The dynamics of hylobatid bipedalism: evidence for an energy-saving mechanism?

Evie E. Vereecke[1,2,*], Kristiaan D'Août[1,3] and Peter Aerts[1,4]

[1]*Laboratorium for Functional Morphology, University of Antwerp, Universiteitsplein 1, Wilrijk B-2610, Belgium,*
[2]*Department of Human Anatomy and Cell Biology, University of Liverpool L69 3GE, UK,* [3]*Centre for Research and Conservation, Belgium and* [4]*Department of Movement and Sports Sciences, University of Ghent, Belgium*

*Author for correspondence at address 2 (e-mail: evie.vereecke@liverpool.ac.uk)

Summary

When gibbons travel through the forest canopy, brachiation is alternated with short bipedal bouts over horizontal boughs. We know, from previous research, that brachiation is a very efficient locomotor mode that makes use of a pendulum-like exchange of energy, but to date, nothing is known about the dynamics of hylobatid bipedalism. We wondered if gibbons also make use of an efficient gait mechanism during bipedal locomotion. To investigate this, we calculated oscillations of the centre of mass (COM), energy fluctuations, recovery rates and power outputs from the 3D ground reaction forces. These ground reaction forces were collected during spontaneous bipedal locomotion of four untrained white-handed gibbons (*Hylobates lar*) over an instrumented walkway (with an AMTI force plate). Excursions of the COM are relatively large during hylobatid bipedalism and the fluctuations of potential and kinetic energy are largely in-phase. Together with the low inverted pendulum recovery rates, this points to a spring-mass mechanism during bipedal locomotion. Although the well-developed Achilles tendon of gibbons seems to be a good candidate for the storage and recoil of elastic energy, this is not supported by kinematical data of the ankle joint. Instead, we suggest that the knee extensor muscle tendon unit functions as an energy-saving mechanism during hylobatid bipedalism, but detailed anatomical data is needed to confirm this suggestion. At low speeds gibbons use either pendular or spring mechanics, but a clear gait transition as seen in most quadrupedal mammals is absent. At moderate to high velocities, gibbons use a bouncing gait, generally without aerial phases. This supports the view that aerial phases are not a prerequisite for spring-mass mechanics and reinforces the claim that duty factor alone should not be used to distinguish between a walk and run.

Key words: white-handed gibbon, *Hylobates lar*, primate locomotion, biomechanics, energy recovery.

Introduction

Humans, like most terrestrial animals, have developed energy-saving mechanisms to reduce the cost of locomotion. Walking uses an 'inverted pendulum' (IP) mechanism, enabling an effective exchange between potential and kinetic energy (Cavagna et al., 1977; Alexander, 1991a; Alexander, 1995) (Fig. 1). Running exploits a 'spring-mass' mechanism, which is based on the storage and recoil of elastic energy in tendons, muscles and ligaments (Blickhan, 1989; Alexander, 1991a; Alexander, 1991b; Farley and Ferris, 1998) (Fig. 1). An even more effective mechanism is used during brachiation of gibbons. In this suspensory gait there is a pendular exchange of potential and kinetic energy, like in the IP mechanism, but the main feature of this gait is the minimization of collisional energy loss (Bertram and Chang, 2001; Usherwood and Bertram, 2003; Bertram, 2004; Gomes and Ruina, 2005). Most arboreal travel is done using this fast and economical progression mode, but from time to time gibbons also locomote bipedally (4–12% of their locomotor activities) (Carpenter, 1964; Fleagle, 1976; Gittins, 1983; Cannon and Leighton, 1994). The question then arises whether an energy-saving mechanism is also applicable during hylobatid bipedalism. Specifically, this paper attempts to answer the following questions. (1) Do gibbons use an energy-saving mechanism during bipedalism? And if so, (2) is this mechanism used at all speeds or is there a speed-related gait transition during hylobatid bipedalism?

Previous kinetic studies on hylobatid bipedalism have shown that all bipedal bouts investigated so far lack a clear double-humped vertical force pattern (Ishida et al., 1976; Kimura et al., 1977; Okada et al., 1983; Vereecke et al., 2005a). Moreover, in a recent publication (Schmitt, 1999), Schmitt remarks that stiff-leg walking does not provide an advantage during arboreal locomotion because it involves high
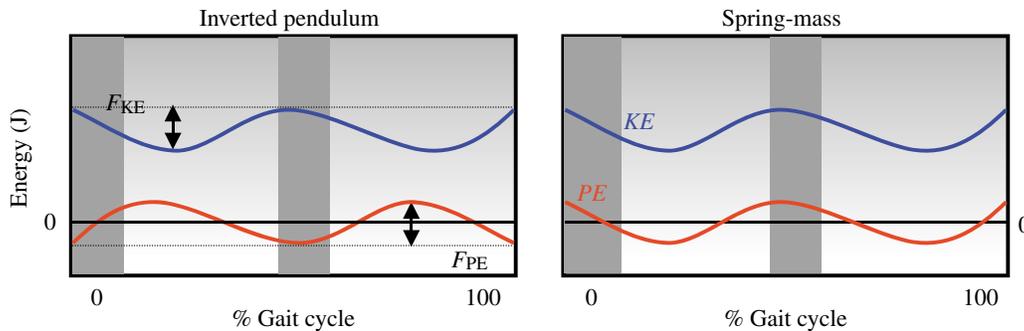
Fig. 1. In an inverted pendulum (IP) gait, the potential (*PE*; red line) and kinetic energy (*KE*; blue line) fluctuate out-of-phase, and energy exchange between *PE* and *KE* is possible. If the amplitudes of the *PE* (F_{PE}) and *KE* fluctuations (F_{KE}) are similar, there will be an optimal energy recovery *via* the IP mechanism. In a spring-mass gait, *PE* and *KE* fluctuate in-phase and there is no energy transfer between *PE* and *KE*. Instead, energy can be stored in elastic tissues during initial stance and released at push-off. This mechanism is active during human running and effectuates an energy recovery of ca. 35%.

impact forces at the hind limbs and creates vertical oscillations of the substrates on which the animals walk. Instead, arboreal primates will generally use a compliant gait in order to flatten the path of the COM and to reduce impact velocity and force (Schmitt, 1999). This makes us expect that an inverted pendulum mechanism will be absent during hylobatid bipedalism, but it does not cancel out the presence of a spring-mass mechanism. In addition, the fact that all bipedal bouts investigated so far have a similar vertical force pattern (Vereecke et al., 2005a) suggests that all bipedal bouts belong to the same locomotor mechanism and that a gait transition is absent. This prediction is also supported by an associated kinematic study, which found no abrupt speed-related change in spatiotemporal and kinematic gait parameters over the entire speed range tested (Vereecke et al., 2006a; Vereecke et al., 2006b).

