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Facilitation of soleus H-reflex amplitude evoked by cutaneous nerve stimulation at the wrist is not suppressed by rhythmic arm movement

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Abstract Neural connections between the cervical and lumbosacral spinal cord may assist in arm and leg coordination during locomotion. Currently the extent to which arm activity can modulate reflex excitability of leg muscles is not fully understood. We showed recently that rhythmic arm movement significantly suppresses soleus H-reflex amplitude probably via modification of presynaptic inhibition of the IA afferent pathway. Further, during walking reflexes evoked in leg muscles by stimulation of a cutaneous nerve at the wrist (superficial radial nerve; SR) are phase and task dependent. However, during walking both the arms and legs are rhythmically active thus it is difficult to identify the locus of such modulation. Here we examined the influence of SR nerve stimulation on transmission through the soleus H-reflex pathway in the leg during static contractions and during rhythmic arm

movements. Nerve stimulation was delivered with the right shoulder in flexion or extension. H-reflexes were evoked alone (unconditioned) or with cutaneous conditioning via stimulation of the SR nerve (also delivered alone without H-reflex in separate trials). SR nerve stimulation significantly facilitated H-reflex amplitude during static contractions with the arm extended and countered the suppression of reflex amplitude induced by arm cycling. The results demonstrate that cutaneous feedback from the hand on to the soleus H-reflex pathway in the legs is not suppressed during rhythmic arm movement. This contrasts with the observation that rhythmic arm movement suppresses facilitation of soleus H-reflex when cutaneous nerves innervating the leg are stimulated. In conjunction with other data taken during walking, this suggests that the modulation of transmission through pathways from the SR nerve to the lumbosacral spinal cord is partly determined by rhythmic activity of both the arms and legs.

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Introduction

During bipedal locomotion both the arms and legs are rhythmically active and it has been suggested that humans make use of quadrupedal neural mechanisms for coordinated limb movement during locomotion (Dietz 2002). This proposition would require neural linkage between the arms and legs although the mechanisms by which this coordination may be mediated remain uncertain. It was shown that electrical stimulation of nerves in the leg could have large reflex effects on arm muscles during locomotion (Dietz et al. 2001; Haridas and Zehr 2003). There is also evidence that activation of sensory nerves in the arm can influence reflexes in the legs. H-reflexes in soleus, an ankle extensor muscle, were facilitated by stimulating the ulnar nerve (Meinck and Piesiur-Strehlow 1981) and the median nerve (Kagamihara et al. 2003) at the elbow.

Kagamihara et al. (2003) attributed this facilitation to reducing presynaptic inhibition of IA afferents to soleus through a long-loop pathway. Quite recently we showed that rhythmic arm movement significantly suppressed H-reflex amplitude in the ankle extensor muscle soleus (Frigon et al. 2004). This provided evidence that isolated rhythmic arm movement could affect reflex excitability in the legs independent of rhythmic leg muscle activity. It was suggested that rhythmic arm cycling suppressed the soleus H-reflex via modification of presynaptic inhibition at the IA afferent terminals.

We have previously shown that cutaneous nerve stimulation at the wrist (superficial radial; SR) evoked interlimb reflexes in many leg muscles (including soleus) during both sitting (Zehr et al. 2001) and walking (Haridas and Zehr 2003). Further, reflex pathways from cutaneous fields in the hand and foot that link leg and arm muscles are modulated during walking (Haridas and Zehr 2003). However, modulation of reflexes in leg muscles after stimulation at the wrist during walking could be affected by both arm and/or leg activity. That is, walking involves the simultaneous activation of arm and leg muscles and thus the locus of modulation (for example, at a cervical or lumbosacral level) of “distant” nerve stimulation has remained unknown. Subtle effects of interlimb reflex linkages can be detected by conditioning the soleus H-reflex using inputs from a cutaneous nerve at the wrist. The present experiments were designed to address two questions: (1) does input from the SR nerve at the wrist influence transmission in the soleus H-reflex pathway in the leg? and (2) does rhythmic arm movement modulate any conditioning effect of SR nerve stimulation on the soleus H-reflex? We hypothesised that SR nerve stimulation would have a significant effect on soleus H-reflexes during static contractions. Since the conditioning effect of cutaneous input from the legs on soleus H-reflex was suppressed by arm cycling (Frigon et al. 2004), we further hypothesised that cutaneous input from the SR nerve stimulation would be similarly suppressed and would not alter soleus H-reflex amplitude when applied during arm cycling.

