Effects of enhanced cutaneous sensory input on interlimb strength transfer of the wrist extensors

Trevor S. Barss1,2,3 | Taryn Klarner1,2,3,4 | Yao Sun1,2,3 | Kristy Inouye1 | E. Paul Zehr1,2,3,5,6

1Rehabilitation Neuroscience Laboratory, University of Victoria, Victoria, BC, Canada
2Human Discovery Science, International Collaboration on Repair Discoveries (ICORD), Vancouver, BC, Canada
3Centre for Biomedical Research, University of Victoria, Victoria, BC, Canada
4School of Kinesiology, Lakehead University, Thunder Bay, ON, USA
5Division of Medical Sciences, University of Victoria, BC, Canada
6Zanshin Consulting Inc., Victoria, BC, Canada

Correspondence
E. Paul Zehr, Rehabilitation Neuroscience Laboratory, PO Box 3010 STN CSC, University of Victoria, Victoria, BC, Canada V8W 3P1.
Email: pzehr@uvic.ca

Funding information
This work was supported by a Grant-in-Aid of Research from the Heart and Stroke Foundation of Canada (BC & Yukon) and NSERC Discovery Grant (to E. Paul Zehr). Funding was also provided by a doctoral fellowship from the Natural Sciences and Engineering Research Council of Canada (NSERC) (to Trevor Barss). As well, funding was provided through doctoral fellowships from the Heart and Stroke Foundation of Canada and the Canadian Stroke Network (to Trevor Barss, Taryn Klarner, and Yao Sun). Funding sources had no involvement in study design, or in data collection, analyses, and/or interpretation.

Abstract
The relative contribution of cutaneous sensory feedback to interlimb strength transfer remains unexplored. Therefore, this study aimed to determine the relative contribution of cutaneous afferent pathways as a substrate for cross-education by directly assessing how “enhanced” cutaneous stimulation alters ipsilateral and contralateral strength gains in the forearm. Twenty-seven right-handed participants were randomly assigned to 1-of-3 training groups and completed 6 sets of 8 repetitions 3x/week for 5 weeks. Voluntary training (TRAIN) included unilateral maximal voluntary contractions (MVCs) of the wrist extensors. Cutaneous stimulation (STIM), a sham training condition, included cutaneous stimulation (2x radiating threshold; 3sec; 50Hz) of the superficial radial (SR) nerve at the wrist. TRAIN + STIM training included MVCs of the wrist extensors with simultaneous SR stimulation. Two pre- and one posttraining session assessed the relative increase in force output during MVCs of isometric wrist extension, wrist flexion, and handgrip. Maximal voluntary muscle activation was simultaneously recorded from the flexor and extensor carpi radialis. Cutaneous reflex pathways were evaluated through stimulation of the SR nerve during graded ipsilateral contractions. Results indicate TRAIN increased force output compared with STIM in both trained (85.0 ± 6.2 Nm vs. 59.8 ± 6.1 Nm) and untrained wrist extensors (73.9 ± 3.5 Nm vs. 58.8 Nm). Providing ‘enhanced’ sensory input during training (TRAIN + STIM) also led to increases in strength in the trained limb compared with STIM (79.3 ± 6.3 Nm vs. 59.8 ± 6.1 Nm). However, in the untrained limb no difference occurred between TRAIN + STIM and STIM (63.0 ± 3.7 Nm vs. 58.8 Nm). This suggests when ‘enhanced’ input was provided independent of timing with active muscle contraction, interlimb strength transfer to the untrained wrist extensors was blocked. This indicates that the sensory volley may have interfered with the integration of appropriate sensorimotor cues required to facilitate an interlimb transfer, highlighting the importance of appropriately timed cutaneous feedback.

KEYWORDS
Cross-education, cutaneous, electrical stimulation, electromyography, plasticity, reflexes, resistance training
Unilateral training for bilateral strength gains has recently been highlighted for its possible use as a rehabilitation strategy during recovery from asymmetrical injuries (Barss, Pearcey, & Zehr, 2016; Farthing & Zehr, 2014; Hendy, Spittle, & Kidgell, 2012). ‘Cross-education’, ‘inter-limb strength transfer’, or the ‘cross-transfer’ effect is a neural adaptation defined as the increase in strength or performance of the untrained contralateral limb after unilateral training (Farthing & Chilibeck, 2003; Lee & Carroll, 2007; Ruddy & Carson, 2013; Scripture, Smith, & Brown, 1894). While its use as an adjunct therapy during rehabilitation from unilateral injury continues to be explored, a major focus of research has shifted into optimizing how unilateral training will be incorporated to maximize strength or performance gains. The idea of “enhanced” sensory integration during unilateral training has recently been explored through the use of mirror box therapy (Howatson, Zult, Farthing, Zijdewind, & Hortobágyi, 2013). It remains unknown if incorporating other sensory modalities (e.g., tactile somatosensory feedback) during resistance training may provide a similar enhancement effect.

While the original work on cross-education by Edward Wheeler Scripture (Scripture et al., 1894) was published over a century ago, its origins stem from Alfred Wilhelm Volkmann (1801–1877) who found that performing unilateral sensory acuity training using a two-point discrimination task, improved performance bilaterally (Volkmann, 1858). This work was not only the first to identify a portion of the phenomenon that would later be coined ‘cross-education’ but also highlights the effect of using cutaneous afferent sensitivity training. It is well established that cutaneous sensory information can have widespread effects in sculpting motor output (Duyens, 1977; Panek, Bui, Wright, & Brownstone, 2014; Zehr & Stein, 1999) by providing accurate perceptual information about joint position and movement proprioception and kinesthesia (Collins & Prochazka, 1996; Collins, Refshauge, & Gandevia, 2000; Collins & KM R. Todd G. Gandevia S., 2005; Proske & Gandevia, 2012). This includes alterations in contralateral muscles with electrical stimulation provided unilaterally to cutaneous nerve branches (Haridas & Zehr, 2003; Zehr, Collins, & Chua, 2001). Previously, electrical stimulation provided to the radial and median mixed peripheral nerves has been shown to alter reciprocal inhibition in the contralateral upper limb. Interestingly, reciprocal inhibition in the contralateral limb was reduced by 16.5% with radial nerve stimulation. However, stimulation of cutaneous branches of each nerve did not alter reciprocal inhibition in the contralateral limb indicating that multiple converging pathways are important to understand interlimb interactions of electrical stimulation (Delwaide & Pepin, 1991). Therefore, one possibility is that providing ‘enhanced’ cutaneous input may interact with mechanisms and pathways responsible for cross-education and alter the transfer of strength to the untrained limb.

Previously, adaptations in spinal reflex pathways have been shown to occur with unilateral training which may contribute to cross-education. On the trained side, previous studies have shown increased H-reflex amplitude (Lagerquist, Zehr, & Docherty, 2006), increased H-reflex amplitude at threshold (Dragert & Zehr, 2011), and increased reciprocal inhibition (Geertsen, Lundbye-Jensen, & Nielsen, 2008). On the untrained side, little evidence of change in H-reflex amplitudes have been noted in the agonist muscle despite an increase in strength (Del Balso and Cafarelli, 2007; Finland et al., 2009; Lagerquist, Zehr, & Docherty, 2006). However, maximal H-reflex amplitude has been shown to be reduced in the antagonist muscle after unilateral plantar flexion training in a neurologically intact group, (Dragert & Zehr, 2011) while spinal reflex excitability and reciprocal inhibition within the untrained more affected tibialis anterior were altered in a poststroke population (Dragert & Zehr, 2013). In recent years, evidence of a cortical contribution to cross-education has been established. Two nonexclusive theories have been proposed: the ‘cross-activation’ and ‘bilateral access’ hypotheses (Aniss, Gandevia, & Burke, 1992; Négyesi et al., 2018; Russmann, Lamy, Shamim, Meunier, & Hallett, 2009). It is clear that the ‘untrained’ motor cortex, ipsilateral to the trained limb, plays a critical role in mediating the cross-transfer effect (Russmann et al., 2009). As well, recent chronic voluntary strength studies using transcranial magnetic stimulation (TMS) and functional magnetic resonance imaging (fMRI) have confirmed that reduced interhemispheric inhibition and increased activation of specific areas in the non-exercised hemisphere are key moderators of cross-education in healthy adults (Geertsen et al., 2008; Hortobágyi, Taylor, Petersen, Russell, & Gandevia, 2003).

