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RESEARCH ARTICLE

Vertical perturbations of human gait: organisation and adaptation of leg muscle responses

V. Bachmann · R. Müller · H. J. A. van Hedel · V. Dietz

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Abstract During the last several years, evidence has arisen that the neuronal control of human locomotion depends on feedback from load receptors. The aim of the present study was to determine the effects and the course of sudden and unexpected changes in body load (vertical perturbations) on leg muscle activity patterns during walking on a treadmill. Twenty-two healthy subjects walking with 25% body weight support (BWS) were repetitively and randomly loaded to 5% or unloaded to 45% BWS during left mid-stance. At the new level of BWS, the subjects performed 3–11 steps before returning to 25% BWS (base level). EMG activity of upper and lower leg muscles was recorded from both sides. The bilateral leg muscle activity pattern changed following perturbations in the lower leg muscles and the net effect of the vertical perturbations showed onset latencies with a range of 90–105 ms. Body loading enhanced while unloading diminished the magnitude of ipsilateral extensor EMG amplitude, compared to walking at base level. Contralateral leg flexor burst activity was shortened following loading and prolonged following unloading perturbation while flexor EMG amplitude was unchanged. A general decrease in EMG amplitudes occurred during the course of the experiment. This is assumed to be due to adaptation. Only the muscles directly activated by the perturbations did not significantly change EMG amplitude. This is assumed to be due to the required compensation of the perturbations by polysynaptic spinal reflexes released following the perturbations. The findings underline the importance of load receptor input for the control of locomotion.

Keywords Locomotion · Body weight support (BWS) · Loading perturbation (LP) · Unloading perturbation (UP) · Loading response

V. Bachmann · R. Müller · H. J. A. van Hedel · V. Dietz (✉)
Spinal Cord Injury Center, University Hospital Balgrist,
Forchstrasse 340, 8008 Zurich, Switzerland
e-mail: Volker.Dietz@balgrist.ch

V. Bachmann · R. Müller
Institute of Human Movement Sciences and Sport,
ETH Zurich, 8092 Zurich, Switzerland
e-mail: v.bachmann@pharma.unizh.ch

Introduction

Proprioceptive feedback contributes in different ways to the neuronal control of locomotion. In cats (Hiebert et al. 1996; McCrea 2001; Donelan and Pearson 2004) and humans (Dietz et al. 1989a, b; Dietz and Duysens 2000; Dietz 2002a) this feedback is important for the modulation of basic locomotor programs, for controlling phase transitions during walking, and for reinforcing ongoing muscle activity. Changes in this feedback, for example, as by limb displacements, evoke complex compensatory leg muscle EMG responses to recover the pre-programmed motor patterns for locomotion. Reflex responses were released following mechanical perturbations of the ankle joint during walking (Grey et al. 2002) or to compensate for ground irregularities (Dietz 2002b). Perturbations induced by obstacles that were dropped on the treadmill in front of the subject during early swing were followed by EMG responses in the ipsilateral leg with spinal onset latencies (Schillings et al. 1996). In all these studies, one or several joints of a limb became displaced. Therefore, the exact source of the relevant afferent input for the leg muscle responses remained unanswered.

Several studies indicated that ground reaction forces acting on the limbs influence locomotor muscle activity and postural control in cats (Duysens and Pearson 1980;

Prochazka et al. 1997) and humans (Horstmann and Dietz 1990; Yang et al. 1998; Bastiaanse et al. 2000; Fouad et al. 2001; Hesse et al. 2001; Dietz 2002b; Ivanenko et al. 2002; Dietz and Harkema 2004). These studies implied that afferent input from hip joints, in combination with that from load receptors, plays a crucial role in the generation of locomotor activity. It is assumed that load sensitive receptors have a facilitatory input to corrective reflex responses. Translational perturbations leading to changes in the body's centre of gravity produced much stronger long-latency responses in the calf muscles compared to rotational perturbations during the stance phase, although stretch of extensor muscles was similar (Dietz et al. 1992). This load information was assumed to be mediated by Ib afferents from extensor muscles (Dietz et al. 1989b; Whelan 1996; Stephens and Yang 1999; Dietz and Duysens 2000). However, little information exists about the direct influence of load information on leg muscle activity during walking.

