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Human neuronal interlimb coordination during split-belt locomotion

Abstract Human interlimb coordination and the adaptations in leg muscle activity were studied during walking on a treadmill with split belts. Four different belt speeds (0.5, 1.0, 1.5, 2.0 m/s) were offered in all possible combinations for the left and right leg. Subjects adapted automatically to a difference in belt speed within 10–20 stride cycles. This adaptation was achieved by a reorganization of the stride cycle with a relative shortening of the duration of the support and lengthening of the swing phase of the "fast" leg and, vice versa, in support and swing duration on the "slow" leg. The electromyogram EMG patterns were characterized by two basic observations: (1) onset and timing of EMG activity were influenced by biomechanical constraints. A shortening of the support phase on the faster side was related to an earlier onset and increase in gastrocnemius activity, while a coactivation pattern in the antagonistic leg muscles was predominant during a prolonged support phase on the slower side. (2) A differential modulation of the antagonistic leg muscles took place. An increase in ipsilateral belt speed in combination with a constant contralateral belt speed was associated with an almost linear increase in ipsilateral gastrocnemius and contralateral tibialis anterior EMG activity, while the contralateral gastrocnemius and ipsilateral tibialis anterior EMG activity were little affected. It is concluded that a modifiable timing within the stride cycle takes place with a coupling between ipsilateral support and contralateral swing phase. The neuronal control of this coupling is obviously based on ipsilateral modulation of leg extensor EMG by proprioceptive feedback and an appropriate central (e.g. spinal) modulation of contralateral tibialis anterior EMG activity.

Key words Split-belt locomotion Interlimb coordination · Leg muscle EMG activity Biomechanical constraints · Human

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Introduction

Several investigations on human locomotion were concerned with the modulation by inputs from proprioceptive (Berger et al. 1984; Dietz et al. 1987), vestibular (Allum et al. 1988) and visual (Berthoz et al. 1975; Dietz et al. 1992b) systems to the programmed leg muscle activation. In addition, the regulation of locomotion is also based on the finely tuned coordination of muscle activation between the two legs. This human interlimb coordination represents a basic requirement of upright stance and gait. Although the control of bilateral leg muscle activation usually takes place at a subconscious level, voluntary interaction with these mechanisms can occur. This potential for independent voluntary control of movements of a single leg, in addition to the more usual automatic coordination of the movements of both legs, requires adequate neuronal mechanisms to achieve task-directed coupling of bilateral leg muscle activation (Dietz and Berger 1984; Dietz et al. 1989). In the latter studies it was shown that during stance a unilateral displacement was followed by an automatic co-activation of the corresponding muscle of the contralateral non-displaced leg. Nevertheless, the contralateral leg muscles are not activated after unilateral displacement when they are not performing a supportive role (Dietz and Berger 1984), i.e. when they are not connected to a postural programme (Horak and Nashner 1986).

A flexible interlimb coordination is known from split-belt locomotion in spinal cats (Forssberg et al. 1980). In this study the hindlimbs of chronic spinal cats were placed on a treadmill and, while the fore part of the cat was supported, different combinations of left and right belt speed were offered. The question arises in how far such flexibility can also be achieved during bipedal gait, where, in comparison with quadrupedal locomotion, body equilibrium control is crucially based on a close interlimb coordination.

The aim of the present study was to get information about interlimb coordination during human bipedal locomotion in a split-belt task, its biomechanical and electrophysiological implications and constraints. For this, adult healthy subjects were asked to walk on a treadmill with split belts. Various differences in speed between the two belts were induced during walking at moderate speeds. Of particular interest was the activity of antagonistic leg muscles in this task where there is a mutual influence of the limb movement and the muscle activation patterns of one leg to the movement and activity in the other leg moving at a different speed. It is hypothesized that, as in quadrupedal locomotion, a flexible interlimb coordination exists and a quick adaptation to a difference in speed between the two legs takes place during such a new walking condition.

Materials and methods

General procedures and experimental conditions

Ethical approval was given by the ethical committee of the University of Freiburg in order to make biomechanical and electrophysiological recordings from ten healthy males (mean age 26.7, SD 2.8 years). Recordings were made when subjects were walking on a treadmill with split-belts (Woodway MTR 250-40). Four belt speeds (0.5, 1.0, 1.5, 2.0 m/s) were combined for the left and right leg. The resulting 16 conditions (normal walking conditions included) were offered in the same order for all subjects. Before recording data subjects were familiarized with both treadmill walking and walking in split-belt conditions over 30 to 40 step cycles. This was done by offering two normal treadmill walking conditions (0.5 m/s and 1.0 m/s) and two split-belt walking conditions (left belt speed at 0.5 m/s and right belt speed at 1.0 and 1.5 m/s, respectively). Each split-belt condition was tested over about one minute of walking. Impact of the right leg (i.e. signal of treadmill force) was taken for triggering biomechanical and electrophysiological signals (right heel strike).

