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Progressive Adaptation of the Soleus H-Reflex With Daily Training at Walking Backward

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Schneider, Cyril and Charles Capaday. Progressive adaptation of the soleus H-reflex with daily training at walking backward. *J Neurophysiol* 89: 648–656, 2003; 10.1152/jn.00403.2002. When untrained subjects walk backward on a treadmill the amplitude of the soleus H-reflex in midswing is equal to or exceeds the value in stance. This is a surprising result because during the swing phase of backward walking the soleus is inactive and its antagonist, the tibialis anterior, is active. We suggested that the high amplitude of the soleus H-reflex in late swing reflects task uncertainties, such as estimating the moment of foot contact with the ground and losing balance. In support of this idea we show that when untrained subjects held on to handrails the unexpected high-amplitude H-reflex during midswing was no longer present. We therefore asked whether daily training at this task without grasping the handrails would adaptively modify the H-reflex modulation pattern. In this event, within 10 days of training for 15 min daily, the anticipatory reflex activity at the beginning of training was gradually abated as the subjects reported gaining confidence at the task. However, when adapted subjects were made to walk backward with their eyes shut, the anticipatory reflex activity in midswing returned immediately. The reflex changes as a result of training were not due to changes in the motor activity or kinematics; they are likely part of the motor program controlling backward walking. This adaptive phenomenon may prove to be a useful model for studying the neural mechanisms of motor learning and adaptive plasticity in humans and may be relevant to rehabilitation programs for neurological patients.

INTRODUCTION

Change of the vestibuloocular reflex gain induced by changes in visual image motion is a classic example of experience-dependent adaptation of a simple reflex (Lisberger 1996). It is a case of motor learning consequent to modification of visual inputs as occurs, for example, when wearing magnifying eyeglasses for several days. Conditioning the eye-blink reflex to respond to an auditory tone is an example of classical conditioning mediated by the cerebellum (Steinmetz 1996). Long-term modifications of simple spinal cord reflexes can also be

induced. Wolpaw (1997) has shown that the H-reflex and the stretch reflex can be enhanced or reduced by operant conditioning, independently of the level of motor activity in rats and monkeys. Similar results were obtained for the biceps stretch reflex in humans (Segal and Wolf 1994). In animals this change persists after spinal transection, establishing that the basic neural substrate is within the spinal cord (Wolpaw 1997). However, the neural mechanisms involved have yet to be established and, more importantly, the functional purpose of this phenomenon remains to be elucidated. A reasonable hypothesis is that the phenomenon reflects the natural adaptation of spinal reflex circuits during motor learning or motor adaptation (Bouyer et al. 2001; Carrier et al. 1997), however, no human model of spinal cord reflex adaptation or plasticity in the context of a natural motor task existed. Here we demonstrate such an experimental model as a direct result of our recent work on central versus feedback control of reflex modulation (Schneider et al. 2000).

In a previous study (Schneider et al. 2000), we showed that when untrained subjects walk backward, the H-reflex of the ankle extensor soleus increased to a high value in midswing just prior to the onset of ankle extensor activity and about 150 ms before toe contact. This was a very surprising result since in midswing the soleus was inactive, but its antagonist the tibialis anterior (TA) was active. The situation is very different while walking forward, during which the soleus H-reflex increases progressively during the stance phase nearly in parallel with the soleus electromyographic (EMG) activity (Capaday and Stein 1986) and is shut off during the swing phase while the TA is active (Andersen and Sinkjaer 1999; Capaday and Stein 1986; Lavoie et al. 1997; Schneider et al. 2000; Yang and Whelan 1993). The modulation pattern of the H-reflex during normal walking thus follows the classic pattern of reciprocal inhibition between antagonistic muscles (Lavoie et al. 1997). We therefore suggested that the high amplitude of the soleus H-reflex in the midswing phase of backward walking is

Address for reprint requests: C. Capaday, Brain and Movement Laboratory, Centre de Recherche Université Laval-Robert Giffard, F-6500, 2601 de la Canardière, Québec City, QC G1J 2G3 Canada (E-mail: charles.capaday@anm.ulaval.ca).

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related to task uncertainties, such as estimating the moment of foot contact with the ground and losing balance (Schneider et al. 2000). Here we provide evidence in support of this idea and, more importantly, show that with daily training at walking backward the anticipatory reflex activity at the beginning of training is gradually abated as the subjects reported gaining confidence at the task. A summary of this work has been published as an abstract (Schneider and Capaday 1999).

METHODS

Subjects and outline of the experiments

The experiments were done on eight normal human subjects ranging in age between 22 and 32 yr (25.5 ± 4 ; mean \pm SD). All subjects gave their consent after being informed of the nature and purpose of the experiment, which was approved by the local ethics committee. None of the subjects had any previous experience at walking backward on a treadmill or were involved in physical activities that required walking or running backward. In all subjects, an initial experiment was done to record the pattern of EMG activity in the ankle muscles, the leg joint kinematics, and the modulation pattern of the soleus H-reflex while walking backward. Thereafter, subjects trained daily at walking backward for 15 min, excluding weekends. Measurements were made, as in the initial experiment, every 3 days throughout a training period of 16 days (i.e., 6 experimental sessions). After the subjects had ceased their training, persistence of the adapted H-reflex modulation pattern was tested once a month over 5 months. In these posttraining experiments, the H-reflex modulation pattern was measured twice, at the beginning and at the end of the experiment that typically lasted 1.25 h. In an additional four untrained subjects, the H-reflex modulation pattern was studied during walking backward with and without grasping the treadmill handrails. In four subjects at the end of their training, the H-reflex modulation pattern was studied while they walked backward with their eyes closed.

EMG recordings and stimulation

EMG recordings were obtained from the soleus and TA of the right leg with bipolar Ag-AgCl electrodes (7-mm-diam recording surface) filled with saline gel. The recording electrodes were placed at the same pen-marked position in each experiment. H-reflexes were elicited by electrical stimuli of 0.5 ms duration to the tibial nerve in the popliteal fossa. The cathode was an Ag-AgCl electrode (7-mm diam) filled with saline gel and held in place by a rubber strap wrapped around the leg. The anode consisted of a thin brass plate (3×7 cm) covered with gauze and moistened with saline placed over the patella above the knee. A large ground plate was placed over the upper part of calf, between the stimulating electrode and the recording electrodes. Electrogoniometers (Biometrics, Newport, Gwent, UK) were used to measure the ankle, knee, and hip angular displacements in the sagittal plane. A pressure-activated switch was placed inside the shoe, under the metatarsal-phalangeal joint of the big toe, and served as a marker for the onset of the backward step cycle (toe contact) and data acquisition.

