knee extension strength increased significantly in both trained and contralateral legs.

Contralateral strength gains are greatest when the mode of testing mirrors the training protocol for the ipsilateral limb. Hortobagyi et al., (1997) compared cross education effects following 12 weeks of isokinetic training of the knee extensors with either concentric or eccentric contractions. Concentrically trained subjects displayed greater (30%) strength increases in the contralateral limb than the eccentrically trained group (18%) when tested concentrically. Conversely, eccentrically trained subjects displayed greater (77%) strength increases than the concentric training group (10%) when tested eccentrically.

Voluntary eccentric contractions appear to produce greater cross education effect compared to voluntary concentric or isometric contractions (Hortobagyi et al., 1997; Hortobagyi et al., 1999). However, EMS-evoked eccentric contractions induce even greater training effects than voluntary contractions. Hortobagyi et al., (1999) found that subjects who trained with unilateral EMS-evoked eccentric contractions showed superior strength gains (104%) when tested in the same mode compared to voluntary eccentric contractions (34%). In addition, eccentric unilateral fatigue protocols appear to have a unique facilitative effect on the contralateral muscles (Grabiner & Owings, 1999). Following a unilateral fatiguing protocol using voluntary eccentric contractions, eccentric strength testing was enhanced by 11%, while no such effect was found following the concentric fatiguing protocol.

Neural Adaptations to Strength Training and Cross Education

It is well established that resistance training can lead to an increase in maximal contractile force of the specific musculature exercised without inducing hypertrophy. However, the specific mechanisms responsible for this adaptation are not well understood. Moritani and deVries (1979) suggested an increased “central neural drive” as a possible factor influencing maximal contractile muscle force in the absence of muscular hypertrophy. Much of the available evidence surrounding neural adaptations to resistance training is based on EMG data, which represents an indirect measure of neural activation, but does not distinguish between spinal or supraspinal mechanisms. Only a few studies have examined evoked spinal motoneuron responses to more closely elucidate the adaptive changes in neural function induced by resistance training (Aagaard, et al., 2000). While it is unclear what neural adaptations are responsible for strength increases due to resistance training, the mechanisms of cross education are even more elusive.

Several neural mechanisms have been proposed for cross education, including diffusion of impulses between hemispheres, coactivation via bilateral corticospinal pathways, afferent modulation and postural stabilization or improved coordination. However, similar to the literature on neural adaptations to strength training, few studies have directly examined supraspinal activation as it relates to cross education, and none have studied evoked spinal motoneuron responses to examine spinal adaptation mechanisms in order to elucidate the precise locus of change.

Supraspinal Mechanisms

Hellebrandt (1951) suggested that diffusion of impulses to the contralateral motor cortex during a unilateral task were responsible for cross education. Hellebrandt speculated that the excitation of a supraspinal motor point during voluntary contraction of a muscle might produce an effect on the contralateral motor cortex, which then elicits a training effect of the contralateral muscle. The findings of Kristeva, Cheyene, and Deecke (1991), support this hypothesis since bilateral topography of the premotor readiness field and motor field for both the unilateral and bilateral movements was found. These results suggest the presence of a bilateral generator and that unilateral voluntary movements involve the activation of the contralateral cortex. The anatomy of the corticospinal tracts may provide further insight into mechanisms of cross education.

Approximately 15% of corticospinal fibres enter the lateral and anterior corticospinal tract of the ipsilateral side, while the remaining fibres cross to the contralateral side (Martini, Timmons, & Tallitsch, 2003). Coactivation of bilateral homologous muscles caused by an overflow of descending signals due to uncrossed portions of the corticospinal tract has been proposed as another mechanism of cross education (Hellebrandt, 1951). Contradicting this hypothesis are the findings of Carr, Harrison, and Stephens (1994), who observed that transcranial magnetic stimulation evoked common activation of homologous muscles, as measured by EMG, in axial musculature that is normally co-activated, but not in muscles that usually act independently. However, these results cannot exclude the possibility that cross education may still occur due to coactivation since EMG measures only muscle activity and not descending efferent volleys that could still induce a training effect in the contralateral limb. Yue and Cole (1992) provided further support for supraspinal contributions to cross education by finding that unilateral training with imagined contractions can induce a strength gain of 11% in the homologous muscle of the other hand. The use of transcranial magnetic stimulation (TMS), transcranial electric stimulation (TES), and motor evoked potentials (MEPs) may provide more appropriate measures for evaluating possible supraspinal and spinal mechanisms of cross education.

The mechanisms of eliciting descending corticospinal volleys differ between TMS and TES. The responses to TES are less strongly influenced by the excitable state of the motor cortex than TMS responses (Carrol, Riek, and Carson, 2002). Consequently, comparing the MEPs elicited from TMS and TES could allow one to infer whether neural adaptations to resistance training, resulting in cross education, occur to a greater extent at supraspinal or spinal sites in the CNS. To date no study has examined cross education in this manner, however, Carrol et al., (2002) used TMS, TES, EMG, and MEPs to examine neural adaptations of the index finger abductor after 4 weeks of resistance training. Carrol and colleagues suggested that resistance training causes changes in the organization of the synaptic circuitry in the corticospinal pathway, but does not substantially affect the motor cortex. How these findings relate to cross education and to what degree spinal circuitry adaptations affect cross education remains to be explored, however, the use of TMS and TES could provide an additional method of evaluating the mechanisms of cross education. In addition, the Hoffman reflex has potential for evaluating changes in human reflex pathways and plasticity of the neuromuscular system.

