RESEARCH ARTICLE

Optimal walking speed following changes in limb geometry

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SUMMARY

The principle of dynamic similarity states that the optimal walking speeds of geometrically similar animals are independent of size when speed is normalized to the dimensionless Froude number (Fr). Furthermore, various studies have shown similar dimensionless optimal speed ($Fr \sim 0.25$) for animals with quite different limb geometries. Here, we wondered whether the optimal walking speed of humans depends solely on total limb length or whether limb segment proportions play an essential role. If optimal walking speed solely depends on the limb length then, when subjects walk on stilts, they should consume less metabolic energy at a faster optimal speed than when they walk without stilts. To test this prediction, we compared kinematics, electromyographic activity and oxygen consumption in adults walking on a treadmill at different speeds with and without articulated stilts that artificially elongated the shank segment by 40 cm. Walking on stilts involved a non-linear reorganization of kinematic and electromyography patterns. In particular, we found a significant increase in the alternating activity of proximal flexors–extensors during the swing phase, despite significantly shorter normalized stride lengths. The minimal metabolic cost per unit distance walked with stilts occurred at roughly the same absolute speed, corresponding to a lower Fr number ($Fr \sim 0.17$) than in normal walking ($Fr \sim 0.25$). These findings are consistent with an important role of limb geometry optimization and kinematic coordination strategies in minimizing the energy expenditure of human walking.

Key words: Froude number, $\dot{V}_{O_2}$, locomotion, stilts.

INTRODUCTION

The 'dynamic similarity' theory has been developed to account for similarities in animal behaviour, allowing invariant features of locomotion in the same gravity field to be characterized (Alexander, 1989). The theory states that geometrically similar animals will walk and run similarly at the same Froude (Fr) number, defined as:

$$Fr = \frac{V^2}{gL} \, , \qquad (1)$$

where V is the speed of locomotion, g is the acceleration due to gravity and L is the leg length. Because it accounts for body size, the Fr number is particularly useful for comparing walking animals of different sizes at the same g (Saibene and Minetti, 2003). Even though the theory emphasizes geometrical similarities for comparing animal motion, Alexander and Jayes (Alexander and Jayes, 1983) went on to show that animals as diverse as rhinoceroses and humans move in essentially dynamically similar ways, as do other animals of varying sizes (Alexander, 1984; Bullimore and Burn, 2004; Griffin et al., 2004; Saibene and Minetti, 2003).

Consistent with this theory, it has been shown that humans and quadrupeds change from walk to run or trot at the same Fr number, close to 0.5 (Alexander, 1989; Biewener, 2006). Adults of average height as well as children (Cavagna et al., 1983; DeJaeger et al., 2001), people with dwarfism (Minetti et al., 2000) and pygmies (Minetti et al., 1994) all have optimal walking speeds that correspond

to the same Fr number, 0.25. Walking speed is optimal when the recovery of energy due to the pendulum mechanism is maximal, and the metabolic cost is minimal (Saibene and Minetti, 2003).

Although there is a common usage of the Fr number for animals with different limb segment configurations (Saibene and Minetti, 2003), the question remains as to whether the most relevant information for calculating the optimal walking speed relies on the total limb length (Eqn 1) or whether compensatory 'distortions' are important for counteracting the effects of size differences (Bullimore and Burn, 2006; Kramer and Sarton-Miller, 2008). The first possibility would imply that the optimal walking speed would not differ following disproportional changes in the limb length if appropriate corrections were made for calculating the Fr number (Eqn 1). If, in contrast, the optimal speed changes, we would argue that it is more likely that compensatory mechanisms play an important role in the adjustment of the limb geometry and optimal energetics of terrestrial locomotion in accordance with the Fr number of 0.25. In addition, such investigations may have important implications related to the construction of biologically inspired robots (Pfeifer et al., 2007) and clinical studies (Dominici et al., 2009; Kuo and Donelan, 2010).

While leg length is most commonly used for computing the Fr number, the importance of a particular limb segment configuration has not been investigated. The issue of evolutionarily adopted 'optimization' of body geometry has also recently received attention

with regard to the so-called locomotor body scheme (Dominici et al., 2009; Pearson and Gramlich, 2010; Ivanenko et al., 2011a). Walking on stilts represents an interesting example of gait adaptation and reorganization of locomotor patterns (Vaida et al., 1981; Wittlinger et al., 2006; Chiou et al., 2008; Akram and Frank, 2009; Dominici et al., 2009; Pan et al., 2009; Wu et al., 2009; Singer et al., 2011). The energetics of walking may also be affected by changes in the limb segment proportions. To our knowledge, there is only one previous study that has reported oxygen consumption measurements for stilt walking (Vaida et al., 1981) and those authors did not specifically address the issue of the optimal Fr number. Moreover, they used 'classic' stilts with restrained ankle flexion. Therefore, we cannot draw definitive conclusions from their study about gait optimality after disproportional changes in limb geometry.

