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Plastic changes in the human H-reflex pathway at rest following skillful cycling training

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Abstract

Objective: The spinal cord is capable of activity-dependent plasticity, but the extent of its participation in human motor learning is not known. Here, we tested the hypothesis that acquisition of a locomotor-related skill modulates the pathway of the H-reflex, a measure of spinal cord excitability that is susceptible to plastic changes.

Methods: Subjects were tested on their ability to establish a constant cycling speed on a recumbent bike despite frequent changes in pedal resistance. The coefficient of variation of speed (CV_{speed}) measured their ability to acquire this skill (decreasing CV_{speed} with training reflects performance improvements). Soleus H-reflexes were taken at rest before and after cycling.

Results: Ability to establish a target speed increased and H-reflex size decreased more after cycling training involving frequent changes in pedal resistance that required calibrated locomotor compensatory action than with training involving constant pedal resistances and lesser compensation. The degree of performance improvement correlated with the reduction in the amplitude of the H-reflex.

Conclusions: Skillful establishment of a constant cycling speed despite changing pedal resistances is associated with persistent modulation of activity in spinal pathways.

Significance: Recalibration of activity in the H-reflex pathway may be part of the control strategy required for locomotor-related skill acquisition.

Keywords: Plasticity; Memory; Spinal cord; Locomotion; H-reflex

1. Introduction

Much of the evidence for activity-dependent plasticity is based on studies demonstrating functional reorganization of the motor cortex following motor skill learning in upper extremity (Classen et al., 1998; Karni et al., 1995; Nudo et al., 1996; Pascual-Leone et al., 1995; Sanes, 2003). However, acquisition of new skills are likely to rely on integrated activity at multiple sites in the CNS (Hikosaka et al., 2002), including the spinal cord (Windhorst, 1996). For instance, basic propulsive locomotion can be generated and maintained by subcortical structures with the aid of peripheral sensory feedback from the moving limb (Bouyer and Rossignol, 2003; Harkema et al., 1997). Activity in the spinal cord appears to contribute to movement planning (Fetz et al., 2000), the accuracy of reaching movements (Alstermark and Isa, 2002; Mazevet et al., 2003), and locomotor function (Burke, 2001). Therefore, it is possible that activity-dependent plasticity in the human spinal cord

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contributes to the set of biological events required for human locomotor learning.

The H-reflex, a physiological response mediated by a largely monosynaptic pathway that includes the Ia afferent neuron, its synapse on the α-motoneurone, and the α-motoneurone (Pierrot-Deseilligny and Mazevet, 2000), is modulated by complex motor behavior (Capaday, 2002; Zehr, 2002), and can convey information on spinal cord plasticity (Wolpaw and Tennissen, 2001). In primates and rodents, the H-reflex is influenced by operant conditioning and long-term training protocols (Chen and Wolpaw, 1995; Wolpaw, 1987) through descending corticofugal output (Chen and Wolpaw, 2002). In humans, H-reflex is modulated by use as in professional ballet dancers (Koceja et al., 1991; Nielsen et al., 1993), or following performance of prolonged balance training (Trimble and Koceja, 2001) or backward walking (Schneider and Capaday, 2003) tasks. However, the degree to which modulation of activity in the spinal monosynaptic reflex arc operates in the setting of different training tasks is incompletely understood. This is important in view of the notion that motor skill training appears to be a critical factor in driving plastic reorganization at various level of the CNS related to motor experience as compared to nonskill training or passive motor training (Jensen et al., 2005; Nudo et al., 1996; Plautz et al., 2000).

The purpose of this study was to test the hypothesis that cycling training (establishment of a constant cycling speed on a recumbent bike exposed to frequent changes in pedal resistance) that requires calibrated compensatory action, produces greater improvement in performance and modulates the excitability of the spinal monosynaptic arc to a larger extent than simple motor activity (maintenance of a constant cycling speed against constant pedal resistance) that requires less compensatory action. We chose these two types of training because they involved comparable physical activity, but only one involved skill acquisition during cycling. This may lead to differential modulation of the SOL H-reflex pathway.

2. Materials and methods

2.1. Subjects

Eighteen healthy volunteers (average age 34±9 years, range=19–48 years, 7 women, 11 men) participated in the experiments. All subjects gave their written informed consent according to the Declaration of Helsinki, and the NINDS Institutional Review Board approved the study protocol. On the basis of a questionnaire concerning his or her usual level of physical activity, each subject was classified as sedentary ($n=5$), active ($n=8$), or highly active ($n=5$). Activity generally consisted in attending a fitness course, jogging or cycling.

2.2. Training protocol

The participants sat comfortably on a recumbent cycle ergometer (Cateye EC 3700, VacuMed. Inc.) that allowed the legs to be loaded in a stable balanced set (Fig. 1a). Subjects participated in 3 different sessions, separated by a week, and were tested on their ability to establish a constant cycling speed of 60 rpm, which they could monitor on the bike digital display (Fig. 1b), against frequent changes in pedal resistance for 4 min. Testing as described was done before and after 16-min training periods (one in each session) consisting of *variable* pedal resistance training, *constant* pedal resistance training, or *no training* (Fig. 1c).