Materials and methods

Subjects

Ten subjects, ranging in age from 22 to 43 years, with no known history of neurological disorders, participated in this study. The subjects gave written consent to participate under the sanction of the Health Research Ethics Board at the University of Alberta. The experiments were conducted in accordance with the Declaration of Helsinki.

Protocol

These data were collected in the same subjects in parallel with the study of Frigon et al. (2004). The experimental

set-up is the same as that shown in Fig. 1 of Frigon et al. (2004). Rhythmic arm cycling was performed in a clockwise direction (viewed from the right side of the body) at a comfortable pace (~60 rpm) using a custom-made hydraulic arm ergometer (described in Zehr et al. 2003) positioned directly in front of the subjects. For each trial, subjects maintained a consistent low-level tonic contraction (~10% MVC) of their right soleus muscle using visual feedback of the filtered and rectified EMG signal. Nerve stimulation (see below) was delivered during cycling and static trials at two positions: (1) right shoulder flexed (~70° in front of the midaxillary line); or (2) right shoulder extended (~10° behind the midaxillary line). In all trials the arms were constrained 180° out of phase.

Nerve stimulation

All nerves were stimulated with bipolar surface electrodes (H69-P; Jason-Kendall LTP, CA) using a Grass S88 (Grass Instruments, AstroMed) stimulator connected in series with SIU5 isolator and CCU1 constant current units. Stimulation was delivered approximately once every two to three cycles during cycling and pseudorandomly between 1 and 3 s during static trials. Averages of 20 stimuli were taken for each condition.

Reflexes were evoked by nerve stimulation in three ways: (1) tibial nerve alone (to evoke an H-reflex in soleus); (2) SR nerve + tibial nerve with a condition-test (C-T) interval of 100 ms (to examine H-reflex conditioning); and (3) SR nerve alone (to identify postsynaptic effects of the cutaneous stimulus on the soleus motoneurons). Each type of nerve stimulation was delivered in a separate set of trials and the order of the trials was randomised across subjects. In five subjects the effect of varying the SR-to-tibial nerve C-T interval was examined across a range of 50–200 ms.

Soleus H-reflex

The tibial nerve was stimulated with single 1-ms square-wave pulses delivered over the right popliteal fossa. M-wave and H-reflex recruitment curves were constructed at the start of each experiment to determine the maximal M-wave (M_{max} ; mean of the three largest M-wave values), and to identify the stimulus intensity required to obtain an H-reflex on the ascending limb of the curve with a small but stable M-wave. For the remainder of the experiment stimulation intensity was set to evoke an M-wave of this size (~10% M_{max}). M-wave amplitude was monitored online and stimulation intensity was adjusted occasionally to maintain consistent amplitude. Stimulation current was measured (mA-2000 Noncontact Milliammeter; Bell Technologies, Orlando, FL).

Superficial radial nerve stimulation

Cutaneous reflexes were evoked with trains (5×1.0-ms pulses at 300 Hz) of isolated constant current stimulation (Grass S88 stimulator with SIU5 and CCU1 constant current units; AstroMed-Grass) applied to the SR nerve at the wrist using flexible surface electrodes. Stimulus intensity was set on the CCU1 unit as a multiple of the threshold at which a clear radiating paresthesia (radiating threshold, RT) into the innervation area of the nerve (dorsolateral portion of the hand) was reported (Zehr et al. 2001; Haridas and Zehr 2003). This level was typically set at ~2×RT.

Electromyography

Electromyography (EMG) was recorded with surface recording electrodes (Vermed, Bellows Falls, VT). EMG signals were preamplified and bandpass filtered at 30–300 Hz (P511 Grass Instruments, AstroMed) as described previously (Frigon et al. 2004).