The aim of this study was to evaluate the leg muscle EMG responses to a sudden change in body load (vertical perturbations) during stepping on a treadmill while changes in leg joint angles were kept to a minimum. These vertical perturbations were released using a special device, the Lokolift® (Hocoma AG, Volketswil, Switzerland). This system allowed loading (LP) and unloading perturbations (UP) of the body within 40–50 ms. We hypothesised that bilateral, complex leg muscle EMG response patterns become evoked by load changes at a spinal level with more activity in LP and less activity in UP condition compared to unperturbed walking. In addition, the course of the leg muscle activation pattern to repeated perturbations over the course of experiment was of interest. We hypothesised that an adaptation of leg muscle activity to body load changes takes place during the course of the experiment.

Methods

Experimental protocol

Twenty-two healthy subjects (age 26 ± 8 years, weight 71 ± 10 kg, and height 1.74 ± 0.08 m) gave informed consent to participate in the experiment. Approval was obtained from the local Ethics Committee according to the Declaration of Helsinki. Leg muscle EMG responses of the lower legs to vertical perturbations during treadmill walking were analysed. Subjects walked within a parachute harness, connected to the body weight support (BWS) system "Lokolift" (Frey et al. 2006). This system provides a precise unloading force during treadmill walking, controlled by a force sensor (Fig. 1a).

Subjects walked on a treadmill with a speed of 0.75 m/s (=2.7 km/h). This speed has been chosen, because this study should also provide data for further research in patients with movement disorders, i.e. who are restricted in their walking speed. To maintain cadence a metronome triggered left and right heel strike. Before the actual experiment was started, the subjects were familiarised to walk on

