

On the Potential Role of the Corticospinal Tract in the Control and Progressive Adaptation of the Soleus H-Reflex During Backward Walking

Roth-Visal Ung, Marie-Andrée Imbeault, Christian Ethier, Laurent Brizzi, and Charles Capaday

CRULRG, Brain and Movement Laboratory, Department of Anatomy and Physiology, Faculty of Medicine, Université Laval, Quebec City, Quebec, Canada

Submitted 22 February 2005; accepted in final form 6 April 2005

Ung, Roth-Visal, Marie-Andrée Imbeault, Christian Ethier, Laurent Brizzi, and Charles Capaday. On the potential role of the cortical tract in the control and progressive adaptation of the soleus H-reflex during backward walking. *J Neurophysiol* 94: 1133–1142, 2005; doi:10.1152/jn.00181.2005. When untrained subjects walk backward on a treadmill, an unexpectedly large amplitude soleus H-reflex occurs in the midswing phase of backward walking. We hypothesized that activity in the corticospinal tract (CST) during midswing depolarizes the soleus α -motoneurons subliminally and thus brings them closer to threshold. To test this hypothesis, transcranial magnetic stimulation (TMS) was applied to the leg area of the motor cortex (MCx) during backward walking. Motor-evoked potentials (MEPs) were recorded from the soleus and tibialis anterior (TA) muscles in untrained subjects at different phases of the backward walking cycle. We reasoned that if soleus MEPs could be elicited in midswing, while the soleus is inactive, this would be strong evidence for increased postsynaptic excitability of the α -motoneurons. In the event, we found that in untrained subjects, despite the presence of an unexpectedly large H-reflex in midswing, no soleus MEPs were observed at that time. The soleus MEPs were in phase with the soleus electromyographic (EMG) activity during backward walking. Soleus MEPs increased more rapidly as a function of the EMG activity during voluntary activity than during backward walking. Furthermore, a conditioning stimulus to the motor cortex facilitated the soleus H-reflex at rest and during voluntary plantarflexion but not in the midswing phase of backward walking. With daily training at walking backward, the time at which the H-reflex began to increase was progressively delayed until it coincided with the onset of soleus EMG activity, and its amplitude was considerably reduced compared with its value on the first experimental day. By contrast, no changes were observed in the timing or amplitude of soleus MEPs with training. Taken together, these observations make it unlikely that the motor cortex via the CST is involved in control of the H-reflex during the backward step cycle of untrained subjects nor in its progressive adaptation with training. Our observations raise the possibility that the large amplitude of H-reflex in untrained subjects and its adaptation with training are mainly due to control of presynaptic inhibition of Ia-afferents by other descending tracts.

INTRODUCTION

It has been hypothesized that backward walking is controlled at the kinematic level by the time-reversed motor program of forward walking (Lacquaniti et al. 1999). Interestingly, the modulation pattern of the soleus H-reflex is not a time-reversed version of the pattern during forward walking. While walking in the normal forward direction, the soleus H-reflex increases progressively during the stance phase nearly in parallel with

the soleus electromyographic (EMG) activity (Capaday and Stein 1986; Crenna and Frigo 1987; Ethier et al. 2003). It is abruptly reduced just before swing and remains essentially shut off throughout the swing phase and early stance while the TA is active (Ethier et al. 2003). 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). The modulation pattern is very different during backward walking. When untrained subjects walk backward on a treadmill, there is a marked increase of the soleus H-reflex in midswing, well before soleus EMG activity and toe contact (Schneider et al. 2000). This was an unexpected result because in midswing, the soleus is inactive while its antagonist, the tibialis anterior (TA), is active. We suggested that the high amplitude of the soleus H-reflex in the midswing phase of backward walking reflects an overall lack of confidence at the task (Schneider et al. 2000). This involves uncertainties such as, estimating the moment of foot contact with the ground, losing balance, etc. In support of this idea, we have recently shown that when untrained subjects held on to handrails the unexpected high-amplitude H-reflex in midswing was no longer present (Schneider and Capaday 2003). More importantly, in the same study, we reported that daily training at this task (without handrail support) resulted in an adaptive modification of the soleus H-reflex modulation pattern. Within 10 days of training, the modulation pattern of the soleus H-reflex became reciprocal—i.e., the H-reflex was high during soleus activity and shut off during TA activity. What occurred during the training period was a progressive time delay of the large H-reflex in midswing until its peak coincided with peak soleus EMG activity at toe contact in early stance. The time of occurrence of the maximal H-reflex thus shifted progressively from midswing to early stance. There also occurred a progressive reduction of the peak H-reflex amplitude despite greater EMG activity in early stance compared with midswing. Thus the anticipatory reflex activity at the beginning of training gradually abated as subjects gained confidence at the task. The reflex changes are not due to changes in ankle muscle activity or leg kinematics and do not involve persistent changes in the spinal cord; they must be part of the motor program controlling backward walking (Schneider and Capaday 2003). This adaptive phenomenon may be a useful model for studying the neural mechanisms of motor learning and adaptation in humans. We suggested two neural mechanisms to explain the unexpectedly high-amplitude H-reflex in the midswing phase

Address for reprint requests and other correspondence: C. Capaday, CRULRG, Brain and Movement Laboratory, F-6500, 2601 Chemin de la Canardière, Québec City, QC G1J 2G3, Canada (E-mail: charles.capaday@anm.ulaval.ca).

The costs of publication of this article were defrayed in part by the payment of page charges. The article must therefore be hereby marked "advertisement" in accordance with 18 U.S.C. Section 1734 solely to indicate this fact.

of backward walking; increased postsynaptic excitability of the soleus α -motoneurons coupled with a reduction of presynaptic inhibition of their Ia-afferent terminals (Schneider and Capaday 2003).

Previous work in animals suggests that the motor cortex (MCx) may have a role during backward walking and reflex control. For example, in the cat, the motor cortex is involved when the animal needs to adapt its gait, such as 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." Related to this is the observation that integrity of the corticospinal tract (CST) is necessary for operant conditioning of the H-reflex in the rat (Chen and Wolpaw 2002). This implies that the CST has access to the neural mechanisms controlling the H-reflex circuitry (Rudomin 1990). Additionally, when untrained subjects walk backward on a treadmill, they all report needing to pay attention to the task. Taken together, these observations suggest a possible role for the MCx in the control of backward walking, including control of the H-reflex pathway.