Recording methods

Electromyograms (EMGs) were recorded by means of surface electrodes (silver chloride electrodes; interelectrode distance 4 cm) over the belly of the following muscles of both legs: rectus femoris, biceps femoris, tibialis anterior and the medial head of the gastrocnemius. Angular displacements in the knee and ankle of both legs were measured using laterally placed goniometers (for details see Dietz et al. 1987, 1989). Each of the two belts of the treadmill was seperately placed over a force-measuring system (Kistler). Thus, from the output of four piezo-elements, fixed at the corners of each belt, the support and swing phases as well as stride cycle duration (T_c) of both legs could be determined (for details see Duysens et al. 1990).

Definition of variables: T_c, the duration of the period between two successive impacts of the right leg; support phase, phase within the stride cycle in which the leg is used to support body weight (measured as an exerted force on the treadmill); swing phase, the phase within the stride cycle in which the leg is moved forward (measured as the absence of force output).

Data analysis

EMG and biomechanical recordings were amplified (FM-microvolt amplifier; time constant 0.15 s, bandwidth 0.1–1000 Hz) and, after rectification of the EMG, transferred on-line to a microcomputer system (Tandon 386/20) via an analog-digital converter sampling at 500 Hz (for details see Dietz et al. 1987). From the last part of the recording periods 20 subsequent cycles were selected for further analysis. These stride cycles were used for calculating means and standard deviations of the different temporal parameters of the stride cycle and mean EMG patterns. This was done for each subject and each condition. The integrated EMG activity of leg muscles was calculated over the individual mean stride cycle. All individual (mean) traces were normalized to a relative time scale starting at zero and ending at 100% of the stride cycle duration (starting and ending with a right heel strike). From these normalized traces group mean traces were calculated.

A quantification of the muscle activity during different conditions was obtained by calculating the mean EMG activity of leg muscles over the individual mean stride cycle. To allow for a comparison of the muscle activity in different conditions, this individual mean EMG activity was expressed as a percentage of the individual mean EMG activity in the conditions where belt speed was 1 m/s on both legs. From these data, group means were calculated for the different conditions.

For the calculation of co-contraction indices, the individual (mean) stride cycles were divided in 20 time segments over which the integrated EMG activity was calculated. Subsequently, these values were expressed as a percentage of the sum of the 20 segment integrals. Then the cross-sectional area of agonist and antagonist EMG activity was determined as a measure of co-activity.

Further statistical analysis of the mean EMG activity (means, standard deviations, MANOVA tests for repeated measurements, and t-tests) was performed using a statistical software package (SPSS/PC).

Results

During walking on a treadmill with split belts all subjects adapted within 15–20 step cycles to a difference in belt speed between both legs. This was true also during greater differences in belt speed (e.g. 1.5 m/s). During adaptation biomechanical and electrophysiological changes occurred. An interesting phenomenon could be seen in the on-line data traces: the adaptation to a split-belt condition usually coincided with EMG patterns which first were rather chaotic but gradually reached a characteristic burst-like activity which was then maintained. After an experimental session, some of our subjects even reported that is was necessary to adapt to the normal walking situation for the following 10–15 step cycles.

Biomechanical adaptations

When left and right belt speed were varied between 0.5 and 2.0 m/s the resulting stride frequency was interme-

Table 1 Changes in the durations of the stride cycle (T_c) and left and right support phases $(T_{sup-l}$ and T_{sup-r}, both expressed as a percentage of $T_c)$ during different combinations of left and right belt speed