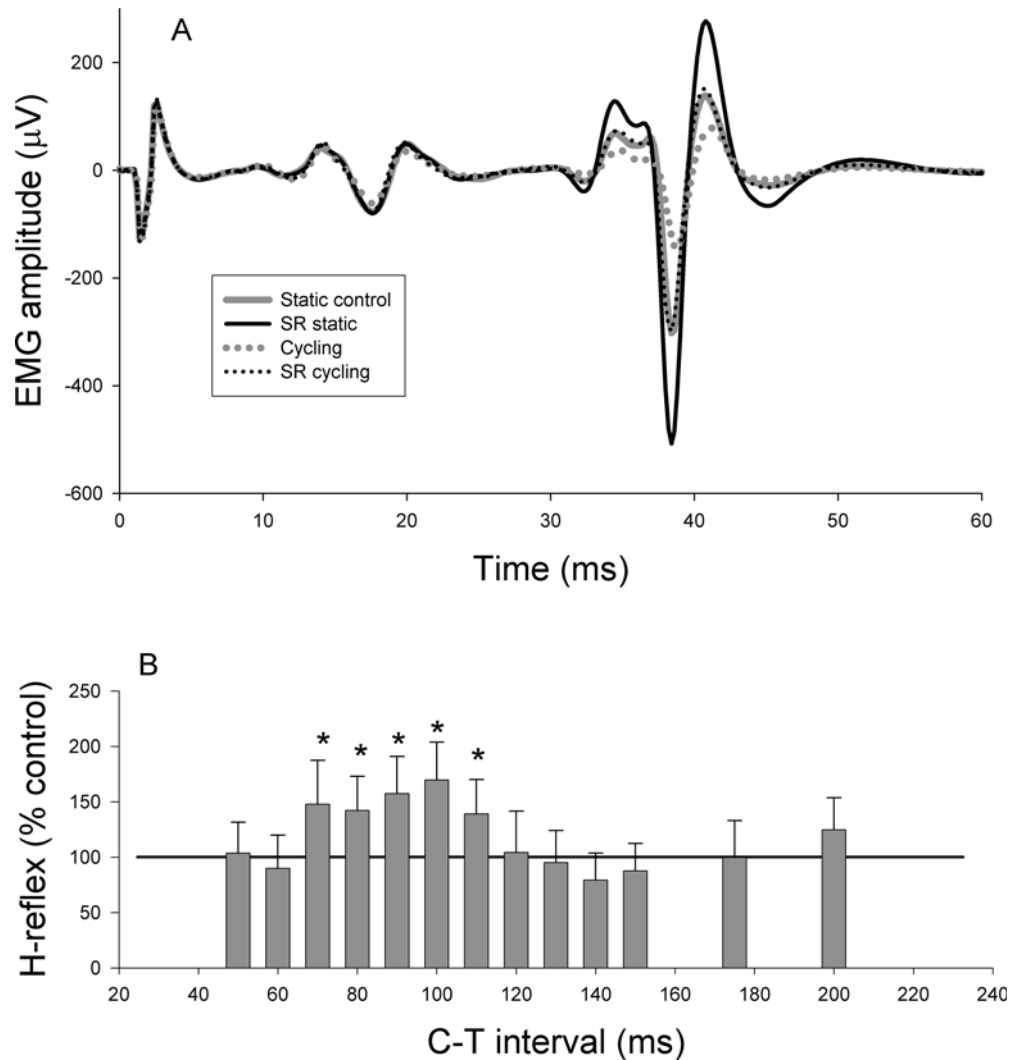
Data acquisition and analysis

Data were sampled at 5,000 Hz with a 12-bit A/D converter controlled by a custom-written computer Lab-View (National Instruments) program. For all trials 20 sweeps (300 ms with 50 ms prestimulus) were collected. Prestimulus EMG was rectified and averaged and used as a measure of muscle activity at the time of nerve stimulation.

H-reflexes

M-wave and H-reflex peak to peak amplitudes were measured off-line (custom-written software; Matlab, Nantick) from the single unrectified sweeps of ipsilateral soleus EMG. M-waves and H-reflexes were normalised to the corresponding M_{max} for each subject. Averages were calculated from all 20 sweeps in each condition.