Here we test the hypothesis that, in untrained subjects, descending CST activity during midswing subliminally depolarizes the soleus α -motoneurons (because the soleus is inactive during the midswing phase) and thus brings them closer to firing threshold. As a consequence, Ia-afferent input would discharge a significant proportion of soleus α -motoneurons, accounting for the unexpectedly large soleus H-reflex. Transcranial magnetic stimulation applied over the leg area of the MCx was used to elicit motor-evoked potentials (MEPs) in the soleus at different phases of the backward walking cycle. We reasoned that if soleus MEPs could be elicited in midswing, while the soleus is inactive, this would be strong evidence for increased postsynaptic excitability of the α -motoneurons. It also follows that with training the modulation pattern of soleus MEPs would change in parallel with that of the H-reflex. Additionally, we measured facilitation of the soleus H-reflex by a conditioning stimulus to the MCx in midswing of backward walking and compared it to that obtained during voluntary plantarflexion and rest. If MCx excitability is increased in midswing, then a conditioning stimulus to the MCx at this time should facilitate the H-reflex. A partial summary of this work was published as an abstract (Ung et al. 2004).

METHODS

Subjects and outline of the experiments

The experiments to measure the H-reflex and MEP modulation pattern during backward walking were performed on 10 healthy human subjects (8 men, 2 women), aged between 23 and 54 yr [30.8 ± 10 (SD) yr]. All subjects gave their consent after being informed of the nature and the purpose of the study in accordance with the Declaration of Helsinki. The study was approved by the local ethics committee. None of the subjects had any previous experience at walking backward on a treadmill or was involved in activities that required walking or running backward on a regular basis. The subjects trained at walking backward on the treadmill every day for 15 min over a period of 16 days, excluding weekends. Subjects walked at their own preferred speed chosen on the first day and kept this speed throughout the training period [3.2 ± 0.9 (SD) km/h, range: 2.6–3.9 km/h]. They were instructed to walk without drifting position on the

treadmill, aided by tape markers placed on the edges of the treadmill. This ensured repeatable cycle times and stance and swing duty cycles. Experiments were done on the 1st, 8th, and 16th days of training. Each experimental session lasted ~2–3 h. In an additional four untrained subjects, the amount by which the soleus H-reflex was facilitated by a conditioning magnetic stimulus to the MCx was measured at rest, during a minimal voluntary isometric contraction, and in the midswing phase of the backward walking cycle.

EMG recordings and stimulation

EMG recordings were made on the soleus and TA muscles of the left leg with active bipolar DE 2.1 electrodes (Delsys, Boston, MA). The placement of the electrodes was marked with a waterproof rub-resistant marker on the first day to ensure that the recording electrodes were placed at the same location in each experimental session. A large brass plate (4×10 cm) was used as the reference electrode and was placed on the upper part of the calf, between the stimulating electrode in the popliteal fossa and the EMG recording electrodes. EMG signals were high-pass filtered at 20 Hz, low-pass filtered at 1,000 Hz, and sampled at a rate of 2 kHz. A pressure-sensitive switch was taped in the shoe under the big toe and served to indicate the onset of the stance phase of the backward walking cycle and for triggering data acquisition.

Magnetic stimuli were applied to the scalp with a coned double-D-shaped focal coil (16×8 cm) connected to a Cadwell MES-10 biphasic stimulator having maximum magnetic field strength of 2 Tesla. The stimulus intensity was measured as a percentage of the maximum stimulator output. The coil was placed in direct contact with the scalp with the handle pointing backward. The center of the coil was placed 1 cm lateral and 1 cm anterior to the vertex. For each subject, fine adjustments were made to find the optimal location for eliciting MEPs in the TA. This location was marked on the scalp and served as a reference against which the coil was positioned. The active motor threshold (AMT) was defined as the lowest stimulus intensity needed to elicit eight MEPs in sixteen trials while the subject contracted the TA isometrically at 10% of maximum voluntary contraction (MVC). The coil was maintained manually at this location by one of the experimenters during the experiment. Its position and orientation were constantly attended to throughout the experiment. These procedures have been shown to evoke stable and reproducible responses in various tasks (Capaday et al. 1999; Devanne et al. 1997; Lavoie et al. 1995). The soleus H-reflex was 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.

Training and experimental procedures

Subjects trained daily at walking backward for 15 min over a period of 16 days excluding weekends. Experiments were performed on the 1st, 8th, and 16th days of the training period. The experimental session was divided in three parts. First, to determine the modulation pattern of the soleus and TA MEPs during the backward step cycle, magnetic stimuli were applied to the MCx at increments of 50 ms, starting at toe contact (TC). Stimuli were applied at random every one to three step cycles, and only one stimulus was delivered in a step cycle. MEPs were evoked during the step cycle at two stimulus intensities, 1.0 and 1.2 times the active motor threshold (AMT) of the TA. These stimulus intensities were chosen because MEPs could be readily evoked in the soleus and TA during their respective phase of activity and did not disrupt the walking cycle. Recordings of the soleus and TA EMG activity during backward walking (i.e., without stimulation) were made several times during the course of the exper-

iment. This ensured that the subjects did not change the duration of their walking cycle nor the duty cycles of flexors and extensors.

Second, the relation between MEP size and the level of EMG activity during voluntary isometric contractions was determined for the soleus and TA. Subjects were seated with the left leg extended and the foot fixed on an adjustable plate. In this way, the subjects could voluntarily dorsiflex and plantarflex the ankle isometrically. The level of EMG activity in the soleus and TA was displayed on separate analog meters placed ~1 m in front of the subject. The subjects were asked to contract tonically either the soleus or the TA at different levels in random order between 0 and 45% of MVC, matching the range of EMG activity in these muscles during walking. The ankle angle was ~90° during the isometric contractions and about equal to that during the midswing phase of backward walking. Two magnetic stimulus intensities were used, 1.0 and 1.2 × AMT. Eight MEPs were averaged at each intensity and prescribed level of EMG activity. The EMG activity of the soleus and TA were continuously monitored on an oscilloscope to ensure that no co-contraction occurred during the experiment. In the third part of the experiment, the H-reflex modulation pattern was determined during the backward step cycle ($n = 6$ subjects). The methods used are described in detail in a previous publication from this laboratory (Schneider and Capaday 2003).

In separate experiments on five additional subjects, the facilitation of the soleus H-reflex produced by a conditioning stimulus (1.0 or 1.2 × AMT of the TA) to the motor cortex was measured in four subjects. The amount of facilitation was measured at rest, during voluntary plantarflexion at 5% of MVC and in the midswing phase of backward walking. The conditioning-testing (C-T) stimulus intervals ranged between -5 and +1 ms, in increments of 1 ms (Petersen et al. 1998). A negative value indicates that the test stimulus preceded the conditioning one. During walking, only two C-T intervals were tested, the interval at which facilitation began (i.e., 1st millisecond of facilitation) and the interval at which facilitation was maximal. Control of the experiment, averaging and sorting of the responses were done in real time on a PC. Facilitation of the test H-reflex by a conditioning stimulus to the motor cortex was calculated as the change of the test response size divided by the control value (test - control/control).

