Dynamics of the body centre of mass during actual acceleration across transition speed

Veerle Segers*, Peter Aerts, Matthieu Lenoir and Dirk De Clerq

Ghent University, Department of Movement and Sport Sciences, Watersportlaan 2, Ghent B-9000, Belgium

*Author for correspondence (e-mail: Veerle.Segers@Ugent.be)

Summary

Judged by whole body dynamics, walking and running in humans clearly differ. When walking, potential and kinetic energy fluctuate out-of-phase and energy is partially recovered in a pendulum-like fashion. In contrast, running involves in-phase fluctuations of the mechanical energy components of the body centre of mass, allowing elastic energy recovery. We show that, when constantly accelerating across the transition speed, humans make the switch from walking to running abruptly in one single step. In this step, active mechanical energy input triples the normal step-by-step energy increment needed to power the imposed constant acceleration. This extra energy is needed to launch the body into the flight phase of the first running step and to bring the trunk into its more inclined orientation during running. Locomotor cycles immediately proceed with the typical in-phase fluctuations of kinetic and potential energy. As a result, the pendular energy transfer drops in one step from 43% to 5%. Kinematically, the transition step is achieved by landing with the knee and hip significantly more flexed compared to the previous walking steps. Flexion in these joints continues during the first half of stance, thus bringing the centre of mass to its deepest position halfway through stance phase to allow for the necessary extension to initiate the running gait. From this point of view, the altered landing conditions seem to constitute the actual transition.

Key words: biomechanics, walking, running, transition, centre of mass.

Introduction

When walking faster and faster, humans will spontaneously start running. Generally, both gaits are distinguished from each other on the basis of the difference in dynamics of the body's centre of mass (Alexander, 2003; Cavagna et al., 1977; Farley and Ferris, 1998; Mochon and McMahon, 1980; Srinivasan and Ruina, 2006; Willems et al., 1995). Walking is characterized by out-of-phase oscillations of kinetic and gravitational potential energy of the body centre of mass (COM), whereas in running these mechanical energy components fluctuate in-phase, often referred to in the literature as the inverted pendulum and spring-mass paradigms, respectively (Blickhan, 1989; Blickhan and Full, 1987; Cavagna et al., 1977; McMahon and Cheng, 1990; Mochon and McMahon, 1980) (see also Farley and Ferris, 1998). Recently, Geyer and co-workers developed a spring-mass model for walking, which showed that limb compliance plays a functional role not only in bouncing gaits but also in the vaulting walk (Geyer, 2005; Geyer et al., 2006).

Next to this dynamic discrimination, a more operational definition based on spatio-temporal characteristics is often used to discern walking from running in human gait analysis: duty factors (DF; the fraction of the stride time a particular limb is in stance) >0.5 are referred to as walking; DF <0.5

characterize running gaits (see Aerts et al., 2000; Ahn et al., 2004; Alexander, 1989; Alexander, 2004; Bramble and Lieberman, 2004; Donelan and Kram, 1997; Donelan and Kram, 2000; Farley and Ferris, 1998; Gatesy, 1999; Grieve and Gear, 1966; Minetti, 1998; Minetti and Alexander, 1997; Nilsson and Thorstensson, 1987; Rubenson et al., 2004; Segers et al., 2006; Van Coppenolle and Aerts, 2004; Verstappen and Aerts, 2000; Zatsiorsky et al., 1994). When this spatio-temporal definition is applied to the natural gaits of humans, the distinction between walking and running is very clear and strict (but see below). A double stance phase (DF>0.5; walking) is either present or not, and the transition between both modes of locomotion when defined on the spatio-temporal basis evidently occurs within one step (Segers et al., 2006).

From animals it is known that transition speeds defined on the basis of the above criteria might differ. Some birds, crabs, primates and elephant, for instance, show dynamic running, while still walking spatio-temporally (DF>0.5) (e.g. Alexander and Jayes, 1978; Blickhan and Full, 1987; Gatesy, 1999; Gatesy and Biewener, 1991; Hutchinson et al., 2003; Kimura, 1996; Muir et al., 1996; Schmitt, 1999; Schmitt, 2003). This is known as 'grounded running' (Rubenson et al., 2004) or Groucho running (McMahon et al., 1987). In humans, it is still

an open question whether gait discrimination according to both definitions concur or not.

Moreover, to date (and despite the common use of COM-dynamics to discern walking from running), nothing is known about precisely how the behaviour of the COM changes at transition. Do the COM-dynamics gradually shift from the walking to the running state? In other words: does the characteristic vaulting pattern of the COM (inverted pendulum) flatten step by step when approaching the transition speed, to pass smoothly into the (spring-like) sagging of the stance limb when running? Or, does a transition in a more mathematical sense exist, being characterized by a sudden and clear discontinuity in mechanical behaviour?

Although many studies discuss aspects of the transition between walking and running in humans, most are based on the analyses of locomotion at steady speeds (Daniels and Newell, 2003; Getchell and Whitall, 2004; Hreljac, 1993a; Hreljac, 1993b; Hreljac, 1995a; Hreljac, 1995b; Hreljac et al., 2001; Mercier et al., 1994; Minetti et al., 1994; Neptune and Sasaki, 2005; Nilsson et al., 1985; Nilsson and Thorstensson, 1989; Prilutsky and Gregor, 2001; Raynor et al., 2002; Sasaki and Neptune, 2006). There are only a few reports of what happens when actually accelerating across the transition between walking and running (Diederich and Warren, 1995; Diederich and Warren, 1998; Li, 2000; Li and Hamill, 2002; Segers et al., 2006; Thorstensson and Roberthson, 1987). Yet, knowledge gained from such conditions allows one to obtain insights into the manner in which COM-dynamics change through transition. In this way, the interplay between neuromuscular control and the physical characteristics of the human locomotor system (Farley and Ferris, 1998), as well as the level of self-organization in motor control (Aerts et al., 2000; Diedrich and Warren, 1995), can be addressed.