Session order was randomized across subjects. In the *variable* training, pedal resistance changed every 15 s in a pre-programmed sequence unknown to the subject. Subjects had no visual information on the workload changes since the relative values were hidden from their sight (white oval in Fig. 1b). In the *constant* training, pedal resistance was fixed at the mean overall torque level of the *variable* training period. Physical effort was measured by the mean maximum heart rate. In the *no training* period, the subject simply sat on the bike without pedaling.

In each session, before (pre) and after (post) the training period (16 min), we measured for 4 min the subject's ability to cycle a constant speed of 60 rpm in the presence of variable pedal resistance. Therefore, subjects were tested on their ability to establish a constant cycling speed on a recumbent bike despite frequent changes in pedal resistance. The coefficient of variation of speed (CV_{speed}) measured their ability to acquire this skill (decreasing CV_{speed} with training reflects performance improvements while maintainance or increases in CV_{speed} reflect lack of changes or deteriorating performance). Subjects rested for 4 min after the pre-testing period (i.e. before training) and the 16-min training period (i.e. before the post-testing period).

2.3. Physiological measures

We were interested in finding whether there might be modification of the resting excitability of the H-reflex outlasting a single training session, as a trace of a persistent change in this spinal pathway and whether this possible modification might be related to a certain type of training. An advantage of measuring the H-reflex in quiescent muscles is that cortical effects on spinal interneurones that are affected by voluntary contraction are likely to be less active and will not confound the results (Katz and Pierrot-Deseilligny, 1999; Pierrot-Deseilligny, 1997). Among the many muscles involved in cycling, we selected the Soleus (SOL) muscle because it is highly active during downstroke (the extension phase of cycling) (Neptune et al., 1997). By adjusting ankle motion in downstroke (Raasch and Zajac, 1999), changes in foot acceleration (the main consequence of varying pedal resistance) can be effectively controlled. In addition, the H-reflex from SOL is strongly modulated during pedaling (Brooke et al., 1992; Pyndt and Nielsen, 2003), as it is during walking (Capaday, 2002). Lower extremity kinetic patterns during recumbent cycling are similar to those exhibited during cycling in the upright position (Gregor et al., 2002). Recumbent cycling minimizes vestibular involvement and avoids the possible risk of balance problems.

EMG was recorded from the right SOL. The skin was cleansed with rubbing alcohol toilettes and surface electrodes were applied in a bipolar configuration with the active electrode 4 cm below the inferior margin of the two heads of the gastrocnemius muscle and the reference over the Achilles tendon. To monitor the level of SOL background activity at rest at the time of collection of the H-reflexes, 20 ms of EMG data prior to H-reflex stimulus onset were collected before and after training for the 3 conditions. In 3 subjects, EMG activity was also recorded from tibialis anterior (TA), rectus femoris (RF) and biceps femoris (BF) muscles while eliciting the Sol H-reflex. Fifty millisecond of EMG data prior to H-reflex stimulus onset were collected before and after training to monitor background activity at rest in multiple leg and knee muscles. In this case surface electrodes were applied in a bipolar configuration over the belly of the aforementioned muscles. The signal was amplified and filtered (5 Hz to 1 kHz) by a Dantec EMG machine, and then digitized at 4 kHz by a PC-based data acquisition and processing system (Labview, National Instruments). Electrical stimulation was delivered from a Grass S88 Stimulator coupled to a SIU5 stimulus isolation unit and a CCU1 constant current isolation unit (Grass Instruments, Astro-Med, Inc.). H-reflexes were