Training and experimental procedures

The training procedure required subjects to walk backward on a treadmill at their preferred speed (on average 4.5 km/h) daily for 15 min, excluding weekends. The treadmill speed chosen in the first experimental session remained the same throughout all subsequent sessions. The first experimental session will be referred to as day 1 and the sixth and last session occurred on day 16. The following experimental procedures were strictly adhered to in all sessions

throughout the training program. To determine the modulation pattern of the soleus H-reflex during the backward step cycle, H-reflexes were obtained at increments of 50 ms starting from toe contact. However, to improve the temporal resolution during the swing phase, H-reflexes were elicited at increments of 20 ms. Electrical stimuli to the tibial nerve were delivered at each selected phase of the step cycle at intervals ranging between one and three steps, at random. Only one stimulus was delivered per step cycle. Eight H-reflexes were averaged at each selected phase of the step cycle. The amplitude of the H-reflex during quiet standing was determined at least twice throughout the experiment (minimally, before walking, and at the end of the experiment). The amplitude and shape of soleus M-wave served as a measure of the effective stimulus strength delivered to the tibial nerve. During the experiment the M-wave was monitored in real-time by a time-amplitude window discriminator implemented in software (Capaday et al. 1995). The M-wave time-amplitude acceptance window was determined from recordings of the M-wave and H-reflex recruitment curves obtained during quiet standing (QS) at the beginning of the experiment. Responses having M-waves that were outside the acceptance window were rejected in real-time. Consequently, coefficients of variation of the averaged M-waves were typically around 10%. The mean value of the soleus and TA EMG activities were measured in real-time from the rectified and filtered EMG signals over a 50-ms time interval prior to stimulus (and see following text).

The H-reflex amplitude in the monkey shows a diurnal rhythm (Downman and Wolpaw 1989), consequently all experiments were done between the hours of 0900 and 1200. Further details on the experimental procedures used in the present study and their neurophysiological basis are described in several publications from this laboratory (Capaday 1997; Capaday et al. 1995; Lavoie et al. 1997; Schneider et al. 2000).

Data reduction and analysis

At the beginning, middle, and end of each experimental session, averages ($n = 32$ steps) of the EMG activities and joint angular displacements were obtained during backward walking, with no stimulation, and stored on computer disk for further analysis. The coefficient of variation between sessions of each subject's stance and swing durations was found to be between 0.05 and 0.3. We therefore were able to express temporal parameters, such as duration of EMG bursts, with respect to a normalized unit step cycle. The normalized duration during which the H-reflex could be elicited was calculated separately for the stance and swing phases. These procedures allowed us to make statistical comparisons between subjects over the course of training, as detailed under RESULTS. The mean value of the soleus EMG background at the time the reflexes were elicited was determined as in the preceding section, as well as from EMG recordings during control steps obtained throughout the experiment. It was calculated from the mean value of the rectified and filtered EMG over a 20-ms time interval centered on the time of occurrence of each H-reflex (not the time of stimulation). The amplitudes of the soleus H-reflexes obtained during backward walking were normalized for each session with respect to the amplitude of H-reflex measured during QS, which was measured several times in the same session. It should be noted that the main result we report involves a change in the timing pattern and is thus independent of any amplitude normalization procedure one cares to adopt. For each subject one H_{\max} to M_{\max} ratio was determined per session from the recruitment curves measured during quiet standing. Time and amplitude variables related to EMG activity were measured in each session. The EMG variables were correlated with the duration during which the H-reflex could be elicited and separately for the swing and stance phases for all sessions.

RESULTS

The results are presented in four sections. We first show that, when untrained subjects hold on to handrails, the unexpectedly

high H-reflex in midswing is no longer present. We then describe the time course of adaptation of the soleus H-reflex modulation pattern in the course of daily training at walking backward. We present evidence that the progressive changes of its amplitude and modulation pattern are unrelated to changes in the pattern and level of motor activity or limb kinematics. In the last section we show that, when subjects are tested monthly over a 5-mo period, after they stopped training, the adapted H-reflex modulation pattern persists.

Effects of postural confidence on the H-reflex modulation pattern

We had noticed at the outset of these experiments that some subjects were unable to securely walk backward on the treadmill unless they could lightly grasp the handrails, but without using them for weight support. We thus asked whether increasing the postural confidence of untrained subjects in this way would at once modify the H-reflex modulation pattern. We thus studied a group of subjects who could walk without grasping

the handrails in two different conditions in a single experimental session. In one condition the untrained subjects were required to walk backward without handrail support and in the other they grasped the handrails. The conditions were tested in random order. As previously described (Schneider et al. 2000), when subjects walked without handrail support, a large H-reflex occurred in midswing before the onset of soleus activity and while the TA was still active (Fig. 1). For the four subjects tested, the peak H-reflex in midswing occurred on average 113 ms (18 ms, SD) before the onset of soleus activity. In contrast, when grasping the handrails, the H-reflex began to increase in late swing, nearly coincident with the onset of soleus EMG activity and after the TA activity had ceased. While grasping the handrails, the H-reflex modulation pattern was thus reciprocal. The change observed during handrail grasping was immediate and consequent to grasping them. All naive subjects reported feeling more confident and secure when grasping the handrails. Figure 1 also shows that the EMG pattern of the soleus and TA in the two conditions was not significantly different in time course or amplitude.