Unfortunately, little to no work has explored the role of cutaneous sensory feedback at any level of the nervous system during resistance training. Understanding if cutaneous sensory information can impact strength gains in the trained or untrained limb will provide information toward a unifying model of cross-education. It has previously been suggested that heightened afferent input associated with electrical muscular stimulation plays a key role in neural adaptations to electrically stimulated strength training (Hortobágyi & Maffioletti, 2011). Providing electrical stimulation to the wrist extensor or flexor muscles has been shown to increase activation of the contralateral primary motor cortex, primary somatosensory cortex, premotor cortex, and numerous other areas important in motor control (Blickenstorfer et al., 2009) with bilateral activation of supplementary motor areas (Han et al., 2003). Providing a large sensory volley during unilateral resistance training may interact with many of these same cortical areas that contribute to cross-education.
The addition of ‘enhanced’ somatosensory input to facilitate the transfer of a motor skill has been proposed in an analytic review by Veldman, Maffiuletti, Hallett, Zijdewind, and Hortobágyi (2014) as prolonged low-amplitude somatosensory electric stimulation (SES) with nerve stimulation can have ‘direct’ and ‘crossed’ effects on brain activation, corticospinal excitability, and motor performance which could enhance transfer effects of unilateral training. An initial study indicated that a single session of both unilateral SES applied to the median and radial nerves alone and performance of a visuomotor performance task at the wrist alone improved task performance in both the trained and untrained limbs (Veldman et al., 2015). However, the addition of SES during the visuomotor task did not enhance the transfer to a greater extent and it was concluded they may be mediated by different mechanisms. This is confirmed in a follow-up study which highlighted that 20 min of low-amplitude SES applied to the median and radial nerves alone facilitates interlimb transfer of visuomotor performance. However, a recent pilot study in healthy young adults found a single session of SES paired with a visuomotor task did not improve the transfer of practice-induced skill transfer to the untrained limb of either SES or skill training alone (Négyesi et al., 2018).

Recently, the effect of a single session of unilateral strength training combined with transcranial direct-current stimulation (tDCS) applied to the ipsilateral (untrained) M1 on strength was assessed (Hendy & Kidgell, 2014). Researchers found that strength of the untrained, left extensor carpi radialis (ECR) increased following training of the right ECR with tDCS of the right M1, but not following training of the right ECR with sham-tDCS or tDCS alone. This was accompanied by neural modulation in the ipsilateral M1, including an increase in corticospinal excitability, a decrease in short latency intracortical inhibition (SICI), and an increase in cross-activation during maximal contractions in the right ECR. This provides specific evidence for experimentally induced plasticity (tDCS) and dependent use plasticity (strength training) working together to provide an enhanced effect above resistance training alone.

While studying the modulation of reflexes can be used to probe interlimb neural activity (Burke, Dickson, & Skuse, 1991; Zehr et al., 2004), no study has directly assessed the relative contribution of cutaneous afferent pathways to an interlimb strength transfer protocol. Providing ‘enhanced’ sensory input via electrical stimulation during resistance training would improve strength gains compared with training alone.

### 2 | METHODS

#### 2.1 | Participants

A total of 27 neurologically intact right-handed participants were recruited and randomly assigned to one of three experimental groups. Handedness was determined using a 10-item version of the Waterloo Handedness Questionnaire (WHQ) which ranged from −20 to +20, where a negative score indicates left handedness and a positive score indicates right handedness. The groups included maximal voluntary training (TRAIN) (7 females; 2 males, 22.1 ± 4.2 years, 168.2 ± 9.7 cm, 69.6 ± 11.0 kg, 14.8 ± 4.4 WHQ), cutaneous nerve stimulation only (STIM) (6 females; 3 males, 23.2 ± 2.8 years, 170.8 ± 12 cm, 64.5 ± 13.2 kg, 18.4 ± 2.8 WHQ), or cutaneous nerve stimulation during maximal voluntary contraction (TRAIN + STIM) (5 females; 4 males, 22.4 ± 2.8 years, 175.1 ± 10.8 cm, 70.3 ± 16.1 kg, 15.9 ± 4.0 WHQ). Protocols used in the experiments were approved by the University of Victoria Human Research Ethics Committee and performed according to the Declaration of Helsinki (1964).

#### 2.2 | Experimental procedures

Each participant completed two pretraining (PRE 1, PRE 2) and one posttraining (POST) session during which dependent measures of strength, muscle activation, and cutaneous

| TABLE 1 | Adjusted Strength measures |
|---------|---------------------------|
| **PRE** | **POST** | **POST** | **POST** | **Sig.** |
|         | ADJUSTED | TRAIN | STIM | TRAIN+STIM |
| Right Handgrip | 36.1 kg | 36.8 ± 2.0 kg | 35.2 ± 1.9 kg | 35.5 ± 2.0 kg | NS. |
| Left Handgrip | 35.6 kg | 34.2 ± 2.3 kg | 34.5 ± 2.2 kg | 34.7 ± 2.3 kg | NS. |
| Right Flexion | 85.0 Nm | 82.3 ± 16.8 Nm | 74.2 ± 16.4 Nm | 89.2 ± 18.2 Nm | NS. |
| Left Flexion | 66.9 Nm | 72.8 ± 17.8 Nm | 64.9 ± 17.5 Nm | 73.5 ± 18.1 Nm | NS. |

*Note:* NS. No significant differences between any groups (p > .05).
*Values are adjusted based on analysis or covariance.*
reflex excitability were assessed. Multiple baseline sessions
were used to account for learning effects. During these ses-
sions, tests were performed in the same order and under the
same environmental conditions (i.e., temperature, noise,
lighting, and participant position) and session time of day
were kept as consistent as possible as established in previous
research (Dragert & Zehr, 2013; Lagerquist, Zehr, Baldwin,
Klakowicz, & Collins, 2006; Zehr, 2002). Participants com-
pleted training in the right arm only within their specified
group 3x/week for 5 weeks, most commonly on Monday,
Wednesday, and Friday. The training program was progres-
sive in nature, beginning with four sets of eight repetitions
and increasing in volume by one additional set each training
day, up to a maximum training volume of six sets of eight
repetitions. The training program included a taper down to
four sets of eight contractions over the final two training
sessions to ensure recovery from training prior to posttest
session. Each training session consisted of six sets of eight
repetitions of the specified training. All training sessions
were performed in a supervised laboratory setting while
sitting with the right arm placed in a secured custom-built
forearm brace. For all training sessions, the forearm was se-
cured in place with joint angles being maintained throughout
training. The TRAIN group protocol consisted of unilateral
maximal voluntary contractions (MVCs) of the right wrist
extensors (Figure 1a). The STIM group received only cu-
taneous stimulation (2 times radiating threshold [RT] for
3 s at 50Hz) of the superficial radial (SR) nerve at the right
wrist. Stimulation was delivered at the same relative inten-
sity, duration, and timing across individuals and groups. This
condition was chosen to provide a sham training condition
as no motor response was evoked with SR stimulation. The
TRAIN + STIM group protocol included MVCs of the right
wrist extensors while the SR nerve was stimulated. MVCs of
the wrist extensors were initiated upon sensation of the SR
stimulation and released when stimulation stopped.

