

The up and down bobbing of human walking: a compromise between muscle work and efficiency

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Human walking has a peculiar straight-legged style. Consequently, the body's centre of mass (CM) moves up and down with each step, which is noticeable in their up and down head bobbing while walking. This vertical CM movement enables humans to save energy via a pendulum-like mechanism but is probably a relatively recent locomotor innovation insofar as earliest bipeds may have walked flexed and flat. We investigated the mechanics, energetics, muscle efficiency and optimization of human walking by decreasing and increasing the vertical CM displacement (flat and bouncy walking) in comparison to normal walking at six speeds (1–6 km h⁻¹). In both flat and bouncy walking, the pendular mechanism was reduced and the energy cost was increased. However, this increase was unexpectedly much sharper in flat walking where muscles provided normal mechanical work but with a decrease in muscle efficiency. In bouncy walking, muscles provided extra mechanical work in an efficient way. Our results showed that not only do humans bob up and down in normal walking to save energy via a pendulum-like mechanism but also to make their muscles work efficiently. Actually, walking flat makes the muscles work in unfavourable conditions that waste energy. Furthermore, we are still close to a flat CM displacement relative to our current ability to change this displacement, which suggests that reducing vertical CM displacement is indeed important but only to certain limits. Evolution may ultimately have chosen the best compromise between flat locomotion that requires little work to move and bouncy locomotion that improves muscle efficiency to minimize energy consumption.

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Bipedalism is considered a hallmark of being human, although we are not alone in walking on two legs. However, the distinctive feature of human bipedalism, compared with other bipedal animals, is that we walk while keeping our legs relatively straight (Alexander, 1992). Consequently, our body's centre of mass (CM) moves up and down during each step by reaching its lowest point when both feet are on the ground and rising to its highest point while we vault over a relatively straight supporting leg. While our CM goes up we slow down and when it goes down we speed up, thus passively converting gravitational potential energy to forward kinetic energy and back again (Cavagna, 1978; Alexander, 1992). This pendulum-like mode of walking, which is a consequence of the straightness of our legs, reduces the mechanical work that our muscles must supply to raise and accelerate the CM, thus reducing the 'cost of work' and saving metabolic energy. On the other hand, while walking straight, the line of action of our body's weight passes close to the leg joints, and little tension is needed in the muscles to prevent the joints from collapsing under the load. Hence, another possibly more important consequence of our

straight-legged style of walking is that it enables us to support our weight without the need for large forces in our leg muscles, thereby reducing the 'cost of force' (Alexander, 1992). This in turn increases the efficiency with which our muscles provide mechanical work (i.e. the proportion of the metabolic energy resulting in mechanical energy) (Cavagna, 1978; Minetti, 2004).

Humans walk straight, but even the apes – our closest relatives – rarely walk on two legs, and when they do, their legs bend in a compliant pattern (Alexander & Jayes, 1978; Alexander, 1992). Compliant gait is paramount for arboreal locomotion because it reduces ground reaction forces and involves little oscillations of the CM (i.e. flat gait), thus enhancing stability and allowing primates to maintain loosely stabilized joints (Schmitt, 2003). Recent studies suggest that our common ancestors with apes, probably ~7 million years ago (Gibbons, 2002), might also have walked flexed and flat, which would have facilitated their transition to terrestrial bipedality when they had not completely forsaken arboreal locomotion (Schmitt, 2003). Hence, the important locomotor innovation characterizing the

human lineage was likely to be the development of straight-legged walking rather than upright walking *per se* (Alexander, 1992; Schmitt, 2003). When did this occur? The australopithecines, as represented by the famous 3.2-million-year-old 'Lucy', were short with poorly stabilized limbs, sacrum and vertebral joints (Stern & Susman, 1983; Ward, 2002). Therefore, scientists believed that they may have walked flexed and flat, and then the shift to a more robust skeleton in *Homo erectus* ~1.8 million years ago may have reflected the adoption of straight-legged walking (Schmitt, 2003). However, recent simulation studies suggest that Lucy already walked straight and moved up and down (Nagano *et al.* 2005; Sellers *et al.* 2005), while its primitive anatomical features were rather associated with a limited ability for endurance running (Bramble & Lieberman, 2004). Hence, straight-legged walking with its inherent vertical CM movement may have appeared well before the genus *Homo*.

The peculiar relatively straight-legged walking in modern humans, and the energy saving that it may induce, may suggest that the straighter we walk the less energy we consume. However, straight legs may induce a bouncy walking characterized by larger vertical CM displacement and abrupt changes in CM path from one arc to the next. This would imply large forces to redirect the CM and to raise the body against gravity during each step, thus increasing energy cost. Hence, Saunders *et al.* (1953) postulated that humans walk as flat as possible, by using some of the flexed joint characteristics seen in our ancestors' compliant gaits, to decrease the energy cost. Recent human experiments have shown that, contrary to Saunders' hypothesis, flat walking costs more energy than normal walking (Ortega & Farley, 2005). On the other hand, a recent breakthrough in a computer optimization model of human locomotion demonstrated that all optimization simulations converged towards a normal walking style but never to a flat gait (Srinivasan & Ruina, 2006). Nonetheless, the physiological reasons that underlie the increased energy cost in flat walking remain unknown, in addition to the questions of why our natural mode of walking is the optimal one in comparison with flat or bouncy walking and where we stand between flatness and bounce.

We set out to test the mechanics, energetics, muscle efficiency and optimization of human walking with regard to the CM displacement and to assess the benefits from our inherent vertical movement. This study will provide insights into the physiological determinants of energy consumption in human walking and the reasons for nature to have chosen our natural modes of locomotion.