Data reduction

The locomotor EMG activity and the time of occurrence (not the time of stimulation) of the MEPs and H-reflexes were normalized with respect to the step cycle duration for each subject in each experimental session. These procedures allowed comparisons between subjects. The mean value of the TA and soleus EMG activity at the time MEPs were elicited was determined from the average rectified and filtered signals recorded during the session without stimulation. The value was calculated over a 20-ms time period centered at the time of occurrence of the MEP.

RESULTS

The results are presented in four sections. We first show that in untrained subjects during the backward walking cycle, the soleus and TA MEPs are modulated in phase with their respective locomotor EMG bursts. By contrast, the soleus H-reflex begins to increase in midswing prior to the onset of soleus EMG activity. Importantly, no soleus MEPs are observed in this phase of the step cycle. We then show that with training, the soleus H-reflex becomes modulated in phase with the soleus EMG activity and its amplitude decreases markedly. However, the soleus MEPs do not decrease in amplitude and remain modulated in phase with the soleus locomotor EMG. In the third section, we demonstrate that soleus MEPs are larger

during voluntary contractions than during backward walking for matched levels of EMG activity. Last, we show that a conditioning stimulus to the motor cortex facilitates the soleus H-reflex when the subject is at rest or voluntarily contracting the soleus but not in the midswing phase of the backward step cycle.

Modulation of the soleus H-reflex and MEPs in untrained subjects

All subjects reported being uneasy when they began walking backward on the treadmill, nonetheless the modulation pattern of their soleus MEPs was in phase with the soleus EMG activity from the outset. An example of data obtained from one subject is shown in Fig. 1. It can be seen that in the stance phase the soleus MEPs decrease, as does the soleus EMG activity (Fig. 1D). At the beginning of the swing phase, while the TA is still active and the soleus inhibited (Fig. 1, A and B), no MEPs were recorded in the soleus muscle. They began to increase at the onset of the soleus burst. By contrast, the H-reflex began to increase earlier as shown in Fig. 1C. On average, the H-reflex increased 129 ± 71 (SD) ms before the soleus MEPs ($n = 5$ subjects). The soleus MEP modulation pattern during the backward step cycle averaged across all 10 subjects is shown in Fig. 2B, along with the likewise averaged soleus locomotor EMG activity (Fig. 2A). It is clear that no soleus MEPs were observed prior to the onset of soleus EMG activity in midswing. Like the soleus MEPs, those of the TA were also modulated in phase with its EMG activity (Fig. 2, C and D).

As previously reported (Schneider and Capaday 2003), the H-reflex modulation pattern was quite different in trained versus untrained subjects. In the first experimental session, an H-reflex is observed in untrained subjects prior the onset of the soleus EMG burst in midswing. By the 16th day of training, this high-amplitude H-reflex was no longer present in midswing and the H-reflex increased in phase with the soleus EMG burst (Fig. 3, C and E). Moreover, there was a dramatic decrease of the H-reflex amplitude that was not due to EMG pattern or amplitude changes (Fig. 3E). For the subject whose data are reported in Fig. 3, the soleus EMG activity happened to be slightly higher on day 16 compared with day 1, but the H-reflex had decreased by a factor of nearly four. By contrast, it can be seen that the soleus MEPs were clearly in phase with the soleus EMG activity on the first day of experiment and remained so after 16 days of training (Fig. 3D). Of greater importance, the amplitude of the soleus MEPs did not decrease with training as did the H-reflexes. For the group as a whole no significant changes in EMG amplitude were observed (paired t -test, for TA, $t = 1.44$, $P = 0.22$; for soleus, $t = -0.25$, $P = 0.82$). It can also be seen in Fig. 3B that the TA MEPs were modulated in phase with the TA EMG activity on the first and last day of training and their amplitude did not change.

MEPs during voluntary contraction versus backward walking

Soleus and TA MEPs recorded during backward walking were compared with MEPs recorded during voluntary contractions of the respective muscle. Linear regression coefficients