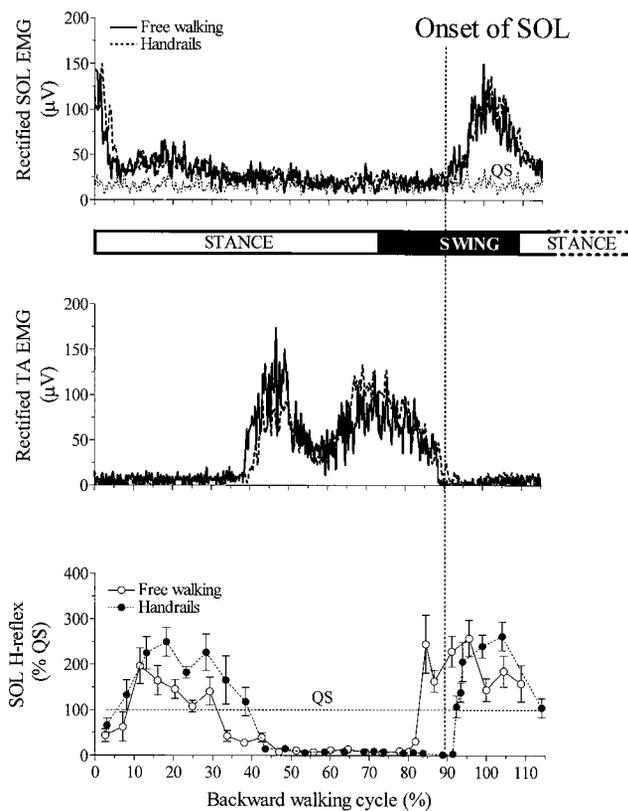


FIG. 1. Example of the effects of grasping the handrails on the soleus H-reflex modulation pattern during walking backward from a single untrained subject. Rectified electromyographic (EMG) activity of soleus (SOL) and tibialis anterior (TA) are shown along with the corresponding soleus H-reflex amplitude (averages of 8 responses, \pm SD). Recordings are superimposed for both conditions, walking backward freely and while grasping the handrails. Data are plotted as a function of normalized time after toe contact. H-reflex values are plotted against the time of their occurrence, not the time of stimulation in this and all other figures. H-reflex amplitude and soleus EMG activity during quiet standing (QS) are indicated. Rectified EMG traces are averages of 32 successive step cycles in each condition. White and black horizontal bars beneath the SOL EMG traces indicate the duration of stance and swing phases, respectively. Dashed vertical line indicates the onset of the soleus EMG activity in swing. Format and trace parameters of this figure apply to all similar subsequent figures.

Time-course and characteristics of the soleus H-reflex adaptation

Recordings of the EMG activity of the soleus and TA and the leg kinematics during the backward step cycle for the 1st and 10th day of training are superimposed in Fig. 2, along with the soleus H-reflex modulation pattern from the 1st to the 10th day. In all subjects the pattern of soleus H-reflex modulation in stance is out of phase with the soleus motor activity, as its peak occurs after the peak of soleus EMG activity near toe contact. In this example, the peak amplitude of H-reflex in stance is not significantly different from that of the H-reflex in QS, despite the fact that the EMG activity is much higher. This was observed in five of eight subjects. From that point on, the H-reflex decreases as the activity in the TA increases in mid-stance. The H-reflex reaches its minimum value (essentially near 0) around the time of peak TA EMG activity. A second burst of TA activity occurs just prior to the onset of swing. This second TA burst maintains the ankle dorsiflexed in swing and is terminated just before the onset of soleus EMG activity. The soleus EMG activity stiffens the ankle for toe contact and thereafter serves to control lowering of the heel toward the ground. In untrained subjects (day 1), the H-reflex unexpectedly begins to increase in early swing prior to onset of soleus burst and while the TA is still active. Remarkably, its amplitude is often highest in this part of the step cycle despite the fact that there is as yet no activity in the extensor soleus and its antagonist, the TA, is still active, having a mean value of about $63 \pm 19 \mu\text{V}$ (mean \pm SD, $n = 8$ subjects).

An important point illustrated in Fig. 2 with respect to the EMG activities and joint kinematics is that they did not change to any significant extent over the course of the training period. In marked contrast, the modulation pattern of the soleus H-reflex and its peak amplitude in midswing change in a systematic manner. Superimposition of H-reflex modulation patterns obtained on day 1 through to day 10 of training shows that the time at which the H-reflex begins to increase in early swing is shifted progressively toward the onset of soleus activity. For this subject the shift was from 75 to 88% of the normalized step cycle and corresponds to a time shift of 146 ms. Thus the main

