Locomotor activity in spinal man: significance of afferent input from joint and load receptors

Volker Dietz, Roland Müller and Gery Colombo

Paraplegic Centre of the University Hospital Balgrist, Zurich, Switzerland

Correspondence to: V. Dietz, ParaCare, Paraplegic Centre, University Hospital Balgrist, Forchstr. 340, 8008 Zurich, Switzerland

E-mail: dietz@balgrist.unizh.ch

Summary

The aim of this study was to differentiate the effects of body load and joint movements on the leg muscle activation pattern during assisted locomotion in spinal man. Stepping movements were induced by a driven gait orthosis (DGO) on a treadmill in patients with complete para-/tetraplegia and, for comparison, in healthy subjects. All subjects were unloaded by 70% of their body weight. EMG of upper and lower leg muscles and joint movements of the DGO of both legs were recorded. In the patients, normal stepping movements and those mainly restricted to the hips (blocked knees) were associated with a pattern of leg muscle EMG activity that corresponded to that of the healthy subjects, but the amplitude was smaller. Locomotor movements restricted to imposed ankle joint movements were followed by no, or only focal EMG responses in the stretched

muscles. Unilateral locomotion in the patients was associated with a normal pattern of leg muscle EMG activity restricted to the moving side, while in the healthy subjects a bilateral activation occurred. This indicates that interlimb coordination depends on a supraspinal input. During locomotion with 100% body unloading in healthy subjects and patients, no EMG activity was present. Thus, it can be concluded that afferent input from hip joints, in combination with that from load receptors, plays a crucial role in the generation of locomotor activity in the isolated human spinal cord. This is in line with observations from infant stepping experiments and experiments in cats. Afferent feedback from knee and ankle joints may be involved largely in the control of focal movements.

Keywords: complete paraplegia; human locomotion; leg muscle EMG activity; load receptors; hip joint receptors

Abbreviations: DGO = driven gait orthosis; GM = medial gastrocnemius muscle; SCI = spinal cord injury; TA = tibialis anterior muscle

Introduction

The regulation of human upright posture and locomotion is based on the finely tuned coordination of muscle activation between the two legs. For example, when a disturbance causes an initiation or prolongation of the swing phase on one side, the stance phase of the contralateral leg becomes initiated or prolonged accordingly in human infants (Yang et al., 1998a, b; Pang and Yang, 2000, 2001) and the cat (Gorassini et al., 1994; Hiebert et al., 1994, 1996; Schomburg et al., 1998). Unilateral leg displacements during stance and gait evoke a bilateral response pattern with similar short (i.e. spinal) onset latencies on both sides (Dietz and Berger, 1984). This interlimb coordination is necessary to keep the body centre of gravity over the feet (Dietz et al., 1989; for a review see Dietz, 1992).

In most studies on the bilateral coordination of leg movements in cat and man, one or both legs became perturbed. By such an approach, several joints of a limb become displaced. However, whether the source of the relevant input for the bilateral coordination is provided by the displacement of a single joint or by the combination of the afferent input from many sensors of joints, muscles and tendons activated by the leg displacement has not been determined. In the cat, there are two main sources of afferent input, that lead to rhythm entrainment and/or resetting of locomotor activity. Such input can either block or induce a switching between the alternating flexor and extensor locomotor bursts. One of these two sources that satisfy these criteria is related to hip position, the other to load (for a review see Dietz and Duysens, 2000). For example, for the initiation of the swing phase, the significance of hip position was stressed for human infant stepping (Pang and Yang, 2000), similarly to what was described for the chronic spinal

Table 1 Data of patients included in the study

Subject	Age (years)	Level of lesion	ASIA	Duration of lesion (years)
P1	19	C 6/7	В	4
P2	62	T 7	A	9
P3	31	T 6	A	5
P4	52	C 6	A	10
P5	40	C 7	В	10
P6	37	T 3/4	A	10

C = cervical; T = thoracic; ASIA = American Spinal Injury Association classification.

cat (Grillner and Rossignol, 1978). However, how similarly organized the coordination of leg movements is to that described for the spinal cat and, indeed, how important is the contribution of afferent input from joint receptors remain unanswered.

