RESEARCH ARTICLE

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Coordinated modulation of locomotor muscle synergies constructs straight-ahead and curvilinear walking in humans

Abstract We describe the muscle synergies accompanying steering of walking along curved trajectories, in order to analyze the simultaneous control of progression and balance-threatening emerging forces. For this purpose, we bilaterally recorded in ten subjects the electromyograms (EMGs) of a representative sample of leg and trunk muscles ($n = 16$) during *continuous* walking along one straight and two curved trajectories at natural speed. Curvilinear locomotion involved a graded, limb-dependent modulation of amplitude *and* timing of activity of the muscles of the legs and trunk. The turn-related modulation of the motor pattern was highly coordinated amongst muscles and body sides. For all muscles, linear relationships were detected between the spatial and temporal features of muscle EMG activity. The largest modulation of EMG was observed in gastrocnemius medialis and lateralis muscles, which showed opposite changes in timing and amplitude during curve-walking. Moreover, amplitude and timing characteristics of muscle activities were significantly correlated with the spatial and temporal gait adaptations that are associated with curvilinear locomotion. The present results reveal that fine-modulation of the muscle synergies underlying straight-ahead locomotion is enough to generate the adequate propulsive forces to steer walking and maintain balance. These findings suggest that the turn-related

command operates by modulation of the phase relationships between the tightly coupled neuronal assemblies that drive motor neuron activity during walking. This would produce the invariant templates for locomotion kinematics that are at the base of human navigation in space.

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Introduction

Human walking differs in many aspects from other terrestrial locomotor modes of vertebrate (Capaday 2002). Contrary to most mammals, which walk on four legs with the trunk roughly parallel to the ground, humans walk erect on two legs. A pendulum-like movement results, which converts kinetic energy into gravitational potential energy, and inversely so, thereby increasing gait efficiency (Cavagna and Margaria 1966; Alexander 1989).

However, bipedal locomotion is naturally unstable, in particular in the medio-lateral plane (Winter et al. 1993; Kuo 2001). Accurate control of propulsion and balance during human locomotion requires the CNS to produce highly coordinated movements of lower limb segments and trunk (Lacquaniti et al. 1999; Courtine and Schieppati 2004). The parallel emergence of lower limb coordination and trunk vertical stability in toddlers (Gramsbergen and Hadders-Algra 1998; Cheron et al. 2001) emphasizes the need for dynamic but separate (Ivanenko et al. 2005) integration of body balance *and* forward motion peculiar to bipedal walking.

The characteristics of neural drive encoding for this dual integration have received little attention so far. How is muscle activation modulated to propel the body and ensure balance during locomotion? This interaction, already present during straight-ahead walking, would become critical during curvilinear locomotion. Indeed, many spatiotemporal parameters of gait are adapted to

the actual curvature of the path: the orientation of nearly all body segments–therefore of the center of mass–shifts inwards with respect to the body trajectory in order to counteract the gravito-inertial forces that destabilize balance, and to implement the planned locomotor path (Patla et al. 1999; Imai et al. 2001; Courtine and Schieppati 2003a, b, 2004). Accordingly, the commands delivered to the leg muscles for proper drive of the chain of limb segments *and* to the trunk muscles to preserve balance necessarily imply demanding computational processes during curve-walking (Bernstein 1967). Evidences of this complexity emerge, when studying turning in aged persons (Thigpen et al. 2000), Parkinsonians (Stack and Ashburn 1999; Morris et al. 2001) and cosmonauts on their return from space (Chekirda et al. 1971).

In a previous study (Courtine and Schieppati 2003a, b, 2004), we disclosed unifying kinematics principles, by virtue of which the CNS achieves inter-segmental coordination during straight- *and* curve-walking: graded, limb-dependent tuning of a basic coordination pattern accounted for the adaptation of left and right leg trajectories to the actual curvature of the path, as well as their coordination with trunk movement, both in the sagittal and frontal planes. However, a common kinematic principle underlying straight- and curve-walking does not imply a similar modulation of muscle activation for both locomotor tasks. For example, Grasso et al. (1998) demonstrated that conservation of kinematic templates during forward and backward locomotion is accomplished at the expense of a complete reorganization of muscle synergies. The emergence of balance-threatening forces during curvilinear locomotion (Imai et al. 2001) may require the restructuring of the motor pattern underlying straight-walking and a significant change in the activity of those muscles that counteract gravito-inertial forces in order to preserve balance.

We previously reported that the SL and TA muscles show a modest modulation of their EMG during curve walking (Courtine and Schieppati, 2003b), certainly not sufficient for the production of successful curvilinear locomotion. Here, we recorded the activity of a much larger sample of muscles acting on the legs and trunk muscles during walking along three trajectories of different curvature, to investigate (1) the amplitude and temporal distribution of lower limb and trunk muscle activity during straight versus *continuous* curvilinear locomotion, (2) the modulation of muscle synergies across several segments, and (3) how adaptive modifications of gait mechanics are encoded in turn-related modification of EMG. We hypothesized that continuous steering along curvilinear locomotor paths would involve graded, coordinated modulation of the muscle synergies underlying straight-ahead walking, which would produce the invariant templates for locomotion kinematics at the base of human navigation in space (Patla et al. 1999; Imai et al. 2001; Courtine and Schieppati 2003a, b, 2004).

Methods

Subjects

Ten healthy male adults volunteered for this experiment. They had never participated in this kind of experiment before. Their mean age was 25 (range 23–28), mean height 175 cm (163–183), and mean weight 70 kg (62–84). The subjects gave written and informed consent and the study conformed to the Declaration of Helsinki. The study was approved by the ethic committee of the University of Bourgogne.

Locomotor task

Figure 1 shows the three locomotor trajectories (black traces) along which the subjects were required to walk. The first trajectory was straight, in the straight-ahead (SA) direction. The two other trajectories were curved with radius of 4.6 and 1.2 m, and were called curve-slight (CS) and curve-tight (CT), respectively. CS and CT paths were curved toward the left side with respect to the walking direction. Preliminary experiments revealed no differences in the motor strategy underlying clockwise versus counterclockwise curvilinear locomotion. Each locomotor path was marked on the floor with a black plastic band. Subjects performed at least three gait cycles along each locomotor trajectory before and after they entered the acquisition volume. The recorded and analyzed gait cycles were therefore extracted from *continuous* curve-walking tasks, i.e., when the locomotor pattern had reached a plateau (Courtine and Schieppati 2003a). Ten repetitions were made along each path. Subjects walked at their preferred (natural) velocity with their eyes open and received no particular instruction concerning body, head or gaze orientation.

Data acquisition and processing

The methods and procedures used in the present study have been detailed in our previous reports on curve-walking (Courtine and Schieppati 2003a, b, 2004) and will be only briefly reported here. Both kinematic and electromyographic (EMG) data were obtained by means of the integrated ELITE system (BTS, Italy).

Kinematics

Eight video cameras (100 Hz) were located around the walking area, creating an acquisition volume of 4 ×4 m (2 m high) for the recording of whole-body movements. Reflective markers (8 mm in diameter) were attached to the skin overlying the following body landmarks: vertex; between the eyebrows; and for both hemi-bodies: the
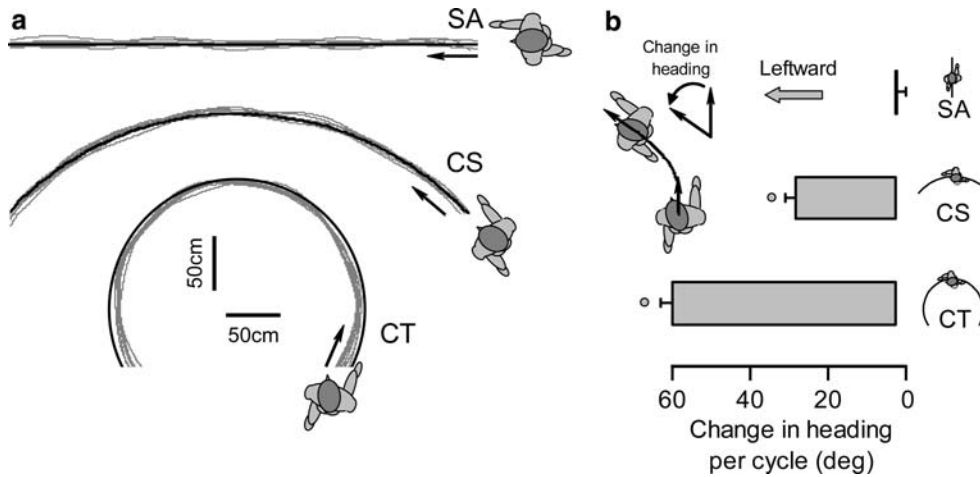
Fig. 1 Description of the locomotor task. **a.** The *black lines* show the shape of the three locomotor paths drawn on the floor, along which the subjects were required to walk. The gray lines depict the actual trajectories covered by the body midpoint during ten successive executions for a typical subject. **b.** The change in heading is defined as the angle between the orientations of the vector velocity at the time of two successive heel strikes for one leg. The mean values ($+$ SD) of the change in heading per cycle (all subjects and all successive strikes of both legs pooled) are reported in the *histogram bars* for each locomotor trajectory. *Circles* indicate significant differences between curve (CS and CT) and straight-walking (SA). A significant difference also exists between CS and CT