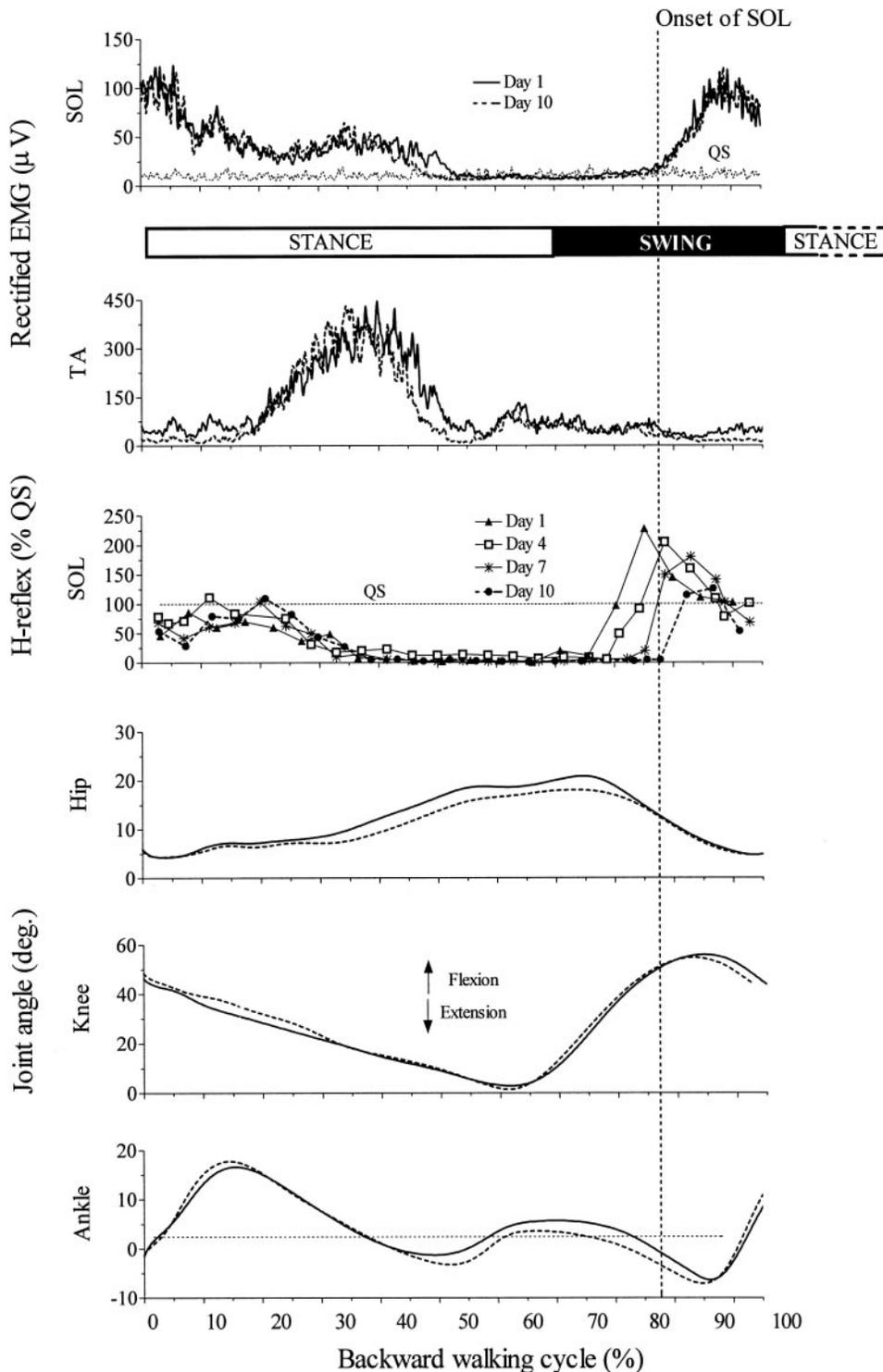


FIG. 2. Example of the progressive adaptation of the soleus H-reflex modulation pattern as a result of daily training at walking backward. Rectified EMG activity of the soleus and the tibialis anterior are shown along with the corresponding soleus H-reflex amplitude and the angular displacement of the hip, knee, and ankle joints. H-reflex modulation patterns from day 1 training to day 10 training are superimposed. EMGs and joint angular displacements are only shown for days 1 and 10. Data are plotted as a function of normalized time after toe contact. Joint flexion corresponds to an upward deflection of the angular displacement trace.

temporal characteristic of the adapted reflex modulation pattern was that the H-reflex began to increase in midswing rather than in early swing and strictly coincident with onset of the soleus burst (Fig. 2). In all subjects this adapted H-reflex modulation pattern was observed by the 10th day of training. No characteristic change in the time course of H-reflex modulation pattern was observed for the stance phase (Fig. 2).

All subjects reported that they felt more confident and secure at the task as a result of training and toward the end of their training the majority of subjects would have liked to have

increased their walking speed, but this was not allowed. Initially the experimenters had to increase the treadmill speed progressively to the subject's desired walking speed. This was no longer necessary toward the end of training since subjects decided, on their own, to set the treadmill speed themselves and began to walk backward with the treadmill already running at the chosen speed.

When adapted subjects are asked to walk backward with their eyes closed, the H-reflex modulation pattern reverts immediately back to that observed in untrained subjects (Fig. 3).

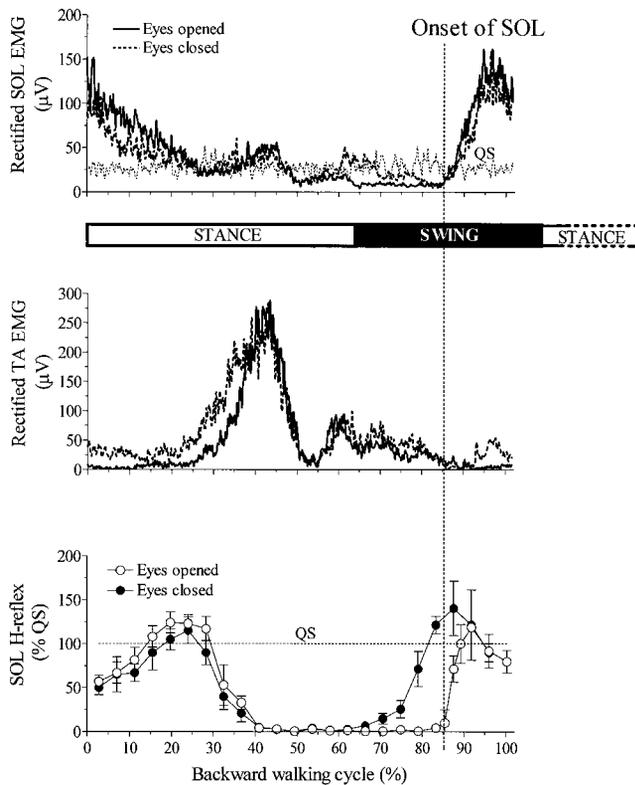


FIG. 3. Example showing that, when adapted subjects are asked to walk backward with their eyes closed, the soleus H-reflex modulation pattern immediately reverts back to that observed at the onset of training. Data shown in this figure were obtained in the same experimental session. The format of the figure is the same as that of Figs. 1 and 2. Note that, in this subject, the EMG activity of the TA in the stance phase began slightly earlier when walking with eyes closed, but this is unrelated to the H-reflex changes in swing.

This was observed in all four subjects tested in this manner. On average, the H-reflex began to increase 180 ± 54 ms ($n = 4$ subjects) before the increase in the adapted state. The peak amplitude of the H-reflex in the swing phase also increased by $22 \pm 8\%$ ($n = 4$ subjects) when walking backward with eyes closed. There were no changes of EMG activity of the soleus or TA in swing (Fig. 3). In two subjects, however, the TA

EMG activity in stance began earlier, as shown in Fig. 3. All four adapted subjects reported feeling some insecurity and greater difficulty when walking backward with their eyes closed.

Quantitative characteristics of the soleus H-reflex adaptation

A quantitative summary of the temporal changes of the H-reflex modulation pattern during the course of training is presented in Fig. 4. The data shown are the group average values of the normalized duration of soleus and TA EMG activity during the step cycle, as well as the normalized duration of the time during which the H-reflex was above zero. For the stance phase none of these variables was significantly changed during the course of training (paired t -test, $n = 8$ subjects). The mean normalized duration of the soleus and TA EMG activity during stance was $39.2 \pm 0.87\%$ and $27.35 \pm 1.2\%$, respectively. The mean normalized duration during which the H-reflex was above zero during stance was $44 \pm 1.87\%$. In the swing phase, duration of soleus H-reflex above zero progressively and significantly decreases from 27 ± 6 to $10.8 \pm 3\%$ during the first 10 days of training (paired t -test, $P = 0.006$, $n = 8$ subjects). In contrast, no significant changes of the mean normalized durations of the soleus ($10.88 \pm 0.75\%$) and TA EMG activity ($26.10 \pm 0.88\%$) were observed during the training period. Figure 4 also shows that the modulation pattern of the H-reflex became progressively more reciprocal with training. It can be seen that by the 10th day of training the soleus H-reflex is high during soleus activity and shut off during activity of the TA.