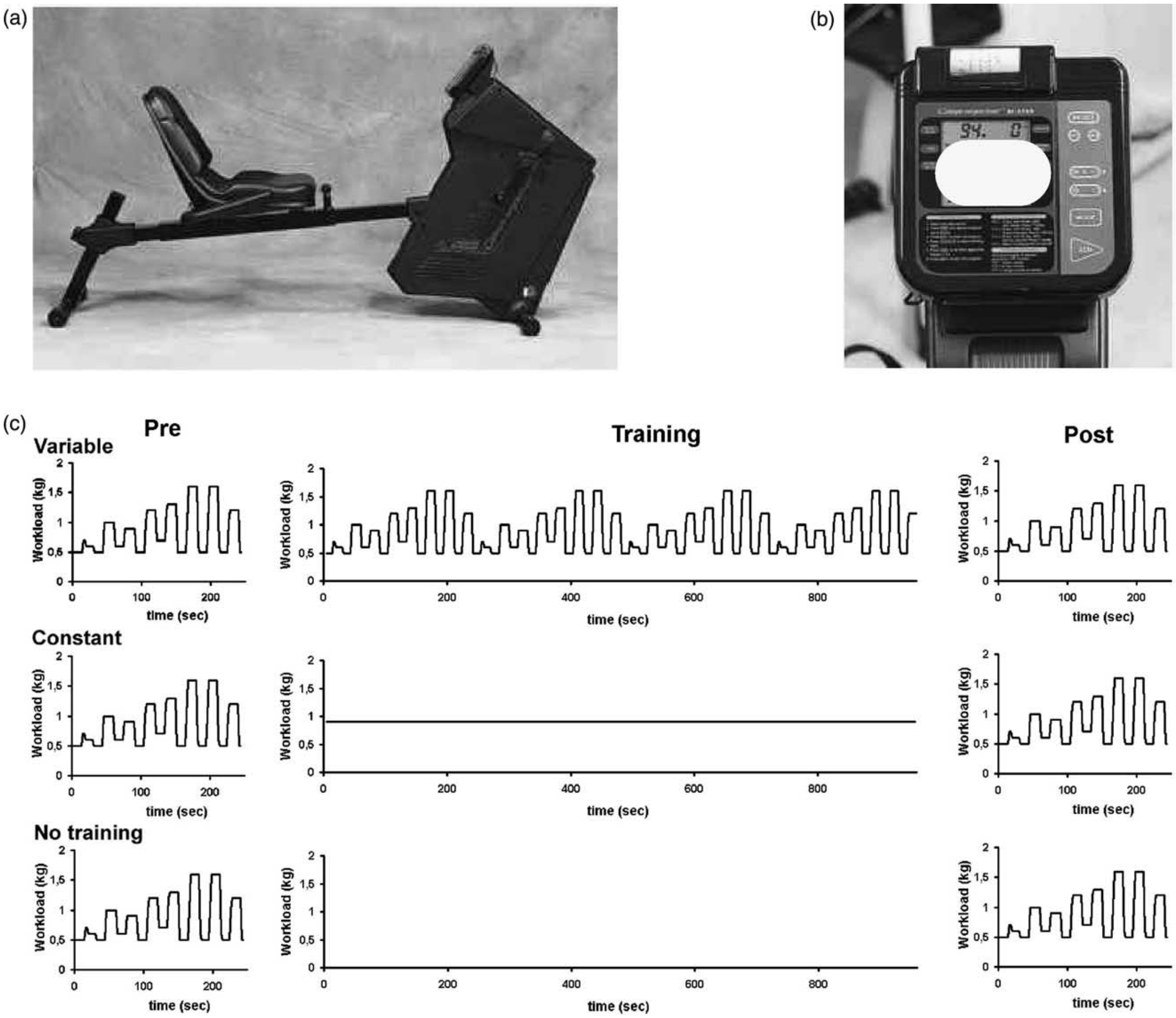

Fig. 1. Experimental set-up. (a) Recumbent cycle ergometer utilized in the experiments and (b) console providing visual feedback of current pedaling rate during performance. Workload values were hidden from sight by attaching a piece of paper to the screen (white oval). (c) Pedal resistance (workload) before (pre), during and after (post) training (*variable*, *constant*, and *no-training*) (c). Note that pre- and post-training test periods consisted of identical patterns of changing workloads (each lasting 4 min).

recorded after stimulation of the tibial nerve with the cathode at the popliteal fossa and the anode over the patella. The position of the cathode was marked on the skin beneath the electrode. For each subject, stimulus duration was 1-ms and stimulus intensity was adjusted at the beginning of the session to elicit an H-reflex equal to about 30% of the maximum M response ($M_{\max}$). $M_{\max}$ is the EMG response produced by direct activation of all the axons of all the α-motoneurones innervating the muscle. Under our conditions, the H-reflex was preceded by a small M response (approximately 0.2 mV). Adjusting the stimulus to keep the M response at this size ensured that effective stimulus strength remained consistent across time and training conditions (Pierrot-Deseilligny and Mazevet, 2000; Zehr, 2002). Additionally, $H_{\max}/M_{\max}$ ratio, an expression of the largest possible fraction of the motoneuron pool activated by the H-reflex stimulus, was measured in 6 subjects. For H-reflex elicitation, the stimulus was delivered every 8 s. Twenty-four H-reflexes were recorded at rest for about 3 min before and after biking (i.e. after the 4-min post-training session) approximately at the same time interval for the 3 sessions. The average H-reflex amplitude was expressed relative to the amplitude of $M_{\max}$ determined at the beginning and end of the session. The raw EMG signal obtained before H-reflex stimulus onset was processed by calculating the root-mean-square (RMS) value.

The corticospinal excitability of the leg motor representation was measured with transcranial magnetic stimulation (TMS) (Siebner and Rothwell, 2003) using a technique that stimulates pyramidal tract neurons mainly transynaptically (Houlden et al., 1999). TMS was applied on the scalp over the leg motor area through a double 70 mm coil (MAGSTIM PN9925) or a double cone coil (MAGSTIM PN9902) connected to a MAGSTIM 200 magnetic stimulator (Magstim, Whitland, UK) with a monophasic current waveform. The optimal coil and scalp position for activating the contralateral SOL muscle was determined as the site where TMS produced consistently the largest motor evoked potential (MEP) at slightly suprathreshold stimulus intensity. This site was referred as the 'hot spot' and marked on the scalp with a pen. In each subject, the same coil was used for the 3 different sessions. The resting motor threshold (RMT) was defined as the minimal stimulus intensity (expressed as a percentage of the maximal stimulator output) that produced MEPs > 50 μV in peak-to-peak amplitude in at least 5 of 10 trials. RMT was determined at the 'hot spot' for activating the SOL muscle at the beginning and end of each session. For MEP determination, the intensity of TMS was adjusted to approximately 1.2 times the SOL RMT, and stimuli were delivered every 6 s. Twenty-four MEP were recorded at rest for about 2 min at the beginning and end of the session, before and after the H-reflex determinations, respectively. The rectified MEP area was averaged and expressed as a ratio of Mmax area.