In order to fill this lacuna, the aim of the present paper was to provide answers to the following questions. How do COM-dynamics change during human locomotion when actually accelerating across the transition speed? What are the dynamical and kinematical aspects behind the observed behaviour of the COM at transition? What is the relationship between the spatio-temporal and dynamical definitions of walking and running in humans?

Materials and methods
Subjects and set-up

To assess transition during constant acceleration we chose to study overground rather than treadmill locomotion, in order to exclude any potential artefacts. Nine female subjects participated in the present study. The influence of anthropometry was minimized by selecting test persons within a limited height and mass range (1.69±0.03 m; 64.89±4.52 kg) (Getchell and Whitall, 2004; Hreljac, 1995a). They were instructed to follow a constantly accelerating running light (0.15 m s^{-2}) along a 50 m long running track. The accuracy with which they did this was visually judged by three experienced researchers. After 35 m along the track, 3D kinematics were recorded over a sufficiently long period (±7 m) to cover 6–7 successive steps (240 Hz using eight infrared cameras (Pro Reflex, Qualisys AB, Gothenburg, Sweden) and Qualisys software). Trials were selected for further analysis when the acceleration was scored as constant by the three observers and when the transition occurred within the period captured by the camera system. Steps (from one heel contact to the next) were labelled in the following way: step 0 = transition step, the first step without double support phase; step $-n$ = nth step before step 0; step $+n$ = nth step after step 0.

Anatomical reflective markers were placed according to McClay and Manal (McClay and Manal, 1999) on the greater trochanter, the medial and lateral femoral condyles, the medial and lateral malleolus, the medial and lateral part of the calcaneus, the head of the first and fifth metatarsals, the anterior superior iliac spine, the top of the acromion, the medial and lateral epicondyle of the humerus and the styloid processes of radius and ulna. The tracking markers consisted of rigid plates secured to the thigh and the shank, and markers on the calcaneus, on top of the foot arch, on the os sacrum and on the 7th cervical vertebra. Three markers were also used to track the movements of the upper and lower arm. Following calibration (recording while standing), subjects were familiarized with the test protocol. Raw displacement data were filtered using a Butterworth low-pass filter at 18 Hz.

COM position and validation

An 11-segment model (forearms, upper arms, head+trunk, thighs, shanks, feet) was used to calculate the position of the COM (Visual 3D v3.19.0, C-motion, Gaithersburg, MD, USA) for the 6–7 steps captured by the camera system. To validate these calculations, a 2 m force plate (AMTI, Watertown, MA, USA) was built into the running track in order to obtain ground reaction forces (GRF) of one (occasionally two) of the video-captured steps. Thus, GRF were randomly obtained within the range of step –3 (i.e. last three walking steps before transition) to step +3 (i.e. first three running steps after transition), depending upon where precisely transition occurred in the 3D-period covered. For 20 steps, COM displacements were calculated from the force recordings [double numerical integration of accelerations deduced from the forces (cf. Eames et al., 1999)] and compared with the associated COM displacements as obtained from the kinematic recordings (example in Fig. 1). Average measures of intra-class correlation coefficients were calculated and resulted in values varying between 0.920 and 0.987 ($P<0.01$). This, together with the fact that COM displacements obtained using both methods fluctuate about the same mean ($P=0.408$), indicated that kinematic measures were highly reliable, supporting the use of the methods in the present study to obtain the instantaneous horizontal and vertical position of the COM for seven successive over-ground accelerating steps, including the transition between walking and running. First and second derivatives of these positions against time yielded velocities (horizontal: v_x, vertical: v_z) and accelerations (horizontal: a_x,
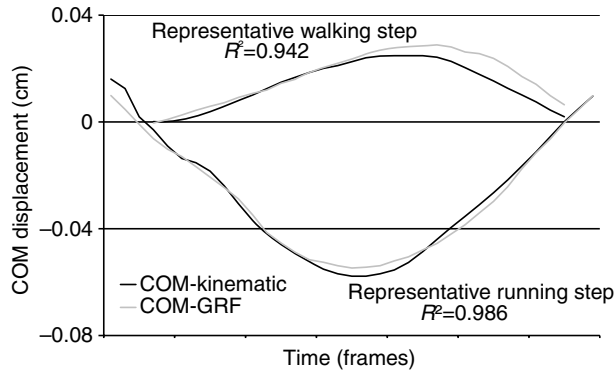
Fig. 1. Comparison of the vertical displacement of the COM by ground reaction forces (GRF) and kinematically. One representative walking and one running step in the present protocol are shown. This comparison is made for available steps (at least one for each subject).

vertical: a_z), respectively, that were filtered using a Butterworth Low Pass filter at 18 Hz.