The changes in the soleus H-reflex modulation pattern and amplitude observed during the training period can be represented in a simple manner by considering the decrease from its peak in stance to its minimum value (essentially 0) and the increase from minimum to its peak in late swing (Fig. 5). The group data were averaged for each experimental session in the training program (i.e., 16 training days that included 6 experimental sessions) and plotted against time relative to the onset of soleus activity in midswing. In the stance phase, the time to reach the peak H-reflex and the time to the H-reflex minimum do not significantly change between sessions (1-way ANOVA, $P = 0.89$ for H-reflex peak and $P = 0.67$ for H-reflex mini-

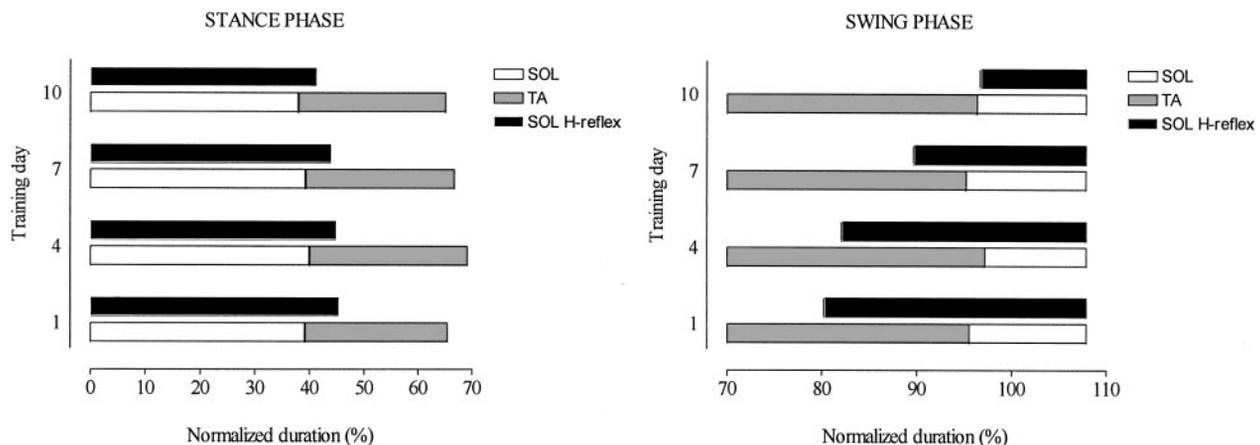


FIG. 4. Normalized duration (i.e., in percentage of backward step cycle) of the soleus and TA EMG activity are shown for each test day. Normalized duration during which the soleus H-reflex could be elicited is also shown. Data are shown separately for the stance and swing phases. The figure summarizes the results obtained in the 8 subjects studied. There was no significant difference in any of the stance phase duration parameters over the course of training. In contrast, the duration during which the soleus H-reflex could be elicited during swing decreased significantly over the course of training.

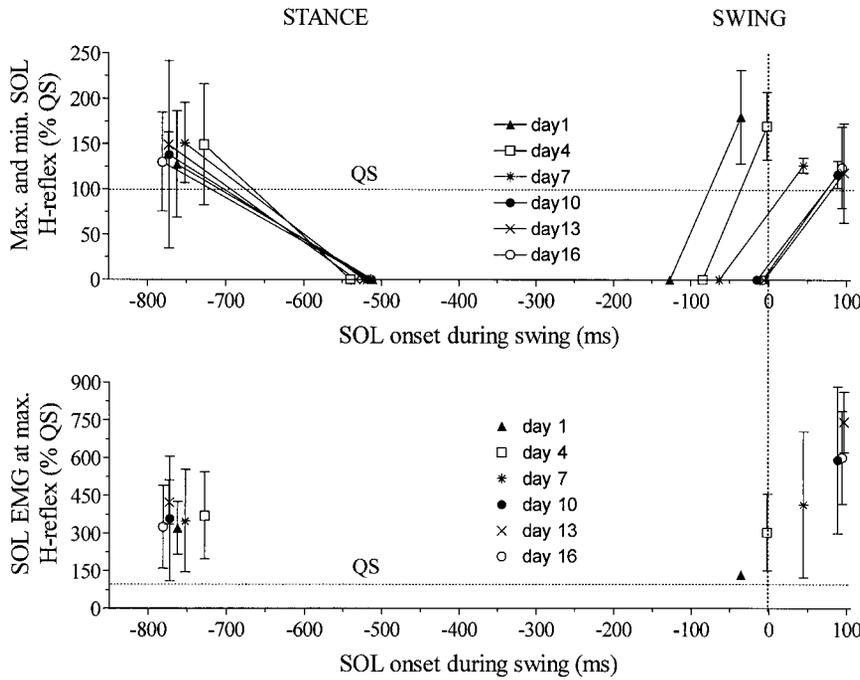


FIG. 5. Characteristics of the soleus H-reflex adaptation (*top*) over the 6 experimental sessions relative to the soleus EMG activity at the time the reflex is elicited (*bottom*). Each data point is the mean \pm SD value for the 8 subjects. H-reflex amplitudes are expressed relative to QS and plotted against time relative to the onset of soleus EMG activity in swing (dashed vertical line). Soleus EMG activity during the backward step cycle is normalized relative to the mean EMG activity during quiet standing. Peak and minimum values of the H-reflex are shown separately for the stance and swing phases. In the stance phase neither the peak value nor the time to peak of the H-reflex are modified in the course of training. In contrast, in the swing phase the time to peak of the H-reflex is progressively delayed in the course of training. Moreover, the peak amplitude of the H-reflex in swing also decreases in the course of training despite the fact that there is more soleus EMG activity at the moment the reflex is elicited.

num). In swing, the time at which the H-reflex begins to increase from its minimum value is shifted from a mean of -127.3 ± 33 ms on day 1 to a mean of -15.6 ± 12 ms on day 10. The values are expressed relative to the onset of soleus activity in swing (Fig. 5). Similarly, the time at which the H-reflex reaches its peak relative to the onset of soleus EMG activity is shifted from -36 ± 20 to 88 ± 40 ms. In swing, the time elapsed between the increase of the H-reflex above minimum and soleus EMG onset becomes significantly smaller by day 7 (paired *t*-test, $P = 0.0044$, $n = 8$ subjects). This decrease achieves a steady value at day 10, as shown by the coincidence of curves for days 10 to 16 in Fig. 5.