The knee angle was 100° and the ankle angle was 90°. These joint positions were monitored and kept the same for the beginning and end of session measurements.

The endpoint measure of this study was the coefficient of variation of speed (CV_{speed}) calculated as the SD/mean speed determined in each 4 min testing period before and after (pre, post) each training type (constant, variable, no training). After determination that CV_{speed} values were comparable preceding the 3 training types (ANOVA, $F=0.67$, $P=0.52$), post-training data was expressed relative to pretraining performance.

2.4. Statistical analysis

Data were collected and averaged for the 3 sessions. They were initially tested for normal distribution (Kolmogorov–Smirnov) and homogeneity of variance (Levene's F). Repeated measures ANOVA ($ANOVA_{RM}$) was used to assess the effect of history of previous physical activity (H/O PhysAct $_{\text{sedentary, active, highly active}}$), type of training ($TRAINING_{\text{constant, variable, no training}}$), gender and time ($TIME_{\text{pre-training, post-training}}$) on CV_{speed} values and physiological measures. Post hoc testing was implemented using Fisher test. The relationships between CV_{speed} values and age, and CV_{speed} values and H-reflex amplitude ($H_{\max}/M_{\max}$ ratio) were examined using a linear regression model. The significance of correlations was determined by F-value (ANOVA regression table). Along the manuscript, variance is expressed as standard error of the mean (SEM) and results were considered significant at a level of $P<0.05$.

3. Results

Before training, there was a significant effect of previous physical activity on CV_{pre} ($F=5.54$, $P=0.007$). Sedentary subjects entered the study with higher CV_{pre} (0.032 ± 0.002) than active (0.024 ± .001) or highly active (0.023 ± 0.002) individuals, reflecting the difficulties in sedentary subjects to establish a constant speed. CV_{pre} was otherwise comparable across age and gender.

3.1. Motor performance

After training, previous physical activity did not influence CV_{post}. Group data showed a significant decrease in CV_{post} ($F=30$, $P<0.0001$) and a significant interaction with the type of training ($F=4.73$, $P=0.013$). Post hoc testing showed that only *variable* and *constant* training resulted in reduction in CV_{post} (variable: $P<0.0001$; constant: $P<0.02$; Fig. 2a). Since, CV_{pre} values were comparable, post-training data were expressed relative to pretraining performance. Improvement in CV_{post} was more prominent with *variable* than with *constant* training or *no-training* ($P=0.007$ and 0.001,

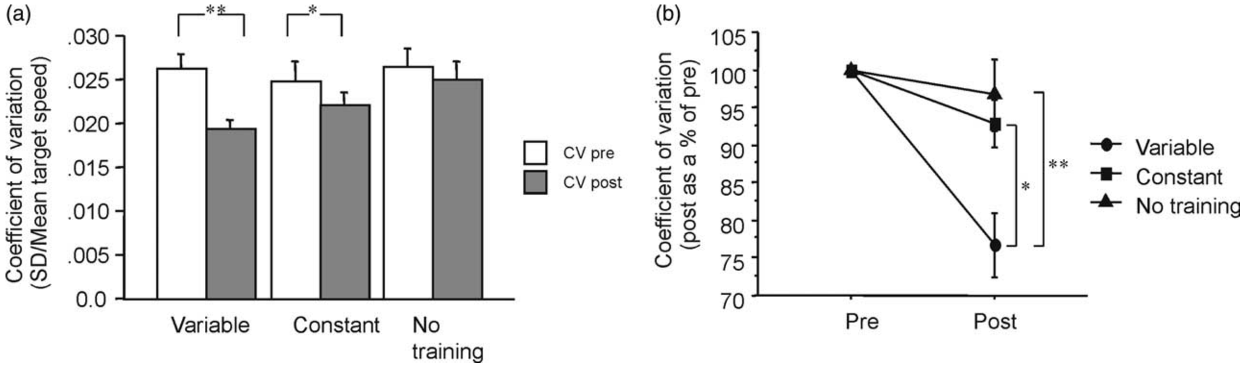

Fig. 2. Training effects on absolute (a) and normalized (b) coefficient of variation of mean speed (CV_{speed}) values. Note that *variable* training was associated with a more prominent decrease in CV_{speed} than *constant* training or *no-training* (b, $^*P<0.007$, $^{**}P<0.001$).

respectively, Fig 2b) in the absence of any correlation with age or gender.

Physical effort, measured as the mean maximum heart rate (118 rpm ± 18), was comparable across the *variable* and *constant* training periods and across subject activity class.

