

## RESEARCH ARTICLE

# Biomechanics of human bipedal gallop: asymmetry dictates leg function

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### SUMMARY

Unilateral skipping or bipedal galloping is one of the gait types that humans are able to perform. In contrast to many animals, where gallop is the preferred gait at higher speeds, human bipedal gallop only occurs spontaneously in very specific conditions (e.g. fast downhill locomotion). This study examines the lower limb mechanics and explores the possible reasons why humans do not spontaneously opt for gallop for steady-state locomotion on level ground. In 12 subjects, who were required to run and gallop overground at their preferred speed, kinematic and kinetic data were collected and mechanical work at the main lower limb joints (hip, knee, ankle) was calculated. In a separate treadmill experiment, metabolic costs were measured. Analysis revealed that the principal differences between running and galloping are located at the hip. The asymmetrical configuration of gallop involves distinct hip actions and foot placing, giving galloping legs different functions compared with running legs: the trailing leg decelerates the body in the vertical direction but propels it forward while the leading leg acts in the opposite way. Although both legs conserve mechanical energy by interchanging external mechanical energy with potential elastic energy, the specific orientation of the legs causes more energy dissipation and generation compared with running. This makes gallop metabolically more expensive and involves high muscular stress at the hips, which may be why humans do not use gallop for steady-state locomotion.

Key words: locomotion, human gait, asymmetric gait, skipping, metabolic cost, energetics, ground reaction force, kinematics, joint moments, joint power, work.

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### INTRODUCTION

Locomotion is an important aspect of human life. For aerobic, steady-state locomotion, people subconsciously select locomotion patterns that are most economical in terms of energy usage so that energy efficiency is maximized (Novacheck, 1998; Sparrow et al., 2000). In order to minimize the metabolic cost during locomotion, fluctuations in total mechanical energy must be kept to a minimum (Cavagna et al., 1977; Novacheck, 1998).

Walking minimizes the metabolic cost of transport at lower speeds and therefore is preferred to running at lower speeds, while the opposite is true for higher speeds (Farley and Ferris, 1998; Hreljac, 1993). Both locomotion patterns are symmetrical, meaning that the legs strike the ground at constant successive intervals (one leg completes its cycle when the other leg is halfway through its cycle) (Whitall and Caldwell, 1992). The basic dynamics of these gaits can be explained by a simple bipedal spring–mass model, the so-called SLIP (spring-loaded inverted pendulum) (Geyer et al., 2006). The model shows that fluctuations in total energy can be minimized by means of two mechanisms: (1) an exchange between gravitational potential energy and kinetic energy, as occurs in an inverted pendulum, and (2) an exchange between mechanical energy stored in the elastic elements of (some) muscles involved and recovered as both kinetic and gravitational potential energy, as in a bouncing ball (Cavagna et al., 1977). Although some elastic energy storage and recoil does occur, walking is primarily dominated by the exchange between gravitational potential and kinetic energy (Sawicki et al.,

2009; Cavagna et al., 1977; Kuo et al., 2005; Geyer et al., 2006; Cavagna and Margaria, 1966; Hof, 1990). In contrast to walking, most energy in running is saved by converting gravitational potential and kinetic energy into elastic potential energy, which is reconverted into kinetic and gravitational potential energy later in stance (McMahon, 1990; Cavagna et al., 1976; Cavagna et al., 1977; Novacheck, 1998; Geyer et al., 2006).

In addition to walking and running, people have alternative options for moving. One option is skipping, a temporally and spatially asymmetrical locomotion pattern where successive foot falls are not evenly spaced and one leg is kept in front of the other, discriminating a trailing and a leading leg with different functions (Minetti, 1998; Caldwell and Whitall, 1995; Whitall and Caldwell, 1992; Getchell and Whitall, 2004). Skipping can be bilateral, i.e. when the left and right leg alternately act as the leading leg, or unilateral, i.e. when the same leg is always kept in front. Unilateral skipping, also called bipedal galloping (Caldwell and Whitall, 1995; Whitall and Caldwell, 1992; Peck and Turvey, 1997), is more natural than bilateral skipping and can be reproduced easily by presenting only the acoustic rhythm whereas bilateral skipping needs to be practiced (Minetti, 1998; Whitall and Caldwell, 1992). Although human gallop is not a gait of choice for steady-state locomotion on level ground, there are some situations where gallop occurs spontaneously. Indeed, human gallop is observed in playing children, in sport-specific situations and when descending stairs and steep slopes (Minetti, 1998; Caldwell and Whitall, 1995; Getchell and Whitall, 2004).

The literature on human gallop is limited. Whitall and Caldwell focused on motor control aspects by investigating the differences in kinematic lower limb behaviour between running and galloping (Whitall and Caldwell, 1992). They discovered that interlimb coordination was clearly different but that intralimb coordination patterns were surprisingly similar. Further, Minetti (Minetti, 1998) and Caldwell and Whitall (Caldwell and Whitall, 1995) investigated the energetic aspects of gallop. According to Minetti, (bilateral) skipping could be modelled as a rimless wheel with two springy spokes [see fig. 4, p. 1231 in Minetti (Minetti, 1998)]. The model has the same essential characteristics as that of Geyer and colleagues (Geyer et al., 2006), i.e. bipedalism and leg compliance, and showed that in skipping, energy is conserved by using elastic mechanisms combined with the pendulum-like motion of the whole-body centre of mass ( $COM_{wb}$ ). The model provides a realistic representation of the mechanical energy fluctuations of the  $COM_{wb}$  (Minetti, 1998; Caldwell and Whitall, 1995) and of the ground reaction forces (GRFs), but no experimental validation of the underlying energetics and kinetics during contact exists.

In contrast to that of most quadrupedal animals, human gallop is not related to a scaling of progression velocity, but is more a matter of voluntary control (Whitall and Caldwell, 1992; Caldwell and Whitall, 1995). When gallop is intentionally chosen, the progression speed is similar to that of run (Whitall and Caldwell, 1992; Caldwell and Whitall, 1995). Consistent with Minetti's findings on bilateral skipping (Minetti, 1998), preliminary results show that metabolic energy consumption is higher for gallop than for run at the same speed. Furthermore, subjects reported soreness at the hip and thigh, indicating high muscular stress after a short period (several minutes) of galloping. Thus, the reason why humans do not spontaneously gallop may lie in the lower economy and/or in the higher muscular load compared with run.

The goals of this study were (1) to determine the biomechanical differences between bipedal gallop and run, (2) to understand how propulsion in bipedal gallop is generated and (3) to gain insight into why humans do not use this gait for steady-state locomotion. Therefore, we provide a comprehensive description of the spatiotemporal parameters, GRFs, and lower limb kinematics and kinetics of gallop and compare these to those of run. Based on the present knowledge, it was hypothesized that, compared with running, (i) the legs have different functions and (ii) at joint level, the largest differences during support are situated in the hips. Further it was expected that in gallop (iii) both mechanical energy-saving mechanisms operate simultaneously and (iv) the higher metabolic cost of transport and the higher level of muscular stress compared with run potentially explain why people do not use gallop.

## MATERIALS AND METHODS

Twelve subjects participated in the first part of this experiment. To minimize the influence of anthropometry, participants were selected based on sex (all female) and height (hip height  $0.862 \pm 0.036$  m, mass  $57.67 \pm 6.50$  kg, age  $20.09 \pm 1.30$  years). All participants were free from disease or injury and gave written informed consent before participating in the study. For the study, ethical approval was granted by the institutional review board of Ghent University Hospital.

Subjects ran (R) and galloped (G) along a 30 m runway at their preferred speed wearing standard running shoes. In the gallop trials, subjects were free to choose their trailing leg, i.e. the leg that lands first after the flight phase (in 8 out of 12 subjects the left leg was the trailing leg). Prior to data collection, practice trials of running and galloping were executed.

Spatiotemporal parameters were calculated. Foot contact (FC) was determined by finding the instant at which the vertical GRF surpasses the 10 N threshold. Toe-off (TO) was the instant at which the vertical GRF dropped below the 10 N threshold. Preferred velocity ( $v_{pref}$ ) was defined as the mean velocity of the  $COM_{wb}$  (derived from the kinematic model as described below) over one stride. Stride length (SL) was the distance the  $COM_{wb}$  travelled in the anterior–posterior direction between two consecutive contacts of the same foot. For gallop, these contacts refer to contacts of the trailing leg. Stride frequency (SF) was calculated as 1/stride time. Compound stance time was the duration of the combined FC in gallop, i.e. from FC of the trailing leg to TO of the leading leg.

To obtain GRF data, six force platforms (five from AMTI, Watertown, MA, USA and one from Kistler AG, Winterthur, Switzerland) were mounted in series along the middle of the runway. GRFs were collected at 1000 Hz and low-pass filtered at 10 Hz with a fourth-order zero-lag Butterworth filter. To obtain a measure of movement consistency for each gait, variability in GRFs was assessed by calculating the coefficients of variation (CV) (Winter, 1984). Net, braking and propulsive horizontal impulses and vertical impulses of the legs were calculated for each stride. Vertical impulses were obtained by integrating the vertical GRFs over stride time. Similarly, net horizontal impulses were computed by taking the time integral of the horizontal GRFs. Horizontal braking and propulsive impulses were calculated by integrating the negative and positive values, respectively, of the horizontal GRFs over stride time.

3D kinematics were recorded at 200 Hz using a passive motion capture system (Qualisys AB, Gothenburg, Sweden). The kinematic marker set consisted of a total of 59 markers: 28 anatomical markers placed on identifiable landmarks to define segment end points and 31 tracking markers placed in clusters of three or four on rigid plates to track segment motion. The marker coordinate data were filtered at 10 Hz using a fourth-order zero-lag Butterworth filter (Winter, 2009).