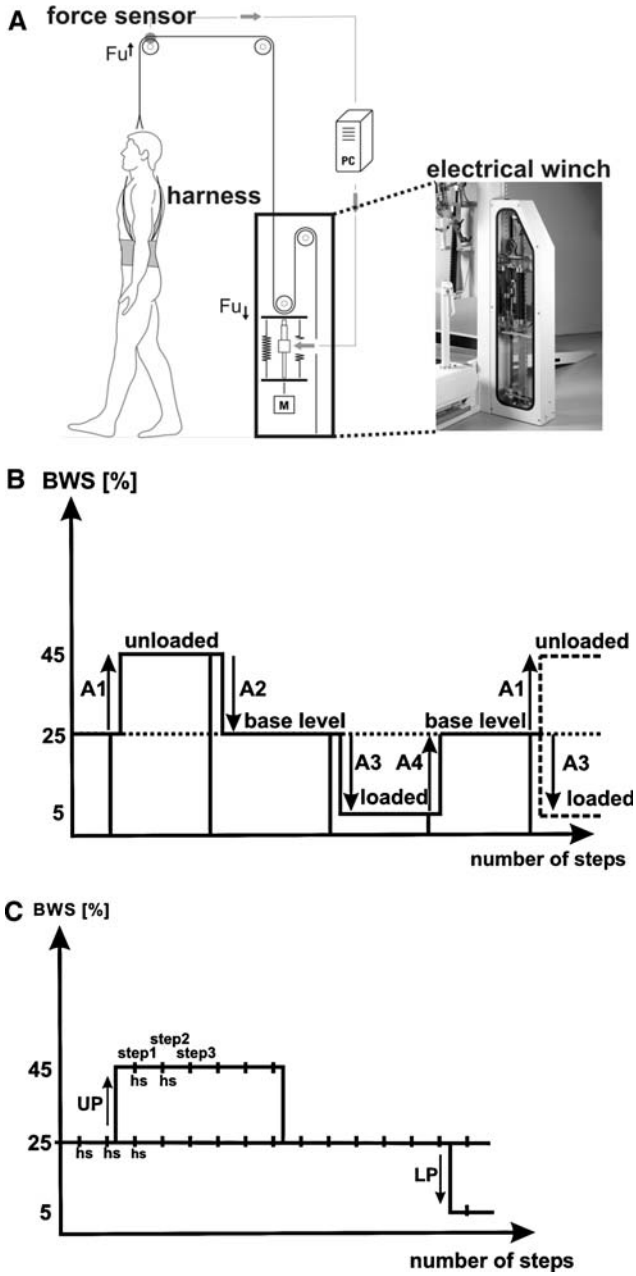

Fig. 1 Experimental set-up. **a** Lokolift System (Hocoma AG, Volketswil, Switzerland) used to unload subjects and to change body weight support during walking on a treadmill. Closed loop control is achieved by a force sensor measuring the actual patient's body weight support. **b** Schematic drawing of the conditions applied to the subjects. Subjects started to walk with 25% body weight support (base level). From this level, the subjects were either loaded to 5% (LP) or unloaded to 45% (UP) of body weight support at left mid-stance. **c** Analysis of steps after a perturbation. Leg muscle EMG analysis was done for the three steps following the unloading perturbation step. *hs* heel strike left

the treadmill at three BWS conditions: 5, 25 and 45% body weight unloading. Each subject walked 100 steps in each condition (data from this familiarisation task were not analysed). In the perturbation experiment subjects started to walk with 25% BWS (Fig. 1b, base level). From this base level, the BWS was suddenly and unexpectedly changed at left mid-stance. The subjects were randomly either loaded (LP) to 5% BWS or unloaded (UP) to 45% BWS every 3–11 steps (Fig. 1b). The new walking condition lasted over 3–11 steps and was always followed by the same amount of steps at base level of 25% BWS. Load changes were accomplished within 40–50 ms. The number of perturbations amounted to 39 ± 3 in LP and 33 ± 5 in UP. Subjects walked 1,600 steps (around 20 min) and did not experience fatigue within this time.

Data acquisition

Flat force sensitive resistors placed on a shoe insole of the subject's left foot detected the four gait events: heel-strike, foot flat, heel-off and toe-off. To assure a physiological gait, an insole of the same dimension, but without resistors, was placed in the right shoe. EMG activity of the biceps femoris and of the mono-articular vastus medialis, tibialis anterior and soleus muscles of both legs was recorded. Surface electrodes (Ag/AgCl) were placed 2 cm apart on the muscle belly parallel to the muscle fibre direction. A reference electrode was put around the left ankle. The raw signals were amplified 5,000 times and band-pass filtered (30–300 Hz). In pilot experiments, ankle and knee joint movements were recorded too, using electro-goniometers (Biometrics Ltd, Gwent, UK). All signals were AD-converted with a sampling rate of 1,000 Hz (resolution 12 bit). The recordings and analyses were performed using Soleasy software (ALEA Solutions GmbH, Zurich, Switzerland).

Data analysis

EMG data

First, all EMG raw data were full-wave rectified, cut into single strides (left heel strike to left heel strike), normalised in time, and filtered (low-pass filter of 20 Hz). Thereafter, these modified data were processed in different ways as explained below.

Leg muscle EMG responses to changes in loading

Leg muscle EMG amplitudes were compared between the base level condition and the steps in which sudden loading (5% unloading) or unloading (45% unloading) was applied. For every perturbed step of each single subject, the root mean square (RMS) was calculated within a period of 300 ms after perturbation onset. Afterwards the median of all steps within each subject was calculated.

The 300 ms time window was chosen because EMG responses generated on a spinal level were the focus of interest for this study. Due to the fact that the data were not normally distributed, differences in amplitudes between base level walking and LP, as well as differences between base level walking and UP perturbation were tested using the Wilcoxon signed ranks test. For all statistical tests, α was set at 0.05.

The latency was defined as the time between onset of perturbation and the leg muscle EMG responses. Latencies were calculated by the net effect of the different vertical perturbations. In order to obtain the net effect of the perturbations on the leg muscle EMG activity, the RMS values of base level walking at 25% BWS were subtracted from those of the LP and UP conditions within the 300 ms time period and median values were built up among the two perturbation conditions, respectively, of every subject. Median values from these data were calculated among all subjects. The time-normalized perturbation median values were again converted back into time to define the latencies visually (cf. Grey et al. 2002).