Adaptation of the soleus H-reflex peak amplitude during swing

Normalized means of the soleus EMG activity measured at the time of occurrence of the H-reflex are also shown in Fig. 5 beneath the normalized H-reflex values. The normalized H-reflex peak value in stance remains constant throughout the 16 days of training ($140.8 \pm 10.4\%$, $n = 8$ subjects), as does the normalized value of the soleus EMG activity ($358 \pm 37\%$, $n = 8$ subjects). The situation was very different for the swing phase. Associated with the progressive delay of the H-reflex increase in swing, its peak amplitude also significantly decreased with training. On day 1 the mean value of the peak H-reflex was $180.4 \pm 37.5\%$ of the control value in QS and it progressively decreased to $116.8 \pm 15\%$ by the 10th day of training (paired *t*-test, $P < 0.0001$, $n = 8$ subjects). By this time, it was significantly smaller than the peak of the H-reflex in stance (unpaired *t*-test, $P = 0.015$, $n = 8$ subjects) and comparable to the control value during QS (unpaired *t*-test, $P > 0.5$, $n = 8$ subjects). The striking observation was that this progressive decrease of the peak H-reflex during training occurred despite the fact that the soleus background EMG activity was considerably greater at the time of the peak H-reflex (from $136 \pm 5\%$ of QS on day 1 to $606 \pm 184\%$ on day 16).

The relationship over the course of training between the peak H-reflex value in swing and the soleus background EMG at the time of its occurrence is shown in Fig. 6A. It can be seen that there is an inverse relation between the peak H-reflex and the soleus background EMG ($r^2 = 0.83$, $P = 0.012$) and stands in contrast to the usual direct relation between these variables (e.g., Capaday and Stein 1986; Schneider et al. 2000). Neither the change in the H-reflex modulation pattern nor the decrease

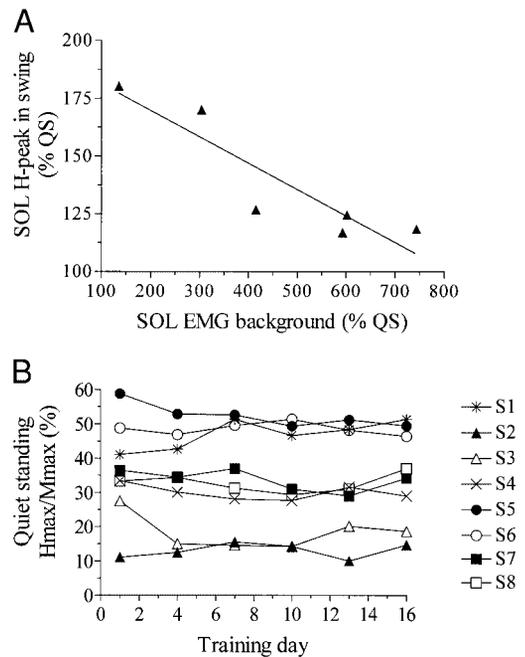


FIG. 6. A: relationship between the peak amplitude of soleus H-reflex in swing versus the mean value of the background soleus EMG at the time the reflex is elicited. Each point is the average obtained from the 8 subjects and represents the value on each of 6 test days (i.e., from day 1 to day 16). B: H_{\max} to M_{\max} ratio measured during QS on each test day after the start of training. Inset: Each symbol represents a different subject (e.g., S1, S2, etc.).

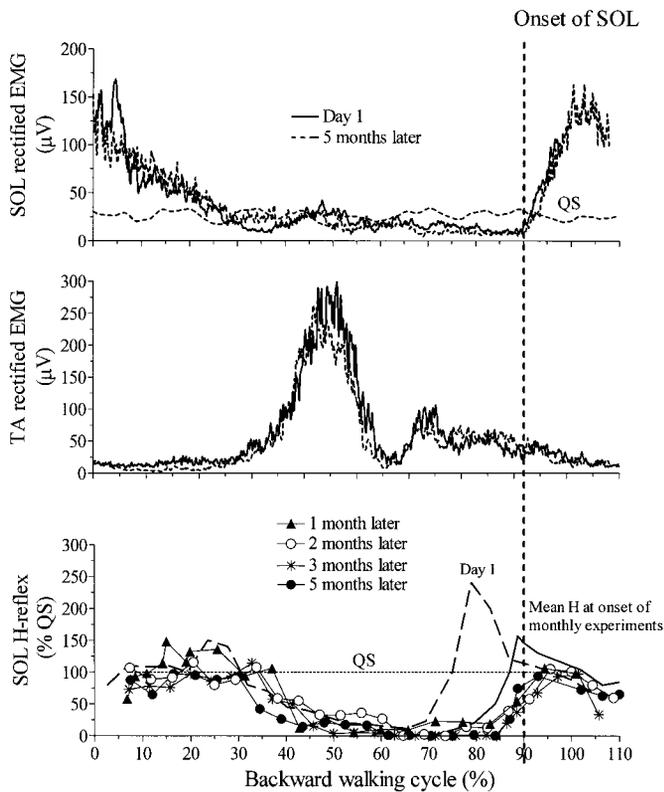


FIG. 7. Example of the persistence of the adapted H-reflex modulation pattern after training stopped. The format of this figure is the same as that of Figs. 1–3. The H-reflex modulation pattern on day 1 is shown by the dashed trace. At the start of each monthly experiment after training had stopped the H-reflex modulation pattern was intermediate between that on day 1 and the fully adapted pattern. This is indicated by the solid trace labeled “Mean H at onset of monthly experiments”. However, in all cases, within 20 min of walking the H-reflex modulation pattern reverted back to that observed in the fully adapted subject. Note that in the adapted pattern the peak amplitude of H-reflex in swing is equal to the value during QS, despite a much higher level of soleus EMG activity.

of the peak H-reflex in swing were associated with changes in the QS H_{\max} to M_{\max} ratio measured over the course of training (Fig. 6B).