A 12-segment, 33 degrees of freedom model (forearms, upper arms, head + trunk, pelvis, thighs, shanks and feet) was developed to calculate the positions of the segments. Locations of segmental centres of gravity and moments of inertia were calculated using a mathematical model (Hanavan, 1964). Segment masses were determined from the total body weight (BW) and Dempster's anthropometric data (see Winter, 2009). Positions of the  $COM_{wb}$  during stance and flight phases of running and galloping were derived from the model and were differentiated to calculate linear velocities. Segmental angles were determined by positioning the segments in the laboratory coordinate system and joint angles by positioning the distal segment coordinate system in the proximal segment coordinate system. To obtain angular velocities, the obtained angles were differentiated.

Gravitational potential energy ( $E_{pot} = mgh_{wb}$ , where  $m$  is the mass of the subject,  $g$  is the gravitational constant and  $h_{wb}$  is the instantaneous  $COM_{wb}$  height), and forward and vertical kinetic energy ( $E_{kin, f/v} = 1/2 m v_{f/v}^2$ , where  $m$  is the mass of the subject and  $v_{f/v}$  is the forward/vertical velocity of the  $COM_{wb}$ ) of the  $COM_{wb}$  were calculated. External energy was calculated as the sum of gravitational potential, forward and vertical kinetic energy.

An inverse dynamics approach (Winter, 2009) was used to calculate net joint moments, which were multiplied by the joint angular velocities to calculate joint power at the ankle, knee and hip. For each joint, angular extensor and flexor impulses during foot contact were calculated by taking the time integral of the corresponding positive or negative joint moment. All kinematic and kinetic calculations were executed using Visual 3D software (Visual

3D v 4.90.0, C-motion, Germantown, MD, USA). Because of practical limitations of the setup, hip moments and power of only four subjects are available for each condition: trailing galloping leg ( $G_{\text{trail}}$ ), leading galloping leg ( $G_{\text{lead}}$ ) and running leg (R). For the ankle and knee moments and power, data from all subjects have been used.

Net joint work was computed as the time integral of joint power over the entire stride. Positive and negative joint work were calculated by time integrating all positive and negative joint power phases over the stride separately. For those four subjects where the power of all joints was available, net positive and net negative limb work were defined as the summation of the positive and negative net joint work (as defined above) per limb, respectively. Total positive and negative limb work were calculated by summation of the positive and negative joint work (as defined above) at the ankle, knee and hip separately. To establish the contribution of a joint to (net/total) positive and (net/total) negative limb work, positive and negative (net) joint work were expressed as a percentage of (net/total) positive and (net/total) negative limb work, respectively.

For each condition (R and G or R,  $G_{\text{trail}}$  and  $G_{\text{lead}}$ ), variables were first averaged per subject. Next, group means and standard deviations were calculated and presented. To compare these variables between conditions, a repeated measures ANOVA was used. When a significant main effect was found ( $P < 0.05$ ), Bonferroni corrected *post hoc* comparisons were performed. To check whether fore–aft ground reaction impulses were different from 0, a one-sample *t*-test with significance defined as  $P < 0.05$  was used.

To assess the metabolic cost of gallop, 13 female subjects (hip height  $0.880 \pm 0.066$  m, mass  $64.58 \pm 8.83$  kg, age  $26.69 \pm 2.75$  years) took part in a separate experiment. Subjects were healthy and gave written informed consent that followed the guidelines of the institutional review board of Ghent University Hospital. After a 5 min stance period, subjects ran and galloped on a motorized treadmill at a speed that guaranteed locomotion within the aerobic range ( $2.78 \text{ ms}^{-1}$ ). Subjects were free to choose the trailing leg (in six out of 13 subjects the trailing leg was the left leg). The running and galloping blocks lasted for a period of 4 min with 6 min of rest between them. Rates of oxygen consumption ( $\dot{V}_{\text{O}_2}$ ,  $\text{ml O}_2 \text{ s}^{-1}$ ) and carbon dioxide production ( $\dot{V}_{\text{CO}_2}$ ,  $\text{ml CO}_2 \text{ s}^{-1}$ ) were measured by using an open-circuit respirometry system (Jaeger, Höchberg, Germany). Average  $\dot{V}_{\text{O}_2}$  and  $\dot{V}_{\text{CO}_2}$  were calculated during the final 90 s of running and galloping after subjects reached steady state. Gross metabolic cost ( $\text{J min}^{-1}$ ) was estimated with Brockway's equation (Brockway, 1987). To derive the metabolic cost of locomotion ( $\text{J kg}^{-1} \text{ m}^{-1}$ ), the metabolic cost of stance was subtracted from the value obtained during gallop and run, and was divided by the progression speed and the subject's mass.

Of the 13 subjects, five were excluded from the sample because they were not able to perform a galloping pattern on the treadmill (one subject) or did not complete the galloping block because of local discomfort or the intensity of the exercise (four subjects). A repeated measures ANOVA was used to compare the metabolic cost of running and galloping. Significance was defined as  $P < 0.05$ .

## RESULTS

### Spatiotemporal data

There was no difference in preferred G and R speed ( $P = 0.354$ ) (Table 1). Despite this, differences were found between the two gait types for some spatiotemporal parameters: SF was higher ( $P = 0.000$ ) and SL was shorter for G than for R ( $P = 0.001$ ). The difference in stride time arises because flight duration in G is shorter than the

summed double flight phase of R ( $P = 0.000$ ). FC times were not different between  $G_{\text{trail}}$ ,  $G_{\text{lead}}$  and R ( $P = 0.217$ ).

### GRFs

No differences were found in the variability of horizontal ground reaction force ( $\text{GRF}_h$ ) between R and G or between  $G_{\text{lead}}$  and  $G_{\text{trail}}$  ( $P = 0.621$ ) (Fig. 1). For the vertical ground reaction force ( $\text{GRF}_v$ ), the variability of  $G_{\text{lead}}$  and  $G_{\text{trail}}$  did not differ ( $P_{G_{\text{trail}}-G_{\text{lead}}} = 0.206$ ). Also, no difference was evident between  $G_{\text{lead}}$  and R ( $P_{R-G_{\text{lead}}} = 1.000$ ) but the variability of  $G_{\text{trail}}$  was smaller than that of R ( $P_{R-G_{\text{trail}}} = 0.019$ ).

The  $\text{GRF}_v$  of both galloping legs shows a pattern that is roughly similar to that of running legs. The maxima of  $G_{\text{lead}}$  were similar to those of  $G_{\text{trail}}$  ( $P_{G_{\text{trail}}-G_{\text{lead}}} = 0.243$ ) but they were smaller than those of R ( $P_{R-G_{\text{trail}}} = 0.001$ ,  $P_{R-G_{\text{lead}}} = 0.002$ ). In addition, the vertical impulses were smaller for G strides than for R strides ( $R = 0.703 \pm 0.048 \text{ BW s}$ ,  $G = 0.625 \pm 0.364 \text{ BW s}$ ;  $P = 0.000$ ).

The largest difference in GRFs between G and R was in  $\text{GRF}_h$ . In run, each leg firstly decelerates and then accelerates the body by an equal amount, leading to a zero net horizontal impulse during FC ( $P = 0.592$ ). In gallop at a constant velocity, the net horizontal impulse is zero over one stride ( $P = 0.214$ ) but the horizontal braking and propulsive impulses are distributed differently over the two legs. Most of the braking is executed by the leading leg ( $G_{\text{trail}} = -0.009 \pm 0.002 \text{ BW s}$ ,  $G_{\text{lead}} = -0.037 \pm 0.008 \text{ BW s}$ ;  $P = 0.000$ ), landing last, while the trailing leg, landing first after the flight phase, provides most of the propulsion ( $G_{\text{trail}} = 0.042 \pm 0.006 \text{ BW s}$ ,  $G_{\text{lead}} = 0.010 \pm 0.005 \text{ BW s}$ ;  $P = 0.000$ ). This is in contrast to running, where braking precedes propulsion. Although braking and propulsive horizontal impulses are distributed differently over the legs, braking ( $R = -0.046 \pm 0.010 \text{ BW s}$ ,  $G = -0.046 \pm 0.009 \text{ BW s}$ ;  $P = 0.945$ ) and propulsive ( $R = 0.044 \pm 0.007 \text{ BW s}$ ,  $G = 0.052 \pm 0.009 \text{ BW s}$ ;  $P = 0.065$ ) horizontal impulses do not differ between gallop and run over one stride.

### Energetics of the $\text{COM}_{\text{wb}}$

As depicted in Fig. 2, energy fluctuations due to movements of the  $\text{COM}_{\text{wb}}$  of R show two minima and two maxima. The minima are associated with the middle of FC while the maxima occur at TO. The mechanical external energy ( $E_{\text{ext}}$ ) decreases during the first half of FC and increases in the second half as the subject pushes off. The forward kinetic ( $E_{\text{kin},f}$ ) and potential energy ( $E_{\text{pot}}$ ) components fluctuate in phase.

The plot of the  $E_{\text{ext}}$  of G also shows two minima and two maxima. As in R, the minima are associated with the middle of FC of both legs and the maxima are coincident with TO. In contrast to R, where the two maxima are similar in size, in G the first maximum

Table 1. Spatiotemporal parameters of run and gallop

	Run	Gallop
$v_{\text{pref}}$ ( $\text{m s}^{-1}$ )	$3.14 \pm 0.33$	$3.01 \pm 0.35$
SL (m)*	$2.30 \pm 0.22$	$1.87 \pm 0.28$
SF (Hz)*	$1.39 \pm 0.05$	$1.64 \pm 0.10$
$t_{\text{stance,comp}}$ (s)	—	$0.431 \pm 0.037$
$t_{\text{flight}}$ (s)*	$0.128 \pm 0.023$	$0.182 \pm 0.022$
$t_{\text{FC}}$ (s)	$0.232 \pm 0.021$	$0.224 \pm 0.025$ ( $G_{\text{trail}}$ )
	—	$0.231 \pm 0.017$ ( $G_{\text{lead}}$ )

$v_{\text{pref}}$ , preferred velocity; SL, stride length; SF, stride frequency;  $t_{\text{stance,comp}}$ , compound stance time;  $t_{\text{flight}}$ , flight time;  $t_{\text{FC}}$ , time of foot contact;  $G_{\text{trail}}$ , trailing leg of gallop;  $G_{\text{lead}}$ , leading leg of gallop.