3.2. Physiological measures

Before training, there was no significant influence of previous physical activity on soleus H-reflex amplitudes and soleus MEP area. The M_{max}, measured to monitor the stability of stimulation and peripheral muscle fatigue across conditions, did not show significant effects on CV_{post} nor a significant interaction with the type of training (Fig. 3).

3.2.1. Soleus H-reflex

After training there was a reduction of H-reflex amplitude ($F=7.8$, $P=0.007$) and a significant interaction with the type of training ($F=3.4$, $P=0.04$). Post hoc testing showed that *variable* training led to a significant reduction in H-reflex amplitude in the absence of significant changes

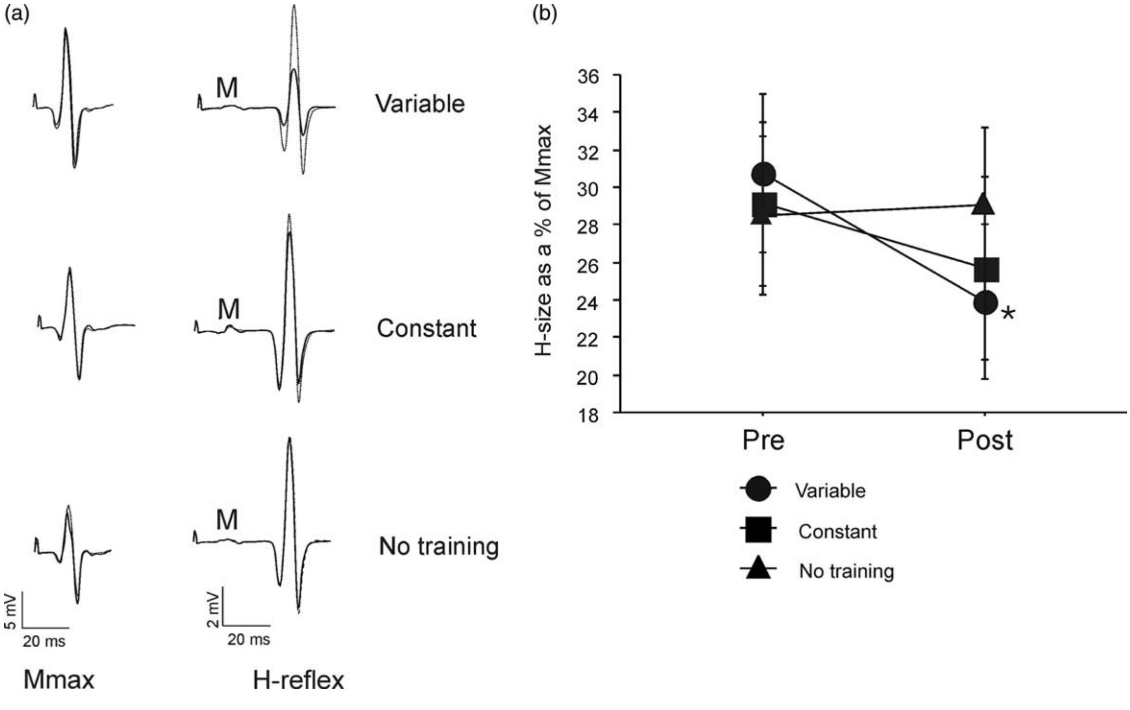

Fig. 3. Training effects on soleus H-reflex. Soleus H-reflexes and maximum M-waves (M_{max}) taken at rest before (thin dashed line) and after (solid line) training in a representative subject (a). Each H-reflex is the average of 24 responses. The reproducible small M-wave preceding the H-reflex was used to monitor the stability of the stimulating conditions before and after training (see Section 2). Note that the M-wave is unchanged by training, while the H-reflex is much smaller after *variable* training and almost unchanged after *constant* or *no-training*. Group data (b) comparing pre- and post-training soleus H-reflex amplitudes (expressed as a percentage of *M*max amplitude) for the 3 interventions. Note that only *variable* training led to a significant reduction in H-reflex amplitude ($^*<0.01$).