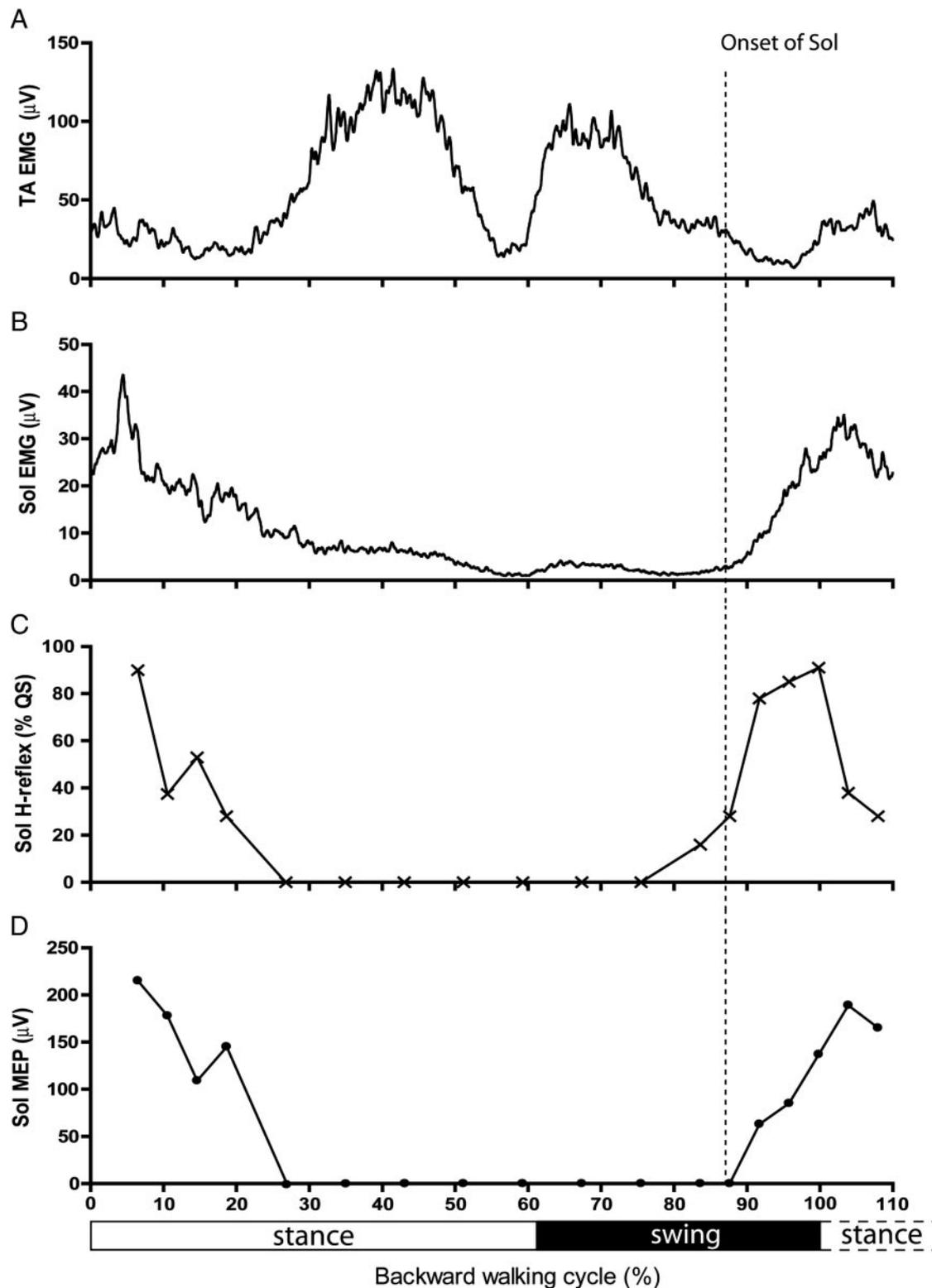


FIG. 1. Example of motor-evoked potentials (MEPs) and H-reflexes recorded during the backward step cycle of an untrained subject in the first experimental session. The H-reflexes are expressed as a percentage relative to the value during quiet standing (QS). The averaged ($n = 64$ steps) locomotor EMGs of the soleus and tibialis anterior (TA) are shown in A and B. Note that soleus H-reflex began to increase in midswing prior to the onset of soleus EMG activity (---) and while the TA was still active. However, the soleus MEPs began to increase at the onset of soleus electromyographic (EMG) activity in midswing.

(slope and y intercept) of MEP amplitude versus background EMG were calculated for each subject in each condition. Figure 4 shows an example of these linear regressions calculated for one subject. In Fig. 4A, soleus MEPs are compared

between walking and voluntary contractions. For all seven subjects tested, the slopes of the linear regressions were steeper for voluntary contractions. An analysis of covariance revealed that the effect was statistically significant in 4/7 subjects (Table 1).

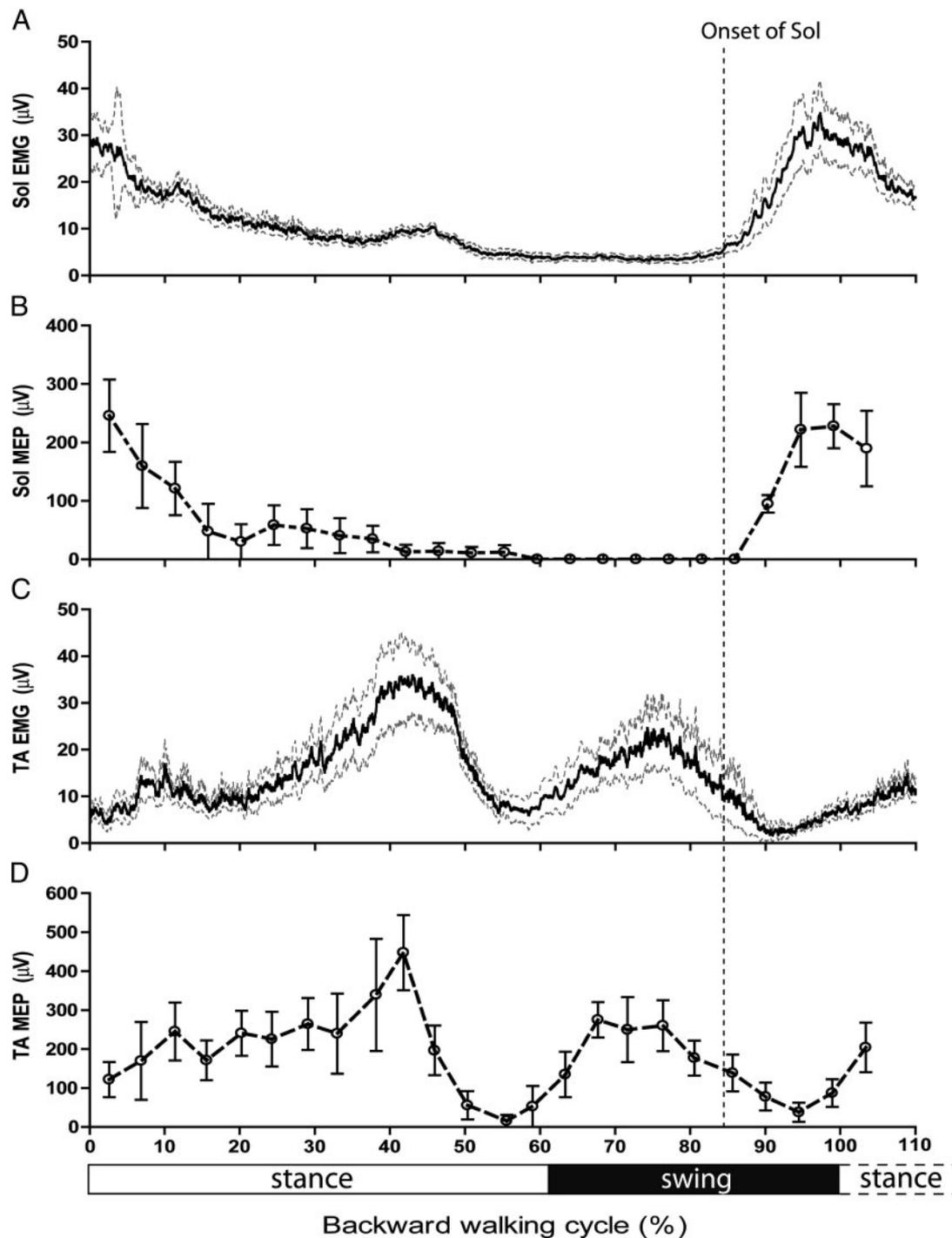


FIG. 2. The traces shown in this figure are grand averages (± 1 SD) of data obtained from 10 subjects on their 1st experimental session. Note how the amplitude of soleus and TA MEPs closely follows the respective locomotor EMG and especially that in midswing the soleus MEPs begin to increase at the onset soleus EMG activity.