\*Significant difference between run and gallop ( $P < 0.05$ ).

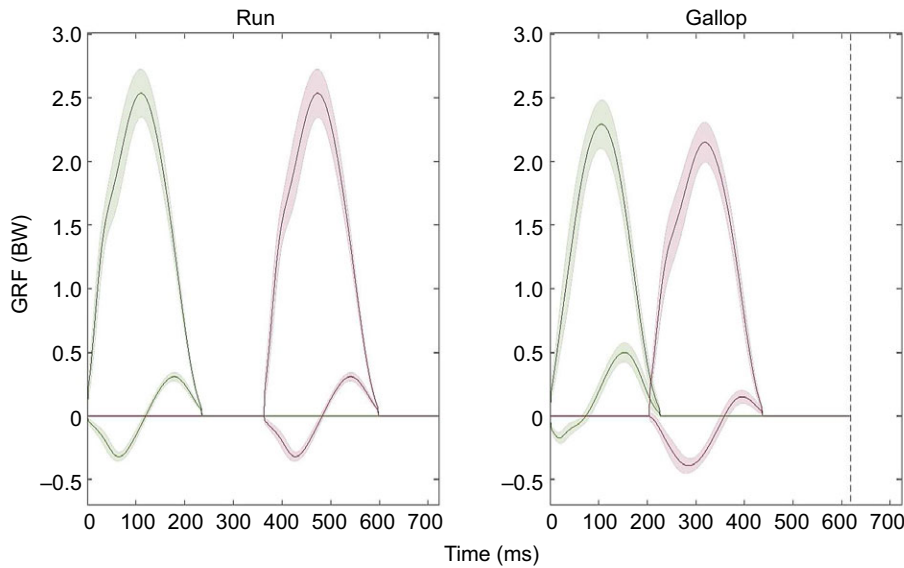


Fig. 1. Ensemble averages and s.d. of the vertical and horizontal ground reaction forces (GRFs) during a stride of run (R) and gallop (G). Green lines represent the left leg and red lines represent the right leg for R. For G, green lines represent the trailing leg of gallop ( $G_{\text{trail}}$ ) and red lines represent the leading leg of gallop ( $G_{\text{lead}}$ ). The dashed line represents foot contact (FC) of  $G_{\text{trail}}$  of the next G stride. y-axis: GRFs in terms of body weight (BW); x-axis: stride time.

associated with the push-off of  $G_{\text{trail}}$  is lower than the maximum associated with the push-off of  $G_{\text{lead}}$  ( $P_{G_{\text{trail}}-G_{\text{lead}}}=0.000$ ). Furthermore, in R the two legs absorb and generate an equal amount of mechanical energy (reflected in a decrease and increase, respectively, of the energy profiles during FC) ( $P_R=0.142$ ), whereas there is an asymmetry in energy generation and absorption between

the legs in G. In G,  $G_{\text{trail}}$  absorbs more energy than it produces ( $P_{G_{\text{trail}}}=0.001$ ) while  $G_{\text{lead}}$  generates more than it absorbs ( $P_{G_{\text{lead}}}=0.000$ ). This asymmetry is also reflected in both the  $E_{\text{pot}}$  and  $E_{\text{kin},f}$ . The amplitude of  $E_{\text{pot}}$  during G is almost twice as large as those in R ( $P_{R-G}=0.000$ ). The  $E_{\text{pot}}$  plateaus around its minimum, i.e. around the middle of compound stance, and shows one distinct

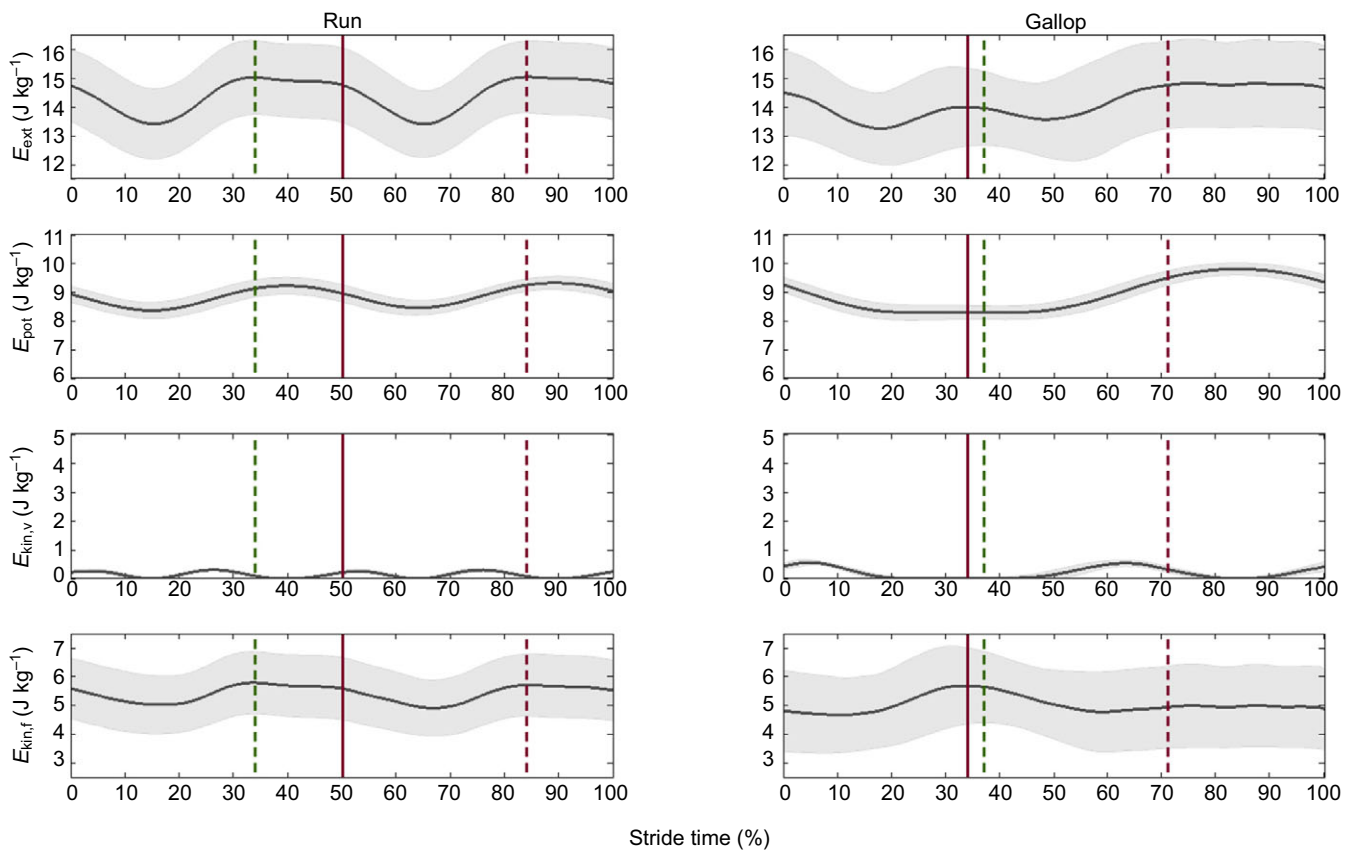


Fig. 2. Instantaneous energy of the whole-body centre of mass ( $\text{COM}_{\text{wb}}$ ; external energy  $E_{\text{ext}}$ , gravitational potential energy  $E_{\text{pot}}$ , vertical kinetic energy  $E_{\text{kin},v}$  and forward kinetic energy  $E_{\text{kin},f}$ ) during a stride of R and G. Solid vertical lines represent FC and vertical dashed lines represent toe-off (TO). For R, green lines represent left legs and red lines represent right legs; for G, green lines represent  $G_{\text{trail}}$  and red lines represent  $G_{\text{lead}}$ . y-axis: BW-normalized energy; x-axis: normalized stride time.



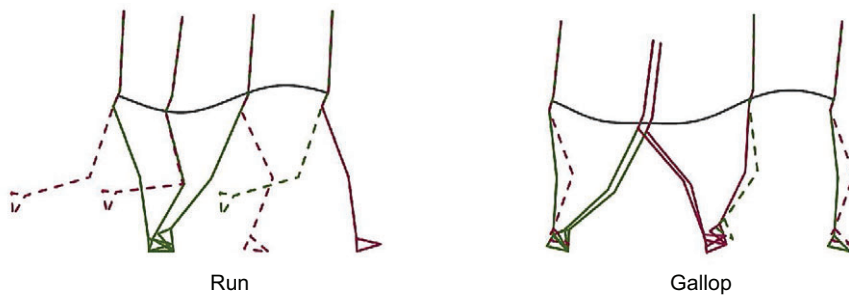


Fig. 3. Kinematics of G and R: average kinematics of a R step and a G stride. For R, green lines represent the right leg and red lines represent the left leg. For G, green lines represent  $G_{\text{trail}}$  and red lines represent  $G_{\text{lead}}$ . Solid lines represent legs in contact with the ground and dashed lines represent legs in flight phase. The trajectory of the  $\text{COM}_{\text{wb}}$  is represented by the grey line. Stick figures were created at key events of a stride. For R: FC right, middle of FC, TO right and FC left. For G: FC of  $G_{\text{trail}}$ , FC of  $G_{\text{lead}}$ , TO of  $G_{\text{trail}}$ , TO of  $G_{\text{lead}}$  and FC of  $G_{\text{trail}}$ .

maximum, during the flight phase.  $G_{\text{trail}}$  lowers the height of the  $\text{COM}_{\text{wb}}$  during the first half of FC and  $G_{\text{lead}}$  again raises the  $\text{COM}_{\text{wb}}$  during push-off. The  $E_{\text{kin},f}$  shows one peak, which is associated with the thrust phase of  $G_{\text{trail}}$ . Acceleration of the  $\text{COM}_{\text{wb}}$  is mainly associated with the push-off of  $G_{\text{trail}}$  and is immediately followed by a deceleration when the foot of  $G_{\text{lead}}$  makes contact with the ground.

