

## RESEARCH ARTICLE

# The quadrupedal walking gait of the olive baboon, *Papio anubis*: an exploratory study integrating kinematics and EMG

François Druelle<sup>1,2,3,\*</sup>, Anthony Supiot<sup>4</sup>, Silke Meulemans<sup>3</sup>, Niels Schouteden<sup>3,5</sup>, Pablo Molina-Vila<sup>2</sup>, Brigitte Rimbaud<sup>2</sup>, Peter Aerts<sup>3,6</sup> and Gilles Berillon<sup>1,2</sup>

## ABSTRACT

Primates exhibit unusual quadrupedal features (e.g. diagonal gaits, compliant walk) compared with other quadrupedal mammals. Their origin and diversification in arboreal habitats have certainly shaped the mechanics of their walking pattern to meet the functional requirements necessary for balance control in unstable and discontinuous environments. In turn, the requirements for mechanical stability probably conflict with mechanical energy exchange. In order to investigate these aspects, we conducted an integrative study on quadrupedal walking in the olive baboon (*Papio anubis*) at the Primatology station of the CNRS in France. Based on kinematics, we describe the centre of mass mechanics of the normal quadrupedal gait performed on the ground, as well as in different gait and substrate contexts. In addition, we studied the muscular activity of six hindlimb muscles using non-invasive surface probes. Our results show that baboons can rely on an inverted pendulum-like exchange of energy (57% on average, with a maximal observed value of 84%) when walking slowly ( $<0.9 \text{ m s}^{-1}$ ) with a tight limb phase ( $\sim 55\%$ ) on the ground using diagonal sequence gaits. In this context, the muscular activity is similar to that of other quadrupedal mammals, thus reflecting the primary functions of the muscles for limb movement and support. In contrast, walking on a suspended branch generates kinematic and muscular adjustments to ensure better control and to maintain stability. Finally, walking using the lateral sequence gait increases muscular effort and reduces the potential for high recovery rates. The present exploratory study thus supports the assumption that primates are able to make use of an inverted pendulum mechanism on the ground using a diagonal walking gait, yet a different footfall pattern and substrate appear to influence muscular effort and efficiency.

**KEY WORDS:** Centre of mass, Electromyography, Primate, Locomotion, Positive reinforcement

## INTRODUCTION

The origin and evolution of primates is closely related to arboreal habitats (e.g. Cartmill, 1974; Hamrick, 2001; Toussaint et al., 2020) and many extant primates continue to live in arboreal environments,

or at least invest a certain amount of time foraging in the trees on thin and flexible branches (Hunt, 2016). Such an environment obviously implies discontinuity, variability, instability and oscillations of the substrates that perturb the inherent mechanical requirements of legged locomotion, i.e. propulsion, balance and stability of the walking gait. It has been shown that primates exhibit a set of morphological adaptations and kinematical adjustments coupled to a behavioural flexibility that allow them to meet the functional requirements demanded by this complex environment (e.g. Cartmill et al., 2020; Demes et al., 1994; Druelle et al., 2020; Hunt et al., 1996; Larney and Larson, 2004; Larson et al., 2001; Schmitt, 1999; Schmitt et al., 2006; Thorpe et al., 2007). During quadrupedal walking, primates use diagonal sequence/diagonal couplet (DSDC) gaits, large limb angular excursions, large elbow yield, long stance phase, low stride frequency and a weight support shifted toward the hindlimbs (see Larson, 2018, for a review). These features can be integrated under the compliant gait model of primate walking (Schmitt, 1999). Overall, these characteristics should particularly allow for control of pitching, yawing and rolling moments, and limit the vertical oscillations of the centre of mass (CoM), and hence branch oscillation, and increase maintenance of balance (e.g. Cartmill et al., 2020, 2002; Schmitt et al., 2006).

Parallel to these functional adjustments, the muscular activity pattern also presents specificities. Electromyography (EMG) studies on non-human primates have provided significant knowledge about muscle basic activity pattern in different locomotor modes such as climbing, brachiating and bipedal walking (e.g. Hirasaki et al., 1995; Ishida et al., 1974; Jungers and Stern, 1981; Stern and Larson, 2001, 1981), but the way muscle recruitment has been altered in non-human primates in relation to the arboreal niche remains poorly understood (Boyer et al., 2007; Courtine et al., 2005; Larson and Stern, 2009; Patel et al., 2015). During primate quadrupedal walking, distal limb muscles are suggested to be under higher cortical control including different speed-related modulations of the limbs compared with other quadrupedal mammals (Courtine et al., 2005). The different inertial properties of non-human primates compared with other quadrupeds (Grand, 1977; Druelle et al., 2019) should also affect the way the work is performed, and the forces transmitted. Overall, more flexible capabilities of the neuromotor control system are suggested in primates (Courtine et al., 2005; Jungers and Anapol, 1985; Shapiro et al., 1997), with the hand and the foot having distinct functional roles (Druelle et al., 2018; Hashimoto et al., 2013; Lawler, 2006; Patel et al., 2015). Furthermore, although the phasic recruitment of muscles is generally similar to that of other quadrupedal mammals (Courtine et al., 2005; Higurashi et al., 2019; Shapiro and Jungers, 1994), specificities have been emphasized for the humeral retractors (Larson and Stern, 1987, 1989, 2007), and hip extensors might also be used for different functions (Larson and Stern, 2009; Reynolds, 1985). As a result, primate quadrupedal control and mechanics are considered atypical compared with that of other (terrestrial) quadrupedal

<sup>1</sup>Histoire Naturelle de l'Homme Préhistorique, UMR 7194, CNRS-MNHN-UPVD, 75116 Paris, France. <sup>2</sup>Primatology Station of the CNRS-Celphedia, UAR 846, 13790 Rousset-sur-Arc, France. <sup>3</sup>Functional Morphology Laboratory, University of Antwerp, 2610 Antwerp, Belgium. <sup>4</sup>Gait and Motion Analysis Laboratory, Assistance Publique des Hôpitaux de Paris (AP-HP), Robert Debré University Hospital, 75004 Paris, France. <sup>5</sup>Monde Sauvage Safari Parc, 4920 Aywaille, Belgium. <sup>6</sup>Department of Movement and Sports Sciences, University of Ghent, 9000 Ghent, Belgium.