2.3 | Strength – maximal voluntary
contractions

MVCs of wrist extension, wrist flexion, and handgrip
were assessed bilaterally at PRE1, PRE2, and POST. Three
MVCs were recorded for each task bilaterally and held for 3 s each with 1 min of rest between contractions. All
MVCs were recorded in a seated position with the non-
tested arm placed in the participant’s lap. Wrist extension
and flexion were assessed in a custom-built forearm sup-
port attached to a Gamma Sensor force transducer (ATI
Industrial Automation, Model FT06598). The forearm
was secured, and all joint angles were maintained across
testing time points. Handgrip MVC was recorded via dy-
namometer in the same seated position at an approximate
45° angle away from the body. All settings were main-
tained through the data collection process. Verbal encour-
agement was provided by the tester in a similar fashion
for all measures and time points. Although wrist exten-
sion was the primary strength measure, forearm strength
assessments were performed in a manipulandum to as-
sess for transfer of strength to the untrained limb across
multiple tasks using the same musculature (Figure 1).
For each task, the contraction with the highest peak force
was used for comparison at each time point. Participants
were familiarized with the isometric strength tasks prior
to MVCs and completed a standardized warm-up prior to
each session.

2.4 | Muscle activation – electromyography

Electromyography was recorded bilaterally from the mus-
cle bellies of the flexor carpi radialis (FCR) and extensor
carpi radialis (ECR) in the forearm. After the skin was
cleaned with alcohol wipes, surface electrodes (Thought
Technologies Ltd.) were placed in a bipolar configuration
on the skin using a 2-cm interelectrode distance, oriented
along the fiber direction, in accordance with SENIAM
procedures (Hermens, Freriks, Disselhorst-Klug, & Rau,
2000). A reference electrode was placed on the medial epi-
condyle to serve as a common ground for the EMG signal.
Electrodes were placed in the same position at each testing
session. Landmarking measurements were recorded at the
initial pretest to ensure correct placement at each subsequent
time point. During MVCs a 0.5 s window of time around
peak muscle activity was used to calculate the peak mean
absolute value (MAV). The peak MAV associated with the
corresponding peak MVC from each baseline and posttest
measure was used for assessment.

EMG was preamplified 5000x (GRASS P511, AstroMed,
Inc.) and band-pass filtered 100–300 Hz. The output was sent
to the A/D interface (National Instruments Corp. TX, USA)
where it was converted into a digital signal and sampled at 1,000 Hz using custom-built continuous acquisition software (LabVIEW, National Instruments) and stored to a computer for off-line analysis.

2.5 | Sensory stimulation

2.5.1 | Cutaneous reflexes

Cutaneous reflexes were evoked via stimulation of the superficial radial nerve (SR) innervating the dorsum of the hand. Electrodes for SR nerve stimulation were placed just proximal to the radial head (Zehr & Chua, 2000; Zehr & Duysens, 2004). Appropriate stimulation location was checked by ensuring that radiating paresthesia was evoked into the appropriate cutaneous innervation area of the SR. To assess cutaneous reflexes, trains of 5 x 1.0 ms pulses at 300 Hz were delivered at an intensity of 3 x RT via isolated constant current stimulator (Grass S88 stimulator with SIU5 stimulus isolation and a CCU1 constant current unit AstroMed-Grass Inc., Canada). To provide the same relative intensity of stimulation between participants, a multiple of the radiating threshold (RT) was used. RT was determined as the minimum intensity that evokes a clear radiating sensation in the entire perceptive field of the SR nerve innervates (Brooke et al., 1997; De Serres, Yang, & Patrick, 1995; Delwaide, Crenna, & Fleron, 1981; Duysens, Trippel, Horstmann, & Dietz, 1990). Cutaneous reflexes were assessed during graded ipsilateral contractions of the wrist extensors of 5, 10, 25, and 50% of EMG<sub>max</sub>. The level of background activity significantly modulates cutaneous responses such that as activity increases, the reflex response also increases in a linear fashion (Aniss et al., 1992; Burke et al., 1991; Komiyama, Zehr, & Stein, 2000; Van Wezel, Ottenhoff, & Duysens, 1997; Yang & Stein, 1990).

2.5.2 | Enhanced sensory stimulation

For the groups that received enhanced cutaneous stimulation during their training, trains of 1.0 ms pulses at 50 Hz were delivered at an intensity of 2 x RT for 3 s (equal duration to training MVCs). Fifty Hz frequency was chosen as it most closely resembles the sensation of surface pressure on the back of the hand during wrist extension. Cutaneous stimulation intensity was set low enough to producing a buzzing or fluttering sensation in the innervation area without producing measurable changes in motor output (Zehr, 2006; Zehr & Stein, 1999). Nonnoxious stimulation intensities were found for each participant to ensure nonnociceptive pathways were stimulated.

2.6 | Data analysis

EMG data were analyzed for background amplitudes and reflexes using custom-written software program (MATLAB, The Mathworks, Inc.). The net effect of cutaneous input on motoneuron excitability is inferred from surface EMG recorded in the muscle of interest. Modulation of ongoing activity can be seen by averaging data that are time locked to the known stimulus. The reflex response was determined by averaging 20 sweeps of SR stimulation then subtracting the prestimulation activity, leaving reflex activity to be assessed (Brooke et al., 1997; Zehr & Stein, 1999). This technique allows for measurement of both facilitatory and inhibitory responses (Baken, Dietz, & Duysens, 2005). Monitoring the effect of cutaneous stimulation on muscle activity provides reasonable temporal resolution to accurately document the amplitude and latency of the responses (Brooke et al., 1997). The stimulus artifact was removed from the subtracted reflex trace and data were then low-pass filtered at 30 Hz using a dual-pass, fourth-order Butterworth filter.

Initially, reflexes were quantified as the average cumulative reflex over 150 ms following stimulation. This value is determined as the integral obtained at 150 ms divided by the time interval of integration to yield the overall reflex effect. If the value is positive, overall facilitation has occurred; if the value is negative, overall inhibition has occurred. This quantification method allows for interpretation of modulation of reflex pathways from spinal, brainstem, and supraspinal centers (Komiyama et al., 2000). Triphasic responses at varying delay latencies, which can be excitatory or inhibitory, were recorded bilaterally in the ECR and FCR during graded ipsilateral wrist extension contractions. (De Serres et al., 1995; Duysens, Tax, Trippel, & Dietz, 1992; Gibbs, Harrison, & Stephens, 1995; Jenner & Stephens, 1982; Van Wezel et al., 1997; Yang & Stein, 1990). An early latency component was identified as occurring before 75 ms, the middle component between 70 and 120 ms, and the late component measured after 120 ms (Brooke et al., 1997; Duysens et al., 1992). The time window for each latency was visually chosen around the peak response which was said to be a significant reflex if the peak was 2 standard deviations outside of the background muscle activity (Zehr & Chua, 2000). Within each time window, all data were averaged together, and a 10 ms band around the maximum response was used to obtain a single value. All reflex measures were normalized to the corresponding maximally evoked motor response (M<sub>max</sub>).