Energy and power

Gravitational potential energy [$E_{pot}=M_b\,\boldsymbol{g}\,h_i$; where M_b=mass of the subject, $\boldsymbol{g}$=gravitational constant (9.81 m s^{-2}), h_i=instantaneous COM-height], and kinetic energy due to horizontal and vertical velocity ($E_{kin}=M_b\,\mathbf{v}_x^2/2$ and $M_b\,\mathbf{v}_z^2/2$, respectively) fluctuations of the COM were determined. Results were normalized over subjects and trials (cf. Fig. 1) by expressing E_{pot} as a fraction of $M_b\,\boldsymbol{g}\,h_r$ (with h_r the height of the COM in resting position) and E_{kin} as a fraction of $M_b\,\mathbf{v}_x^2/2$ (where v_{trans} is the trial-specific horizontal speed at which transition occurred). Instantaneous power profiles for the COM were calculated [$P_x=M_b\,\mathbf{a}_x\mathbf{v}_x$; $P_z=M_b(\boldsymbol{g}+\mathbf{a}_z)\mathbf{v}_z$; $P_{ext}=P_x+P_z$]. To estimate pendular energy transfer [R_{step} (cf. Cavagna et al., 2002)], the positive work done on the COM in the horizontal (^+W_x) and vertical (^+W_z) directions and the positive external work in the sagittal plane ($^+W_{ext}$) were calculated by integrating the positive phases of the associated power profiles (P_x, P_z, P_{ext}, respectively) during single stance. The fraction of mechanical energy exchange is given by: ($^+W_x+^+W_z-^+W_{ext}$)/ ($^+W_x+^+W_z$), yielding in essence the calculation method used in Heglund et al. (Heglund et al., 1982).

Regressions and statistical comparisons

The kinetic energy regressions against time were calculated for walking and running steps separately. As kinetic energy is a function of the velocity squared, an accelerated movement yields a non-linear relationship between E_{kin} and time, by definition. However, because of the limited velocity range considered, exponential and linear regressions are virtually identical (very similar R^2-values). Therefore, linear regressions were used for simplicity: their slopes represent the average power necessary to accelerate over the involved velocity ranges under consideration.

A repeated-measures ANOVA with *post-hoc* Bonferroni tests was used to examine differences in R_{step} and kinematic variables between the seven successive steps and in slopes and intercepts between walking, transition and running. Values are reported as means ± s.d.

Results
General

Based on the kinematics of the body centre of mass (COM), the forward speed at the heel contact initiating step 0=2.17 m s^{-1} (±0.02 m s^{-1}; see also Table 1). This is presently considered the walk-to-run transition (WRT) speed. Measured over the time intervals coinciding with step –3 to step –1, as well as step +1 to step +3, the acceleration of the COM=0.15 m s^{-2} (±0.02 m s^{-2} and 0.03 m s^{-2}, respectively). This is identical to the imposed acceleration of the running light (see Materials and methods). Over the course of step 0, however, the measured velocity increase of the COM corresponds to an acceleration of 0.23 m s^{-2} (±0.03 m s^{-2}). This is reflected in a tripling of the net work and mean step power required for step 0, when compared to that required for the preceding walking, respectively succeeding running, steps (see below). Table 1 presents the step durations and velocities at initial contact for all examined steps (–3 to +3).

Kinetic and potential energy fluctuations

Fig. 2A shows that fluctuations in kinetic and gravitational potential energy of the COM abruptly change from an out-of-phase (red arrows) to an in-phase (blue arrows) pattern. As a result, the pendular energy transfer drops in one step from 43% to 5% (Fig. 2A). Potential energy (Fig. 2A) naturally fluctuates about $M_b\,\boldsymbol{g}\,h_r$ (relative=1, purple horizontal line in Fig. 2A), but amplitudes double when subjects start running. This is because at step 0 the COM keeps lowering when leaving the vaulting pattern of the previous walking step (step –1; Fig. 2A).

Fig. 2B presents linear regression of total kinetic energy against time for both walking (step –3 to step –1) and running (step +1 to step +3), separately. Slopes equal 22.37±4.86 W and 23.53±9.45 W and are a measure for the average power input needed to accelerate in the speed range covered during the last three walking steps and the first three running, respectively. As test persons followed a constantly accelerating running light, these slopes are not statistically different

