Similar muscles contribute to horizontal and vertical acceleration of center of mass in forward and backward walking: implications for neural control

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Running head: Similar muscles control COM in forward and backward walking

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ABSTRACT

Leg kinematics during backward walking (BW) is very similar to the time-reversed kinematics during forward walking (FW). This suggested that the underlying muscle activation pattern could originate from a simple time-reversal as well. Experimental EMG studies have confirmed that this is the case for some muscles. Furthermore, it was hypothesized that muscles showing a time-reversal, should also exhibit a reversal in function (from accelerating the body center of mass (COM) to decelerating). However, this has not been verified yet in simulation studies. In the present study, forward simulations have been used to study the effects of muscles on the acceleration of COM in FW and BW. It was found that a reversal in function was indeed present in the muscle control of the horizontal movement of COM (e.g. tibialis anterior and gastrocnemius). In contrast, muscles antigravity contributions maintained their function for both directions of movement. An important outcome of the present study is therefore that similar muscles can be used to achieve opposite functional demands at the level of control of the COM when walking direction is reversed. However, some muscles showed direction-specific contributions (i.e. dorsiflexors). It was concluded that the changes in muscle contributions imply that a simple time-reversal would be insufficient to produce BW from FW. It is therefore proposed that BW utilizes extra elements, presumably supraspinal, in addition to a common spinal drive. These additions are needed for propulsion and require a partial reconfiguration of lower level common networks.

KEYWORDS

Induced acceleration; human locomotion; forward dynamic simulation; gait control; central pattern generator
INTRODUCTION

In humans, there is substantial evidence for the presence of central pattern generators (CPGs) during locomotion (Duysens and Van de Crommert 1998). In addition, the suggestion was made that such generators can be used for locomotion in various directions including forward (FW) and backward (BW) walking (Duysens et al. 1996; Lamb and Yang 2000). The idea was suggested that BW was basically FW in reverse (Winter et al. 1989; Thorstensson 1986; Duysens et al. 1996). The kinematics seemed to support this idea since joint angles at the hip show a simple time reversal during BW and FW. Nevertheless this is somewhat less true for the knee and ankle angles (Winter et al. 1989; Thorstensson 1986; Grasso et al. 1998; van Deursen et al. 1998). The similarity between FW and BW is so striking that most subjects cannot distinguish videos from FW and reversed BW (Viviani et al. 2011). Likewise, joint torques of ankle and hip are highly correlated in the two conditions, but less for the knee joint (Winter et al. 1989).

Surface electromyography (EMG) indicated more or less similar muscle activation patterns, with time reversal of the activation patterns in BW, especially for upper leg muscles (Winter et al. 1989; Thorstensson 1986). Such reversal was much less present for ankle muscles (Thorstensson 1986). Several other studies confirmed that activation patterns can differ significantly between the two movement directions. Grasso et al. (1998) reported different EMG patterns for FW and BW, indicating different muscle synergies, and different EMG amplitudes over the gait cycle. Likewise, van Deursen et al. (1998) reported a phase shift for all muscles except quadriceps. Ivanenko et al. (2008) also noted important differences. Based on a principal component analysis of spinal maps derived from surface EMG, they concluded that these spinal maps differed considerably between FW and BW, although the main components of FW and BW were highly correlated. Some authors have used mechanical parameters to tackle the BW-FW issue. Joint power patterns during FW and BW were found to be mirrored due to the reversal of joint velocity
Winter et al. 1989; Thorstensson 1986). This suggests that reversal in walking direction induces a reversal of muscle function at joint level with muscles changing from energy generator to absorber and vice versa. Interestingly, similar conclusions came from some of the cat studies. For example, Buford and Smith (1990) found that the anterior biceps muscle was active in stance both in FW and BW, suggesting that for this muscle there was a reversal in function from shortening to lengthening contraction.

From a neural control perspective, it seems advantageous that the same muscle can be used for different functions in FW and BW as it would allow the activation pattern to simply time-reverse to produce similar lower limb kinematics patterns that induce opposite accelerations of the center of mass (COM). However, the EMG studies mentioned above suggest that for specific muscles a simple time reversal cannot account for the observed differences in muscle activity between FW and BW. These observations suggest that the idea of pattern generators working in reverse may be too simple to explain BW. Instead, it is more attractive to consider the option of generators with elements that can be reconfigured to subserve different locomotion patterns (Koch et al. 2011; Frigon 2011). In such scheme, there is room for some common synergies but in addition the option exists to use part of the network for specific purposes depending on the specific locomotor function e.g. BW versus FW. In that case, it can expected that some muscles show a simple reversal of the activity patterns but that others would show quite different patterns for FW and BW.