Furthermore, in recent studies, the significance of load receptor input for the regulation of stance and gait was stressed for the cat (Prochazka *et al.*, 1997) and man (Dietz *et al.*, 1992). It was assumed that this effect is mediated by group Ib afferent input (for a review see Dietz and Duysens, 2000).

Further studies have indicated that even in complete paraplegic patients, a locomotor pattern can be evoked (Dietz *et al.*, 1995; Harkema *et al.*, 1997). In these studies, it was emphasized that load receptor input is essential for leg muscle activation during stepping movements of these patients.

The aim of the current study was to evaluate the differential effects of proximal and distal leg joint movements in combination with actual body load on the leg muscle activation pattern in complete paraplegic patients. This was achieved by walking within a driven orthotic device, which enabled the induction of stepping movements restricted to specific joints and with different body loads. It was hypothesized that, in addition to body load, hip, knee and ankle joints differentially contribute to coordinated leg muscle activation during locomotion.

Methods

General procedures and subjects

With the permission of the local Cantonal ethics committee and the informed consent of the volunteers, the leg muscle EMG during assisted locomotion was analysed in six patients with a chronic (>2 years) complete para-/tetraplegia (see Table 1) and in three healthy subjects (age 24–29 years). According to the classification of the ASIA (American Spinal Injury Association; see Maynard *et al.*, 1997), the patients included were sensory incomplete but motor complete (ASIA B) or sensory and motor complete (ASIA A) with a level of lesion between C 6 and T 7. During walking with a driven gait orthosis (DGO) 'Lokomat' (Hocoma AG, Zurich) on a treadmill, the EMG activity of right and left leg muscles [rectus femoris, biceps femoris, tibialis anterior (TA) and medial gastrocnemius (GM)] was recorded. Surface elec-

trodes were fixed over the muscle belly with a distance between the electrodes of 1.5 cm. Hip and knee joint movements of the orthosis were recorded by potentiometers.

DGO

A detailed description of the device can be found elsewhere (Colombo et al., 2000, 2001). Briefly, the DGO provides drives for the hip and knee joint movements of each leg, whereas the dorsiflexion of the ankles during the swing phase is achieved by passive foot lifters (elastic straps) (see Fig. 1A). The drives consist of linear actuators with a precision ball screw driven by a DC motor via a toothed belt. Four separate position controllers implemented in a computer-based real time system (Lokomaster-PC) control the angles of the hip and knee joints. The desired angle values for hip and knee are taken from a database of healthy subjects walking within the DGO (see Fig. 1B) and are identical for all subjects. Feedback of the actual angles of the orthosis is provided by potentiometers attached to the lateral aspect of the hip and knee joints of the orthosis. Ankle joint movements are recorded by mechanical potentiometers attached to the lateral aspect of the lower leg and foot. Unloading is achieved by a parachute harness connected to counterweights (see Fig. 1A).

The DGO is fixed to the treadmill by a flexible parallelogram (see Fig. 1A). A compensation mechanism for the weight of the orthosis is provided. The orthosis is fixed to the subjects with straps around the waist, the thigh and the shank. The orthosis can be adjusted in size at the different segments and therefore can be adapted to different subjects.

Walking conditions

During treadmill walking, speed was kept constant at 1.9 km/h. Stepping cadence had to be adjusted slightly according to the leg length of the different subjects. Before the experiment was started, subjects walked for ~5 min to habituate to walking within the orthosis. Although there were some restrictions of arm swing due to the orthosis, after habituation subjects reported little impairment of their walking movements. Healthy subjects were instructed to walk as normally as possible within the DGO and not to intervene with the movements imposed by the DGO for the