The Hoffman Reflex in Cross Education

The Hoffman (H) reflex is considered the electrical equivalent of the stretch reflex (Zehr, 2002). Evoking the H reflex involves electrically stimulating both motor and sensory axons of peripheral nerves. Gradually increasing intensity of stimulation will cause the larger diameter Ia afferent sensory fibres to be recruited before the smaller diameter motor fibres. The H reflex is recorded when electrical stimulation of the Ia afferents causes adequate neurotransmitter release via depolarization of the afferent terminals leading to a postsynaptic depolarization of alpha motoneurons. Subsequent neurotransmitter release at the neuromuscular junction leads to depolarization and contraction of the muscle fibres, which is recorded as the H reflex (Zehr, 2002). The H-reflex has been reported to be a measure of α-motoneuron excitability, while also reflecting presynaptic inhibition in Ia afferent synapses. The V wave is a variant of the H reflex and is recorded only during voluntary muscular contraction (Aagaard et al., 2002). The V-wave has been suggested to reflect the overall magnitude of efferent motor output from the α-motoneuron pool because of activation from descending central pathways (Aagaard et al., 2002). However, Zehr (2002) suggests that great care be exercised when interpreting changes in the H reflex or the V wave as representing changes in motoneuron excitability due to the effects of presynaptic inhibition.

Recently Aagaard et al., (2002) monitored changes in evoked V-waves during maximal muscle contraction and H-reflexes to examine neural adaptive changes induced by resistance training. Elevated V-wave and H-reflex amplitudes were observed in response to 14 weeks of progressive resistance training. This suggests adaptations at both spinal and supraspinal levels *potentially* indicating changes in the α-motoneuron excitability and descending neural drive respectively. To date no study on cross education has utilized the H-reflex to determine spinal or supraspinal loci of adaptation. Although caution must be exercised when interpreting changes in the H reflex as a measure of α-motoneuron excitability, or increases in the V wave as an indication of increases in central neural drive, careful use of these tools may elucidate the mechanisms of cross education. Recent studies using electrical muscle stimulation (EMS) have provided compelling evidence of spinal mechanisms as the main effector in cross education.

Spinal Mechanisms

As previously discussed, EMS training has been shown to elicit greater gains in cross education than volitional training (Hortobagyi, et al., 1999). Electrical muscle stimulation artificially stimulates muscle and consequently eliminates supraspinal control of muscle activity. Electrically elicited muscular contractions can induce training effects in the stimulated limb, as well as the non-stimulated contralateral limb (Hortobagyi, et al., 1999). EMS can stimulate both α-motorneurons and sensory afferent fibres. Therefore, simultaneous activation of afferent sensory fibres may contribute to cross education by altering the excitability of motor neurons and interneurons affecting the contralateral limb (Zhou, 2000).

Hortobagyi et al., (1999) suggested that "central neural drive" was not the dominant mechanism of cross education during EMS training. Three reasons were offered in support of the mechanisms of cross education residing at the spinal level. First, the degree of EMG activity recorded from the contralateral quadriceps during training was not proportional to the amount of strength gained. During unilateral leg extension, the EMG activity from the contralateral quadriceps of the volitional training group was 5% of that during maximal contraction. Likewise, during unilateral training with EMS, EMG activity of the contralateral quadriceps did not exceed 15% of that during maximal contraction. These results cannot exclude the possibility that cross education may still occur since EMG measures only muscle activity and not descending efferent volleys that could still induce a training effect in the contralateral limb. Following six weeks of training, the EMG activity in the contralateral quadriceps during an MVIC increased 20% and 33%, for all subjects, in response to isometric and eccentric testing, respectively. Such increases in EMG activity correspond well with contralateral strength gains due to voluntary testing (15-34%) and could be due to an increased central drive.

However, the much greater increase in contralateral strength (37-104%) that was evident with EMS training and testing suggests that enhanced neural drive alone could not be the dominant mechanism. Second, EMS training was more effective than voluntary training in eliciting cross education strength gains, and must thus be able to access different mechanisms of adaptation not influenced by central drive during voluntary training. Third, the discomfort associated with EMS is not likely to cause supraspinal adaptations great enough to induce the extent of cross education observed. After EMS training, stimulated eccentric strength increased 104% while voluntary eccentric strength increased 34%. If pain caused adaptations in central drive, via afferent nociceptor input, it would be expected that voluntary and stimulated strength would increase by same extent. These findings suggest the presence of a spinal modulation to mediate cross education. The mechanisms underlying spinal modulations are not well understood, however, involvement of group IIa muscle afferents and the crossed extension reflex is suspected to be involved.

Stimulation of group Ia afferent fibres causes excitation of flexor muscles and inhibition of extensor muscles ipsilaterally, and excitation of contralateral extensors and inhibition of flexors. This phenomenon has been termed the crossed extension reflex (Vander, Sherman, & Luciano 1994). It has been speculated that such a mechanism may contribute to cross education by strengthening excitatory synaptic interactions intraspinally on the contralateral extensors (Hortobagyi et al., 1999). For example, it has been shown that ipsilateral cutaneous stimulation increased motoneuron excitability in the contralateral homologous muscle

(Robinson, McIian, & Hayes, 1979). However, no direct evidence exists linking afferent modulation, associated with EMS training, and spinal mechanisms, such as the crossed extensor reflex. Methodologies comparing EMS and voluntary training, in conjunction with EMG of the agonist and antagonist muscle of the contralateral limb, are needed to verify or refute this mechanism. Possibly, unilateral training elicits inhibition of the homologous contralateral antagonist muscle, excitation of the homologous contralateral agonist muscle, or a combination of both. Either of these possibilities could result in greater force production of the contralateral limb. For example, Carolan and Cafarelli (1992) examined the training effects on coactivation of agonists and antagonist muscles in the contralateral limb during unilateral knee extension. They reported a 16% increase in knee extensor strength accompanied by a 13% reduction in coactivation of the hamstring muscles. This decrease in EMG activity of the contralateral hamstring musculature did not change after the first week of training, whereas strength in contralateral limb continued to increase with subsequent training. This suggests that other mechanisms were contributing to the continued cross education effect. However, this is an isolated finding and further research needs to examine the effect of cross education on contralateral agonist and antagonist muscle activation. Postural stability may also involve coactivation of agonist and antagonist muscles.