Such a scheme fits well with insights gained from studies on backward pedaling (Ting et al. 1999). Using experimentally measured EMG, Ting et al. (1999) confirmed that direction reversal in cycling depends on the temporal reorganization of basic synergies. Simulations of pedaling (Raasch et al. 1997; Ting et al. 1999) previously indicated that six basic biomechanical functions per limb suffice to produce a range of pedaling tasks, including forward and backward pedaling.
These six functions can be organized into three pairs (namely extension/flexion, anterior/posterior and dorsiflexion/plantarflexion) that form the basis for a neural control strategy of forward and backward pedaling (Raasch et al. 1997). Analyzing phase reversal of the major lower limb muscles, Ting et al. (1999) confirmed that a phase reversal of the anterior/posterior pair is sufficient to produce backward pedaling. The flexion/extension synergy does not require a major phase-shift since this synergy opposes gravity which imposes similar constraints in both cycling directions. Ting and colleagues further suggested that a similar grouping into muscle synergies could be applicable to FW and BW, but that BW would require a phase reversal of two (anterior/posterior and dorsiflexion/plantarflexion) instead of one function pairs. This suggestion has not been verified so far.

Even more fundamentally, it remains unclear if muscle functions that directly actuate the individual lower limb joints during backward and FW have a similar control on the COM when walking direction is reversed. To address this question, simulations of FW and BW need to be developed to identify and classify individual muscle function in terms of the control to the COM. This approach is similar to the study of Neptune et al. (2000), who used cycling simulations to demonstrate that some muscles contributed to identical biomechanical functions in forward and backward pedaling. Similarly, muscle-actuated simulations of FW were already previously used to identify muscles that contribute to horizontal and vertical acceleration in FW at a typical walking speed (Liu et al. 2006, 2008; Neptune et al. 2001, 2004). Vasti and gluteus maximus act mainly to decelerate the COM during the first half of stance, while plantarflexors propel the body forwards in the second half of stance. Furthermore, these muscles are found to provide the majority of support during stance.

These studies all relate to FW and there are no studies available that identify the role of the individual muscles in accelerating or decelerating the COM during BW. In the present study, we
use subject-specific simulations of FW and BW to determine which muscles contribute predominantly to the horizontal (anterior-posterior) and vertical (up-down) accelerations of COM during BW and FW. Based on the biomechanical function of individual muscles in terms of their contribution to the horizontal and vertical acceleration of the COM, we hypothesize that in FW and BW similar muscles groups remain responsible for accelerations of the COM. This hypothesis is based on the proposal of a similar control scheme for FW and BW formulated by Ting et al. (1999) and on the observations by Winter et al. (1989) that with reversal of gait direction some muscles change from energy absorber to accelerators and vice versa. Hence, a reversal of muscle function in the horizontal direction is expected, with decelerators becoming accelerators and vice versa, while muscle function in the vertical direction remains unchanged. If similar muscles can be identified to be responsible for the control of the COM in both FW and BW, this supports the previously suggested hypothesis of a common neural basis for both walking conditions. Deviations from this pattern may reveal instances were additional control is required.

METHODS

Subjects and protocol

Ten healthy subjects (6 male, 4 female, mean age 26.1 ± 4.3 years) walked forward and backward for 10-15 minutes on a split-belt treadmill (Forcelink, The Netherlands) at a speed of 4 km/h. Before data collection, we allowed the subject to habituate to walking on the treadmill. All subjects gave their informed consent and the protocol was approved by the institutions ethical committee.
Experimental setup

Three-dimensional kinematics were collected at 100Hz using 2 Krypton cameras (Nikon Metrology NV, Belgium) placed at both sides of the treadmill. Six technical clusters, each containing three markers, were positioned bilaterally on shank, thigh, pelvis and on the upper trunk. Sixteen individual markers were placed on anatomical landmarks (Fig. 1). Force-plates integrated into the split-belt treadmill measured ground reaction forces and torques at 1000Hz. EMG activity was recorded bilaterally for tibialis anterior (TA), gastrocnemius lateralis (LGAS), soleus (SOL), vastus lateralis (LVAS), rectus femoris (RF), biceps femoris (BF) and semitendinosus (ST) using a wireless EMG system (Zero-wire EMG, Aurion, Italy) at 1000 Hz (Fig. 2A).

Data processing and data analysis

To process the kinematic data, a dedicated workflow in OpenSim was used (Delp et al. 2007):

1. A generic musculoskeletal model with 27 degrees of freedom and 92 Hill-type muscle-tendon actuators was scaled to match the anthropometry of the subject using the marker positions during a static trial.