To examine whether modifications in the limb segment proportions affect the optimal Fr number for walking (Fr ~0.25), we studied how the relative changes in limb geometry alter metabolically optimal walking speed and electromyography (EMG) patterns. To this end, we compared locomotor patterns and oxygen consumption rates in adults walking at different speeds normally and on specially designed stilts imitating elongation of the shank segments.

MATERIALS AND METHODS
Subjects
Kinematic, metabolic and EMG data were collected from 10 healthy adult volunteers (3 females and 7 males, age 24±3 years, mass 71±9 kg, height 1.76±0.06 m, leg length 0.94±0.05 m, means ± s.d.). All subjects were free from documented neurological or metabolic impairment. The experimental procedure was explained to the subjects and they signed an informed consent form approved by the local ethics committee of the Université Libre de Bruxelles. The procedure conformed to the directives of the Declaration of Helsinki and involved no discomfort or inherent health risks.

Stilts
We sought to use stilt walking as a model to uncover modifications in gait dynamics caused by changes in lower limb segment lengths and proportions. To simulate the biomechanical consequences of a disproportional increase in leg length, we asked adult subjects to perform the experimental tasks while walking on stilts (Giraffe Stilts™ 40 cm height, 1.5 kg each; Plasteringsupplies, Lysterfield, VIC, Australia) that displaced the 'functional' axis of ankle joint rotation during stance and thus elongated the 'functional' length of the shank segment. This type of stilt provided both mobility at the ankle joint and a stable base of support, so that all participants could stand and walk. The stilt for each leg consisted of a long stick (leg support strut) and a rotational parallelepiped attached to its lower part. Its four axes of rotation represented hinge joints, so that rotation of the parallelepiped was possible only in the sagittal plane (Fig. 1A). Contact with the ground occurred at the lower part (floor plate) of the parallelepiped. The shank segment was fixed to the upper leg support strut using a wide belt, while the foot was fixed to the footplate of the rotational parallelepiped, allowing rotary motion of the ankle joint [see Dominici et al. and Singer et al. for a detailed description of this type of stilt (Dominici et al., 2009; Singer et al., 2011)]. The 40 cm shank elongation caused the total limb length to be increased accordingly.

Experimental procedure
Before the test session the subjects performed two training sessions, in which they walked at different self-selected speeds on a treadmill (Cosmed, Rome, Italy) in order to get used to first normal treadmill walking and second stilt walking. To avoid injury in the case of a fall, subjects were secured to the laboratory ceiling by means of a light harness. However, no actual falls occurred during this experiment. These training sessions lasted for approximately 20 min, until the subjects felt comfortable, exceeding the minimum treadmill habituation time of 10 min recommended for healthy subjects (Van de Putte et al., 2006). At the end of each training session, the speed of the treadmill was progressively increased in steps of 0.2 km h⁻¹ by the experimenter, until the moment the subject spontaneously started to run, in the case of normal waking, or until the subject could not match the belt speed in the case of stilt walking. This speed will be referred to as 'maximum walking speed' (V_{max}) for each subject.

During the test session, the subjects were asked to walk on the treadmill at different constant speeds (2, 3, 4, 5, 6, 7 and 8 km h⁻¹ until reaching V_{max}) presented in a random order across the subjects and separated by rest periods long enough to allow the oxygen consumption and heart rate to return to resting values. These resting values were determined for each subject by computing the mean rate of oxygen consumption over 2 min after a 15 min rest period following the training session, while the subject was sitting comfortably on a chair. The same procedure was repeated with each subject wearing stilts. During the resting and test sessions, the metabolic data were continuously collected. For each speed level, the subjects walked for at least 3 min until a steady metabolic state was reached. Our criterion for steady state was no more than 10% variance in the rate of oxygen consumption between successive 20 s intervals.