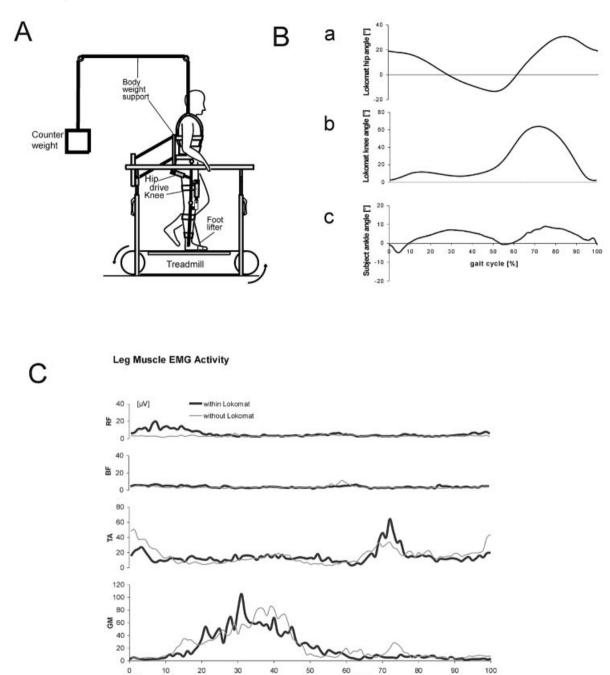


Fig. 1 Experimental set-up. (**A**) Locomotion on the treadmill within a DGO. (**B**) Hip (a) and knee (b) joint movement trajectories were imposed by the DGO. For the ankle joint movements (c), support for foot dorsiflexion during the swing phase was provided by passive foot lifters (elastic straps). (**C**) EMG activity of upper and lower leg muscles during stepping within and without the DGO.

stance phase

normal walking condition. There was little difference between the locomotor pattern obtained during walking within or without the DGO (see Fig. 1C).

The different walking conditions performed by all six patients and three healthy subjects were the following: (i) bilateral normal walking; (ii) bilateral 'hip walking', i.e. walking with the knees fixed in an extended position; and (iii) unilateral walking, i.e. normal walking on the right side and rhythmic loading of the extended and static left leg during

right swing. All three conditions were performed with partial body unloading of 70% body weight. Such an unloading is necessary to allow stepping movements to be induced in complete paraplegic patients (cf. Dietz *et al.*, 1995) and to prevent stumbling. In three patients and two healthy subjects, (i) normal walking movements were also induced with full body unloading and (ii) simulated 'walking' movements were imposed only on the left ankle joint with or without loading the foot sole (~30% of body weight).

swing phase

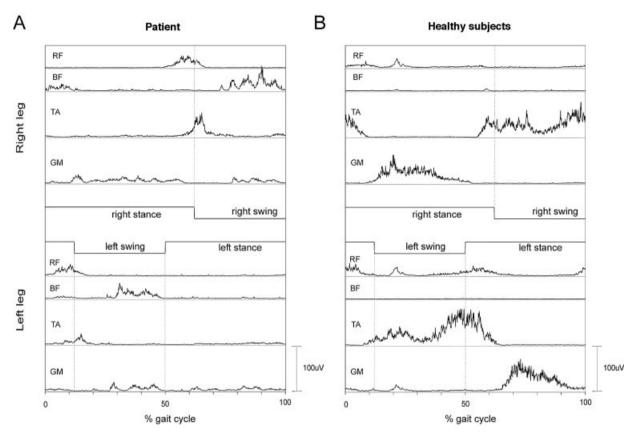


Fig. 2 Locomotor activity of individual examples. Averaged (n = 20 gait cycles) leg muscle EMG activity of both legs during normal walking within the DGO with body weight support (70%) from (**A**) a patient with complete paraplegia (level of lesion T 6) and, (**B**) a healthy subject. RF = rectus femoris: BF = biceps femoris

The duration of one experiment was \sim 30 min; subjects did not experience fatigue within this time. For the bilateral hip walking as well as for the unilateral walking, additional measures had to be undertaken, either to get enough clearance of the foot during the swing phase (hip walking) or to allow the static extended posture of the left leg over the moving belt during stance (unilateral walking), respectively. This required that a platform (a 35 \times 20 cm rectangle of 10 cm height) was interposed manually between foot and treadmill on either side in order to achieve an appropriate loading (30% body weight) of the respective extended leg during the stance phase.

Data analysis

For data recording and signal analysis, Soleasy Software (ALEA Solutions GmbH, Zurich) was used. EMG recordings were amplified (microvolt amplifier; band pass filter 30–300 Hz) and transferred to a PC via a 12 bit AC/DC converter. In addition, the following signals were recorded: reference signals for hip and knee joint movement of both orthotic legs, recordings of actual hip and knee joint angle trajectories of both orthotic legs, and two trigger signals identifying the beginning of the right and left stance phases. All data were sampled at 600 Hz.