2. A Kalman smoothing algorithm was used to calculate the joint angles during walking using the marker trajectories and based on the musculoskeletal model definition (De Groote et al. 2008, not part of the OpenSim workflow) (Fig. 3A).

3. An inverse dynamics procedure was used to calculate the joint moments (Fig. 3B) and powers (Fig. 3C) at hip, knee and ankle.

The raw EMG signal was band-pass filtered between 10-500Hz using a fourth order digital Butterworth filter and RMS was calculated using a 50 ms time window.

All data was time normalized and expressed with respect to the gait cycle. Kinetic data was normalized to body weight. Correspondence of the kinematics, kinetics and EMG curves for FW
and BW was evaluated statistically using a Pearson’s correlation analysis. Coefficient of variation (CV) scores were calculated for all joint moments similar to Winter et al. (1989).

**Muscle driven simulations and perturbation analysis**

To quantify the contributions of the individual muscles and gravity to the acceleration of the body COM during both FW and BW, we generated subject-specific simulations for both conditions. For FW, each simulation started with ipsilateral heel contact (iHC) and ended with toe off (iTO). Loading response (LR) and single stance (SS) were analyzed for the ipsilateral limb, whereas preswing (PSW) and swing (SW) for the contralateral side (Fig. 1).

For BW, simulation started with ipsilateral toe contact (iTC) and ended with heel off (iHO). However, all BW data were time-reversed i.e. presented from iHO to ipsilateral iTC, followed by swing. This procedure therefore relates phases with similar kinematics in FW and BW. Therefore, for BW, SS and PSW were analyzed for the ipsilateral side, while SW and LR were analyzed for the contralateral side.

Based on the previously described workflow in OpenSim, the muscle driven simulations were generated:

1. To reduce dynamic inconsistencies between the model kinematics and the measured ground reaction forces, a residual reduction algorithm (RRA) was used (Thelen and Anderson 2006).
2. Computed Muscle Control (CMC) was used to compute a set of muscle excitations needed to track the experimental walking task (Thelen and Anderson 2006). After amplitude normalization, measured EMG and calculated muscle activations were visually verified (Fig. 2A-B).
3. A fixed-force perturbation analysis (Liu et al. 2006) computed the contribution of a specific muscle or gravity to the horizontal and vertical acceleration of the COM: the force of the muscle was increased with 1N and the equations of motion were integrated forward over a time window of 0.03 seconds, using a 10 ms time step. To test the validity of the simulations, the summed
contributions of all muscles and gravity to the acceleration of the COM were compared to the acceleration of the COM in the reference simulation (Fig. 4).

(7) In a post processing step, the contributions (muscles or gravity) that generated ≥80% of the horizontal and vertical acceleration in each of the phases were identified and averaged over all subjects. Contributions of smaller muscles with similar function were summed; GMED is the summed function of the three parts of the gluteus medius, GMAX includes the different parts of gluteus maximus. Dorsiflexors (DF) consist of contributions from tibiaalis anterior, extensor digitorum and extensor hallucis; GAS consists of the medial and lateral part of the gastrocnemius, VAS are the combined accelerations of vastus lateralis, intermedius and medialis, OPF (other plantarflexors) are tibiaalis posterior, flexor digitorum/hallucis, peroneus longus/brevis. ILIPSO are the combined contribution of iliacus and psoas. Relevant contributions were also found for biceps femoris short head (BFsh) and semimembranosus and tendinosus (SM+ST).

(8) Significance of differences in % muscle contributions between FW and BW were statistically assessed using a Wilcoxon’s test for matched pairs (Statistica, Statsoft Inc, USA).

RESULTS

Experimental data collection

The experimental data on FW and BW on which the simulations were based will be presented first.

Kinematics

Hip and knee joint angles correlate highly (respectively r=0.99 and r=0.95) between FW and BW, while correlation of ankle joint angle is somewhat lower (r=0.65, Fig. 3A).
Ankle and knee moments during FW and BW are highly correlated (respectively r=0.99 and r=0.73). For the hip joint (r=0.54) the correlation is less pronounced (Fig. 3B). BW joint moments show higher CV scores than FW (hip: 79.0 vs. 53.6 %, knee: 129.3 vs. 68.0 %, ankle: 69.2 vs. 31.8 %).

Joint powers during FW and BW are highly correlated for the ankle (r=-0.86) and knee (r=-0.93). Similar to the hip moments, the power in the hip joint shows a lower correlation (r=-0.63) (Fig. 3C).

EMG

Average normalized RMS profiles of BF and ST show a high correlation between FW and BW (r=0.8 and r=0.91). Lower correlations are found for GAS (r=0.39) and SOL (r=0.27). Limited agreement is found for the muscle activity of RF (r=0.16), VAS (r=0.15) and especially TA (r=0.09) (Fig. 2A).

