Differential Regulation of Cutaneous and H-Reflexes During Leg Cycling in Humans

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Zehr, E. Paul, Kathryn L. Hesketh, and Romeo Chua. Differential regulation of cutaneous and H-reflexes during leg cycling in humans. J Neurophysiol 85: 1178–1184, 2001. Reflexes undergo modulation according to task and timing during standing, walking, running, and leg cycling in humans. Both cutaneous and Hoffman (H-) reflexes are modulated by movement and task. However, recent evidence suggests that the modulation pattern for cutaneous and H-reflexes may be different. We sought to clarify this issue by reducing the effect of movement phase and altering the level of background muscle activation (low and high) in static and dynamic (leg cycling) conditions. Electromyography was recorded from the ankle extensors soleus and medial gastrocnemius (MG) and the knee extensor vastus lateralis (VL). Reflexes were evoked during the downstroke of stationary leg cycling. Cutaneous reflexes were evoked with trains of 5 × 1.0 ms pulses at 300 Hz delivered to the distal tibial nerve, whereas H-reflexes were evoked in soleus by stimulation with single 1.0-ms pulses. There were two main observations in this study: 1) middle latency cutaneous reflexes were facilitatory during static contraction but were dramatically attenuated or reversed to suppressive responses during cycling (task-dependent modulation); 2) soleus H-reflexes were larger in the high muscle activation condition but were unaffected by task (no task-dependent modulation). Thus opposite results were obtained in the two reflex pathways. It is concluded that cutaneous and H-reflexes are modulated by different mechanisms during active locomotor-like movements.

I N T R O D U C T I O N

Cutaneous and muscle afferent (particularly the Hoffman or H-reflex) reflex pathways have been studied during rhythmic leg movement (Brooke et al. 1997). The extent to which these two pathways are similarly controlled during movement has received recent study. Brooke et al. (1999) showed that during passive movement, cutaneous reflexes have quite different behavior than H-reflexes. There was little passive movement-related modulation of cutaneous reflexes, perhaps in keeping with the suggestion that a central pattern generator (CPG) controls this pathway during rhythmic movement (Duyssens and Van de Crommert 1998). In contrast, H-reflexes seem to show features of both central (Schneider et al. 2000) and peripheral (Brooke et al. 1997) control. Cutaneous and H-reflexes in soleus show some similarities in that they are phase and task modulated. For example, under certain circumstances, both types of reflexes can be of greatest magnitude while the muscle is contracting. It is not yet known how they behave under varying conditions of voluntary muscle activity during rhythmic movement. An emerging concept is that while these reflexes may share similar features, the nature of the modulation they undergo may be quite different. Thus both types of reflexes were elicited under the same conditions to remove this as a factor affecting the two reflex pathways. If the reflexes behave similarly, it might point to some common mechanism for controlling reflexes during rhythmic locomotor movements of the lower limb.

In recent years, there have been many studies examining the modulation of reflexes during leg cycling. Researchers have mainly focused on the study of the soleus H-reflex (Brooke et al. 1997). These studies have suggested that discharge from velocity-sensitive stretch receptors in heteronymous and contralateral muscles is a possible influence (Brooke et al. 1992a, 1997; Cheng et al. 1995b, 1998; McIlroy et al. 1992; Misiaszek et al. 1995). Other experimental results indicate that a more central influence is responsible for reflex behavior during rhythmic movements such as treadmill locomotion (Capaday and Stein 1986, 1987; Duyssens 1998; Duyssens and Van de Crommert 1998; Duyssens et al. 1990, 1992; Lavoie et al. 1997; Yang and Stein 1990). However, there has only been limited investigation into the effects of muscle activity on reflex modulation during cyclic movement (Boorman et al. 1992). Evidence from static comparisons of background electromyographic (EMG) levels indicates that the H-reflex should scale with background muscle activity (Crenna and Frigo 1987; Verrier 1985).

M E T H O D S

All methods and procedures were approved by the Health Research Ethics Committee at the University of Alberta. Twelve adults who were healthy and free of any known neuromuscular disease participated with informed, written consent.

EMG

EMG was collected from the medial gastrocnemius (MG), soleus (SOL), tibialis anterior (TA), vastus lateralis (VL), and biceps femoris...
stimulus and lasted 100 ms, at a sampling frequency of 2,000 Hz. Participants were instructed to maintain the same head, neck, and torso orientation during data collection. During movement conditions, participants pedaled for bouts of approximately 5 min while data were collected, with brief rest periods in between trials. During static trials, participants held contractions for 1 min at a time (15–20 sweeps) then were allowed to rest for a few minutes to avoid fatigue effects. Stimuli were delivered pseudorandomly during static trials, approximately every 3–4 s.