Postural Stabilization

Unilateral training may activate the contralateral limb musculature in order to achieve postural stability. Such activation has been speculated to contribute to the cross education effect (Hellebrandt, 1951). However, the small magnitude of EMG in the contralateral limb appears to be insufficient to generate the magnitude of strength gains associated with cross education. For example, Hortobagyi et al., (1999), found that EMG activity of the contralateral muscle during EMS training was less than 15% while the strength gain caused by cross education was104%. It therefore seems unlikely that postural stabilization greatly influences the effects of cross education.

Conclusion

Cross education has been observed under multiple conditions and demonstrates specificity of training. Training with eccentric or EMS-evoked contractions appears to obtain greater cross education effects than concentric or isometric voluntary contractions. The mechanisms of cross education continue to be elusive, with supporting evidence for both spinal and supraspinal sites of adaptation. The use of the H reflex and its variant, the V wave, as well as TMS and TES have been neglected as possible tools for the evaluation of plasticity in the neuromuscular system during cross education. Systematic utilization of these tools could provide insight into the neural adaptations responsible for cross education. Likewise, collecting EMG data from the contralateral agonist and antagonist muscles could help elucidate the mechanisms concerning the crossed extensor reflex and its influence on cross education. A better understanding of the mechanisms surrounding cross education would benefit not only future neuromuscular rehabilitation programs for persons incapable of exercising a limb, but also further our understanding of human motor control.

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Appendix C

Neural Adaptations to Chronic Physical Activity:
The Influence of Presynaptic Inhibition

The capabilities and adaptations of the human neuromuscular system are affected by both the volume and type of physical activity that are imposed. A person engaged in regular, intense resistance training will have greater lean body mass and strength than if they were inactive. Alternatively, a person subjected to bed rest, or who has a limb immobilized will experience muscle atrophy and a decline in strength. Observations such as these highlight the plasticity of the human neuromuscular system evoked by physical activity. While certain myogenic mechanisms surrounding resistance training have been elucidated, little is known concerning the loci of adaptation concerning neural adaptations to strength training.

It is well established that chronic physical activity such as resistance training causes myogenic adaptations in the form of hypertrophy and other cellular morphologies as well as influencing neural processes. Strong evidence supporting neural adaptations in resistance training has come from studies utilizing electromyography, unilateral training (cross education), and imagined contractions. The mechanisms surrounding these adaptations are not entirely understood, although maximizing muscle activation and/or modifying the specificity and pattern of neural drive to muscle are likely contributors.

Few studies have examined changes in evoked spinal responses to adaptive changes induced by chronic physical activity such as resistance training. Attempts have been made to utilize the Hoffman (H) reflex as a measure of alpha motoneuron excitability in order to clarify neurological adaptations to chronic physical activity. However, previous studies have utilized different methodologies and neglected to account for the strong effects of presynaptic inhibition (PSI) on the H-reflex. Thus, earlier exercise studies reporting adaptations in the H-reflex need to be interpreted carefully and with some caution.

It is well documented that unilateral strength training can effect performance of the homologous, non exercised muscles in the contralateral limb. This effect, termed cross education, occurs in the absence of myogenic adaptations in the untrained muscle and is thought to result from undetermined neural mechanisms (Zhou 2000). The influence of a strength-training program on PSI and PSI's relevance to cross education has yet to be determined. This is an area that warrants further investigation since altering PSI in the trained and untrained musculature may affect the efficacy of alpha-motoneuron pool excitability as well as influence the cross education effect.

Strength Training Studies

The following section will review the evidence for neuromuscular adaptations to chronic physical activity by exploring myogenic adaptations, electromyographic evidence, imagined contractions and cross education in strength training studies. This brief review of select key points is by no means exhaustive. For more complete reviews please refer to Enoka, (1997), McComas, (1994), Kraemer, Fleck, and Evans (1996), and Duchateau and Enoka (2002).

Onset of myogenic adaptations

It is well established that repetitive resistance training induces muscular hypertrophy via increased protein synthesis (Goldberg, Ettinger, Goldspink, &

Jablecki, 1975; Macdougal, Sale, Always, & Sutton, 1984). It is also well established that strength increases occurring during the first few weeks of training precede any significant increase in muscle mass (Hickson et al., 1994; Komi, 1986; Jones and Rutherford, 1987; Sale, 1988). Although protein synthesis has been shown to increase following a single bout of heavy-resistance exercise, no significant hypertrophy of muscle fibres is apparent until the exercise program has been continued for about eight weeks (Staron et al., 1994). This suggests that initial strength gains are largely due to neural adaptations. Further evidence for neuromuscular adaptations occurring without the aid of muscular hypertrophy is provided by the occurrence of cross education.

Cross education in strength training

Several studies have reported that chronic unilateral motor activity can affect performance of the homologous muscles in the contralateral limb. This phenomenon, termed cross education, has been shown to result in contralateral strength improvements of 10-15% in the untrained limb, that are specific to the prescribed mode of training (Hortobagyi, Scott, Lambert, Hamilton, & Tracy, 1999). The contralateral strength improvements gained through cross education have never been found to accompany *any* myogenic adaptations and occur in the absence of activity in the contralateral muscles during training of the ipsilateral muscles (Zhou, 2000). Thus it has been assumed that neural mechanisms are solely responsible for the strength gains in the contralateral muscle.

In an attempt to explain the initial increase in strength without the accompaniment of muscular hypertrophy in both bilateral and cross education protocols a number of electromyographic studies have been performed.