On the contrary, an analysis of covariance between TA MEPs and background EMG did not reveal a task dependent difference of slopes (Table 1). An example is shown in Fig. 4B, note also that the data points are much more scattered around the best-fitting regression lines compared with those for the soleus. This was in fact a consistent finding across all subjects. The correlation coefficients (r^2) of MEP amplitude versus EMG level are shown for all subjects in Table 1. When looking at the r^2 values for the soleus during voluntary contractions and

during backward walking, the average value is quite high (0.766 ± 0.136 and 0.859 ± 0.067 , respectively). For the TA during voluntary contractions, the average r^2 value was 0.883 ± 0.069 and in all cases statistically significant. However, the mean value for backward walking was very low 0.385 ± 0.262 and in all cases not statistically significant. Thus the variance of TA MEP amplitude accounted for by the level of TA EMG activity is markedly lower during walking. This result did not depend on differences between soleus and TA

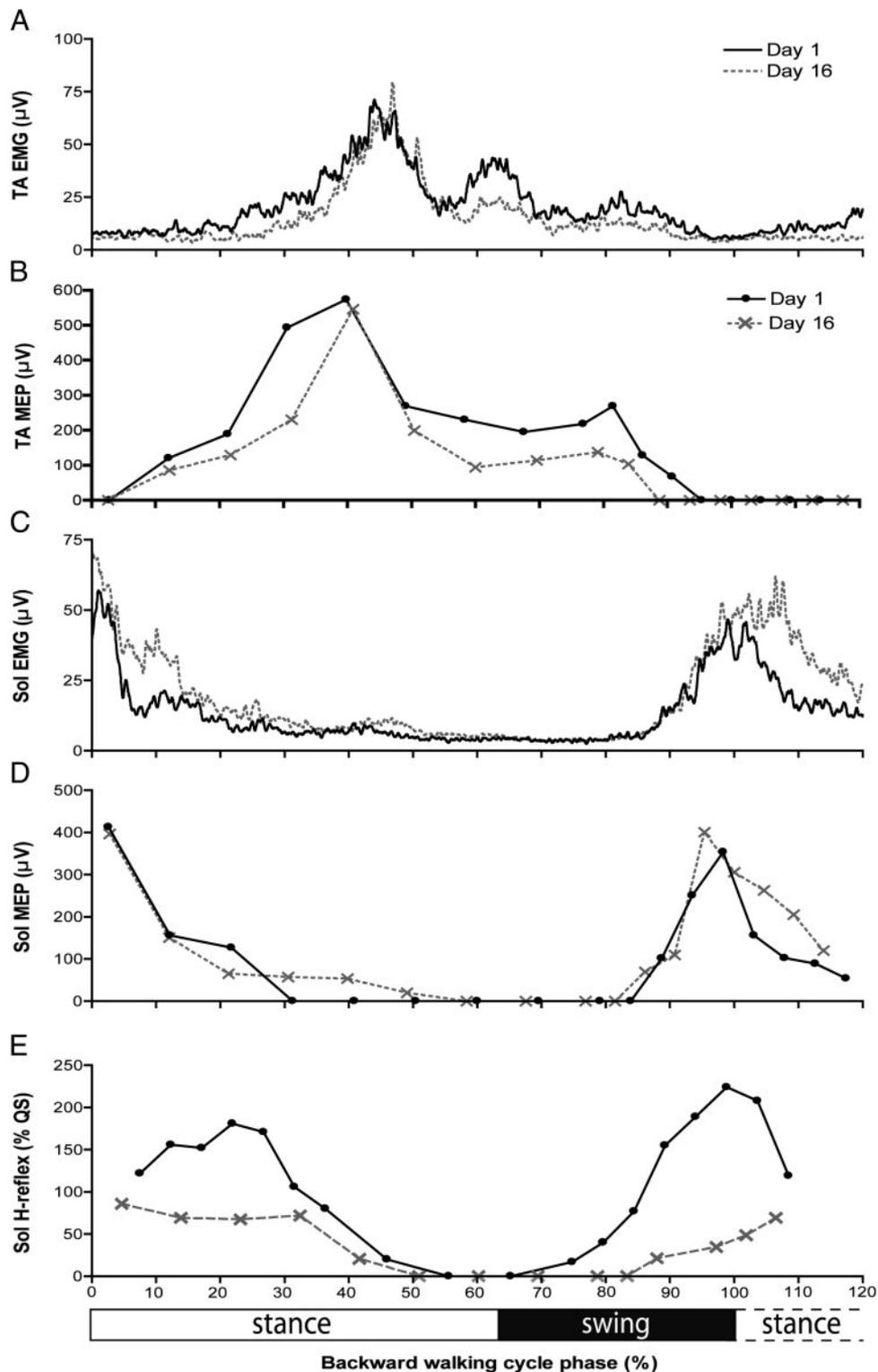


FIG. 3. Comparison of the results obtained from 1 subject on the 1st and last experimental session. In the midswing phase of the 1st experimental session the soleus H-reflex began to increase prior to the soleus EMG activity, but the soleus MEP increased at the onset of soleus EMG activity. When the subject was tested 16 days after the start of training, the soleus H-reflex decreased throughout the step cycle and markedly in midswing and early stance. The amplitude and modulation pattern of soleus and TA MEPs were comparable on the 1st and last experimental session.

MEP amplitude, which were nearly in the same range as can be inferred from Fig. 5. Variability of MEPs, as measured by the coefficient of variation (CV), decreases with increasing MEP amplitude (Capaday et al. 1999). As shown in Fig. 5, the relation between MEP amplitude and CV was not different for the soleus and TA MEPs (ANCOVA, $F = 0.7754$, $P = 0.3794$). The greater variability of TA MEPs during the backward step cycle was thus not related to their amplitude.

Facilitation of the soleus H-reflex by conditioning stimulus to MCx

An example of facilitation of the soleus H-reflex by a conditioning stimulus to the MCx is shown in Fig. 6. The data were obtained from one subject in the same experimental session and the size of the test H-reflex was adjusted to be nearly equal in the different tasks. The conditioning stimulus to