Methods

Subjects and experimental procedure

Mechanical, metabolic and electromyographic data were acquired from six healthy adult volunteers (5 female

and 1 male, age 24 ± 1 years, weight 60.3 ± 11 kg, height 1.7 ± 0.1 m (mean \pm s.d.)). All were moderately active, but none were specialists in any particular sport. Before the experiment, the subjects signed an informed consent approved by the local ethics committee after the nature of the study was explained. The experiments involved no discomfort and were performed according to the *Declaration of Helsinki*.

The subjects walked barefoot on a custom-built motorized treadmill mounted on four 3-D strain-gauge force transducers (Dierick *et al.* 2004). All six subjects walked at all six speeds (1, 2, 3, 4, 5 and 6 km h⁻¹). For each speed, they walked in three different conditions: normally, with minimum vertical CM displacement (flat walking), and with maximum vertical CM displacement (bouncy walking). In all, 18 walking trials were carried out in a random order to eliminate any possible order effects and in two testing sessions on two different days to avoid physical fatigue. Before testing sessions, the subjects walked on the treadmill in a practice session during which they were given at least 30 min to become accustomed to the treadmill and the three types of walking at different speeds. This practice session exceeded the minimum treadmill habituation time of 10 min recommended in the literature for healthy subjects (Wall & Charteris, 1981; Van de Putte *et al.* 2006). The habituation time was similar for both flat and bouncy walking and a resting time was given between the practice and the testing session.

Metabolic data were continuously measured during the experiments. A baseline standing metabolic rate was taken at the beginning of each measurement session, for at least 3 min. Each walking trial was maintained as long as necessary to obtain a steady metabolic state for at least 3 min, during which we simultaneously collected metabolic, kinematic, EMG and ground reaction force data of 10 consecutive walking strides (i.e. the time between two successive instants of initial floor contact of the same foot). After each walking trial, a resting time was given until metabolic data and pulse rate returned to initial standing values $\pm 10\%$ and showed a steady state for at least 3 min.

Subjects were provided with real-time visual feedback to help them modulate the vertical displacement of their CM. A marker over the mid-sacrum was video-taped from a posterior view and projected onto a screen projector in front of the subject. The position of the marker was chosen according to the literature, which has shown that a sacral marker is accurate and sensitive to estimate the changes in vertical CM displacement (Thirunarayan *et al.* 1996). The camera was calibrated so that 1 cm displacement of the marker appeared as 10 cm on the screen. The only instruction given was to modulate the vertical displacement of the marker regardless of the strategy used. At the beginning of the practice session, the participants tried several techniques to achieve this goal. However, by the end of the practice session they all showed a similar strategy to modulate the marker

displacement and similar changes in the mechanical, metabolic and EMG variables as reflected later by the relatively small standard deviations in the results.

Positive mechanical work and CM displacement over a walking stride

Segmental kinematics was measured with an Elite system (Elite V5, BTS, Italy) at a sampling rate of 100 Hz. Six infrared cameras measured the 3-D bilateral co-ordinates of reflective markers positioned on specific anatomical landmarks to compute angular displacements as described in detail by Davis *et al.* (1991). The internal work, W_{int} , i.e. the work required to move the limbs relative to the CM, was computed from kinematic data following the method described by Willems *et al.* (1995) and Detrembleur *et al.* (2003). The body was divided into seven rigid segments: head–arm–trunk (HAT), and both thighs, shanks and feet. The internal mechanical energy of the body segments corresponded to the sum of rotational and translational energies of these segments due to their movements relative to the CM. For each lower limb, the internal mechanical energy–time curves of the thigh, shank and foot were summed. The W_{int} of each lower limb and HAT segment were then calculated separately as the sum of the increments of the respective internal mechanical energy curves. Finally, the W_{int} during gait corresponded to the sum of the W_{int} done to move the lower limbs and the HAT segment and was expressed per kilogram body mass and per metre travelled.

Vertical, forward and lateral ground reaction forces were recorded by means of the strain gauges of the force measuring treadmill at a sampling rate of 100 Hz and were digitized synchronously with the Elite system. The external work, W_{ext} , i.e. the work performed to lift and accelerate the CM relative to the surroundings, was computed following the method described in detail by Cavagna (1975) and Willems *et al.* (1995). The 3-D accelerations of the CM were computed from the vertical, lateral and forward components of the ground reaction forces and the mass of the subject. The mathematical integration of the 3-D accelerations gave the velocity changes of the CM in all three directions (V_v , V_f , V_l). From the instantaneous V_v , V_f and V_l and the body mass (M), we computed the instantaneous vertical ($E_{\text{kv}} = 1/2MV_v^2$), forward ($E_{\text{kf}} = 1/2MV_f^2$) and lateral ($E_{\text{kl}} = 1/2MV_l^2$) kinetic energies of the CM. A second mathematical integration of V_v was performed to determine the vertical CM displacement (S_v) of the CM. The amplitude of vertical CM displacement (A_v) was measured as the peak-to-peak amplitude on the S_v curve over a stride. A stride was selected for analysis only when the sum of the increments in V_v , V_f and V_l changes did not differ by more than 25% from the sum of the decrements, thus revealing a relatively constant

average height and speed per stride (Cavagna, 1975). The instantaneous gravitational potential energy ($E_p = MgS_v$) was computed from the vertical displacement (S_v) of the CM, the body mass and the gravity constant (g). The total external mechanical energy (E_{ext}) of the CM was calculated as the sum of E_{kf} , E_{kv} , E_{kl} and E_p . The increments of the E_{kf} , E_{kv} , E_{kl} and E_p curves represented, respectively, the positive work (W_{ekf} , W_{ekv} , W_{ekl} and W_{ep}) necessary to accelerate the CM in the three directions and to lift the CM during a stride. W_{ext} was obtained by summing the increments of E_{ext} over a stride. W_{ekf} , W_{ekv} , W_{ekl} , W_{ep} and W_{ext} were expressed per kilogram body mass and per distance travelled. The ‘recovery’, quantifying the percentage of mechanical energy saved via a pendulum-like exchange between gravitational potential energy and kinetic energy of the CM, i.e. an index reflecting the effectiveness of the pendulum-like mechanical mode of walking, was calculated as:

$$\text{Recovery (\%)} = 100 \times \frac{W_{\text{ek}} + W_{\text{ep}} - W_{\text{ext}}}{W_{\text{ek}} + W_{\text{ep}}}$$

where $W_{\text{ek}} = W_{\text{ekf}} + W_{\text{ekv}} + W_{\text{ekl}}$. The maximum positive work one should do without energy shift is $W_{\text{ek}} + W_{\text{ep}}$, and W_{ext} represents the work actually done (Cavagna *et al.* 1976). A 100% recovery would require the kinetic and potential curves to be exactly out of phase and of equal shape and amplitude according to an ideal frictionless pendulum.

The total mass-specific muscular work per distance travelled (W_{tot}) was calculated as the sum of W_{ext} and W_{int} and expressed in $\text{J kg}^{-1} \text{ m}^{-1}$.

Metabolic cost and efficiency of positive work production

Breath-by-breath rate of oxygen consumption, rate of carbon dioxide production and heart rate were measured with an ergospirometer (Quark b², Cosmed, Italy). Values were automatically converted by a software program (Cosmed, Quark b² win, v. 7.6.a) to standard temperature, pressure and dry oxygen consumption. After steady state was reached, metabolic data were collected. The mass-specific gross energy consumption rate (W kg^{-1}) was obtained from the oxygen consumption rate using an energy equivalent of oxygen, taking into account the measured respiratory exchange ratio (RER) (i.e. the ratio between the rate of carbon dioxide production and the rate of oxygen consumption) (McArdle *et al.* 1996). Only trials with $\text{RER} \leq 1.0$ were retained and analyzed. The mass-specific net energy consumption rate (W kg^{-1}) was calculated from the energy consumption attributed to the walking *per se*, i.e. the energy consumption rate while walking minus the energy consumption rate while standing. Finally, the mass-specific net cost of transport,

C_{net} ($\text{J kg}^{-1} \text{m}^{-1}$), was calculated by dividing the net energy consumption by the walking speed in m s^{-1} .

Efficiency of positive work production by the muscles and tendons during walking (η) was calculated as the ratio of W_{tot} to C_{net} and expressed as a percentage (Cavagna & Kaneko, 1977).

Electromyographic activity

The EMG activity of the vastus lateralis (VL), biceps femoris (BF), tibialis anterior (TA) and medial gastrocnemius (MG) muscles in both lower limbs was recorded by a telemetry system (Telemg, BTS, Milan, Italy). Circular

surface electrodes were used with a diameter of 1 cm and an interelectrode distance of 2 cm (Medi-Trace, Graphic Controls Corporation, NY, USA) after hair shaving, skin abrasion and application of alcohol and ether so that the interelectrode resistance was below 5 k Ω . For each muscle, a pair of recording electrodes were placed close to each other, parallel with the muscle fibres and close to the motor point (Perotto, 1994), and care was taken not to place the electrodes over the peripheries of the muscles to minimize EMG cross talk between muscles (Winter, 2005).

The EMG signal was digitized at 1000 Hz, full-wave rectified and filtered (bandwidth 25–300 Hz). The onset