\*Author for correspondence (francois.druelle@mnhn.fr)

DOI: 10.1242/jeb.242587 F.D., 0000-0001-9680-6401; A.S., 0000-0001-8551-2950

mammals. However, basic biomechanical and physiological data regarding the typical quadrupedal walking pattern of non-human primates is, unfortunately, non-existent. Integrative studies examining the kinematics, the dynamics of the CoM and the muscular activity (EMG) all together are very rare (see Courtine et al., 2005).

To explore the quadrupedal walking gait of non-human primates and the suggested neuromotor flexibility, we conducted an integrative analysis exploring the limb kinematics, the CoM mechanics (using kinematics) and the muscle activity of six extrinsic hindlimb muscles in olive baboons, *Papio anubis*. Baboons can be considered as (semi-)terrestrial primates as they have developed a set of cursorial adaptations that mean they are more suited for terrestrial locomotion and for long-distance walking. For instance, they have been shown to move between 3.6 and 9.5 km per day, making them the non-human primates with the longest daily travel distance (Garland, 1983); their limbs are relatively extended with a digitigrade hand posture when walking, they display convergent natural pendular periods of their forelimbs and hindlimbs and their proximal limb mass distribution suggests good propulsive action capacities (Druelle et al., 2017a; Patel, 2009; Patel et al., 2012; Raichlen, 2004; Zeininger et al., 2017).

In this study, animals were trained to voluntarily cooperate using positive reinforcement techniques. Our refined experiment used surface probes (sEMG) that did not need surgical procedures. We first recorded the muscular activity of two female baboons walking quadrupedally using their typical DSDC gait over flat regular ground at their voluntary walking speed. This allowed us to describe their typical quadrupedal walking gait in terms of spatio-temporal parameters and muscular activity. We then recorded the gait of one female baboon when walking DSDC on a suspended horizontal and cylindrical substrate (branch) and while spontaneously using lateral sequence/lateral couplet (LSLC) gaits for a few strides on the ground. We thus provide a preliminary picture of the normal quadrupedal walking pattern in baboons and its flexibility (through kinematic modulation) in the context of different gait and substrate. First, and because the baboon is defined as an adapted quadrupedal walker, we expected it to be able to make use of an inverted pendulum mechanism when walking steadily on the ground using its preferred walking gait (DSDC; as previously observed in ring-tailed lemurs and capuchin monkeys: O'Neill and Schmitt, 2012; Demes and O'Neill, 2013). Second, we specifically evaluated whether the usual muscle activation pattern observed in DSDC walking is altered in other gait and substrate contexts. When the baboon uses the unusual LSLC gait on the ground, changes are expected in proximal muscles (i.e. in the main limb motors), whereas walking on a different substrate, such as a branch (imposing higher balance requirements and certainly higher control), should mainly affect the recruitment of distal muscles (Boyer et al., 2007; Courtine et al., 2005; Patel et al., 2012). Exploring the kinematics, the movements of the CoM and the muscle activity together should provide an integrative picture of the quadrupedal walking pattern in the baboon and how these are connected (see Courtine et al., 2005). In this context, a reduced efficiency in the mechanics of the CoM (for example, walking on a branch requires kinematical adjustments that tend to reduce the vertical oscillations of the CoM; see Gálvez-López et al., 2011; Schmitt, 1999) should match an alteration of the muscular activity toward an increased activation.

## MATERIALS AND METHODS

### Experiment context, training and study subjects

The olive baboons, *Papio anubis*, were housed at the Primatology Station of the CNRS (Rousset-sur-Arc, France). The experiments

presented in this study and conducted inside the primatology centre are part of a large ongoing project on bipedal walking skills in non-human primates (G.B. and F.D., unpublished data). The heterogeneous character of the quadrupedal data presented here results from opportunistic periods of data collection that were not initially intended to be considered together. All the procedures that are described in this study were approved by the ethical committee on animal experimentation no. 14 (Projet 68-19112012, CEEA-14 Marseille).

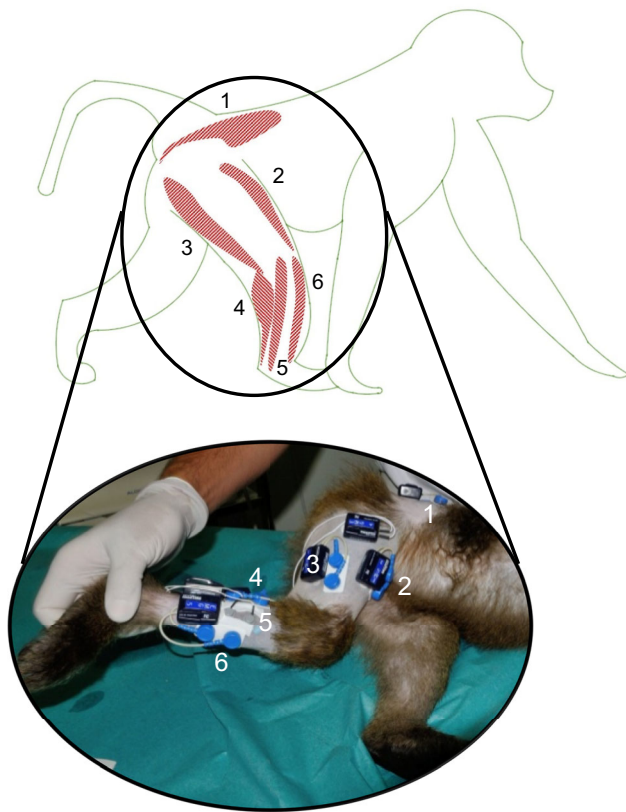
Prior to the experiments, primates were trained over a period of 18 months and focused on the habituation and desensitization of individuals to the whole experimental setup. All training was based on positive reinforcement techniques and systematic desensitization (Prescott and Buchanan-Smith, 2016; Schapiro et al., 2003) and was conducted by the same two trainers, P.M.-V. and B.R. The first training period was carried out in a large indoor cage where the two individuals were pair-housed for 18 months. During this period, individuals were mainly habituated to the close proximity of and interaction with trainers by means of training other basic behaviours such as target or parking training. After 6 months of training (46 sessions of training of approximately 30–45 min), individuals cooperated to get out of their enclosure on a leash and to walk quadrupedally beside the trainer on the experimental setup. Individuals were then moved to a bigger indoor/outdoor enclosure where they could move freely. This training allowed us to lead the baboons to the technical platform for data collection.