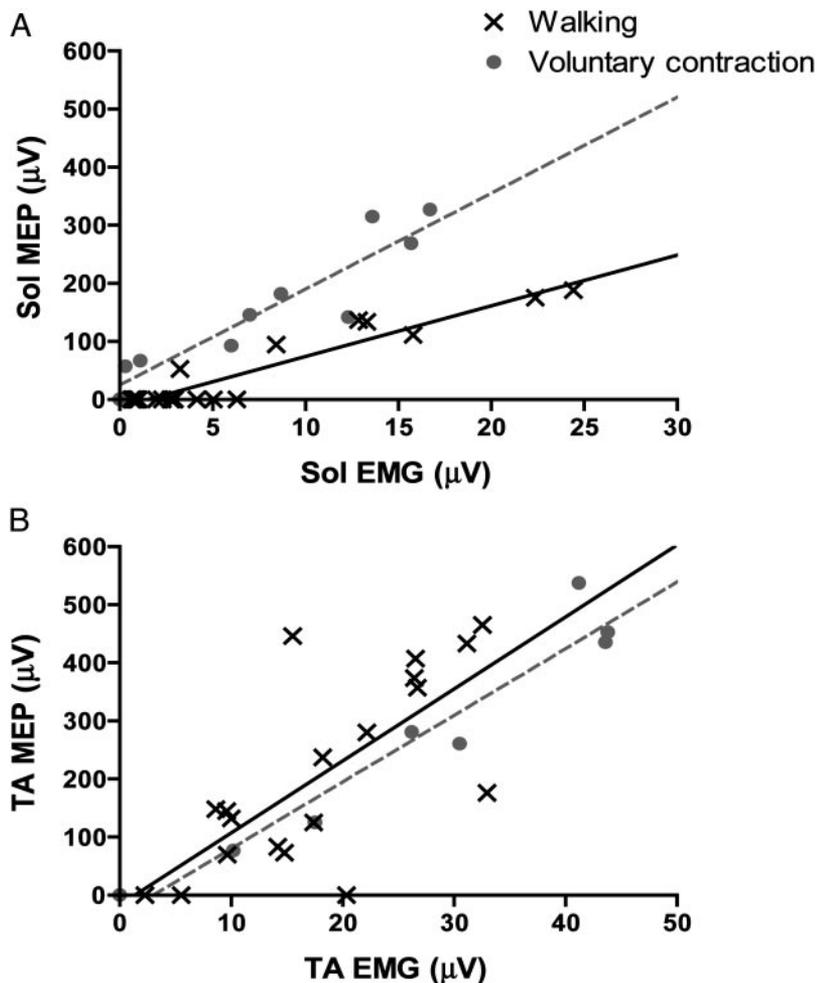


FIG. 4. The data were obtained from a single subject in the same experimental session. *A*: soleus MEPs increased roughly linearly with the background level of EMG activity during voluntary contractions and backward walking. Analysis of co-variance (ANCOVA) revealed a significant difference ($P < 0.001$) between the slopes of the best fitting regression lines. The slope of the regression line was steeper for voluntary contractions. *B*: TA MEPs also increased roughly linearly with background EMG in both tasks. However, the correlation between MEP amplitude and EMG level was higher during voluntary contractions. An ANCOVA did not reveal a significant difference between the slopes of the best fitting lines, or their y intercept.

the motor cortex was $1.2 \times$ AMT of the TA and on its own elicited no response in the soleus. When the subject was at rest, the conditioning stimulus facilitated the H-reflex by 69% (Fig. 6A). During voluntary isometric contraction of the soleus at 5%

of MVC, the facilitation increased to 109% (Fig. 6B). In the midswing phase of backward walking no facilitation was observed (Fig. 6C). The box-whisker plot in Fig. 6D summarizes the grouped results. On average, the conditioning stimu-

TABLE 1. Summary of linear regression analysis and ANCOVA of soleus and TA MEPs

Subjects	Backward Walking		Voluntary Contraction		ANCOVA, P Value	Significance	y Intercept
	Slope	r^2	Slope	r^2			
Soleus							
1	4.98	0.800	6.70	0.811	0.110	NS	NS
2	3.33	0.560	5.68	0.739	0.145	NS	NS
3	5.28	0.655	8.53	0.902	0.049	S	-
4	8.73	0.900	16.49	0.862	<0.001	S	-
5	3.40	0.929	8.41	0.867	<0.001	S	-
6	14.94	0.832	18.95	0.877	0.301	NS	NS
7	8.50	0.688	12.52	0.952	0.050	S	-
TA							
1	7.79	0.402	7.73	0.740	0.982	NS	NS
2	5.75	0.717	5.87	0.885	0.911	NS	S
3	1.27	0.034	2.73	0.890	0.267	NS	NS
4	9.58	0.244	11.47	0.935	0.676	NS	NS
5	4.79	0.257	5.63	0.873	0.700	NS	NS
6	6.57	0.750	7.88	0.948	0.390	NS	S
7	8.34	0.289	8.27	0.913	0.982	NS	NS

The slopes and squared correlation coefficients (r^2) of the best fitting regression lines relating motor-evoked potential (MEP) amplitude and background electromyographic (EMG) level are shown for the soleus and tibialis anterior (TA). All r^2 values for TA MEPs during voluntary contractions were statistically significant, but none was for backward walking. The column labeled significance refers to the results of the ANCOVA. Differences in y intercepts between regression lines can't be tested if the slopes are different; this is indicated by a dash.

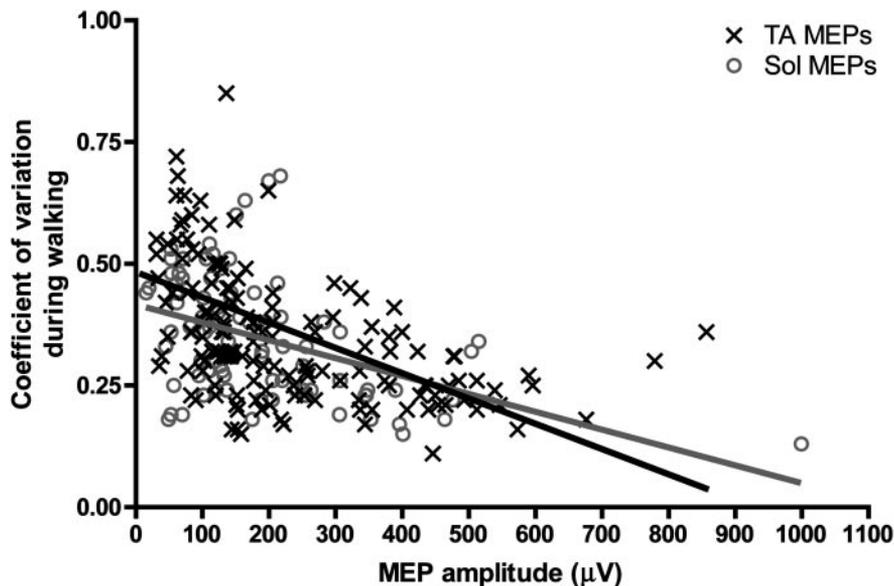


FIG. 5. The coefficient of variation of soleus and TA MEPs decreases as a function of MEP amplitude. There was no significant difference between the regression lines relating the CV to MEP amplitude.

lus to the motor cortex facilitated the soleus H-reflex by 40% at rest and by 49% during a voluntary contraction of 5% MVC. In both cases, the facilitation was significant (t -test $P < 0.02$). In the midswing phase of backward walking, no facilitation was observed in any subject.

DISCUSSION

In this study, we demonstrated that in untrained subjects TMS applied to the MCx in the midswing phase of backward walking does not elicit a MEP in the soleus but that stimulation of the tibial nerve at the same phase readily elicits a soleus H-reflex. With daily training at walking backward, the time at which the H-reflex began to increase was progressively delayed until it coincided with the onset of soleus EMG activity, and its amplitude was considerably reduced compared with its value on the first experimental day. By contrast, no changes were observed in the timing or amplitude of soleus MEPs with training. Soleus MEPs were smaller during backward walking compared with voluntary contractions. The soleus H-reflex was facilitated by a conditioning stimulus to the motor cortex when subjects were at rest or voluntarily plantarflexing the ankle but not in the midswing phase of backward walking. Taken together these observations suggest that in untrained subjects the soleus H-reflex that occurs unexpectedly in midswing is unlikely to be due to CST activity as we had hypothesized. The results also suggest that the CST is unlikely to be involved in the progressive adaptation of the H-reflex with daily training because neither the timing nor amplitude of MEPs changed in the course of training. From the aforesaid, we suggest that in untrained subjects the unexpectedly large soleus H-reflex in the midswing phase of backward walking may be due to a reduction of presynaptic inhibition of the Ia-afferent terminals projecting to the α -motoneurons. The adaptive changes of the H-reflex with training may likewise be explained by a progressive increase of presynaptic inhibition. Subcortical descending pathways such as the vestibulospinal and reticulospinal tracts can affect presynaptic inhibition of intraspinal afferent terminals (Rudomin 1990) and may be involved in the control of the H-reflex during backward walking and its adaptation with training.