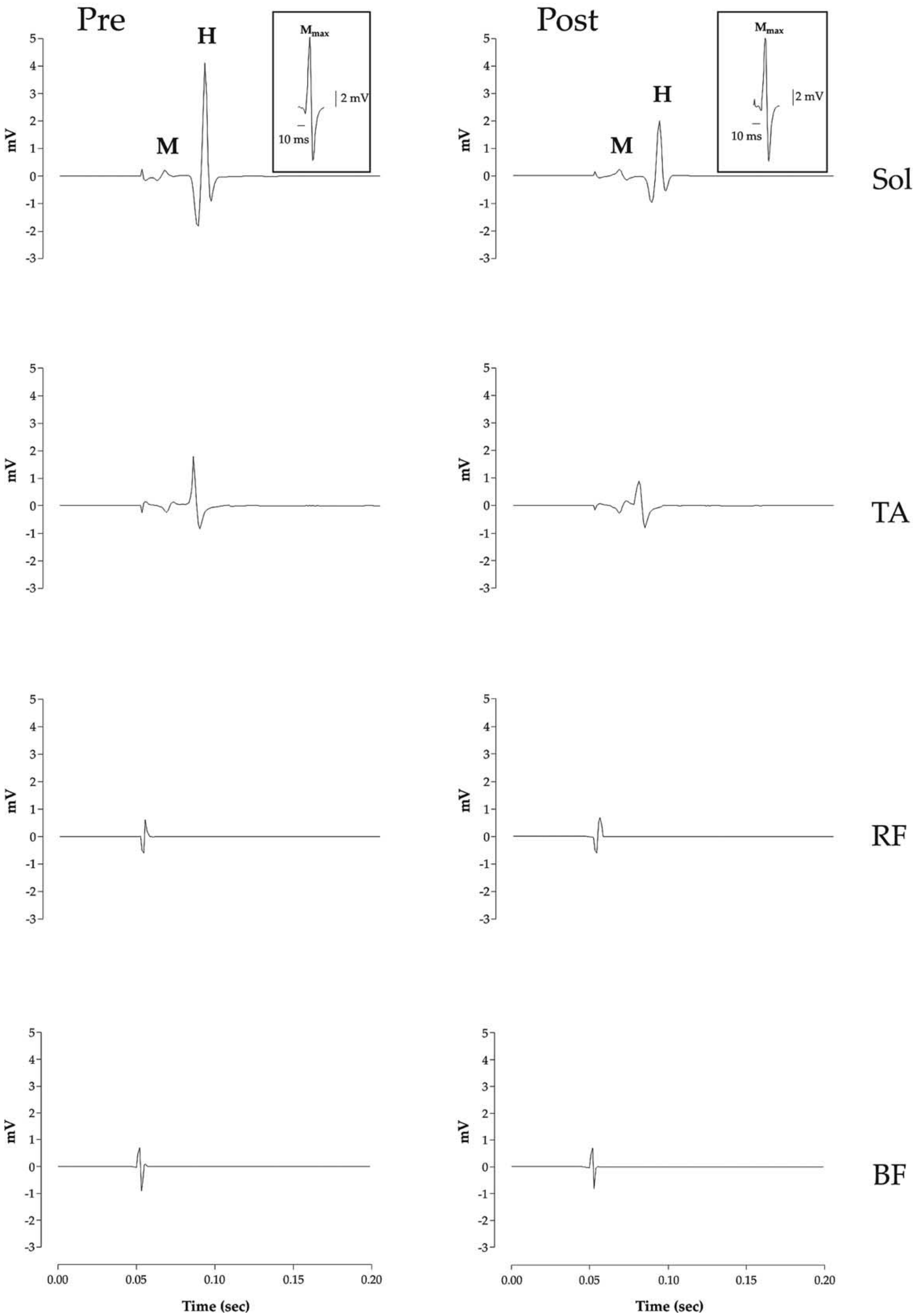

Fig. 4. H-reflexes from the Soleus (SOL) muscle, and EMG activity from tibialis anterior (TA), rectus femoris (RF) and biceps femoris (BF) before (pre) and after (post) *variable* resistance training in one representative subject. Each trace is the average of 24 sweeps. The Sol H-reflex (preceded by a small M-wave of the same size) is consistently reduced after training while the maximum M-wave (insert) recorded from the same muscle is unchanged. Note that in TA, volume conduction responses are recorded, while in RF and BF only the stimulus artifact for the H-reflex is present.

Table 1
RMS (mV^2) of EMG activity 50 ms prior to SOL H-reflex stimulus

$N=3$	Soleus	Tibialis anterior	Rectus femoris	Biceps femoris
Pre	0.0058 ± 0.0006	0.0032 ± 0.0001	0.0040 ± 0.0008	0.0026 ± 0.0005
Post	0.0044 ± 0.001	0.0044 ± 0.001	0.0041 ± 0.0009	0.0024 ± 0.0006

$\text{Pre/Post}_{\text{variable}} = \text{ns}$.

with *constant* training or *no-training* (variable: $P=0.007$; Fig. 3a,b). ANOVA also showed significant effects on $H_{\max}/M_{\max}$ ratio after training ($F=6.4$, $P=0.02$) and a significant interaction with the type of training ($F=7.6$, $P=0.005$). Only *variable* training elicited a significant reduction in $H_{\max}/M_{\max}$ ratio (from 0.56 ± 0.02 to 0.41 ± 0.03, $P=0.01$), while constant and no-training produced no significant effects.

To rule out that changes in reflex amplitude might be due to differences in SOL activity, we measured prestimulus background EMG between conditions. After training, ANOVA showed no significant effect on soleus RMS. Pre/post H-reflex results were similar when pre/post EMG activity in other leg and knee muscles was controlled (see representative example in Fig. 4 and Table 1).

3.2.2. Soleus MEP

ANOVA on soleus MEP area showed no significant difference between the 3 different sessions before training. After training, there was no significant effect on soleus MEP area or RMT nor any interaction with the type of training and physical activity (Fig. 5).