Left belt speed (m/s)	Right belt speed (m/s)							
	0.5		1		1.5		2	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
2 T_c (ms)	1018.53	188.43	945.40	83.35	904.47	57.69	863.99	59.70[a]
T_{sup-l} (% of T_c)	46.29	6.46	52.15	2.23	55.05	1.33	58.57	0.65[a]
T_{sup-r} (% of T_c)	73.38	3.68	66.92	1.60	62.20	0.61	58.48	0.78[a]
1.5 T_c (ms)	1120.76	182.50	1014.56	65.99	967.46	51.37[a]	898.60	63.07
T_{sup-l} (% of T_c)	50.96	6.00	57.04	1.52	60.46	1.13[a]	62.51	0.79
T_{sup-r} (% of T_c)	70.69	3.08	64.38	1.00	60.20	1.05[a]	55.76	1.16
1 T_c (ms)	1242.17	171.94	1127.38	47.71[a]	1010.87	82.06	933.62	74.42
T_{sup-l} (% of T_c)	57.51	5.44	62.28	1.48[a]	64.52	0.66	67.33	1.04
T_{sup-r} (% of T_c)	67.92	2.41	61.63	1.19[a]	57.05	1.35	52.00	1.75
0.5 T_c (ms)	1559.84	89.22[a]	1253.52	107.98	1095.26	104.39	982.95	121.73
T_{sup-l} (% of T_c)	66.52	2.81[a]	68.47	0.83	70.90	1.76	73.80	2.35
T_{sup-r} (% of T_c)	66.30	3.02[a]	58.73	2.67	52.13	3.53	47.13	4.41

[a] Normal walking conditions

Fig. 1A–D Rectified and averaged muscle activity in rectus femoris (*RF*), biceps femoris (*BF*), tibialis anterior (*TA*), gastrocnemius (*GM*) and angular displacements in knee (*KNEE*) and ankle (*ANK*) of the right leg of one subject in split-belt conditions. The six traces are mean traces calculated from 20 stride cycles at each condition. The mean traces were normalized to one stride cycle duration (starting and ending with a right heel strike) to allow for a comparison between conditions. The *solid lines* below each condition indicate right support (*upward deflection*) and swing (*downward deflection*) phases, left support and swing phases are indicated by *dashed line*
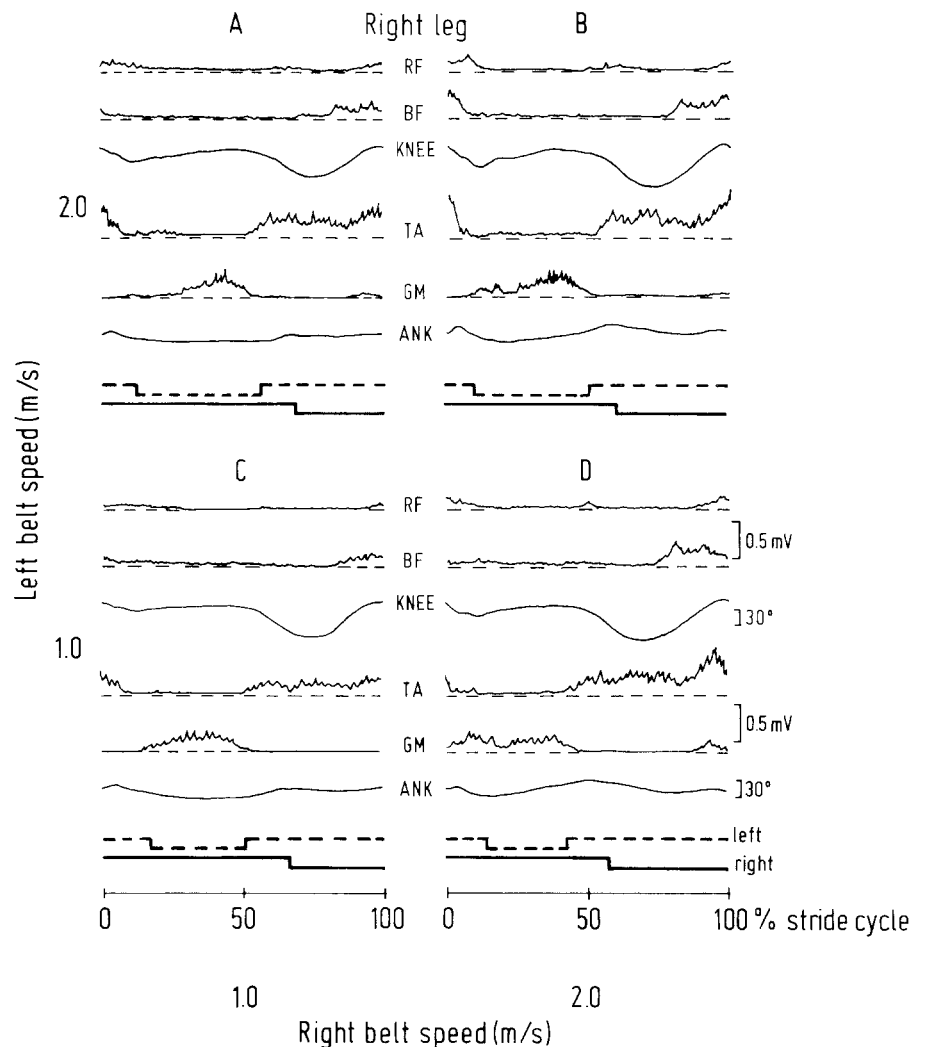
diate to the normal values for stride frequency for both speeds. However, the adaptation to speed differences for both legs was not symmetrical; there was a predominance of the faster leg over the slower one, leading to stride durations which tended more to the normal value for the fast speed (see Table 1).