When subject balance on an unstable rocking platform soleus and TA MEPs increase by more than can be accounted for by changes in the background level of EMG activity (Solopova et al. 2003). However, the soleus H-reflex decreases when on the rocking platform (Solopova et al. 2003). The situation is very different during backward walking, soleus MEPs are reduced throughout the step cycle. This suggests a greater degree of corticospinal control of the ankle musculature on the rocking platform than during backward walking. Indeed, Lavoie et al. (1995) had previously suggested that the MCx may be engaged during voluntary postural control on the basis of the relation between MEP size and the background level of EMG activity in various tasks. Recently, Bonnard et al. (2002) demonstrated a greater involvement of the CST during voluntarily controlled gait modifications (see also Schubert et al. 1999). All this leads to the idea that the MCx may be more engaged in the control of voluntary postural activities and gait modifications than in backward walking. The latter appears more of an automatic task controlled by the time-reversed kinematic program of forward walking (Lacquaniti et al. 1999). Voluntary control appears to attenuate reflexes and exert more direct control of the spinal circuitry. The decrease of H-reflexes during walking on a narrow beam (Llewellyn et al. 1990) or balancing on a rocking platform (Solopova et al. 2003) may be examples of this potentially general principle. Conversely, automatic tasks may rely more on reflexes to counter unexpected external events and uncertainties in motor programming. The specific enhancement of the soleus H-reflex at the transition from swing to stance, a critical phase of the backward step cycle, may be an example of this.

The reduction of soleus MEPs during backward walking is not due to co-contraction of the soleus and TA. On an unstable rocking platform, the soleus and TA co-contrast, yet in this task the soleus and TA MEPs are enhanced (Solopova et al. 2003). Moreover, during forward walking there is no co-contraction of the ankle muscles during the step cycle, yet the soleus MEPs are reduced compared with voluntary activation (Capaday et al. 1999). Thus the reduction of soleus MEPs in backward walking is a specific feature of this task and leads us to suggest that other descending tracts and the stretch reflex

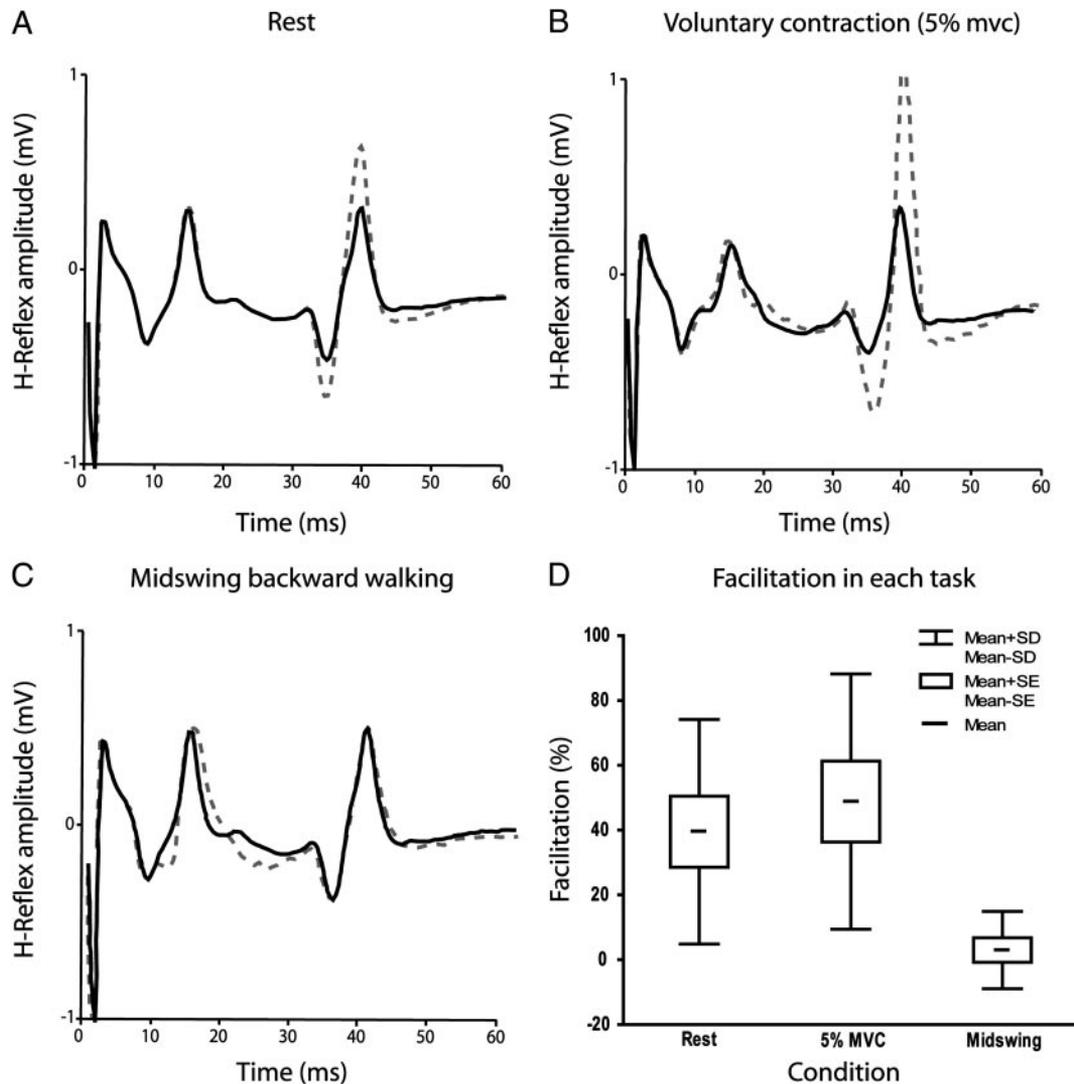


FIG. 6. Examples of the effects of a conditioning stimulus to the motor cortex [$1.2 \times$ active motor threshold (AMT)] on the soleus H-reflex at rest (A), during a voluntary contraction of 5% MVC (B), and in the midswing phase of backward walking (C). The conditioning-testing interval was -2 ms. Control H-reflex traces are shown in solid black, those conditioned by a stimulus to the motor cortex as dashed gray tracings. The box-whisker plot in D summarizes the data obtained on the 4 subjects tested.

contribute to soleus activation (Bennett et al. 1996; Capaday et al. 1999; Stein and Capaday 1988; Yang et al. 1991). An unexpected finding was that the poor correlation between TA MEP amplitude and the locomotor TA EMG during the backward step cycle, which differs markedly from the strong correlation obtained during voluntary activity (see also, Bawa et al. 2002). This relation was not specifically determined in previous studies of forward walking (Capaday et al. 1999; Schubert et al. 1997). Thus a detailed comparison between forward and backward walking would be worthwhile as it may further our understanding of the relation between motor cortex activity and TA locomotor activity.