Training sessions started when the baboons were 1.5 and 2 years old. The collection of the data presented in this study was performed during three recording sessions for individual 1 (Id1), 4 July 2013, 31 July 2013 and 15 December 2017, and during one recording session for individual 2 (Id2), 3 December 2013. At the time of data collection, Id1 was 3 years old and weighed 8.14 kg in 2013 and 7.5 years old and weighed 13.5 kg in 2017. Id2 was 3.5 years old and weighed 8.05 kg in 2013. At 3 years of age, olive baboons have already experienced significant growth-related changes in body morphometrics and their general morphotype is very similar to that of adults (see fig. 6 in Druelle et al., 2017a). The maturation of their neuromotor control also appears to be largely complete (see Druelle et al., 2017b; Rose, 1977), as has also been observed in other cercopithecoid species at this age (e.g. Vilensky and Gankiewicz, 1990; Zeininger et al., 2017; Dunbar and Badam, 2000).

### Data collection

#### Surface electromyography (sEMG)

Muscle activity was recorded at 2000 Hz using a wireless Zerowire system (Aurion Srl, Milan, Italy) with MyoResearch XP Master Edition software (Noraxon®). We focused on 6 muscles commonly studied as actuators of the three main joints of the hindlimb (hip, knee and ankle), and easily identifiable at the surface of the skin: gluteus medius, biceps femoris, rectus femoris, tibialis anterior, gastrocnemius (medialis or lateralis) and peroneus longus, of the right side (Fig. 1). To ensure accurate electrode placement, the muscular topography was previously assessed on olive baboon cadavers of a similar size and age that were available at the primatology station. Baboons were instrumented during a short period of anaesthesia (~60 min); the anaesthesia was initiated with an intra-muscular injection of ketamine (4 mg kg<sup>-1</sup>) and medetomidine (40 µg kg<sup>-1</sup>) and maintained with gas isoflurane (1%). This anaesthesia was short and light enough to shorten the recovery period using atipamezole as an antagonist. After locally shaving, cleaning and degreasing the skin, electrodes were taped at the level of the muscle belly (approximately at mid-length of each



**Fig. 1. Schematic diagram of a baboon walking quadrupedally including the average position of the 6 recorded extrinsic muscles (in red).** The positioning of the electrodes (connected to their respective wireless battery) for the 6 muscles studied can be seen in the photograph below: 1, gluteus medius (hip extensor and rotator); 2, rectus femoris (hip flexor and knee extensor); 3, biceps femoris (hip extensor and knee flexor); 4, medial gastrocnemius (plantar flexion and knee flexion); 5, peroneus (foot eversion); 6, tibialis anterior (dorsiflexion of the foot and inversion).

muscle and electrode pairs and always parallel to fibre direction). We used fabric legwear and trunkwear (close-fitting clothes, see Fig. 6B) to ensure a good adhesion of the equipment and to protect the electrodes. In the context of the present study, we have worked on the technical platform for biomechanics (Motion Analysis of Primates, MAP) that is permanently installed in an outdoor enclosure of the primatology centre (see Berillon et al., 2011, for details). The experiments started after the baboons were totally recovered from the anaesthesia (i.e. they were fully active and able to climb and run), between 60 and 90 min after their arrival in the enclosure.

### Kinematics

The animals walked on a straight and horizontal calibrated walkway and on a horizontal branch (diameter 0.16 m, positioned at approximately 1 m above the ground), where they could easily be video-captured using an integrated multicamera system (Norpix Inc.) with 3 synchronized HD-video cameras running at 200 frames  $s^{-1}$  (Baumer HXC1) (see Berillon et al., 2010, for a general description of the experimental setup); synchronized recording was proceeded with Streampix 4 (Norpix Inc.). Two cameras were laterally placed perpendicular to the walkway, to accurately record in a large field of view the main sagittal spatio-temporal and joints kinematics. One additional camera was positioned obliquely to increase the accuracy for visually

identifying the locomotor events, i.e. touch-down and lift-off of the limbs. EMG and video recordings were synchronized using an external digital signal; in addition, a fourth lateral video camera (running at 60 frames  $s^{-1}$ ) was driven by the MyoResearch XP software and thus software-synchronized with the EMG recording.

We first qualitatively selected appropriate quadrupedal sequences during which the individual was walking steadily, along the platform or the branch. The quadrupedal strides were defined from a right hindlimb touchdown to the next right hindlimb touchdown. As we noticed some speed variation between consecutive quadrupedal strides, we calculated an acceleration/deceleration index as follows:  $(\text{average speed stride}_{n+1} - \text{average speed stride}_n) / \text{average speed stride}_n$ . For the present analysis, we removed the quadrupedal strides for which speed variations were above 10% between consecutive strides [note that given the small number of lateral sequences recorded ( $n=6$ ), we kept one stride for which the speed variation was 26% in order to keep a sample of 4 strides and, therefore, use non-parametric statistics, see below]. Table 1 shows the dataset included in the present analysis after applying this strong selective criterion.

### Analysis

#### Basic kinematics

We calculated the following spatio-temporal parameters: cycle duration (time period between two right hindlimb touchdown events), frequency (inverse of cycle duration), duty factor (proportion of stance phase of the right hindlimb relative to cycle duration), stride length (horizontal displacement of the tip of the right foot during one stride), speed (estimated from the horizontal displacement of the CoM; see below) and limb phase (time period between the right hindlimb touchdown and the right forelimb touchdown relative to the cycle duration;  $<50\%$  is a lateral sequence,  $>50\%$  is a diagonal sequence). The spatio-temporal parameters were made dimensionless using geometric scaling equations (Hof, 1996) and the shank length was used as the scaling factor (Aerts et al., 2000). A total of 20 anatomical reference points were digitized by S.M. and N.S. using the *DLTdv7* application developed in MATLAB by the T. Hendrick Lab (Fig. 2). Video footage was analysed for one individual and the kinematics were therefore extracted for Id1 in different contexts (see Table 1). When the tracked anatomical references were obscured by the movement of other limbs, we applied a piecewise linear interpolation to add the missing datapoints. Movement patterns were visually checked using a custom-made script in MATLAB to ensure a satisfactory digitization result, i.e. a smooth movement with no anomaly. Data were then filtered per stride using a 4th order zero phase shift low-pass Butterworth filter with a cut-off frequency of 5 Hz. We then applied a cubic spline interpolation over a time base with 100 points in order to stride-normalize the individual quadrupedal cycles. Tracking the joints and body segments during the walking strides allowed us to measure 6 internal joint angles (joint extension corresponds to their increase) (Anvari et al., 2014): the ankle [estimated between the foot taken as a whole (from heel to tip) and the shank segment], the knee, the hip, the shoulder, the elbow and the wrist; as well as 5 external joint angles (with respect to the horizontal): the shank, the thigh, the trunk, the humerus and the forearm.