The kinematics and EMG data were collected for 10 gait cycles during the last minute of metabolic steady-state acquisition. At the
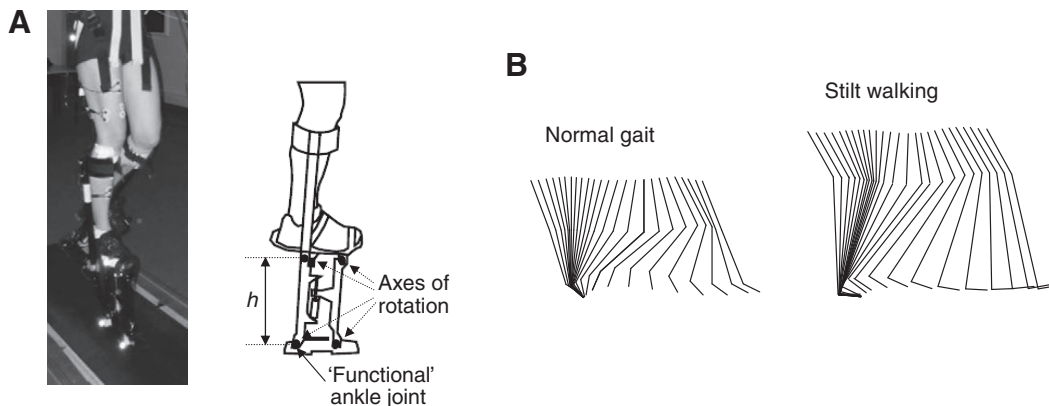
Fig. 1. Experimental conditions. (A) Schematic view of stilts imitating shank elongation. Shank segment elongation was emulated by attaching a rotational parallelepiped-like support of height (*h*) 40 cm so that the functional axis of ankle rotation was displaced downward to a distal part of the stilts (schematically shown on the right). The picture on the left illustrates walking on stilts. (B) Stick diagrams (one stride) of walking without and with stilts at 5 km h⁻¹ in one representative subject.

end of the recording session, we performed anthropometric measurements on each subject. These included the mass and stature of the subject, and the length and circumference of the main segments of the body (Zatsiorsky et al., 1990).

Metabolic energy cost

Breath-by-breath rates of O_2 consumption and CO_2 production ($\dot{V}_{O_2}$ and $\dot{V}_{CO_2}$) were measured using an open-circuit breath analyser (MedGraphics CPX Express System, MedGraphics, St Paul, MN, USA). The subjects were asked to breathe through a lightweight pneumotach mouthpiece. BreezeSuite Software (MedGraphics) allowed immediate on-screen access to the collected values, adjusted for standard temperature and pressure conditions. Only trials with a respiratory exchange ratio (the ratio between $\dot{V}_{CO_2}$ and $\dot{V}_{O_2}$) below 1 were retained and analysed (McArdle et al., 1996).

The metabolic cost of transport (ml O_2 kg^{-1} m^{-1}) was determined for each subject and each speed by dividing the rate of O_2 consumption in ml kg^{-1} min^{-1} by the velocity expressed in m min^{-1}. In the case of walking on stilts, we normalized the metabolic cost to overall body mass, including the mass of the stilts. Based on these metabolic profiles as a function of walking speed, for each subject we determined the optimal walking speed (V_{opt}), for which the oxygen consumption per unit distance (O_2 cost) was minimal.

Gait kinematics

Gait kinematics was acquired by means of the ELITE Biomech opto-electronic system (BTS, Milan, Italy) at a sampling rate of 100 Hz, including six infrared cameras placed at a distance of ~3 m around the treadmill. Retro-reflective passive markers were fixed on the skin overlying the following bony landmarks on both sides of the body: lateral malleolus (LM), fifth metatarsal head (MT), lateral condyle of the knee (LE), greater trochanter (GT) and tubercule of the anterosuperior iliac crest (IL). In the case of walking on stilts, two markers were also placed on the distal part of the stilts imitating the foot segment, to measure its rotation relative to the shank segment. The temporal gait cycle events, namely heel strike (HS) and toe off (TO), were determined using SMART310 analysis software (BTS), from the kinematics of the LM (anterior–posterior maximum) and the MT (anterior–posterior minimum) markers, respectively. The same software was used to compute the elevation angles of the thigh (GT–LE), shank (LE–LM) and foot (LM–MT) segments relative to the vertical (Cheron et al., 2001).

EMG activity

Surface EMG activity of the following muscles was measured using a telemetry system (Telemg, BTS): tibialis anterior (TA), gastrocnemius medialis (MG), vastus lateralis (VL), biceps femoris (BF), rectus femoris (RF) and semi-tendinosus (ST). To reduce skin resistance, the electrode location was prepared by shaving and light abrasion of the skin followed by cleaning with isopropyl alcohol. Muscle activity was recorded by using pairs of silver–silver chloride electrodes positioned at the approximate centre of the muscle belly with an inter-electrode distance of 2 cm (Medi-Trace, Graphic Controls Corporation, Yonkers, NY, USA). Raw EMG signals were amplified (×1000) and digitized at 1000 Hz, full-wave rectified, high-pass filtered with a cut-off frequency of 30 Hz and smoothed by means of a third-order averaging filter with a time constant of 20 ms.