gleno-humeral joint, anterior superior iliac spine, great trochanter (GT), knee (lateral femur epicondyl, K), lateral malleolus (M) and fifth metatarso-phalangeal joint of the foot (F). In addition, two markers were placed along the anterior and posterior body midlines, 2 cm below the belly button and at the level of L3 (see Fig. 2b). The average value of the coordinates of these two markers and the left (L) and right (R) markers located on the ilium and great trochanter was calculated. The resulting point, labeled body midpoint (x_B; x_B; z_B), provided a good approximation of the displacement of the center of mass. The *limb axis* was for each limb the virtual straight line connecting the lateral malleolus to the great trochanter.
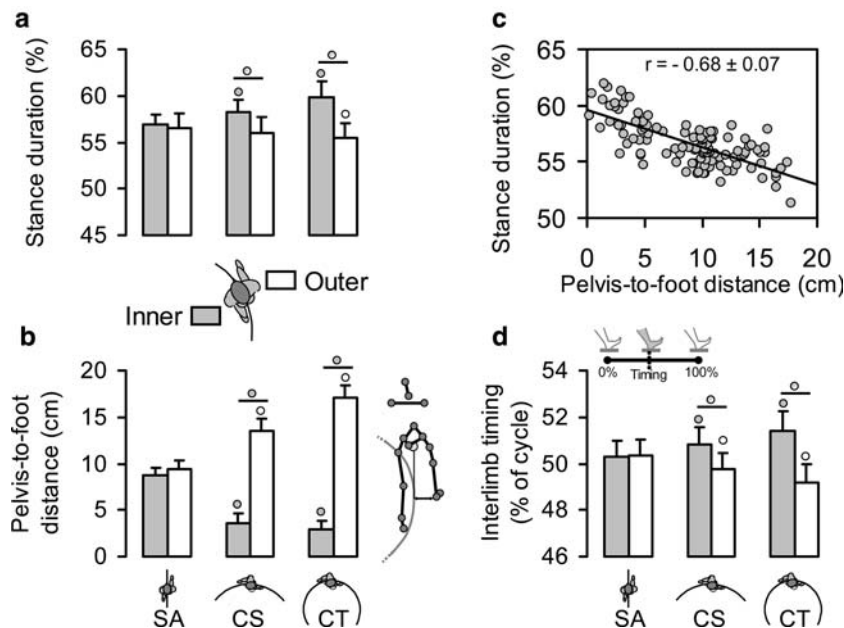

Fig. 2 Spatiotemporal patterns of limb and pelvis movements. **a.** Mean values ($+$ SD) of stance duration expressed as a percentage of cycle duration. **b.** Mean distance ($+$ SD) between the pelvis, represented by the body midpoint (*open circle* in the inset), and the stance foot at mid-stance. **c.** Relationship between stance duration and pelvis-to-foot distance for one typical subject. The mean value ($+$ SD) of the correlation coefficients (*r*) computed for all subjects is reported in the plot. **d.** Inter-limb timing refers to the time of heel contact of one foot relative to the heel contact of the contralateral foot, expressed as the percentage of the duration of the cycle period of the contralateral limb. *Open* and *filled circles* indicate significant differences between curve- and straight-walking for the inner and outer legs, respectively. *Bars* associated with a circle show significant differences between inner and outer leg

Electromyogram (EMG)

The skin was cleaned with alcohol swabs before applying two electrodes (1 cm in diameter, 2 cm inter-electrode distance) for recording the surface EMG. The electrodes were placed over seven muscular groups of each leg: tibialis anterior (TA), soleus (SL), gastrocnemius medialis (GM) and gastrocnemius lateralis (GL), vastus lateralis (VL), biceps femoris (BF), and gluteus medialis (GLU) as well as bilaterally on the erector spinae (ES) muscle. The electrodes were positioned as follows: for the GM, GL, VL, BF, and GLU on the belly of the muscle, midway between the proximal and distal insertions; for the SL, on the midline, posteriorly, 2 cm below the insertion of the gastrocnemii in the Achilles' tendon; for the TA, on the anterior aspect of the upper third of the leg, just close to the shin; for the ES 3 cm laterally with respect to L3 (Thorstensson et al. 1982). Successful recordings were obtained from all muscles of all subjects, except for BF ($n = 8$). EMG activity of the VL muscle was recorded in six subjects. Signals were pre-amplified (x 100), digitized, and transmitted to the remote amplifier via telemetry. Signals were sampled at 1,000 Hz, band-pass filtered (10–500 Hz), and full-wave rectified.

Reference frame

The coordinate frames that describe body motion while moving through space were defined in a hierarchical manner as described in previous papers (Courtine and Schieppati 2003a, 2004). Briefly, the instantaneous heading direction was defined as the angle of the instantaneous linear velocity vector of the *body midpoint* in the horizontal plane with respect to the space-fixed reference frame. The coordinates of the different markers were converted in the body-centered reference frame, whose X axis matched the heading direction, through coordinate transformation. The amplitude of the walking direction change during each gait cycle was calculated as the difference in heading between two successive heel strikes of one leg (see inset of Fig. 1b).

Gait parameters

The gait cycle was defined as the time interval between two successive heel strikes of one leg. Successive heel strikes were set at the zero crossings of the rate of change of the elevation angle of the *limb axis*. On an average, 20 ± 5 cycles were examined for each leg, each locomotor path, and for each subject, thus representing a total of 120 cycles per subject and 1,200 locomotor cycles as a whole. Onsets of swing phases were based on rates of change of foot (foot marker, F) vertical translations. A threshold of foot clearance was set at 10% of maximal peak velocity of foot vertical displacement during the swing phase. Classical gait parameters such as total gait duration, stance duration, mean velocity, stride length, and inter-limb timing were evaluated (Courtine and Schieppati 2003b). The distance between the stance foot and the body (pelvis) in the medio-lateral plane was measured (see inset of the Fig. 2b). This was the distance at mid-stance between the position of the malleolus marker and the trajectory described by the position of the *body midpoint*. The difference between the stride length of the left and right legs during the time interval of a gait cycle was computed as the difference between the distance covered by the left and right malleolus during this period (Courtine and Schieppati 2003a, 2004).

Timing of muscle activity

EMG activity from each trial was ensemble-averaged after time-interpolation over individual gait cycles to fit a normalized 1,000-point time base. The procedure was applied individually for each leg, each locomotor path and each subject. The timing of muscle activity was evaluated on each of these mean traces. Onsets and ends of EMG burst activity were established at the points at which muscle activity exceeded and fell below (for at least 50 ms), respectively, the mean activity plus 1.5 SD recorded during a period (200 ms) when this muscle was least active. A mobile average (40 ms width) was first applied on the signal to reduce the effects of signal oscillation. The recorded muscles generally presented a single burst during the gait cycle. However, the TA muscle showed a well-identified double burst and was divided into two distinct bursts whose separation was set as the trough occurring around the center of the double burst. Furthermore, the ES muscle exhibited two periods of activity: a phasic burst coincided with heel strike and was followed by a period of tonic activity. These two periods were separately analyzed.

Amplitude of muscle activity

The mean activity was calculated as the integral of the muscle envelope during the time-interval of the gait cycle. In addition, the amplitude of the muscle bursts during each cycle was computed by integrating the activity of each individual EMG burst during the time interval (onset-end) defined during walking along each locomotor path, as described above. The difference between EMG activity of left and right muscles during each gait cycle was also assessed. The procedure consisted in normalizing the amplitude of EMG activity of each muscle to the mean activity of the same muscle during straight-walking. The normalization was independently applied to each muscle and each leg as well as to each subject. The ratio between EMG activity of left and right muscles during each gait cycle was subsequently evaluated by expressing the activity of the muscle most active as a percentage of the activity of the muscle less active.

Statistical analysis

For each subject, we calculated the mean values of the different parameters computed and their SD over all trials according to the experimental condition. Except otherwise specified, values reported in the figures are the averaged mean and SD values of all subjects. Repeated-measure ANOVA was used to test the effect of the different conditions on the experimental parameters. The factors examined were locomotor path (SA, CS, CT) and body side (left or right). Post hoc differences were assessed by means of the Newman–Keuls test.

Results

This section contains three parts. Firstly, we confirm that successful curve-walking requires a number of graded, side-dependent adaptations of gait (Courtine and Schieppati, 2003a, b). The aim of this first section is twofold: (1) to point out the continuity of the steering process across trajectories of different curvature that was not described in our precedent reports, (2) to provide the reader with a comprehensive view of how segment movements are adjusted to steer the body along a curve in order to better understand the accompanying changes in muscle activity. In the second part, we detail the amplitude and temporal characteristics of EMG bursts and show the graded, side-dependent modulation of EMG pattern of nearly all muscles across curved paths of different tightness. Finally, we report that the modulations of muscle activities are well coordinated and properly correlated with the adaptations of body kinematics required to ensure accurate *and* balanced steering of the body through space.

Spatial trajectory

The subjects easily followed the required locomotor paths (black lines in Fig. 1a). Their locomotor trajectories (gray traces in Fig. 1a) and changes in heading per cycle were highly reproducible from cycle-to-cycle and trial-to-trial; change in body direction per cycle gradually increased with path tightness (curve effect,

$P < 0.001$, Fig. 1b). No significant difference was found for the heading change between left and right cycles ($P > 0.3$). The consistency of the change in heading per cycle when walking along each of the three curves indicates that the locomotor system had reached a plateau during the recorded gait cycles.