To compare leg muscle EMG amplitudes of the first three steps following a LP or an UP step (Fig. 1c), RMS values were evaluated for each of the three steps among the whole trial and median values were determined for each individual trial and afterwards among all subjects.

RMS for the left soleus (SOL) was calculated between 15 and 55% after heel strike and for the right tibialis anterior (TAR) between 65 and 5% of gait cycle (Vaughan et al. 1992). To recognise differences in EMG activity within these three steps the Friedman test was performed.

Adaptation in leg muscle EMG activity to repeated perturbations

To evaluate the changes in leg muscle EMG amplitudes immediately after perturbation during the course of experiment, RMS values were calculated over the period of 300 ms after perturbation onset for the LP, UP and base level walking condition, respectively. A linear regression line was fitted through these data points for each condition and each subject separately to account for the EMG step-to-step variability. The value of the regression line at the final step was presented as a percentage of the value of the first step (first step = 100%), representing the slope of the regression line. Differences between the conditions were compared using the Wilcoxon signed ranks test, because the values were not normally distributed.

The interaction between loading direction and adaptation in leg muscle EMG activity to repeated perturbations has also been tested using an ANOVA with repeated measure (Compound Symmetry Model).

Duration of gait cycle and stance phase

To control the possible changes in gait cycle phase due to vertical perturbations, the step-cycle, and the stance phase durations for each LP and UP step for the ipsi- and contralateral legs were determined. Median values of these data were calculated and compared to the step-cycle and stance phase duration of base level walking of 25% BWS. Statistical analysis was performed by the Wilcoxon signed ranks test.

Results

Leg muscle EMG responses to changes in body load

Vertical perturbations released at left mid-stance evoked consistent EMG responses in the SOL and the TAR muscles during the 300 ms. Depending on the perturbation condition, the SOL EMG amplitude was observed to change during left stance, and the timing of the EMG bursts in the TAR changed during right swing (Fig. 2a). The ipsilateral tibialis anterior (TAL), the contralateral soleus (SOR) and the upper leg muscles did not show relevant EMG responses following perturbations and thus, they were not further described. Angular displacements of the leg joints (for an individual example see Fig. 2b) were small and consisted of a decrease in ankle joint movement following LP and UP and a decrease in knee flexion angle following UP.

The EMG patterns were compared between base level walking and the two perturbation conditions. The ipsilateral SOL amplitude showed a stronger excitation following LP ($p < 0.05$) and the amplitude decreased following UP ($p < 0.05$) compared to base level walking. Burst time activity in the contralateral flexor TAR was shortened following LP ($p < 0.05$) and extended following UP ($p < 0.05$). Moreover, TAR EMG activity started with a delay following LP and earlier following UP compared to base level walking. However, the maximum TAR EMG amplitude varied little among all three conditions.

The latencies of the SOL and TAR EMG responses of the population median value varied between 90 and 105 ms in both muscles for the two perturbation conditions (Fig. 2c).

The ongoing swing phase after the perturbations ($p < 0.05$), and therefore, cycle duration was shortened, following LP and prolonged following UP compared to walking at base level. Stance phase duration did not change.

The effect of a change in body load was restricted to one step cycle, as the leg muscle amplitudes did not differ between the three steps after the perturbation step ($p > 0.05$).

Adaptation in leg muscle EMG activity to repeated perturbations

In Fig. 3, the change in muscle activity following LP and UP as well as during walking at base level is shown.

The amplitude of the compensatory EMG responses in SOL and TAR decreased significantly during the course of the experiment ($p < 0.05$) for both perturbation conditions, except for the TAR during UP. This decrease in EMG amplitude was smallest for the muscles directly involved in the compensation of the perturbations, i.e. SOL (LP) and TAR (UP). This decrease of SOL EMG amplitude was stronger following UP and less following LP, compared to walking at 25% BWS and the TAR decreased stronger following LP and less following UP compared to walking at base level.

The interaction of loading direction and adaptation in leg muscle EMG activity to repeated perturbations showed a significant difference in the SOL ($p < 0.05$) and TAR ($p = 0.05$).