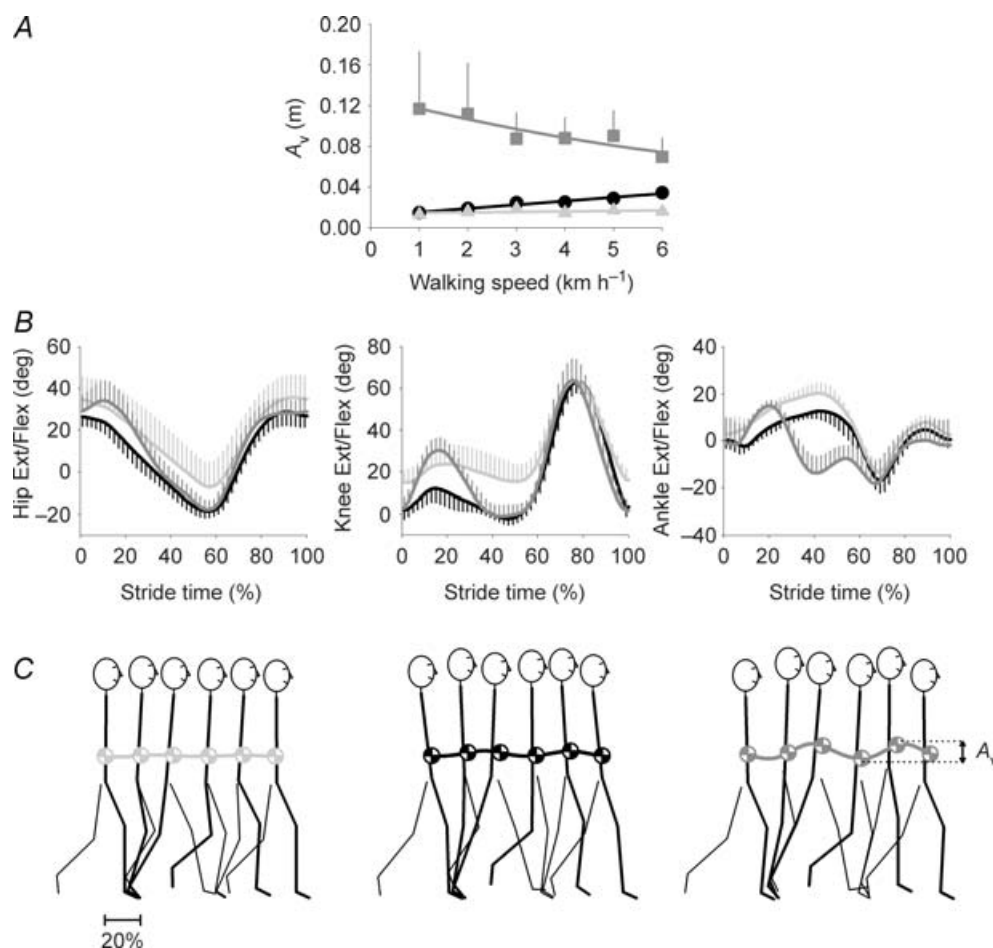


Figure 1. The body's centre of mass and kinematics during walking

A, amplitude of vertical CM displacement (A_v) versus walking speed for the six subjects in normal (black circle), flat (light grey triangle), and bouncy walking (dark grey square). Each data point represents mean value, vertical bars indicate one standard deviation from the mean, and lines are least squares regressions. B, mean angular displacement in sagittal plane of the right hip, knee and ankle for the six subjects at 4 km h^{-1} are presented from right to left, respectively, in normal (black traces), flat (light grey traces), and bouncy walking (dark grey traces) as a percentage of the walking stride. Negative values denote extension and positive values denote flexion position. Vertical bars indicate one s.d. from the mean. C, the stick figures show the segments' positions (right limb in thick lines) every 20% of the stride (from heel-strike to heel-strike of the right foot) for a female (21 years old, 1.6 m height) walking at 4 km h^{-1} in flat, normal and bouncy styles from left to right, respectively. The hourglass circle depicts the centre of mass displacement in flat (light grey curve), normal (black curve), and bouncy walking (dark grey curve).

and cessation of muscle activity were both visually (Basmajian, 1979) and mathematically determined by computing the EMG threshold voltage as described in detail by Van Boxtel *et al.* (1993). By combining the visual and mathematical methods, we obtained the EMG packets (onset to cessation) for each muscle. The strides were normalized to 100% in time before averaging the EMG activity of each muscle (Winter, 1991). Finally, the index of co-contraction between the BF and VL muscles (BF–VL) and between the TA and MG muscles (TA–MG) was temporally quantified as the percentage of the gait stride during which these antagonistic muscles were simultaneously activated (Yang *et al.* 1998).

Statistical analysis

For each walking trial, data obtained during 10 strides were averaged and the mean values were used for statistical analysis. The effects of walking conditions (normal, flat and bouncy) and speed on metabolic, mechanical and EMG variables were tested using a two-way repeated measures analysis of variance (ANOVA) (SigmaStat version 2.0, SPSS Sciences Software GmbH, Erkrath, Germany) and Tukey's *post hoc* tests where appropriate. The assumption of homoscedasticity was verified for all the comparisons, and the significance level α was set at 0.05.

Results

Flat walking

In normal walking, the amplitude of vertical CM displacement, A_v , increased linearly with speed from about 0.015 ± 0.003 m (mean \pm s.d.) at the lowest speed to 0.034 ± 0.004 m at the highest speed (Fig. 1A). In flat walking, the subjects were able to significantly decrease A_v to a constant amplitude for all speeds (0.015 ± 0.002 m, $P < 0.001$) corresponding to the half of A_v measured during normal walking at an intermediate speed of 4 km h^{-1} . To walk flat, all the subjects adopted a flexed-legged pattern although no specific instructions were given regarding the strategy to use (Fig. 1B and C).

The decrease in A_v reduced the work necessary to raise the CM, W_{ep} , from an average of $0.35 \pm 0.04 \text{ J kg}^{-1} \text{ m}^{-1}$ in normal to $0.22 \pm 0.04 \text{ J kg}^{-1} \text{ m}^{-1}$ in flat walking ($P = 0.001$). It also decreased the work necessary to accelerate the CM, W_{ek} , from $0.30 \pm 0.1 \text{ J kg}^{-1} \text{ m}^{-1}$ in normal to $0.25 \pm 0.1 \text{ J kg}^{-1} \text{ m}^{-1}$ in flat walking ($P = 0.016$) (Fig. 2). However, the work necessary to move the CM relative to the surroundings, W_{ext} , did not change significantly ($P = 0.620$) due to a reduction in the pendular recovery from $52.49 \pm 16.1\%$ in normal to $41.59 \pm 12.2\%$ in flat walking ($P = 0.04$). Nonetheless, the internal work done to move the limbs relative to the CM, W_{int} , decreased

significantly from $0.27 \pm 0.1 \text{ J kg}^{-1} \text{ m}^{-1}$ in normal to $0.24 \pm 0.1 \text{ J kg}^{-1} \text{ m}^{-1}$ in flat walking ($P = 0.003$) (Fig. 3A). The total positive mechanical work provided by the muscles, W_{tot} , did not change significantly ($P = 0.181$). However, the net energy cost, C_{net} , nearly doubled from $2.11 \pm 0.4 \text{ J kg}^{-1} \text{ m}^{-1}$ in normal to $3.74 \pm 0.7 \text{ J kg}^{-1} \text{ m}^{-1}$ in flat walking ($P < 0.001$) due to a significant decrease in the muscle efficiency of positive work production, η , from $27.91 \pm 6.4\%$ in normal to $14.34 \pm 4.8 \text{ J kg}^{-1} \text{ m}^{-1}$ in flat walking ($P < 0.001$) (Fig. 3B).

In regards to the EMG activity in flat walking, all muscles showed increased activation timing relative to the walking stride time (Table 1, Fig. 4). Muscle co-contraction timing also increased significantly in shank muscles from $17.78 \pm 15.9\%$ in normal to $30.25 \pm 16.8\%$ in flat walking ($P = 0.033$) but not in thigh muscles ($P = 0.398$).