General gait parameters

Average values of spatial and temporal features of the gait pattern for all subjects when walking along the three locomotor paths are detailed in Table 1. Gait cycle duration was hardly affected by the curvature of the path. Only the tighter curve caused a modest (40 ms, 4%), though significant increase in cycle duration (curve effect, $P < 0.01$; SA vs. CT post hoc comparison, $P < 0.05$). Conversely, mean body velocity steadily decreased with the increase in curve tightness (curve effect, $P < 0.0001$; $P < 0.01$ for all post hoc comparisons). This slowing was the consequence of the increasing divergence between the stride length of the left and right legs (curve × side effect, $P < 0.0001$). The outer (right) leg conserved or minimally reduced its stride length during curve- with respect to straight-walking (only SA and CS vs. CT post hoc comparisons reached significance, $P < 0.001$ for both comparisons). In turn, the stride length of the inner (left) leg markedly diminished when curve tightness increased ($P < 0.001$ for all post hoc comparisons).

Spatiotemporal patterns of leg and pelvis movements

There was an interaction effect on stance duration ($P < 0.0001$) between leg (left or right) and locomotor paths (SA, CS, CT) (Fig. 2a). The left and right legs exhibited similar stance durations during straight-walking ($P > 0.3$) but showed opposite modifications of stance duration during curve-walking ($P < 0.0001$ for both CS and CT comparisons). Stance duration of the left inner leg significantly increased with curve tightness (all post hoc comparisons, $P < 0.005$). Changes in stance duration of the right outer foot were less pronounced. Stance duration decreased but significantly so only when

Table 1 General gait parameters. Average values (all subjects) of gait cycle duration, mean velocity and left (inner) and right (outer) stride length according to the characteristics of the locomotor path

	SA		CS		CT	
Gait duration (s)	1.13 ± 0.06		1.14 ± 0.06		1.17 ± 0.08	
Mean velocity (m.s^{-1})	1.19 ± 0.12		1.14 ± 0.10		0.98 ± 0.10	
	Inner	Outer	Inner	Outer	Inner	Outer
Stride length (m)	1.34 ± 0.09	1.33 ± 0.08	1.26 ± 0.08	1.34 ± 0.09	1.08 ± 0.07	1.27 ± 0.1

stepping along the CT curve (SA vs. CT post hoc comparison, $P = 0.01$).

The pelvis, reflected by its midpoint, substantially modified its position with respect to the stance foot during curve-walking. The histograms of Fig. 2b report mean values of the pelvis-to-foot distance at mid-stance according to leg and locomotor path—at this time, the leg is fully extended and carries the body weight. Dramatic side-dependent changes accompanied the progression along a curve (curve × leg effect, $P < 0.0001$). While the pelvis-to-foot distance was similar for the left and right legs during straight-walking ($P > 0.4$), the outer and inner foot gradually moved away from and closer to the pelvis trajectory, respectively, when curve tightness increased (all post hoc comparisons, $P < 0.0001$). The stance phase duration of both legs was negatively correlated with the pelvis-to-foot distance in all the subjects (Fig. 2c, $P < 0.001$; $r = -0.68 \pm 0.07$). The slope of this relationship significantly depended on the subject's weight, being larger in the heaviest subjects (correlation between body weight and slope, $r = 0.64$, $P < 0.05$). A concomitant changes in the mean roll trunk orientation also was observed. The trunk significantly (curve effect, $P < 0.01$) tilted toward the inner part of the curve on passing from SA to CS ($0.9 \pm 0.8°$) and from CS to CT ($1.8 \pm 1.1°$).

A slight but significant change in timing between the displacement of inner and outer legs was a regular feature of the progression along the curved paths. Mean values of the inter-limb timing, i.e., the time of contralateral heel contact, are reported in Fig. 2d. The timing of inner and outer heel contacts slightly but significantly changed, in opposite sense, with curve tightness (curve × leg effect, $P < 0.0001$); as a consequence, the inner leg led with respect to the outer leg when turning (all post hoc comparisons, $P < 0.05$). Instead, the left and right legs moved near perfectly out of phase during straight-walking: the contralateral heel contact occurred at $50.3 \pm 0.7\%$ of cycle duration. Further details on gait adaptations to curve-walking in humans can be found in Courtine and Schieppati (2003a, b, 2004).

Curve-dependent adjustment of patterns of muscle activation

Figures 3, 4, and 5 illustrate the characteristics of the muscle activation patterns of the two legs and the trunk when walking along the SA, CS, and CT locomotor paths. Figure 3 shows the average EMG profile (average of the mean traces of all subjects) of trunk, hip, thigh, and leg muscle activity over the normalized time interval of the cycle period when walking along the three locomotor paths. EMG waveforms recorded on the left (inner) and right (outer) legs are aligned on the time of heel contact, and identified by dark and light traces, respectively. The timing characteristics of the EMG bursts are sketched in Fig. 4; the left and right borders of each box indicate the onset and end of the EMG burst. Finally, the histograms of Fig. 5 report the mean values of EMG burst amplitude normalized on SA baseline.

Overall muscle activity

The EMG activity picked-up from the left and right muscles was remarkably similar during straight-walking. Accordingly, left and *right* EMG envelopes were highly correlated regardless of the muscle considered ($P < 0.0001$, mean of correlation coefficients from all muscles of all subjects, $r = 0.97 \pm 0.01$). Walking along the curved paths did not imply a dramatic re-organization of the basic EMG patterns required for walking straight-ahead. Rather, the progression along the two curves required a subtle and graded modulation of amplitude and temporal characteristics of EMG bursts, which was opposite in inner and outer muscles. These adaptations of muscle activity that accompanied steering of the body are detailed in the subsequent sections muscle by muscle.

Leg muscles

Soleus and GM muscles showed similar features during straight- and curve-walking. Both muscles developed a burst beginning 100–200 ms after the onset of the stance phase ($13 \pm 2\%$ and $14 \pm 4\%$ of cycle duration for SL and GM) and ending approximately with swing onset ($59 \pm 2\%$ and $57 \pm 3\%$ of cycle duration for SL and GM). During straight-walking, the amplitude and timing of SL and GM bursts did not differ between the left and right legs (all statistical tests on amplitude and timing, $P > 0.1$). During curve-walking, SL burst onset remained unchanged; instead, GM burst onset was significantly advanced and delayed (Figs. 3, 4) on the outer and inner legs, respectively (curve × leg effect, $P = 0.001$). These changes were small (1–2% of cycle duration), though significant ($P < 0.01$ for all inner versus outer post hoc comparisons for CS and CT curves). Conversely, the end of GM burst did not depend on path curvature ($P > 0.3$), whereas the end of SL bursts significantly changed when walking in a curve (curve × side effect, $P < 0.05$). Post hoc test revealed that, when stepping along the tighter curve, the end of inner and outer SL bursts was significantly ($P < 0.05$) delayed and advanced (2% of cycle duration), respectively (Fig. 4). Not only was the timing of SL and GM bursts changed during curve-walking, but their amplitude also was modulated (curve × side effect, $P < 0.001$). The EMG activity increased for GM (SA vs. CS, $P > 0.3$; SA vs. CT, $P < 0.001$) or remained unchanged for SL ($P > 0.8$) muscles in the outer leg (Fig. 5). On the other hand, the amplitude of EMG bursts decreased in both SL and GM inner muscles during curve-walking ($P < 0.001$) for all post hoc comparisons). This modulation was progressive, the depression being more evident when walking

Fig. 3 Muscle activity during straight- and curve-walking. Mean EMG waveforms computed from all trials of all subjects, separated according to body side and locomotor path. Traces from the muscles of the outer (*black*) and inner (*gray*) body segments are aligned on the time of heel strike (HS). The *horizontal bars* at the bottom of the figure specify the duration of stance and swing phases. The time of toe off (TO) is also indicated. The *short vertical white lines* depict the time of contralateral heel strike (CHS). The EMG activity was bilaterally recorded from soleus (SL), gastrocnemius medialis (GM), gastrocnemius lateralis (GL), tibialis anterior (TA), vastus lateralis (VL), biceps femoris (BF), gluteus medius (GLU), and erector spinae (ES) muscles, from top to bottom
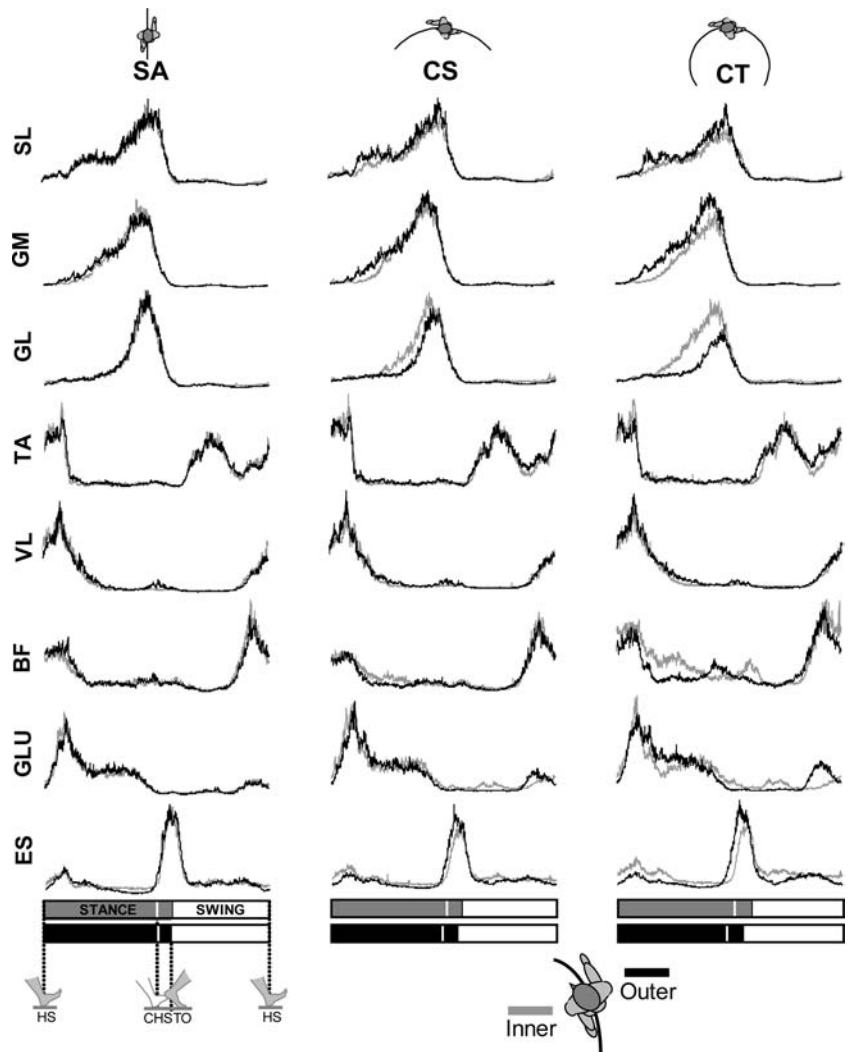
along CT than CS curve (CS vs. CT, $P < 0.001$ for both SL and GM muscles, Fig. 5). The activity decreased by 11% for SL and 17% for GM along CS, and about 21% for both muscles along CT.