For data analysis, the EMG was rectified. Twenty gait cycles of each condition were normalized in time and averaged. The population mean values were calculated for the groups of three healthy subjects and of six patients for the walking conditions (i)–(iii).

Statistics

EMG mean values per leg muscle and for one gait cycle were calculated individually for both the patients and healthy subjects. Differences between the groups of healthy subjects and of patients were tested statistically using the Wilcoxon two-sample test. The significance level was set at P < 0.05.

Results

Leg muscle activity during normal stepping movements

Figure 2 shows an individual example of the locomotor pattern of a patient with complete paraplegia (level of lesion T 6) (Fig. 2A) and of a healthy subject (Fig. 2B) during walking within the DGO. Both the patient and the healthy subject were unloaded by 70% of their body weight. There was a distinct pattern of bilateral leg muscle activation in the

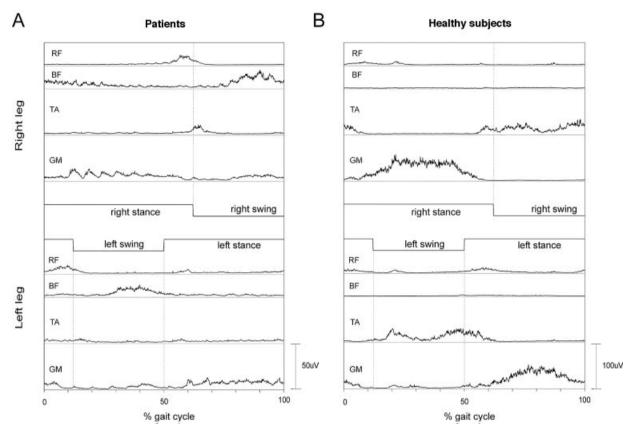


Fig. 3 Normal walking. Averaged (20 gait cycles) leg muscle EMG activity of (A) six complete spinal cord injury (SCI) patients and (B) three healthy subjects during normal walking within the DGO with body weight support (70%). Note the different EMG calibration in A and B.

patient, which in several aspects was similar to that obtained in the healthy subject. The main difference observed was that the amplitude of EMG activity, especially of TA and GM, was considerably smaller in the patient. Furthermore, TA was only active at the beginning of swing and not during the whole swing phase as it was in the healthy subject. During swing, low amplitude EMG activity was present in the GM. A reciprocal mode of upper and lower leg muscle activation was present in both the patient and the healthy subject.

Figure 3 shows the mean of the locomotor pattern obtained from six subjects with complete para-/tetraplegia (Fig. 3A) and three healthy subjects (Fig. 3B). The body unloading (70%) and the movements imposed by the DGO were the same in patients and healthy subjects. The leg muscle activation on both sides in the patients was similar to that of the healthy subjects in several aspects (e.g. reciprocity of EMG activity in antagonistic leg muscles and appearance of leg extensor and flexor EMG activity during the stance and swing phases, respectively). However, the EMG amplitude in the lower leg extensor muscles of the patients was significantly (P < 0.05) smaller (about half amplitude) than that recorded in the healthy subjects. In contrast, in most patients, the EMG amplitude of upper leg muscles was larger than in the healthy subjects. However, because of the great variability, the difference was not significant.

Effect of joint afferents

The DGO enabled the evaluation of the effect of blocking knee joint movements during the performance of 'stepping movements'. Figure 4 shows the mean of the bilateral pattern of leg muscle activation obtained from all patients during walking with blocked knee movements. The pattern of leg muscle activity was about the same as seen with normal leg movements (Fig. 3A).

In a further experiment, only the right leg performed physiological stepping movements. The movements of the whole left leg were blocked. This leg was only loaded (30% of body weight) during the swing phase of the right leg, i.e. the corresponding 'stance phase' of the left static leg. Under these conditions, the 'normal' pattern of leg muscle activation (cf. Figs 2 and 3) appeared only in the right, moving leg in the patients (Fig. 5A) with no visible EMG activity in the static left leg. In contrast, the healthy subjects also showed a pattern of leg muscle activation in the left, non-moving leg. This pattern was similar to that during normal locomotion for the leg flexor muscles but of smaller amplitude (Fig. 5B). In the left RF and GM (the extensor muscles), only little EMG activity was apparent.