Reduction in CV_{post} (reflecting improved control) correlated significantly with the reduction in soleus H-reflex amplitude after *variable* training ($r=0.55$, $P=0.02$) but not after *constant* training or *no-training* (Fig. 6).

4. Discussion

The main finding of this study was that a brief period of cycling led to changes in a spinal cord pathway expressed as a persistent decrease of the H-reflex amplitude that correlated with skill acquisition.

4.1. Skill acquisition during cycling

Motor learning entails the acquisition of novel movement patterns by simple repetition, by the establishment of new spatiotemporal routines and/or by acquiring arbitrary, context-dependent rules (Shadmehr and Mussa-Ivaldi, 1994; Toni et al., 2001). While these processes have been described in relation to cortical functions, they are likely to operate in subcortical sites involved in locomotor control as well (Burke, 2001; Grillner, 1981).

In this study, subjects were tested on their ability to establish stable speed during 4-min cycling test periods with changing pedal resistances preceding and following 3 interventions (*variable* and *constant* training, and *no training*). During *variable* training, subjects learned to

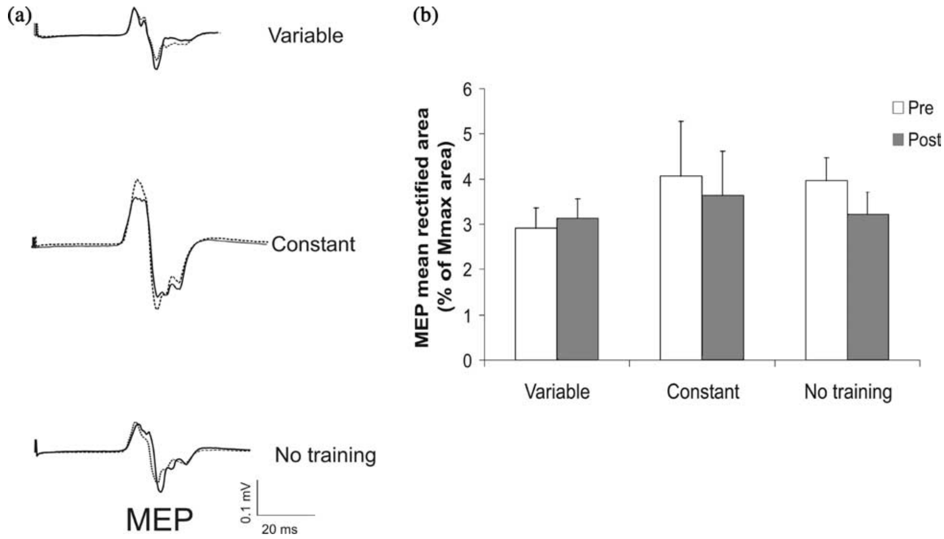

Fig. 5. Training effects on the soleus motor evoked potential (MEP). MEP waves at rest before (thin dashed line) and after (solid line) training in a representative subject (a) and group data (b). In (a), each MEP is the average of 24 responses. In (b), the ratio of MEP mean rectified areas versus *M*max mean rectified areas showed no significant changes following the 3 different interventions.

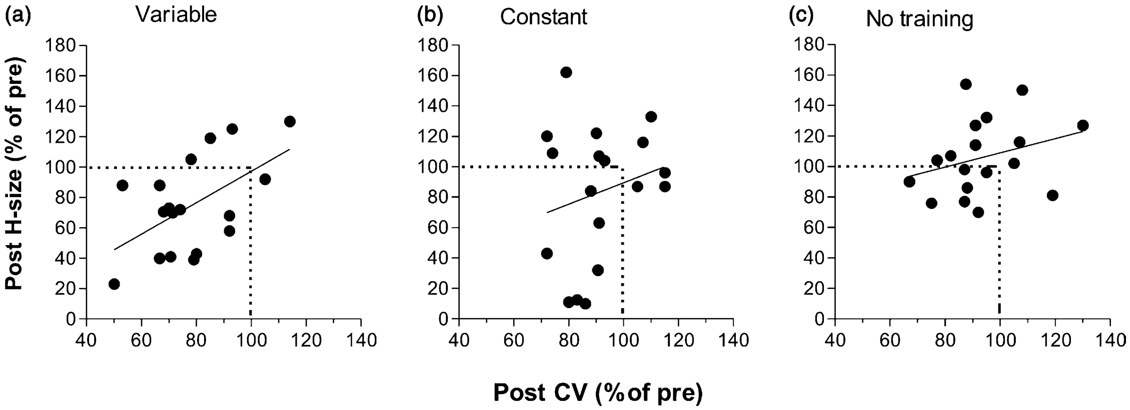

Fig. 6. Training-dependent changes in H-reflex amplitude (ordinate) as a function of training-dependent changes in coefficient of variation of mean speed (CV_{speed}) (abscissa) following the 3 different interventions. In both axes, the dashed lines (100) indicate absence of training-dependent changes. Values below 100 reflect training-dependent improvements in CV_{speed} (abscissa) and decreases in H-reflex amplitude (ordinate). Performance improvements correlated well with H-reflex decreases for the *variable* (a) training only ($r=0.55$, $P<0.02$).