EMG patterns were time-normalized to the percentage of stride for each subject. EMG amplitudes during all walking conditions were normalized by setting the maximum amplitude for each muscle to 100% for walking at 5 km h^{-1}. This amplitude normalization allowed for inter-muscular and inter-subject comparisons of EMG amplitude.

Statistics

Statistical analysis was performed using Statistica software (Statsoft, www.statsoft.com). Repeated measures (RM) ANOVA was used to compare the amplitude of angular motion and EMG activity during walking with and without stilts at different absolute speeds. Paired *t*-tests were used to compare changes in the metabolically optimal dimensionless speed of progression (*Fr* number). Reported results are considered significant for $P<0.05$. Descriptive statistics show means ± s.d.

RESULTS
Kinematic and EMG patterns during stilt walking

Fig. 2 illustrates changes in the general gait parameters during walking on stilts relative to those during normal gait (without stilts) when compared at the same absolute speeds. RM ANOVA detected which parameters were significantly different between conditions (with/without stilts, criterion of $P<0.05$). Namely, with stilts the cycle duration increased, the relative stance duration decreased and the stride length increased (Fig. 2). Nevertheless, it is worth emphasizing that increases in stride length were significantly smaller than those predicted from the proportional increment of the leg length (Fig. 2C, dashed line), consistent with previous studies (Dominici et al., 2009; Singer et al., 2011). All 10 subjects managed to walk on stilts up to 6 km h^{-1}, while only 8 of them reached $V_{max} \geq 7$ km h^{-1} and only one subject could walk on stilts at 8 km h^{-1}. Normal walking was recorded in all subjects at 7 km h^{-1} and in 7 subjects at 8 km h^{-1}.

The analysis of gait kinematics (Fig. 3) revealed that shank and foot segments oscillated drastically less during walking on stilts than
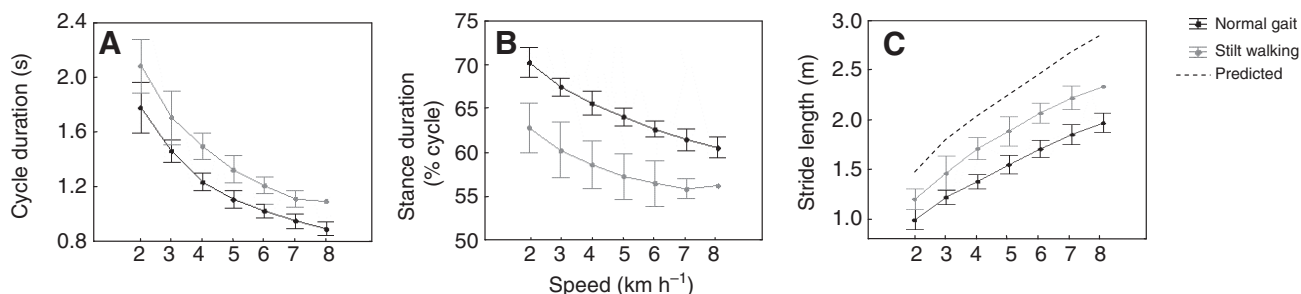

Fig. 2. General gait parameters (A, cycle duration; B, stance duration; C, stride length) during walking with and without stilts at different speeds. The dashed line in C represents the stride lengths for stilt walking predicted from the proportional increment of the leg length due to stilt wearing.
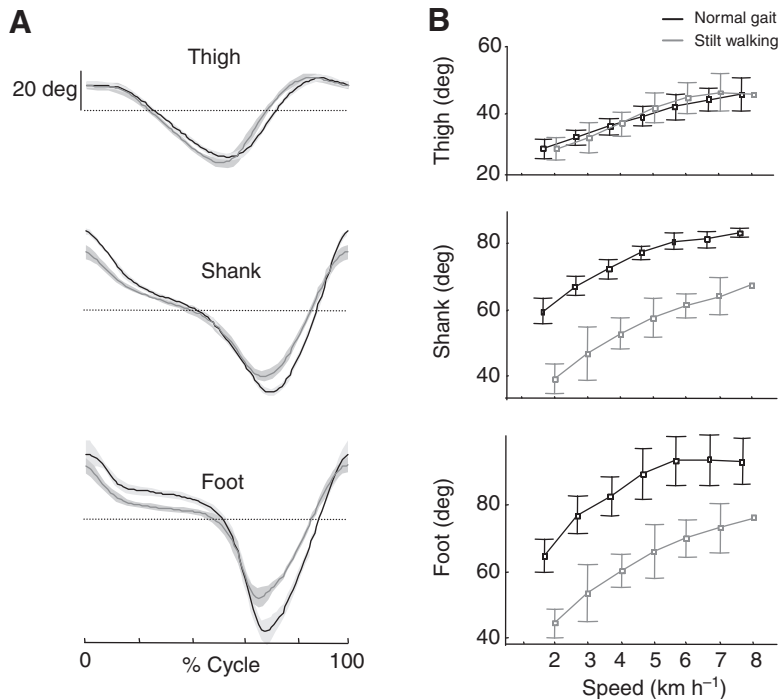
Fig. 3. Changes in the kinematic patterns during stilt walking with respect to normal gait. (A) Ensemble averaged (±s.d.) segment elevation angles in one subject walking at 5 km h⁻¹ with and without stilts. (B) Peak-to-peak amplitude (±s.d., N=10) of elevation angles as a function of walking speed. Note the significantly smaller oscillations of the distal segments with stilts (A,B).