Furthermore, 'stepping' movements were imposed at the left ankle joint only (see Fig. 1Bc), with a corresponding loading at the foot sole during the simulated 'stance phase' of

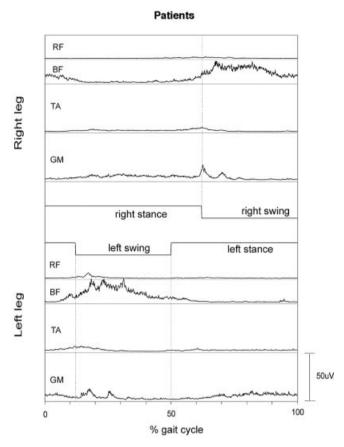


Fig. 4 Hip walking. Averaged (20 gait cycles) leg muscle EMG activity of six complete SCI patients during hip walking (knee joints in a fixed extended position) within the DGO with body weight support (70%).

the static leg while the right leg performed normal stepping movements. In the patient and the healthy subject, an increase of EMG activity was restricted to the GM muscle (not shown).

Effect of body unloading

From earlier studies on the locomotor training of incomplete paraplegic patients, it became apparent that body unand reloading is of crucial importance for its success (Dietz *et al.*, 1995). In order to facilitate leg movements, body unloading was required for the training in patients with a spinal cord injury (SCI). The degree of unloading depended predominantly on the severity of the spinal cord lesion. However, with the course of training, a successive reloading was possible and, therefore, it was suggested that this might be the adequate stimulus to obtain training effects (cf. Harkema *et al.*, 1997).

By the application of the DGO, it also became possible to impose the same physiological locomotor movements as in the previous experiments with full (100%) body unloading (i.e. without ground contact during the step cycle). Since the DGO exerted only hip and knee joint locomotor movements,

the corresponding movements of the feet were imposed manually (without loading the foot sole). Figure 6 shows the leg muscle EMG activity with 70% (above) and 100% (below) body unloading during walking movements in a patient with complete paraplegia (Fig. 6A) and a healthy subject (Fig. 6B). Compared with the partial unloading, EMG activity recorded in the proximal and distal leg muscles was reduced or lacking in both patients and healthy subjects when air stepping movements were performed.

Discussion

The aim of this study was to evaluate the afferent sources and their contribution to the organization of stepping movements in spinal man. Earlier investigations have shown that it is possible to induce locomotor activity in patients with complete paraplegia (Dietz et al., 1995; Harkema et al., 1997). However, from these studies, the requirements to achieve a patterned leg muscle activation remained unresolved. The main observations made here on the locomotor activity of the isolated spinal cord were the following: (i) stepping movements induced by the DGO only in combination with afferent input from 'load receptors' lead to a patterned leg muscle activation, similar to the case in healthy subjects; (ii) in addition to load receptor input, afferent information from hip joints seems to be essential for the generation of a locomotor pattern; and (iii) in contrast to healthy subjects, unilateral stepping movements do not lead to a bilateral pattern of leg muscle activation. These results will be discussed in the context of what is known about the organization of locomotion from humans and cats and with respect to their functional relevance.

Significance of load receptor input

The significance of load receptors for the regulation of stance and gait had been established previously in healthy subjects (Dietz *et al.*, 1992) as well as in the cat (Duysens and Pearson, 1980; Prochazka *et al.*, 1997). Also, the essential contribution of load receptor input to the generation of a locomotor pattern has been recognized earlier in paraplegic patients (Dietz *et al.*, 1995; Harkema *et al.*, 1997).

By the application of the DGO in the present study, we could show that physiological locomotor-like leg movements alone (100% body unloading) do not lead to a leg muscle activation in either healthy subjects or patients with complete para-/tetraplegia. Obviously, cyclical leg movements only in combination with loading of the legs lead to an appropriate leg muscle activation. Therefore, it is not surprising that body un- and reloading plays an essential role in the success of locomotor training in incomplete paraplegic (Dietz *et al.*, 1995) and hemiplegic (Hesse *et al.*, 1997) patients. The differential strength of upper and lower leg muscle activation in the patients compared with the healthy subjects with a greater EMG amplitude in upper muscles might reflect the phylogenetically earlier locomotor pattern observed in infants