2.7 | Statistics

Using commercially available software (SPSS 20.0, Chicago, IL), strength data were analyzed using a one-way ANCOVA.
with the between-subjects factor of group, using pretest scores as the covariate and posttest scores as the dependent variable. This was performed due to baseline differences in strength between groups in both the right and left arms. Peak muscle activity, PT, and RT data were analyzed using a between-within 3 (Group; TRAIN, STIM, TRAIN + STIM) x 2 (Time; PREavg, POST) ANOVA with each muscle tested separately. Background muscle activity and cutaneous reflex data were analyzed using a between-within 3 (Group) x 2 (Time) x 4 (Contraction intensity; 5, 10, 25, 50% EMGmax) ANOVA. For cutaneous reflex data, a priori comparisons within each training group were also assessed by a 2 (Time) x 3 (Contraction intensity) repeated-measures ANOVA. Mmax data were analyzed using a between-within 3 (Group) x 2 (Time) ANOVA. For second set of measures ANOVA. Mmax was used to normalize peak muscle activity and reflex measures at each time point. If significant main effects or interactions were detected, simple main effects analysis followed using one-way ANOVA and LSD post hoc or pairwise comparisons where appropriate. A Cohen’s d value of effect size was determined for all significant results. Assumptions for ANOVA and paired-samples t tests were evaluated for parametric tests for a within-subject design. Statistical significance was set at \( p \leq .05 \).

3  |  RESULTS

3.1  |  Strength – maximal voluntary contractions

Results indicate that 5 weeks of voluntary wrist extension training increases strength in the trained wrist extensors regardless of cutaneous stimulation. One-way ANCOVA indicated a significant effect of GROUP (\( F_{(2,23)} = 4.809, p = .018 \)). Adjusted wrist extension torque at POST was significantly higher than STIM in both the TRAIN (85.0 ± 6.2 Nm vs. 59.8 ± 6.1 Nm; \( p = .004 \)) and TRAIN + STIM Groups (79.3 ± 6.3 Nm vs. 59.8 ± 6.1 Nm; \( p = .037 \)) with no difference between TRAIN and TRAIN + STIM (\( p = .538 \)) (Figure 2).

In the untrained contralateral limb, results indicate that the TRAIN group increased peak wrist extension torque after the intervention. One-way ANCOVA indicated a significant effect of GROUP (\( F_{(2,23)} = 5.101, p = .015 \)). After the intervention, adjusted wrist extension torque was significantly higher in the TRAIN group compared with STIM (79.3 ± 6.3 Nm vs. 59.8 ± 6.1 Nm; \( p = .037 \)) with no difference between TRAIN and TRAIN + STIM (\( p = .538 \)) (Figure 2).

There were no significant differences in peak strength after training for any group during peak handgrip and wrist flexion contractions (\( p > .05 \)) (Table 1).

3.2  |  Peak muscle activation

After 5 weeks of voluntary wrist extension training there is a differential response in peak muscle activation of the
trained ECR between TRAIN and TRAIN + STIM compared with STIM only (Figure 3). Repeated-measures ANOVA indicated a significant GROUP x TIME interaction (F(2,23)=3.816, p = .037). Pairwise comparisons indicate significant reduction in peak muscle activation for STIM after the intervention (9.2 ± 4.0 vs. 7.7 ± 3.4; p = .032). Pairwise comparisons indicate there was no significant difference in peak muscle activation after the training intervention for TRAIN or TRAIN + STIM (p > .05).

Results of ANOVA indicate no differences in peak muscle activation of the trained ECR for handgrip or wrist flexion for any group in the untrained limb (Table 2). Results of ANOVA indicate no differences in peak muscle activation of the FCR for wrist extension, flexion, or handgrip in either limb after the intervention (p > .05).

### 3.3 | Maximally evoked motor responses (M_max)

Results indicate maximally evoked motor responses (M_max) were similar across time points providing a valid normalization technique for EMG and reflex measures. A 3 x 3 repeated-measures ANOVA indicated a significant effect of GROUP in the right FCR (F(2,24)=4.083, p = .030), left FCR (F(2,24)=5.367, p = .012), and left ECR (F(2,24)=3.398, p = .050). Group differences were expected as there were significant differences in baseline strength between groups. There was a significant main effect of TIME in the left ECR only (F(2,48)=4.057, p = .024). Pairwise comparisons indicate that PRE2 was significantly lower than both PRE1 (1293.6 ± 67.9 µV vs. 1388.5 ± 66.2 µV; p = .022) and POST (1293.6 ± 67.9 µV vs. 1395.4 ± 67.9 µV; p = .012). There were no significant differences in M_max over any time point in the right FCR, right ECR, and left ECR (p > .05).

### 3.4 | Background EMG during cutaneous reflexes

Results from the 3 x 2 x 4 ANOVA indicate there were no significant interactions or main effects of group or time for background muscle activity during cutaneous reflex measurement (p > .05) (Figure 4). There was a significant effect of contraction intensity in both the right FCR (F(3,72)=96.724, p < .001) and left ECR (F(3,72)=76.194, p < .001). Pairwise comparisons indicate that there was a significant increase in muscle activity between all levels of contraction in both the right and left ECR (p < .001).

### 3.5 | Cutaneous reflexes

Results from the 3 x 2 x 4 ANOVA assessing ACRE 150, early latency, and middle latency reflexes indicate there were no significant interactions or main effects for GROUP or TIME (p > .05). For ACRE 150 there was a significant main effect of
contraction intensity in both the trained right ($F_{(3,72)}=28.380$, $p < .001$) and untrained left limb ($F_{(3,72)}=21.494$, $p < .001$).

For early latency reflexes there was a significant main effect of contraction intensity in both the trained right ($F_{(3,72)}=78.231$, $p < .001$) and untrained left limb ($F_{(3,72)}=53.081$, $p < .001$).

For middle latency in the untrained left limb there was a main effect of time pooled across contraction intensity and group ($F_{(1,24)}=6.550$, $p = .001$). Results from a priori 2 x 3 ANOVAs for each group indicate no significant interactions or main effects of time for either limb ($p > .05$). There was a significant main effect of contraction intensity in both the trained right ($F_{(3,72)}=5.129$, $p = .003$) and untrained left limb ($F_{(3,72)}=6.427$, $p = .001$) (Figure 5).

For long latency reflexes in the trained right limb there was a significant Contraction x Time Interaction ($F_{(3,24)}=4.487$, $p = .006$). Results from a priori 2 x 3 ANOVAs for each group indicate no significant interactions or main effects of time for TRAIN or STIM ($p > .05$). However, for the TRAIN + STIM group there was a significant Contraction x Time Interaction ($F_{(3,24)}=8.574$, $p < .001$) and time main effect ($F_{(1,8)}=14.201$, $p = .005$). Paired samples $t$ tests indicate a significant difference in reflex amplitude at 25% ($p = .010$) and 50% ($p = .006$) contraction intensities (Figures 6 and 7).

3.6 | Perceptual and radiating thresholds

Results of the 2 x 3 ANOVA indicate that there was no change over time or across group for either perceptual or radiating threshold as no significant interactions or main effects were present ($p > .05$) (Table 3).

4 | DISCUSSION

Unilateral wrist extension training alone (TRAIN) increased peak force output in the trained wrist extensors. Providing ‘enhanced’ cutaneous sensory input via electrical stimulation during training (TRAIN + STIM) led to a similar increase in strength in the trained limb compared with TRAIN. However, the major finding of the current investigation is that providing ‘enhanced’ cutaneous input in the TRAIN + STIM group blocked interlimb strength transfer to the untrained wrist extensors. This is the first study to directly assess the cutaneous sensory contribution to interlimb strength transfer from unilateral resistance training. While it was hypothesized that providing ‘enhanced’ cutaneous input would facilitate the strength gain in the untrained contralateral side, it appears the large sensory volley may have interfered with the integration of appropriate sensorimotor cues required to facilitate an interlimb transfer and improvements in the untrained limb.