Discussion

The aim of this study was to evaluate the effect of vertical perturbations (i.e. body loading/unloading) on leg muscle activation during treadmill walking. The following results were obtained: (1) complex bilateral SOL and TAR muscle EMG responses were evoked with spinal onset latencies (2) leg muscle EMG activity did not change within the first three steps after the perturbation step walking with constant body weight support and (3) a decrease in EMG activity took place during the course of the experiment, which was smallest for the muscles directly activated by the perturbations.

In earlier studies, translational (Dietz et al. 1989a) or rotational perturbations (Schillings et al. 1996; Grey et al. 2004) were applied during the stance phase of locomotion, which evoked bilateral corrective leg muscle EMG reflex responses. In these studies, a mixture of group Ia, Ib and II afferent input was assumed to be involved in the generation of the corrective EMG response patterns. Rapid dorsiflexion-perturbations, for example, mainly induced group Ia mediated short-latency stretch reflex bursts (Grey et al. 2004). However, other studies indicated that perturbations inducing changes in the body's centre of gravity evoked activation locomotion rather of group II or/and group Ib than of group Ia afferents (Dietz 2002b; Sinkjaer 2000). Also feedback from cutaneous afferents might not contribute significantly to the extensor activation during walking, as blocking their transmission by lidocaine had no effect on the extensor EMG response to a displacement of ankle trajectory during locomotion (Mazzaro et al. 2006). In our