The adaptation to split-belt conditions required a reorganization of ipsi- and contralateral support and swing phases within the stride cycle to allow for the differences in amplitude of leg movements in both legs. When right belt speed was low and left belt speed became faster (left column in Table 1), right support became proportionally longer and left support correspondingly shorter.

Figure 1 shows the muscle activity and angular displacements in the *right* leg of an individual walking in normal (Fig. 1B, C) and split-belt (Fig. 1A, D) conditions. It can be seen from the indicated support and swing phases below each figure that the right support phase was shortened and the right swing phase was lengthened when the right leg was the "fast" moving leg (Fig. 1D). The reverse took place when the right leg was the "slow" side (Fig. 1A). Corresponding changes in the timing of support and swing phases were observed in the left leg (interrupted line) when the left leg was either the "fast" or the "slow" leg.
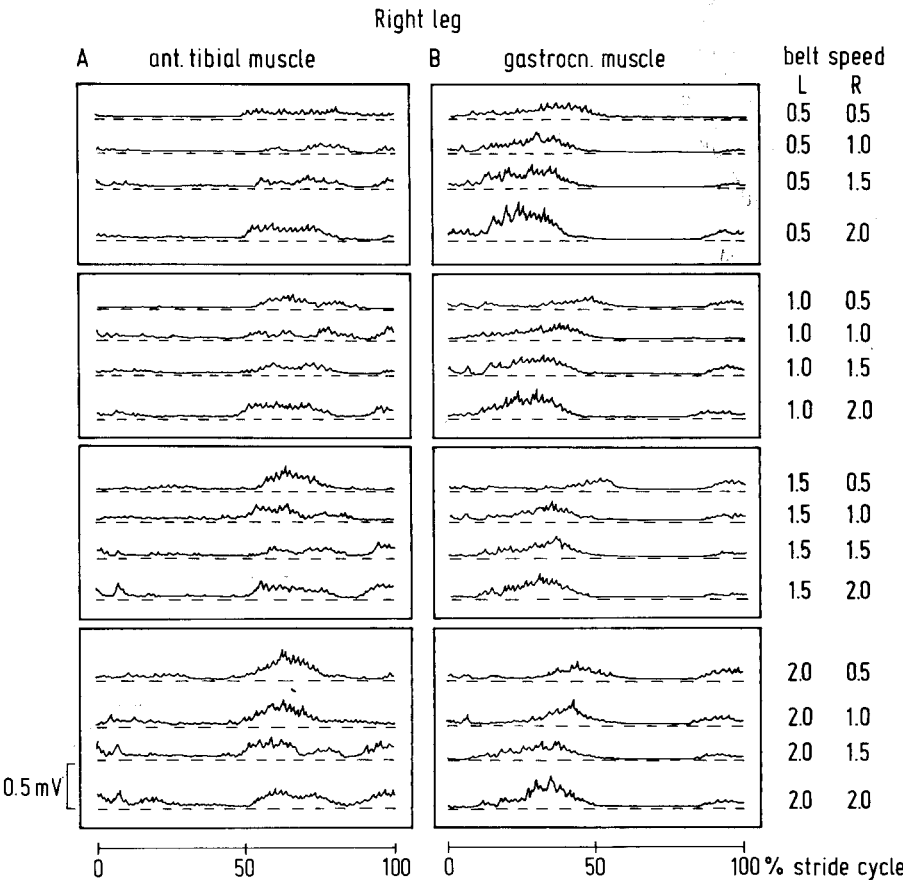
In Fig. 1 speed-dependent changes in angular displacements in the right ankle and knee joint can be seen

(compare C with B, A with B, and C with D). The timing of angular displacements differed, as could be expected on the basis of the changes in the duration of the phases of the stride cycle. The amplitudes of the angular displacements in knee and ankle were always larger in the "fast" leg.