**Data reduction**

EMG signals from each muscle were amplified (×500–5,000) using Grass P-511 amplifiers and band-pass filtered at 30–300 Hz. Data from each EMG channel and the potentiometer were digitized using an A/D interface, sampled at a rate of 1,000 Hz (cutaneous reflexes) or 2,000 Hz (H-reflex) using Labview (National Instruments) data acquisition software, then stored on an IBM compatible microcomputer. A custom-designed computer program (MATLAB, MathWorks, Nantick, MA) was used to process the raw data. Each EMG channel was rectified and stimulus artifacts removed. The latency and peak-to-peak amplitude for M-wave and H-reflex of the unrectified EMG for soleus, as well as the mean and standard deviation of the prestimulus level of activity of each channel were determined. These values were used for further calculations.

**Analysis**

**BACKGROUND EMG.** Background muscle activity was quantified by averaging the mean EMG level over a 150-ms poststimulus period for each sweep of control trials. The sweeps were then each normalized to MVC and averaged.

**CUTANEOUS REFLEXES.** Raw data were examined using an interactive computer program. The stimulus artifact was removed, and the EMG was filtered using a 21-point moving average filter. The control EMG traces were subtracted from the stimulated EMG. The resultant subtracted traces were used for subsequent analysis of the latency and magnitude of all significant facilitations and suppressions of the EMG signal. To be considered significant, reflexes had to exceed a 2 SD band centered about the mean prestimulus EMG. The responses were divided into early (40–65 ms), middle (70–120 ms), and late (130 ms and longer) latencies. These distinctions are similar to those used in other papers (Duyssens et al. 1990; Yang and Stein 1990). Additionally, as with previous studies, we focused on the middle latency response that typically shows the most interesting patterns of modulation (Duyssens and Tax 1994). Reflexes were normalized to background EMG levels for each trial.

**H-reflexes**

M-H curves were generated in each condition. Analyses were performed on three sizes of H-reflex: 1) 30% of $M_{\text{max}}$, 2) $H_{\text{max}}$, and 3) $H$ that occurred at the midpoint of the descending limb of the M-H curve. These three points were compared to see whether there were any differences in the behavior of the H-reflex with changing background levels at different points on the M-H curve. These points of the M-H curve were chosen as there had been some differences in the H-reflex sizes used previously (Brooke et al. 1992b; Capaday and Stein 1987; Cheng et al. 1995a; Taylor et al. 1990). $M_{\text{max}}$ was calculated by averaging the five highest peak-to-peak M-waves.

To have consistent M-wave size within a type of analysis for individual subjects, M-H pairs were chosen by using the specific criteria for each type (e.g., M-wave size where the H-reflex was 30% of $M_{\text{max}}$) from the low muscle activation cycling condition. Next, this M-wave size was used to choose M-H pairs in the other conditions (e.g., low muscle activation during static contraction). This is an extension of a method we have used previously to examine H-reflex...
modulation in different conditions (Zehr and Stein 1999). Eight to 10 M-H pairs were taken from each participant in each condition to find an average for each subject. Since no difference in behavior of the reflex across the M-sizes was found (see RESULTS), 20–30 sweeps of consistent M-wave size (on the ascending limb of the M-H curve) from each subject were averaged for further analyses.

To make direct comparisons between cutaneous and H-reflexes, SOL middle latency responses were normalized to $M_{\text{max}}$ and compared with H-reflexes in the same conditions. Obviously, this was only possible to do with SOL, since M and H data were only available for this muscle.

**Statistics**

Background muscle activity and peak-to-peak M-wave and H-reflex amplitude comparisons as well as H-reflex behavior at different points on the M-H curve were made using repeated measures ANOVA (RM ANOVA). When analyzing cutaneous reflex data, it was not possible to use a RM ANOVA, since not all of the participants exhibited a significant reflex response at each latency, particularly in VL. A one-way ANOVA was performed on the significant responses for early, middle, and late latencies comparing the magnitudes of all significant responses in each condition. A separate ANOVA was calculated for each muscle and latency. Values are given as means ± SD, and statistical significance was set at $P < 0.05$.

**RESULTS**

**Background EMG**

Background EMG levels were larger during the high versus low load condition in MG ($P < 0.05$), SOL ($P < 0.01$), and VL ($P < 0.01$). However, the EMG levels were not different between static and movement trials. That is, background EMG was matched in the static low versus movement low and static high versus movement high conditions. As we attempted to manipulate background EMG by changing workload, this result allows for comparisons of reflex amplitudes at different levels of muscle activation and between movement or static conditions.