Calculated muscle contributions

In Figure 5, the time evolution of the contribution to horizontal and vertical as well as the combined acceleration over stance phase is presented for specific muscles of the lower limbs. Muscle contributions to horizontal acceleration of the COM are similar for FW and BW. However, muscles responsible for acceleration in FW decelerate BW and muscles that impede progression in FW, contribute to acceleration in BW. These basic results are summarized in Figure 6, based on the calculated percentage of contribution of the various muscles to horizontal accelerations or decelerations of COM and to the vertical accelerations or decelerations of COM (Fig. 7).

Horizontal acceleration (Fig. 6)

Forward walking
During double-limb support of FW, the plantarflexors of the preswing limb contribute most to accelerating the COM (GAS: 19.4 %, SOL: 19.1 %). This is further supported bilaterally by the hamstrings (LR: 12 %, PSW: 7.8 %) and iliopsoas during PSW (7.56 %). During loading response, the dorsiflexors first decelerate the COM immediately after heel contact till foot-flat (-7.6%, Fig. 5, left pane), but then contribute to forward acceleration (14.25 %). Deceleration is provided by the vasti during loading response (-20.7 %) and to a lesser extent during preswing (-11.9 %, Fig. 5, left pane), as well as by RF of both limbs (LR & PSW: -9.3 %) and soleus during loading response (-9.4 %). Additional deceleration is induced by the dorsiflexors of the preswing limb (-9.6 %) and to a lesser extent gravity (-4 %).

During single-limb support of FW, gastrocnemius decelerates progression of the stance limb during the first half of single-limb support (-11.1 %), but then forcefully accelerates the COM (13.6 %, Fig. 5, left pane). This acceleration is supported by the hamstrings (16.6 %), gravity (13.5 %), dorsiflexors (11.1 %), iliopsoas (10.2 %) and gluteus medius (9.9 %). On the swing side, only iliopsoas (6.1 %) contributes substantially to acceleration. Deceleration of the COM is induced by the stance limb quadriceps (RF: -23.4 %, VAS: -15.2 %), soleus (-21.9 %) and the other plantarflexors (-3.9 %). Swing limb gluteus medius (-4.7 %) and dorsiflexors (-4.1 %) further support this.

**Backward walking**

During double-limb support of BW, the function of dorsiflexors during PSW (22.1 %) and vasti during LR (18.7 %) is to accelerate the COM. This is assisted by bilateral contributions of the rectus femoris (PSW: 9.4 %, LR: 6.6 %) and the vasti during PSW (8.6 %). Smaller contribution of gravity (3.2 %) is present as well. Plantarflexors (GAS:-21.2 %, SOL: -13.2 %) decelerate the COM during LR, assisted bilaterally by the hamstrings (PSW: -9.2 %, LR: -9.5 %).
and iliopsoas (LR & PSW: -4.3 %). Gastrocnemius (-8.2 %) and soleus (-6.6 %) also decelerate the COM during PSW.

During single-limb support of BW, soleus of the stance limb is the main accelerator of the COM (26.7 %) assisted by the knee extensors (RF: 14.8 %, VAS: 13.6 %) and gastrocnemius (12.5 %). Swing limb gluteus medius (3.1 %) has a minor contribution. Stance limb dorsiflexors (-20.7 %) are the main decelerators of the COM, assisted by the hamstrings (-13.9 %), gluteus medius (-14.4 %), mono-articular hip extensors (GMAX: -5.7 %) and gravity (-12 %). After its initial contribution to acceleration, gastrocnemius decelerates the COM during most of the remainder of stance (-4.6 %, Fig. 5, left pane). Likewise, dorsiflexors contribute to acceleration (3.9 %) at the end of single stance, after first decelerating COM (Fig. 5, left pane). At the swing limb side, only iliopsoas contributes to decelerating the COM (-3.3 %).

In summary, it appears that most muscles show a reversal in function from FW to BW. Furthermore, this reversal of function did significantly affect the magnitude of the % contribution in most muscles: whereas the amplitudes of some muscles (e.g. soleus) did not differ between FW and BW, for most other muscles the % contribution differed significantly.

**Vertical acceleration (Fig. 7)**

Similar muscles that contribute to horizontal acceleration and deceleration of the COM also provide vertical support in FW and BW. However, in contrast to the horizontal component, a reversal of function almost never occurred. This is illustrated in Figure 7.