4.1 | Absence of interlimb strength transfer with ‘enhanced’ cutaneous input

The group that received the 50 Hz enhanced cutaneous sensory stimulation during the maximal wrist extension training protocol saw no transfer of strength to the untrained limb.
While this result is contrary to our hypothesis, this study highlights the important role of cutaneous afferent feedback during movement tasks.

It remains likely the timing and amplitude properties of the enhanced sensory volley which was not linked to the actual intention to contract interfered with the integration of sensory cues required to transfer strength to the untrained limb. If we consider the human nervous system to exhibit properties of a “Hebbian” synapse with “neurons firing together and wiring together”, providing a mismatched sensory volley may have altered fundamental properties associated with acquisition of novel motor skills (Carson, 2006; Cooper & Donald, 2005). Neurons that release action potentials at the same time have an increased probability of forming synaptic connections, while uncorrelated activity diminishes functional connectivity (Russmann et al., 2009). In typical motor behavior sensorimotor integration is tightly related to motor output and anticipated sensory afference. The compelling observation here that mis-timed sensory input could completely abolish a robust neural transfer effect argues strongly for future work exploring timing.

4.2 | Possible cortical interactions with ‘enhanced’ cutaneous feedback

Providing a large and asynchronous sensory volley during unilateral resistance training may interact with many of the same cortical areas which contribute to cross-education. Changes in multiple cortical areas in both hemispheres have been shown after unilateral training via fMRI (Farthing, Borowsky, Chilibeck, Binsted, & Sarty, 2007; Farthing et al., 2011), positron emission tomography (PET) (Dettmers et al., 1995), and TMS (Boroojerdi, Ziemann, Chen, Butefisch, & Cohen, 2001; Hortobágyi et al., 2003; Kristeva, Cheyne, & Deecke, 1991; Perez et al., 2007). As well, adaptations in connections between primary motor cortices (M1) through transcallosal routes have shown significant plasticity with training (Hortobagyi et al., 2011; Perez et al., 2007). Plasticity of interhemispheric connections mediating cross-education of a simple motor task likely also contribute to such effects of transfer (Hortobágyi et al., 2011). While the current investigation cannot provide insight into areas of possible integration, it is likely that interference with the cortical mechanisms of adaptation interfered with the transfer of strength to the untrained limb.

While this study is unique in that enhanced cutaneous input appears to ‘block’ the interlimb transfer of strength, previous investigators have shown an ability to alter transfer of skill or strength which may provide information regarding possible sites of interference within the current investigation. Unilateral practice of a ballistic finger abduction task has been shown to improve performance by 82% in the untrained...
left hand and was accompanied by bilateral increases in corticospinal excitability (Carroll, Lee, Hsu, & Sayde, 2008). A follow-up paper found bilateral increases in performance and corticospinal excitability after unilateral training of a ballistic motor task (Lee, Kilbreath, Singh, Zeman, & Davis, 2010). Most interestingly, repetitive TMS was applied to the trained and untrained motor cortex to induce a ‘virtual lesion’. This was induced by applying repeated TMS (rTMS) to either the right or left cortex, which reduced performance gains in the contralateral limb. Researchers concluded that early retention of ballistic performance improvements in the untrained limb is due to adaptations in the untrained motor cortex.

The ability to alter the acquisition of a novel motor task through interhemispheric excitability of both sensory and motor areas of the cortex has been shown using a diverse array of tasks. After completing a single unilateral exercise session of pinch grip, participants improved their error of force in the untrained contralateral hand by almost one third. However, when rTMS was applied to the contralateral cortex during the exercise session, no transfer of improved error of force occurred (Goodall et al., 2013). Local tonic cutaneous pain induced by capsaicin cream also interferes with the retention of a newly learned locomotor adaptation task despite the finding that baseline gait and motor acquisition were unimpaired by pain (Bouffard, Bouyer, Roy, & Mercier, 2014). Taken together, these studies indicate that cutaneous sensory information can have dramatic effects on the retention of a novel motor task, and interference of interhemispheric connections may be a contributing site of adaptation. Interestingly, providing a combination of anodal tDCS over M1 during a single session increased force production in the untrained limb, while training with sham tDCS or anodal tDCS alone showed no increase in contralateral strength (Hendy & Kidgell, 2014). This was accompanied with changes in interhemispheric inhibition and corticospinal excitability in the untrained limb in the group that received anodal tDCS. It becomes apparent that learning, regardless of the type or task, can be transferred between hemispheres and directly impacted by altering excitability of the cortex facilitating this transmission.

The main result from the current investigation of a ‘block’ of transfer between limbs may be due to the unilateral training task being paired with a mismatched sensory volley not allowing for appropriate integration of sensory cues for transfer. This is similar to recent work where ‘enhanced’ somatosensory input via prolonged low-amplitude somatosensory electric stimulation (SES) with nerve stimulation was provided. SES stimulation alone has been shown to facilitate transfer of performance of visuomotor task to the untrained contralateral limb (Veldman et al., 2014). However, while SES applied to the median and radial nerves alone as well as visuomotor task training improve performance in both the trained and untrained limbs, little to no additional benefit appears to be provided by applying low-amplitude nerve stimulation during the visuomotor training task (Négyesi et al., 2018; Veldman et al., 2015).

### 4.3 Possible spinal mechanisms with enhanced cutaneous feedback

Here, cutaneous reflexes provided a measure of whether the integration of sensory information from the skin was differentially relayed after resistance training, electrical stimulation, or a combination of both. Once cutaneous mecanoreceptors are activated, sensory information diverges through an unknown number of polysynaptic connections and is integrated at multiple levels of the nervous system, and subsequently modulates ongoing muscle activity (Zehr, 2006; Zehr & Stein, 1999). Within the current investigation there was a significant facilitation of long latency reflex amplitude in the trained limb after the intervention for the TRAIN + STIM group. This demonstrates interaction between the ascending afferent pathways and the sensorimotor connections, facilitating reflex transition after resistance training in the trained limb. This is the first evidence of altered transmission of cutaneous afferent information with resistance training (Figure 6c). The multicomponent EMG response to cutaneous nerve stimulation is thought to arise due to differences in the number of interneurons in a particular pathway within the spinal cord (Zehr, 2006; Zehr & Stein, 1999). Based on the latency of the earliest responses, it is assumed that the earliest components of cutaneous reflexes can be mediated by pathways in the spinal cord (Baken et al., 2005; Dimitrijevic & Nathan, 1969; Zehr & Stein, 1999). Responses at longer latencies are likely the result of transmission through longer pathways which may contain multiple interneurons at multiple levels of the nervous system including cortical contributions (Eccles & Lundberg, 1959; Jenner & Stephens, 1982; Nielsen, Petersen, & Fedirchuk, 1997). As the facilitation was only seen in the group that received cutaneous stimulation during voluntary training, there appears to be an interaction between the two conditions which led to a long-term alteration in excitability. This change in excitability may be related to the lack of strength transfer to the untrained cortex within this group as there were no changes in early and middle latency reflex excitability within this or any group.