The GL was the muscle in which the maximum changes in EMG activity were detected during curve- with respect to straight-walking. In spite of their synergistic action around the ankle joint, GL and GM muscles showed opposite temporal *and* spatial EMG modulation during curve-walking (Fig. 3). GL burst onset was significantly (curve × leg effect, $P < 0.0001$) advanced and delayed in the inner and outer legs, respectively, regardless of the curve followed ($P < 0.01$ for all post hoc comparisons, Fig. 4). Changes in GL burst amplitude were also observed (curve × leg effect, $P < 0.0001$). Indeed, contrary to SL and GM muscles, activity of the GL muscle of the inner leg remained unchanged (SA vs. CS, $P > 0.2$) or increased (26%, SA vs. CT, $P < 0.05$) during curve- with respect to straight-walking (Fig. 5). Conversely, the EMG activity dropped in the outer muscle when steering along CS (21%) and CT (41%) paths compared to SA path ($P < 0.01$).

The changes in TA muscle activity during curve-walking were modest with respect to those detected in the ankle extensors. Modulation of ankle flexor activity was however consistent with the turn-related adaptations of the gait parameters. During straight-walking, the TA muscles exhibited a double-peak burst that began at the onset of swing ($62 \pm 2\%$ of cycle duration) and lasted up to the first third of the subsequent stance phase ($13 \pm 3\%$ of cycle duration). Opposite phase shift in the TA EMG burst onset between inner and outer legs emerged during curve-walking (curve × leg effect, $P < 0.0001$, Fig. 3 and 4). The outer burst was anticipated and the inner was delayed during CS and CT walking with respect to the straight-ahead condition (all post hoc comparisons, $P < 0.05$). Interestingly, TA burst onset was significantly ($p < 0.01$) correlated with the end of stance in seven out of the ten subjects ($r = 0.73 \pm 0.19$). No systematic changes were detected for the other temporal features of TA activity (Fig. 4). Significant changes in amplitude also were observed (curve effect, $P < 0.01$): EMG activity (8%) slightly decreased at the
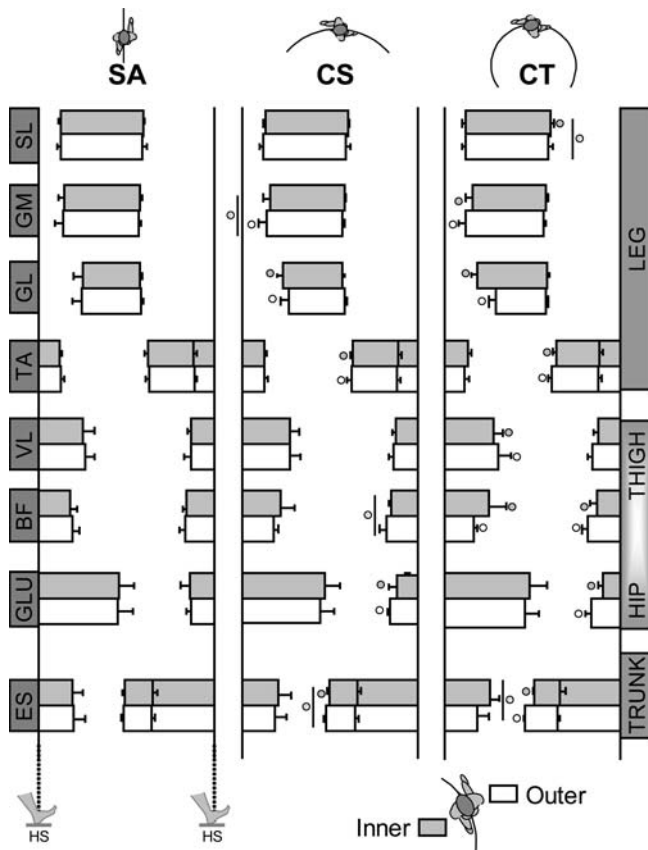
Fig. 4 Schematic representation of muscle activity during straight- and curve-walking. *Left and right borders* of each box indicate the onset and end (+ SD) of muscular bursts, respectively, referred to the normalized duration of the cycle period (HS, heel strike). *Open* and *filled circles* indicate significant differences in muscle timing between straight-walking and curve-walking (both CS and CT) conditions for the inner and outer legs, respectively. Bars associated with a circle show significant differences between the timing of the inner and outer muscle activity within a given condition of walking

beginning of stance for both inner and outer muscles during CT vs. SA walking ($p < 0.05$).

Thigh muscles

The activity of VL muscle has been recorded in six subjects. Except for one subject, who showed significant changes but a low level of EMG activity, walking along either curve hardly altered the activity of the VL muscle (Fig. 3). The only significant difference observed during curve-walking was a weak change in the timing during the stance phase of gait (curve effect, $P < 0.001$). Both inner and outer muscles significantly prolonged their burst by 3% of the cycle duration when walking along CT vs. SA or CS paths ($P < 0.01$; Fig. 4). Together with our previous observation that the rectus femoris muscle shows no adaptation in EMG activity during curve- compared to straight-walking (Courtine and Schieppati, 2003b), the current finding suggests that knee extensors contribute little to the production of a curvilinear trajectory during human walking. We cannot exclude, however, that the other heads of the quadriceps muscle might show significant modifications when walking in a curve as presently observed within the triceps surae group.

The activity of the BF muscle was more strongly modulated during curve-walking. During straight-ahead walking, it normally exhibited a single burst that overlapped the swing-to-stance transition (Fig. 3). Burst onset and end respectively occurred at $84 \pm 3\%$ and $19 \pm 3\%$ of cycle duration in straight-ahead condition, but significantly changed during curve-walking (curve × side effect, $P = 0.001$ and $P < 0.05$ for onset and end, respectively). BF EMG activity rose earlier ($p < 0.05$) and later ($P < 0.05$) in the outer and inner muscles, respectively, when walking along the CT versus SA path (Fig. 4). This difference was also significant between inner and outer muscles for CS ($P < 0.001$). The BF burst end was significantly delayed and advanced in the inner and outer muscles, respectively (CT *vs.* SA post hoc comparison, $P < 0.01$). Significant changes in burst amplitude also were observed (curve × side effect, $P < 0.05$). The activity of the inner muscle progressively increased with curve tightness compared to the activity of the outer muscle (inner vs. outer post hoc comparisons, $P < 0.01$ for both curved paths; Fig. 5). Furthermore, an additional burst emerged in both inner and outer muscles at the stance-to-swing transition when stepping along the tighter curve (Fig. 3). This burst appeared earlier in the outer with respect to the inner muscles, as reported for the stance phase duration (Fig. 2a). It is noteworthy that this additional burst was only observed in those subjects who already exhibited a small EMG activity at the stance-to-swing transition in the straight-ahead condition.

Hip muscle

Hip rotation and lateral trunk leaning are important determinants for the production of a curved path in humans (Courtine and Schieppati 2003a). Accordingly, the activity of the GLU muscle, a thigh abductor, might be substantially modulated during curve-walking. However, GLU EMG pattern did not show major modifications when walking along either curve (Fig. 3). Timing changed, though: GLU muscle activity increased at the end of the swing phase in straight-ahead condition ($86 \pm 4\%$ of cycle duration), but significantly changed its temporal occurrence during curve-walking (curve × leg effect, $P < 0.0001$). The onset of GLU activity was delayed and advanced for the inner and outer muscles (Fig. 4), respectively, regardless of the tightness of the path followed ($P < 0.05$ and $P < 0.01$ for CS and CT paths, respectively). In any case, the GLU muscle burst was fully developed only after heel contact. At this time, a peak emerged, which ceased with the end of BF and VL bursts (Fig. 3). A high tonic activity was then maintained throughout the remaining period of single stance (end at $45 \pm 8\%$ of cycle duration). Whereas the