Our finding that in untrained subjects the MCx via the CST may not contribute to the unexpectedly high-amplitude H-reflex in midswing nor in its progressive adaptation with training is not at odds with the essential role of the CST in the operant conditioning of the H-reflex (Chen and Wolpaw 2002; Chen et al. 2002). We studied neural mechanisms during an unconstrained natural motor task, the control mechanisms involved may be very different from those involved in operant

conditioning. For example, changes in presynaptic inhibition are not thought to be involved in operant conditioning of the H-reflex (Wolpaw 1997; Wolpaw and Tennissen 2001), whereas from the aforesaid it may be a prime candidate mechanism in controlling the H-reflex during backward walking and its adaptation with training.

Conclusion

In untrained subjects, the temporal modulation pattern of soleus MEPs and H-reflexes do not follow the same time course during the backward step cycle. In midswing, the H-reflex begins to increase prior to the soleus locomotor EMG activity, whereas the MEPs begin to increase at EMG onset. A conditioning stimulus to the MCx in midswing does not facilitate the soleus H-reflex. This is strong evidence that the excitability of the MCx is reduced in this phase of the step cycle. Moreover, with training, the time at which the soleus H-reflex begins to increase changes from midswing to early stance and its amplitude is markedly reduced. Neither the

amplitude nor the temporal modulation pattern of soleus MEPs change with training. We thus conclude that in untrained subjects the MCx is not involved in producing the unexpectedly high-amplitude H-reflex in midswing nor in its progressive adaptation with daily training.

ACKNOWLEDGMENTS

We thank F. Roy and P. Vachon for dedicated and expert technical assistance.

GRANTS

This work was supported by the Canadian Institutes of Health Research. L. Brizzi is supported by a postdoctoral fellowship from the Fondation Médicale Pour la Recherche.

REFERENCES

- Bawa P, Chalmers GR, Stewart H, and Eisen AA.** Responses of ankle extensor and flexor motoneurons to transcranial magnetic stimulation. *J Neurophysiol* 88: 124–132, 2002.
- Bennett DJ, De Serres SJ, and Stein RB.** Gain of the triceps surae stretch reflex in decerebrate and spinal cats during postural and locomotor activities. *J Physiol* 496: 837–850, 1996.
- Bonnard M, Camus M, Coyle T, and Pailhous J.** Task-induced modulation of motor evoked potentials in upper-leg muscles during human gait: a TMS study. *Eur J Neurosci* 16: 2225–2230, 2002.
- Capaday C, Lavoie BA, Barbeau H, Schneider C, and Bonnard M.** Studies on the corticospinal control of human walking. I. Responses to focal transcranial magnetic stimulation of the motor cortex. *J Neurophysiol* 81: 129–139, 1999.
- 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.
- Chen XY, Carp JS, Chen L, and Wolpaw JR.** Corticospinal tract transection prevents operantly conditioned H-reflex increase in rats. *Exp Brain Res* 144: 88–94, 2002.
- Chen XY and Wolpaw JR.** Probable corticospinal tract control of spinal cord plasticity in the rat. *J Neurophysiol* 87: 645–652, 2002.
- Crenna P and Frigo C.** Excitability of the soleus H-reflex arc during walking and stepping in man. *Exp Brain Res* 66: 49–60, 1987.
- Devanne H, Lavoie BA, and Capaday C.** Input-output properties and gain changes in the human corticospinal pathway. *Exp Brain Res* 114: 329–338, 1997.
- Drew T.** Motor cortical activity during voluntary gait modifications in the cat. I. Cells related to the forelimbs. *J Neurophysiol* 70: 179–199, 1993.
- Ethier C, Imbeault MA, Ung V, and Capaday C.** On the soleus H-reflex modulation pattern during walking. *Exp Brain Res* 151: 420–425, 2003.
- Lacquaniti F, Grasso R, and Zago M.** Motor patterns in walking. *News Physiol Sci* 14: 168–174, 1999.
- Lavoie BA, Cody FW, and Capaday C.** Cortical control of human soleus muscle during volitional and postural activities studied using focal magnetic stimulation. *Exp Brain Res* 103: 97–107, 1995.
- 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.
- Llewellyn M, Yang JF, and Prochazka A.** Human H-reflexes are smaller in difficult beam walking than in normal treadmill walking. *Exp Brain Res* 83: 22–28, 1990.
- Petersen N, Christensen LO, and Nielsen J.** The effect of transcranial magnetic stimulation on the soleus H reflex during human walking. *J Physiol* 513: 599–610, 1998.
- Rudomin P.** Presynaptic inhibition of muscle spindle and tendon organ afferents in the mammalian spinal cord. *Trends Neurosci* 13: 499–505, 1990.
- Schneider C and Capaday C.** Progressive adaptation of the soleus H-reflex with daily training at walking backward. *J Neurophysiol* 89: 648–656, 2003.
- 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.
- Schubert M, Curt A, Colombo G, Berger W, and Dietz V.** Voluntary control of human gait: conditioning of magnetically evoked motor responses in a precision stepping task. *Exp Brain Res* 126: 583–588, 1999.
- Schubert M, Curt A, Jensen L, and Dietz V.** Corticospinal input in human gait: modulation of magnetically evoked motor responses. *Exp Brain Res* 115: 234–246, 1997.
- Solopova IA, Kazennikov OV, Deniskina NB, Levik YS, and Ivanenko YP.** Postural instability enhances motor responses to transcranial magnetic stimulation in humans. *Neurosci Lett* 337: 25–28, 2003.
- Stein RB and Capaday C.** The modulation of human reflexes during functional motor tasks. *Trends Neurosci* 11: 328–332, 1988.
- Ung VR, M. Imbeault MA, Ethier C, and Capaday C.** On the potential role of the corticospinal tract in the progressive adaptation of the soleus H-reflex during backward walking training. *Soc Neurosci Abstr* 187.16, 2004.
- Wolpaw JR.** The complex structure of a simple memory. *Trends Neurosci* 20: 588–594, 1997.
- Wolpaw JR and Tennissen AM.** Activity-dependent spinal cord plasticity in health and disease. *Annu Rev Neurosci* 24: 807–843, 2001.
- Yang JF, Stein RB, and James KB.** Contribution of peripheral afferents to the activation of the soleus muscle during walking in humans. *Exp Brain Res* 87: 679–687, 1991.