### Kinematics

Patterns of the lower limb joint angles for R are similar to reference values published elsewhere (Novacheck, 1998; Whitall and Caldwell, 1992) and will be not described in detail. Patterns for G are in accordance with those observed in figs 3 and 4 of Whitall and Caldwell (Whitall and Caldwell, 1992).

In G,  $G_{\text{trail}}$  strikes the ground with a more extended hip ( $P_{\text{R-Gtrail}}=0.027$ ) and with a more plantarflexed ankle ( $P_{\text{R-Gtrail}}=0.003$ ) compared with run (Figs 3, 4). Because of the extended configuration, initial contact (IC) is made with the forefoot

and takes place just in front of the vertical projection of the position of the  $\text{COM}_{\text{wb}}$ . IC is immediately followed by ankle flexion and knee flexion as loading is accepted. The ankle flexes to the same degree as in R ( $P_{\text{R-Gtrail}}=1.000$ ) but the maximum flexion of the knee is less than in R ( $P_{\text{R-Gtrail}}=0.001$ ). During the second part of FC, the ankle extends to a similar degree to that in R ( $P_{\text{R-Gtrail}}=0.639$ ), the knee extends  $\sim 10^\circ$  less than it is initially flexed ( $P_{\text{Gtrail}}=0.000$ ) and the hip gradually extends till TO. Maximum hip extension is reached at TO and is comparable to that in R ( $P_{\text{R-Gtrail}}=1.000$ ). The foot leaves the ground far behind the vertical projection of the position of the  $\text{COM}_{\text{wb}}$ .

$G_{\text{lead}}$  strikes the ground well in front of the vertical projection of the  $\text{COM}_{\text{wb}}$  and in a more flexed configuration compared with R: the hip is more flexed ( $P_{\text{R-Glead}}=0.015$ ) while the knee ( $P_{\text{R-Glead}}=0.223$ ) and ankle angle ( $P_{\text{R-Glead}}=1.000$ ) are similar to those in R. IC occurs with the heel and is immediately followed by a plantarflexion of the ankle until the foot is flat on the ground. During the first part of FC of the leading leg, loading is accepted

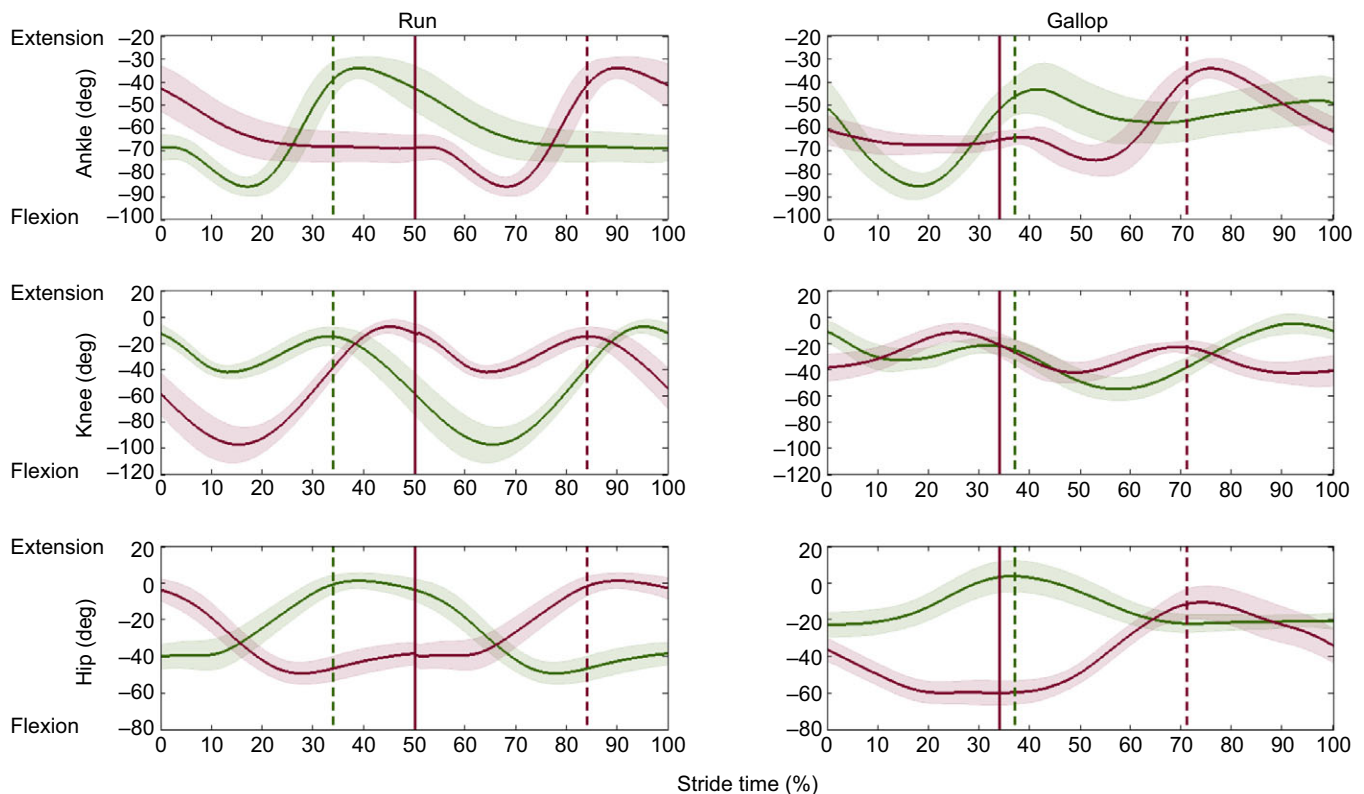


Fig. 4. Instantaneous joint angles (ankle, knee and hip) during a stride of R and G. For R, green lines represent the left leg and red lines represent the right leg; for G, green lines represent  $G_{\text{trail}}$  and red lines represent  $G_{\text{lead}}$ . Solid vertical lines represent FC and vertical dashed lines represent TO (colour relates to leg). y-axis: joint angle not normalized to standing posture; x-axis: normalized stride time.

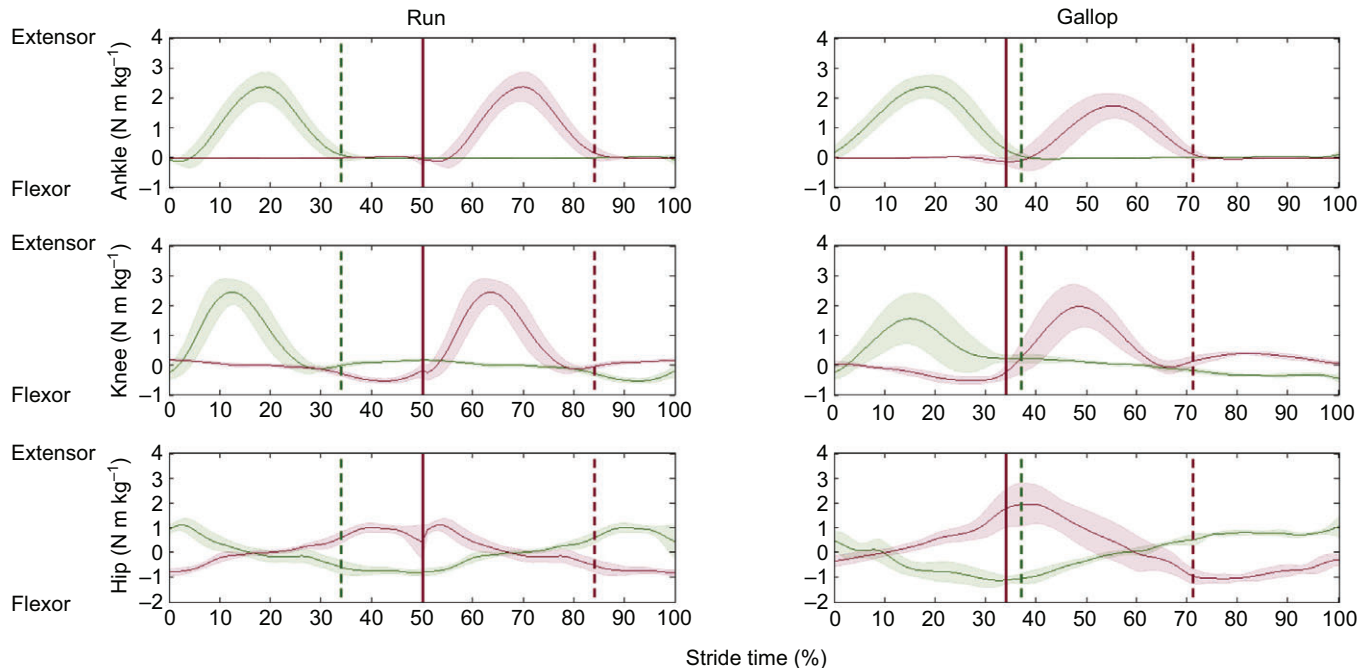


Fig. 5. Instantaneous joint moments (ankle, knee and hip) during a stride of R and G. Green lines represent left legs and red lines represent right legs for R. For G, green lines represent  $G_{\text{trail}}$  and red lines represent  $G_{\text{lead}}$ . Solid vertical lines represent FC and vertical dashed lines represent TO (colour relates to leg). y-axis: joint moments in N m normalized to BW; x-axis: normalized stride time.

by flexing the ankle and knee. After loading, the leading leg extends till TO: maximum ankle plantarflexion is similar to that in R ( $P_{R-G_{\text{lead}}}=0.506$ ) and the knee extends to a similar position as at IC ( $P_{G_{\text{lead}}}=0.115$ ). Throughout FC of  $G_{\text{lead}}$ , the hip is gradually extended till maximum extension is reached at TO. This maximum is smaller than in R or in the trailing leg ( $P_{R-G_{\text{lead}}}=0.046$ ,  $P_{G_{\text{trail}}-G_{\text{lead}}}=0.072$ ). In contrast to R and  $G_{\text{trail}}$ , where the feet leave the ground far behind the horizontal position of the  $\text{COM}_{\text{wb}}$ , TO of  $G_{\text{lead}}$  takes place just behind the horizontal position of the  $\text{COM}_{\text{wb}}$ .