Electromyographic studies

Electromyographic studies have provided the majority of indirect evidence of neural adaptations to training. These studies have focused primarily on motor unit activation before and after training via the use of surface electrodes. Recorded motor unit activation in muscle is quantified as an integrated electromyogram (IEMG) (Sale, 1988). The relationship between IEMG and force is such that the greater the number of motor units activated, and/or the greater the rate of motor unit firing, the greater the force production and hence greater the IEMG. Early strength increases have been found to accompany increases in maximum IEMG activity (Komi, 1998; Sale, 1988). IEMG has been shown to increase after many different modes of training including dynamic resistance (Hakkinen, &, Komi, 1983), isokinetic contractions (Komi, & Buskirk, 1972) and isometric contractions (Komi, Vitasalo, Raurama, & Vihko, 1978). Increased IEMG with associated increases in strength, especially in the absence of significant muscular hypertrophy, has been interpreted as indicating that trained subjects can more fully activate muscles during maximal voluntary contractions through some form of neural adaptation. However, the majority of studies have been limited to examining surface electrode IEMG and force producing capabilities in the leg extensor muscles, vastus lateralis especially (Hakkinen, Kallinen, Komi & Kauhanen, 1991). The mechanism responsible for increased

IEMG in conjunction with increases in strength has yet to be determined. However, the phenomenon of cross education indicates that the adaptations in the CNS are not focused only on the motor neuron pool of the trained muscle but also affect neurons that modulate the activity of the contralateral muscle (Enoka, 1997). The effect of imagined contractions provides evidence that further supports the existence of neural factors in strength gains.

Imagined contractions

In support of neural mechanisms leading to strength gains, Yue and Cole (1992) found that subjects who performed unilateral contractions increased maximum isometric force by 30% in the trained hand whereas those who simply imagined the contractions experienced a 22% increase. Since no IEMG was detected in the test muscle during the mental training, the authors deemed the neural adaptation to be upstream from the motorneuron pool. In contrast to this theory, it is possible that mental rehearsal increases muscle spindle activity even though no IEMG is detectable, and that enhanced spindle sensitivity can facilitate force production via a more effective stretch shortening cycle or reciprocal inhibition. However, no evidence of increased spindle activity in the absence of IEMG was found in tibialis anterior or forearm muscles when participants imagined performing motor tasks (Gandevia, Wilson, Inglis & Burke, 1997). Instead, Gandevia et al. (1997) found that mental practice of motor tasks always accompanied increased IEMG activity and H-reflex excitability and concluded that mental rehearsal usually involves unintentional performance of the planned motor task. In support of these findings, Gandevia and Burke (1985) found that muscle spindle afferents could not voluntarily be activated without also activating low-threshold alpha-motoneurons. Thus it seems that altered muscle spindle activity is not a likely contributing factor in increasing force production due to mental practice in studies that have documented zero increase in IEMG activity. In addition, training with imagined contractions caused a statistically significant increase in the strength of the homologous muscle in the contralateral untrained hand. Subjects who trained with actual contractions increased the strength of the contralateral hand by 14.4% while the subjects who performed the imagined contractions increased by 10.5%. Consistent with these findings, Gandevia and Rothwell (1987) established that when subjects focused attention (presumably through subliminal motor commands) on a hand muscle the recruitment threshold of motor units to percutaneous electrical stimulation of the motor cortex was reduced. If mental practice of a motor task is capable of reducing the PSI to specific motoneurons this may lower the threshold of motor unit activation, leading to a facilitation of strength, although this possibility has yet to be explored. Change does seem to occur in the gain of reflexes and adaptations of muscle afferents due to training and a conditioning stimulus. Wolpaw (1987) established that operant conditioning with monkeys changed triceps surae Hoffman (H-) reflex amplitude without a change in background IEMG, while other studies examining neural adaptations in training humans have found evidence of increased H-reflexes due to strength training (Aagaard, Simonsen, Andersen, Magnusson & Dhyre-Poulsen, 2002). However, the examination of reflex potentiation in exercise studies, has often been misinterpreted.

Evoked Spinal Motoneuron Responses to Adaptive Changes Induced by Physical Activity

In an attempt to elucidate neural adaptations to strength training and chronic physical activity, exercise studies have examined reflex pathways by using electromyography in conjunction with muscle and nerve stimulation. The H-reflex is possibly the most widely studied reflex due to the ease with which it can be elicited in various muscles. Many exercise studies have examined the H-reflex with various hypotheses as to why it may be potentiated or attenuated due to chronic physical activity. However, no exercise studies utilizing the H-reflex have accounted for the strong effects of presynaptic inhibition (PSI) in modulating the H-reflex, thus severely limiting the interpretation of existing literature. Properly conducted exercise studies utilizing the H-reflex in conjunction with measures of PSI are needed in order to further elucidate how reflex mechanisms may be affected by chronic physical activity such as strengthening programs.

Presynaptic inhibition

When an action potential in the presynaptic cell reduces the probability of an action potential occurring in the postsynaptic cell it is referred to as presynaptic inhibition (PSI). The concept of PSI began in 1957 when Frank and Fourtes described a depression of monosynaptic excitatory potentials (EPSPs) occurring without a change in the post synaptic potential or change in motoneuronal excitability. The mechanism responsible for PSI is thought to vary depending on the nerve fiber type, but are believed to be mediated through both

$GABA_A$ and $GABA_B$-type receptors (Rudomin & Schmidt, 1999). However, axo-axonic GABAergic synapses having $GABA_A$-type receptors are thought to induce the greatest PSI on motoneurons by inducing primary afferent depolarization (PAD) (Rudomin & Schmidt, 1999). $GABA_A$-receptors are believed to be linked to chloride ion (Cl-) channels which upon activation causes an efflux of Cl- and consequently K+ efflux. The net result of the K+ efflux moves the membrane potential back towards its resting value (Alvarez-Leefmans, Gamino, Giraldez & Nogueron, 1998). Possibly, this inhibition of action potential invasion into the primary afferent terminal reduces the amplitude of propagated action potentials, thereby reducing or blocking Ca2+ influx and decreasing the release of excitatory neurotransmitters, most likely glutamate (Rudomin & Schmidt 1999). Conclusive evidence for this hypothesis is lacking, however, $GABA_A$ receptor activation has been shown to gate Cl- channels in the rat (Jackson & Zhang 1995), and in the bullfrog, $GABA_A$ receptor activation has been shown to induce PSI effects at synapses between muscle spindle afferents and motoneurons accompanied by a reduction in action potentials invading the afferent terminals (Peng & Frank 1989a).