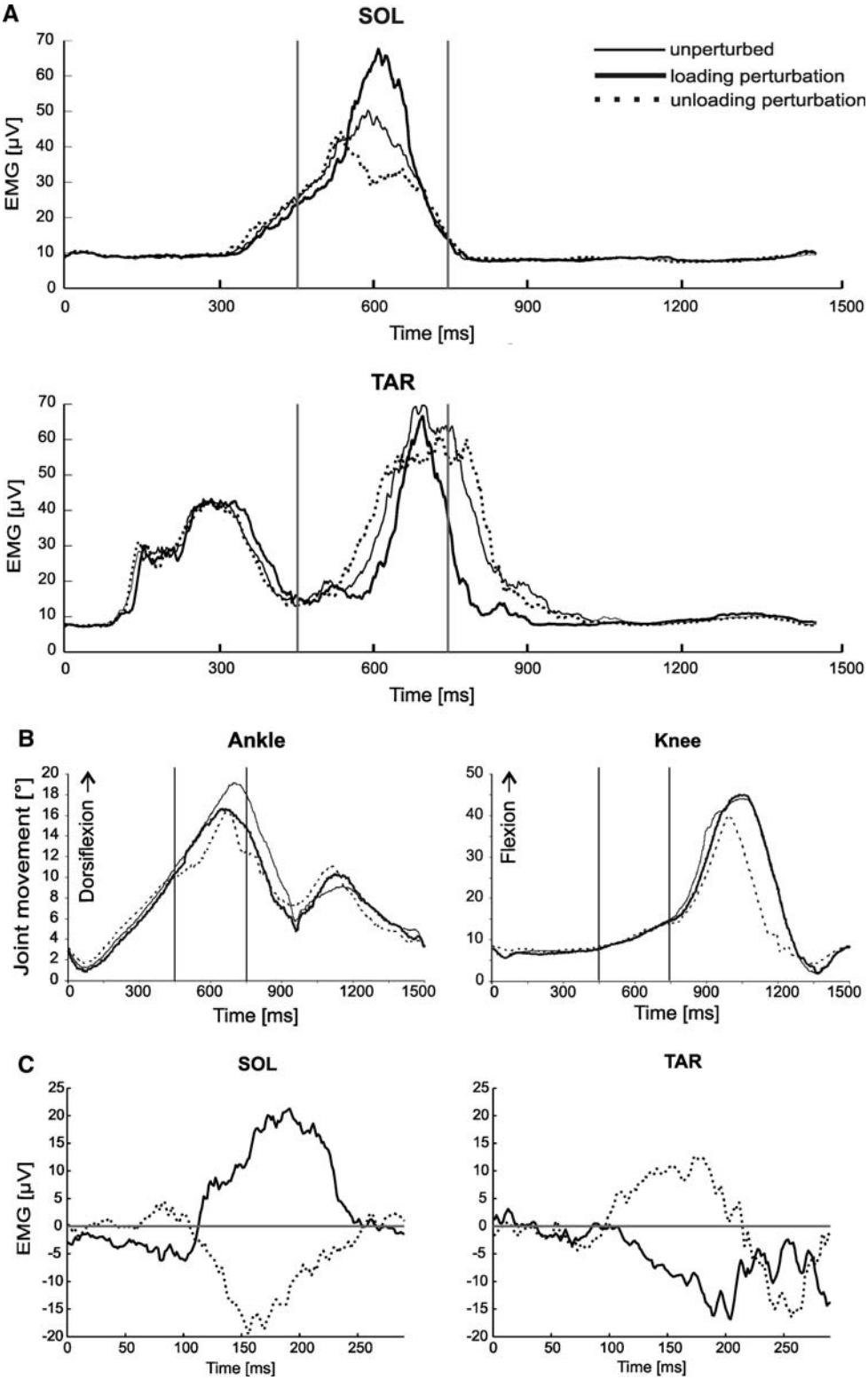

Fig. 2 Leg muscle EMG responses to perturbations. **a** Median EMG responses of the left soleus (SOL) and the right tibialis anterior (TAR) during loading perturbations (25 to 5% of BWS), unloading perturbations (25 to 45% of BWS) and walking at base level (25% BWS), among all subjects. Perturbations were released at left midstance. $t = 0$: left heel strike. EMG activity was analysed within a time window of 300 ms after perturbation onset, represented by the two vertical lines. **b** Individual example of left ankle and knee joint excursions to loading and unloading perturbation (median slopes of multiple measurements). Perturbation responses were analysed within a time window of 300 ms represented by the two vertical lines. **c** Net EMG responses (perturbed step minus base level step of 25% BWS) within the period of 300 ms after perturbation onset among all tested subjects. $t = 0$: onset of perturbation

study, it is unlikely that the results were influenced by short- or long-latency stretch reflexes, as latencies were not compatible and angular displacements at the ankle joints even decreased within the time window of 300 ms after the perturbation.

Leg muscle EMG responses to perturbations

The EMG response patterns observed in this study led to functionally significant responses: in the supporting leg, the extensor activity was increased to compensate for the LP

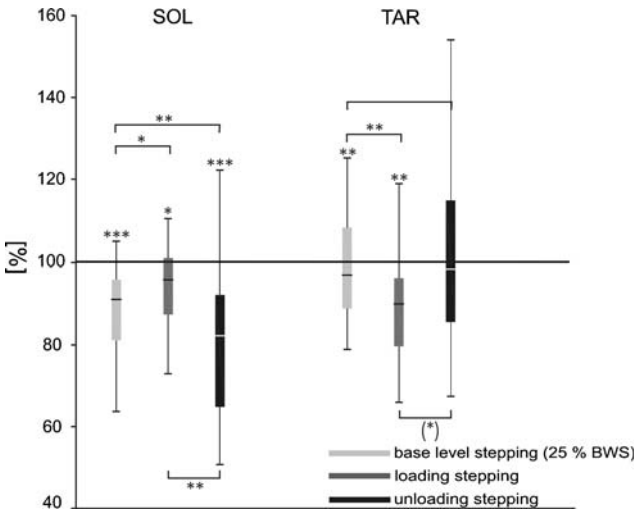

Fig. 3 Changes in amplitude of EMG activity during the course of the experiment, i.e. over 36 ± 5 changes in load (duration about 20 min). *grey* loading perturbation LP; *black* unloading perturbation UP. Muscle activity is plotted as RMS values (calculated within the period of 300 ms after onset of perturbation). *Box plots* show the median, quartile and min/max of activity among all subjects. The *box plot values* at the end are presented as a percentage of the values of the first steps (first step = 100%). *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, (*) $p = 0.05$

and was decreased following UP. These results are in line with other studies using translational perturbations (Finch et al. 1991; Harkema et al. 1997; Stephens and Yang 1999; Dietz and Duysens 2000; Ivanenko et al. 2002). The observations indicate that EMG activity in the antigravity leg muscles is load dependent (Faist et al. 2006). This effect might be mediated by group Ib afferents. According to the latencies, it can be assumed that the EMG responses to load changes were generated within the spinal cord.