Fig. 1 **A** Modulation of soleus H-reflex amplitude by remote cutaneous nerve stimulation (SR) and by arm cycling. Averaged sweeps from a single subject are shown. Note the facilitation of the H-reflex from control amplitudes (static control) during SR stimulation with no arm movement (SR static). Arm cycling (cycling) reduces H-reflex amplitude. However, when SR stimulation is provided during cycling (SR cycling; seen superimposed upon static control trace) reflex amplitude is returned to static control size. **B** Plot showing the effect of various condition-test (C-T) intervals on the SR nerve facilitation of soleus H-reflex amplitude for a single subject. Note the emergence of significant facilitation at C-T intervals of 70–110 ms (asterisks)



Superficial radial nerve stimulation

To assess whether changes in H-reflex amplitude induced by the conditioning methods were due to changes in motoneuron excitability (change in EMG of soleus) responses in soleus evoked by stimulating the SR nerve were quantified for each subject from subtracted EMG traces by analysing for peak responses at early (50–80 ms) and middle (80–120 ms) latencies (see Zehr et al. 2001). Reflexes were considered to be significant when they exceeded a two standard deviation band calculated from the 50-ms prestimulus EMG.

Statistics

A three-factor [two conditions (H-reflex with or without somatosensory conditioning) \times two tasks (static or cycling) \times two positions (flexed or extended shoulder)] with repeated measures analyses of variance test (ANOVA) was used to identify significant effects of conditioning, task and position (independent variables) on the amplitude of soleus H-reflexes, M-waves, prestimulus EMG levels and responses in the averaged ($n=20$ sweeps) surface EMG evoked by SR nerve stimulation (STATISTICA, StatSoft). Planned comparisons were used to evaluate specific differences between conditions. Descriptive statistics are given as the mean \pm 1 SE and an alpha level of $P \leq 0.05$ was used for statistical significance.

Results

Superficial radial conditioning of the soleus H-reflex

Superficial radial stimulation evoked significant (main effect, $P < 0.01$) facilitation of the soleus H-reflex during static contraction. This can be seen for a single subject in Fig. 1A (compare solid black line with grey line) and across all subjects in Fig. 2. Across all subjects statistical significance was seen only at the shoulder extended position (Fig. 2B).

For the five subjects in whom C-T interval effects were examined, facilitation typically peaked at a C-T of ~ 100 ms. Data from one such subject (stimulus amplitude $2.5 \times RT$) are shown in Fig. 1B. Significant facilitation emerged at a C-T of 70 ms, reached a peak at 100 ms and continued out to 110 ms.

Effect of arm cycling on SR conditioning of soleus H-reflexes

Arm cycling significantly ($P < 0.001$) reduced the soleus H-reflex (Fig. 1A; compare solid grey line for control static contraction with large dotted line during cycling) for both shoulder flexion (Figs. 1A, 2A) and extension (Fig. 2B). This result was documented previously (see Frigon et al. 2004) and the data on the effect of arm cycling from that