Bouncy walking

In bouncy walking, the subjects were able to increase A_v from an average of 0.024 ± 0.01 m in normal to 0.094 ± 0.02 m in bouncy walking ($P < 0.001$), corresponding to up to ~ 8 times greater than normal at 1 km h^{-1} and ~ 3.5 times greater than normal at 4 km h^{-1} (Fig. 1A). The relatively small standard deviations in the

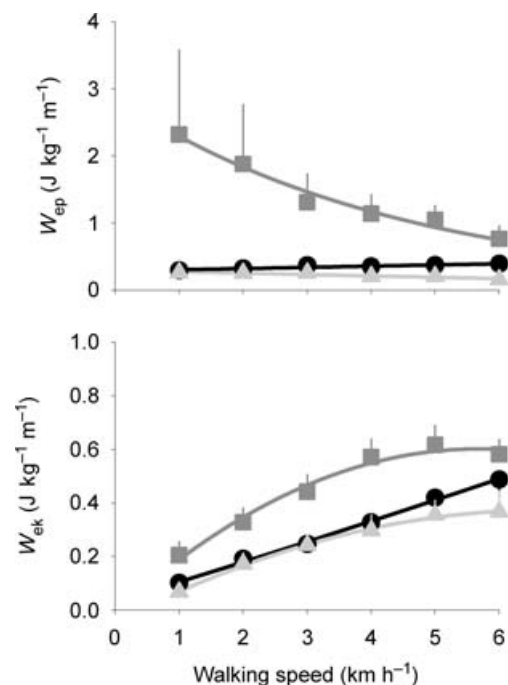


Figure 2. Work to move the centre of mass of the body

The top panel shows the mass-specific work necessary to raise the CM in the vertical direction per distance travelled *versus* walking speed for the subjects in normal, flat and bouncy walking. The bottom panel presents the mass-specific work necessary to accelerate the CM to travel a metre (symbols as in Fig. 1).

Table 1. EMG activity timing in lower limbs† as a percentage of walking stride time in normal versus flat and bouncy walking

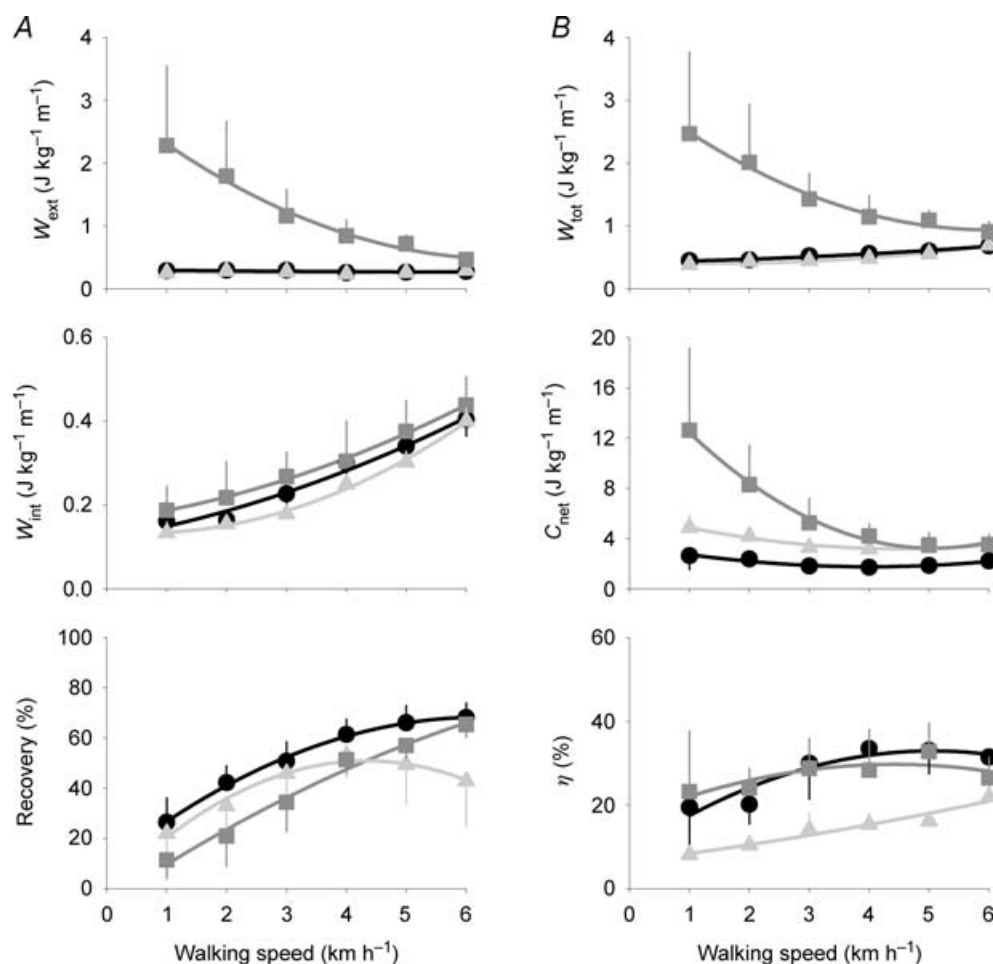
	Tibialis anterior (TA) (%)	Medial gastrocnemius (MG) (%)	Muscle co-contraction in shank (TA – MG) (%)	Biceps femoris (BF) (%)	Vastus lateralis (VL) (%)	Muscle co-contraction in thigh (BF – VL) (%)
Normal	60.61 ± 12.8	44.97 ± 9.2	17.78 ± 15.9	43.36 ± 13.7	39.76 ± 16	32.47 ± 12.9
Flat	69.22 ± 12.6	54.56 ± 12.3	30.25 ± 16.8	49.47 ± 14.3	62.61 ± 12.1	35.67 ± 12.8
P_{\ddagger}	0.015	0.005	0.033	0.175	< 0.001	0.398
Bouncy	77.06 ± 11.9	57.50 ± 10.4	43.81 ± 16.2	54.97 ± 11.9	55.00 ± 15.7	30.56 ± 14.2
P	0.005	0.006	0.001	< 0.001	0.009	0.194

Values are means ± s.d. †Right lower limb (left lower limb showed similar EMG activity). ‡Significant P values are emboldened.

kinematics also show the limited variability in the strategy between the subjects (Fig. 1*B* and *C*).