Long-term persistence of the training effect

After they had ceased their daily training subjects were tested monthly over a period of 5 mo. An example comparing the H-reflex modulation pattern on day 1 with those obtained at monthly intervals is shown in Fig. 7. For all subjects, in the initial 20 min of walking backward, the soleus H-reflex began to increase slightly before the onset of the soleus EMG activity in midswing, but much later than in untrained subjects (day 1). In other words, at the start of each monthly experiment after training had stopped, the H-reflex modulation pattern was intermediate between that on day 1 and the fully adapted pattern. Thereafter, there was no essential difference in the time course of the H-modulation pattern after 20 min of walking and the adapted reflex modulation pattern obtained up to 5 mo previously, i.e., the waveforms superimpose nearly exactly (Fig. 7). The characteristics of the adapted H-reflex modulation pattern displayed by this subject are typical; the time of occurrence of the peak H-reflex is shifted toward late swing and the peak H-reflex amplitude is smaller despite a greater level of

background motor activity (Fig. 7). The time of occurrence of the peak H-reflex shifted from early swing on day 1 to midswing after day 10 by an average of 89 ± 21 ms, $n = 8$ subjects), or equivalently $11.1 \pm 2.3\%$ of the cycle. There were no significant changes in the EMG activity of the soleus or the TA in going from day 1 to 5 mo posttraining (Fig. 7).

DISCUSSION

In this study we showed that, in untrained subjects, the unexpectedly large H-reflex that occurs in the midswing phase of backward walking—well before ankle extensor activity and toe contact—is related to task uncertainties, such as estimating the moment of foot contact and losing balance. This was demonstrated by the observation that, immediately upon grasping the handrails, the H-reflex in midswing dropped to zero and peaked, as expected, at the peak of soleus activity at toe contact. This is consistent with other studies showing that reflex responses to mechanical perturbation during walking or standing are reduced when subjects are provided greater postural support or when the mechanical perturbation has a lesser effect on disturbing balance per se (Misiasek et al. 2000; Rietdyk and Patla 1998). The most important new finding of this study, however, was that, with daily training at walking backward, the H-reflex modulation pattern changed progressively until it had the same temporal characteristics as those observed in untrained subjects who secured themselves by grasping the handrails. Moreover, in adapted subjects who were asked to walk backward with their eyes shut, the anticipatory reflex activity in midswing returns immediately. We also showed that the reflex changes that occurred with training were not due to changes in the motor output pattern or limb kinematics; they are likely part of the motor program controlling backward walking.

The other important observation made in this study was that, in adapted subjects, the size of the H-reflex at toe contact was smaller than its value in early swing at the beginning of training, despite a larger level of soleus EMG activity at toe contact. This observation reinforces our interpretation that, in untrained subjects, the high value of the H-reflex in midswing reflects heightened stretch reflex excitability in anticipation of unexpected disturbances during the backward step cycle, as does the result obtained in adapted subjects walking backward with eyes shut. These observations also demonstrate and add to the evidence that the soleus H-reflex amplitude can be controlled independently of the level of motor activity (Andersen and Sinkjaer 1999; Capaday and Stein 1986, 1987; Edamura et al., 1991). Here we have shown that this control, whatever its mechanism, can be exerted progressively in the course of training at a motor task.

In what follows, we discuss the functional significance of our observations and the neural mechanisms potentially involved.

Functional significance

We have shown that the motor output pattern and the movement kinematics were essentially unchanged in the course of training. Plainly, this simply means that mature human subjects know how to walk backward. In contrast, the soleus H-reflex modulation pattern did change in the course of training. The

results therefore suggest that the motor program is composed of at least two separate but not necessarily independent processes. One is involved in controlling the motor output to the muscles, the other in controlling spinal reflex pathways. The latter process, as we have shown, is adaptable on a moment-to-moment basis as well as more gradually over the course of daily training. Our observations also add to the evidence that H-reflex measurements reflect functional characteristics of the motor program (Capaday 2002; Stein and Capaday 1988).

In the course of training, adaptive changes of the H-reflex modulation pattern were observed in the swing phase, but no changes were observed for the stance phase. This suggests that, once the foot is placed on the ground, the dynamics of the body are known to the CNS and readily controlled. The observation also reinforces our interpretation that the uncertainties during backward walking are related to the swing phase and are reflected by an unexpectedly high H-reflex.

Potential neural mechanisms

It is now clear that the spinal cord on its own is capable of some adaptive plasticity (Bouyer et al. 2001; Carrier et al. 1997). However, it seems unlikely that the progressive adaptation of the H-reflex observed here in normal human subjects was produced by the spinal circuitry itself. We suggest that the progressive adaptation we have observed reflects dynamic control of the reflex circuit by descending pathway(s). The observation that at the start of each monthly experiment after training had stopped the H-reflex modulation pattern was intermediate between that on day 1 and the fully adapted pattern and within 20 min reverted back to the fully adapted pattern supports this suggestion. In untrained subjects, the unexpectedly high amplitude of the H-reflex in the swing phase of backward walking may be explained by two neural mechanisms: increased postsynaptic excitability of the soleus α -motoneurons coupled with a reduction of presynaptic inhibition of their Ia-afferent terminals. This may be due to subliminal anticipatory activity in the corticospinal tract, for example. This is consistent with several observations. In the cat, the motor cortex has been shown to be involved when the animal needs to adapt its gait, such as, for example, when walking across a horizontal ladder or stepping over obstacles in its path. Drew (1993) summarized these results by stating "... these experiments show that there is an increase of cortical activity when an animal adapts its locomotor gait to the exigencies of the external environment". Coupled to this is the observation that integrity of the corticospinal tract is necessary for operant conditioning of the H-reflex in animals (Chen and Wolpaw 2002). Additionally, when untrained subjects walk backward on a treadmill, they all report needing to pay attention to the task and a general sense of uneasiness. Taken together, these observations suggest a role for the motor cortex in the control of backward walking, including control of the H-reflex circuit. Further, we hypothesize that this descending control subsides with training, accounting for the observed changes in the H-reflex modulation pattern. Whatever the neural mechanisms turn out to be, they are readily testable in intact behaving human subjects (Capaday 1997; Rothwell 1997).