These predictions are evaluated by calculating the centre of mass (COM) and associated energy fluctuations from the ground reaction forces during spontaneous hylobatid bipedalism. This should reveal if gibbons use an energy-saving gait mechanism during their bipedal locomotion and also clarify whether or not gait transitions are present in hylobatid bipedalism. In addition, we also calculated the external mechanical work to get an idea of the mechanical energy cost of the bipedal locomotion of gibbons.

Materials and methods
Data collection

Data were obtained from four untrained white-handed gibbons (*Hylobates lar* L.), two adults, one adolescent (6 years) and one juvenile (3–4 years), during voluntary bipedal locomotion over an instrumented walkway in the Wild Animal Park Planckendael, Belgium. The experimental set-up consists of a 4 m-long instrumented walkway with a built-in force plate (AMTI, 1.0 m×0.4 m) and pressure mat (footscan®, 1.0 m×0.4 m). The pressure mat and force plate were synchronized with four S-VHS cameras that recorded

the oblique views. A detailed description of the set-up is given elsewhere (Vereecke et al., 2005a). We analyzed the ground reaction forces during one full stride, i.e. from touchdown of one foot to the subsequent touchdown of the same foot, for each sequence (*N*=43). The position of the hip was digitized in the corresponding video recordings [using Kwon3D software (Kwon, 1994)] to calculate the average velocity of the bipedal bouts and to obtain the average hip height of each individual. A detailed description of the digitization process is given in a related paper on the kinematics of hylobatid bipedalism (Vereecke et al., 2006b). The average velocity was assessed from the linear regression of the horizontal displacement of the hip against stride duration. The hip height of each animal was calculated as the average vertical position of the hip during the stance phase. As this measure showed some stride-to-stride variation within each individual, hip height was averaged over the selected sequences (±s.d. = 1 cm).

Centre of mass (COM) excursions

The ground reaction forces are used to calculate the fluctuations of the centre of mass *via* the procedure first described in 1975 (Cavagna, 1975), and which has been applied in a large number of recent publications (Farley and Ko, 1997; Roberts and Scales, 2002; Ahn et al., 2004; Griffin et al., 2004; Hallemans et al., 2004; Parchman et al., 2003). In this method, body mass is obtained by integration of the total vertical force (of both hind limbs) over stride duration. Dividing the lateral (F_x) and forward (F_y) forces (of both hind limbs) by body mass yields the lateral (A_x) and forward (A_y) acceleration. Subtracting body weight from the vertical force (F_z), followed by subsequent division by body mass, yields the vertical acceleration (A_z). Numerical integration of the 3D accelerations gives the velocity components (V_x, V_y and V_z). Integration constants are so defined that the average 3D velocities (V_x, V_y and V_z) over a stride match the velocities as measured on the video images. Subsequent integration of the 3D velocities yields the position of the centre of mass (*X, Y*

and *Z*), which is then plotted as a function of stride duration to calculate the stride length and illustrate the vertical oscillations of the COM.

Acceleration

The zoo protocol did not allow direct interaction with the animals, hence we could not control for speed and animals were free to choose their own locomotor speed. This resulted in a speed range of 0.79–3.53 m s^{-1}, of which the highest speeds presented substantial acceleration. As previous research (Roberts and Scales, 2002; Roberts and Scales, 2004) has demonstrated that acceleration can have a major effect on the dynamics of locomotion, we have excluded the strides with substantial acceleration or deceleration ($A_y < -0.2$ or $A_y > 0.2$ m s^{-2}) from our statistical analyses, finally resulting in a speed range of 0.79–2.08 m s^{-1} (N=26; Fig. 2). The average acceleration of each trial was calculated by dividing the average forward force component (F_y) by body mass (M_b). The remaining 'unsteady' trials are shown in the regression plots to illustrate the effect of velocity and/or acceleration, but these relationships are not tested statistically.

Gait mechanism

The 3D velocities (V_x, V_y and V_z) are used to calculate the potential (*PE*) and kinetic energies (*KE*) following Heglund et al. [(Heglund et al., 1982); see Table 1]. Based on the relationship between the fluctuations in *PE* and *KE* during a stride, we can identify the applied gait mechanism (Fig. 1). If the *PE* and *KE* are out-of-phase, energy exchange *via* the 'inverted pendulum' (IP) mechanism is possible. If the *PE* and *KE* are in-phase than a 'spring-mass' mechanism might be active. We calculated the following parameters to evaluate the energy exchange mechanism (the formulae are shown in
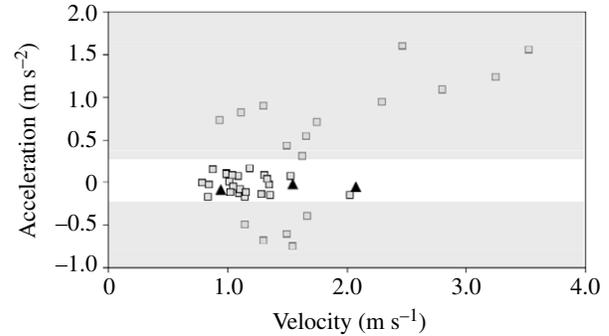

Fig. 2. Scatter plot showing the variation in velocity and acceleration of all collected bipedal strides (*N*=43). Only the trials with little or no acceleration (*A*=0±0.2 m s^{-2}; white band on plot) are included in the statistical analysis. The triangles (at 1 m s^{-1}, 1.5 m s^{-1} and 2.0 m s^{-1}) indicate the example strides that are illustrated in Fig. 3.