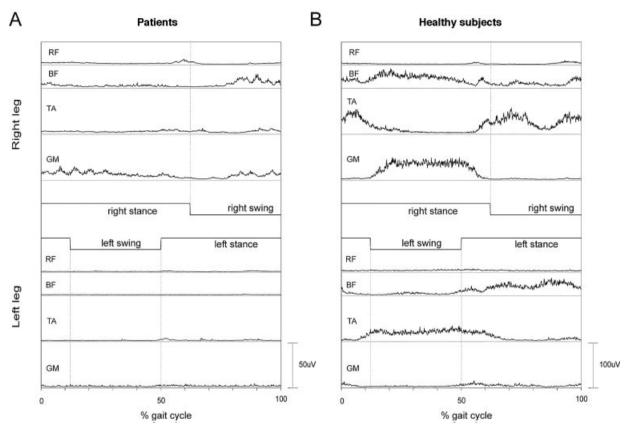


Fig. 5 Unilateral walking. Averaged (20 gait cycles) leg muscle EMG activity of (A) six complete SCI patients and (B) three healthy subjects during unilateral walking within the DGO with body weight support (70%). The left static leg was loaded rhythmically (30%) during the swing phase of the right, physiologically stepping leg.

(Pang and Yang, 2000) and cats (Hiebert *et al.*, 1994). Alternatively, this difference might be compensatory for the reduced lower leg muscle activation. From the present experiments and the earlier reports, it still remains unclear whether Ib afferents, as suggested for the cat (see Dietz and Duysens, 2000), are responsible for the effects of actual body load during locomotion in human subjects.

The absence of leg muscle EMG activity in the patients when physiological stepping movements were imposed during full body unloading indicates that pathological stretch reflexes contribute little to the leg muscle activation in normal walking conditions.

In addition, in the patients, an appropriate rhythmic loading of the ipsilateral stationary, extended leg while stepping movements are performed by the contralateral leg did not lead to an activation of the static leg. This indicates that a combination of different afferent inputs is required to achieve a locomotor-like leg muscle activation. It is still unresolved as to how far this really represents a 'locomotor' activity.

Significance of hip joint afferents

Here, for the first time, the effect of controlled movements applied to proximal leg joints on leg muscle activation was studied in complete paraplegic patients. A major observation was that the pattern of leg muscle activation was almost unchanged after the knee joint movements were blocked. Furthermore, isolated foot joint movements (simulated stepping with or without loading of the foot sole) evoked only local responses, which is in line with the findings of earlier reports (Gottlieb and Agarwal, 1979; Dietz *et al.*, 1992; Sinkjaer *et al.*, 1996). This indicates that hip joint afferents play a major role in leg muscle activation in the isolated spinal cord.

Afferent input from hip joints obviously is important for the leg muscle activation during locomotion. This is especially the case for initiating the stance to swing transition with the appropriate leg muscle activation, as was shown earlier for stepping in human infants (Pang and Yang, 2000, 2001). The significance of hip joint afferents was also emphasized for cat locomotion (Grillner and Rossignol, 1978). In the latter experiments, it was observed that preventing the hip from obtaining an extended position in chronic spinal cats inhibited the generation of the flexor burst and the onset of the swing phase. Furthermore, entrainment of a locomotor rhythm was obtained by using rhythmic hip movements in immobilized spinal (Andersson and Grillner, 1981, 1983) and decerebrate (Kriellaars *et al.*, 1994) cats.

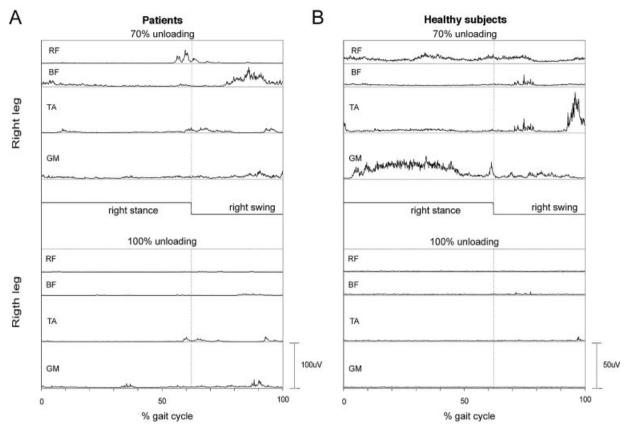


Fig. 6 Air stepping. Averaged (20 gait cycles) right leg muscle EMG activity of (**A**) a complete SCI patient (T 3/4) and (**B**) a healthy subject during walking within the DGO with 70% (above) and 100% (below) body unloading.