**Forward walking**

During double-limb support, the contribution of the plantarflexors in preswing (SOL: 25.3 %, GAS: 14 %) provides the majority of upward acceleration of the COM. In the loading response this is supplemented by the vasti (10.3 %), dorsiflexors (8.7 %), gluteus maximus (6.9 %) and medius (7.1 %). Gravity (-47 %), bilateral iliopsoas (LR: -8.6 %, PSW: -7.3 %) and dorsiflexors
(LR: -8.3 %, PSW: -7.2 %) decelerate the COM. During single-limb support, gluteus medius (19.5 %) and plantarflexors (GAS & SOL: 17.6 %) continue to accelerate the body upward, assisted by the knee extensors (RF: 7.3 %, VAS: 7 %) and gluteus maximus (5.1 %). Gravity (-67 %) remains the main decelerator of the COM, assisted by the iliopsoas and dorsiflexors of the stance limb (ILIPSO: -5.4 %, DF: -4 %) and gluteus medius of the swing limb (-6 %).

**Backward walking**

Similar to FW, dorsiflexors during PSW (35.3 %) combined with the plantarflexors (SOL: 16.8 %, GAS: 12.2 %) in LR, produce most of vertical support during double-limb support, assisted by vasti during LR (5.7 %). Plantarflexors during PSW (GAS: -9 %, SOL: -10.8 %) and dorsiflexors (-5.6%) during LR decelerate the COM together with gravity (-47.1 %).

During single-limb support, stance side gluteus medius (22.8 %) and maximus (11.8 %), knee extensors (VAS: 12.3 %, RF: 6.4 %), soleus (13.6 %) and dorsiflexors (11.5 %) account for most of the upward acceleration. Plantarflexors (GAS: -2.7 %, SOL: -3.4 %) continue to decelerate in the single-limb support, assisted by dorsiflexors (-5.2 %), iliopsoas (-7.3 %) and gravity (-57 %). Unlike in FW, iliopsoas only contributed substantially to deceleration in the single-limb support phase.

In summary, a reversal of function for the vertical acceleration was not seen for most muscles. However, there was a significant difference in the percentage contribution for FW and BW e.g. the contribution of the gastrocnemius to vertical acceleration during single support of FW was not confirmed during BW and support provided by dorsiflexors during LR during BW was four times larger compared to FW.
In this study, we investigated the effect of gait direction reversal on the contributions of muscles and gravity to horizontal and vertical accelerations of the COM. Previously, BW was only analyzed using kinematics, kinetics and EMG. Based on these parameters, it was stated that FW is a simple time reversal of BW (see introduction). The present study is the first to test the role of individual muscles in inducing progression and support of the COM using subject-specific simulations based on experimental data for both FW and BW. From a neural control perspective, it seems advantageous that the same muscle can be used for different functions in FW and BW. This would allow the activation pattern to simply time-reverse to produce similar lower limb kinematics patterns that induce opposite accelerations of the center of mass (COM), therefore confirming the suggestions made by Ting et al. (1999) based on the cycling simulations.

The simulations results indeed confirm a time-reversal of the muscle contributions to the horizontal and vertical acceleration of the COM as this was explicitly imposed during the data analysis.

More interestingly, in the horizontal direction, the simulation results clearly show a function reversal: the same muscles induce opposite horizontal accelerations of the COM during FW as compared to BW. This finding confirms the idea that time reversal of a common neural basis can generate the opposite functional demands for both FW and BW. When walking direction changes to BW, some muscle activity profiles are simply time reversed and additionally muscle contributions to horizontal acceleration invert: In the presence of similar muscle activity profiles, the muscle function in the horizontal control of the COM is opposite in FW and BW, with horizontal accelerators becoming decelerators and vice versa. For example, VAS contributes to deceleration of the COM in the entire gait cycle of FW, while it contributes to horizontal acceleration during BW (Fig. 5, left pane). This agrees with previous experimental studies (Flynn
and Soutas-Little 1993; Cipriani et al. 1995). These authors conclude that the eccentric, decelerating contractions of the quadriceps during FW are replaced by an isometric, stabilizing function during single stance and a concentric, accelerating contraction during preswing in BW. The specific role of the gastrocnemius in deceleration during first half of single stance, and to forward acceleration of the COM during the second half of single stance and preswing in FW is reversed in BW. During BW, the muscle contributes to the deceleration of the COM during loading response and preswing, while it contributes to acceleration during single stance. This finding agrees with the experimentally described function of the ankle plantarflexors in decelerating the COM at toe contact and acceleration of the COM during single support by pulling the leg backward around the ankle joint during BW (Winter et al. 1989). Thus, in general, prime horizontal accelerators during FW are prime decelerators during BW and vice versa.

In contrast, no reversal in the contribution of muscles to the vertical acceleration of the COM is found: similar muscles accelerate the body COM upwards in both FW and BW. Indeed, in both walking directions muscle have to oppose gravity. Therefore a reversal in muscle function in the vertical direction would be inappropriate.