in normal walking ($P<0.001$ for both segments), whereas the amplitude of thigh motion was comparable in the two walking conditions ($P>0.05$). In summary, the intersegmental coordination significantly changed when wearing stilts, providing a possible explanation for the modification of the intrinsic relationship between stride length and limb length (Fig. 2C).

EMG activity demonstrated non-linear changes comparable with previous studies (Dominici et al., 2009; Landy et al., 2009; Wu et al., 2009). An example of ensemble-averaged EMG patterns in one representative subject is shown in Fig. 4A. During stilt walking, smaller movements in the distal segments were accompanied by smaller mean EMG activity in the TA muscle ($P<0.05$), while EMGs of MG and proximal (RF, VL, BF and ST) leg muscles showed larger amplitudes with stilts than without ($P<0.05$) (Fig. 4B).

Metabolic profile (oxygen consumption) for stilt walking
Mean oxygen consumption over 1 min was computed once a steady metabolic state was reached (>3 min after the beginning of the trial on the treadmill). To obtain the metabolic cost of locomotion, the oxygen consumption was divided by the subject's mass and normalized per unit time (Fig. 5A,C) or per unit distance (Fig. 5B,D). The metabolic cost per unit time was somewhat higher during stilt walking and increased faster with dimensionless walking speed (Fig. 5C). Normalization to distance is typically used to assess the optimal speed of locomotion. The normalized O_2 cost normally has a minimum around Fr 0.25 during normal walking (Saibene and Minetti, 2003). Our results confirmed this notion (Fig. 5, mean Fr 0.24); however, they clearly demonstrated significantly lower ($P=0.0005$ paired t-test) optimal dimensionless speeds during stilt walking for all subjects (mean Fr 0.17, Fig. 5D) while the minimum metabolic cost occurred at a similar absolute speed with and without stilts (5.47 and 5.36 km h⁻¹, respectively, Fig. 5B).

The data in Fig. 5 were obtained by normalizing the walking speed to the leg length (the vertical distance between GT and the sole during standing) using the Fr number. Although leg length is commonly used for calculating Fr number (Saibene and Minetti,

2003), other lengths might be more appropriate. For example, the centre of mass (COM) is located higher than the hip joint (approximately at the level of the ilium). Moreover, adding the extra mass of the stilts (2×1.5 kg) to the leg may slightly displace the COM. Therefore, we verified whether the main findings would change significantly after normalization to the distance from the supporting foot to the COM rather than to the limb length. COM was estimated for each subject using anthropometric measurements (Ivanenko et al., 2004), taking into account the weight of the stilts. This procedure shifted the results slightly towards lower Fr numbers (for both normal gait and walking on stilts). However, even following this adjustment, the absolute optimal walking speed was still significantly ($P<0.001$) slower for stilt walking. Thus, our findings (Fig. 5) did not depend on whether normalization was performed on the total limb length (leg + stilt) or on the distance between the foot and COM. Here, we report the results using the limb length normalization as this is commonly accepted in the literature.