Fig. 5 Amplitude of muscle activity during straight- and curve-walking. Mean values (+ mean SDs) of muscle burst amplitude according to the body side and the locomotor path. All the values are normalized on the averaged activity computed for each leg and subject during straight-walking. The same convention as in Fig. 2 indicates significant differences. The *shaded area* in the schematic representation of the EMG activity depicted above each *histogram* indicates the considered muscle burst, i.e., the temporal interval during which the amplitude of muscle activity was computed and reported in the *bar histograms* below
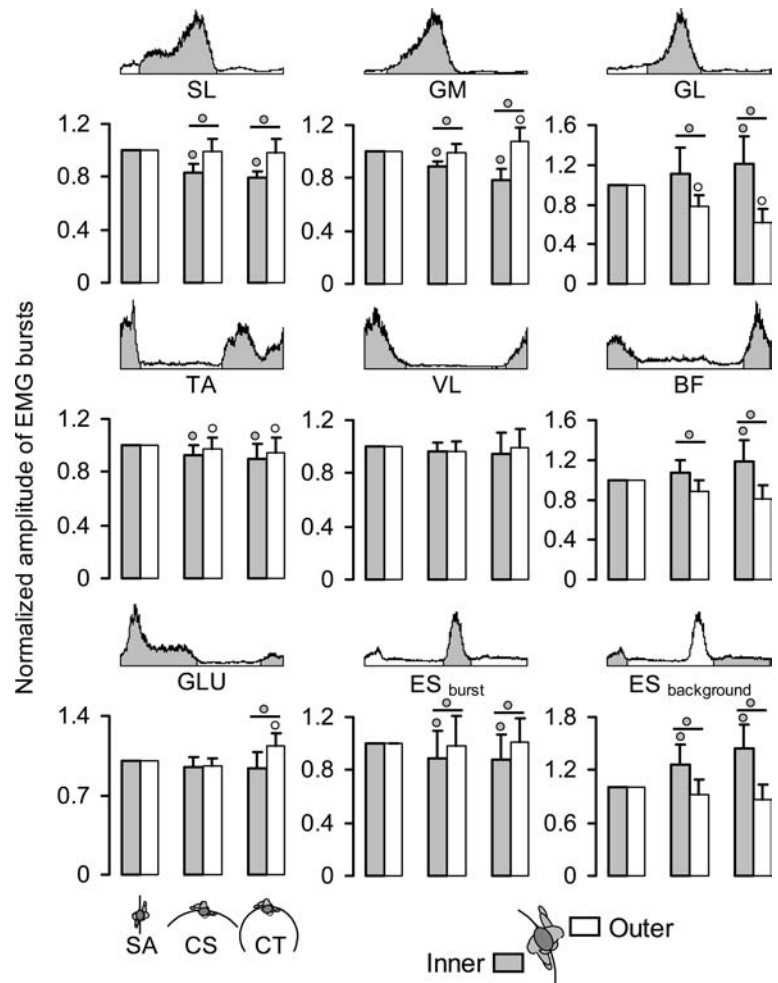
amplitude of the phasic burst tended to decrease, this tonic activity significantly (curve × side effect, $P < 0.05$) increased in the outer muscle during curve-walking (CT path) as did its initial burst at the end of the swing phase ($P < 0.01$; Fig. 5).

Trunk muscles

The lumbar (L3) ES muscle showed two distinct periods of activity, phasic and tonic (Fig. 3). The phasic burst occurred in relation with the contralateral heel strike ($48 \pm 1\%$ of cycle duration) and lasted up to swing onset ($65 \pm 2\%$ of cycle duration). Afterward, a weak tonic activation of trunk muscles was maintained throughout the period of leg oscillation and during the first part of the subsequent stance phase, i.e., this activity ended at around $21 \pm 6\%$ of cycle duration. The timing of the ES phasic burst was substantially modified during curve- with respect to straight-walking (curve × side effect, $P < 0.0001$). Burst onset was advanced for the inner ($P < 0.01$) and delayed for the outer muscle, respectively (SA vs. CT, $P < 0.001$; SA vs. CS, $P = 0.09$; Fig. 4). Interestingly, a significant relationship between ES burst

onset and the time of contralateral heel strike was found for eight out of the ten subjects ($P < 0.001$; $r = 0.77 \pm 0.17$). Significant modulation of amplitude of ES EMG activity accompanied the smooth body steering along a curve. The activity of the phasic burst significantly decreased (curve × side effect, $P < 0.01$) in the inner with respect to the outer muscle when walking along both curves as well as compared to the activity of the same muscle in the straight-ahead condition ($P < 0.01$ for all comparisons; Fig. 5). The inner muscle conversely increased its level of tonic activity during curve- compared to straight-walking (curve × side effect, $P < 0.001$, all post hoc comparisons, $P < 0.01$). No significant changes in the amplitude of the outer ES muscle activity were observed during curve- compared to straight-walking.

Coordinated spatial and temporal modulation of muscle activity and its relation with stride length

To explore how the CNS coordinates the modulation of muscle activity for successful body steering along a curved path, we evaluated the degree of correlation

between muscle burst features, both in spatial and temporal domains. Figure 6 shows typical relationships between the activity of ankle extensors (GM and GL), i.e., the muscles exhibiting large modulation during curve-walking, and the activity of the other recorded muscles; the number of subjects for which significant correlations ($P < 0.05$) were found is reported in each plot. The EMG amplitude of the inner and outer legs was inversely modulated during curve-walking; as a consequence, their data points evolved in opposite directions when walking along either curve. No correlation or weak correlations were found in those subjects who exhibited modest modulation in the activity of a particular muscle; accordingly, the slope of the corresponding relationship was close to zero, and the correlation was not or weakly significant. In these instances, however, a similar dissociation between inner and outer burst amplitudes was clearly observed.

Inter-muscle coordination was also apparent at the time of onset or end of the inner and outer leg muscle EMG bursts relative to the onset of the ES EMG (Fig. 7). In general, the inner and outer leg muscles were activated prior to ES muscle. Also, during curve-walking, the outer leg muscles were activated prior to the inner leg ones; when combining the inner and outer muscle onsets for each stepping paradigm (SA, CS, and CT), there was a positive slope for each muscle except for the GL. These relationships were consistent across subjects; mean values of regression coefficients are reported to the right of each plot ($P < 0.001$). This analysis of the spatial *and* temporal structures of the motor pattern points out the high degree of coordination in the command to *bilaterally* modulate bursts of leg and trunk muscles during straight- *and* curve-walking.

We also investigated whether this coordinated modulation of inner and outer muscle activity could account for the turn-related asymmetrical adaptation of stride length, a necessary event for curvilinear locomotion (Courtine and Schieppati 2003b). The percent change in EMG amplitude between inner and outer homonymous muscles when walking along the three locomotor paths was compared to the difference in the distance traveled by the inner and outer malleolus during the same time interval. Significant correlations were detected for GM, SL, GL, GLU, ES, and BF muscles in several subjects ($P < 0.05$; from 5 to 8 according to the comparisons, reported in Fig. 8). The differences between the stride length of the left and right legs were equal to zero during straight-walking as was the normalized EMG ratio. As a result, SA-related data points are clustered around zero in Fig. 8. Gradual decrease in inner compared to outer stride length is a regular feature of curve-walking (see above) and CS–CT related data points indeed shifted upward in the plots of Fig. 8, i.e., the outer to inner stride length difference increased. Interestingly, gradual divergence in inner-outer EMG activity accompanied this adaptation of inner–outer stride length. Opposite modulation of inner and outer muscle activity resulted in

differences as large as 300% between EMG amplitude of both muscles for the tighter direction changes.

A number of significant correlations between EMG activity and the different measured gait parameters were observed in some subjects. For example, linear regressions were detected between the changes in body midpoint positioning/trunk roll and the activity of the triceps surae and/or trunk muscles. However, the correlations reached significance only in those subjects showing substantial modifications in both muscle activation and gait mechanics during curve- compared to straight walking. Accordingly, these relationships are not reported in the present communication, and would probably require additional conditions, such as increase in walking speed, to emerge clearly.

Discussion

The aim of this study was to investigate the spatial and temporal characteristics of muscle synergies during straight versus *continuous* curvilinear locomotion, to relate those EMG features to gait mechanics, and to assess the degree of coordination in the turn-related modulation of muscle synergies. For this purpose, we bilaterally recorded the EMG activity of a representative sample of leg and trunk muscles during walking along three paths of increasing curvature. We show that *continuous* curvilinear locomotion involved coordinated, side-dependent modulation of amplitude and timing of leg and trunk muscle activity, and that this pattern was correlated with the adaptations of gait mechanics that are required to simultaneously control balance and propulsion when stepping in a curve. Our findings suggest that, to implement curvilinear locomotor trajectories, the descending command finely modulates the basic oscillating circuits that shape the activity of the muscles during straight-walking in humans. The intrinsic coupling between spinal neuronal assemblies would guarantee the coordinated modulation of motor pool activity and the conservation of kinematic principles that ensure well-balanced human bipedal stepping in a variety of locomotor tasks (Courtine and Schieppati, 2004; Lacquaniti et al. 2002).