Fig. 2. Energy fluctuations of the COM. (A) Out-of-phase (walking; red arrows) and in-phase oscillations (running; blue arrows) of kinetic energy and gravitational potential energy of the COM on a normalized time-basis with an indication of the efficiency of energy exchange (%=percentage of recovery pendulum). (B) Total kinetic energy (black line) is presented as a fraction of the total kinetic energy at transition (blue line). The red lines are the regressions for walking and running steps. (C) Kinetic energy due to vertical velocity of the COM, with horizontal regressions for walking and running steps. The black line indicates the mean of the average of all trials (N=3–5) with each subject (N=9). Grey lines indicate standard deviation (s.d.) between subjects. Grey and black bars on the x-axis represent contact with the ground by alternate feet.
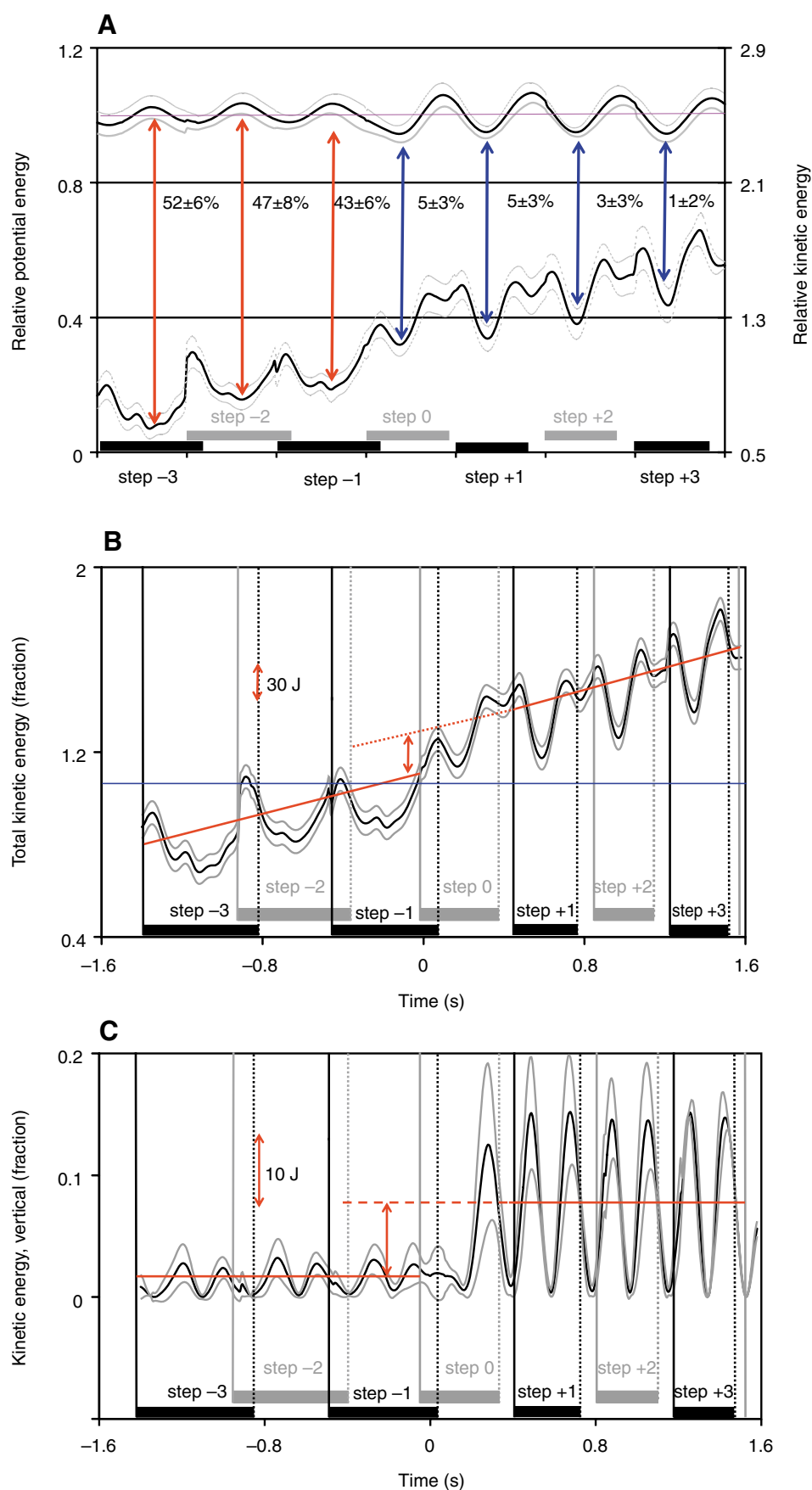
A

B

C

Fig. 2. See previous page for legend.

Step	Walking steps			Transition step	Running steps		
	−3	−2	−1	0	+1	+2	+3
Velocity (m s^{-1})	1.95±0.15	2.03±0.14	2.10±0.16	2.17±0.19	2.31±0.19	2.38±0.22	2.45±0.21
Step duration (s)	0.48±0.02	0.48±0.02	0.46±0.02	0.47±0.05	0.41±0.03	0.41±0.04	0.40±0.04

Values are means ± s.d. (*N*=9).

(P=0.398). The intercepts, however, do differ significantly (P<0.01), representing a definite energy jump during step 0 (double-headed red arrow in Fig. 2B).

This means that at transition (step 0), active mechanical energy input (=33.86±8.70 J) triples the step-by-step energy increment needed to power the constant acceleration of progression at the transition speed (=9.66±1.09 J: the energy solely required to follow the accelerating running light during step 0). Apart from the latter component for overall acceleration, being approximately one third of the energy jump, another third (=9.99±1.99 J) of the energy input at step 0 is required to increase the average vertical kinetic energy from the walking to the running level (red double-headed arrow in Fig. 2C). The work for this extra kinetic energy is delivered during the second half of stance of step 0 to accelerate the COM upwards in order to initiate the first small flight phase (Fig. 2C). The remaining third of the kinetic energy jump in step 0 relates to a short-lasting increase in forward velocity of the COM, coming on top of the expected step-by-step velocity increase as a result of the overall acceleration. This is because the HAT-segment (head-arms-trunk) rotates further forward during stance of step 0 compared to the preceding walking steps (step −3 to step −1) (Fig. 3A; i.e. increased range of motion). This results in a significantly larger forward displacement (hence forward velocity) of the COM during that step (Δ*v*=0.06±0.03 m s^{-1}, resulting in an increase of 11.74±4.00 J). In the subsequent running steps (step +1 to step +3) the angular range of motion of the HAT decreases again, becoming similar in magnitude to that observed in walking, but oscillations now occur about a more inclined position. Due to the latter, the forward velocity increase observed in step 0 (to bring the trunk in the running configuration) was not observed in the running steps. So the slopes of the regressions in kinetic energy due to horizontal velocity of walking and running steps did not differ (Fig. 2B).

Kinematical realization of the transition step

Fig. 3A illustrates how the switch from walking to running is realized kinematically. In step 0, the foot placement occurs more in front of the hip, with significantly more plantar, hip and knee flexion (P<0.05) compared to the landing configurations in the previous walking steps (step −3 to step −1). This altered landing condition is only prepared late in the preceding swing phase (last 15% of swing phase duration, Fig. 3B). During the subsequent stance, hip knee and ankle first go further in deeper flexion, lowering the COM (instead of the typical upwards vaulting motion observed in the previous walking steps). This

allows for more powerful leg extension during the second part of stance, sufficient to propel the body in its first flight phase. As a result, the change in dynamics (from out-of-phase to in-phase fluctuations) and the transition according to the kinematical definition [duty factor <0.5 (Alexander, 1989; Farley and Ferris, 1998; Segers et al., 2006)] occur in the same step.