Modulation of EMG activity

Modulation of EMG activity during split-belt walking occurred preferentially in the lower leg muscles (see Fig. 1). Therefore, further analysis was done for gastrocnemius and tibialis anterior muscles. Figure 2 shows an individual example of the EMG pattern in the right leg muscles during the various split-belt walking conditions. When the right belt speed was increased, while left belt speed remained constant, a strong increase in right gastrocnemius EMG activity always occurred. Contrary to this the tibialis anterior EMG changed only little. In conditions where left belt speed was changed and right belt speed was constant, the right tibialis anterior EMG activity increased with left belt speed and the gastrocnemius EMG activity remained about constant. In addition to these changes, a constant left belt speed and an increasing right belt speed led to a time shift of gastrocnemius activity to the early part of the stride cycle. The adaptation of the EMG pattern to an increas-

Fig. 2 Rectified and averaged ($n=20$) EMG activity in right tibials anterior (**A**) and right gastrocnemius (**B**) muscles of one subject walking in split-belt conditions. The mean traces were normalized to one stride cycle duration (starting and ending with a right heel strike) to allow for a comparison between conditions. On the *right*, left (L) and right (R) belt speed are indicated in metres per second

	Right leg	belt speed	
A ant. tibial muscle	**B** gastrocn. muscle	**L**	**R**
		0.5	0.5
		0.5	1.0
		0.5	1.5
		0.5	2.0
		1.0	0.5
		1.0	1.0
		1.0	1.5
		1.0	2.0
		1.5	0.5
		1.5	1.0
		1.5	1.5
		1.5	2.0
		2.0	0.5
		2.0	1.0
		2.0	1.5
		2.0	2.0

0.5 mV
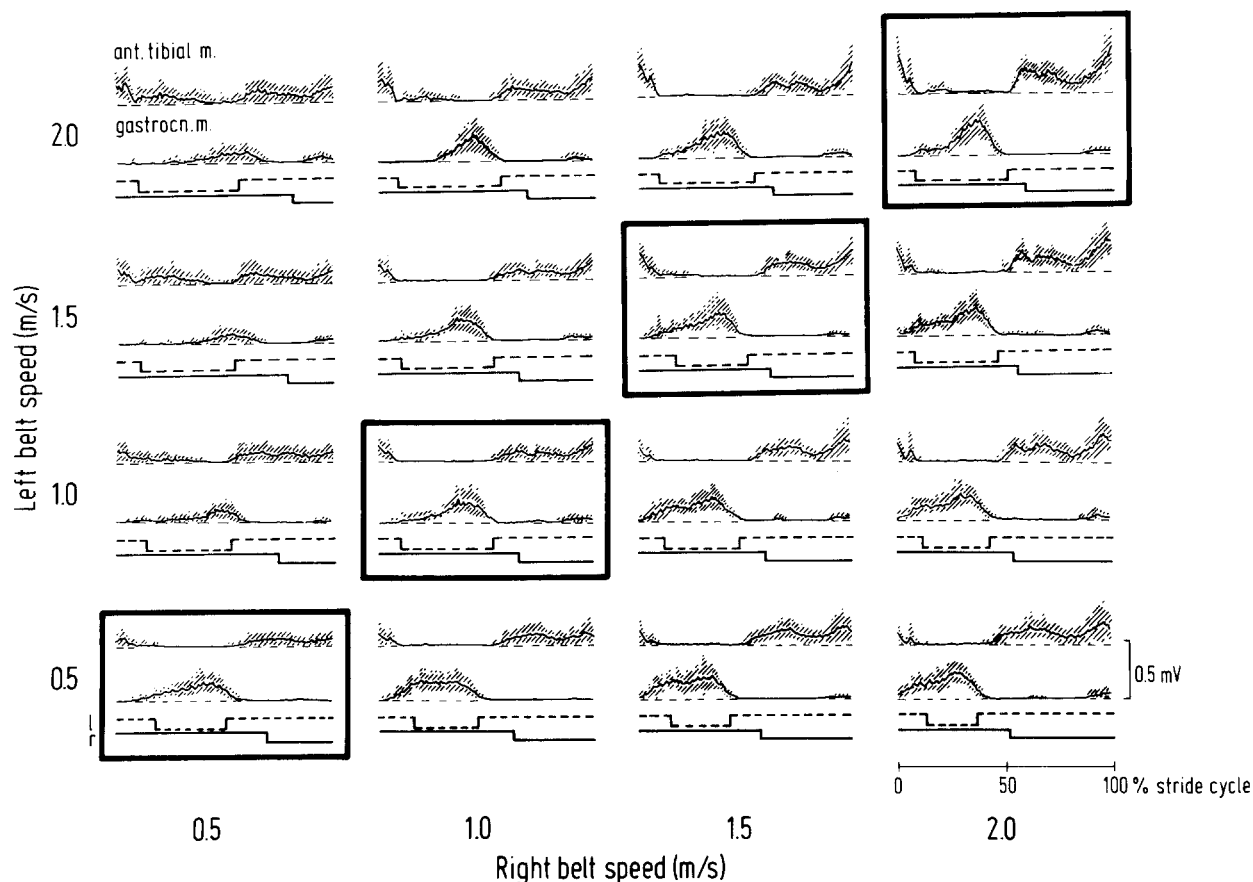
0   50   100 0   50   100 % stride cycle