#### CoM mechanics

The position of the body centre of mass (BCoM) can be estimated using body segment displacement and morphometrics (kinematic method; Maus et al., 2011). In 2013 and 2017, morphometrics



**Table 1. Studied individuals and data collected**

Individual and date (dd/mm/yyyy)	n/n	EMG	Spatio-temporal	Kinematics (joint+BCoM)	Gait type/substrate
ID1					
04/07/2013	3/4	X	X	X	Diagonal/on ground
	2/3	X	X	X	Lateral*/on ground
31/07/2013	9/14	X	X	–	Diagonal/on ground
15/12/2017	12/16	X	X	X	Diagonal/on ground
	2/3	X	X	X	Lateral/on ground
	6/8	X	X	X	Diagonal/on branch
ID2					
03/12/2013	19/39	X	X	–	Diagonal/on ground

n/n, the number of strides kept in the present analysis (left) and the total number of strides recorded before applying the acceleration selection criterion (right) (see Materials and Methods). BCoM, body centre of mass. \*Given the small amount of data for the lateral walking gait (2 in 2013 and 2 in 2017), we pooled these data in the analyses. X, data were collected; –, no data were collected.

of the studied individual (Id1) were collected using external measurements (when the individual was anaesthetized). The geometric model of Crompton et al. (1996) was used to estimate the body proportions (segment volume and length) as well as the position of the segment's CoM (i.e. head, trunk, arm, forearm, hand, thigh, shank, foot and tail). Based on these data, we calculated the weighted arithmetic mean CoM of all segments to estimate the instantaneous position of the BCoM. By using BCoM displacement, we estimated the variations in kinetic and potential energy during the quadrupedal strides. The kinetic energy (KE) was calculated as follows:

$$KE = \frac{1}{2} M_b (V_v^2 + V_{f-a}^2), \quad (1)$$

where  $M_b$  is the body mass,  $V_v$  is the vertical velocity of the BCoM in the sagittal plane and  $V_{f-a}$  is the velocity in the fore–aft direction. The potential energy (PE) was calculated as follows:

$$PE = M_b g h, \quad (2)$$

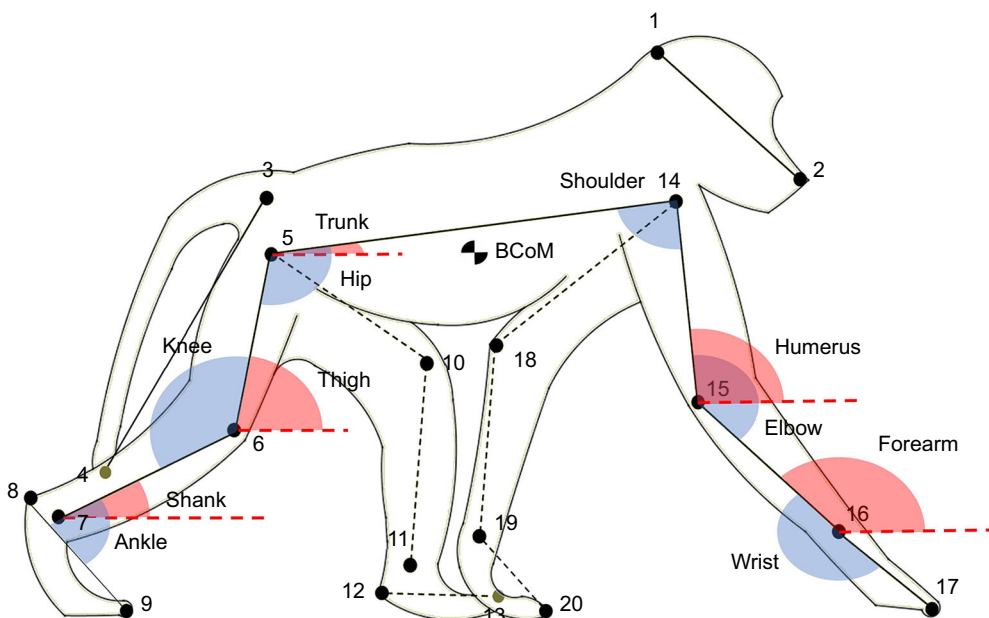
where  $g$  is the gravitational acceleration ( $9.81 \text{ m s}^{-2}$ ) and  $h$  is the height of the BCoM. The total external mass-specific

mechanical energy ( $W_{\text{ext}}$ ;  $\text{J kg}^{-1} \text{ m}^{-1}$ ) is defined as the sum of the positive increments of the total energy ( $\Delta^+ \text{TE}$ ) within a cycle, divided by the body mass and the stride length (SL) of the respective cycle:

$$W_{\text{ext}} = \frac{\Delta^+ \text{TE}}{M_b \text{SL}}. \quad (3)$$

During walking, the BCoM trajectory in relatively large animals ( $>1 \text{ kg}$ ; Reilly et al., 2007) generally follows an inverted pendulum movement. In this context, PE and KE fluctuate out of phase and energy exchange between PE and KE is possible. During the rise of the BCoM, energy is converted from KE to PE, while during the fall, PE is converted back into KE. If the amplitudes of the two energy fluctuations are very similar and they fluctuate perfectly out of phase, there will be an optimal energy recovery via the inverted pendulum mechanism (i.e. 100% recovery). Hence, the percentage recovery allows us to evaluate the efficiency of the pendular exchange of energy and is estimated as follows:

$$\% \text{Recovery} = \frac{\Delta^+ \text{PE} + \Delta^+ \text{KE} - \Delta^+ \text{TE}}{\Delta^+ \text{PE} + \Delta^+ \text{KE}} \times 100. \quad (4)$$



**Fig. 2.** Schematic diagram showing the position of the digitized anatomical points, the internal (blue) and external (red) angles measured and the body centre of mass (BCoM) in the middle of the trunk.