An important outcome of the present study is therefore that similar muscles can be used to achieve opposite functional demands at the level of horizontal control of the COM when walking direction is reversed, while the vertical function is maintained. This arrangement simplifies neural control since basically the same automatisms can be used for the two directions, without elaborate need for a separate control. This agrees with the concept of basic neural structures/circuits that drive the neural control of gait. One such type of structure is the spinal CPG, as demonstrated in the early cat work (Graham-Brown 1911). It is thought that these CPGs have the potential to generate FW as well as BW on a treadmill after training (Barbeau et al. 1987; Musienko et al. 2007). This indicates that the same locomotor generators
can be used to control opposite functional demands during FW and BW. In line with this, Musienko et al. (2007) showed that epidural stimulation of segments L4-5 of the spinal cord in the cat elicited well coordinated walking in the hind limbs on a moving treadmill band, irrespective of the direction of the belt movement. Current thinking makes a distinction between a rhythm generating part and a pattern generator (Burke et al. 2001; Ivanenko et al. 2006). Furthermore, a direct link from the rhythm generator to the flexor burst generator was suggested (Duysens 2006).

In humans there is only indirect evidence for CPGs (Duysens and Van de Crommert 1998). Nevertheless, it is reasonable to expect that the same ‘spinal’ automatisms are used for FW and BW (as also proposed by Earhart et al. 2001 and Ivanenko et al. 2008). The best evidence comes from infant stepping, where BW can be generated, despite the absence of mature corticospinal projections (Lamb and Yang 2000).

Exceptions

However, some muscles in our simulations also showed specific contributions independent of the walking direction, i.e. not a simple time and/or function reversal. For instance, our simulation results show that TA and VAS have similar functions during both FW and BW, suggesting that their function does not depend on a reversal of their control: Despite their role as prime accelerators of the COM during loading response in FW, dorsiflexors (including TA) are also the main accelerators of the COM during BW preswing (Fig. 6, left bottom pane). This agrees with the dominant role of the dorsiflexors in propulsion of the COM during BW as previously described in experimental studies (Thorstensson 1986). The timing of VAS contribution to vertical acceleration might indicate that a time reversal for this extensor muscle would not be
necessary, because in both conditions peak contributions appear during loading response (Fig. 5, middle pane).

In these cases additional (supraspinal) inputs have to be taken into consideration to enforce the observed function at the level of the COM. This is related to the very different control of the ankle in FW and BW. During BW, VAS activations and functions deviate strongly from a simple reversed pattern. This differential role of VAS can be linked to the modified control strategy at the ankle due to the modified foot roll off during BW (i.e. an inverted plantigrade-digitigrade sequence) on the one hand, but also to the anatomical asymmetry of the foot and leg muscles along the anteroposterior axis. For instance, anterior thigh muscles (VAS + RF) and posterior calf muscle (GAS, SOL) have a higher mass and strength than muscles on the respective other sides (Grasso et al. 1998, Lacquaniti et al. 1999). This can explain why the minimal propulsive role of the triceps surae during BW is compensated by a large contribution of the VAS (see also Ivanenko et al. 2008). Similarly TA does not show a simple reversal. The absence of heel strike in BW strongly affects the role of TA and therefore imposes specific demands to the control of the ankle in BW. This control is likely to come from the motor cortex. Indeed, an important contribution of the motor cortex to the control of TA was previously suggested by Dietz (1992).

Previous studies on backward locomotion in lampreys (Zelenin 2011) and cats (Zelenin et al. 2011) also show supraspinal participation in both forward and backward locomotion. It was suggested that supraspinal neurons are involved in activating the CPGs in forward or backward mode (Zelenin 2011), thereby generating the basic locomotor pattern. In addition, Zelenin et al. (2011) suggested that cortical input is responsible for the reconfiguration of the spinal networks controlling forward and backward locomotion. This modulation of cortical neurons would allow that the same spinal signals address different muscles in different modes of locomotion or to change the timing of the spinal signals.
Is this also the case in humans? In adults with spinal cord injury, BW can be induced using the remaining spinal circuits, provided some training was given (Grasso et al. 2004). However, in the latter study it was found that there was no transfer of learning to walk FW on the performance of (untrained) BW indicating that BW may require a “higher level of supraspinal control” (see also Schneider and Capaday 2003). Similarly, Choi and Bastian (2007) failed to find transfer of FW adaptation on BW, therefore suggesting that in humans there may be more differentiation in the control of FW and BW. This indicates increased cortical control of some muscles such as TA and VAS in human gait.