Table 1). The relative amplitude (RA) gives the ratio between the *PE* and *KE* amplitudes, the percentage congruity (%C) reflects the phase relationship between the *PE* and (forward) *KE* fluctuations (*PE* and *KE* are out-of-phase when %C=0 and in-phase when %C=1), and the recovery (R) quantifies the amount of energy transfer between *PE* and (forward) *KE* *via* the IP mechanism. Energy exchange *via* the IP mechanism (or R=100%) is optimal when RA=1 and %C=0. To estimate the potential amount of energy recovery *via* the spring-mass mechanism, we calculated the power fluctuations during a stride by differentiating energy change with respect to stride duration. At touchdown, kinetic and potential energy are dissipated as heat or stored in elastic structures (e.g. tendons), coinciding with a negative power peak ('absorption phase'). During the second half of the stance phase, the muscles have

Table 1. *The mechanical gait parameters (abbreviation, definition and unit of measurement)**

Parameter	Abbreviation	Definition	Unit
Vertical COM excursion	deltaZ	$Z_{(max-min)}$/hip height	
Kinetic energy	*KE*	$KE_x + KE_y + KE_z = \frac{1}{2}M_b(V_x^2 + V_y^2 + V_z^2)$	J
Potential energy	*PE*	$9.81 M_b Z$	J
Total energy	*TE*	$PE + KE$	J
PE fluctuation	F_{PE}	$PE_{(max-min)}/M_b SL$	J kg^{-1} m^{-1}
KE fluctuation	F_{KE}	$KE_{(max-min)}/M_b SL$	J kg^{-1} m^{-1}
Relative amplitude	RA	$PE_{(max-min)}/KE_{(max-min)}$	
Recovery	R	$[\Delta^+(PE+KE_z)+\Delta^+ KE_y - \Delta^+ TE]/[\Delta^+(PE+KE_z)+\Delta^+ KE_y] \times 100$	%
Percentage congruity	%C	0=*PE* and *KE* are in-phase	(0–1)
		1=*PE* and *KE* are out-of-phase	
Positive work	+*W*	$\Sigma(\Delta TE > 0)$ or $\Delta^+ TE$	J
Negative work	−*W*	$\Sigma(\Delta TE < 0)$ or $\Delta^- TE$	J
External work	W_{ext}	+W/$M_b SL$	J kg^{-1} m^{-1}
Positive power	+*P*	$\Sigma[(\Delta TE/\Delta t) > 0]$	W
Negative power	−*P*	$\Sigma[(\Delta TE/\Delta t) < 0]$	W
Power output	P_{max}	Maximum (+*P*)	W
Power ratio	PR	+*P*/−*P*	

*M_b=body mass; *SL*=stride length; KE_x, KE_y and KE_z=lateral, forward and vertical components of the kinetic energy; V_x, V_y and V_z= velocity components; *Z*=vertical position of the COM; $\Delta^+ TE$=sum of positive increments in *TE* over an integral number of steps.

to generate mechanical work ('generation phase'), which is associated with a positive power peak. Depending on the properties of the tendon (stiffness, elastic modulus, hysteresis), a certain amount of energy can be stored in the tendons during the 'absorption phase' and recovered during the 'generation phase' (by recoil of the muscle–tendon units), thereby contributing to the total mechanical work of the body during locomotion (Biewener and Blickhan, 1988; Ettema, 1996; Lindstedt et al., 2002; Lichtwark and Wilson, 2005). By calculating the power ratio (PR), i.e. the ratio of positive to negative power, we can evaluate the potential energy recovery *via* the spring-mass mechanism during a stride. We also calculated the maximal power output during a stride, i.e. the positive power peak, and plotted it as a function of stride duration. The definitions of all calculated parameters are given in Table 1.

The sum of *PE* and *KE* gives the total mechanical energy, *TE*, and the sum of the positive time increments of *TE* over a complete stride gives us the total external mechanical energy, W_{ext}. To allow comparison with humans and other animals, W_{ext} is divided by body mass and stride length and expressed in $J\,kg^{-1}\,m^{-1}$. The fluctuations in *PE* and *KE* over a stride are also expressed in $J\,kg^{-1}\,m^{-1}$ (Table 1 and Fig. 1).

Data analysis

The animals varied in body mass (range=3.5–7.5 kg) and size (ankle to knee distance; range=0.146–0.177 m), and to allow comparison of the different-sized animals, we scaled the dynamic parameters to body mass (F_{PE}, F_{KE} and W_{ext}, see Table 1) or hip height (for deltaZ, see Table 1). Hip height is obtained from digitization of the corresponding video images (see above). The gait parameters are plotted as a function of dimensionless velocity (DV), which is the square root of the Froude number (Alexander and Jayes, 1983). The *DV* is calculated as the average velocity over a complete stride, as measured on the video images, normalized to hip height (Alexander and Jayes, 1983):

$$DV = \text{Velocity} / (9.81 \times \text{hip height})^{1/2}.$$

The relationship between dimensionless velocity and the dynamic gait parameters was evaluated using a least-squares regression analysis. Different regression curves were estimated, of which we selected the best-fitting curve based on the highest R^2 value (significance level: $P<0.05$). Data for the four animals were pooled in the regression analysis, because the effect of individual was not significant as determined by a mixed linear model analysis in SAS software (SAS Institute, 1999).