During swing, both  $G_{\text{lead}}$  and  $G_{\text{trail}}$  are kept extended, which differs significantly from R, where the legs are flexed ( $P_{R-G_{\text{trail}}}=0.000$ ,  $P_{R-G_{\text{lead}}}=0.000$ ).

#### Joint moments

The course of the joint moments of the G and R legs was roughly similar for the ankle and knee (Fig. 5). In  $G_{\text{trail}}$ , an initial ankle flexor moment was absent because of forefoot IC. The ankle moments throughout contact of both feet were extensor moments but the angular ankle extensor impulse was smaller in  $G_{\text{lead}}$  than in  $G_{\text{trail}}$  and R ( $P_{R-G_{\text{lead}}}=0.003$ ,  $P_{G_{\text{trail}}-G_{\text{lead}}}=0.000$ ). During FC, both knee moments were extensor moments. The angular knee extensor impulse in  $G_{\text{trail}}$  was smaller than that in R but was not different to that in  $G_{\text{lead}}$  ( $P_{R-G_{\text{trail}}}=0.007$ ,  $P_{G_{\text{trail}}-G_{\text{lead}}}=1.000$ ). The largest differences in joint moments between G and R legs occurred at the hip. For R, the hip moment was an extensor moment during the first half of FC and changed to a flexor moment during the second half of FC. The hip moment of  $G_{\text{trail}}$  was an extensor moment during the first third of FC only, while in  $G_{\text{lead}}$  only the last third of FC was an extensor moment. During FC, the angular hip flexor impulse of  $G_{\text{trail}}$  was larger than those in R and  $G_{\text{lead}}$  ( $P_{R-G_{\text{trail}}}=0.001$ ,  $P_{G_{\text{trail}}-G_{\text{lead}}}=0.000$ ). In  $G_{\text{lead}}$ , the extensor moment at the hip at IC ( $P_{R-G_{\text{lead}}}=0.043$ ,  $P_{G_{\text{lead}}-G_{\text{trail}}}=0.007$ ) and the angular hip extensor impulse during FC ( $P_{R-G_{\text{lead}}}=0.001$ ,  $P_{G_{\text{trail}}-G_{\text{lead}}}=0.000$ ) were larger than those in  $G_{\text{trail}}$  and R.

#### Joint power

As indicated by the eccentric activity of the ankle plantar flexors and the knee extensors, the ankle and knee of both G and R legs absorbed power in the first half of FC (Fig. 6). In second half, these muscles showed concentric activity; thus, power was generated. In comparison with R, the  $G_{\text{trail}}$  ankle absorbed more power, while the absorption of power by the  $G_{\text{lead}}$  ankle was smaller. The knee power in  $G_{\text{trail}}$  was smaller than that in R but was not different from that in  $G_{\text{lead}}$  ( $P_{R-G_{\text{trail}}}=0.000$ ,  $P_{G_{\text{trail}}-G_{\text{lead}}}=0.348$ ). In contrast to the ankle and knee power, hip joint power was remarkably different between G and R. The maxima and minima of the hip joint power in R were rather low compared with those in G, though not significantly different (minimum hip power:  $P_{R-G_{\text{trail}}}=0.101$ ; maximum hip power:  $P_{R-G_{\text{lead}}}=0.106$ ). In G there is a phase of large eccentric activity of the hip flexors of  $G_{\text{trail}}$  starting at one third in FC and continuing until TO. For  $G_{\text{lead}}$ , the hip extensors generate power during the first two thirds of FC followed by power absorption by the hip flexors during the last third of stance.

#### Work

Total positive work performed over one stride did not differ between G and R ( $R=3.12\pm0.36\text{ J kg}^{-1}$ ,  $G=2.96\pm0.59\text{ J kg}^{-1}$ ;  $P_{R-G}=0.461$ ) (Fig. 7). However, when scaled to the travelled distance, the work performed in G was larger than that in R ( $R=1.41\pm0.06\text{ J kg}^{-1}\text{ m}^{-1}$ ,  $G=1.62\pm0.15\text{ J kg}^{-1}\text{ m}^{-1}$ ;  $P_{R-G}=0.030$ ). In R, the two legs contributed equally to the total positive work, while in G,  $G_{\text{trail}}$  delivered  $\pm 35\%$  of the total positive work and  $G_{\text{lead}}$   $\pm 65\%$  ( $P_{R-G_{\text{trail}}}=0.050$ ,  $P_{R-G_{\text{lead}}}=0.050$ ,  $P_{G_{\text{trail}}-G_{\text{lead}}}=0.050$ ).

The difference in work generation between G and R legs was not limited to the amount that each leg contributed to the total positive work but was also evident in the relative contribution of the joints to total positive leg work. The relative contribution of the ankle in  $G_{\text{trail}}$  was larger than that in R and  $G_{\text{lead}}$  ( $P_{R-G_{\text{trail}}}=0.083$ ,

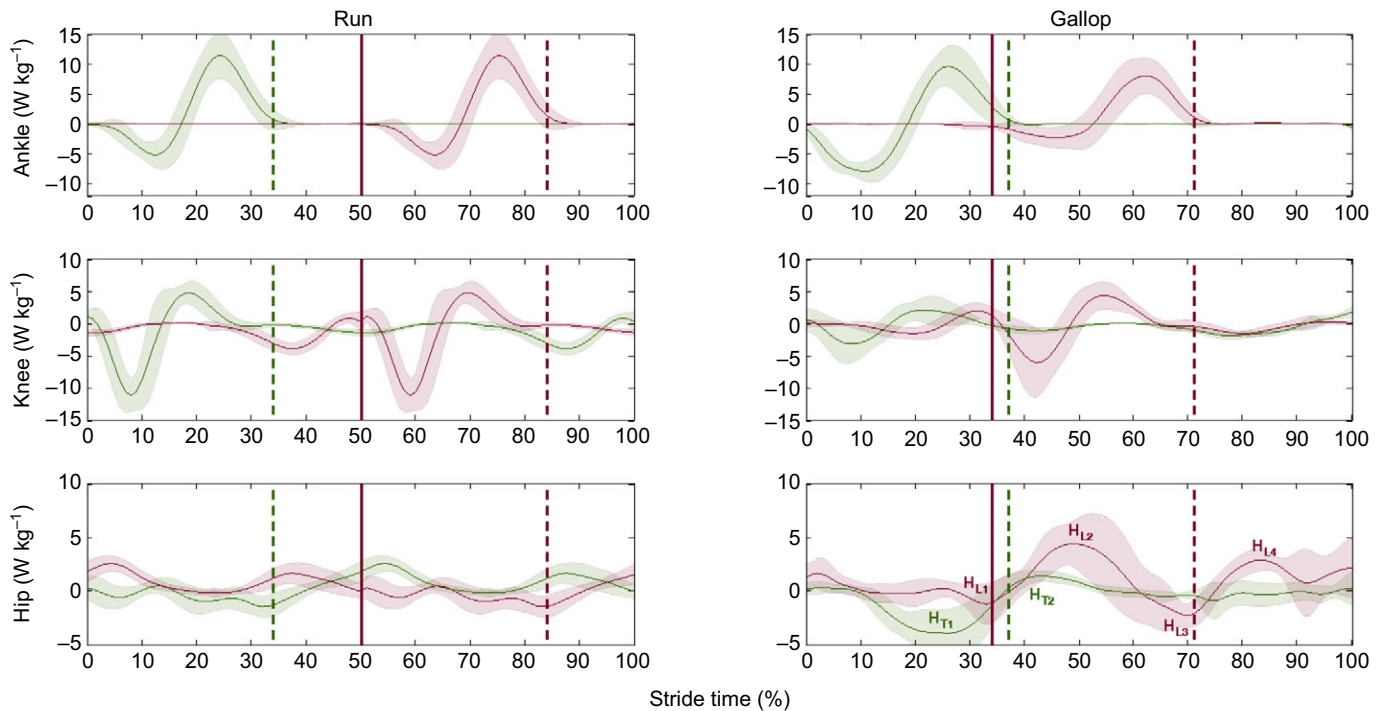


Fig. 6. Instantaneous joint power (ankle, knee and hip) during a stride of R and G. For R, green lines represent left legs and red lines represent right legs. For G, green lines represent  $G_{\text{trail}}$  and red lines represent  $G_{\text{lead}}$ . Solid vertical lines represent FC and vertical dashed lines represent TO (colour relates to leg).  $H_{T1,2}$ , hip flexors, trailing leg;  $H_{L1,2}$ , hip extensors, leading leg;  $H_{L3,4}$ , hip flexors, leading leg. y-axis: joint power, negative values indicate power absorption, positive values indicate power generation; x-axis: normalized stride time.