Power of the COM
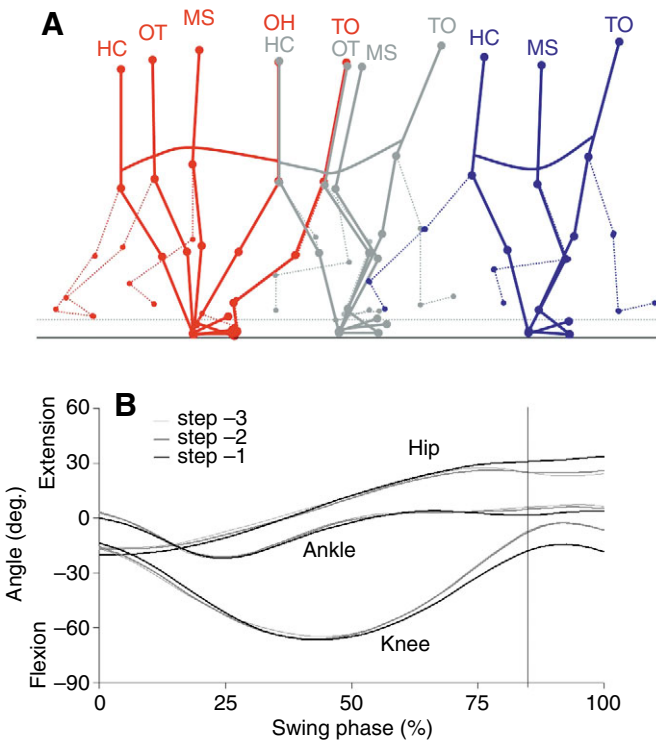
Instantaneous COM power profiles presented in Fig. 4

Fig. 3. Kinematics of the transition. (A) Average kinematics of the last walking step, the transition step and the first running step. The red line represents the last walking step, the grey line the transition step and the blue line the first running step. Stick figures were created at specific key events of each step, being heel contact (HC), opposite toe-off (OT), midstance (MS), opposite heel contact (OH) and toe-off (TO). (B) Hip, knee and ankle angles during swing in the last walking steps. Light grey line, step −3; dark grey line, step −2; black line, step −1. Negative sign stands for flexion (ankle, dorsiflexion), a positive sign for extension (ankle, plantar flexion). The vertical blue line indicates the beginning of the final 15% of the swing phase.
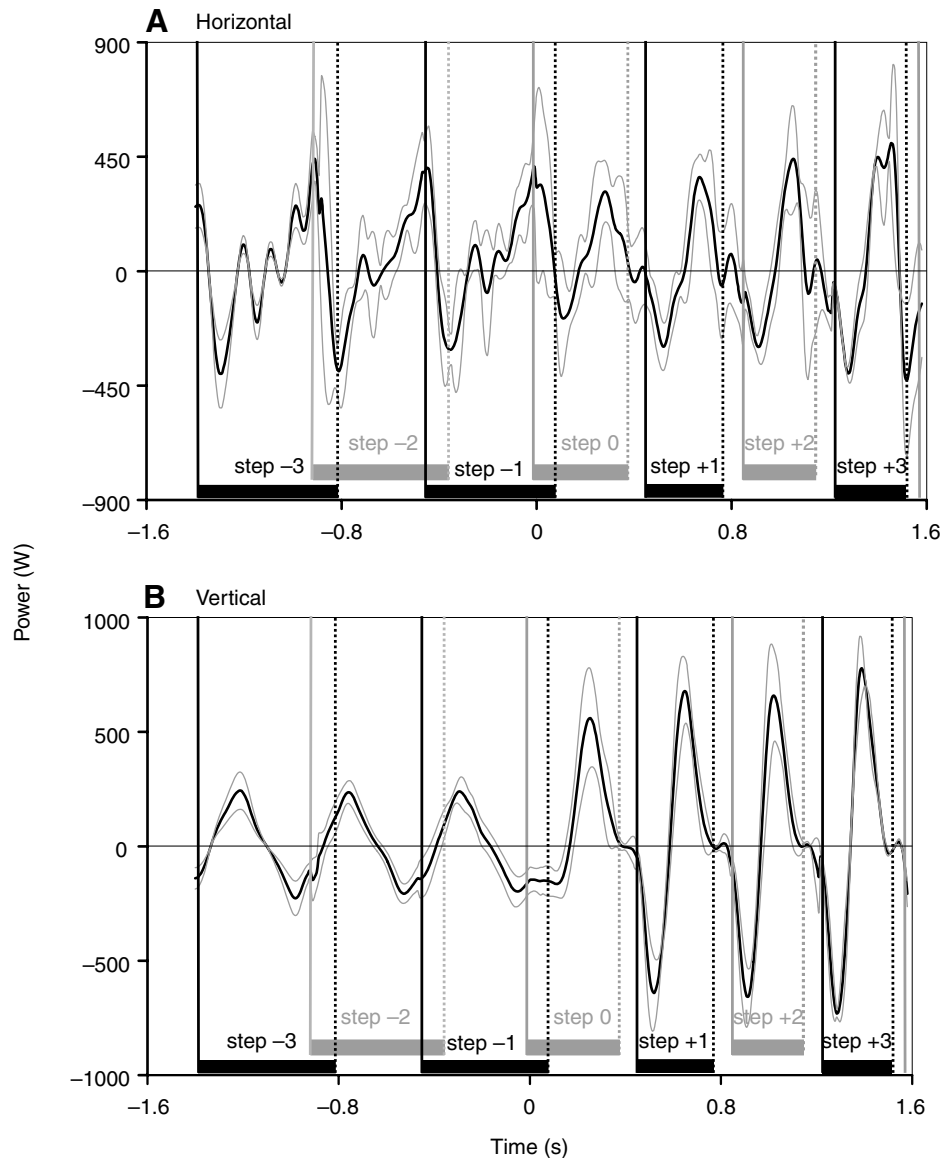
Fig. 4. Average power fluctuations of the COM; (A) horizontal, (B) vertical. The black line indicates the mean of the average of all trials (*N*=3–5) of each subject (*N*=9). Grey lines indicate s.d. between subjects. Grey and black bars on the *x*-axis represent contact with the ground by alternate feet.

confirm the above conclusions. For running steps, negative COM power early in stance represents energy extracted from the system, either dissipated as heat or temporarily stored as elastic energy in tendinous structures. In the latter case, this energy can be recovered during the second part of stance when energy is added to the system again (positive COM power). For step 0, however, negative COM power levels during the first part of stance remains very small, both in fore–aft (Fig. 4A) and vertical (Fig. 4B) directions.