Results

COM fluctuations and gait mechanics

The absolute vertical COM fluctuations, as calculated from the ground reaction forces, are on average 2.6 cm during hylobatid bipedalism. The position of the COM is highest during the double stance phases and lowest during the single

Table 2. *Mechanical gait parameters, together with the R^2 value and significance level of their relationship with dimensionless velocity (DV)*

Parameter	Mean	s.d.	R^2	~DV
deltaZ	0.084	0.053	–	n.s.
F_{PE}	$0.32\ J\,kg^{-1}\,m^{-1}$	$0.16\ J\,kg^{-1}\,m^{-1}$	–	n.s.
F_{KE}	$0.35\ J\,kg^{-1}\,m^{-1}$	$0.09\ J\,kg^{-1}\,m^{-1}$	0.20	$P<0.05$
RA	0.94	0.41	–	n.s.
R	16.86%	19.75%	0.44	$P<0.001$
%C	68.28%	22.77%	0.29	$P<0.05$
+W	3.56 J	1.42 J	0.39	$P<0.001$
−W	−3.60 J	1.60 J	0.42	$P<0.001$
W_{ext}	$0.72\ J\,kg^{-1}\,m^{-1}$	$0.29\ J\,kg^{-1}\,m^{-1}$	0.22	$P<0.05$
+P	891.39 W	257.21 W	0.36	$P<0.001$
−P	−900.65 W	400.12 W	0.41	$P<0.001$
P_{max}	21.23 W	12.25 W	0.75	$P<0.0001$
PR	1.07	0.34	–	n.s.

s.d., standard deviation; n.s., not significant.
The corresponding regression equations are given in Fig. 4.

stance phases (Fig. 3). The vertical fluctuations of the COM create fluctuations in *PE* and, to a lesser extent, in *KE*, which both average about $0.33\ J\,m^{-1}\,kg^{-1}$ during a steady-state stride (Table 2, Fig. 4B). As a result, the relative amplitude (RA) averages 1 for the steady-state trials (Table 2, Fig. 4C), which allows an optimal energy exchange between *PE* and *KE* if they fluctuate out-of-phase. The %C, which evaluates the phase relationship between *PE* and *KE*, indicates, however, that *PE* and *KE* fluctuate more or less in-phase: 22 out of 26 trials have a %C higher then 50% (Fig. 3 and Fig. 4E). Efficient energy recovery between *PE* and *KE* seems thus not possible during most trials, and this also explains the low IP recovery rates of the bipedal bouts: 84% of the bouts have an IP recovery lower than 25% (Fig. 4D). These low IP recovery rates and the in-phase fluctuations of *PE* and *KE* might point to the use of a spring-mass mechanism in hylobatid bipedalism (compare Fig. 1 with Fig. 3). In addition, the average power ratios (PR) equal 1 for the steady-state strides (Table 2 and Fig. 4H), meaning that, in theory, all negative work can be recovered to generate positive work during the subsequent propulsive phase. However, it should be noticed that although the greater part of the bipedal bouts are characterized by an in-phase fluctuation of *PE* and *KE*, some of the slower trials (4 out of 26) have a more or less in-phase fluctuation of *PE* and *KE*. This results in relatively high IP recovery rates (Fig. 4D) and suggests that gibbons either use a spring-mass or an IP-like mechanism during slow bipedal locomotion.

Mechanical energy and effect of locomotor speed

The net external mechanical work (W_{ext}) delivered during a steady-state stride amounts on average to $0.72\ J\,kg^{-1}\,m^{-1}$ (Table 2) for hylobatid bipedalism. W_{ext} increases almost linearly with increasing dimensionless velocity ($P<0.05$, Fig. 4I), and shows no speed-related discontinuity within the
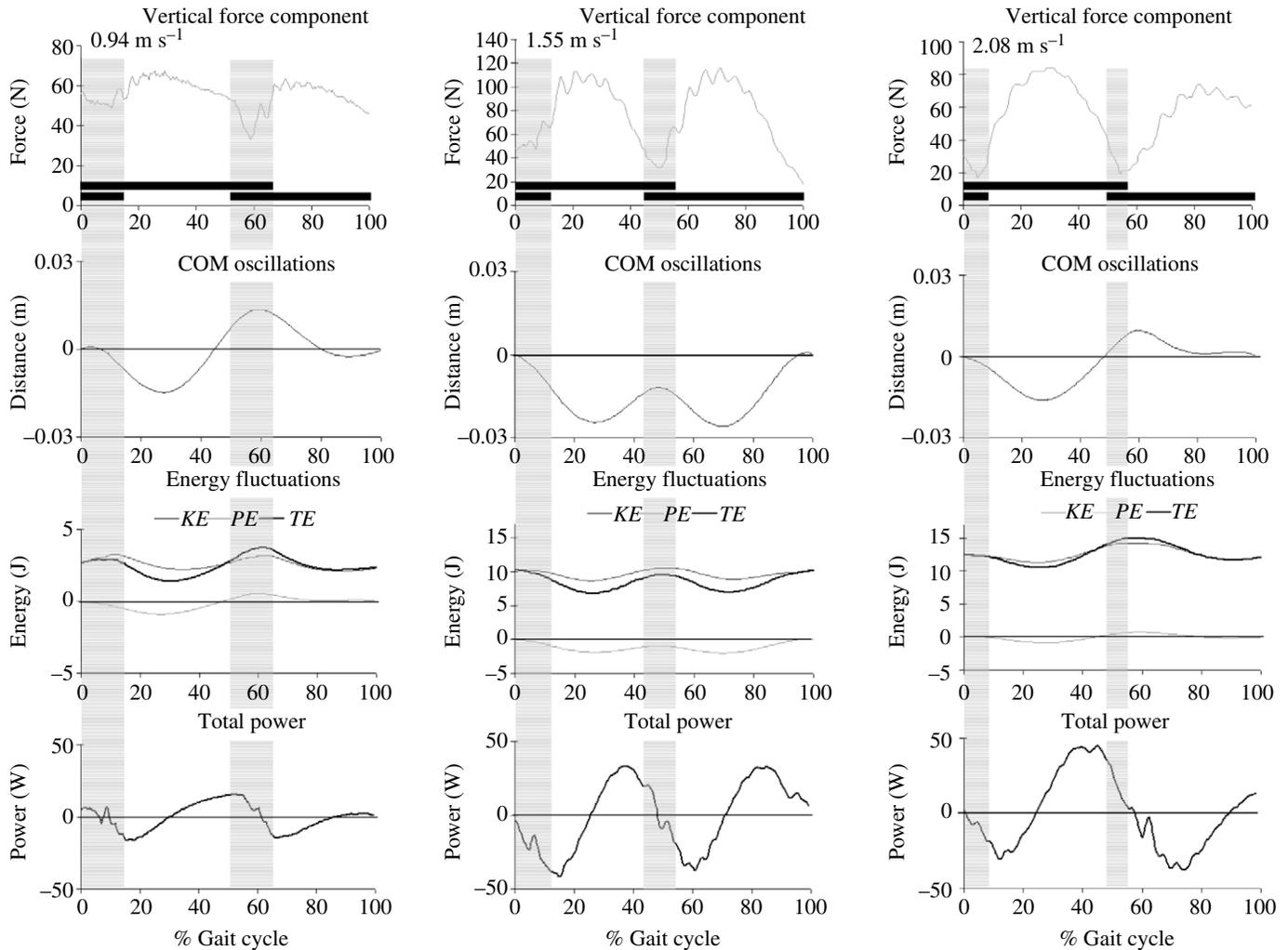
Fig. 3. Vertical force component, vertical COM oscillations and energy and power fluctuations during a complete stride of a slow (0.94 m s^{-1}; left), moderate (1.55 m s^{-1}; middle) and fast (2.08 m s^{-1}; right) bipedal sequence. Black horizontal bars on the top graphs indicate the stance phase of each foot; hatched vertical bars indicate the double support phases. For abbreviations, see Table 1.