DISCUSSION
The results highlight a reorganization of kinematic and EMG patterns during walking on stilts. In particular, prominent modifications occurred in the relative changes of angular segment motion, in agreement with previous studies (Dominici et al., 2009; Singer et al., 2011). The distal segments (shank and foot) showed much smaller oscillations relative to the normal gait, while the proximal thigh segment displayed comparable oscillations (Fig. 3A). As a consequence, the stride length was shorter than that predicted from the proportional increment of the leg length (Fig. 2C, dashed line). We also observed a significant increase of activity of the proximal flexor and extensor muscles (Fig. 4) (see also Landy et al., 2009; Wu et al., 2009). Furthermore, the results clearly demonstrate that the optimal dimensionless walking speed (i.e. the speed at which the metabolic cost per unit distance is minimal) significantly decreased during walking on our stilts (Fig. 5D).
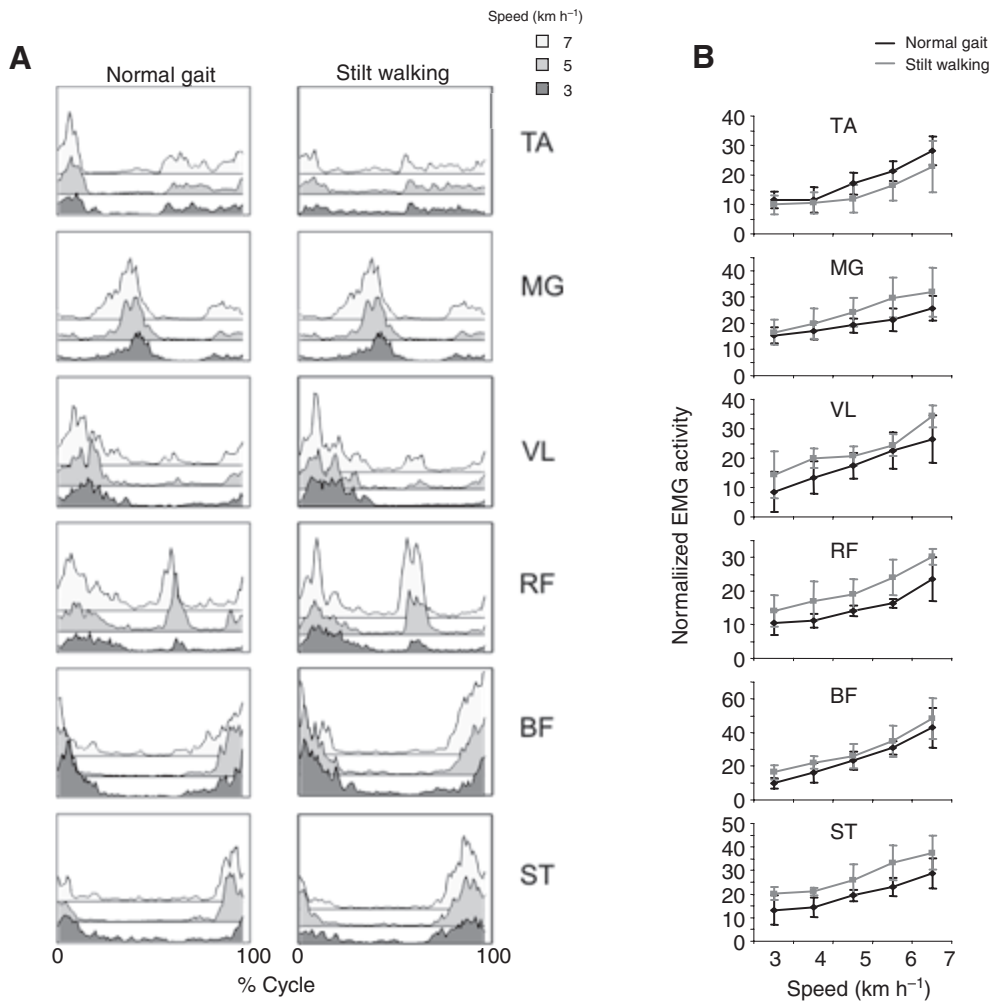
Fig. 4. Electromyography (EMG) activity during stilt walking and normal gait. (A) An example of EMG patterns in one representative subject during walking with and without stilts at different speeds (3, 5 and 7 km h^{-1}). The amplitude of EMG activity for each muscle was normalized to the EMG maximum during normal gait at 5 km h^{-1}. (B) Mean (±s.d.) EMG activity as a function of speed. Note the higher activation of MG and proximal muscles (VL, RF, BF, ST) during stilt walking with respect to normal gait. TA, tibialis anterior; MG, gastrocnemius medialis; VL, vastus lateralis; RF, rectus femoris; BF, biceps femoris; and ST, semi-tendinosus.