Increasing A_v led to a dramatic increase in W_{ep} from $0.35 \pm 0.04 \text{ J kg}^{-1} \text{ m}^{-1}$ in normal to $1.41 \pm 0.6 \text{ J kg}^{-1} \text{ m}^{-1}$

in bouncy walking ($P = 0.003$). It also increased W_{ek} from 0.30 ± 0.1 to $0.46 \pm 0.2 \text{ J kg}^{-1} \text{ m}^{-1}$ ($P < 0.001$) (Fig. 2). A dramatic increase also occurred in W_{ext} from $0.28 \pm 0.02 \text{ J kg}^{-1} \text{ m}^{-1}$ in normal to $1.21 \pm 0.7 \text{ J kg}^{-1} \text{ m}^{-1}$

**Figure 3. Mechanical work, energy cost and muscle efficiency**

A, from top to bottom, the work provided to move the centre of mass relative to the surroundings, the work necessary to move the limbs and trunk relative to the centre of mass and the pendular recovery of mechanical energy versus walking speed. *B*, from top to bottom, the total mechanical work, the net energy cost and the efficiency of work production by muscles versus walking speed (symbols as in Fig. 1).

in bouncy walking ($P = 0.004$) associated with a significant decrease in the recovery from $52.49 \pm 16.1\%$ in normal to $40.08 \pm 21.3\%$ in bouncy walking ($P = 0.002$). On the other hand, W_{int} remained close to normal ($P = 0.121$) (Fig. 3A). Consequently, a dramatic increase occurred in the total mechanical work, W_{tot} , particularly at the lowest speed from $0.55 \pm 0.1 \text{ J kg}^{-1} \text{ m}^{-1}$ in normal to $1.51 \pm 0.6 \text{ J kg}^{-1} \text{ m}^{-1}$ in bouncy walking ($P = 0.004$) as well as in the net energy cost, C_{net} , from $2.11 \pm 0.4 \text{ J kg}^{-1} \text{ m}^{-1}$ in normal to $6.23 \pm 3.6 \text{ J kg}^{-1} \text{ m}^{-1}$ in bouncy walking ($P = 0.004$). However, the efficiency, η , remained close to normal walking values ($P = 0.591$) (Fig. 3B).

In bouncy walking, all muscles showed increased activation timing relative to the walking stride time (Table 1, Fig. 4). Muscle co-contraction timing also increased significantly in shank muscles from $17.78 \pm 15.9\%$ in normal to $43.81 \pm 16.2\%$ in bouncy walking ($P = 0.001$) but not in thigh muscles ($P = 0.194$).

Optimization of human walking

The optimal combination of A_v and walking speed, which minimizes C_{net} , was $\sim 3 \text{ cm}$ for A_v at $\sim 4 \text{ km h}^{-1}$ corresponding to A_v at the spontaneously adopted speed in normal human walking (Fig. 5). In bouncy walking, C_{net} increased only a little with a quite large increase of A_v from the optimum, particularly at high speeds, where in flat walking, C_{net} was highly sensitive to reductions of A_v .

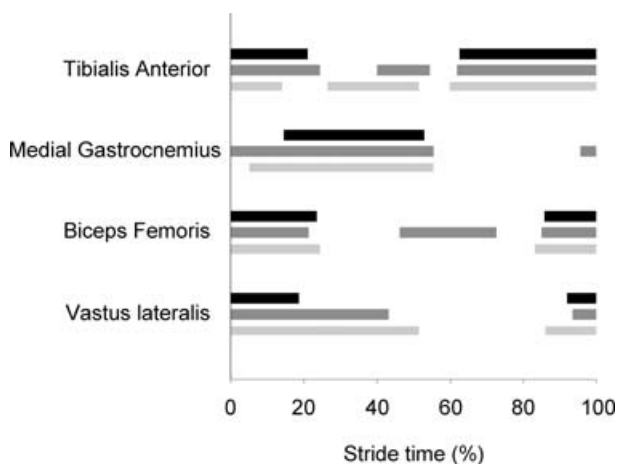


Figure 4. Electromyographic activity

The figure shows typical EMG activity timing of a female subject (21 years old, 1.6 m height) walking at 4 km h^{-1} in normal (black bars), flat (light grey bars) and bouncy walking (dark grey bars). Onset and cessation of EMG are presented as separate bars and normalized as a percentage of stride time. From top to bottom are, respectively, depicted the EMGs of the major antagonistic shank and thigh muscles. The index of co-contraction between the tibialis anterior and medial gastrocnemius muscles, and between the biceps femoris and vastus lateralis muscles, was calculated as the time overlap between their corresponding EMG activity bars.

For instance, at around 4 km h^{-1} the subjects were able to reduce A_v by nearly half (from about 0.025 to 0.015 m) which nearly doubled their C_{net} (from about 1.7 to $3.2 \text{ J kg}^{-1} \text{ m}^{-1}$); however, they were able to increase A_v up to ~ 3 – 4 times higher (from about 0.025 to 0.088 m), but their C_{net} only doubled (from about 1.7 to $4.2 \text{ J kg}^{-1} \text{ m}^{-1}$).

Discussion

Human walking seems to be spontaneously optimized to minimize energy consumption. In fact, energy cost increased in flat walking due to unfavourable muscular efficiency although the mechanical work provided by muscles was small, and it increased in bouncy walking due to an extra mechanical work although the muscles provided this work efficiently.