**Cutaneous reflexes**

In MG, the middle latency response (70–120 ms poststimulus) reversed from excitatory under static conditions to suppressive during movement ($P < 0.01$). Sample reflex data from one subject are plotted in Fig. 1, and mean subject data averaged across all subjects are shown in Fig. 2 (top). There were no significant effects at the other latencies, an observation in keeping with previous studies in which the middle latency response is most sensitive to modulation (Duysens and Tax 1994). SOL demonstrated the same general pattern as in MG: there was also a task-dependent modulation of the middle latency cutaneous reflex ($P < 0.01$) with very small or inhibitory responses during movement and larger excitatory responses predominating during static contraction (Fig. 2, middle). As with MG, there was no significant difference in SOL response between conditions at either the early or late latency.

**FIG. 1.** Task-dependent reflex reversal of middle latency response to distal tibial nerve stimulation in medial gastrocnemius (MG) muscle. The subtracted reflex traces represent averaged sweeps ($n = 30$) from one subject during static and dynamic (movement) muscle contraction. Background electromyographic (EMG) levels were the same in both conditions. The stimulus artifact has been removed and replaced by a flat line from time 0 until ~35 ms. The middle latency component is highlighted by the gray rectangle.

**FIG. 2.** Peak amplitudes of the middle latency cutaneous reflex for the leg extensor muscles during static and dynamic muscle activation at low and high levels. Reflexes have been normalized to the background EMG in each condition to create ratios. For MG, soleus, and vastus lateralis (VL), there was a main effect for condition but no effect for muscle activation level. Thus the middle latency response was significantly task modulated. Values are means ± SE for 11 subjects. The asterisk and horizontal line indicate significant differences ($P < 0.05$) between movement conditions.
Reflexes in VL were similar to MG and SOL except that both early ($P < 0.05$) and middle ($P < 0.05$) latency responses were either very small or inhibitory during movement and larger excitatory responses during matched static contractions (Fig. 2, bottom). There was no effect of background EMG (as influenced by workload) on cutaneous reflex amplitude.

**H-reflexes**

The SOL H-reflex was significantly smaller at low levels of muscle activation ($P < 0.05$), but there was no difference in H-reflex size between movement and static conditions (Fig. 3, top). Hence there was no task-dependent modulation of the H-reflex. M-wave amplitude ($14.5 \pm 7\% M_{\text{max}}$, mean $\pm$ SD) did not differ significantly across conditions (see Fig. 3, bottom), and thus the intensity of stimulation was consistent across all conditions. When analyzing the data from different points on the M-H curve, it was determined that neither the M-wave nor H-reflex showed any significant differences across movement conditions or contraction level when comparing these different points on the M-H curve. Thus the size of the “test” H-reflex is not a confounding factor in these types of experiments.

**Direct comparison of cutaneous and H-reflexes in SOL**

We wanted to have a direct comparison between the cutaneous and H-reflex pathways, and thus SOL middle latency cutaneous responses were normalized to $M_{\text{max}}$. Following this procedure, the same significant difference between tasks was observed. This is shown in Fig. 4 (top). In the bottom panel of Fig. 4, the H-reflex data have been replotted to better show the difference between the cutaneous and H-reflexes.

**DISCUSSION**

In these experiments a novel approach was taken to examine the issue of reflex control in different pathways. The main observation from this experiment was that cutaneous and H-reflexes behaved differently in the same controlled, experimental situation. We observed task-dependent reflex modulation only in middle latency cutaneous reflexes and background-
dependent were kept constant so that the velocity of muscle
shortening would be consistent across all conditions. The un-
derlying assumption was that both the central pattern for gen-
erating the cycling movements and the dynamic input from the
Ia afferents were similar in all conditions due to the control of
movement velocity and joint angle. In previous animal exper-
iments Ia input from VL has been reported to be the major
afferent source affecting H-reflex modulation associated with
cyclical movement of the limb in dogs (Misiaszek et al. 1995).
However, we observed modulation of the reflex with a pre-
sumed tonic level of Ia input. We also observed that the
H-reflex is graded simply by the background level of excitation
of the motoneuronal pool, and this is maintained during con-
trolled movement as well as static contraction. This was an
unexpected observation. However, one must be cautious in
oversimplifying this relationship since measurements here
were made only at one point in the movement cycle. Further,
Yang and Whelan (1993) observed that SOL H-reflex ampli-
tudes were different at comparable EMG levels during swing
and stance. Thus the H-reflex amplitude scales with other
factors including EMG level during movement.