All 10 subjects showed a substantial decrement in the metabolically optimal dimensionless speed (from Fr ~0.25 to ~0.15, Fig. 5). These findings are consistent with the preferred walking speed on stilts that often (though not necessarily) corresponds to the most energetically advantageous speed (Saibene and Minetti, 2003). For instance, Chiou and colleagues reported that experienced construction workers tend to walk more slowly using stilts compared with normal walking (Chiou et al., 2008), Singer and colleagues reported similar absolute speeds (Singer et al., 2011), while stilt walking was found to be faster for stilt users in sports or leisure activities (Vaida et al., 1981). It is important to stress, however, the fundamental difference between the classical stilts used by Vaida and colleagues (Vaida et al., 1981) and our stilts. The former are rigid segments, while the latter are articulated at an artificial ankle joint. Even though stilt walking experience may improve performance, in all these studies the 'natural' dimensionless walking speed on stilts was found to be slower than that predicted from the proportional increment in the limb length. Indeed, Vaida and colleagues found only small increments in the absolute preferred and maximal walking speeds (Vaida et al., 1981). Note, however, that their stilts were much longer than ours (1 m vs 40 cm) and they found similar rates of oxygen consumption when wearing stilts, assuming the lower optimal Fr number (Eqn 1). For instance, the natural preferred dimensionless walking speed (Fr) was 2.1 without stilts and only 1.4 with stilts [see tables 1 and 2 in Vaida et al. (Vaida et al., 1981)]. It is also worth noting the significantly shorter

dimensionless stride lengths (Fig. 2C) and inability to walk on stilts at speeds faster than 7 km h^{-1} (Fr ~0.3) for most of our subjects.

In our previous study, we also reported slower walking in adults wearing stilts and in an achondroplastic child after a surgical procedure of shank segment elongation (Dominici et al., 2009). The slower speeds were observed even when the experimenter held the subject's arm in order to increase postural stability and confidence in walking, suggesting that postural instability is unlikely to be the main cause of this phenomenon.

Given the disproportional lengthening of the limb segments, one would expect to detect changes in the locomotor pattern after limb elongation. Indeed, maintaining the same joint angle motion would be unfeasible because this would result in unrealistic anterior–posterior and vertical hip displacements and anatomically impossible trunk deformations [see simulation results in Ivanenko et al. (Ivanenko et al., 2011a)]. Therefore, the neural control system must adapt to the new limb proportions. In fact, all subjects adapted by decreasing oscillations in the distal leg segments (Fig. 3) accompanied by a significant decrement in the optimal dimensionless speed (Fig. 5D). Adding mass (1.5 kg) to the foot may also affect the metabolic rate (Browning et al., 2007), though it is not clear whether the optimal speed would change as well. In addition, in a recent study (Ivanenko et al., 2011b) we found that the dimensionless walk–run transition speed (Fr ~0.5) did not significantly change after adding 2×1.5 kg of mass to the leg. On the other hand, manipulations of the leg segment proportions [either
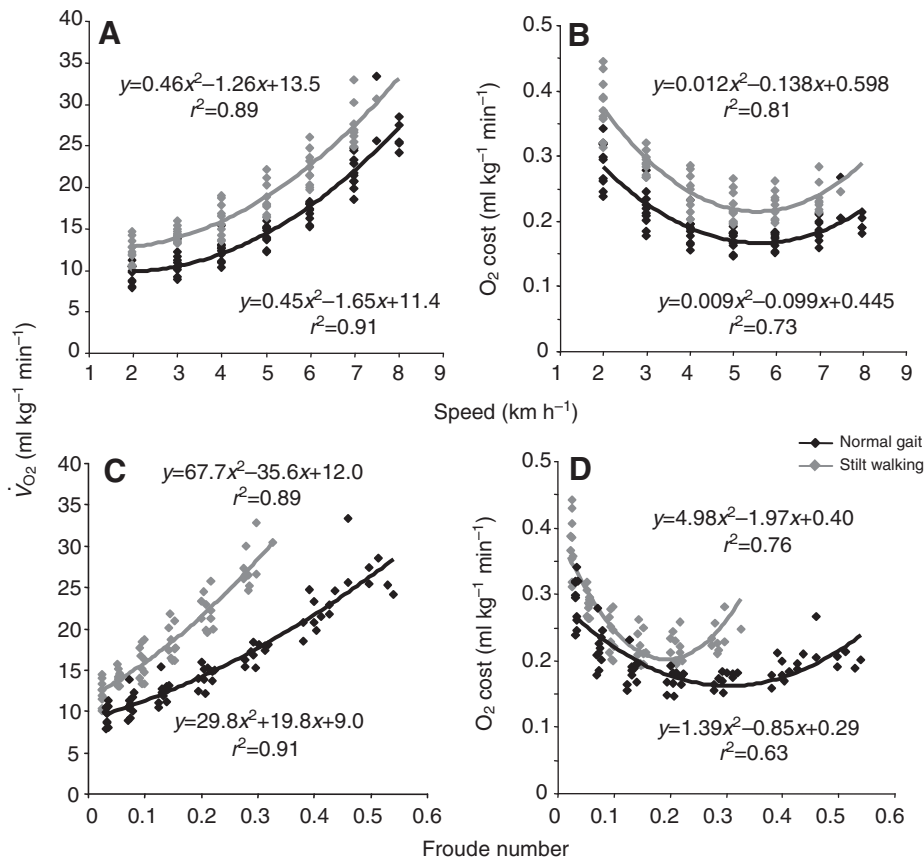
Fig. 5. Metabolic measurements of walking with and without stilts on a treadmill at different speeds. (A,C) Metabolic cost of transportation per minute ($\dot{V}_{O_2}$ expressed in ml O_2 kg^{-1} min^{-1}) as a function of absolute (A) and dimensionless (Froude number, Fr; C) speed. The data for all subjects were pooled; each point indicates the data obtained from one trial. (B,D) Metabolic cost per unit distance (ml O_2 kg^{-1} m^{-1}). Regression lines represent second-order polynomial fittings. Note a steeper increment of energy expenditure with speed (A) and a shift of the $\dot{V}_{O_2}$ minimum towards slower speeds (B,C) for stilt walking.