observed speed range. The *KE* fluctuations also increase with increasing dimensionless velocity (*P*<0.05; Fig. 4H), since *KE* is correlated with forward speed. There is, however, no significant effect of dimensionless speed on the magnitude of the *PE* fluctuations (F_{PE}), due to the absence of increase in vertical excursion of the COM (delta*Z*) with increasing dimensionless velocity. Yet, the small positive trend between the dimensionless speed and delta*Z* and F_{PE} makes that the relative amplitude (RA=*PE*/*KE*) does not increase with increasing dimensionless velocity (Table 2).

The positive and negative power increase with increasing dimensionless velocity (*P*<0.001, Table 2), but since we are looking at steady-state locomotion, both increase proportionally, resulting in a similar power ratio at all speeds (*P*>0.05, Fig. 4H). The increase in positive power with increasing dimensionless speed is also reflected in the maximal power output, which increases sharply with dimensionless speed (*P*<0.0001, Fig. 4G). The %congruity increases with increasing dimensionless velocity (*P*<0.05), with *PE* and *KE*

being more out-of-phase at lower velocities and more in-phase at higher velocities (Fig. 4E). This results in higher IP recovery rates at slower speeds, but even at these low velocities, the IP recovery rarely rises above 25%.

Discussion

With this paper we wanted to investigate: (1) if gibbons use an energy-saving mechanism during their bipedal locomotion and (2) if this gait mechanism is used at all speeds or if we find indications for a speed-related gait transition. In addition, the results for gibbon bipedalism are compared with the locomotion of other primates and a number of vertebrates.

Energy-saving mechanism

In most bipedal bouts, the *PE* and *KE* fluctuate largely in-phase, being highest during double-support and lowest during midstance (Fig. 3). This pattern is also seen in human running and points to the use of a spring-mass mechanism (Novacheck,
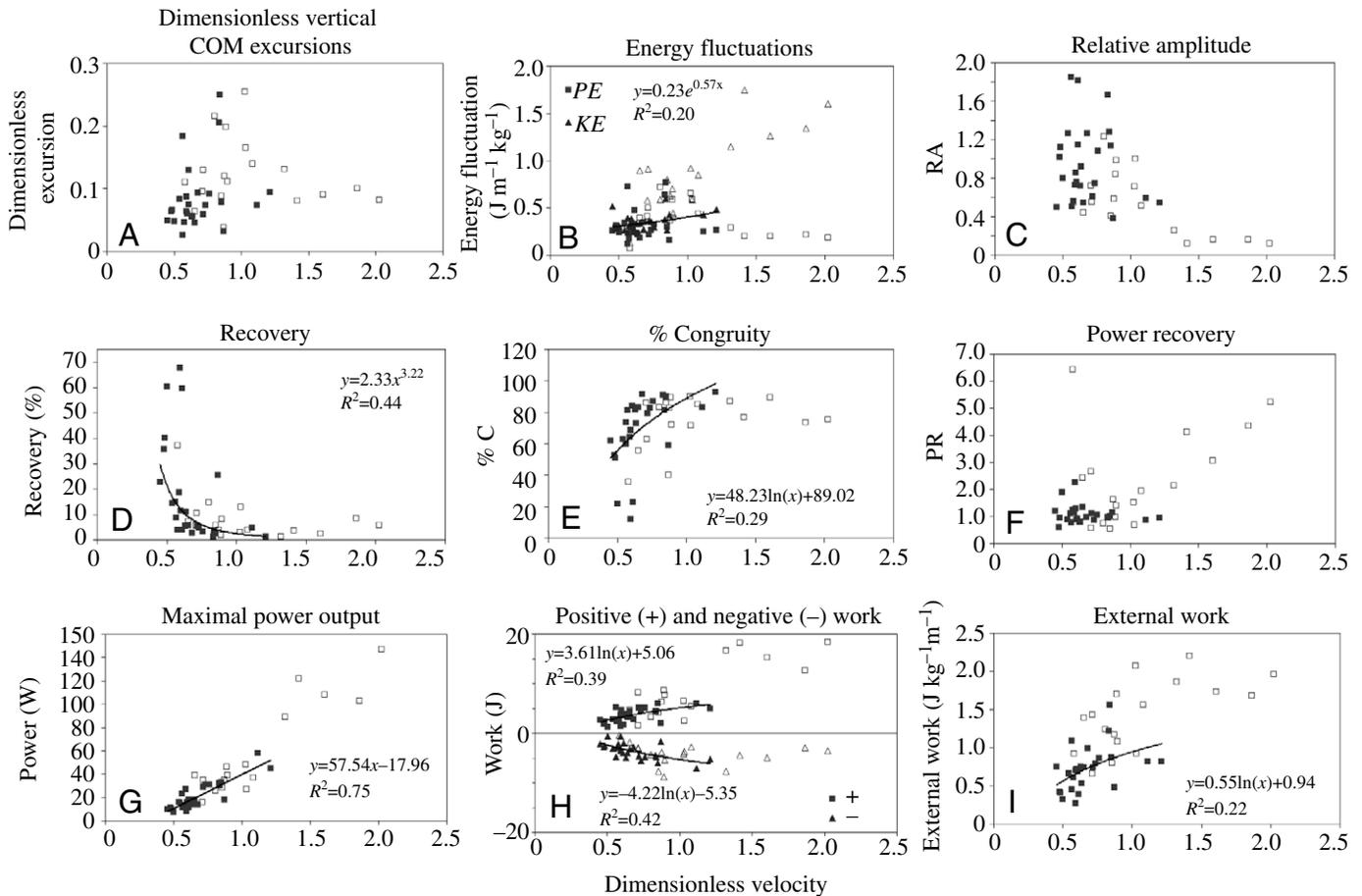
Fig. 4. Scatter plots of the dynamic gait parameters as a function of dimensionless velocity. Filled squares/triangles represent the steady state trials, open squares/triangles represent the 'unsteady' trials. Regression lines and equations are only shown for the statistically significant relationships ($P<0.05$) and include only the steady state trials. For abbreviations, see Table 1.