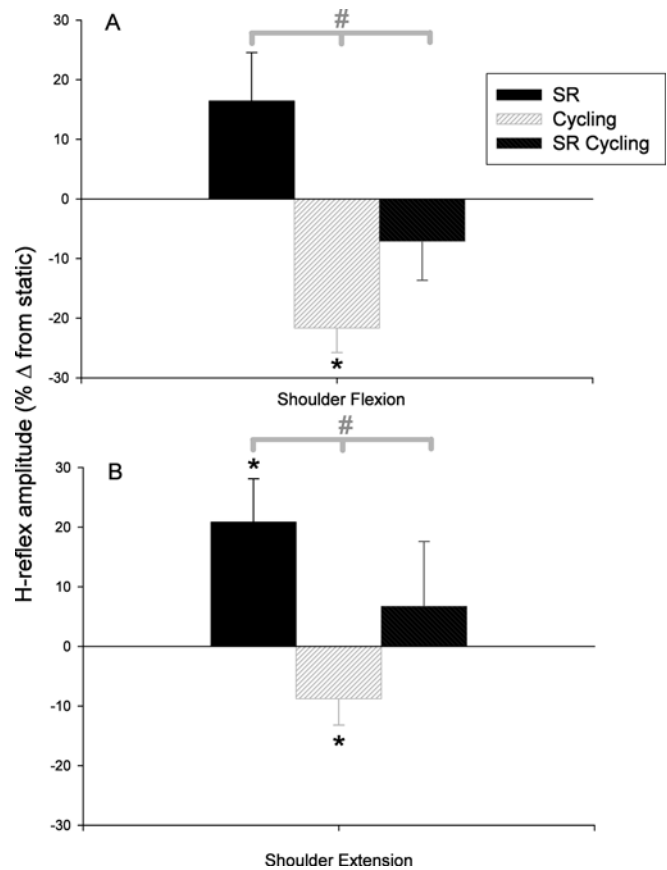


Fig. 2A, B Interaction of SR nerve facilitation and arm cycling suppression of soleus H-reflex amplitude averaged across all subjects. Data from the right shoulder flexed position are shown in **A** while **B** shows data from the shoulder extended position. Note that the data on unconditioned effects during cycling (*middle bars* in **A** and **B**) are replotted data from Frigon et al. (2004) shown for reference. Data are mean values \pm SEM expressed as percentage changes in reflex amplitude from the static unconditioned amplitudes at each position. *Black asterisks* indicate significant differences from control static unconditioned reflex amplitude. *Grey lines* and *number sign* indicate significant differences between conditions at $P \leq 0.05$.

paper are replotted in Fig. 2 and shown here for reference. There was no significant difference in H-reflex amplitude between the two shoulder positions during static contraction and thus changes in arm position alone did not significantly affect SR conditioning. However, during rhythmic arm movement there was an interaction between movement-induced inhibition and SR facilitation (see Figs. 1A, 2). In Fig. 2 the grey number sign over the grey line indicates that all conditions were significantly different from each other. The black asterisk indicates conditions that were different from static control H-reflex amplitude. The suppression of soleus H-reflex amplitude with arm cycling was offset by the facilitation induced by SR stimulation. That is, H-reflex amplitude when SR stimulation was given during cycling (SR cycling; see Fig. 2) was significantly larger than H-reflex amplitude during cycling without SR stimulation and was not significantly different from control values with no movement or conditioning. In the single subject traces shown in

Fig. 1A it can be seen that SR stimulation could evoke facilitation of the H-reflex during cycling. Combined with the inhibitory effect of cycling alone, this restored the reflex amplitude to the unconditioned static value (compare dotted grey line with solid black line).

Effect of arm cycling on interlimb cutaneous reflexes in soleus

Stimulation of the SR nerve evoked interlimb cutaneous reflexes in soleus at early latency in 22.5% of subjects and in 42.5% for middle latency when examined across all conditions. The middle latency response was inhibitory and had peaked at a latency that corresponded well with the SR H-reflex C-T interval (~100 ms). Arm cycling did not significantly ($P>0.2$) modulate these SR nerve interlimb cutaneous reflexes in soleus. Averaged across all subjects there was no significant ($P>0.12$) effect of either static arm position or rhythmic arm cycling on cutaneous reflex amplitudes in soleus.

Discussion

In this paper we report two novel findings. Firstly, activation of cutaneous afferents in the SR nerve at the wrist facilitates soleus H-reflexes in the leg. Secondly, contrary to our hypothesis, this facilitation persists during arm cycling, despite the suppressive influence of arm cycling on the soleus H-reflex (Frigon et al. 2004) and the well-documented attenuation of afferent transmission during movement (Brooke et al. 1997). That is, even in the presence of inhibitory conditioning evoked by rhythmic arm movement SR conditioning facilitated H-reflex amplitude in the direction of control amplitude.

Superficial radial nerve stimulation facilitates soleus H-reflexes

Meier-Ewert et al. (1973) demonstrated that stimulation of “remote” cutaneous fields (for example, the skin on the forehead) could evoke reflexes in leg muscles such as tibialis anterior and gastrocnemius. Stimulation of various skin areas in the torso and upper limb evoked responses in leg muscles (Piesiur-Strehlow and Meinck 1980). Thus, cutaneous stimulation from remote skin areas could have strong effects on distant motor pools. Further experiments suggested that the remote effects in leg muscles evoked by stimulation of the brachial plexus in the upper limb could be carried via a propriospinal pathway (Meinck and Piesiur-Strehlow 1981). Later, it was shown that stimulation of the cutaneous SR nerve at the wrist could evoke interlimb cutaneous reflexes and, at least in some subjects, with latencies compatible with propriospinal pathways (Zehr et al. 2001). However, propriospinal interlimb reflexes have only been conclusively demonstrated in

complete spinal cord injured humans (Calancie 1991; Calancie et al. 1996).