Gait adaptations during curvilinear locomotion

Bipedal locomotion is naturally unstable in the lateral plane during straight-ahead walking (Winter et al. 1993; Kuo 2001). Curve-walking adds further complexity to body propulsion and balance, since the change in direction of body masses causes a significant outward tilt of the gravito-inertial acceleration vector that threatens lateral stability (Imai et al. 2001). We previously showed that successful walking along a curve requires a number of adaptations of spatial and temporal determinants of gait. This turn-related adjustment of locomotion kine-

Fig. 6 Coordinated spatial tuning of muscle activity during straight- and curve-walking. Relationships between burst amplitudes of ankle extensor muscles and the other muscles recorded. Burst amplitudes of each muscle are normalized with respect to their mean activity during straight-walking. The coordinates of each dot represent the activity (burst amplitude) of the indicated pair of muscles during the same gait cycle. *Open* and *filled circles* differentiate the outer and inner muscles, respectively. All the data from a typical subject are represented in each plot. The mean values of the correlation coefficients (mean plus SD) are reported as well as the number of subjects for which the linear regression analysis reached significance ($p < 0.01$)
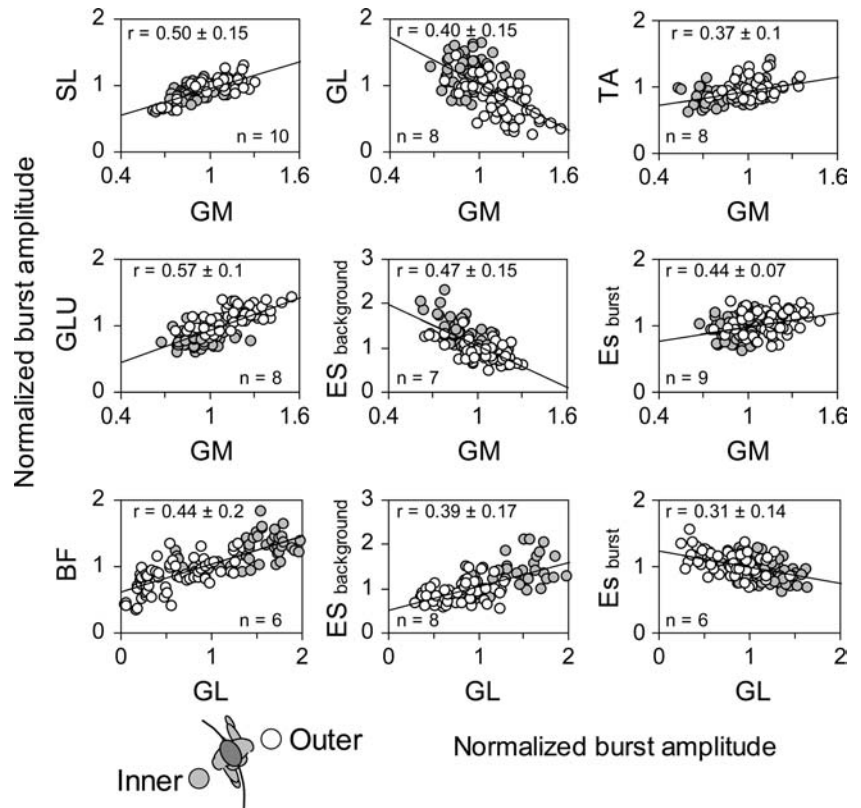
matics notably includes whole-body tilt toward the inner part of the curve, and discrepancy in the stride length of the inner and outer legs. The former adaptation is directed to counteract the outward-oriented gravito-inertial forces in order to preserve balance (Patla et al. 1999; Imai et al. 2001; Courtine and Schieppati 2003a, 2004), while the latter generates the curved trajectory of the body center of mass to implement the planned locomotor path (Courtine and Schieppati 2003b). Both activities must be coordinated in a feed-forward mode. In the current study, we confirm that the CNS substantially accommodates gait mechanics in order to successfully fulfill the complex balance *and* propulsion requirements accompanying curvilinear locomotion. This includes side-dependent changes in stride length and stance duration, modification of inter-limb coordination, and shift of the pelvis segment toward the inner part of the locomotor trajectory (Table 1, Fig. 2). Furthermore, the use of the medium-curvature path allowed us to illustrate the continuity of the steering process, i.e., the progressive adaptation of gait features to curve tightness.

Modulation of muscle activity during curvilinear locomotion

Significant changes in balance constraints emerging during curvilinear locomotion may necessitate drastic adjustments of muscle activity. We pointed out in the

Introduction that conservation of locomotion kinematics across gait directions might be achieved at the expense of a complete reorganization of muscle synergies, as demonstrated during backward compared to forward walking (Grasso et al. 1998). However, we recorded the activity of a representative sample of leg and trunk muscles and found that *continuous* curvilinear locomotion did not require major changes in the pattern of muscle activation underlying straight-ahead walking: successful curve-walking was accomplished through fine-modulation in amplitude and timing of the basic motor pattern for straight-ahead locomotion. Significant differences in the activity of inner and outer muscles resulted, which paralleled increase in curve tightness (Fig. 3). Interestingly, these adaptations of muscle activity matched the curve-dependent changes in spatial and temporal parameters of gait that are required to construct the assigned locomotor trajectory while preserving balance.

For example, leg- and curve-dependent changes in TA burst onset were significantly correlated with the concurrent modifications of the stance phase duration for both legs. Similarly, a significant relationship was found between the onset of the phasic burst in lumbar trunk muscles and the timing of inter-limb displacement. During curve-walking, a gradual delay in onset of the inner ES muscle activity accompanied the progressive lag of the heel strike of the outer leg, and inversely for the outer ES muscle. These results confirm that locomotor-related activity of lumbar trunk muscles is closely
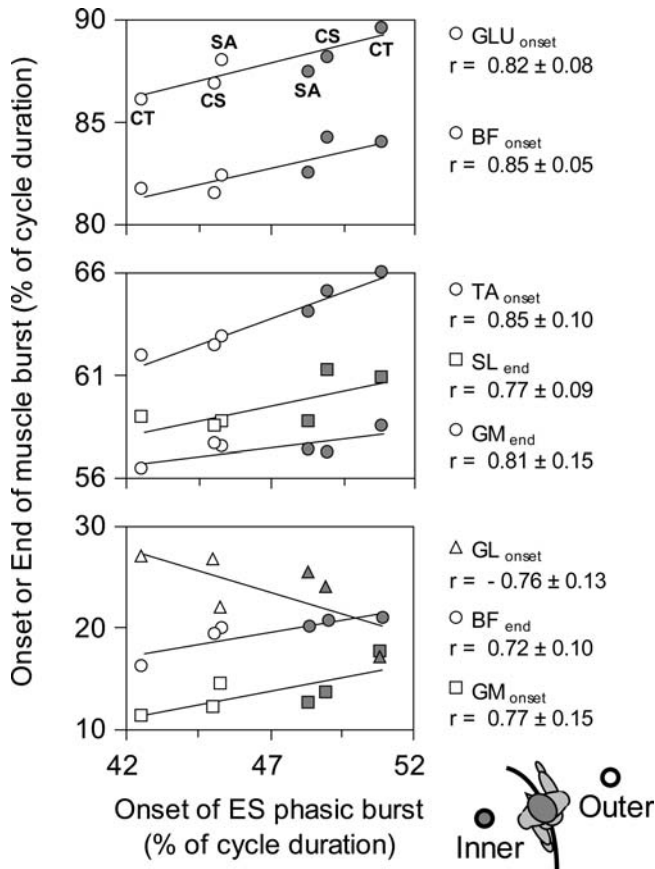
Fig. 7 Coordinated temporal tuning of muscle activity during straight- and curve-walking. Relationships between onset of erector spinae burst and onset or end (as indicated nearby each plot) of SL, GM, GL, TA, BF, and GLU muscle bursts for a typical subject. Each point represents the mean timing value when walking along SA, CS, and CT paths for inner (*square*) and outer (*circle*) muscles, from left to right and right to left, respectively. Since all the plots are from a typical subject, the onset of the ES phasic burst is the same in each plot, and therefore, SA, CS, and CT data points are vertically aligned. The average values (+ SD) of the regression coefficients computed from all individual subjects are reported beside each scatter plot

coordinated with the timing of contralateral stance beginning (Waters and Morris 1972; Thorstensson et al. 1982). Likewise, turn-related increase in abduction and adduction of outer and inner legs, respectively, detected before heel contact (Courtine and Schieppati 2004), may explain the anticipation of the onset of the activity of the outer gluteus medius muscle at the end of swing during curve-walking while the inner muscle remained quiescent. Lastly, concomitant changes in the SL burst timing and stance phase termination have been observed when walking along the tighter curve in the present study (Fig. 4). A similar modification of the peroneus longus muscle burst was found in our previous study on curve-walking (Courtine and Schieppati 2003b).

These new experimental results thus show that side- and curve-dependent timing modulation of the activity of a variety of muscles are required to produce well-balanced propulsion when stepping in a curve. The accuracy of this turn-related temporal modulation of

muscle activity may be critical since bipedal walking is inherently unstable, even when progressing along a straight path, and less flexible than quadrupedal locomotion (Patla et al. 1991). Alterations to the temporal (and spatial) features of left and right leg displacements, for example, provoke gait instability during straight-walking in toddlers (Clark 1995), Parkinsonian patients (Dietz et al. 1997), and cosmonauts following their return from space (Courtine and Pozzo 2004).