Relation to previous studies

Our study showed that the exceptionally flat walk is never optimal as is also the case with an exceptional increase in CM undulations, which confirms the prediction of Srinivasan and Ruina's computer optimization model that showed that normal walking is the most optimal (Srinivasan & Ruina, 2006). However, our study showed the physiological grounds of this optimization and revealed an additional physiological complexity to the simple mathematical model insofar as the conditions in which the muscles provided mechanical work efficiently differed with respect to CM displacement (Fig. 3). A part of our results is also in agreement with

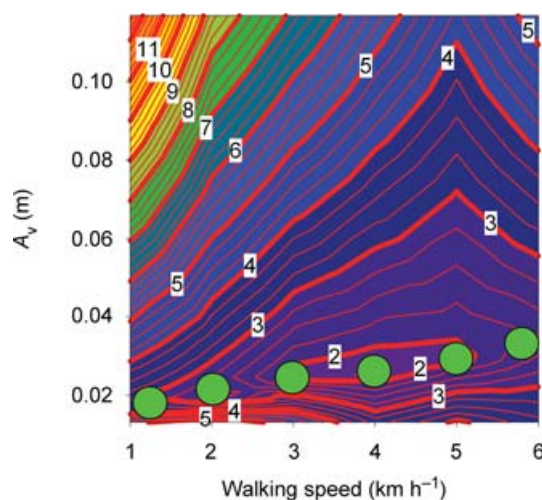


Figure 5. Gait optimization

Contours show the energy cost C_{net} (in $\text{J kg}^{-1} \text{ m}^{-1}$) against the amplitude of vertical CM displacement A_v and walking speed. Each contour indicates a higher cost than the one inside. A central contour surrounds the minimum cost region that looks like a valley on a map. The mean C_{net} for our subjects in normal walking (green circles) are plotted at the corresponding speed and vertical CM displacement.

the recent human experiments done by Ortega & Farley (2005). In fact, they showed that subjects spontaneously adopted a flexed-legged pattern to walk flat, but contrarily to the long-lasting theory of Saunders (Saunders *et al.* 1953), flat walking costs more, even twice more, than normal walking although the external work necessary to move the CM remains normal. However, the physiological reasons that underlie this increased energy cost remained unknown because they assessed neither muscle efficiency, as they only measured the external work that is only a part of the total mechanical work, nor muscle activity to examine the role of co-contraction in increasing the energy cost. We have also examined the effect of the increase in the vertical CM displacement above normal and directly compared all three walking styles at a large range of speed, which enabled us to see the effect of the inherent vertical movement seen in normal human walking and to find that bouncy walking is even better than flat walking for muscles to provide efficient work. Thus, we were able to deduce that not only do humans move up and down in normal walking to save energy via a pendulum-like mechanism (Cavagna *et al.* 1976; Ortega & Farley, 2005) but also to make their muscles work efficiently.

Factors influencing the energy cost and muscle efficiency in flat and bouncy walking

An efficient locomotion is one where most of the metabolic energy input is transformed into mechanical work (Minetti, 2004). The efficiency in our study takes into account the efficiency of the positive work derived from the contractile engine and that derived from energy storage and release by muscles and tendons (Cavagna & Kaneko, 1977). Consequently, it mainly depends on the shortening velocity of the muscles, stretching of elastic musculotendon structures before contraction and frictional losses within the body (Cavagna, 1978; Heglund & Cavagna, 1985). Isolated muscle experiments *in vitro* showed that muscle efficiency is low when the velocity of contraction is too low or too high, whereas the maximal efficiency of unstretched human muscles is about 25% (Dickinson, 1929; Heglund & Cavagna, 1985). However, stretching muscles and tendons before work production increases the efficiency above 25% by providing positive work, free of cost, during the recoil of the previously stretched structures, which is taken as evidence of the pre-stretching mechanism *in vivo* (i.e. during human walking) (Cavagna & Kaneko, 1977; Heglund & Cavagna, 1985; Willems *et al.* 1995). Recent studies have indeed shown the *in vivo* spring-like behaviour of the stretched musculotendon structures such as the tendon in the calf muscles in particular (Fukunaga *et al.* 2001; Ishikawa *et al.* 2005). On the other hand, *in vivo*, frictional losses

mainly occur within antagonistic muscles doing work on each other as measured during co-contraction, which would decrease the efficiency by using metabolic energy no apparent work produced (Cavagna, 1978; Heglund & Cavagna, 1985; Minetti, 2004).

In our study, muscle activation increased in both flat and bouncy walking as exemplified by the vastus lateralis being likely to counter an increased knee flexion in flat walking and to straighten the knee to increase the CM amplitude in bouncy walking by raising the CM further when it has to be at a maximum (Figs 1 and 4). The increase in muscle activation associated with an increase in muscle co-contraction may also have occurred because flat and bouncy walking were unfamiliar tasks. However, our study included two practice sessions that exceeded the recommended treadmill habituation time, and the constant strategy that subjects showed suggests that they had become relatively habituated with both walking types. Nonetheless, any remaining habituation effect would have influenced flat and bouncy walking in a similar way, as both had a similar habituation time. Unexpectedly, the increase in muscle co-contraction did not seem to be a determining factor influencing the muscle efficiency, as this latter variable remained normal in bouncy walking. This is similar to recent experiments in our laboratory that also showed that muscle efficiency may remain normal, for instance in hemiparetic spastic patients pedalling with one leg on an ergometer (Stoquart *et al.* 2005) or walking with a pathological increase in the vertical CM displacement (Detrembleur *et al.* 2003), although muscle co-contraction timing was increased. The less determinant role of muscle co-contraction timing may be due to the fact that, as measured at present, it does not necessarily reflect the amount of useless force, as EMG activity is not necessarily correlated to muscle tension during walking (Winter, 2005) and, consequently, is not directly correlated to the energy consumed by the muscles. However, to our knowledge, it is not yet possible to measure the force developed and the energy consumed by individual muscles *in vivo* to better explain the relation between the energy cost, the mechanical work and the muscular efficiency during exercise.