$GABA_B$ receptors are also believed to effect PSI via their effect on presynaptic Ca2+ currents, mediated through a second messenger system (Dolphin, Huston & Scott 1990). A decrease in Ca2+ influx would decrease the likelihood of excitatory neurotransmitter release. $GABA_B$ receptor activation has also been suggested to activate K+ efflux in presynaptic terminals, resulting in a return of resting membrane potential and therefore a blocking of action potential invasion (Gage 1992). However, the role of $GABA_B$ receptors in modulating PSI is currently not as well understood as the influence of $GABA_A$ receptors.

A classic technique for demonstrating PSI in animals is to show that the membrane potential and conductance of the postsynaptic neuron are not altered at the same instant as the size of the synaptic potential is reduced (Frank & Fourtes, 1957). This establishes that the inhibition is not generated at the post synaptic cell, and must instead be elicited presynaptically with the release of afferent neurotransmitters. The most widely used method of studying PSI in humans is by measuring changes in the H-reflex.

The Hoffmann reflex

Simply put, the H-reflex is considered the electrical equivalent of a stretch reflex and is predominantly characterized by the monosynaptic projections of group Ia afferents onto homonomous motoneurons (Zehr, 2002; Misaiszek, 2003). Evoking the H-reflex involves percutaneously stimulating both motor and sensory axons of peripheral nerves. Increasing the intensity of stimulation causes the larger diameter Ia afferent sensory fibers to be recruited before the smaller diameter motor fibers. The H-reflex is recorded when the electrical stimulation of the Ia afferents causes enough neurotransmitter release via depolarization of the afferent terminals leading to a depolarization of alpha motoneurons. Consequent neurotransmitter release at the neuromuscular junction leads to depolarization and muscular contraction, which is recorded as the H-reflex (Zehr, 2002). The H-reflex has long been reported to be a measure of α-motoneuron pool excitability due to the direct synaptic connections of Ia afferents and alpha motoneurons

(Angel & Hoffman, 1963). This notion has since proven to be somewhat misleading due to the strong modulatory effects of PSI on the H-reflex.

Pre-Synaptic Inhibition and the Hoffmann Reflex

Due to the direct anatomical synaptic connection between Ia afferents and alpha motoneurons, the H-reflex has been examined in exercise and motor control studies where neural adaptations relating to motoneuron excitability are of interest. However, synaptic connections between Ia afferents and α-motoneurons are subject to powerful adjustment through PSI. Postsynapic inhibition/excitation can also alter the H-reflex, however it also simultaneously alters the EMG level of the recorded muscle. Presynaptic inhibition on the other hand changes the H-reflex while maintaining a constant level of EMG. The effects of PSI on the H-reflex in humans have been known for almost twenty years (Morin, Pierrot-Deseiligny, & Hultborn, 1984), and have been extensively supported (see reviews in Zehr, 2002; Stein 1995).

PSI is believed to be mediated by inhibitory interneurons acting on Ia afferent terminals, causing a reduction in neurotransmitter release and thereby reducing motoneuron depolarization induced by Ia activity (Zehr, 2002). Originally demonstrated in the cat by Frank and Fourtes (1957), PSI enables afferent transmissions to be altered without a subsequent effect on the postsynaptic membrane. Consequently it is not possible to determine if H-reflex amplitude modulations are due to motoneuron pool excitability without specifically controlling for and testing the influence of presynaptic inhibition.

Several factor are known to influence presynaptic inhibition of the H-reflex. These include, but are not limited to, peripheral afferent feedback from muscle spindles, Golgi tendon organs, and mechanoreceptors, as well as descending supraspinal commands (Zehr, 2002). The H-reflex can be modulated in a variety of ways that need to be carefully controlled for in order to have any degree of certainty that presynaptic inhibition is not an influence.

In humans, PSI of the H-reflex can be initiated and measured by heteronomous afferent activation (Misiaszek, 2003). This afferent activation can be elicited through vibration (Iles & Roberts, 1987), and electrical stimulation (Morin et al, 1984) of heteronomous musculature. H-reflex modulation hypothesized to occur via presynaptic mechanisms has been shown through a host of paradigms, including changes in posture (Angulo-Kinzler, Mynark, & Koceja, 1998), passive movement of ipsilateral and contralateral limbs (McIlroy, Collins, & Brooke, 1992; Cheng, Brooks, Misiaszek & Staines, 1998) use of the Jendrassic manoeuvre (Zehr & Stein, 1999a), as well as others (see Stein, 1995; Zehr, 2002; and Misiaszek, 2003 for more comprehensive reviews). Several exercise studies have also reported changes in the H-reflex due to physical activity, although none of these studies have accounted for PSI.

Exercise studies and the H-reflex

Adaptive plasticity in human reflex pathways due to training has been examined using the H-reflex in a number of different situations with conflicting results. In lieu of consistent methodologies across studies, these discrepancies may be due to the sensitive of the H-reflex to the effects of presynaptic inhibition.

However, to date no exercise study has directly examined the degree to which presynaptic inhibition influences measures of the H-reflex after strength training.

Casabona, Polizzi and Perciavalle (1990) found that athletes trained for explosive movements (volleyball players and sprinters) presented a reduced Hmax:Mmax ratio in the soleus and lateral gastrocnemius muscles upon electrical stimulation of the tibial nerve. The authors concluded that this effect could be due to lesser synaptic strength of type Ia excitatory afferents on small and intermediate motoneurons in the soleus and lateral gastrocnemius motoneuron pools. This implies that explosively trained subjects may be genetically predisposed to have a weaker synaptic connection between Ia afferents and small motoneurons, or it could be a training induced phenomenon which results in a small motoneuron to large motoneuron transformation. Seemingly in conflict with these results Perot, Goubel, and Mora (1991) found that the Hmax:Mmax ratio was also reduced after eight weeks of endurance training. To confuse the issue even more reduced Hmax:Mmax ratios in the soleus have even been found after 20 days of bed rest (Yamanaka et al. 1999), and in highly trained ballet dancers (Nielsen, Rone, & Hultborn, 1992). Voigt, Chelli and Frigo (1998) have suggested that short term adaptations in the H-reflex amplitude disappear during chronic training. This hypothesis has yet to be substantiated as different methodologies utilized across studies in this area make interpretation of available data difficult. However, it would seem odd that a seemingly acute adaptation of a reflex pathway would shift completely after a certain specified amount of training. This is an area that warrants systematic replication with consistent methodologies.