While there are no direct connections between motoneurons on the contralateral side, afferents do modulate interlimb coordination (Sherrington, 1910) and are most likely mediated through commissural interneurons (Jankowska, Krutki, & Matsuyama, 2005) and propriospinal paths (Burke, Gracies, Mazevet, Meunier, & Pierrot-Deseilligny, 1992; Jankowska, 2001). Activation of group 1a afferents inhibit contralateral homologous motoneurons (McCrea, 2001) via the Ia inhibitory interneurons (Delwaide & Pepin, 1991). This has been functionally demonstrated as contraction of an
ipsilateral limb has been shown to depress H-reflex amplitude in the homologous contralateral muscle (Carson et al., 2004; Hortobágyi et al., 2003).

There was no change over time and between any of the groups for early latency subtracted reflex amplitude indicating effects are unlikely to be occurring purely in the spinal cord. The current investigation indicates excitability of cutaneous spinal reflex pathways is not altered with unilateral resistance training or repeated sensory volleys evoked with electrical stimulation. Other studies that have found alterations in spinal reflex excitability have done so using techniques such as the H-reflex (Dragert & Zehr, 2011; Lagerquist, Zehr, Baldwin, et al., 2006) or reciprocal inhibition (Dragert & Zehr, 2013; Geertsen et al., 2008) which assess predominantly muscle afferents.

4.4 | Possible measures of altered cutaneous transmission

We thought that receiving cutaneous stimulation at a reasonably strong intensity over a period of 5 weeks may induce some type of chronic adaptation in detection thresholds of cutaneous afferents (Volkmann, 1858). If so, it could be detected by measuring either the PT or RT of the SR nerve at the wrist before and after the intervention. However, after 5 weeks of electrical nerve stimulation applied to the superficial radial cutaneous nerve, there were no differences for any group or time point for PT or RT indicating little adaptation to the detection thresholds or excitability of transmission with repeated activation or resistance training.

4.5 | Controls within the current investigation

A type of sham condition was used as the control group to test whether repeated cutaneous stimulation alone would provide alterations in excitability or strength changes in the trained or untrained limb. Participants who were assigned to the STIM group only received passive SR stimulation which did not produce any motor response. This passive stimulation was the same volume and in the same position as the groups completing voluntary contractions. The participants who only received STIM did not increase in strength, muscle activation, or reflex excitability, indicating that cutaneous stimulation by itself had little to no impact on motor output during voluntary contractions.

4.6 | Limitations and future directions

A limitation in the current investigation was the timing and intensity of electrical stimulation used to ‘enhance’ sensory input. In the TRAIN + STIM group, each maximal wrist extension contraction throughout the training protocol was initiated by the electrical stimulator, therefore, a volley of cutaneous sensory information was provided prior to initiation of the contraction. In contrast, initiating the movement produces the appropriate volley of sensory information based on timing, intensity, and task. Not only was the timing of the stimulation provided mismatched but also the intensity of the stimulation remained constant throughout each contraction for the duration of the study. A more natural type of stimulation would have been to increase the stimulation frequency proportionally as muscle activation increased. As well, the intensity of the sensory volley may have been too high, bombarding sensorimotor cortical areas (Blickenstorfer et al., 2009; Han et al., 2003). This may not have allowed appropriate sensory cues from the wrist extension contractions to be incorporated and shared between hemispheres (Ruddy & Carson, 2013). It remains possible that an appropriately timed stimulus that is more natural and with intensity-dependent frequency and amplitude may have shown different results under the same experimental settings.

Another limitation of the current investigation was the inability to assess the effect cutaneous stimulation to the SR nerve during wrist extension contractions had on the peak force production within each training session. It is possible that the voluntary drive during each training session was altered due to the large sensory volley. However, the similar improvement in strength between the TRAIN + STIM and TRAIN in the trained limb indicates a similar level of effectiveness of the training intervention.

Future research should explore how ‘enhanced’ cutaneous sensory information would have impacted strength transfer if applied to the untrained arm during unilateral training. Results from a recent cross-sectional investigation indicate that enhanced stimulation on the nondominant arm amplifies interneuronal excitability in interlimb cutaneous pathways during a static task (Sun & Zehr, 2019). While this was initially part of the study design, due to constraints on the number of conditions and comparisons it was determined to be beyond the scope of the current investigation. Taking into consideration the results from the current investigation, this may be a valuable approach which could provide the ‘enhancement’ of strength in the untrained limb we initially hypothesized. The results of the current investigation provide a clear example of the specific nature of cutaneous sensory information and the necessity to provide functionally meaningful information to the nervous system.

5 | CONCLUSIONS

Providing ‘enhanced’ sensory input via electrical stimulation during training (TRAIN + STIM) led to similar increases in strength in the trained limb compared with
TRAIN. However, providing a large sensory volley during training in the TRAIN + STIM group alleviated any inter-limb strength transfer to the untrained wrist extensors. It appears that the large mismatched sensory volley may have interfered with the integration of appropriate sensorimotor cues required to facilitate improvement in the untrained limb. Voluntary wrist extension training or repeated electrical stimulation to a cutaneous nerve does not appear to alter cutaneous reflex transmission across contraction intensity or latencies of response. However, receiving a large sensory volley during wrist extension training altered long-latency cutaneous reflex amplitude from inhibition to facilitation at high levels of muscle contraction on the trained right side. While it appears that stimulation delivered under the current conditions without specific timing will not facilitate cross-education, this provides important insight into the important contribution of appropriate cutaneous information on motor output.

ACKNOWLEDGMENTS

The authors wish to acknowledge the participants for their contributions during data acquisition.

CONFLICT OF INTEREST

None of the authors have potential conflicts of interest to be disclosed.

ORCID

Trevor S. Barss https://orcid.org/0000-0003-3466-2750

REFERENCES

Aniss, A. M., Gandevia, S. C., & Burke, D. (1992). Reflex responses in active muscles elicited by stimulation of low-threshold afferents from the human foot. *Journal of Neurophysiology, 67*, 1375–1384.

Baken, B. C. M., Dietz, V., & Duysens, J. (2005). Phase-dependent modulation of short latency cutaneous reflexes during walking in man. *Brain Research, 1031*, 268–275.

Barss, T. S., Pearcey, G. E. P., & Zehr, E. P. (2016). Cross-education of strength and skill : An old idea with applications in the aging nervous system. *The Yale Journal of Biology and Medicine, 89*, 81–86.

Blickestoerfer, A., Kleiser, R., Keller, T., Keisker, B., Meyer, M., Rienner, R., & Kollias, S. (2009). Cortical and subcortical correlates of functional electrical stimulation of wrist extensor and flexor muscles revealed by fMRI. *Human Brain Mapping, 30*, 963–975.

Boroojerdi, B., Ziemann, U., Chen, R., Butefisch, C. M., & Cohen, L. G. (2001). Mechanisms underlying human motor system plasticity. *Muscle and Nerve, 24*, 602–613.

Bouffard, J., Bouyer, L. J., Roy, J.-S., & Mercier, C. (2014). Tonic pain experienced during locomotor training impairs retention despite normal performance during acquisition. *Journal of Neuroscience, 34*, 9190–9195.

Brooke, J. D., Cheng, J., Collins, D. F., McIlroy, W. E., Misiaszek, J. E., & Staines, W. R. (1997). Sensory-sensory afferent conditioning with leg movement: Gain control in spinal reflex and ascending paths. *Progress in Neurobiology, 51*, 393–421.

Burke, D., Dickson, H. G., & Skuse, N. F. (1991). Task-dependent changes in the responses to low-threshold cutaneous afferent volleys in the human lower limb. *Journal of Physiology, 432*, 445–458.

Burke, D., Gracies, J., Mazevet, D., Meunier, S., & Pierrot-Deseilligny, E. (1992). Convergence of descending and various peripheral inputs onto common propriospinal-like neurones in man. *Journal of Physiology, 449*, 665–671.