Fig. 3 Mean values (with SD) of the rectified and averaged ($n = 20$) EMG activity of right gastrocnemius and tibialis muscles obtained from all subjects. All conditions tested are displayed. All traces were normalized to one stride cycle duration (starting and ending with a right heel strike) to allow for a comparison between subjects and conditions. The EMG pattern obtained during equal speeds of each belt are indicated by frames (*left bottom to right top*). Below the EMG traces the support and swing phases of both legs are indicted, as in Fig. 1

ing right belt speed was mainly achieved by an increase in amplitude and shortening of gastrocnemius activity, while the tibialis anterior EMG pattern roughly remained constant.

Figure 3 shows the mean (with SD) EMG traces of right gastrocnemius and tibialis anterior muscles of the group of subjects during split-belt walking. Below the EMG traces the (mean) right and left support and swing phase durations are indicated. From left bottom to top right the EMG activity is displayed when the belt speed was equal at both sides (patterns displayed within boxes). In these normal walking conditions there was a shortening of the support and a relative lengthening (normalized stride cycles) of the right swing phase with increasing speed. This was connected with a continuously increasing gastrocnemius activity during the second half of the support phase. When the gastrocnemius was silent, the tibilialis anterior was active and its amplitude also increased with speed. Its maximum amplitude occurred around impact. When the right belt was faster

than the left belt, the main change in the stride cycle consisted in a disproportional shortening of support and lengthening of swing at the right leg (vice versa at the slow left leg) related to a premature gastrocnemius activation during early support while tibialis anterior EMG activity was little changed.

When the left belt was faster than the right one, the right support and left swing phases became relatively longer. Right gastrocnemius EMG activity became expanded and flattened over the prolonged right support phase with a maximum during the last third of the support phase. With increasing difference between right (low) and left (high) belt speed, the right tibialis anterior became increasingly active throughout the whole stride cycle, with a minimum activity during the time when the gastrocnemius was maximally active. The phase shifts of EMG activity seen in the various conditions of Fig. 3 could not be assessed quantitatively mainly because of a great interindividual variability.

Quantitative EMG assessment

The observations made in the EMG recordings were also clearly reflected in the quantitatively evaluated data. Figure 4A shows the mean EMG activity of the right tibialis anterior and gastrocnemius in conditions where the belt speed was the same for both legs. There was an almost linear increase in gastrocnemius activity
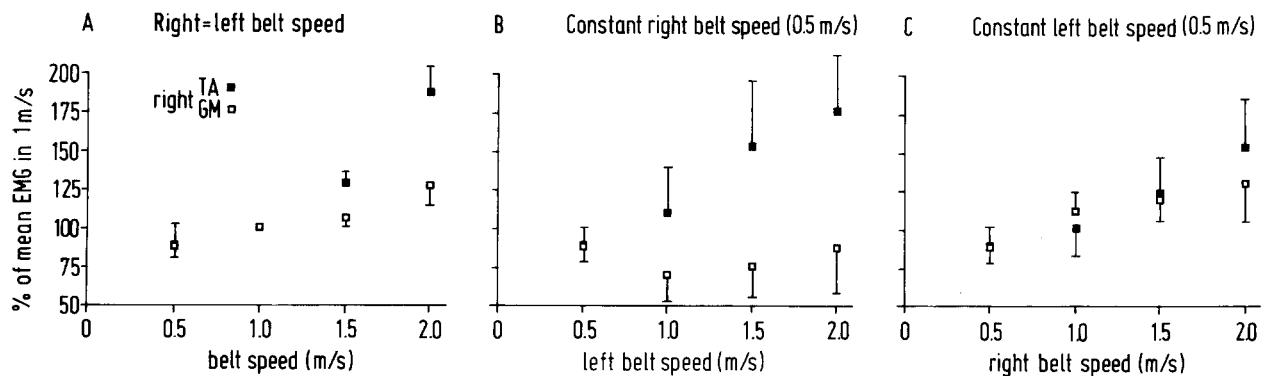
A   Right=left belt speed   B   Constant right belt speed (0.5 m/s)   C   Constant left belt speed (0.5 m/s)