As mentioned, no training study has examined changes to the H-reflex as a result of chronic training while controlling for and evaluating the effects of presynaptic inhibition. Proposed mechanisms of neural adaptation to chronic physical activity would be further clarified by an understanding of the influence of presynaptic inhibition. Currently there is evidence for supraspinal as well as spinal modulation of presynaptic inhibition.

Supraspinal control of presynaptic inhibition

Soleus H-reflexes are decreased following head and body tilts compared with an upright standing posture (Miziaszek, 2003). Consistent with previous work by Rudomin and Schmidt (1999), this modulation was proposed to be due to involvement of the vestibular system in altering presynaptic inhibition of Ia afferent pathways. Mental rehearsal has also provided evidence for supraspinal control of presynaptic inhibition.

Gandevia, Wilson, Inglis and Burke (1997) found that mental rehearsal increased background EMG in forearm and lower leg muscles while also increasing H-reflex amplitude independent of EMG changes. These findings were suggested to be indicative of changes in presynaptic inhibition of the afferent Ia pathway residing at a supraspinal level. Also in support of supraspinal control of PSI, Hasbroucq, Kaneko, Akamatsu and Possamai (1999) found a decreased H-reflex and MEPs response in the flexor pollicis brevis muscle during the foreperiod of a choice reaction time. The authors concluded that mental preparation is simultaneously implemented by an increase of presynaptic inhibition and a reduction of the excitability of the corticospinal tract.

Spinal level control of presynaptic inhibition

Frank and Fourtes (1957) were the first to provide evidence of presynaptic inhibition residing at the level of the spinal cord in the cat, and shortly thereafter this was investigated by Eccles and colleagues (Eccles, Schmidt & Williams, 1962). These investigators noted that activation of distant muscle afferents led to presynaptic inhibition of Ia afferents, and subsequently depression of the H-reflex. The effect of presynaptic inhibition due to stimulation of heteronymous muscle afferents in man has since been documented (Iles & Roberts, 1987).

Modulation of presynaptic inhibition is also implicated in the control of afferent feedback from the legs during locomotion although some have argued against this being mediated at the level of the spinal cord. Gosgnach, Quevedo, Fedirchuck & McCrea (1999) have shown that inducing fictive locomotion in the decerebrate cat results in tonic presynaptic inhibition of Ia afferents prior to movement. This implies that spinal cord circuitry can affect the level of presynaptic inhibition. It should be noted that some evidence has been presented that contradicts these findings (Misziaszek, De Serres, Stein, Jiang & Pearson, 2000).

Presynaptic inhibition might also be a factor in spinally mediated afferent modulations during voluntary locomotion. Previous studies have suggested this as far back as 1986 when it was established that the H-reflex is depressed when walking compared to standing (Capaday & Stein, 1986). Ferris, Aagaard, Simonsen, Farley & Dyhre-Poulsen (2001) have also recently demonstrated evidence suggesting spinal modulation of the stretch reflex during human locomotion by assessing soleus H-reflex gains over a range of muscle activity levels during running and walking. The benefits of increased presynaptic inhibition during running versus walking are currently not clear. Ferris et al., (2001) suggest that the nervous system might use presynaptic inhibition during locomotion to produce a relatively constant H-reflex response independent of muscle activation and rely on fusimotor activity to adjust the stretch reflex response to different gaits.

Presynaptic inhibition appears to have both spinal and supraspinal levels of control. The relative importance of these two sources remains unclear. However, while some evidence exists regarding the role of PSI during locomotion, none exists in regards to the role of PSI in the development of strength. The following section will review some proposed neural mechanisms for strength gains due to chronic physical activity.

Proposed Neural Mechanisms Due to Chronic Physical Activity and Strength Increases

Despite strong evidence indicating that neural factors mediate changes in strength, there has been less progress in elucidating the specific mechanisms responsible for these adaptations. Explanations are general and the evidence for proposed mechanisms are vague and incomplete. Neuromuscular adaptations are likely to vary across conditions, but in general, have been related to maximizing muscle activation, the specificity of the neural drive, and the pattern of neural drive (Sale, 1988; Enoka, 1997). As well, the influence of presynaptic inhibition on influencing these neural adaptations has not yet been systematically examined. As previously discussed, there is ample evidence that the H-reflex is modulated via presynaptic inhibition. Since there is also evidence (albeit with inconsistent methodologies and a failure to control for the effects of presynaptic inhibition) that the H-reflex is modulated with chronic physical activity, it leads one to the conclusion that presynaptic inhibition may have influenced the findings in previous exercise studies. The following section will review mechanisms of neuromuscular adaptations to physical activity and briefly discuss the possible influence of PSI.

Maximizing muscle activation

If an individual is unable to voluntarily activate a muscle maximally then improving his capacity to do so will increase strength. While there is variability from person to person and between muscle groups, normally active persons usually find it difficult to maximally activate musculature during a voluntary contraction (Enoka & Fuglevand, 1993). However, the degree of muscle activation appears to change with training. The degree of neuromuscular recruitment and muscle activation has also been found to differ between concentric, eccentric and isometric contractions with no clear understanding as to why this occurs (Kay, St Clair Gibson, Mitchell, Lambert & Noakes, 2000). The maximality of a muscle contraction can be tested via the twitch interpolation technique, originally described by Merton (1954) (for a recent review see Herbert and Gandevia, 1999). Allen, Gandevia, and McKenzie (1995) found that subjects could maximally activate the elbow flexors in 25% of the trials, and that maximum voluntary activation ranged from 90.3% to 99.8% in the remaining trials.