perform an initially unfamiliar task to compensate for the variable load changes. Eventually, they learned to optimize pedal force adjustments to establish stable speed, as reflected by a consistent decrease in CV_{speed}. During *constant* training, subjects soon attained and easily maintained target cycling speed against a constant training load, but were later less effective in compensating for changing pedal resistances during the testing period that followed training, as reflected by a lesser decrease in CV_{speed}. These results also emphasize the view that in the locomotor domain, as previously demonstrated in other systems, complex training paradigms and not only physical activity are required for motor learning and most profound plastic changes (Jensen et al., 2005; Nudo et al., 1996; Plautz et al., 2000). It is important to note that both *variable* and *constant* training involved the same mean pedal resistance and resulted in comparable effort (measured as maximal heart rate). The *no-training* condition controlled for the possible effects of test repetition.

The finding that *variable* training, challenging individuals with frequent unexpected changes in sensory input, led to a greater ability to establish target cycling speed than *constant* training or than *no training* is consistent with the view that changes in sensory input represent a crucial factor in the acquisition of locomotor-related skills (Lam and Pearson, 2002). Age, gender and history of previous physical activity did not exert overt influences on training effects.

4.2. Physiological changes following performance improvements

H-reflexes recorded at rest decreased only with *variable* training and the magnitude of this change correlated with the subjects' ability to control speed (reflected as lower CV_{speed}). The correlation between changes in H-reflex size and performance improvements is suggestive of a connection between excitability changes in this spinal pathway and performance improvements, but cannot be interpreted as proof of a cause-effect link. We have not tested H-reflexes during cycling, and therefore, do not know if the changes described at rest were maintained during performance of the same task, if they were cancelled by motor activity (Ridding and Rothwell, 1995), or if they were further enhanced (Aagaard et al., 2002). Interestingly, it has been proposed that fusimotor activity is stronger during more demanding tasks (Hulliger et al., 1989; Kakuda et al., 1996, 1997). It is also known that during ankle tracking tasks there is differential regulation of the amplitude of soleus H-reflexes and tibial nerve somatosensory evoked potentials (Staines et al., 1997). Perhaps then the attenuation of the H-reflex is required during the learning task to gate the increased afferent drive that presumably is directed toward the higher centres.

It is unlikely that motor fatigue or attention influenced our results, since maximal *M* responses and MEPs, sensitive indicators of peripheral (Duchateau et al., 2002; Garland and McComas, 1990) and central (Brasil-Neto et al., 1993; Lentz and Nielsen, 2002) fatigue did not change. Furthermore, behavioral contexts that require increased attention are often associated with larger H-reflex amplitudes (Hess et al., 2003; Schneider and Capaday, 2003), and not smaller as found in our study.

It may be surprising that MEPs to TMS did not change as a function of training regimen. Many explanations are possible for this negative finding. (1) Corticospinal drive to SOL motoneurones is only in part reflected by MEP changes, as tested here by TMS (Nielsen et al., 1999). (2) A single session of training may not be enough to elicit changes in corticospinal tract function (Thomas and Gorassini, 2005). (3) Learning of a cycling task may be accompanied by reorganizational changes involving multiple neural sites not tested by TMS (Christensen et al., 2000).

In the absence of changes in descending drive to soleus motoneurones, as reflected by lack of differences in MEPs at rest between pre- and post-training, the decrease in H-reflex may be the consequence of an increase in extrinsic presynaptic inhibition, which relies on primary afferent depolarization (PAD) (Rudomin, 1990), in turn modulated by activity in cutaneous and muscle afferents as well as descending pathways (Seki et al., 2003). Homosynaptic depression (Lev-Tov and Pinco, 1992) that does not rely on PAD (Miller, 1998) could also be responsible for the down regulation of H-reflexes after the *variable* training. Long lasting post-activation depression induced by heightened Ia afferent activity may explain why CV_{speed} decreased after both *variable* and *constant* training but that H-reflexes were only reduced after the more demanding training task (see above). It could then be argued that the decrease in H-reflex is not due to an adaptation resulting from a motor learning task but is a phenomenon associated with increased fusimotor drive and Ia activity. However, the improvement in CV_{speed} after constant training may also reflect a better compliance in the musculature due to motor use in the absence of significant changes in spinal pathways. One more point to consider is that we cannot rule out that compensation for the changing loads during variable training engaged muscle groups different from those engaged by the constant training. If so, it is possible that this phenomenon contributes to the differential changes identified in H-reflexes from the SOL muscle, although no pre-post difference in the level of activity of TA, RF and BF muscles was observed after variable training. Altogether, our results show that performance improvements with the *variable* training correlated with SOL H-reflex modulation while this was not the case for the *constant* training.

In summary, engagement in a single training session involving acquisition of a cycling skill results in plastic changes of the H-reflex at rest that is detected after the end of training. We suggest that recalibration of the H-reflex may be part of the control strategy for learning this skill in the context of a task that requires integration of input originating in different sensory modalities.

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