**Experimental data**

The time reversal of the muscle contribution to the control of the acceleration of the COM with walking direction relate to the observed time reversal of the joint kinematics and kinetics during FW and BW. In agreement with Winter et al. (1989), good correlations of the ankle moments were found between BW and FW, more pronounced differences in joint moments of hip and knee joint are reported here compared to Winter et al. (1989). These differences in joint moments of the proximal joints induce the reversal of joint accelerations and change individual muscle function from energy generator to absorber between FW and BW. Evidence of an identical common neural structure responsible for both walking conditions was previously based on the time reversal of the EMG profiles. Our experimental EMG data during BW and FW are largely in agreement with previously published studies. In agreement with Winter et al. (1989), TA, GAS, SOL and hamstrings exhibit very similar EMG patterns in FW and BW. However, quadriceps shows a prolonged burst of activity during the stance phase in BW, as previously described by Thorstensson (1986).
Methodological considerations

For a proper comparison in gait studies one usually chooses to control either for constant speed or constant cadence. In the present study we compared FW and BW at the same speed on a treadmill. This means that cadence could be different. In fact, this was verified and a Wilcoxon test for matched pairs showed indeed a significant difference in cadence between FW and BW (55.1 ± 2.4 and 62.0 ± 3.4 strides/min respectively; p = 0.004).

During BW, an increase in stride frequency is needed to maintain the predefined walking speed, in the presence of a shorter stride length. Shorter stride lengths in BW as compared to FW were previously reported both for treadmill (Vilensky et al. 1987) as for overground BW (Grasso et al. 1998). Previous studies (Umberger and Martin 2007) have shown that stride frequency influences joint kinematics and kinetics. Hence it can be expected that it will also have an effect on the calculated muscle contributions. However, this would only be important for the calculation of the absolute muscle contributions. In the present study we evaluated the relative % contribution rather than the absolute muscle contributions. Therefore we feel that the influence of stride frequency on the interpretation of our results is negligible.

Another potential limitation of this study is the use of a treadmill instead of overground walking. While several studies investigated temporal gait parameters, joint kinematics, joint kinetics and muscle activation patterns between overground and treadmill FW, their results were often inconclusive. For instance, Lee and Hidler (2008) reported differences in joint powers, moments and muscle activations between overground and treadmill FW; however the overall patterns were quite similar. Riley et al. (2007) found significant differences in kinematics and kinetics, nevertheless these differences were within the range of variability. Therefore, they concluded that overground and treadmill FW are qualitatively and quantitatively quite similar for FW. For BW there are no studies that compared overground and treadmill walking within the
same subjects but some potential differences in kinematics were suggested. Winter et al. (1989) reported a bias towards ankle dorsiflexion during half of the stride cycle during overground BW, while this bias was shown during the entire gait cycle in treadmill BW (Thorstensson 1986, Vilensky et al. 1987). Strikingly, our ankle kinematics, obtained on a treadmill, show more agreement with the ankle angles during overground BW reported by Winter et al. (1989) than with the previous treadmill data (Thorstensson 1986, Vilensky et al. 1987). Hence, if differences exist they are minor and we therefore feel that the extrapolation to overground walking is still quite feasible.

Conclusions

The present simulation results allow us therefore to conclude that during FW and BW the muscle activity profiles are either time-reversed or modulated so that each muscle exhibits a combined control of the horizontal and vertical acceleration of the body COM. Hence, this study basically supports the concept of one neural structure capable of inducing direction reversal by simple modulation of a time-reversed muscle activity profile, although it is clear that additional control is required (presumably from supraspinal sources) to meet the specific constraints of BW, in particular those related to the ankle joint.
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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).
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Fig. 1. Musculoskeletal model used to generate subject-specific simulations of forward and backward walking.

Six technical clusters, each containing three markers, were positioned on shank, thigh, pelvis and upper trunk and 16 individual markers were placed on anatomical landmarks (bilateral heel, midfoot, malleolus lateralis, epicondylus lateralis femoris, spina iliaca anterior superior, acromion, epicondylus lateralis humeri and between processus styloideus ulnaris and radialis). The relation between the clusters and the anatomical markers was defined during an anatomical calibration procedure in which the position of selective anatomical points (malleolus lateralis/medialis, epicondylus lateralis/medialis femoris, spina iliaca anterior superior, sternum and acromion) was registered to the cluster position using a measurement probe. The simulation of forward walking starts with ipsilateral heel contact (HC) and ends at ipsilateral toe off (TO). Backward walking starts with ipsilateral toe contact (TC) and ends with ipsilateral heel off (HO). The stance phase was further divided in the first double-limb support phase (DLS), single-limb support (SLS) and second double-limb support. Therefore, for FW, loading response (LR) and single stance (SS) were analyzed for the ipsilateral limb, whereas preswing (PSW) and swing (SW) for the contralateral side. For BW, SS and PSW were analyzed for the ipsilateral side, while SW and LR were analyzed for the contralateral side.