1998). In human running, the Achilles tendon (and plantar aponeurosis) is stretched when the ground reaction force increases (at touchdown) and energy is stored (negative power). At the end of the stance phase, the force falls and the Achilles tendon and plantar aponeurosis recoil, thereby releasing the stored elastic energy, which can be re-utilized for forward propulsion (positive power). However, the amount of energy that can be stored in the (Achilles) tendon and the amount of stored energy that can be recovered varies with the tendon properties (Ettema, 1996; Lichtwark and Wilson, 2005). The tendon should have a suitable stiffness and low hysteresis to allow storage and recoil of elastic energy during bipedal locomotion. From detailed dissections, we know that gibbons have a well-developed Achilles tendon (Vereecke et al., 2005b), but we have no information about the tendon properties so the energy-saving capacity of the Achilles tendon remains unverified. The energy-saving role of the plantar aponeurosis seems negligible during hylobatid bipedalism because gibbons have a weak plantar aponeurosis and lack a longitudinal foot arch (but see Alexander, 1991b) (Fig. 2).

Apart from suitable material properties, we also need appropriate joint motions and muscle activation patterns to effectuate an efficient spring-mass mechanism. Therefore, we combined the power oscillation patterns with corresponding kinematical data, which were presented in a related kinematic study analyzing the same bipedal sequences (Vereecke et al., 2006b). In Fig. 5 the angular time profiles of the hind limb joints and the corresponding oscillations of the total power of a single bipedal stride are shown. During the initial stance phase, the ankle dorsiflexes, herewith stretching the plantarflexor muscle tendon unit (triceps surae and Achilles tendon) and enabling storage of elastic energy. The ankle continues to dorsiflex until terminal stance when the ankle finally starts to extend (or plantarflex). However, at that time the power has already dropped to negative values, pointing to energy absorption. This suggests that the Achilles tendon and ankle plantarflexors do not act as effective elastic springs during hylobatid bipedalism. Still, muscle tendon units at the knee and/or hip joint could behave like elastic springs. The power/angular time profile of the knee joint shows knee flexion at initial contact, enabling storage of elastic energy, and knee extension during midstance when there is a positive power peak (Fig. 5). At terminal stance, the knee starts to flex, attaining a maximal flexed position during the swing phase.
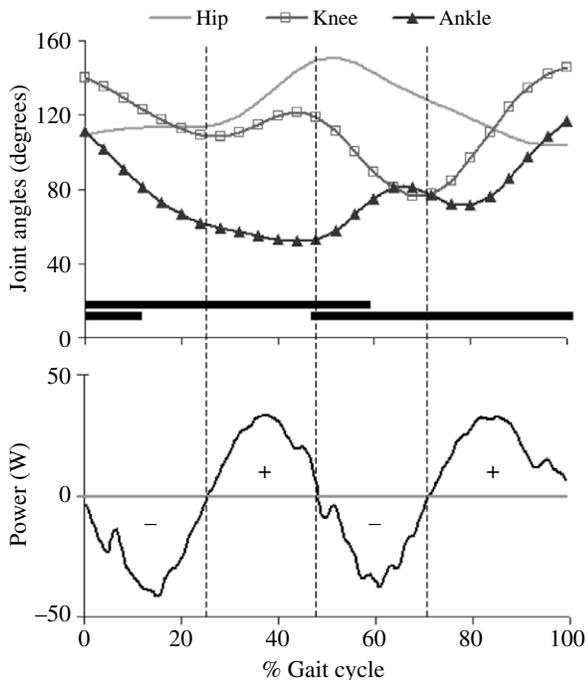
Fig. 5. Angular time profile and power oscillations during a bipedal stride. The top graph shows the 3D joint angles at hip (solid line), knee (squares) and ankle (triangles) of the stance limb (as indicated by the horizontal black bar). The bottom graph shows the power oscillations during the same bipedal stride.

Hence, the knee extensor group might act as an elastic spring, although the small amount of knee flexion and extension during the stance phase (compare ankle and knee flexion in Fig. 5) will probably limit its energy-saving capacity. The angular time profile of the hip shows no hip flexion at touchdown, which excludes storage of elastic energy in the hip extensors.

In summary, the power/angular time profiles are compatible with storage and recoil of elastic energy in the knee extensors (the quadriceps), which suggests that a spring-mass mechanism might be active during hylobatid bipedalism. However, the energy-saving capacity of the system is probably limited compared to the efficiency of human running.