Nonetheless, other factors seem to have influenced muscle efficiency. In fact, in bouncy walking, the efficiency reached a maximum (~35%) at intermediate speeds and then decreased with higher speeds, which is expected when the positive mechanical work is mainly derived from the transformation of chemical energy by the contractile machinery of muscles, as in cycling (Dickinson, 1929) and normal walking (Cavagna & Kaneko, 1977), according to the force–velocity relationship and the measurements of the ‘initial efficiency’ of muscle (Hill, 1964). Hence, in bouncy walking, the role played by the contractile machinery prevails over that of the elastic component, although this last element cannot be neglected. In flat

walking, the efficiency increased continuously with speed, which is expected when the positive work is mainly due to the recoil of elastic structures and to a lesser extent to the active shortening of the contractile machinery, as in running (Cavagna & Kaneko, 1977), in accordance with the fact that the useful effect of stretching continuously increases with the speed of stretching (Cavagna *et al.* 1968). However, the low efficiency in flat walking, below 25%, suggests that energy losses other than co-contraction may also have contributed to mask this underlying elastic mechanism, such as the chemical energy spent during isometric contractions and that to overcome internal frictions (Willems *et al.* 1995), for which to our knowledge, no attempt has yet been made to precisely quantify their contribution during walking.

Interestingly, humans also walk flat to achieve higher walking speeds in competition, but contrary to what we have found at common walking speeds, flat walking is intriguingly more efficient and less costly than normal walking in competition walkers at high speeds above 6–7 km h⁻¹. The efficiency in competition walking also shows continuous increase at high speed while the pendular recovery decreases steeply, as in our study, indicating a smaller utilization of the pendulum-like mechanism characteristic of walking and a greater elastic storage of mechanical energy (Cavagna & Franzetti, 1981). This suggests that athlete walkers may have discovered an efficient way to walk flat, which may be due to the fact that they are constrained by the race rules to keep their legs straight, while using a peculiar hip movement to flatten their CM displacement (Alexander, 1992), contrary to the spontaneously flexed-legged pattern adopted by common subjects to walk flat.

Significance to the evolution of human locomotion

Even if ~7 million years or more separate us from our common ancestor with apes, we are still close to a flat CM displacement relative to our current ability to change this displacement (Fig. 5). Hence, a reduced vertical CM displacement in normal walking is indeed important to minimize energy cost but only to certain limits beyond which energy cost increases dramatically due to a sharp decrease in muscle efficiency. In other words, tracing human walking back to its origin is much more costly, although the track is much shorter.

Our experiments showed that an efficient straight-legged gait does not waste as much energy as a primitive flat and flexed-legged gait does. This was probably a primary objective of natural selection, which is likely to have been achieved if Lucy walked straight. This may explain in part why its minimum energy cost was estimated to be close to that of humans although it occurred at lower speeds (around 2 J kg⁻¹ m⁻¹ at 2 km h⁻¹) (Sellers *et al.* 2005). This minimum would

probably have been doubled for similar muscle work if Lucy had walked flexed and flat. However, Lucy may have showed a much larger energy cost with increasing speeds (Heglund & Schepens, 2003; Sellers *et al.* 2005). Thus, the stasis of Lucy's anatomy over 3 million years may be explained in part by this efficient gait that is not necessarily economical at high speeds for a species living in less-open habitats. The increase in leg length and modern anatomy seen in *H. erectus*, being probably the first hominid to leave Africa to feed its voracious larger brain (Leonard, 2002), would have made it possible to cover longer distances more economically (Steudel-Numbers & Tilkens, 2004; Wang *et al.* 2004). Hence, natural selection may have maximized muscle efficiency 3 million years before reducing energy costs at higher speed to prepare *H. erectus* for its legendary travel, which was probably vital for our large-brained species.

Future perspectives and other applications

Modern humans take advantage of both primitive flat and modern straight-legged walking styles. Apart from their ability to shortcut in a few seconds millions of years of evolution by walking smoothly while, for instance, carefully holding their brimful cup of boiling coffee, humans walk flat to achieve higher walking speeds in competition as mentioned above. On the other hand, recent backpack design generates electricity from our natural vertical CM displacement to power an increased number of portable devices (Rome *et al.* 2005). It is also interesting to note that a similar decrease in the amount of pendulum recovery is seen in reduced gravity such as on Mars (0.4 g) (Cavagna *et al.* 2000) to that in flat walking in our study. This is probably due to the fact that decreasing the vertical CM displacement by half would have had a similar effect on the potential energy as a similar decrease in the constant gravity *g*.

Finally, humanoid robots have gone through an evolution similar to that of humans. Although some robots walk flat while others move up and down, efficiency and energy consumption remain the main challenges. Some state-of-the-art robots use sophisticated motor control to walk smoothly while demonstrating appalling inefficiency with excessive energy cost, whereas recent robots rival human efficiency by relying on passive dynamic mechanisms with much simple active control of actuators (Collins *et al.* 2005), which echoes what we have found as crucial physiological determinants of optimal human walking.

In conclusion, our study showed that not only do humans move up and down in normal walking to save energy via a pendulum-like mechanism (Cavagna *et al.* 1976; Ortega & Farley, 2005) but also to make their muscles work efficiently. In fact, walking flat makes the muscles work in unfavourable conditions that waste energy. The

experience of million of years of marriage between extreme solutions in search for optimal bipedalism, which seems to have managed the compromise between muscle work and efficiency and come to a halt halfway between flatness and bounce, may provide a lesson in walking physiology for future robots.

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