Not only the timing but also the amplitude of muscle activity was consistent with the adaptations of locomotor movements during curve-walking. For example, the ratio between the activity of the muscles of the inner and outer sides with respect to the direction of the curved trajectory was significantly correlated with the difference between the stride length of the inner and outer legs during the same gait cycle. This linear relationship, significant in most subjects for the GM, GL, SL, ES, BF, and GLU muscles, may simplify implementation of the required trajectory (Fig. 8). Indeed, we previously showed that the inner-to-outer stride length discrepancy is tightly related to the curvature of the whole-body trajectory, i.e., the locomotor path actually covered (Courtine and Schieppati 2003a). This notwithstanding, leg-dependent modulation of muscle activity during curve-walking is intended not only to change the locomotor direction but also to preserve balance. The opposite modulation pattern we detected between GM and GL may appropriately fit propulsion- and balance-related requirements associated with curve-walking. The activity was anticipated and augmented in the inner versus outer muscles for the GL, whereas the inverse modulation pattern was observed in the inner versus outer GM muscles when walking in a curve. Such changes in plantar flexor activity may favor an exorotation moment in the outer leg (Duysens et al. 1996; Arndt et al. 1999), thereby producing the change in walking direction—body turn mainly takes place on the outer foot (Imai et al. 2001; Courtine and Schieppati 2003a). On the other hand, the concurrent increased activity in the inner GL and BF muscles during the stance phase may contribute to body support by increasing knee stability (Williams et al. 2001); it is worth noting that inner GL and BF muscle activities appreciably increased during the single stance phase, i.e., when inward body leaning loads the inner leg (Fig. 3). We also showed significant modulation of the inner erector spinae muscle during curve-walking; the amplitude of its phasic burst significantly decreased with curve tightness whereas its tonic activity increased steadily. This modulation of lumbar trunk muscle activity is likely required to conserve trunk stability (Imai et al. 2001; Courtine and Schieppati 2003a) and thus whole-body balance under demanding equilibrium conditions. Interestingly, both the phasic and tonic periods of lumbar trunk muscle activity nicely correlated with the amplitude of GL and GM bursts (Fig. 6). Dynamical simulation studies (review in Zajac et al. 2003) showed that ankle plantar-flexors are the main contributors to

support and promote progression in human bipedal walking. In particular, Neptune et al. (2001) demonstrated that the gastrocnemii muscles provide trunk support during single-leg stance and pre-swing. Indeed, these muscles may be critical for ensuring lower limb and trunk stability when performing movements in the medio-lateral direction, i.e., the direction in which the bipedal erect stance shows its greatest instability (Winter et al. 1993; Kuo 2001). This idea is consistent with findings in the cat that showed that GM and GL muscles exert substantial torques outside the sagittal plane (Lawrence et al. 1993). In this line, the BF and semitendinosus muscles, which share their proximal insertion at the hip but insert at the outer and inner parts of the knee, respectively, might also show opposite modulation pattern during curve-walking (Duysens et al. 1998). It is worth noting that all these modifications of trunk and leg muscle activation patterns are specific to curvilinear locomotion. Indeed, split-belt treadmill walking, which similarly requires to slow down a leg with respect to the other, does not imply such adaptations in the activity of leg and trunk muscles (Dietz et al. 1994; Jensen et al. 1998). This points out that the dramatic postural changes that accompany curve-walking put specific constraints on the muscle control characteristics in order to maintain balance. Flexible adaptations of muscle activity and gait features to split-belt treadmill locomotion were taken as evidence that spinal neuronal networks ensure adaptation of the walking pattern to speed in human locomotion. Whether curve-walking specificities in muscular control rely upon different neuronal mechanisms should be the focus of future investigations.

Central neural mechanisms for implementation of curvilinear locomotion

The brain orchestrates the transformation of the internal representation of the path to be followed into the relevant motor coordinates (Berthoz and Viaud-Delmon 1999; Vieilledent et al. 2001; Ma et al. 2004). This planning of walking direction change implies anticipatory modification of body movements including head and feet rotation toward the future traveled path (Grasso et al. 1996; Hollands et al. 2001; Imai et al. 2001; Courtine and Schieppati 2003a). We showed in this study that the activation of many muscles is modified during curve-walking compared to straight-walking, thus revealing a significant modulation of the motor pattern evoked by the descending command to turn. Our results, however, suggest that implementation of this motor task does not necessarily imply a transfer of the detailed instruction for muscle activity directly onto the relevant motoneuronal pools. We argue instead that the descending command for steering globally tunes the spinal oscillating circuits that shape motoneuronal activity during straight-locomotion (Bussel et al. 1996; Dimitrijevic et al. 1998; Edgerton and Roy 2002; Ivanenko et al. 2004). We addressed this possibility by evaluating the coordination amongst muscles' activity, both in the spatial (Fig. 6) and temporal (Fig. 7) domains. Tight relationships were detected between burst characteristics of muscles of the two legs and the trunk, both in amplitude and timing, regardless of the actual walking direction. Furthermore, these relationships were
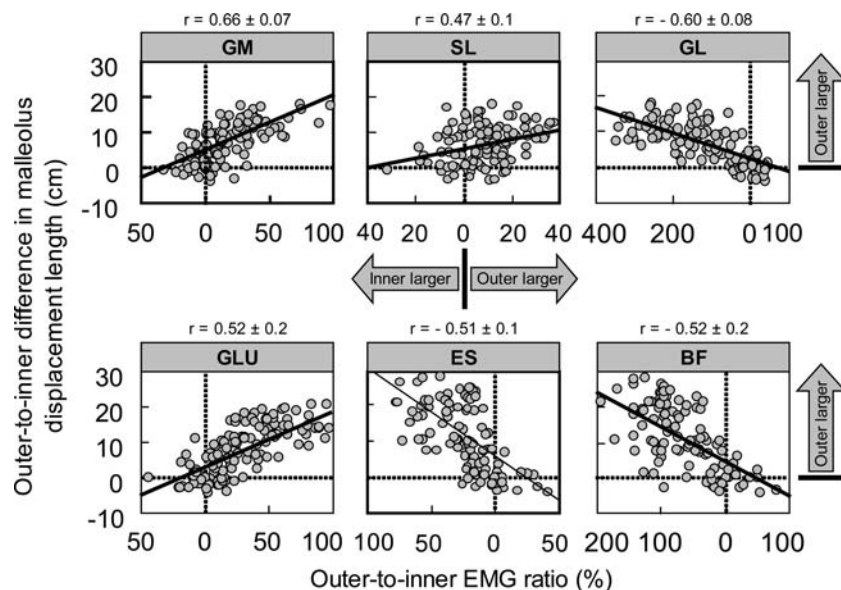

Fig. 8 Relationship between muscle activity and stride length. The difference between the distance traveled by the inner and outer malleolus during the time interval of a gait cycle is represented as a function of the ratio between the activity of inner and outer GM, SL, GL, GLU, ES and BF muscles during the same time interval. The EMG ratio was computed for each gait cycle by expressing the activity of the muscle most active as a percentage of the activity of the muscle less active −100. As such the value was 0 when the inner and outer muscles exhibited the same activity. The mean value (+ SD) of regression coefficients computed in each subject (n = 8, 6, 7, 5, 6, 5 for GM, SL, GL, GLU, ES, and BF muscles, respectively) for whom a significant relationship (p < 0.01) was found is reported above the graphs

virtually identical for inner and outer muscles in spite of their opposite modulation patterns. Our data are compatible with the notion that a unifying principle is responsible for shaping the spatiotemporal activity of the muscles of the two body sides during straight-ahead *and* curve-walking. This is consistent with the conclusion of our previous kinematics study, showing that a basic elementary function was enough to explain the coupling of the two legs and the trunk during straight- *and* curve-walking, both in the frontal *and* sagittal planes (Courtine and Schieppati 2004). Limb-dependent tuning of this intersegmental coordination pattern accounted for the changes in the temporal coupling between lower limb oscillations, and produced adequate modifications of joint angle trajectories to steer walking. The same neural strategy appears to be used to generate different locomotor modes including backward walking or changes in gait posture (see review in Lacquaniti et al. 2002). In the present study, we showed that the timing and amplitude characteristics of muscle bursts were linearly related to the temporal and spatial features of body movements required to progress along a given curved path. Similarly, linear relationships were detected between the amplitude of walking direction change and the modifications of the intersegmental coordination pattern in the kinematics study (Courtine and Schieppati 2004).

Taken together, the data from our kinematics and EMG studies strongly suggest that graded, side-dependent modulation of spinal oscillating circuits that shape the activity of motoneurons during straight-locomotion (Ivanenko et al. 2004) creates the coordinated pattern of muscle activation to successfully steer walking while preserving balance. This would allow the command to turn to be readily incorporated into the ongoing locomotor activity, and significantly facilitate the implementation of the centrally planned walking path. However, the current findings provide no information regarding the way the internal representation of the path to be followed is converted into the relevant motor coordinates, nor do they indicate which descending pathways funnel the turn-related command to the spinal pattern generators. Future investigations will have to assess whether the steering-related supraspinal command is transferred through the corticospinal projections, or whether the bulbospinal pathways convey the sufficient information to achieve a balanced and spatially oriented locomotion in humans (see Discussion in Courtine and Schieppati, 2004).

Putative sensory-related mechanisms during curvilinear locomotion

Side-dependent sensory activity emergent from the neck-vestibular system and the proprioceptors of both legs and the spine may strengthen the influence of the turn-related descending command on the spinal circuitry and favor the production of curvilinear walking. For example, asymmetrical neck and vestibular afferent inputs resulting from the anticipatory head rotation that systematically accompanies steering (Grasso et al. 1996; Hollands et al. 2001; Imai et al. 2001; Courtine and Schieppati 2003a; Mergner and Rosemeier 1998) likely facilitate the production of a curved trajectory (Bove et al. 2001; Courtine et al. 2003; Fitzpatrick et al. 1999; Bent et al. 2000). In the walking system of mammals, the feedback from receptors signaling the loading of the leg influences the level of extensor muscle activity (Harkema et al. 1997) and partly determines the onset of flexor burst generation, i.e., stance end (Duysens and Pearson 1980; Pang and Yang 2002). Accordingly, we show in the present study that the duration of the stance phase as well as the onset of the TA burst are significantly correlated with the change in body midpoint to foot distance (Fig. 2c). Similarly, the opposite amplitude and timing modulation of gastrocnemii medialis and lateralis activity observed during curve-walking is consistent with the selective loading and unloading of inner and outer leg muscles that may result from the inward body leaning (Duysens et al. 1996; 2000). The asymmetric afferent input from trunk proprioceptors may also be a source of relevant input, as shown by the capacity of unilateral erector spinae vibration to produce involuntary, but otherwise normal, curved trajectory during blindfolded walking (Schmid et al. 2005).