(Pseudo)-elastic springs

Detailed morphological data of the knee extensor muscle–tendon complex is needed to confirm the energy-saving function of the quadriceps, but it seems not unlikely that they behave like elastic springs during hylobatid bipedalism. Energy storage and elastic recoil in the quadriceps has amongst others been observed in human and galago jumping (Prilutsky and Zatsiorsky, 1994; Aerts, 1998; Novacheck, 1998), and it seems compatible with the organization and structure of the quadriceps of gibbons. Detailed dissections of gibbon hind limbs have shown that the external part of the knee extensor tendon accounts for ca. 26% of the total knee extensor muscle tendon length (Payne et al., 2006) (E.E.V., personal

observation). If we take the internal part of the tendon into account, this ratio augments to approximately 70% (E.E.V., personal observation). In addition, a previous study of our group has shown that both ankle and knee extensors are important for speed modulation during hylobatid bipedalism (Vereecke et al., 2006b), implying that the knee extensors contribute significantly to propulsion generation at push-off.

Besides the potential energy-saving role of the knee extensors, both knee and ankle joint might reduce the cost of locomotion by acting as pseudo-elastic springs (Ruina et al., 2005). In such structures, energy is stored during the initial stance phase (absorption phase) but there is no recovery in the following phase of the gait cycle (generation phase). Instead, all energy needed for propulsion is actively generated by the muscles. Although this mechanism is certainly not as efficient as a purely elastic spring [cf. human running (Blickhan, 1989)], it is still four times less costly than a mechanism without energy storage (Ruina et al., 2005).

All things considered, it remains puzzling why gibbons have such a well-developed Achilles tendon. In view of the broad locomotor repertoire of gibbons, it might be possible that the Achilles tendon has an energy-saving role during other, commonly used, locomotor modes. The stiffness of the tendon might, for instance, be too high to function as an energy-saving mechanism during bipedal locomotion but might be suitable for energy storage and recoil during jumping [as is observed in humans (Bobbert et al., 1986)], which involves high take-off and landing forces (Demes et al., 1999). Alternatively, the relatively long Achilles tendon of gibbons might be an adaptation for brachiation because it contributes to a reduction of the distal hind limb mass (Payne et al., 2006).

Gait transition

Most legged animals use two basic patterns of locomotion: a walk at low speeds, corresponding to an inverted pendulum mechanism, and a run, trot, hop or gallop at high speeds, corresponding to a spring-mass mechanism (Farley and Ko, 1997). The change from one locomotor pattern to another is called a gait transition and goes along with abrupt changes in one or more determinants of the gait type considered [spatiotemporal parameters, kinematic patterns, dynamic patterns (Alexander, 1989; Hreljac, 1995)]. This is, for example, seen when humans change from walking to running (Segers et al., 2006) or when a trotting horse starts galloping (Farley and Taylor, 1991). Such speed-related discontinuities in kinetic (this study), spatiotemporal and kinematic parameters (Vereecke et al., 2006a; Vereecke et al., 2006b) are not apparent, however, within the observed speed range of hylobatid bipedalism. In addition, the ground reaction forces show a similar pattern during all bipedal bouts, with a single-humped vertical force curve (Vereecke et al., 2005a). These observations suggest that all bipedal bouts belong to the same locomotor mechanism, namely a spring-mass model, and that a clearcut gait transition is absent in gibbon bipedalism. This is also supported by calculation of the net mechanical work, averaging 0.72 J kg^{-1} m^{-1} in hylobatid bipedalism [cf. other

vertebrates: $W=1.15\pm0.43$ J kg^{-1} m^{-1} (Heglund et al., 1982; Full, 1989)], and which rises continuously with increasing speed. As the mechanical work is correlated with the metabolic cost of locomotion (Minetti et al., 1999; Rubenson et al., 2004) and the transition from one gait to another is generally associated with a minimization of the metabolic cost of locomotion (Hoyt and Taylor, 1981; Rubenson et al., 2004), this might indicate that (bipedal) gibbons do not change gaits, or alternatively, that the gait transition is not triggered by metabolic cost.

However, if we look at the IP recovery rates, which reflect the applied gait mechanism, we can observe a gradual change in IP recovery rates in the lower speed range (Fig. 4B,E). Below a dimensionless velocity of 0.7 or a Froude number of 0.5, which coincides with the transitional speed at which most vertebrates generally change gaits (Alexander, 1989; Kram et al., 1997), the variation in %congruity and IP recovery rates increases and the IP recovery rate may rise up to 70% (Fig. 4B,E). High IP recovery rates are typically seen in slow locomotion of large mammals, such as humans, dogs and horses, and point to the use of a relatively stiff-legged gait (Griffin et al., 2004; Willems et al., 1995; Minetti et al., 1999). In contrast, small animals that generally adopt a compliant gait, such as frogs, lizards (Ahn et al., 2004; Farley and Ko, 1997), kangaroo rats, opposums and most birds (Heglund et al., 1982; Muir et al., 1996; Parchman et al., 2003, Rubenson et al., 2004), have relatively low IP recovery rates. Gibbons fit in the latter group, but unlike opposums and kangaroo rats which never use pendular mechanics (Heglund et al., 1982; Parchman et al., 2003), gibbons occasionally adopt an IP-like gait at slow speeds. This is very similar to the situation in lizards (Farley and Ko, 1997) and in some birds [e.g. quails and chicks (Heglund et al., 1982; Muir et al., 1996)], which generally use spring mechanics, but are capable of using either pendular or spring mechanics at low speeds. A large variation in IP recovery rates is also typical for the transitional speed of quadrupedal mammals (Hoyt and Taylor, 1981; Farley and Taylor, 1991), but, in contrast to the situation in mammals, we did not observe a range of very low speeds at which gibbons only use pendular mechanics. Such slow bouts might fall below the sampled speed range, but our personal observations make us doubt that gibbons ever use such low locomotor speeds.

Thus, at moderate to high speeds, we observed no indication for the presence of a gait transition, but a gradual change from a spring-mass to a more IP-like in gait mechanism might be seen in the lower speed range. This is unlike the clearcut gait transition seen in humans, but comparable to the situation in birds. In avian locomotion, the transition from a (grounded) run to a walk comes along with abrupt changes in recovery rate and %congruity, but is not associated with any other speed-dependent kinematic discontinuities (Gatesy and Biewener, 1991; Muir et al., 1996; Gatesy, 1999; Rubenson et al., 2004). In gibbons this 'walk–run' transition is even less apparent as no sharp change in IP recovery rate and %congruity is observed within the observed speed range.