Leg flexor muscle activity on the contralateral non-displaced side showed little change in amplitude, but did exhibit a modulation in timing of the EMG burst following perturbations. This stands in contrast to studies on translational leg displacements in adults (Nashner 1980; Harkema et al. 1997) and human infants (Pang and Yang 2001; Lam et al. 2003), where amplitude rather than a time-dependent modulation of flexor activity was found. However, the EMG responses observed in our study might be explained from a biomechanical point of view. The increased torque in the frontal plane following LP becomes compensated not only by an increased ipsilateral SOL activation but also by a shortening of the swing phase and TAR activity. The opposite applies following UP. Correspondingly, earlier studies showed that swing phase was shorter when carrying a load on the back compared to normal walking (Ghori and Luckwill 1985; Bastiaanse et al. 2000). A vestibular contribution to the compensatory EMG responses might be expected in this kind of experiment. Such an input can hardly be separated from the overall responses. On the basis of earlier experiments using head tilts (Horstmann and Dietz 1988) we assume a rather minor contribution by the vestibular system to the EMG responses.

In line with other studies in humans (Berger et al. 1984, 1987; Dietz et al. 1989a; Duysens and Tax 1994; Tang et al. 1998; Dietz and Duysens 2000; Ting et al. 2000; Ferris et al. 2003; Reisman et al. 2005), afferent input from one limb influences the control of the opposite limb. The perturbations in our experiment led to leg muscle EMG responses also on the contralateral side with the same onset latencies, indicating the activation of polysynaptic reflex responses in the flexor and extensor muscles of both sides. This assumption is in agreement with the responses described following translational and loading perturbations. For the loading perturbations, subjects were wearing a belt with evenly distributed weights placed close to the centre of mass (Gollhofer et al. 1986; Dietz 2002b; Grey et al. 2002; Nakazawa et al. 2004).

The perturbation effect was restricted to one step cycle. In the following steps, the leg muscle EMG pattern was adopted to the new loading or unloading condition. In the three steps following the perturbation, no change in EMG activity occurred. This suggests that no long lasting effects due to the change in BWS were present, i.e. no after-effect occurred. However, it has to be noted that leg muscle EMG activity was analysed only for the three steps following the perturbation step. In earlier studies leg muscle EMG activity responses did not immediately return to the baseline level after removal of an additional body load (Fouad and Pearson 1997; Fouad et al. 2001). However, in these studies the subjects walked over a longer period with the same BWS, before loading was changed.

Adaptation of leg muscle EMG pattern to repeated perturbations

Over the course of the experiment, leg muscle EMG activity following LP and UP decreased in the ipsi- and contralateral legs, most probably due to adaptive changes. Obviously, muscle activation took place in a more economical way to prevent muscle fatigue. The decrease in EMG amplitudes was small or even absent in muscles that were directly involved in compensating for the new body load, i.e. in the leg extensor following the perturbations during loading, and in the contralateral flexor muscle during unloading. This might be due to the fact that a constant activation was required for compensation, provided by spinal reflexes. This assumption would fit with observations made in subjects with chronic spinal cord injury, where H- and flexion reflex response amplitudes remained constant while the locomotor EMG activity decreased within a few minutes during a walking session (Muller and Dietz 2006).

The effects of the perturbations on EMG response amplitude might be influenced by the predictability of the perturbations (every 3–11 steps). This seems, however, rather unlikely for the following reasons: (1) not only the timing but also the direction of the perturbation was randomized (see Methods). (2) The change of EMG amplitudes during the course of an experiment did not show a uniform adaptation as it would be expected in the case of predictability but differed between the conditions. For example, during unloading perturbations TAR response showed little change over the course while the SOL response became significantly smaller at the end of the experiment. This reduction in SOL amplitude again was in the range of that seen in the baseline condition (25% BWS).

In summary, the findings made in this study underline the importance of load information in the control of locomotion. The present findings may contribute to the optimization of locomotor training in subjects with movement disorders during their rehabilitation process. Variable load feedback might enhance training efficacy (Bernstein 1967).

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