$P_{R-G_{\text{lead}}}=0.071$ ,  $P_{G_{\text{trail}}-G_{\text{lead}}}=0.029$ ), while the relative contribution of the hip was smaller than in R ( $P_{R-G_{\text{trail}}}=0.175$ ,  $P_{R-G_{\text{lead}}}=0.147$ ,  $P_{G_{\text{trail}}-G_{\text{lead}}}=0.042$ ). In  $G_{\text{lead}}$ , the proportional contribution of each joint to total positive leg work was opposite to the pattern in  $G_{\text{trail}}$  and R: the contribution of the hip was larger, while that of the ankle was smaller. The relative contribution of the knee was similar in both  $G_{\text{lead}}$  and  $G_{\text{trail}}$  and in R ( $P=0.213$ ).

In G, total negative work over a stride ( $R=-3.01\pm0.71\text{ J kg}^{-1}$ ,  $G=-2.50\pm0.54\text{ J kg}^{-1}$ ;  $P_{R-G}=0.131$ ) and for the same distance travelled ( $R=-1.35\pm0.20\text{ J kg}^{-1}\text{ m}^{-1}$ ,  $G=-1.36\pm0.11\text{ J kg}^{-1}\text{ m}^{-1}$ ;  $P_{R-G}=0.937$ ) did not differ from that in R. As for total positive work, differences were observed between R and G for the contribution of each leg to total negative work. In fact, the proportion of power absorbed by each leg was opposite to the proportion of power generated:  $G_{\text{lead}}$  absorbed only  $\pm 35\%$  of the work while  $G_{\text{trail}}$  absorbed  $\pm 65\%$  of the work ( $P_{R-G_{\text{trail}}}=0.028$ ,  $P_{R-G_{\text{lead}}}=0.028$ ,  $P_{G_{\text{trail}}-G_{\text{lead}}}=0.028$ ). In R, the largest absorption of power was carried out by the knee and only a small amount was performed by the hip. In  $G_{\text{trail}}$ , most of the power was absorbed by the ankle, whereas in  $G_{\text{lead}}$  most of the power was absorbed by the knee, although this was less than that absorbed in R.

#### Metabolic energy consumption

At a speed of  $2.78\text{ m s}^{-1}$ , the cost of locomotion was higher for G than for R ( $G=4.95\pm0.31\text{ J kg}^{-1}\text{ m}^{-1}$ ,  $R=4.01\pm0.31\text{ J kg}^{-1}\text{ m}^{-1}$ ;  $P=0.000$ ).

#### DISCUSSION

The purpose of this study was threefold: first, to explore the differences between bipedal gallop and run; second, to show how propulsion in gallop is generated; and third, to understand why people do not use gallop spontaneously for steady-state locomotion.

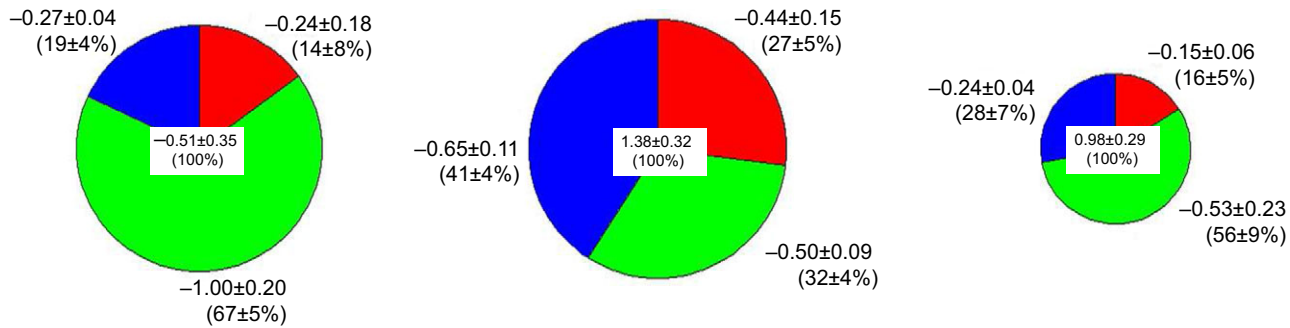
In the first part of the Discussion, differences between gallop and run will be assessed. In the second part, we argue that gallop mainly makes use of elastic energy storage and recoil to minimize the energetic cost of locomotion. This will be followed by an explanation of why humans do not use gallop for steady-state locomotion and why it may be the preferred gait at high speed in animals.

The results of the running test are in agreement with reference studies (Novacheck, 1998; Winter, 1983; Milliron and Cavanagh, 1990; Belli et al., 2002). Considering intra- and inter-subject variability in the horizontal and vertical GRFs as a net measure of movement variability, movement consistency was found to be comparable between running and galloping legs. Apparently, although it is rarely used, gallop is a familiar gait for humans. Moreover, energetics of the  $\text{COM}_{\text{wb}}$  and kinematics of gallop are similar to those reported in earlier studies (Caldwell and Whittall, 1995; Whittall and Caldwell, 1992). Reference data for joint moments and power of gallop only exist for the swing phase (Caldwell and Whittall, 1995). The calculated joint moments and power during swing of this study correspond with the reference data found in that study.

As in gallop, one leg is always kept in front of the other, representing different configurations with respect to the  $\text{COM}_{\text{wb}}$ ; indeed, we found specific movement patterns and functions for each leg, which concurs with previous results (Whittall and Caldwell, 1992). Compared with run, the point where the trailing leg in gallop touches the ground is closer to the  $\text{COM}_{\text{wb}}$  and when this leg leaves the ground the horizontal distance with the  $\text{COM}_{\text{wb}}$  is larger. Touch down of the leading leg is farther in front of the body and at TO the horizontal position of the  $\text{COM}_{\text{wb}}$  almost coincides with that of the foot. This difference in foot positioning results in different leg functions (see Introduction, hypothesis i): (i) the trailing leg



## Negative work



## Positive work

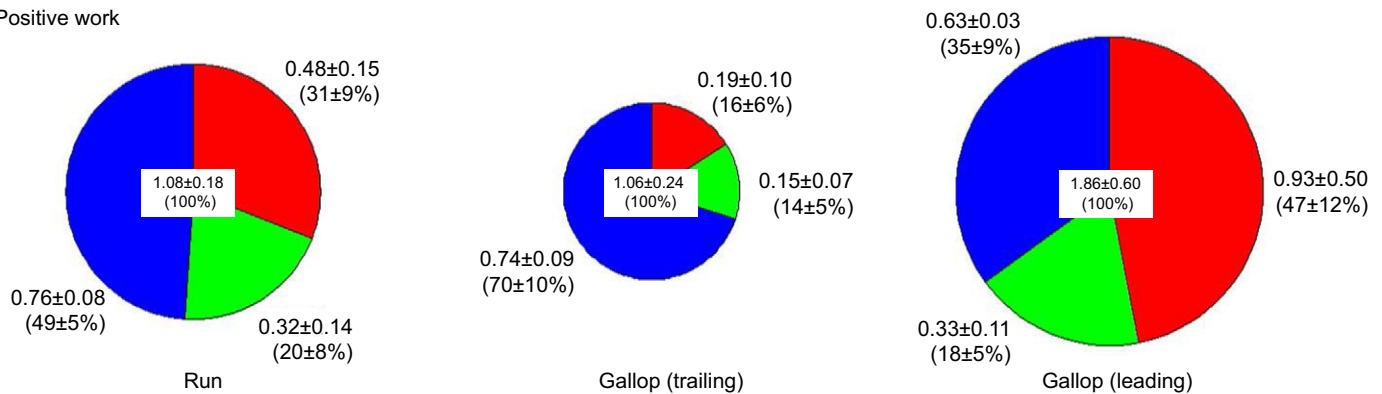


Fig. 7. Pie charts showing the relative contribution ( $\text{J kg}^{-1}$ ) to total negative and positive limb work by the hip (red), knee (green) and ankle (blue) joints of one limb during one stride. The sizes of the pie charts are scaled to total work absorbed/generated by a limb, the value of which is superimposed on the pie chart (in  $\text{J kg}^{-1}$ ).

decelerates the downward velocity of the body during the first part of contact and propels it forward during push-off, (ii) the leading leg does the opposite: it decelerates forward movement of the body during the first part of contact and raises it during push-off. To propel the body forward, the trailing leg transfers  $E_{\text{pot}}$  and  $E_{\text{kin,v}}$  into  $E_{\text{kin,f}}$ , while the leading leg does the opposite to raise the body. In contrast to run, the trailing leg of gallop strikes the ground with the forefoot but similar to run, loading is accepted by flexing the ankle and knee (Novacheck, 1998; Winter, 1983; Milliron and Cavanagh, 1990; Belli et al., 2002). During the second part of foot contact, the ankle and knee are extended to propel the body forward. The leading leg is more flexed (than the trailing leg and running leg) when its foot strikes the ground and flexes further during the first half of contact compared with running and trailing galloping legs. During push-off the leg extends, leaving the ground with the same knee angle as at touchdown. In swing, galloping legs are less flexed than in run to return them to footstrike position.

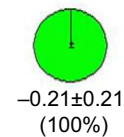
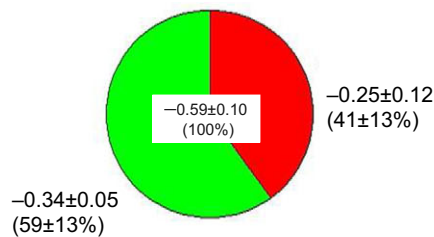
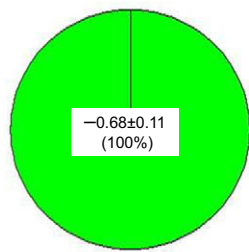
Another hypothesis put forward in the Introduction (hypothesis ii) was that during support the major difference at joint level is situated in the hip. The results of this study confirm this hypothesis. At foot contact, the hip of the trailing leg is already more extended than in running and continues to extend until toe-off. The hip of the leading leg is more flexed throughout contact. The extensor–flexor hip moments reveal the function of the hip musculature in bipedal locomotion: balancing the mass above the pelvis during support (Winter et al., 1990; Winter, 1983; Winter, 1995) and control of the swing leg. As during the support phase in running (Novacheck, 1998; Winter, 1983), the hip moments are extensor moments as long as the feet are in front of the  $\text{COM}_{\text{wb}}$ ,

causing deceleration of the body, and become flexor moments when the  $\text{COM}_{\text{wb}}$  has passed the horizontal position of the feet, facilitating push-off. During flight, an extensor moment at the hip of the trailing leg slows down the forward movement of the trailing leg and prepares it for foot contact. At the same time, the leading leg swings forward because of a flexor moment at the hip. The two moments counteract each other, facilitating upper body stability. Because of the asymmetric foot placing in gallop, the hip moments are larger and distributed differently over the course of one cycle compared with that in running.