Conclusion

Our previous study (Courtine and Schieppati 2004) associated with the present results provides a novel insight into the organizational principles that allow the CNS to adjust the propulsive forces in order to steer walking while preserving body balance in human locomotion. We show that the coordinated modulation of the basic pattern of muscle activation underlying straight-walking generates the appropriate changes in spatial and temporal determinants of gait for successful implementation of a curved locomotor path. The coordinated synergies of leg and trunk muscles suggest that the motor pattern for stepping in a curve emerges from the modulation of phase relationships between the neuronal assemblies distributed along the spinal cord that drive motor neuron activity during walking. The operations of the spinal circuitry coupled with the mechanical properties of limb oscillators would produce the invariant templates for locomotion kinematics that ensure equilibrated bipedal stepping in the variety of locomotor tasks found in humans (Lacquaniti et al. 2002; Courtine and Schieppati 2004).

References

Alexander RM (1989) Optimization and gaits in the locomotion of vertebrates. Physiol Rev 69:1199–1227

Arndt A, Bruggemann GP, Koebke J, Segesser B (1999) Asymmetrical loading of the human triceps surae: II. Differences in calcaneal moments. Foot Ankle Int 20:450–455

Bent LR, McFadyen BJ, Merkley VF, Kennedy PM, Inglis JT (2000) Magnitude effects of galvanic vestibular stimulation on the trajectory of human gait. Neurosci Lett 279:157–160

Bernstein N (1967) The co-ordination and regulation of movements. Pergamon, Oxford

Berthoz A, Viaud-Delmon I (1999) Multisensory integration in spatial orientation. Curr Opin Neurobiol 9:708–712

Bove M, Diverio M, Pozzo T, Schieppati M (2001) Neck muscle vibration disrupts steering of locomotion. J Appl Physiol 91:581–588

Bussel B, Roby-Brami A, Nerris O, Yakovleff A (1996) Evidence for a spinal stepping generator in man. Paraplegia 34:91–92

Capaday C (2002) The special nature of human walking and its neural control. Trends Neurosci 25:370–376

Cavagna GA, Margaria R (1966) Mechanics of walking. J Appl Physiol 21:271–278

Chekirda IF, Bogdashevskiy AV, Yeremin AV, Kolosov IA (1971) Coordination structure of walking of Soyuz-9 crew members before and after flight. Kosmicheskaia Biologiia I Aviakosmicheskaia Meditsina 5:48–52

Cheron G, Bouillot E, Dan B, Bengoetxea A, Draye JP, Lacquaniti F (2001) Development of a kinematic coordination pattern in toddler locomotion: planar covariation. Exp Brain Res 137:455–466

Clark JE (1995) On becoming skillful: Patterns and constraints. In: Research quarterly for exercise and sport, vol 66, pp 173–183

Courtine G, Schieppati M (2003a) Human walking along a curved path. I. Body trajectory, segment orientation and the effect of vision. Eur J Neurosci 18:177–190

Courtine G, Schieppati M (2003b) Human walking along a curved path. II. Gait features and EMG patterns. Eur J Neurosci 18:191–205

Courtine G, Pozzo T (2004) Recovery of the locomotor function after prolonged microgravity exposure. I. Head-trunk movement and locomotor equilibrium during various tasks. Exp Brain Res 158:86–99

Courtine G, Schieppati M (2004) Tuning of a basic coordination pattern constructs straight-ahead and curved walking in humans. J Neurophysiol 91:1524–1535

Courtine G, Papaxanthis C, Laroche D, Pozzo T (2003) Gait-dependent integration of neck muscle afferent input. Neuroreport 14:2365–2368

Dietz V, Zijlstra W, Duysens J (1994) Human neuronal interlimb coordination during split-belt locomotion. Exp Brain Res 101:513–520

Dietz V, Leenders KL, Colombo G (1997) Leg muscle activation during gait in Parkinson's disease: influence of body unloading. Electroencephalogr Clin Neurophysiol 105:400–405

Dimitrijevic M, Gerasimenko Y, Pinter M (1998) Evidence for a spinal central pattern generator in humans. Ann N Y Acad Sci 860:360–376

Duysens J, Pearson KG (1980) Inhibition of flexor burst generation by loading ankle extensor muscles in walking cats. Brain Res 187:321–332

Duysens J, van Wezel BM, Prokop T, Berger W (1996) Medial gastrocnemius is more activated than lateral gastrocnemius in sural nerve induced reflexes during human gait. Brain Res 727:230–232

Duysens J, van Wezel BM, van de Crommert HW, Faist M, Kooloos JG (1998) The role of afferent feedback in the control of hamstrings activity during human gait. Eur J Morphol 36:293–299

Duysens J, Clarac F, Cruse H (2000) Load-regulating mechanisms in gait and posture: comparative aspects. Physiol Rev 80:83–133

Edgerton VR, Roy RR (2002) Paralysis recovery in humans and model systems. Curr Opin Neurobiol 12:658–667

Fitzpatrick RC, Wardman DL, Taylor JL (1999) Effects of galvanic vestibular stimulation during human walking. J Physiol 517:931–939

Gramsbergen A, Hadders-Algra M (1998) Development of postural control, a basic aspect of neuro-ontogeny. Neurosci Biobehav Rev 22:463–464

Grasso R, Glasauer S, Takei Y, Berthoz A (1996) The predictive brain: anticipatory control of head direction for the steering of locomotion. Neuroreport 7:1170–1174

Grasso R, Bianchi L, Lacquaniti F (1998) Motor patterns for human gait: backward versus forward locomotion. J Neurophysiol 80:1868–1885

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

Hollands MA, Sorensen KL, Patla AE (2001) Effects of head immobilization on the coordination and control of head and body reorientation and translation during steering. Exp Brain Res 140:223–233

Imai T, Moore ST, Raphan T, Cohen B (2001) Interaction of the body, head, and eyes during walking and turning. Exp Brain Res 136:1–18

Ivanenko YP, Poppele RE, Lacquaniti F (2004) Five basic muscle activation patterns account for muscle activity during human locomotion. J Physiol 556:267–282

Ivanenko YP, Dominici N, Cappellini G, Lacquaniti F (2005) Kinematics in newly walking toddlers does not depend upon postural stability. J Neurophysiol 94(1):754–763

Jensen L, Prokop T, Dietz V (1998) Adaptational effects during human split-belt walking: influence of afferent input. Exp Brain Res 118:126–130

Kuo AD (2001) A simple model of bipedal walking predicts the preferred speed-step length relationship. J Biomech Eng 123:264–269

Lacquaniti F, Grasso R, Zago M (1999) Motor patterns in walking. News Physiol Sci 14:168–174

Lacquaniti F, Ivanenko YP, Zago M (2002) Kinematic control of walking. Arch Ital Biol 140:263–272

Ma YY, Ryou JW, Kim BH, Wilson FA (2004) Spatially directed movement and neuronal activity in freely moving monkey. Prog Brain Res 143:513–520

Mergner T, Rosemeier T (1998) Interaction of vestibular, somatosensory and visual signals for postural control and motion perception under terrestrial and microgravity conditions–a conceptual model. Brain Res Brain Res Rev 28:118–135

Morris ME, Huxham F, McGinley J, Dodd K, Iansek R (2001) The biomechanics and motor control of gait in Parkinson disease. Clin Biomech (Bristol, Avon) 16:459–470

Neptune RR, Kautz SA, Zajac FE (2001) Contributions of the individual ankle plantar flexors to support, forward progression and swing initiation during walking. J Biomech 34:1387–1398

Pang MY, Yang JF (2002) Sensory gating for the initiation of the swing phase in different directions of human infant stepping. J Neurosci 22:5734–5740

Patla AE, Prentice SD, Robinson C, Neufeld J (1991) Visual control of locomotion: strategies for changing direction and for going over obstacles. J Exp Psychol Hum Percept Perform 17:603–634

Patla AE, Adkin A, Ballard T (1999) Online steering: coordination and control of body center of mass, head and body reorientation. Exp Brain Res 129:629–634

Schmid M, De Nunzio AM, Schieppati M (2005) Trunk muscle proprioceptive input assists steering of locomotion. Neurosci Lett 384:127–132

Stack E, Ashburn A (1999) Fall events described by people with Parkinson's disease: implications for clinical interviewing and the research agenda. Physiother Res Int 4:190–200

Thigpen MT, Light KE, Creel GL, Flynn SM (2000) Turning difficulty characteristics of adults aged 65 years or older. Phys Ther 80:1174–1187

Thorstensson A, Carlson H, Zomlefer MR, Nilsson J (1982) Lumbar back muscle activity in relation to trunk movements during locomotion in man. Acta Physiol Scand 116:13–20

Vieilledent S, Kerlirzin Y, Dalbera S, Berthoz A (2001) Relationship between velocity and curvature of a human locomotor trajectory. Neurosci Lett 305:65–69

Waters RL, Morris JM (1972) Electrical activity of muscles of the trunk during walking. J Anat 111:191–199

Williams GN, Chmielewski T, Rudolph K, Buchanan TS, Snyder-Mackler L (2001) Dynamic knee stability: current theory and implications for clinicians and scientists. J Orthop Sports Phys Ther 31:546–566

Winter DA, MacKinnon CD, Ruder GK, Wieman C (1993) An integrated EMG/biomechanical model of upper body balance and posture during human gait. Prog Brain Res 97:359–367

Zajac FE, Neptune RR, Kautz SA (2003) Biomechanics and muscle coordination of human walking: part II: lessons from dynamical simulations and clinical implications. Gait Posture 17:1–17