Carroll, T. J., Lee, M., Hsu, M., & Sayde, J. (2008). Unilateral practice of a ballistic movement causes bilateral increases in performance and corticospinal excitability. *Journal of Applied Physiology, 104*, 1656–1664.

Carson, R. G. (2006). Changes in muscle coordination with training. *Journal of Applied Physiology, 101*, 1506–1513.

Carson, R. G., Rieke, S., Mackey, D. C., Meichenbaum, D. P., Willms, K., Forner, M., & Byblow, W. D. (2004). Excitability changes in human forearm corticospinal projections and spinal reflex pathways during rhythmic voluntary movement of the opposite limb. *Journal of Physiology, 560*, 929–940.

Collins, D. F., & Prochazka, A. (1996). Movement illusions evoked by ensemble cutaneous input from the dorsum of the human hand. *Journal of Physiology, 496*, 857–871.

Collins, D. F., Refshauge, K. M., & Gandevia, S. C. (2000). Sensory integration in the perception of movements at the human metacarpophalangeal joint. *Journal of Physiology, 529*, 505–515.

Collins, D., Refshauge, K. M., Todd, G., & Gandevia, S. (2005). Cutaneous receptors contribute to kinesthesia at the index finger, elbow, and knee. *Journal of Neurophysiology, 94*, 1699–1706.

Cooper, S. J., & Donald, O. (2005). Hebb’s synapse and learning rule: A history and commentary. *Neuroscience and Biobehavioral Reviews, 28*, 851–874.

De Serres, S. J., Yang, J. F., & Patrick, S. K. (1995). Mechanism for reflex reversal during walking in human tibialis anterior muscle revealed by single motor unit recording. *Journal of Physiology, 488*, 249–258.

Del Balso, C., & Cafarelli, E. (2007). Adaptations in the activation of human skeletal muscle induced by short-term isometric resistance training. *Journal of Applied Physiology, 103*, 402–411.

Delwaide, P. J., Crenna, P., & Fleron, M. H. (1981). Cutaneous nerve stimulation and motoneuronal excitability: I, soleus and tibialis anterior excitability after ipsilateral and contralateral sural nerve stimulation. *Journal of Neurology, Neurosurgery and Psychiatry, 44*, 699–707.

Delwaide, P. J., & Pepin, J. L. (1991). The influence of contralateral primary afferents on inhibitory interneurons in humans. *Journal of Physiology, 439*, 161–179.

Dettmers, C., Fink, G. R., Lemon, R. N., Stephan, K. M., Passingham, R. E., Ridding, M. C., ... Frackowiak, R. S. (1995). Relation between cerebral activity and force in the motor areas of the human brain. *Journal of Neurophysiology, 74*, 802–815.

Dimitrijevic, M. R., & Nathan, P. W. (1969). Changes in the flexor reflex with repetitive cutaneous stimulation in spinal man. *Electroencephalography and Clinical Neurophysiology, 27*, 721–722.

Dragert, K., & Zehr, E. P. (2011). Bilateral neuromuscular plasticity from unilateral training of the ankle dorsiflexors. *Experimental Brain Research, 208*, 217–227.

Dragert, K., & Zehr, E. P. (2013). High-intensity unilateral dorsiflexor resistance training results in bilateral neuromuscular plasticity after stroke. *Experimental Brain Research, 225*, 93–104.
Duysens, J. (1977). Reflex control of locomotion as revealed by stimulation of cutaneous afferents in spontaneously walking premammary cats. *Journal of Neurophysiology*, 40, 737–751.

Duysens, J., Tax, A., Trippel, M., & Dietz, V. (1992). Phase-dependent reversal of reflexly induced movements during human gait. *Experimental Brain Research*, 90, 404–414.

Duysens, J., Trippel, M., Horstmann, G. A., & Dietz, V. (1990). Gating and reversal of reflexes in ankle muscles during human walking. *Experimental Brain Research*, 82, 351–358.

Eccles, R. M., & Lundberg, A. (1959). Supraspinal control of interneurones mediating spinal reflexes. *Journal of Physiology*, 147, 565–584.

Farthing, J. P., Borowsky, R., Chilibeck, P. D., Binsted, G., & Sarty, G. E. (2007). Neuro-physiological adaptations associated with cross-education of strength. *Brain Topography*, 20, 77–88.

Farthing, J. P., & Chilibeck, P. D. (2003). The effect of eccentric training at different velocities on cross-education. *European Journal of Applied Physiology*, 89, 570–577.

Finland, M. S., Helgerud, J., Solstad, G. M., Iversen, V. M., Leivseth, G., & Hoff, J. (2009). Neural adaptations underlying cross-education after unilateral strength training. *European Journal of Applied Physiology*, 107, 723–730.

Geertsen, S. S., Lundbye-Jensen, J., & Nielsen, J. B. (2008). Increased central facilitation of antagonist reciprocal inhibition at the onset of dorsiflexion following explosive strength training. *Journal of Applied Physiology*, 105, 915–922.

Gibbs, J., Harrison, L. M., & Stephens, J. A. (1995). Cutaneousmuscular reflexes recorded from the lower limb in man during different tasks. *Journal of Physiology*, 487, 237–242.

Goodall, S., St Clair Gibson, A., Voller, B., Lomarev, M., Howatson, G., Dang, N., & Hallett, M. (2013). Repetitive transcranial magnetic stimulation attenuates the perception of force output production in non-exercised hand muscles after unilateral exercise. *PLoS ONE*, 8, e80202.

Han, B. S., Jang, S. H., Chang, Y., Byun, W. M., Lim, S. K., & Kang, D. S. (2003). Functional magnetic resonance image finding of cortical activation by neuromuscular electrical stimulation on wrist extensor muscles. *American Journal of Physical Medicine & Rehabilitation*, 82, 17–20.

Haridas, C., & Zehr, E. P. (2003). Coordinated interlimb compensatory responses to electrical stimulation of cutaneous nerves in the hand and foot during walking. *Journal of Neurophysiology*, 90, 2850–2861.

Hendy, A. M., & Kidgell, D. J. (2014). Anodal-tDCS applied during unilateral strength training increases strength and corticospinal excitability in the untrained homologous muscle. *Experimental Brain Research*, 232, 3243–3252.

Hendy, A. M., Spittle, M., & Kidgell, D. J. (2012). Cross education and immobilisation: Mechanisms and implications for injury rehabilitation. *Journal of Science and Medicine in Sport*, 15, 94–101.

Hermens, H. J., Freriks, B., Disselhorst-Klug, C., & Rau, G. (2000). Development of recommendations for SEMG sensors and sensor placement procedures. *Journal of Electromyography & Kinesiology*, 10, 361–374.

Hortobágyi, T., & Maffiuletti, N. A. (2011). Neural adaptations to electrical stimulation strength training. *European Journal of Applied Physiology*, 111, 2439–2449.

Hortobágyi, T., Richardson, S. P., Lomarev, M., Shamim, E., Meunier, S., Russman, H., … Hallett, M. (2011). Interhemispheric plasticity in humans. *Medicine and Science in Sports and Exercise*, 43, 1188–1199.

Hortobágyi, T., Richardson, S., Lomarev, M., Shamim, E., Sabine, M., Russman, H., … Hallett, M. (2011). Interhemispheric plasticity in humans. *Medicine & Science in Sports & Exercise*, 43, 1188–1199.

Hortobágyi, T., Taylor, J. L., Petersen, N. T., Russell, G., & Gandevia, S. C. (2003). Changes in segmental and motor cortical output with contratralateral muscle contractions and altered sensory inputs in humans. *Journal of Neurophysiology*, 90, 2451–2459.