Discussion

In the present study, we provide for the first time evidence that the transition between walking and running emerges as an abrupt change in the dynamics of the system. Furthermore, this transition is initiated just prior to foot placement of step 0. At this stage, it is unclear whether this ultimate adaptation of the swing phase is controlled or whether it reflects the intrinsic dynamics of the system. Similarly it remains an open question whether the deeper limb flexion in the first half of stance of step 0 is actively controlled or is just the result of the altered mechanical conditions at landing of step 0. Regardless, it seems plausible that the deeper flexion and associated extensor lengthening trigger a simple reflex loop, which initiates the increased extensor activity that generates the observed energy jump. The latter aspects need further research as it is impossible to speculate about the existence and the exact timing of this preparation without recording muscle activity.

During step 0 negative COM power levels remain small. Consequently, the subsequent positive COM power peak must be delivered to a large extent by concentric muscle activity. Assuming 100% elastic storage and recovery of the negative COM power, 68±14% of the observed energy jump at transition (23.02 J) must still be generated in this way. Given the observed kinematics (Fig. 3A,B), this is probably at the expense of the large extensor muscle groups of the knee and ankle of the stance limb.

Obviously the sudden shift in average position of the trunk resulting in the short-lasting forward velocity increase of the COM (see above) also requires work to be delivered to a large extent by muscles. Simple modelling of the forward rotation of the HAT during stance of step 0 as a result of the moment induced by gravity only (in practice: double integration of the angular equation of motion with gravity as the sole input) results in a rotation of 1.33°, which is merely a fraction of the observed displacement of 8.53±0.94°. Therefore, active input from the muscles flexing the hip is also required for the forward movement of the trunk during step 0. Clearly, the muscles are capable of delivering the necessary power, as in other tasks the requirements are much higher, for example in countermovement jumping (Vanrenterghem et al., 2004).

How do these findings compare to *quasi*-static approaches in which steady state locomotion at different speeds is examined? The trajectory of the COM was found to be dramatically different between walking and running at the transition speed (Lee and Farley, 1998). At midstance the COM reaches its highest point during walking and its lowest point during running. In the present study these findings were confirmed, as the COM had already reached it lowest point at mid-stance during the transition step 0. Moreover, at heel contact of step 0 even the stance-limb touchdown angle was adapted, which is indicated by more flexion of knee and hip. According to Lee and Farley this is one of the essential differences leading to the different dynamics of walking and running (Lee and Farley, 1998). Comparison with other studies is difficult as the COM has not been closely examined.

Recently, a published abstract (Lipfert et al., 2006) reported on subjects walking on a treadmill at a constant speed near the transition speed. Test persons performed the WRT on an acoustic signal, but without changing the overall locomotor speed (i.e. the belt speed). These authors found a difference in leg compliance (more knee flexion) and steeper angle of attack of the lower leg during step 0. Despite the differences in the experimental protocols (constant velocity, conditional transition *versus* constant acceleration, spontaneous transition), these findings are in agreement with our conclusions.

As mentioned in the Introduction, very few papers deal with aspects of transition during actual acceleration. The WRT-speed in the present study is comparable (2.17 m s^{-1}) to these studies examining acceleration across transition speed on a treadmill (Diederich and Warren, 1995; Diederich and Warren, 1998; Li, 2000; Li and Hamill, 2002; Segers et al., 2006; Thorstenson and Robertson, 1987). In contrast to recent findings concerning ground reaction forces (Li and Hamill, 2002) and spatiotemporal factors (Segers et al., 2006), WRT is only initiated shortly before landing of the transition step WRT and is completed during the course of the transition step. Furthermore, the methodology of the treadmill is a factor that should not be neglected. To explore the latter, further research in the transition phenomenon should examine kinematics and the behaviour of the COM in an accelerated protocol on a treadmill to explore differences and similarities with the results of the present research.

List of abbreviations

$^{+}W_{x}$, $^{+}W_{z}$, $^{+}W_{ext}$	positive work done on the COM in horizontal, vertical direction, sagittal plane
$\mathbf{a}_{x}$, $\mathbf{a}_{z}$	horizontal, vertical accelerations
COM	centre of mass
DF	duty factor
E_{kin}	kinetic energy
E_{pot}	gravitational potential energy
g	gravitational constant
GRF	ground reaction force
HAT	head-arms-trunk
h_{i}	instantaneous COM-height
h_{r}	height of the COM in resting position
M_{b}	mass of subject
P_{x}, P_{z}, P_{ext}	instantaneous power profiles for the COM in horizontal, vertical direction, sagittal plane
R_{step}	pendular energy transfer
v_{trans}	trial-specific horizontal speed at which transition occurred
$\mathbf{v}_{x}$, $\mathbf{v}_{z}$	horizontal, vertical velocities
WRT	walk-to-run transition

References

Aerts, P., Van Damme, R., Van Elsacker, L. and Duchene, V. (2000). Spatio-temporal gait characteristics of the hind-limb cycles during voluntary bipedal and quadrupedal walking in bonobos (*Pan paniscus*). *Am. J. Phys. Anthropol*. **111**, 503-517.