Our current observation of facilitation of soleus H-reflexes by SR stimulation at the wrist is in agreement with previous investigations in which mixed nerve stimulation (for example median nerve) in the upper limb facilitated the soleus H-reflex (Delwaide et al. 1981; Meinck and Piesiur-Strehlow 1981; Delwaide and Crenna 1984; Kagamihara et al. 2003). The general shape of the C-T curves is also similar to that shown for median nerve stimulation at the wrist (Kagamihara et al. 2003) and for median, ulnar and radial nerve stimulation at the elbow (Meinck and Piesiur-Strehlow 1981). Kagamihara et al. (2003) suggested that the facilitation after median nerve stimulation was likely due in large part to contributions from cutaneous afferents. The data on SR stimulation (purely cutaneous nerve) here may be taken as support of a strong effect from cutaneous afferents in the upper limb onto the soleus H-reflex pathway. It is of interest to note that the general effect of remote cutaneous input from different nerves innervating the upper limb is facilitation on the soleus H-reflex pathway. This may suggest that feedback associated with upper limb activity plays a role in modifying lower limb reflex excitability.

Arm cycling does not block SR facilitation of the soleus H-reflex

It has been suggested that the descending facilitatory conditioning of the soleus H-reflex evoked by stimulation of the median nerve at the wrist may act via a reduction in segmental group IA presynaptic inhibition (PSI; Kagamihara et al. 2003). The time course of the peak SR facilitation shown here (~100 ms) is consistent with what has been ascribed to PSI effects evoked by cutaneous (Iles and Roberts 1987; Iles 1996) and mixed nerve (Capaday et al. 1995; Zehr and Stein 1999) stimulation. Furthermore, the facilitation of the H-reflex occurred despite a corresponding inhibition of the ongoing rectified and averaged EMG evoked by SR stimulation delivered alone. This combined with the results of our earlier study on arm cycling and soleus H-reflex suppression, lends support for the view that modification of the H-reflex amplitude is likely occurring via modification of PSI. We showed previously that arm cycling could suppress soleus H-reflex amplitudes (Frigon et al. 2004). In that study it was further demonstrated that there is an interaction between segmental conditioning of IA PSI and arm cycling. The CP and sural nerves were stimulated at C-T intervals of 100 (to increase IA PSI) and 80 ms (to reduce IA PSI), respectively, in separate trials during arm cycling and without arm cycling. Arm cycling was shown to significantly reduce the sural nerve facilitation and further increase the CP nerve inhibition of soleus H-reflex amplitude. Further, in the Frigon et al. paper H-reflex amplitudes conditioned by sural nerve stimulation during cycling were not significantly different from the H-reflex amplitudes during cycling alone (see Figs. 4A and 5A of

that paper). The data on the effect of SR stimulation are in contrast to the sural nerve stimulation effect; H-reflex amplitude when SR stimulation was applied during cycling was larger than cycling alone (see Fig. 2). To better appreciate this difference, data for the flexion and extension position for SR nerve and sural nerve (taken from Frigon et al. 2004) have been combined and replotted in Fig. 3. For the data presented in Fig. 3, both SR and sural nerve stimulation significantly ($P < 0.01$) facilitated soleus H-reflex amplitude during static contraction and cycling significantly ($P < 0.001$) suppressed H-reflex amplitude. It can be seen from this figure that cycling induces significant suppression of H-reflex amplitude which is brought back to control values during cycling by application of SR (indicated by the solid black line from cycling to SR cycling showing significance at $P < 0.02$) but not sural nerve stimulation ($P > 0.12$; see dotted line from cycling to sural cycling).