Fig. 4A–C Mean values of EMG activity in right gastrocnemius (□) and right tibialis anterior (■) of all subjects. A Conditions with an equal belt speed on both sides; B conditions with a constant right belt speed (0.5 m/s) and an increasing left belt speed; and C conditions with a constant left belt speed (0.5 m/s) and an increasing right belt speed. The mean activity is calculated as the mean of the individual integrated EMG activity normalized to the mean EMG activity during the 1 m/s condition

and a (curvi-) linear increase in tibialis activity when belt speed was increased. These increases in muscle activity with belt speed were highly significant in the two muscles ($P < 0.001$, tested with MANOVA test for repeated measurements).

Figure 4B shows the mean EMG activity in conditions with a constant right belt speed (0.5 m/s) and an increasing left belt speed. No significant effect of left belt speed on the activity in the right gastrocnemius muscle was observed (tested with MANOVA test for repeated measurements). When left belt speed was 2.0 m/s the mean right gastrocnemius EMG activity was not greater than the condition when the speed on both sides was 0.5 m/s. In contrast to this, for the right tibialis anterior a higher left belt speed had an effect on the amplitude of EMG activity ($P < 0.001$, tested with MANOVA test for repeated measurements). This dependency of right tibialis anterior activity on left belt speed was most obvious during the combination of high speeds on the left side (2.0 m/s and 1.5 m/s) and low right belt speed (0.5 m/s).

In conditions where a constant left belt speed (0.5 m/s) was combined with an increasing right belt speed (Fig. 4C) both gastrocnemius and tibialis anterior showed significant increases in muscle activity ($P < 0.001$, tested with MANOVA test for repeated measurements). It can, however, be seen that the right tibialis anterior EMG activity was less dependent on the right belt speed than in the normal condition (Fig. 4A) and that the gastrocnemius showed an almost normal dependency on right belt speed (compare Fig. 4A and C). No significant differences could be detected when gastrocnemius EMG activity in conditions shown in Fig. 4C were compared with the corresponding normal conditions (Fig. 4A), whereas tibialis anterior activity showed a significant difference to normal walking when the right belt speed was 2.0 m/s and the left belt speed 0.5 m/s ($P < 0.001$, tested with t-test pairs).

The changes in the patterns of the right tibialis anterior and gastrocnemius activation for the various split-belt conditions shown in Fig. 3 can also quantitatively be assessed by the calculation of co-contraction values for these muscles (listed in Table 2). In normal walking conditions, there was a slight but significant decrease of co-contraction in these muscles wiht increasing speed ($P < 0.05$, tested with MANOVA). The strong increase in co-contraction in conditions with constant low (0.5 m/s) right belt speed and increasing left belt speed was highly significant ($P < 0.001$, MANOVA). Only minor changes (not significant) were observed in the conditions with constant low (0.5 m/s) left belt speed and increasing right belt speed.

Discussion

The aim of the present work was to investigate the inter-limb coordination during split-belt walking. Hitherto,

Table 2 Mean co-contraction indices of the right tibialis anterior and gastrocnemius muscles

Left belt speed (m/s)	Right belt speed (m/s)							
	0.5		1		1.5		2	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
2	66.42	12.06	55.02	11.70	49.62	8.74	45.05	8.45[a]
1.5	65.30	11.41	52.83	11.37	46.58	9.03[a]	46.10	8.22
1	61.19	11.16	49.05	9.82[a]	44.58	10.18	45.97	7.16
0.5	49.39	8.18[a]	45.18	8.34	44.77	7.58	45.77	5.10

[a] Normal walking conditions

split-belt walking experiments were restricted to spinal cats (Forssberg et al. 1980) and 7-month-old infants (Thelen et al. 1987). These investigations showed that differences in treadmill speed between the two legs can produce specific adjustments to the speed of each limb, indicating that the spinal cord contains networks responsible for each limb which can be connected in a variety of ways. From the present work this behavior can be extended to adult humans also. All subjects adapted automatically within 10–20 s to a difference in belt speed.

The coordination between the two legs can, in addition, be specified for two main points: (1) Biomechanically, a split-belt condition is characterized by a relative shortening of support and lengthening of swing phases on the faster leg and, vice versa, on the slower one. In addition, although intermediate stride cycle frequencies can be observed, the faster side dominates over the slower one. (2) Electrophysiologically, the gastrocnemius EMG activity is mainly influenced by the ipsilateral speed and less so by the speed of the contralateral belt. In contrast to this, the tibialis anterior EMG activity is more influenced by the speed of the contralateral belt. These points will be discussed in the light of neuronal control of interlimb coordination during gait and its functional implications.