Ahn, A. N., Furrow, E. and Biewener, A. A. (2004). Walking and running in the red-legged running frog, *Kassina maculata*. *J. Exp. Biol.* **207**, 399-410.

Alexander, R. McN. (1989). Optimization and gaits of locomotion in vertebrates. *Physiol. Rev.* **4**, 1199-1227.

Alexander, R. McN. (2003). Modelling approaches in biomechanics. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **358**, 1429-1435.

Alexander, R. McN. (2004). Bipedal animals and their differences from humans. *J. Anat.* **204**, 321-330.

Alexander, R. McN. and Jayes, A. S. (1978). Vertical movements in walking and running. *J. Zool. Lond.* **185**, 27-40.

Blickhan, R. (1989). The spring-mass model for running and hopping. *J. Biomech.* **22**, 1217-1227.

Blickhan, R. and Full, R. J. (1987). Locomotion energetics of the ghost crab. II. Mechanics of the centre of mass during walking and running. *J. Exp. Biol.* **130**, 155-174.

Bramble, D. M. and Lieberman, D. E. (2004). Endurance running and the evolution of *Homo*. *Nature* **432**, 345-352.

Cavagna, G. A., Heglund, N. C. and Taylor, C. R. (1977). Mechanical work in terrestrial locomotion: two basic mechanisms for minimizing energy expenditure. *Am. J. Physiol.* **233**, R243-R261.

Cavagna, G. A., Willems, P. A., Legramandi, M. A. and Heglund, N. C. (2002). Pendular energy transduction within the step in human walking. *J. Exp. Biol.* **205**, 3413-3422.

Daniels, G. L. and Newell, K. M. (2003). Attentional focus influences the walk-run transition in human locomotion. *Biol. Physiol.* **63**, 163-178.

Diedrich, F. J. and Warren, W. H. (1995). Why change gaits? Dynamics of the walk-run transition. *J. Exp. Psychol. Hum. Percept. Perform.* **21**, 183-202.

Diedrich, F. J. and Warren, W. H. (1998). The dynamics gait transitions: grade and load. *J. Mot. Behav.* **30**, 60-78.

Donelan, J. M. and Kram, R. (1997). The effect of reduced gravity on the kinematic of human walking: a test of the dynamic similarity hypothesis for locomotion. *J. Exp. Biol.* **200**, 2193-3201.

Donelan, J. M. and Kram, R. (2000). Exploring dynamic similarity in human running using simulated gravity. *J. Exp. Biol.* **203**, 2405-2415.

Eames, M. H. A., Cosgrove, A. and Baker, R. (1999). Comparing methods of estimating the total body centre of mass in three-dimensions in normal and pathological gaits. *Hum. Mov. Sci.* **18**, 637-646.

Farley, C. T. and Ferris, D. P. (1998). Biomechanics of walking and running: from center of mass movement to muscle action. *Exerc. Sport Sci. Rev.* **26**, 253-285.

Gatesy, S. M. (1999). Guineafowl hind limb function. I. Cineradiographic analysis and speed effects. *J. Morphol.* **240**, 115-125.

Gatesy, S. M. and Biewener, A. A. (1991). Bipedal locomotion: effects of speed, size and limb posture in birds and humans. *J. Zool.* **224**, 127-147.

Getchell, N. and Whitall, J. (2004). Transitions to and from asymmetrical gait patterns. *J. Mot. Behav.* **36**, 13-27.

Geyer, H. (2005). Simple models of legged locomotion based on compliant limb behaviour. PhD thesis, University of Jena, Germany.

Geyer, H., Seyfarth, A. and Blickhan, R. (2006). Compliant leg behaviour explains basic dynamics of walking and running. *Proc. Biol. Sci.* **273**, 2861-2867.

Grieve, D. W. and Gear, R. J. (1966). The relationships between length of stride, step frequency, time of swing and speed of walking for children and adults. *Ergonomics* **5**, 379-399.

Heglund, N. C., Cavagna, G. A. and Taylor, C. R. (1982). Energetics and mechanics of terrestrial locomotion. III. Energy changes of the centre of mass as a function of speed and body size in birds and mammals. *J. Exp. Biol.* **79**, 41-56.

Hreljac, A. (1993a). Preferred and energetically optimal gait transition speeds in human locomotion. *Med. Sci. Sports Exerc.* **25**, 1158-1162.

Hreljac, A. (1993b). Determinants of the gait transition speed during human locomotion: kinetic factors. *Gait Posture* **1**, 217-223.

Hreljac, A. (1995a). Effects of physical characteristics on the gait transition speed during human locomotion. *Hum. Mov. Sci.* **14**, 205-216.

Hreljac, A. (1995b). Determinants of the gait transition speed during human locomotion: kinematic factors. *J. Biomech.* **28**, 669-677.

Hreljac, A., Arata, A., Ferber, R., Mercer, J. A. and Row, B. R. (2001). An electromyographical analysis of the role of the dorsiflexors on the gait transition during human locomotion. *J. Appl. Biomech.* **17**, 287-296.

Hutchinson, J. R., Famini, D., Lair, R. and Kram, R. (2003). Are fast-moving elephants really running? *Nature* **422**, 493-494.

Kerdok, A. E., Biewener, A. A., McMahon, T. A., Weyand, P. G. and Herr, H. M. (2002). Energetics and mechanics of human running on different surfaces. *J. Appl. Physiol.* **92**, 469-478.

Kimura, T. (1996). Centre of gravity of the body during the ontogeny of chimpanzee bipedal walking. *Folia Primatol.* **66**, 126-136.