Howatson, G., Zilt, T., Farthing, J. P., Zijdewind, I., & Hortobágyi, T. (2013). Mirror training to augment cross-education during resistance training: A hypothesis. *Frontiers in Human Neuroscience*, 7, 396.

Jankowska, E. (2001). Spinal interneuronal systems: Identification, multifunctional character and reconfigurations in mammals. *Journal of Physiology*, 533, 31–40.

Jankowska, E., Krutki, P., & Matsuyama, K. (2005). Relative contribution of Ia inhibitory interneurones to inhibition of feline contralateral motoneurones evoked via commissural interneurones. *Journal of Physiology*, 568, 617–628.

Jenner, J. R., & Stephens, J. A. (1982). Cutaneous reflex responses and their central nervous pathways studied in man. *Journal of Physiology*, 333, 405–419.

Komiyama, T., Zehr, E. P., & Stein, R. B. (2000). Absence of nerve specificity in human cutaneous reflexes during standing. *Experimental Brain Research*, 133, 267–272.

Kristeva, R., Cheyne, D., & Deecke, L. (1991). Neuromagnetic fields accompanying unilateral and bilateral voluntary movements: Topography and analysis of cortical sources. *Electroencephalography and Clinical Neurophysiology Evoked Potentials*, 81, 284–298.

Lagerquist, O., Zehr, E. P., Baldwin, E. R. L., Klakowicz, P. M., & Collins, D. F. (2006). Diurnal changes in the amplitude of the Hoffmann reflex in the human soleus but not in the flexor carpi radialis muscle. *Experimental Brain Research*, 170, 1–6.

Lagerquist, O., Zehr, E. P., & Docherty, D. (2006). Increased spinal reflex excitability is not associated with neural plasticity underlying the cross-education effect. *Journal of Applied Physiology*, 100, 83–90.

Lee, M., & Carroll, T. J. (2007). Cross education: Possible mechanisms for the contralateral effects of unilateral resistance training. *Sports Medicine (Auckland, N. Z.)*, 37, 1–14.

Lee, M.-J., Kilbreath, S. L., Singh, M. F., Zeman, B., & Davis, G. M. (2010). Effect of progressive resistance training on muscle performance after chronic stroke. *Medicine and Science in Sports and Exercise*, 42, 23–34.

McCrea, D. (2001). Spinal circuitry of sensorimotor control of locomotion. *Journal of Physiology*, 533, 41–50.

Négyesi, J., Veldman, M. P., Berghuis, K. M. M., Javet, M., Tihanyi, J., & Hortobágyi, T. (2018). Somatosensory electrical stimulation does not augment motor skill acquisition and intermanual transfer in healthy young adults - A pilot study. *Motor Control*, 22, 67–81.

Nielsen, J., Petersen, N., & Fedirchuk, B. (1997). Evidence suggesting the transcortical pathway from cutaneous foot afferents to tibialis anterior motoneurons in man. *Journal of Physiology*, 501, 473–484.
Panek, I., Bui, T., Wright, A., & Brownstone, R. (2014). Cutaneous afferent regulation of motor function [Online]. *Acta Neurobiologiae Experimentalis*, 74, 158–171. http://www.wyuz.ane.pl/pdf/7416. pdf.

Perez, M. A., Tanaka, S., Wise, S. P., Sadato, N., Tanabe, H. C., Willingham, D. T., & Cohen, L. G. (2007). Neural substrates of intermanual transfer of a newly acquired motor skill. *Current Biology*, 17, 1896–1902.

Proske, U., & Gandevia, S. C. (2012). The Proprioceptive senses: Their roles in signaling body shape, body position and movement, and muscle force. *Physiological Reviews*, 92, 1651–1697.

Ruddy, K. L., & Carson, R. G. (2013). Neural pathways mediating cross education of motor function. *Frontiers in Human Neuroscience*, 7, 397.

Russmann, H., Lamy, J., Shamim, E., Meunier, S., & Hallett, M. (2009). Associative plasticity in intracortical inhibitory circuits in human motor cortex. *Clinical Neurophysiology*, 120, 1204–1212.

Scripture, E., Smith, T., & Brown, E. (1894). On the education of muscular control and power. *Stud Yale Psychol Lab*, 2, 114–119.

Sherrington, C. S. (1910). Flexion-reflex of the limb, crossed extension-reflex, and reflex stepping and standing. *Journal of Physiology*, 28, 29–121.

Sun, Y., & Zehr, E. P. (2019). Sensory enhancement amplifies interlimb cutaneous reflexes in wrist extensor muscles. *Journal of Neurophysiology*, 122(5), 2085–2094. https://doi.org/10.1152/jn.00324.2019

Van Wezel, B. M. H., Ottenhoff, F. A. M., & Duysens, J. (1997). Dynamic control of location-specific information in tactile cutaneous reflexes from the foot during human walking. *Journal of Neuroscience, 17*, 3804–3814.

Veldman, M. P., Maffiuletti, N. A., Hallett, M., Zijdewind, I., & Hortobágyi, T. (2014). Direct and crossed effects of somatosensory stimulation on neuronal excitability and motor performance in humans. *Neuroscience and Biobehavioral Reviews*, 47, 22–35.

Veldman, M. P., Zijdewind, I., Solnik, S., Maffiuletti, N. A., Berghuis, K. M. M., Javet, M., … Hortobágyi, T. (2015). Direct and crossed effects of somatosensory electrical stimulation on motor learning and neuronal plasticity in humans. *European Journal of Applied Physiology*, 115, 2505–2519.

Volkman, A. (1858). Ueber den einfuse der usbung auf das erkennen taktit distansen. Berlin K-Sachs Ges D Weiss Math Phys X.

Yang, J. F., & Stein, R. B. (1990). Phase-dependent reflex reversal in human leg muscles during walking. *Journal of Neurophysiology*, 63, 1109–1117.

Zehr, E. P. (2002). Considerations for use of the Hoffmann reflex in exercise studies. *European Journal of Applied Physiology*, 86, 455–468.

Zehr, E. P. (2006). Training-induced adaptive plasticity in human somatosensory reflex pathways. *Journal of Applied Physiology*, 101, 1783–1794.

Zehr, E. P., Carroll, T. J. T., Chua, R., Collins, D. F., Frigon, A., Haridas, C., … Thompson, A. K. (2004). Possible contributions of CPG activity to the control of rhythmic human arm movement. *Canadian Journal of Physiology and Pharmacology*, 82, 556–568.

Zehr, E. P., & Chua, R. (2000). Modulation of human cutaneous reflexes during rhythmic cyclical arm movement. *Experimental Brain Research*, 135, 241–250.

Zehr, E. P., Collins, D. F., & Chua, R. (2001). Human interlimb reflexes evoked by electrical stimulation of cutaneous nerves innervating the hand and foot. *Experimental Brain Research*, 140, 495–504.

Zehr, E. P., & Duysens, J. (2004). Regulation of arm and leg movement during human locomotion. *Neuroscientist*, 10, 347–361.

Zehr, E. P., & Stein, R. B. (1999). What functions do reflexes serve during human locomotion? *Progress in Neurobiology*, 58, 185–205.

**How to cite this article:** Barss TS, Klarner T, Sun Y, Inouye K, Zehr EP. Effects of enhanced cutaneous sensory input on interlimb strength transfer of the wrist extensors. *Physiol Rep*. 2020;8:e14406. [https://doi.org/10.14814/phy2.14406](https://doi.org/10.14814/phy2.14406)