Conclusion

It has been shown that the strength of the soleus H-reflex is positively correlated with physical activity (Nielsen et al. 1993), but in ballet dancers it is weaker despite the fact that they were the most physically active group studied by Nielsen et al. (1993). However, it is not clear why the reflexes are smaller in ballet dancers; they may be related to the type of physical activity, as suggested by Nielsen et al. (1993), or the result of nonmotor factors such as pain and inflammation. It has also been shown that adaptation of the H-reflex occurs in a single session with repeated short bouts of balancing on an unstable platform (Trimble and Kocreja 1994). What we demonstrate here, for the first time, is that progressive adaptation of a spinal reflex is possible in normal humans as a result of daily training at a natural motor task. This adaptive phenomenon may prove to be a useful model for studying the neural mechanisms of motor learning and natural adaptation of spinal cord circuits in humans. Elucidating these mechanisms is also important for understanding the nature of reflex dysfunction that results from damage to the brain and spinal cord (Stein et al. 1991). For example, in most spinal cord-injured subjects, the H-reflex remains high throughout the stance phase and is only slightly depressed during swing (Yang et al. 1991). The H-reflex modulation pattern is thus not reciprocal, as it is in normal subjects. Abnormally strong reactions to muscle stretch were observed at times in the step cycle when the H-reflex was abnormally high and it was suggested that these exacerbate the patients' walking deficits (Yang et al. 1991). Our results suggest the possibility that training neurologically impaired subjects at walking may lead to a more normal stretch reflex modulation pattern, which will assist rather than hinder walking.

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REFERENCES

- Andersen JB and Sinkjaer T. The stretch reflex and H-reflex of the human soleus muscle during walking. *Motor Control* 3: 151–157, 1999.
- Bouyer LJ, Whelan PJ, Pearson KG, and Rossignol S. Adaptive locomotor plasticity in chronic spinal cats after ankle extensors neurectomy. *J Neurosci* 21: 3531–3541, 2001.
- Capaday C. Neurophysiological methods for studies of the motor system in freely moving human subjects. *J Neurosci Methods* 74: 201–218, 1997.
- Capaday C. The special nature of human walking and its neural control. *Trends Neurosci* 25: 370–376, 2002.
- Capaday C, Lavoie BA, and Comeau F. Differential effects of a flexor nerve input on the human soleus H-reflex during standing versus walking. *Can J Physiol Pharmacol* 73: 436–449, 1995.
- Capaday C and Stein RB. Amplitude modulation of the soleus H-reflex in the human during walking and standing. *J Neurosci* 6: 1308–1313, 1986.
- Capaday C and Stein RB. Difference in the amplitude of the human soleus H reflex during walking and running. *J Physiol (Lond)* 392: 513–522, 1987.
- Carrier L, Brustein E, and Rossignol S. Locomotion of the hindlimbs after neurectomy of ankle flexors in intact and spinal cats: model for the study of locomotor plasticity. *J Neurophysiol* 77: 1979–1993, 1997.
- Chen XY and Wolpaw JR. Probable corticospinal tract control of spinal cord plasticity in the rat. *J Neurophysiol* 87: 645–652, 2002.

- Dowman R and Wolpaw JR.** Diurnal rhythms in primate spinal reflexes and accompanying cortical somatosensory evoked potentials. *Electroencephalogr Clin Neurophysiol* 72: 69–80, 1989.
- Drew T.** Motor cortical activity during voluntary gait modifications in the cat. I. Cells related to the forelimbs. *J Neurophysiol* 70: 179–199, 1993.
- Edamura M, Yang JF, and Stein RB.** Factors that determine the magnitude and time course of human H-reflexes in locomotion. *J Neurosci* 11: 420–427, 1991.
- Lavoie BA, Devanne H, and Capaday C.** Differential control of reciprocal inhibition during walking versus postural and voluntary motor tasks in humans. *J Neurophysiol* 78: 429–438, 1997.
- Lisberger SG.** Learning and memory in the vestibuloocular reflex. In: *The Acquisition of Motor Behavior in Vertebrates*, edited by J. R. Bloedel, T. J. Ebner, and S. P. Wise. Cambridge, MA: MIT Press, 1986, pp. 7–28.
- Misiaszek JE, Stephens MJ, Yang JF, and Pearson KG.** Early corrective reactions of the leg to perturbations at the torso during walking in humans. *Exp Brain Res* 131: 511–523, 2000.
- Nielsen J, Crone C, and Hultborn H.** H-reflexes are smaller in dancers from The Royal Danish Ballet than in well-trained athletes. *Eur J Appl Physiol Occup Physiol* 66: 116–121, 1993.
- Rietdyk S and Patla AE.** Context-dependent reflex control: some insights into the role of balance. *Exp Brain Res* 119: 251–259, 1998.
- Rothwell JC.** Techniques and mechanisms of action of transcranial stimulation of the human motor cortex. *J Neurosci Methods* 74: 113–122, 1997.
- Schneider C and Capaday C.** Long-term H-reflex adaptation during acquisition of motor skill. *Soc Neurosci Abstr* 25: 120, 1999.
- Schneider C, Lavoie BA, and Capaday C.** On the origin of the soleus H-reflex modulation pattern during human walking and its task-dependent differences. *J Neurophysiol* 83: 2881–2890, 2000.
- Segal RL and Wolf SL.** Operant conditioning of spinal stretch reflexes in patients with spinal cord injuries. *Exp Neurol* 130: 202–213, 1994.
- Stein RB and Capaday C.** The modulation of human reflexes during functional motor tasks. *Trends Neurosci* 11: 328–332, 1988.
- Stein RB, Yang J, Edamura M, and Capaday C.** Reflex modulation during normal and pathological human locomotion. In: *Neurobiological Basis of Human Locomotion*, edited by Shimamura M, Grillner S, and Edgerton VR. Tokyo: Japan Scientific Societies Press, 1991, p. 335–346.
- Steinmetz JE.** The brain substrates of classical eyeblink conditioning in rabbits. In: *The Acquisition of Motor Behavior in Vertebrates*, edited by J. R. Bloedel, T. J. Ebner, and S. P. Wise. Cambridge, MA: MIT Press, 1986, pp. 89–114.
- Trimble MH and Koceja DM.** Modulation of the triceps surae H-reflex with training. *Int J Neurosci* 76: 293–303, 1994.
- Wolpaw JR.** The complex structure of a simple memory. *Trends Neurosci* 20: 588–594, 1997.
- Yang JF, Fung J, Edamura M, Blunt R, Stein RB, and Barbeau H.** H-reflex modulation during walking in spastic paretic subjects. *Can J Neurol Sci* 18: 443–452, 1991.
- Yang JF and Whelan PJ.** Neural mechanisms that contribute to cyclical modulation of the soleus H-reflex in walking in humans. *Exp Brain Res* 95: 547–556, 1993.