To evaluate the energy exchange mechanism, we calculated two parameters: (1) the relative amplitude (RA) between the kinetic and potential energy:

$$RA = \frac{PE_{\max} - PE_{\min}}{KE_{\max} - KE_{\min}}; \quad (5)$$

and (2) the percentage congruity (%C), which is an indication of the phase relationship between PE and KE:

$$\%C = \frac{\sum_{i=1}^{n-1} [(PE_{i+1} - PE_i)(KE_{i+1} - KE_i) > 0]}{n - 1}, \quad (6)$$

where  $n$  is the number of values (i.e. 100 data points after stride normalization, see above). The percentage congruity measures the proportion of the gait cycle during which PE and KE change similarly in direction (Ahn et al., 2004). A perfect energy exchange via the inverted pendulum mechanism (i.e. 100% recovery) should result in RA=1 and %C=0.

### sEMG

We first visually checked the signals to ensure the absence of abnormalities and artefacts. We used MATLAB (R2019a) to analyse, filter and create an envelope of the EMG signals (see Supplementary Materials and Methods 1 for an evaluation of different methods, and Fig. S1). The following successive steps were applied: band-pass 4th order Butterworth filter (5 Hz to 500 Hz), centred, rectified (full-wave), low-pass 4th order Butterworth filter (10 Hz), rectified (full-wave) (see Supplementary Materials and Methods 1 for Matlab script). We then applied a cubic spline interpolation over a time base with 200 points in order to stride normalize the individual quadrupedal cycles. This provides an envelope of the muscular activity pattern on which we then applied different statistical analyses (see below). Each individual muscle amplitude was also normalized per day of experiment based on the maximum peak contraction value of the set of quadrupedal walking sequences. Because of these treatments, we were able to average the multiple strides per individual.

### Statistics

We proceeded with two analyses: (1) interindividual differences (Id1 versus Id2; Table 1) when walking quadrupedally on the ground using the typical DSDC gait; and (2) the effect of gait (diagonal versus lateral) and substrate (ground versus branch). For both analyses, the stride represents the independent statistical unit. Given the small sample size and the heterogeneity, we applied exact (non-parametric) tests: the Permutation tests for independent samples. (1) Duty factor, dimensionless stride length and dimensionless stride frequency (and duration) were compared between individuals using Permutation tests for independent samples and were regressed against dimensionless speed; the Pearson correlation ( $r$ ) allowed us to test for significant relationships. (2) Differences in angle average values over a stride are tested between diagonal walking on the ground and diagonal walking on the branch, and diagonal walking on the ground and lateral walking on the ground using Permutation tests for independent samples, as well as the range of motion (angle amplitude over a stride), the spatio-temporal parameters (duty factor, stride length, stride duration, speed) and the CoM mechanics (%C, RA, Recovery,  $W_{\text{ext}}$ ).

In order to evaluate potential differences between the walking contexts, we divided the EMG signals into 4 phases of equal duration, representing 25% of the cycle duration. The numerical

integration of these different phases allowed us to estimate the proportion of EMG activation per phase and its distribution across phases. We conducted a Chi-square test of independence ( $\chi^2$ ) to assess whether there is a significant relationship between the distribution of the activation pattern between individuals (1), and within individual for the different contexts studied (2), i.e. walking on the ground using a diagonal sequence, walking on a branch using a diagonal sequence and walking on the ground using a lateral sequence. Because the data collected in 2017 were obtained the same day on the same individual, we were also able to compare for this specific day and individual the maximal activation values between gaits and substrates using Permutation tests for independent samples. The statistics were conducted using the software for exact non-parametric inference StatXact 3.1 (Cytel, Inc., Cambridge, MA, USA). The significance threshold was set at  $P < 0.05$ .