Interlimb coordination

During walking a different belt speeds the support phase became shorter on the faster side and the swing phase became longer. The inverse behaviour was observed on the slower side. This shortening and lengthening of support and swing phases, respectively, was always more pronounced compared with the corresponding conditions when speed was equal on both sides. The results obtained in the latter conditions were in agreement with those obtained during normal locomotion at different speeds (see Nilsson et al. 1985; Nilsson and Thorstensson 1987). These biomechanical changes were accompanied by corresponding EMG changes. The shortening of support phase of the faster leg was related to an earlier onset and increase in gastrocnemius EMG activity, in order to achieve an early push-off of the leg. In contrast to this, a lengthening of support phase on the slower leg was related to an increased activity of the leg flexor and coactivation of antagonistic leg muscles, which is necessary to stabilize the body equilibrium during the prolonged swing of the contralateral leg. Therefore, each limb affects the strength of muscle activation and the time-space behaviour of the other one, i.e. both legs act in a cooperative manner in functional terms as already described for spinal cats (Forssberg et al. 1980) and infants (Thelen et al. 1987).

All intermediate swing and support phase durations were seen when differences between right and left belt speed were introduced. Nevertheless, the "fast" leg was more influential on the common stride frequency than the slower one, i.e. the faster leg was always the leading leg. The coupling between swing and contralateral support obviously represents a basic requirement of bipedal walking: during swing, the contralateral leg has to provide a support which lasts long enough to allow the ipsilateral swing to be made. The appropriate interlimb coordination which is necessary to make these adjustments in support and swing phases may be achieved in a similar way, as suggested on the basis of experimental work in the cat (Grillner 1981). Proprioceptive information about velocity and direction of angular displacement in the leg joints and/or about (un)loading of the legs (Duysens and Pearson 1980; Dietz et al. 1992a) is assumed to be able to influence and reset the locomotor activity generated by the spinal central pattern generator (Grillner 1981).

Differential control of antagonistic leg muscles

One aspect of neuronal control of antagonistic leg muscle activation was closely related to bilateral adjustments in support and swing phases; the onset and timing of EMG activity in gastrocnemius and tibialis anterior muscles. Another aspect concerns the differential behaviour of the leg muscles to a difference in belt speed, i.e. differential responsiveness to changes in ipsi- and contralateral belt speed, respectively.

An ipsilateral increase in belt speed was related mainly to an increase in ipsilateral gastrocnemius and contralateral tibialis anterior EMG activity. The modulation of ipsilateral gastrocnemius EMG activity is suggested to be mainly achieved by proprioceptive feedback mechanisms mediated on a spinal level (Berger et al. 1984; Dietz et al. 1987). On the other hand, there are several observations which indicate that the neuronal control of leg flexor muscles during functional movements is predominantly achieved by central mechanisms (Brouwer and Ashby 1992; Dietz et al. 1992b). The latter exert a pace-maker function on the flexor muscles. This differential control of the antagonistic leg muscles is in the line with a strong interlimb coordination which most probably takes place on a spinal level (Dietz et al. 1989 for review see Dietz1992). Such a control has to be seen in a functional context: adaptation of EMG activity to the actual ground conditions is predominantly required for the antigravity muscles, while the activity of the flexor muscles may be triggered by a peripheral or central event and released by a central pattern generator. For the present experiments it is suggested that adaptation to the ipsilateral belt speed is achieved by proprioceptive modulation of gastrocnemius EMG activity. The ipsilateral peripheral feedback to the spinal cord again influences the generation of the programmed activity pattern in the contralateral tibialis anterior muscle. In this context it is noteworthy that peripheral feedback in the spinal cat is not only re-setting the locomotor activity but can entrain the rhythm and control the onset of various phases of the step cycle

(Andersson and Grillner 1981; Andersson et al. 1981). Thus it seems probable that human neuronal control of bipedal gait shares a similar "spinal mechanism" to quadrupedal mammals.

All observations indicate that interlimb coordination during gait is hard-wired in some basic aspects of ipsi- and contralateral leg muscle activation. Interlimb coordination is, however, flexible in so far that a quick automatic adaptation to differences in speed is achieved. This indicates that each leg is controlled by its own neuronal apparatus, which can be coupled in a variety of ways between the two legs. It is assumed that such a behaviour is innate and based on interactions between peripheral sensors and spinal interneuronal circuits.

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