During static contraction, as the level of excitability in-
creases, the amplitude of the H-reflex increases (Pierrot-De-
seilligny 1997). However, Capaday and Stein (1986, 1987)
showed that there were significant differences in H-reflex size
at similar EMG levels when comparing the static task of
standing to the dynamic task of walking. They observed that
the H-reflex amplitude was larger at a given level of EMG
during standing than during walking (and also larger while
walking than running) and concluded that reflex amplitude
was independent of EMG drive. They attribute this difference
to central mechanisms acting at a premotoneuronal locus and
causing an increase in presynaptic inhibition of the SOL Ia
afferents. In contrast, the recent study of Simonsen and Dyhre-
Poulsen (1999) suggests a task independence of H-reflex am-
plitude between walking and running. The discrepancy be-
tween their observations and those of Capaday and Stein
(1986, 1987) could be due to the fact that the method of
Simonsen and Dyhre-Poulsen (1999) accounts for variations in
M_max throughout the movement cycle. It is of interest to
compare these observations during walking to our task inde-
pendence here during leg cycling, where variations in M_max
were also taken into account by sampling M_max in each con-
dition. Further, Misiaszek and Pearson (1997) observed that,
during locomotion in decerebrate cats, large H-reflexes (i.e.,
with M-waves present) did not modulate when background
EMG was also high. They suggest that the effect of presynaptic
inhibition can be overcome with high levels of muscle activa-
tion. Although it is uncertain how large an effect this might
have had in this study, it is possible that there was some
saturation in the H-reflex pathways of our subjects, which
could have masked any task-dependent modulation.

Another possibility is that input from force-sensitive recep-
tors (i.e., Golgi tendon organs) from extensor muscles (VL,
SOL, or MG) make excitatory synaptic connections via inter-
neuronal pathways, as demonstrated in the cat (Pearson and
Collins 1993) and suggested in the human (Stephens and Yang
1996). An increase in muscle activation would lead to in-
creased Golgi tendon organ firing, which would in turn cause
increased Ia discharge onto a network. Whether Ia input causes
increased excitation or decreased inhibition, the result would
be a larger reflex amplitude.
Differences between H- and cutaneous reflex modulation

Our results indicate that central drive and peripheral feedback (from changing background muscle activity) had an effect on the resultant amplitude of the H-reflex. Therefore the control of the H-reflex seems to be a complicated interaction between peripheral and central factors. On the other hand, cutaneous reflexes seem to be influenced more centrally. The absence of load-dependent modulation, in addition to the observation of task dependence in our results suggests that cutaneous reflexes are likely governed by central influences, either from the brain or spinal cord. There is ample evidence from previous work to support this idea (Brown and Kukulka 1993; De Serres et al. 1995; Duyssens et al. 1992; Komiyama et al. 2000; Van Wezel et al. 1997; Yang and Stein 1990). Brown and Kukulka (1993) observed phase-dependent modulation of cutaneous reflexes during cycling movements, but not during matched static positioning and activity of the lower leg muscles. In concert with the evidence that cutaneous reflexes are unaffected by passive leg cycling movement (Brooke et al. 1999), our data would seem to corroborate the assertion that cutaneous reflexes are modulated during movement only in the presence of a rhythm-generating network. However, a limitation of this experiment was that we were not able to control all types of afference. It is not known how differences in acceleration between the two types of activity (moving and static contraction) might have affected the results, or if they even play a role in controlling cutaneous reflex activity.

Therefore while cutaneous and H-reflexes show some similarities in behavior under certain conditions (e.g., phase modulation), they do not appear to be controlled by the same mechanisms. When a direct comparison of cutaneous and H-reflexes was made (Fig. 4), H-reflexes scale to background muscle activity, while cutaneous reflex behavior was dependent on task. During cycling, the H-reflex has been shown previously to be highly sensitive to the velocity of movement (Cheng et al. 1995a; McIlroy et al. 1992), and our results also indicate a sensitivity to muscle activity levels. Cutaneous reflexes have not been shown to change with either of these variables but do change as the mode of locomotion changes as we have observed in these experiments, as well as in previous research (Komiyama et al. 2000). Thus the changes in reflex response will be different as the context of movement changes for each type of reflex.

In summary, the main observation in this study was a reflex reversal of a middle latency cutaneous when comparing static contraction to movement. Overall, cutaneous responses were larger and excitatory during static contraction but much smaller and/or inhibitory during movement. H-reflexes were not task modulated in these experiments, which adds to the accumulating evidence that cutaneous and H-reflexes may be modulated by completely separate mechanisms.

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