Grounded running, ambling and tölting

Although gibbons seem to use a bouncing gait at most speeds, aerial phases are generally absent. Only at the highest speeds, might the duty factor drop below 0.5 and an 'aerial-running gait' be observed. Such a bouncing gait with no aerial phase is also found in birds, where it is called a 'grounded-running gait' (Rubenson et al., 2004). Both in birds and gibbons, the transition from a grounded to an aerial run comes along with a gradual drop in duty factor with increasing speed, but is not associated with any other discontinuities in kinematic or kinetic parameters (Gatesy and Biewener, 1991; Rubenson et al., 2004). Thus, according to duty factor the grounded and aerial runs might be classified as distinct gait types, but according to the gait dynamics, they belong to the same locomotor mechanism, namely a bouncing gait. It has been suggested that such spring-mass or 'running' gaits without aerial phase are used by several vertebrates to ensure continuous contact with the substrate and to reduce the vertical oscillations of the COM (Schmitt et al., 2006). Examples of such gaits are the amble of primates (Schmitt et al., 2006) and elephants (Hutchinson et al., 2003), the walking run of frogs and lizards (Ahn et al., 2004), the tölt of Icelandic horses (Biknevicius et al., 2004) or the Groucho run of humans (McMahon et al., 1987).

This paper reinforces the concept that aerial phases are not a prerequisite for spring-mass mechanics (Biknevicius et al., 2004) and, in line with some previous publications (McMahon et al., 1987; Gatesy and Biewener, 1991), it supports the claim that duty factor alone should not be used to distinguish a walk from a run. In addition, the bipedal locomotion of gibbons clearly demonstrates that the grounded-run is more than an 'intermediate' or 'transitional' gait pattern and we suggest that it should be regarded as a full-fledged gait.

Primate bipedalism

Finally, we can compare the results of hylobatid bipedalism to prevailing kinetic data of bipedalism in other primates. This should give us an idea about the different styles of bipedalism within the primates, which can be helpful for the reconstruction of the locomotor behaviour of our hominin ancestors. In gibbon bipedalism the vertical force curve is typically single-humped during gibbon bipedalism, even during bipedal bouts with relatively high %congruity and IP recovery rate. A similar pattern is observed during bipedal locomotion of other primates, such as baboons, Japanese monkeys, chimpanzees (Kimura et al., 1977) and bonobos (personal observation). The vertical force curve might have a broad peak or plateau phase during bonobo and (untrained) chimpanzee bipedalism, but a clear double-humped pattern as seen in human walking is rare (Li et al., 1996). This single-humped vertical force pattern is linked to an in-phase fluctuation of the kinetic and potential energy and to the adoption of a bent-hip, bent-knee posture (Li et al., 1996). The adoption of such compliant gait can be advantageous in an arboreal setting because it enhances the maneuverability and balance and reduces the magnitude of the peak vertical force (McMahon et al., 1987; Gatesy and

Biewener, 1991; Li et al., 1996; Schmitt, 1999). Indeed, arboreal primates generally use a compliant gait in order to flatten the path of the COM and to reduce impact velocity and force (Schmitt, 1999).

Gibbons also adopt a bent-hip, bent-knee posture during bipedal locomotion, using long stride lengths (Vereecke et al., 2005a; Vereecke et al., 2006a) and large angular excursions of the hind limb (Vereecke et al., et al., 2006b). However, the in-phase fluctuation of *PE* and *KE* during (overground) bipedalism of gibbons point to a *running* gait, whereas most (quadrupedal) arboreal primates adopt a compliant *walk*. Associated with this bouncing gait, the vertical oscillations of the COM are also relatively high during gibbon bipedalism. The average vertical excursion of the COM is 2.6 cm during gibbon bipedalism and 3 cm during human walking (Lee and Farley, 1998). Taking size differences into account, gibbons (with a hind limb length of 0.37 m) seem to have relatively larger vertical oscillations of the COM than during human walking (with an average human hind limb length of 0.85 m). Thus there is no evidence for a flattened path of the COM, or the so-called 'rope-walker' pattern (Tardieu et al., 1993), during overground bipedalism of gibbons. It might, however, be possible that gibbons adopt a modified compliant gait during arboreal bipedalism, although there are no indications to suspect that gibbons alter their gait dynamics to substrate type (see also Alexander, 1991b; Bonser, 1999). Observations of wild gibbons indicate that gibbons select thick branches for bipedal locomotion (Fleagle, 1976; Gittins, 1983; Sati and Alfred, 2002) (S. Cheyne, K. Kakati, V. Nijman, personal communication), which leads us to assume that a similar spring-mass mechanism is used during both terrestrial and arboreal bipedalism.

Conclusion

This study suggests that gibbons make use of a spring-mass mechanism during bipedal locomotion. A requisite for this is the presence of a suitable muscle–tendon complex that allows storage and recoil of elastic energy during bipedal locomotion. Although gibbons posses a well-developed Achilles tendon, the kinematics of the ankle joint do not support an energy-saving role of the ankle plantarflexor complex. A limited amount of elastic energy storage and recoil seems, however, possible in the knee extensor muscle tendon unit of gibbons, although this still needs to be confirmed by detailed anatomical data. In conclusion, a spring-mass mechanism might be active during hylobatid bipedalism, but the energy-saving capacities are probably limited.

In the lower speed range, gibbons either use a spring-mass or an inverted pendulum mechanism, but no speed range with an exclusive use of an inverted pendulum gait was observed. In contrast to the locomotor patterns of most mammals, there are no abrupt changes in the dynamics (current study) or in the kinematic, kinetic and spatiotemporal parameters (previous studies) within the observed speed range of hylobatid bipedalism. However, a more gradual change in gait pattern, as seen in some birds, might be observed.

Gibbons use a bouncing gait without an aerial phase at most speeds, probably as an adaptation for locomotion in an arboreal environment. In line with several other publications, this study shows that aerial phases are not a prerequisite for a spring-mass mechanism and it supports the claim that the distinction between walking and running should not solely be based on duty factor.

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