Alternatively, measuring transverse relaxation time of muscle water with magnetic resonance imaging is also a highly sensitive index of muscle activation (Fisher, Meyer, Adams, Foley, & Potchen 1990). Fisher and colleagues (1990) established that maximum voluntary contraction torque could be achieved by electrical stimulation of 71% of the cross sectional area of the quadriceps femoris. These observations suggest that not all muscle are activated during a maximum voluntary contraction. There is evidence to suggest that training may influence the degree of muscle activation and therefore the increase in I EMG that is accompanied with initial strength increases may be related to the degree of motor unit activity.

Maximum isometric force has been found to increase significantly within two testing sessions in both young and elderly participants (9 and 13 %

respectively). This strength increase was accompanied by an increase in maximum discharge rates of motor units (Patten, Kamen, Rowland, & Du, 1995). With such few training sessions it is unlikely that any hypertrophic adaptations occurred, and thus neural adaptations are the likely explanation. Similarly, Leong, Kamen, Patten, and Du (1995) compared motor unit discharge rates in the rectus femoris muscle of elderly weightlifters with those of age-matched controls. For a maximum voluntary contraction the discharge rates were significantly greater for the weightlifters, indicating that strength training appears to evoke rapid, sustainable increases in the maximum discharge rates of motor units. A study by

McCartney, Moroz, Garner, and McComas (1988) found that subjects with various muscular dystrophies could not fully activate the elbow flexor muscles, (as measured by twitch interpolation), however, after nine weeks of resistance training 75% of subjects were able to fully activate their trained muscle. The mechanisms responsible for maximizing muscle activation are not clear. It is possible that changes in presynaptic inhibition may facilitate the increased motor unit discharge rates and motor unit recruitment to enhance maximal activation following chronic physical activity.

Although evidence of altered presynaptic inhibition following chronic physical activity is lacking, some findings can be interpreted as supportive for this possibility. For example, the H-reflex is facilitated about 100 ms before the onset of the I EMG activity in the tested muscle during voluntary movement (Coquery & Coulmance, 1971). This facilitation of the H-reflex may reflect a decreased presynaptic inhibition. A change in the general excitability of spinal systems as an individual prepares to execute a movement, may increase the possibility of maximal contractions. Therefore, modulation of presynaptic inhibition may be advantageous in the development of maximal force via facilitation of maximal motor unit activity.

Specificity

Performance improvements are highly specific to the training imposed. Specific adaptations have been shown to exist with respect to the type of muscular contraction and velocity of contraction. Eccentric contractions have received special attention due to their unique properties, while evidence obtained from intended contractions and cross education studies also support the existence of task specific neural adaptations.

When an individual performs a strength-training program, increases in strength are greatest for tasks that are identical to the type of muscular contraction (Higbie, Cureton, & Warren, 1996), speed of contraction (Almasbakk & Hoff, 1996), and even the specific posture that was employed during the training program (Wilson, Murphy & Walshe, 1996). This does not imply that there are *no* adaptations beyond the exact training methods used to cause increases in performance, rather the improvements are stronger the more closely the testing protocol mimics the actual training. Out of the 4 possible muscular contractions (concentric, isometric, eccentric, and isotonic), eccentric contractions have received special attention.

Eccentric contractions

Nardone, Romano and Schiepati (1989) discovered that eccentric contractions display altered patterns of motor unit recruitment compared to other contractions. They reported that eccentric contractions may involve the selective recruitment of high-threshold motor units. Furthermore, there is reduced muscle activation during maximal eccentric contractions, altered recruitment order of motor units during submaximal eccentric contractions, and a decrease in the size of the potentials evoked in muscle by transcranial and peripheral nerve stimulation during eccentric contractions (Enoka, 1996). As well, Abbruzzese, Morena, Spadavecchia and Schieppati, (1994) found that both transcranial magnetic and electrical stimulation evoked reduced amplitude potentials in brachioradialis and biceps brachii during eccentric contractions compared to isometric contractions. This occurred despite equal levels of background I EMG. The same study also found that amplitudes of H-reflexes observed in brachioradialis decreased during eccentric contractions and increased during concentric contractions. Collectively, these findings suggest that eccentric contractions require unique activation patterns as suggested previously by Enoka (1996). To date no study has examined if eccentric contractions are associated with modulation of presynapic inhibition. Perhaps the modulation of presynaptic inhibition plays a role in the unique activation patterns observed in eccentric contractions. Intended contractions have also provided strong support for the concept of neurally mediated specificity of training.

Intended contractions

A clever study by Behm and Sale (1993) examined both the specificity of velocity and the effect of the *intended* contraction versus the actual movement velocity in subjects training on isokinetic devices. Subjects performed quick (5.23 rad/s) unilateral contractions with the dorsiflexor muscles for 16 weeks. However, one foot of each subject was restrained so that only isometric contractions were possible. After training, subjects were told to make quick movements with both feet, at various velocities. Both legs showed the greatest training adaptation at 5.23 rad/s, indicating that the intended movement velocity during training was more decisive than actual movement velocity for the specific effect on peak torque. This suggests that descending supraspinal motor commands play a strong role in determining task specificity. Other studies have shown a lack of transfer between training with isometric contractions and performance with dynamic contractions (Young and Bilby, 1993; Wilson, Young, Hurnall, Hood & Steinbronn 1994), however, in these instances the *intended* contraction was always the actual end result. Finally, the phenomenon of cross education has shown a great deal of evidence for neurally mediated specificity due to training.

Cross education

Numerous studies have reported that chronic unilateral motor activity can affect performance of the homologous muscles in the contralateral limb. This phenomenon, known as cross education, occurs during both improvements in strength and the learning of motor skills, and displays specificity to the training of the opposite limb (Hortobagyi, Scott, Lambert, Hamilton, & Tracy, 1999). Structural and functional adaptations due to resistance training are specific to the exercised musculature and the greatest training effect is displayed when testing procedures matches the training protocol (Sale, 1988). However, cross education of the contralateral limb displays evidence of neuromuscular adaptations *despite* never being involved in the tasks that are performed during training.