The observations made here indicate that a combination of hip with other afferent input, especially from load receptors (Dietz *et al.*, 1992; Dietz and Colombo, 1996; for a review see Dietz and Duysens, 2000), contributes to the functionally reasonable pattern of leg muscle activation during human locomotion.

Interlimb coordination

Earlier studies in healthy subjects on interlimb coordination during stance and locomotion indicated a coordination of bilateral leg muscle activation at a spinal level (for a review see Dietz, 1992). A bilateral coordination of leg muscle activation is already present in early infancy, i.e. well before the onset of independent walking (Pang and Yang, 2001). An interlimb neuronal mechanism which coordinates the activity between muscles of both legs was also described for pedalling movements (Ting *et al.*, 2000). In these experiments, an influence of contralateral extensor phase afferent input on the ipsilateral flexion movements indicated a bilateral coupling of gain control mechanisms.

On the basis of this interlimb coordination, it was suggested that unilateral stepping movements lead to an activation of the contralateral static, but rhythmically loaded leg. The discrepancy between the preserved activation of leg flexor but strongly reduced EMG activity in the leg extensor

muscles observed here in the group of healthy subjects might be attributed to the well established differential neuronal control of these muscles with a central dominance in the control of leg flexor activity (for a review see Dietz, 1992). During normal locomotion, the leg extensor activity is modulated continuously by proprioceptive feedback during the stance phase. Therefore, in the present condition, with a lack of roll off of the body over the standing leg, this EMG activity is expected to be diminished.

In contrast, no significant EMG activity was present in the muscles of the non-moving leg in the group of patients with an SCI independent of the level of lesion. Therefore, it is assumed that for the walking condition studied here, the spinal coordination of bilateral leg muscle activation depends on a facilitation by supraspinal centres. Indeed, a cerebellar contribution via reticulus spinal neurones has been suggested in both cats (Ito, 1984) and humans (Bonnet *et al.*, 1976), and evidence was presented for a cortical (supplementary motor area) control of interlimb coordination (Debaere *et al.*, 2001).

Acknowledgements

We wish to thank Rachel Jurd for correcting the English text. This work was supported by the Swiss National Science Foundation (No. 31-64792.01) and the NCCR on Neural Plasticity and Repair.

References

Andersson O, Grillner S. Peripheral control of the cat's step cycle. I. Phase dependent effects of ramp-movements of the hip during 'fictive locomotion'. Acta Physiol Scand 1981; 113: 89–101.

Andersson O, Grillner S. Peripheral control of the cat's step cycle. II. Entrainment of the central pattern generators for locomotion by sinusoidal hip movements during 'fictive locomotion'. Acta Physiol Scand 1983: 118: 229–39.

Bonnet M, Gurfinkel S, Lipchits MJ, Popov KE. Central programming of lower limb muscular activity in the standing man. Agressologie 1976; 17: 35–42.

Colombo G, Joerg M, Schreier R, Dietz V. Treadmill training of paraplegic patients using a robotic orthosis. J Rehabil Res Dev 2000; 37: 693–700.

Colombo G, Wirz M, Dietz, V. Driven gait orthosis for improvement of locomotor training in paraplegic patients. Spinal Cord 2001; 39: 252–5.

Debaere F, Swinnen SP, Beatse E, Sunaert S, Van Hecke P, Duysens J. Brain areas involved in interlimb coordination: a distributed network. Neuroimage 2001; 14: 947–58.

Dietz V. Human neuronal control of automatic functional movements. Interaction between central programs and afferent input. [Review]. Physiol Rev 1992; 72: 33–69.

Dietz V, Berger W. Interlimb coordination of posture in patients with spastic paresis: impaired function of spinal reflexes. Brain 1984; 107: 965–78.