Fig. 2. EMG and calculated muscle activations during forward and backward walking.

A: Normalized RMS value of the major lower limb muscles measured over the gait cycle. B: Average calculated muscle activities during the simulations of FW and BW over the gait cycle. The grey line and shaded area indicate average ± 1SD of the signal during FW. Average value during BW is superimposed in black. The shaded bars indicate periods of double-limb support.
Muscle EMG/activations are shown for biceps femoris (BF, long head: BFlh), semitendinosus (ST), rectus femoris (RF), lateral vastus (LVAS), lateral gastrocnemius (LGAS), soleus (SOL) and tibialis anterior (TA).

**Fig. 3. Kinematics and kinetics of hip, knee and ankle joint during forward and backward walking.**

Average joint angles ($A$), joint moments ($B$) and joint powers ($C$) are shown for all 10 subjects. The gray line and shaded area indicate average ± 1SD during forward walking, the black line shows the average during backward walking. The shaded bars indicate periods of double-limb support.

**Fig. 4. Superposition.**

Comparison of the summed contributions of muscles and gravity to the horizontal and vertical acceleration of the COM and the unperturbed acceleration of the COM in forward (left pane) and backward walking (right pane). The grey line and shaded area indicate average ± 1SD of the unperturbed acceleration. Average value of the summed contributions of individual muscles and gravity is superimposed in black. The shaded bars indicate periods of double-limb support.

**Fig. 5. Muscle contributions to horizontal and vertical acceleration of the COM.**

Average muscle contributions to the horizontal (left pane) and vertical (middle pane) acceleration of the COM over the stance phase as well as representation of the combined contributions (right pane) during forward and backward walking. The grey line and shaded area indicates average ± 1SD of the signal during FW. Average value during BW is superimposed in black. The shaded bars indicate periods of double-limb support.
**Fig. 6. Muscle contribution to horizontal acceleration.**

Percentage (%) muscle contributions and gravity to horizontal deceleration and acceleration of the COM (average ± 1 SD), during double- and single-limb support of forward (light grey) and backward walking (dark grey). Contributions of muscles below the predefined threshold for forward walking (white) and backward walking (black) are shown for comparison. The left panes relate to the muscle contribution during double-limb support with the limb in loading response being presented in the bottom pane and the limb in preswing being presented in the upper pane for forward walking, and vice versa for backward walking. The right panes relate to the muscle contribution during single-limb support with the limb in single stance being presented in the bottom pane and the limb in swing being presented in the upper pane for both forward and backward walking. Statistically significant differences (p>0.05) are indicated with *.

**Fig. 7. Muscle contribution to vertical accelerations.**

Percentage (%) muscle contributions to vertical deceleration and acceleration of the COM (average ± 1 SD), during double- and single-limb support of forward (light grey) and backward walking (dark grey). Contributions of muscles that were below the predefined threshold for forward walking (white) and backward walking (black) are shown for comparison. The top panes relate to the muscle contribution during double-limb support with the limb in loading response being presented in the left pane and the limb in preswing being presented in the right pane for FW and vice versa for BW. The bottom panes relate to the muscle contribution during single-limb support with the limb in single stance being presented in the left pane and the
limb in swing being presented in the right pane for both FW and BW. Statistically significant differences (p>0.05) are indicated with *.
FIGURE 1

Joint angle (deg)

knee

% gait cycle

FORWARD

1st DLS  SLS  2nd DLS

HC TO  cTO  cHC  iHC  cTO  cHC  iHC

FW  BACKWARD  BW

TC  HO  HO  TC

% gait cycle

Joint angle (deg)

knee

% gait cycle

FORWARD

BACKWARD
FIGURE 2

A

EMG

B

activations

% gait cycle

% gait cycle

% gait cycle

% gait cycle
FIGURE 4

[Graph showing horizontal and vertical acceleration for FW and BW conditions with muscle+gravity and unperturbed lines.]

% stance phase

HC

TO

HC

TO
FIGURE 5
FIGURE 6

Double-limb support

Loading response

Preswing

% muscle contribution

Single-limb support

Loading response

Preswing

% muscle contribution

FW

BW

DF
OPF
SOL
GAS
VAS
RF
ILIPO
GMAX
BFsh
SM + ST
GMED

% muscle contribution

FW

BW

GRAV

← dec

acc →

% muscle contribution

FW

BW

← dec

acc →

% muscle contribution

FW

BW