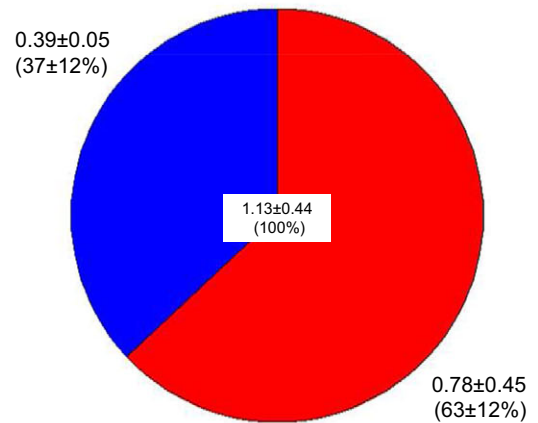
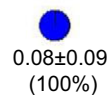
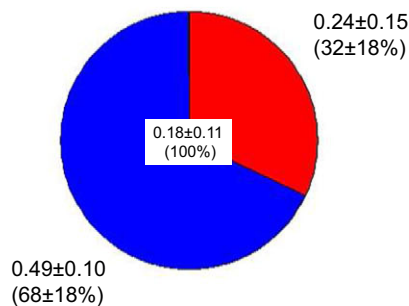
Although Minetti concluded that in gallop the two basic strategies for mechanical energy saving operate simultaneously (Minetti, 1998), no experimental proof has been provided. The first basic energy-saving mechanism consists of the exchange between  $E_{\text{pot}}$  and  $E_{\text{kin}}$  as occurs in an inverted pendulum (Cavagna et al., 1977). If the body behaves like an inverted pendulum in gallop, an increase in  $E_{\text{pot}}$  should be accompanied by a decrease in  $E_{\text{kin}}$  and *vice versa*. In the current experiment, when the trailing foot touched the ground,  $E_{\text{pot}}$  decreased but an increase in  $E_{\text{kin}}$  was only noticed when  $E_{\text{pot}}$  had reached its minimum. During contact of the leading leg, an opposite sequence was observed:  $E_{\text{kin}}$  decreased during the first part of foot contact but  $E_{\text{pot}}$  only increased when  $E_{\text{kin}}$  was already at a minimum. Although ‘energy recovery’ – a parameter reflecting the ability to save mechanical energy through pendulum-like motions (Cavagna et al., 1976) – for gallop is  $51 \pm 10\%$ , which is high, galloping legs do not behave like inverted pendulums (as argued above) and little energy is saved by an exchange between  $E_{\text{kin,f}}$  and  $E_{\text{pot}}$ . The second basic energy-saving mechanism is the exchange between external mechanical energy and elastic energy, as in a spring



## Net negative work



## Net positive work



Run

Gallop (trailing)

Gallop (leading)

Fig. 8. Pie charts showing the relative contribution ( $\text{J kg}^{-1}$ ) to net negative and positive limb work by the hip (red), knee (green) and ankle (blue) joints of one limb during one stride. The sizes of the pie charts are scaled to net work absorbed/generated by a limb, the value of which is superimposed on the pie chart (in  $\text{J kg}^{-1}$ ).

(Cavagna et al., 1977). Usually, the potential for this mechanism is identified by a simultaneous rise and fall in  $E_{\text{pot}}$  and  $E_{\text{kin}}$  of the  $\text{COM}_{\text{wb}}$ , as in run. In gallop, because of the asymmetrical leg configuration, such a pattern is not observed, making the use of this energy-saving mechanism not obvious at the whole-body level. However, judging by the joint kinematics and kinetics, there is potential for elastic energy storage and recoil in gallop. In order to make use of elastic energy, shortening of the muscle-tendon unit must be preceded by a lengthening while force is developed, i.e. concentric activity must be preceded by eccentric activity (Van Ingen Schenau et al., 1997; Komi, 1992). The present data of ankle and knee moments and power during gallop (Figs 5, 6) seem to be in agreement with such an energy-saving mechanism. During contact of galloping legs as well as running legs with the ground, positive work at the ankle and knee is preceded by negative work. Although actual muscle length changes are unknown, it seems reasonable to assume that most of the negative work at the ankle is stored as elastic energy and released during push-off (Ishikawa et al., 2007; Van Ingen Schenau et al., 1997; Komi, 1992), while only a part of the negative work at the knee is converted into elastic energy (Sasaki and Neptune, 2006).

In gallop, the leading leg functions as an elastic vaulting pole, while the trailing leg functions in the reverse manner. The trailing leg converts  $E_{\text{pot}}$  and  $E_{\text{kin,v}}$  into elastic energy that is released into  $E_{\text{kin,f}}$  during push-off. This  $E_{\text{kin,f}}$  is converted into elastic energy by the leading leg and during push-off is released into  $E_{\text{pot}}$  and  $E_{\text{kin,v}}$ . In contrast to hypothesis iii (see Introduction), which stated that in

gallop the two energy-saving mechanisms are operating simultaneously, most energy is saved by exchange between mechanical and elastic energy and only a little energy is saved by exchange between  $E_{\text{kin}}$  and  $E_{\text{pot}}$ .

The fourth purpose of the study was to investigate why people do not gallop spontaneously for steady-state locomotion. On the basis of the current set of data, two possible explanations can be considered: the first one involves the metabolic cost of transport and the second one relates to local muscular stress.

Gallop is metabolically  $24 \pm 5\%$  more expensive than running at the same speed. The higher metabolic cost of gallop may be related to an increase in total work generation and a difference in power contribution.

Over a stride, the total positive and negative work in gallop and run are similar but in relation to the distance covered,  $15 \pm 7\%$  more work is generated during gallop. In addition to the difference in work generation, the contribution of the two legs to the total power in gallop and run is different too. In run, each limb absorbs and generates an equal amount of negative and positive power, whereas in gallop, because of its asymmetrical nature, power is distributed unevenly across the two limbs (Fig. 7). The trailing leg generates only  $\pm 35\%$  of the total average positive power, while it absorbs  $\pm 65\%$  of the total average negative power. If there was a perfect exchange of eccentric and concentric power within a leg, the positive power generated by the trailing leg could be completely regained from the negative power. In the leading leg, only  $\pm 50\%$  of the positive power could be regained out of the negative power. The

implication is that at least  $\pm 0.50 \text{ J kg}^{-1} \text{ m}^{-1}$  must be generated at the expense of metabolic energy.

Furthermore, the amount of absorbed and generated power is distributed differently across the joints. In gallop, most of the work is generated at the ankle of the trailing leg and at the ankle and hip of the leading leg. In run, the ankles generate most of the work, while both hips generate slightly less compared with the positive work done by both galloping hips (Fig. 7).

Assuming that over a stride and within a joint all negative work is temporally stored and recovered into positive work (Fig. 8), in run the ankle and hip generate work, while the knee absorbs an equal amount of work. In gallop, the knee and hip of the trailing leg absorb work while little work is generated at the ankle. Almost all positive work in gallop is generated by the ankle and hip of the leading leg. Because of the asymmetrical nature and the different distribution of power among the joints, more power is generated by proximal muscles in gallop compared with run. The proximal muscles such as the hip extensors do not have long tendons, as found in the distal muscles (Ker et al., 1988), which makes power generation more costly compared with power generation at the ankle. There, the longer tendons can take up much of the muscle–tendon length change, causing the muscle fibers to operate isometrically or at relatively slow velocities, providing power in an efficient manner (Roberts, 2002; Roberts et al., 1997; Ishikawa et al., 2007; Lichtwark et al., 2007).

Examination of instantaneous joint power (Fig. 6) shows that during gallop energy is indeed dissipated at the hip. The hip flexors of the trailing leg ( $H_{T1}$ ) absorb large amounts of power, followed by little power generation in early swing ( $H_{T2}$ ). Moreover, the joint power profiles confirm that in gallop the hip of the leading leg generates a large amount of work that cannot be gained from previously stored elastic energy. During contact, the hip extensors generate lots of concentric power ( $H_{L2}$ ) that is preceded by little eccentric activity ( $H_{L1}$ ). At the end of the stance phase, there is a small amount of eccentric activity of the hip flexors ( $H_{L3}$ ), which is again followed by a much larger concentric activity ( $H_{L4}$ ). Therefore, elastic storage and return, if present, will be minimal. Compared with the hip actions during running, more energy is likely to be dissipated and generated at the expense of metabolic energy in gallop. In both gallop and run, the knee extensors first show eccentric activity, which is followed by equal (gallop) or less (run) concentric activity. Just as in the knees, in the ankles an eccentric–concentric coupling occurs for both running and galloping. The eccentric and concentric peaks are equal in magnitude for the ankle of the trailing leg but differ in magnitude for the ankle of the leading leg and for the running leg, with the eccentric activity being only about 35% of the subsequent concentric activity.

As such, these temporal profiles of joint power in the three lower limb joints demonstrate that in gallop, the orientation of the legs causes energy dissipation through the hip flexors of the trailing leg and metabolic expensive power generation by the hip extensors of the leading leg. This power dissipation and generation may be reflected in the higher metabolic costs compared with run.