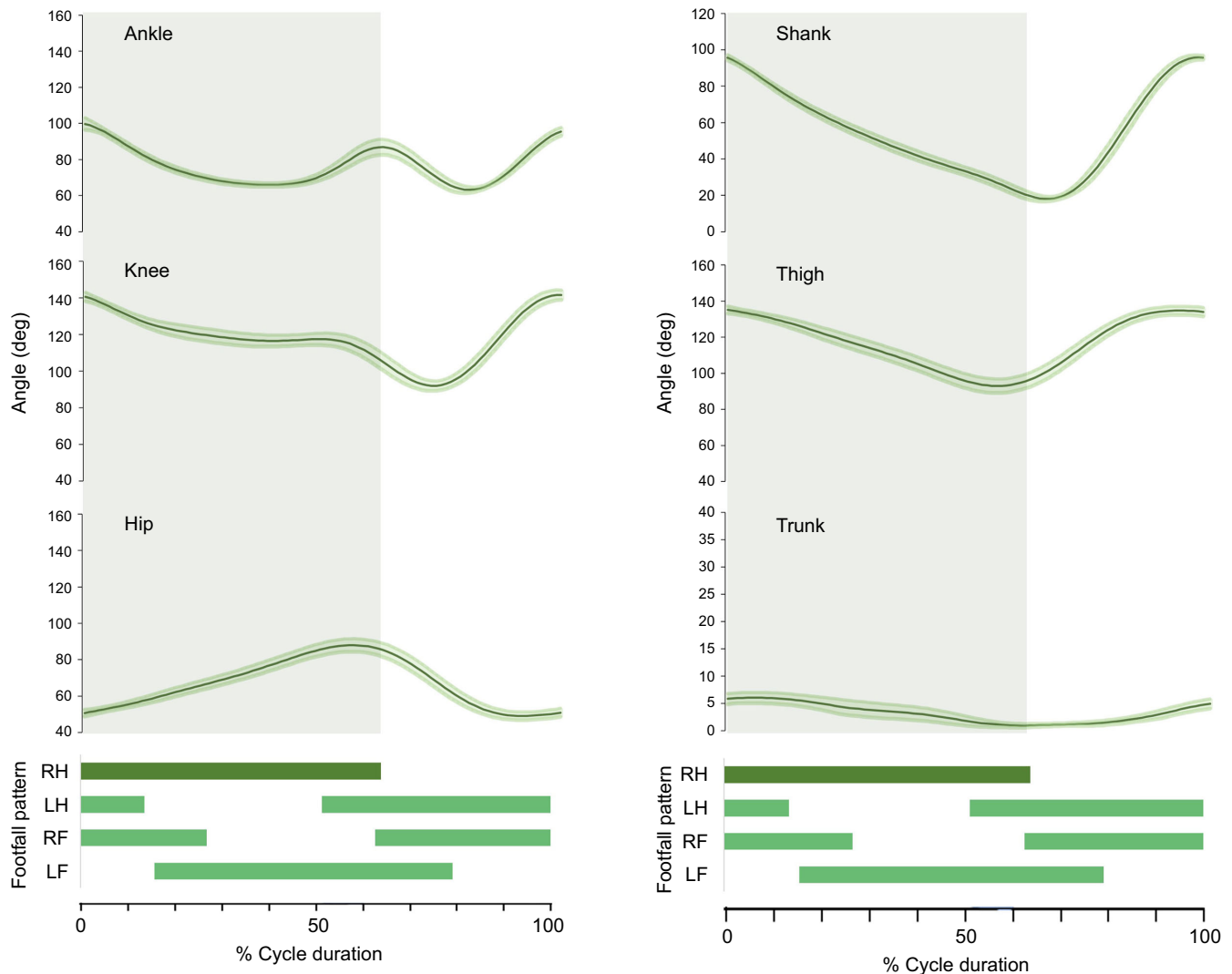
## RESULTS

### Average kinematics

The data used here were from Id1, 15 December 2017 (diagonal/ground  $n=12$ ; Table 1). Time plots of the hindlimb and forelimb joint and segment angles are shown in Figs 3 and 4, respectively. During baboon quadrupedal walking, the hip extends gradually during the stance phase up to  $\sim 90$  deg. It flexes rapidly during the swing phase until it reaches  $\sim 50$  deg and remains in a constant position at the end of the swing phase just before the foot touches the ground and while the knee is extending. The knee starts flexing slowly during the stance phase and reaches a plateau around mid-stance, but the flexion increases rapidly just before lift-off when the ankle is rapidly extending from 65 to 90 deg. The swing phase is characterized by a rapid flexion of the knee up to 90 deg during one-third of the swing phase and then by a rapid extension, reaching 140 deg at touch-down. The ankle shows the same pattern as the knee but is slightly delayed. The trunk angle is maintained around 3 deg on average and remains stable during the quadrupedal stride; the movement amplitude is  $\sim 7$  deg. The shoulder shows a reverse pattern compared with the hip; it flexes gradually during the stance phase of the forelimb until reaching  $\sim 40$  deg and increases during the swing phase until 80 deg. The range of motion of the humerus is 39 deg while the amplitude of the thigh (femur) is 44 deg. The elbow flexes during the beginning of the swing phase from  $\sim 130$  deg to  $\sim 90$  deg and then extends during the second part of the swing phase up to 120 deg. It increases slowly during the stance phase, but it reaches a plateau around mid-stance, as also observed in the knee. The end of the stance phase is characterized by an extension of the elbow from 130 deg to 140 deg. The wrist shows an extreme extension around 220 deg in the last third of the stance phase that precedes a significant roll off before lift-off. The wrist flexes to  $\sim 100$  deg and then extends again in preparation for touch-down at  $\sim 180$  deg. The high wrist extension corresponds to the typical digitigrade hand posture in baboons and the wrist dorsiflexes gradually during two-thirds of the stance phase until reaching an extreme extension when the ipsilateral hindlimb touches down.

### Average BCoM mechanics

The data used here were from Id1, 15 December 2017 (diagonal/ground  $n=12$ ) and 4 July 2013 (diagonal/ground  $n=3$ ). In our sample, the recovery rate of energy was 57% on average when the walking speed was under  $0.9 \text{ m s}^{-1}$  and tended to decrease at higher speed (Fig. 5A). Note that although we provided a linear regression model for this relationship, a second-degree polynomial might be a better fit for the data ( $R^2=0.34$  versus  $R^2=0.26$  for the linear model). A broader speed range would enable confirmation of the linear or



**Fig. 3. Average hindlimb joint and segment angles for Id1 during quadrupedal walking.** Angles ( $\pm 95\%$  confidence interval) were measured on the right side during diagonal sequence/diagonal couplet (DSDC) walking at comfort speed ( $\sim 0.92 \text{ m s}^{-1}$ ). The average footfall pattern at the bottom (gait diagram) shows average stance phase (solid bars) of the right hindlimb (RH), left hindlimb (LH), right forelimb (RF) and left forelimb (LF). The right hindlimb is the limb of reference. It is darker on the gait diagram and the stance phase is indicated on the graphs above by light shading.

the upside-down U-shaped relationship between recovery rate and speed in baboons. Recovery rate was significantly negatively correlated with congruity, i.e. the more the KE and PE fluctuate out of phase, the better the recovery (Fig. 5B). The percentage recovery was also significantly correlated with limb phase. A limb phase value closer to 0.55 corresponded to a higher level of recovery (Fig. 5C). There was no relationship between recovery rate and the relative amplitude of the KE and PE (Fig. 5D).

#### Interindividual differences

The data used here were from Id1, July 2013 ( $n=3+9$ ) and from Id2, December 2013 ( $n=19$ ; see Table 1).