Whether it be a fine motor skill or a simple resistance training test, cross education appears to be confined to the homologous musculature of the contralateral limb. As an example, Hortobagyi et al., (1999) found no changes in hand grip strength after six weeks of unilateral knee extension training although knee extension strength increased markedly in both trained and contralateral, untrained legs.

Contralateral strength gains are greatest when the mode of testing mirrors the training protocol for the ipsilateral limb. Hortobagyi et al., (1997) compared cross education effects following 12 weeks of isokinetic training of the knee extensors with either concentric or eccentric contractions. Concentrically trained subjects displayed greater (30%) strength increases in the contralateral limb than the eccentrically trained group (18%) when tested concentrically. Conversely, eccentrically trained subjects displayed greater (77%) strength increases than the concentric training group (10%) when tested eccentrically. It was previously discussed that eccentric contractions appear to display unique neural activation characteristics, interestingly voluntary eccentric unilateral training has been shown to induce greater cross education effects compared to concentric or isometric training (Hortobagyi, Lambert & Hill, 1997).

Several neural mechanisms have been proposed for cross education, including diffusion of impulses between hemispheres, coactivation via bilateral corticospinal pathways, afferent modulation (influenced by the cross extension reflex), and postural stabilization or improved coordination (see Zhou, 2000, for review). However, similar to the literature on neural adaptations to strength training, few studies have directly examined supraspinal activation as it relates to cross education, and none have studied evoked spinal motoneuron responses to examine spinal adaptation mechanisms in order to elucidate the precise locus of change.

The proposed mechanism of cross education involving afferent modulation might be especially influenced by presynaptic inhibition, although this has yet to be examined. Afferent modulation, possibly influenced by the cross extensor reflex, may play a role in cross education suggesting that modulation of presynaptic inhibition may also be involved due to the strong effect of presynaptic inhibition from flexor to extensor Ia afferents (Iles & Roberts, 1987).

Considering the preceding evidence it appears clear that neuromuscular adaptations to exercise can display large degrees of specificity. How this specificity is achieved has yet to be determined. However, if presynaptic inhibition can be specific to a trained task, contraction type or velocity of contraction then modifying the level of presynaptic inhibition may allow for a greater expression of muscle activation for a *particular* task. Perhaps descending motor commands that are "trained" can selectively alter the level of presynaptic inhibition to specific muscles? Or alternatively, perhaps specific spinal reflex pathways such as those involved in reciprocal inhibition experience selective modulation via presynaptic inhibition, allowing for optimization of muscular contraction between agonists and antagonist muscles. The latter suggestion is related to the pattern of neural drive.

Pattern of Neural Drive

Chronic physical training may cause changes within the nervous system that allow better co-ordination of relevant musculature, thus positively affecting the net torque exerted about a joint. The third proposed area of neural adaptation involves synchronization of motor unit discharge. and modulating the distribution of activation among muscle groups.

Motor Unit synchronization

Milner-Brown, Stein, and Lee (1975) first suggested that increased motor unit synchronization may increase muscle strength. This was based on the observation that six weeks of strength training increased the amount of motor unit synchronization assessed by surface EMG. However, it is not clear how an increase in motor unit synchronization is responsible for increasing the force of voluntary contractions and there is contradicting evidence. Contrary to the notion of motor unit synchrony increasing muscle force, force output was greater with asynchronous motor unit activation than with synchronous activation in the cat (Rack and Westbury, 1969). The validity of using EMG for assessing motor unit synchronization has also come under scrutiny (Yue, Nordstrom and Enoka, 1995a). However, the more accurate cross-correlogram method (determining the correlation between firing pattern of two neurons) also suggests that synchrony of motor units varies from person to person (Nordstrom, Fuglevand & Enoka, 1992), as well as from muscle to muscle (Enoka, 1997). Unfortunately the role of increased synchrony in enhancing force output is unclear. However, the significance of changes in motor-unit synchronization may be important in that it indicates changes in neural connectivity among last-order interneurons and motor neurons (Kirkwood & Schmid, 1991).

Muscle co-ordination and co-contraction

Maximizing the torque about a joint depends not only on full activation of agonists, but also on proper de-activation of antagonists. In an extreme case, when agonist and antagonist muscles of identical joint-movement capabilities are maximally co-activated, net torque will be zero. Therefore, to maximize muscle torque about a joint it is advantageous to minimize co-activation of antagonist musculature. The co-contraction of antagonists may provide stabilization during ballistic and precise movements and is present in subjects that are untrained in the task. However, this co-contraction may also impair maximal muscle activation via the actions of reciprocal inhibition (Sale, 1988). Subjects introduced to a novel and complicated task may therefore not be capable of exerting maximal force. Carolan and Cafarelli (1992) found that an increase in knee extensor strength was accompanied by a marked reduction in the level of co-activation of the knee flexor muscles. The mechanism for this adaptation is unknown, however, modification of the reciprocal inhibition spinal reflex pathway via altered presynaptic inhibition may play a factor.

Conclusion

The evidence for neural adaptations due to chronic physical activity is strong and supports that neural adaptations are present during strength training and cross education. Mechanisms for these neural adaptations are possibly related to altering the degree of muscular activation and specificity and/or pattern of neural drive. However, the loci of control of these proposed mechanisms are not well understood. The H-reflex has been used in an attempt to clarify neural adaptations during chronic physical activity, and wrongfully reported to convey information regarding the excitability of alpha motoneuron pool excitability in exercise studies. However, methods have been inconsistent across studies, and no one has accounted for the strong modulatory effects of presynaptic inhibition on measures of the H-reflex making interpretation of previous results difficult. Currently there is a paucity of knowledge surrounding the role of presynaptic inhibition in eliciting neural adaptations due to strength training and the cross education effect. A better understanding of the role of presynaptic inhibition due to chronic physical activity would further our understanding of human motor control.

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