Dietz V, Colombo G. Effects of body immersion on postural adjustments to voluntary arm movements in humans: role of load receptor input. J Physiol 1996; 497: 849–56.

Dietz V, Duysens J. Significance of load receptor input during locomotion. [Review]. Gait Posture 2000; 11: 102–10.

Dietz V, Horstmann GA, Berger W. Interlimb coordination of leg muscle activation during perturbation of stance in humans. J Neurophysiol 1989; 62: 680–93.

Dietz V, Gollhofer A, Kleiber M, Trippel M. Regulation of bipedal stance: dependency on 'load' receptors. Exp Brain Res 1992; 89: 229–31.

Dietz V, Colombo G, Jensen L, Baumgartner L. Locomotor capacity of spinal cord in paraplegic patients. Ann Neurol 1995; 37: 574–82.

Duysens J, Pearson KG. Inhibition of flexor burst generation by loading ankle extensor muscles in walking cats. Brain Res 1980; 187: 321–32.

Gorassini MA, Prochazka A, Hiebert GW, Gauthier MJ. Corrective responses to loss of ground support during walking. I. Intact cats. J Neurophysiol 1994; 71: 603–10.

Gottlieb GL, Agarwal GC. Response to sudden torques about ankle in man: myotatic reflex. J Neurophysiol 1979; 42: 91–106.

Grillner S, Rossignol S. On the initiation of the swing phase of locomotion in chronic spinal cats. Brain Res 1978; 146: 269–77.

Harkema SJ, Hurley SL, Patel UK, Requejo PS, Dobkin BH, Edgerton RV. Human lumbosacral spinal cord interprets loading during stepping. J Neurophysiol 1997; 77: 797–811.

Hesse S, Helm B, Krajnik J, Gregoric M, Mauritz KH. Treadmill training with partial body weight support: influence of body weight release on the gait of hemiparetic patients. J Neurol Rehabil 1997; 11: 15–20.

Hiebert GW, Gorassini MA, Jiang A, Prochazka A, Pearson KG. Corrective responses to loss of ground support during walking. II. Comparison of intact and chronic spinal cats. J Neurophysiol 1994; 71: 611–22.

Hiebert GW, Whelan PJ, Prochazka A, Pearson KG. Contribution of hindlimb flexor muscle afferents to the timing of phase transitions in the cat step cycle. J Neurophysiol 1996; 75: 1126–37.

Ito M. The cerebellum and neural control. New York: Raven Press; 1984.

Kriellaars DJ, Brownstone RM, Noga BR, Jordan LM. Mechanical entrainment of fictive locomotion in the decerebrate cat. J Neurophysiol 1994; 71: 2074–86.

Maynard FM Jr, Bracken MB, Creasey G, Ditunno JF Jr, Donovan WH, Ducker TB, et al. International standards for Neurological and Functional Classification of Spinal Cord Injury. Spinal Cord 1997; 35: 266–74.

Pang MY, Yang JF. The initiation of the swing phase in human infant stepping: importance of hip position and leg loading. J Physiol 2000; 528: 389–404.

Pang MY, Yang, JF. Interlimb co-ordination in human infant stepping. J Physiol 2001; 533: 617–25.

Prochazka A, Gillard D, Bennett DJ. Positive force feedback control of muscles. J Neurophysiol 1997; 77: 3226–36.

Schomburg ED, Peteresen N, Barajon I, Hultborn H. Flexor reflex afferents reset the step cycle during fictive locomotion in the cat. Exp Brain Res 1998; 122: 339–50.

Sinkjaer T, Andersen JB, Larsen B. Soleus stretch reflex modulation during gait in humans. J Neurophysiol 1996; 76: 1112–20.

Ting LH, Kautz SA, Brown DA, Zajac FE. Contralateral movement and extensor force generation alter flexion phase muscle coordination in pedaling. J Neurophysiol 2000; 83: 3351–65.

Yang JF, Stephens MJ, Vishram R. Infant stepping: a method to study the sensory control of human walking. J Physiol 1998a; 507: 927–37.

Yang JF, Stephens MJ, Vishram R. Transient disturbances to one limb produce coordinated, bilateral responses during infant stepping. J Neurophysiol 1998b; 79: 2329–37.

Received June 12, 2002. Revised July 9, 2002. Accepted July 10, 2002