using stilts as in Figs 2–5 or after surgery (Dominici et al., 2009)] elicited remarkable changes in the intersegmental coordination and preferred and maximal walking speeds.

Our results showed that the minimum metabolic cost occurred at roughly the same absolute speed with and without stilts (Fig. 5B). Therefore, minimum metabolic cost appears to be related to absolute walking speed rather than to Fr, at least under our experimental conditions. One reason for the failure of Eqn 1 to predict the optimal speed could be that it assumes that the total limb length represents the primary determinant of energy expenditure in walking. Instead, it is likely that, in addition to the geometrical factors, the ensuing kinematic strategies also play a key role in the energetics of walking. Thus, Bianchi and colleagues reported that, for normal walking, the specific kinematic intersegmental coordination is a robust predictor of the mechanical energy expenditure of each subject (Bianchi et al., 1998a; Bianchi et al., 1998b). Moreover, several previous studies have shown that the metabolic cost of locomotion depends largely on the muscle forces necessary to support body weight and to swing the limbs (Kram and Taylor, 1990; Kram, 1991; Taylor, 1994; Roberts et al., 1998a; Roberts et al., 1998b; Wickler et al., 2001; Griffin et al., 2003; Biewener et al., 2004; Marsh et al., 2004; Pontzer, 2005; Gottschall and Kram, 2005; Ivanenko et al., 2008). All these factors are tightly inter-related and depend on neural control, in addition to biomechanics. Finally, it is likely that our musculoskeletal apparatus and limb geometry represent the end product of a long evolutionary optimization, favouring endurance walking (Rolian et al., 2009). A drastic alteration in the limb geometry and function of the musculoskeletal apparatus resulting from wearing the stilts may perturb the optimal allocation of muscle volume and forces.

Currently, there are no experimental or model studies that incorporate specific limb segment proportions into a method of predicting metabolic energy consumption. Based on the force production hypothesis of Kram and Taylor (Kram and Taylor, 1990), Pontzer suggested a new mechanical formulation, called the LiMb model, that predicts the energy cost of locomotion from anatomical and kinematic variables (Pontzer, 2005; Pontzer, 2007). However, this model uses the whole limb length as an input. Furthermore, a recent study by Kramer and Sarton-Miller on adults and children also failed to predict accurately the effect of limb length on the energetics of human walking, thus challenging the usage of the Fr number or the LiMb model to compensate for the effect of leg length (Kramer and Sarton-Miller, 2008).

In conclusion, the present study does not suggest a violation of the dynamic similarity theory. Rather, we highlight that animal anatomy and individualized limb segment distortions are optimized in such a way that Eqn 1 can explain optimal walking velocity. In our experimental conditions, full optimization does not occur and care should be taken when manipulating limb segment proportions. Our findings demonstrate that specific limb segment proportions may play an essential role in the kinematics and energetics of walking. This kinematic adaptation and altered metabolic profile support the popular creed on optimal body proportions and may provide further insight into the adaptation of bipedal gait.

LIST OF SYMBOLS AND ABBREVIATIONS

BF	biceps femoris
COM	centre of mass of the body
EMG	electromyography
Fr	Froude number

GT	greater trochanter
HS	heel strike
IL	tubercule of the anterosuperior iliac crest
L	leg length
LE	lateral epicondyle of the femur
LM	lateral malleolus
MG	gastrocnemius medialis
MT	fifth metatarsal head
O_2 cost	oxygen consumption per unit distance
RF	rectus femoris
ST	semi-tendinosus
TA	tibialis anterior
TO	toe off
V	walking speed
$\dot{V}_{CO_2}$	rate of carbon dioxide production
VL	vastus lateralis
V_{max}	maximum walking speed
$\dot{V}_{O_2}$	rate of oxygen consumption
V_{opt}	optimal walking speed

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