Lee, C. R. and Farley, C. T. (1998). Determinants of the centre of mass trajectory in human walking and running. *J. Exp. Biol.* **201**, 2935-2944.

Li, L. (2000). Stability landscapes of walking and running near gait transition speed. *J. Appl. Biomech.* **16**, 428-435.

Li, L. and Hamill, J. (2002). Characteristics of the vertical ground reaction force component prior to gait transition. *Res. Q. Exerc. Sport* **73**, 229-237.

Lipfert, S., Dittrich, E. and Seyfarth, A. (2006). A strategy for walk-run transitions at constant speeds. *J. Biomech.* **39**, S509.

McClay, I. and Manal, K. (1999). Three-dimensional kinetic analysis of running: significance of secondary planes of motion. *Med. Sci. Sports Exerc.* **31**, 1629-1637.

McMahon, T. A. and Cheng, G. C. (1990). The mechanics of running: how does stiffness couple with speed? *J. Biomech.* **23**, 65-78.

McMahon, T. A., Valiant, G. and Frederick, E. C. (1987). Groucho running. *J. Appl. Physiol.* **62**, 2326-2337.

Mercier, J., Le Gallais, D., Durand, M., Goudal, C., Micallef, J. P. and Préfaut, C. (1994). Energy expenditure and cardiorespiratory responses at the transition between walking and running. *Eur. J. Appl. Physiol.* **69**, 525-529.

Minetti, A. E. (1998). A model equation for the prediction of mechanical internal work of terrestrial locomotion. *J. Biomech.* **31**, 463-468.

Minetti, A. E. and Alexander, R. McN. (1997). A theory of metabolic costs for bipedal gaits. *J. Theor. Biol.* **186**, 467-476.

Minetti, A. E., Ardigo, L. P. and Saibene, F. (1994). The transition between walking and running in humans: metabolic and mechanical aspects at different gradients. *Acta Physiol. Scand.* **150**, 315-323.

Mochon, S. and McMahon, T. A. (1980). Ballistic walking. *J. Biomech.* **13**, 49-57.

Muir, G. D., Gosline, J. M. and Steeves, J. D. (1996). Ontogenity of bipedal locomotion: walking and running in the chick. *J. Physiol.* **493**, 589-601.

Neptune, R. R. and Sasaki, K. (2005). Ankle plantar flexor force production is an important determinant of the preferred walk-to-run transition speed. *J. Exp. Biol.* **208**, 799-808.

Nilsson, J. and Thorstensson, A. (1987). Adaptability in frequency and amplitude of leg movements during human locomotion at different speeds. *Acta Physiol. Scand.* **129**, 107-114.

Nilsson, J. and Thorstensson, A. (1989). Ground reaction forces at different speeds of human walking and running. *Acta Physiol. Scand.* **136**, 217-227.

Nilsson, J., Thorstensson, A. and Halbertsma, J. (1985). Changes in leg movements and muscle activity with speed of locomotion and the mode of progression in humans. *Acta Physiol. Scand.* **123**, 457-475.

Prilutsky, B. I. and Gregor, R. J. (2001). Swing- and support-related muscles differentially trigger human walk–run and run–walk transitions. *J. Exp. Biol.* **204**, 2277-2287.

Raynor, A. J., Yi, C. J., Abernethy, B. and Jong, Q. J. (2002). Are transitions in human gait determined by mechanical, kinetic or energetic factors? *Hum. Mov. Sci.* **21**, 785-805.

Rubenson, J., Heliams, D. B., Lloyd, D. G. and Fournier, P. A. (2004). Gait selection in the ostrich: mechanical and metabolic characteristics of walking and running with and without and aerial phase. *Proc. R. Soc. Lond. B Biol. Sci.* **271**, 1091-1099.

Sasaki, K. and Neptune, R. R. (2006). Differences in muscle function during walking and running at the same speed. *J. Biomech.* **39**, 2005-2013.

Schmitt, D. (1999). Compliant walking in primates. *J. Zool.* **248**, 149-160.

Schmitt, D. (2003). Insights into the evolution of human bipedalism from experimental studies of humans and other primates. *J. Exp. Biol.* **206**, 1437-1448.

Segers, V., Aerts, P., Lenoir, M. and De Clercq, D. (2006). Spatiotemporal characteristics of the walk-to-run and run-to-walk transition when gradually changing speed. *Gait Posture* **24**, 247-254.

Srinivasan, M. and Ruina, A. (2006). Computer optimization of a minimal biped model discovers walking and running. *Nature* **439**, 72-75.

Thorstensson, A. and Roberthson, H. (1987). Adaptations to changing speed in human locomotion: speed of transition between walking and running. *Acta Physiol. Scand.* **131**, 211-214.

Van Coppenolle, I. and Aerts, P. (2004). Terrestrial locomotion in the white stork (*Ciconia ciconia*): spatio-temporal gait characteristics. *Anim. Biol.* **54**, 281-292.

Vanrenterghem, J., Lees, A., Lenoir, M., Aerts, P. and De Clercq, D. (2004). Performing the vertical jump: movement adaptations for submaximal jumping. *Hum. Mov. Sci.* **22**, 713-727.

Verstappen, M. and Aerts, P. (2000). Terrestrial locomotion in the black-billed magpie. I. Spatio-temporal gait characteristics. *Motor Control* **4**, 150-164.

Willems, P. A., Cavagna, G. A. and Heglund, N. C. (1995). External, internal and total work in human locomotion. *J. Exp. Biol.* **198**, 378-393.

Zatsiorsky, V. M., Werner, S. L. and Kaimin, M. A. (1994). Basic kinematics of walking. Step length and step frequency. A Review. *J. Sports*