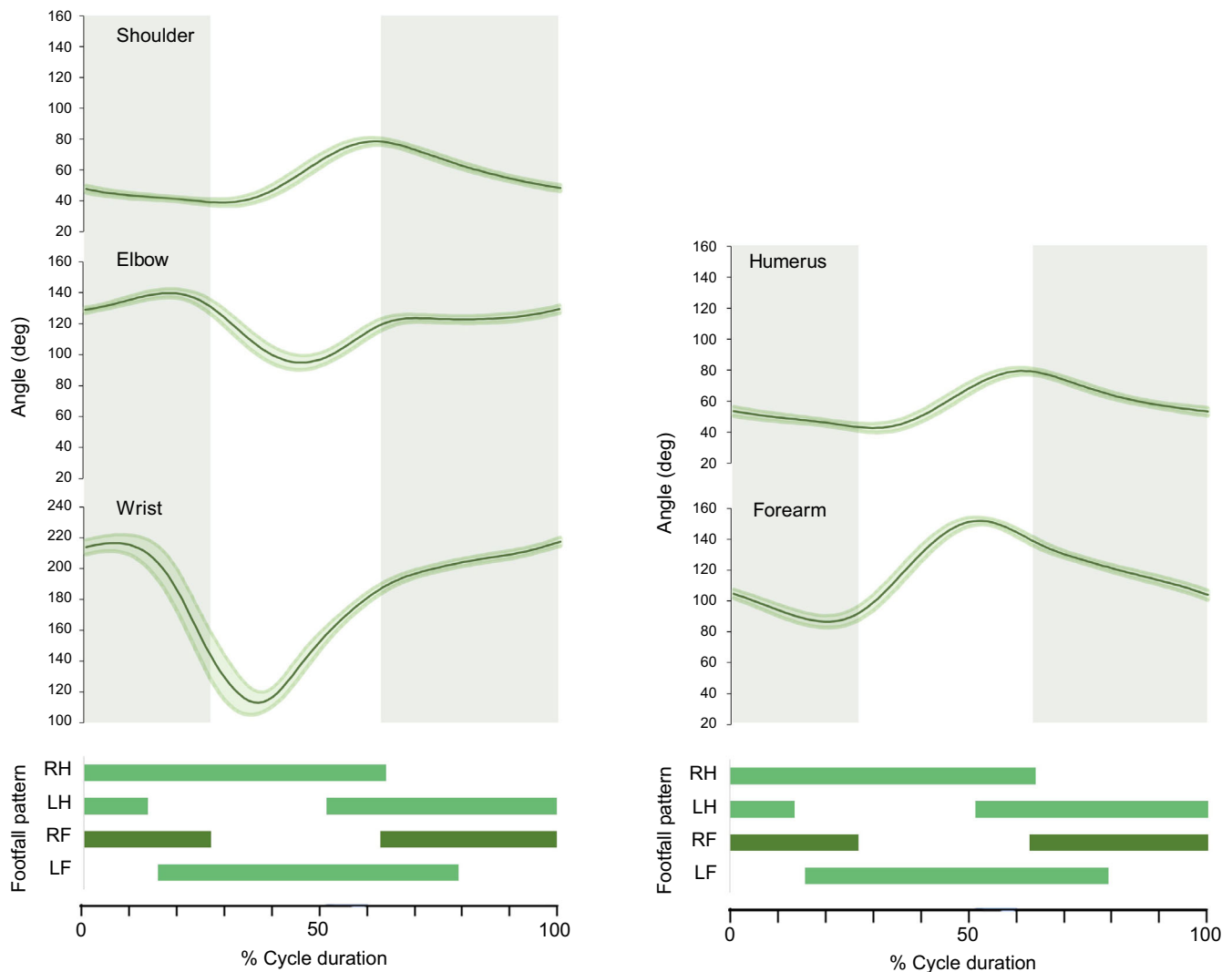
#### Spatio-temporal parameters

Table 2 shows the average values per individual of the spatio-temporal parameters for walking quadrupedally at comfort speed on the ground using DSDC gait. The two individuals studied adjusted their spatio-temporal parameters the same way according to speed (see Fig. S2). Both individuals modulated their walking pattern by altering both their frequency and stride length. Id1 tended to

increase walking speed mainly by increasing stride frequency (Id1: slope=0.12; Id2: slope=0.04), whereas Id2 increased speed mainly by increasing stride length (Id1: slope=3.6; Id2: slope=5.7). Duty factor was significantly greater in Id1 than in Id2, although the absolute difference was small (67% and 64%, respectively, Permutation test: 3.538,  $P=0.0001$ ). Within the limited speed range observed, duty factor was not significantly related to speed for either of the individuals studied. The dimensionless stride length was longer in Id2 than in Id1 (4.76 and 4.22, respectively, Permutation test:  $-3.108$ ,  $P=0.0004$ ).

#### Muscular activity

The bursting EMG patterns were very consistent between the two individuals (Fig. 6). The gluteus medius (hip extensor and rotator muscle), the biceps femoris (hip extensor and knee flexor), the gastrocnemius (ankle extensor muscle) and the peroneus (foot evtor muscle) were active at the beginning of the stance phase. The maximum burst activity was approximately 25% of the stance phase, i.e. when the right hindlimb is still in a protracted posture and when the (contralateral) left hindlimb starts to swing and the left



**Fig. 4. Average forelimb joint and segment angles for Id1 during quadrupedal walking.** Angles ( $\pm 95\%$  confidence interval) were measured on the right side during DSDC at comfort speed ( $\sim 0.92 \text{ m s}^{-1}$ ). The average footfall pattern at the bottom (gait diagram) shows average stance phase (solid bars) of the right hindlimb (RH), left hindlimb (LH), right forelimb (RF) and left forelimb (LF). The right forelimb is the limb of reference. It is darker on the gait diagram and the stance phase is indicated on the graphs above by light shading.

forelimb touches the ground. The rectus femoris (hip flexor and knee extensor) showed a reverse pattern, with a burst of activity when the limb starts to be retracted and the knee maintained around 120 deg. This occurred at approximately 75% of the stance phase and corresponds to the (contralateral) left hindlimb touching the ground. There was also a certain level of recorded activation of the rectus femoris in Id1 at the beginning of stance phase, when the gluteus medius, the biceps femoris and the gastrocnemius are very active. The distinct activation pattern of the rectus femoris was the only significant difference found between the two individuals ( $\chi^2=12$ , d.f.=3,  $P=0.0069$ ). While the activity of the muscles located in the thigh showed very short bursting patterns, the burst activity of the gastrocnemius and peroneus remained during a longer period of the stance phase, i.e. until touch-down of the left hindlimb. The tibialis anterior (dorsiflexion of the foot and inversion) started its activity at the very end of stance phase, just after the (ipsilateral) right forelimb touch-down and showed a burst of activity just after the right hindlimb lift-off when the ankle is rapidly flexed. Its activity then decreased during the second period of the swing phase. There was no activity of the gluteus medius, rectus femoris, biceps