It is interesting to note that our findings bear some resemblance to the asymmetric walking pattern of people with hemiplegia caused by stroke. Research by Teixeira-Salmela and colleagues (Teixeira-Salmela et al., 2001) showed that post-stroke walking is characterized by an asymmetric distribution of power over the two legs. A large proportion of the total leg work is generated by the hip, whose role is to assist propulsion and to balance the upper body. Consistent with our findings for gallop, the increase in work at the level of the hip in hemiplegic gait is associated with a rise in metabolic costs (Lamontagne et al., 2007).

It should be acknowledged that an increase in force generation could also affect the cost of transport. Biewener (Biewener, 1990) and Kram and Taylor (Kram and Taylor, 1990) argued that the amount of force generated by the muscles determines the metabolic cost. Although we cannot measure muscle forces, ground reaction impulses may be a good proxy for the relative demands of muscle force. Taking this into consideration and taking account of the differences in SL, total force generated per unit distance is 12% larger for gallop than for run and thus could also contribute to the higher cost of transport.

As argued above, the relative increase in metabolic cost of galloping compared with running at a given speed (i.e. gallop is  $\pm 24\%$  more expensive than run) is largely similar to the relative increase in mechanical cost of transport (i.e. gallop being 15% more expensive). The higher mechanical cost of galloping could be traced back in the segmental analysis to differences primarily occurring at the hips. One difference between galloping and running is the presence of the double support phase (compound stance), such as in walking when the  $\text{COM}_{\text{wb}}$  is redirected (Kuo et al., 2005; Ruina et al., 2005; Lee et al., 2011). At the whole-body level (centre of mass approach), this redirection comes at a cost and it seems plausible that the double support in galloping explains the higher costs in a similar way. However, the present results show that the period of double stance is very short ( $\pm 0.024 \text{ s}$ ) and, more importantly, that no redirection of the  $\text{COM}_{\text{wb}}$  occurs during this double stance (i.e. no collision; cf. plateau in the  $E_{\text{pot}}$  profile for galloping in Fig. 2), suggesting that the extra costs measured are not related to the double support. In a recent paper, Lee and colleagues proposed a method to estimate (dimensionless) mechanical costs over a stride from a collisional perspective (Lee et al., 2011). Applied to our results, this method on the one hand confirms the above suggestion (no large costs related to double stance) but on the other hand provides puzzling results. Over one stride, both the mechanical costs of motion [eqn 8 in Lee et al. (Lee et al., 2011)] and the equivalent collision angles [eqn 7 in Lee et al. (Lee et al., 2011)] are lower for galloping (0.22) than for running (0.26). However, when normalized to distance covered, costs are identical for the two gaits ( $0.11 \text{ m}^{-1}$ ). This contrasts with the metabolic and segmental–mechanical ratios (1.24 and 1.15; cf. above) measured in this study. In the light of the collision approach, this probably points to a better elastic recovery during running compared with galloping, as is also suggested by the differences in the calculated collision fractions. For running, collision fraction amounts to 0.97, which is consistent with the compliant SLIP model (Lee et al., 2011), whereas for bipedal galloping the collision fraction equals 0.78, similar to what was found for galloping quadrupeds (Lee et al., 2011). Further resolution of this issue is out of the scope of the present study, but may be relevant in view of the further development of the collisional perspective of gait dynamics (Lee et al., 2011).

In addition to the higher metabolic cost of transport, a more local mechanism may also determine why people do not use gallop. In our second experiment, subjects all perceived galloping on a treadmill as physically demanding and uncomfortable. They reported feelings of fatigue and muscular stress at both thighs and hips, causing four out of 13 subjects to stop the galloping pattern early, i.e. they could not keep the galloping pattern going for the whole 4 min. During gallop, the leading leg produces more power than the trailing leg or a running leg, which means that there is an increase in volume-specific muscle force per unit time and thus higher muscle stresses. It is conceivable that this increase in power production causes such high stresses and fatigue

that we place ourselves at risk of an injury, so the galloping pattern cannot be maintained. Indeed, inspection of the joint moments shows that the maximal hip extensor moment and the angular hip extensor impulse in the leading leg are higher than those in the trailing leg and in a running leg, suggesting higher muscular stress and possibly inducing fatigue of the hip extensors of the leading leg. To verify this, hip extensor muscle stresses were calculated using a method that combines published muscle moment arms and physiological cross-sectional areas with our own measured joint angles and moments (Thorpe et al., 1998). Peak stresses in the hip extensors of the leading leg ( $84.7 \text{ kNm}^{-2}$ ) were almost twice as high as those in the trailing leg ( $43.8 \text{ kNm}^{-2}$ ) and  $\sim 1.75$  times higher than those in a running leg ( $48.6 \text{ kNm}^{-2}$ ). Thus, the different movements and functions of both galloping legs cause high local muscular stresses and possible fatigue of the hip extensors of the leading leg, which may be a second (though not mutually exclusive) reason why people do not select gallop spontaneously for overground steady-state locomotion.

Thus, higher metabolic costs of transport as well as higher local muscular stress at the thigh and hip may be the reasons why people do not gallop for steady-state locomotion at higher speeds, which confirms hypothesis iv (see Introduction).

The finding that gallop in humans is metabolically more demanding than running at the same speed is in contrast with findings in horses, where gallop and trot have the same economy at similar speeds (Hoyt and Taylor, 1981; Minetti et al., 1999). This discrepancy may be related to the transfer of energy between the limbs and/or in the function of the hip and shoulder joint. Horses have a flexible spine that bends and extends during galloping strides. Alexander and colleagues suggested that this bending and extending serves as an energy-saving spring in gallop that transfers energy from the hindlimbs to the forelimbs and *vice versa* (Alexander et al., 1985; Alexander, 1990; Alexander, 2002). In humans, such energy transfer is not possible. The implication is that energy dissipates at the hip of the trailing leg and energy needs to be generated by the hip of the leading leg. Moreover, stabilizing the mass on top of the limbs is less demanding in quadrupeds because most of the mass is situated between the hindlimbs and forelimbs, which may free the hip and shoulder of their balancing task and thus enhance their capacity to assist in propulsion (Lee et al., 1999; Usherwood and Wilson, 2005; Dutto et al., 2006; Williams et al., 2009).

Finally, the following limitations of this study should be noted. To assess muscle–tendon work, joint work was calculated by integrating joint power, which was calculated using inverse dynamics. Although this approach is commonly used, it is not without flaws. Joint work is an approximation of muscle–tendon work because it cannot take co-contraction of antagonistic muscles, biarticular muscle work and passive joint work into account. Muscle co-contractions cause the net moment to be smaller than the sum of the individual muscle flexor and extensor moments and thus underestimates joint work/muscle–tendon work. Biarticular muscles (because work is calculated at each joint separately) and passive joint work overestimate muscle–tendon work (Sasaki et al., 2009). The inverse dynamics approach is also unable to measure isometric muscle contractions that consume metabolic energy but are not taken into account in the joint mechanical work. Furthermore, the study focuses on the work absorbed and generated at the joints of the lower limbs. Joint power of, and work generated or absorbed by, the upper limbs were calculated but were considered small compared with those of the lower extremities and are therefore not reported. Another methodological limitation is that hip joint kinetics and

therefore also work at the hips and total leg work were limited to four subjects because of practical limitations of the setup. However, as kinematics, GRFs and ankle and knee joint kinetics show similar patterns for all subjects and because joint kinetics link GRFs to whole-body behaviour, it seems very plausible that hip joint kinetics are similar for all subjects, too.

In conclusion, the present study showed that the specific configuration of galloping legs involves different hip actions and feet placement, giving galloping legs different functions. Although energy is saved by interchanging external mechanical and elastic energy, the metabolic cost of locomotion is higher for gallop than for run. This higher metabolic cost of gallop is caused by larger amounts of work generated per unit distance combined with a shift of power generation to more proximal joints. The asymmetrical pattern not only influences the metabolic cost of locomotion but also involves higher muscular stress at the hips, which may be another reason why humans do not use gallop for steady-state locomotion on level ground.

#### LIST OF SYMBOLS AND ABBREVIATIONS

BW	body weight
COM <sub>wb</sub>	whole-body centre of mass
CV	coefficient of variation
$E_{\text{ext}}$	mechanical external energy
$E_{\text{kin}}$	kinetic energy
$E_{\text{kin,f}}$	forward kinetic energy
$E_{\text{kin,v}}$	vertical kinetic energy
$E_{\text{pot}}$	gravitational potential energy
FC	foot contact
$g$	gravitational constant
G	gallop
G <sub>lead</sub>	leading leg of gallop
GRF <sub>h</sub>	horizontal ground reaction force
GRFs	ground reaction forces
GRF <sub>v</sub>	vertical ground reaction force
G <sub>trail</sub>	trailing leg of gallop
HL <sub>1</sub>	power absorption by the hip extensors of the leading leg
HL <sub>2</sub>	power generation by the hip extensors of the leading leg
HL <sub>3</sub>	power absorption by the hip flexors of the leading leg
HL <sub>4</sub>	power generation by the hip flexors of the leading leg
HT <sub>1</sub>	power absorption by the hip flexors of the trailing leg
HT <sub>2</sub>	power generation by the hip flexors of the trailing leg
$h_{\text{wb}}$	height of the COM <sub>wb</sub>
IC	initial contact
$m$	mass
R	run
SF	stride frequency
SL	stride length
SLIP	spring-loaded inverted pendulum
TO	toe-off
$v_{\text{f}}$	instantaneous forward velocity of the COM <sub>wb</sub>
$v_{\text{pref}}$	preferred velocity
$v_{\text{v}}$	instantaneous vertical velocity of the COM <sub>wb</sub>

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