The current observation that suppression induced by arm cycling does not fully block the SR nerve facilitation of soleus H-reflex amplitude suggests a differential effect of arm cycling on modulation of H-reflex facilitation from cutaneous sources in different places. That is, “local” facilitatory cutaneous conditioning (for example, sural nerve from the ipsilateral leg in Frigon et al. 2004) and “distant” (after SR stimulation at the wrist) conditioning during arm cycling are controlled differently. The former facilitatory inputs appear to be “gated out” by the arm cycling whereas the latter inputs from the upper limb are still present while superimposed on a background of inhibition. We have shown that there is phase-dependent modulation of SR nerve cutaneous reflexes in arm muscles during arm cycling (Zehr and Kido 2001) and walking (Zehr and Haridas 2003) and have argued previously that these observations may be due in part to CPG activity associated with arm movement (Zehr and Duysens 2004). We have also shown significant modulation of SR nerve

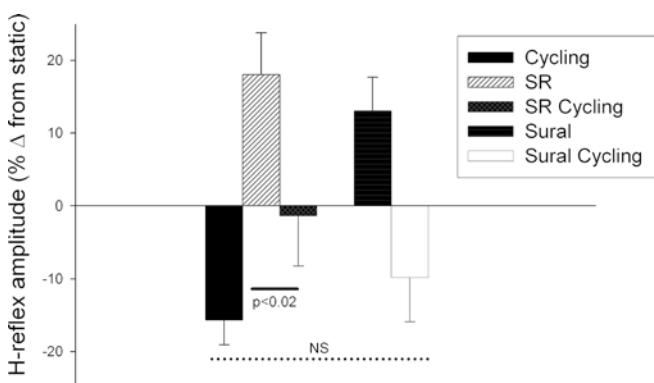


Fig. 3 Effect of SR and sural nerve stimulation on soleus H-reflex amplitude combined for both flexion and extension positions. Data are means \pm SEM as percentage changes in reflex amplitude relative to reflexes taken during control static contraction. Data on sural nerve have been taken from Frigon et al. (2004) and re-analysed. Note that statistical significance ($P < 0.01$) was shown for SR, sural and cycling conditioning (not indicated). The effect of SR nerve facilitation in removing cycling suppression ($P < 0.02$) is shown by the *solid line* while the lack of a similar effect for sural nerve during cycling ($P > 0.12$) is shown by the *dotted line*

interlimb reflexes in leg muscles during locomotion (Haridas and Zehr 2003). It could be that the effect of arm cycling on the descending SR conditioning represents observations on the remote effect of arm CPG activity. Possibly the conditioning from the arm CPG and from the SR nerve stimulation travel through different descending pathways (since the arm CPG does not seem to modulate the SR nerve effect (i.e. the facilitation effect of $\sim 20\%$ is the same during static and cycling trials) before descending to the legs but they may impinge on the same presynaptic interneurons.

Functional implications

As can be seen in the example from a single subject in Fig. 1A, the SR facilitation cancelled the suppression induced by arm cycling. It is of note that the facilitation evoked by SR nerve stimulation is not suppressed during rhythmic arm movement. In many ways this runs contrary to the majority of observations in the literature showing a reduction in efficacy of sensory feedback during movement (for example, H-reflex and somatosensory-evoked potentials; see Brooke et al. 1997 for review). This is also opposite to the effect seen when segmental cutaneous input (for example, from the sural nerve) was evaluated: facilitation of the soleus H-reflex evoked by stimulation of the sural nerve was annulled by arm cycling (Frigon et al. 2004). In contrast, here we observed that the facilitation of the soleus H-reflex induced by SR stimulation persisted even during arm cycling (see Figs. 1A, 2A, B, 3). Indeed there can be seen to be a near linear summation of the effects of suppression by arm cycling and facilitation by cutaneous input from the hand. We speculate that sensory feedback from cutaneous fields in the hand may assist in interlimb coordination between movement of the arms and activity in leg muscles during locomotion by altering the access of sensory feedback from remote sources to the motoneuronal pools of leg muscles. In this way remote inputs (for example, from the arms) still have access while local inputs (for example, from the legs) have reduced access during rhythmic arm movement. It is possible that the state of activity of the limbs from which the somatosensory conditioning is evoked have priority over inputs evoked from limbs that are not moving.

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