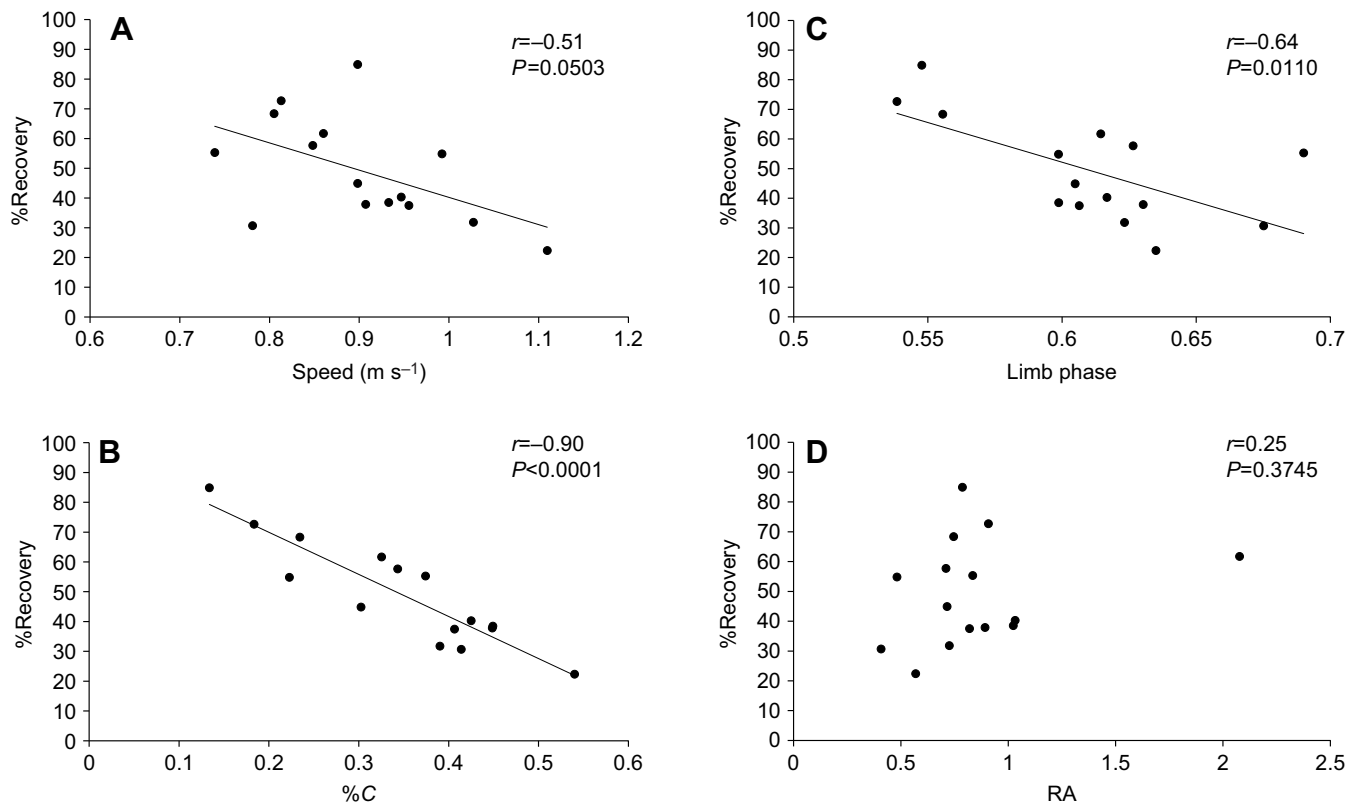
femoris, peroneus and gastrocnemius during the swing phase, but the biceps femoris and gastrocnemius appeared to start their activity at the very end of swing phase, in preparation for touch-down.

#### Variations around the quadrupedal gait: effects of gait and substrate

The data used here were from Id1, 15 December 2017 (diagonal/ground  $n=12$ , lateral/ground  $n=2$ , diagonal/branch  $n=6$ ), and to increase the sample for the lateral walking gait, also from Id1, 4 July 2013 (lateral/ground  $n=2$ ; see Table 1).

#### Spatio-temporal parameters and BCoM mechanics

Table 3 shows the average values of the spatio-temporal parameters for walking quadrupedally on the ground using diagonal sequences (DS-G), for walking quadrupedally on the branch using diagonal sequences (DS-B) and for walking quadrupedally on the ground using lateral sequences (LS-G). We observed a significant difference in stride frequency (and duration) between diagonal and lateral gaits ( $1.26$  and  $1.44 \text{ s}^{-1}$ , respectively, Permutation test:  $2.193$ ,  $P=0.0209$ ) as well as in the percentage congruity (%C) of the



**Fig. 5. Influence of various walking variables on recovery rate during quadrupedal locomotion.** A significant relationship exists between speed and recovery rate (A), the congruity of the fluctuations of kinetic and potential energy (%C) and recovery rate (B) and the diagonality and recovery rate (C), but not between the relative amplitude of the fluctuation of kinetic and potential energy (RA) and recovery rate (D).

BCoM (38.7% and 53.6%, respectively, Permutation test:  $-2.272$ ,  $P=0.0159$ ). There was a significant difference in stride length and speed when walking on the ground versus the branch (stride length: 0.73 m and 0.66 m, respectively, Permutation test: 2.277,  $P=0.0197$ ; speed:  $0.92 \text{ m s}^{-1}$  and  $0.79 \text{ m s}^{-1}$ , respectively, Permutation test: 2.089,  $P=0.0335$ ).

### Kinematics

The ankle angle was more extended and the shank angle more flexed during lateral gait compared with diagonal gait (ankle: 82.1 deg and 76.4 deg, respectively, Permutation test:  $-2.509$ ,  $P=0.0121$ ; shank: 51.4 deg and 53.7 deg, respectively, Permutation test: 2.157,  $P=0.0247$ ). The range of motion (ROM) of the knee angle was greater during diagonal walking than during lateral walking (51.5 deg and 47.3 deg, respectively, Permutation test: 1.914,  $P=0.0247$ ).

On the branch, the baboon increased the ankle extension and the ROM of the ankle as well as the shank extension compared with the ground (ankle: 82.3 deg and 76.4 deg, respectively, Permutation test:  $-3.165$ ,  $P=0.0004$ ; ankle ROM: 44.9 deg and 38.3 deg, respectively, Permutation test:  $-2.08$ ,  $P=0.0339$ ; shank: 56.6 deg and 53.7 deg, respectively, Permutation test:  $-2.79$ ,  $P=0.0023$ ). The ROM of the trunk angle was reduced on the branch compared with the ground (4 deg and 6.3 deg, respectively, Permutation test: 2.862,  $P=0.0015$ ). For the forelimb, the shoulder angle was kept more extended on the branch compared with the ground and the wrist was more dorsiflexed (shoulder: 58.4 deg and 55.3 deg, respectively, Permutation test:  $-2.09$ ,  $P=0.0326$ ; wrist: 187 deg and 180.8 deg, respectively, Permutation test:  $-2.53$ ,  $P=0.0081$ ). Fig. S3 shows the average pattern for each joint and segment angle studied in each gait and substrate context.

### Muscular activity

The bursting EMG profiles were very consistent across gaits and substrates (Fig. 7). There was no difference between the lateral and the diagonal sequences performed on the ground as far as the bursting EMG profiles were concerned. But the maximal burst of activity of the biceps femoris, gastrocnemius and tibialis anterior significantly increased in lateral sequences (Permutation test:  $-1.909$ ,  $P=0.0467$ ; Permutation test:  $-2.042$ ,  $P=0.0379$ ; and Permutation test:  $-2.595$ ,  $P=0.0055$ , respectively).

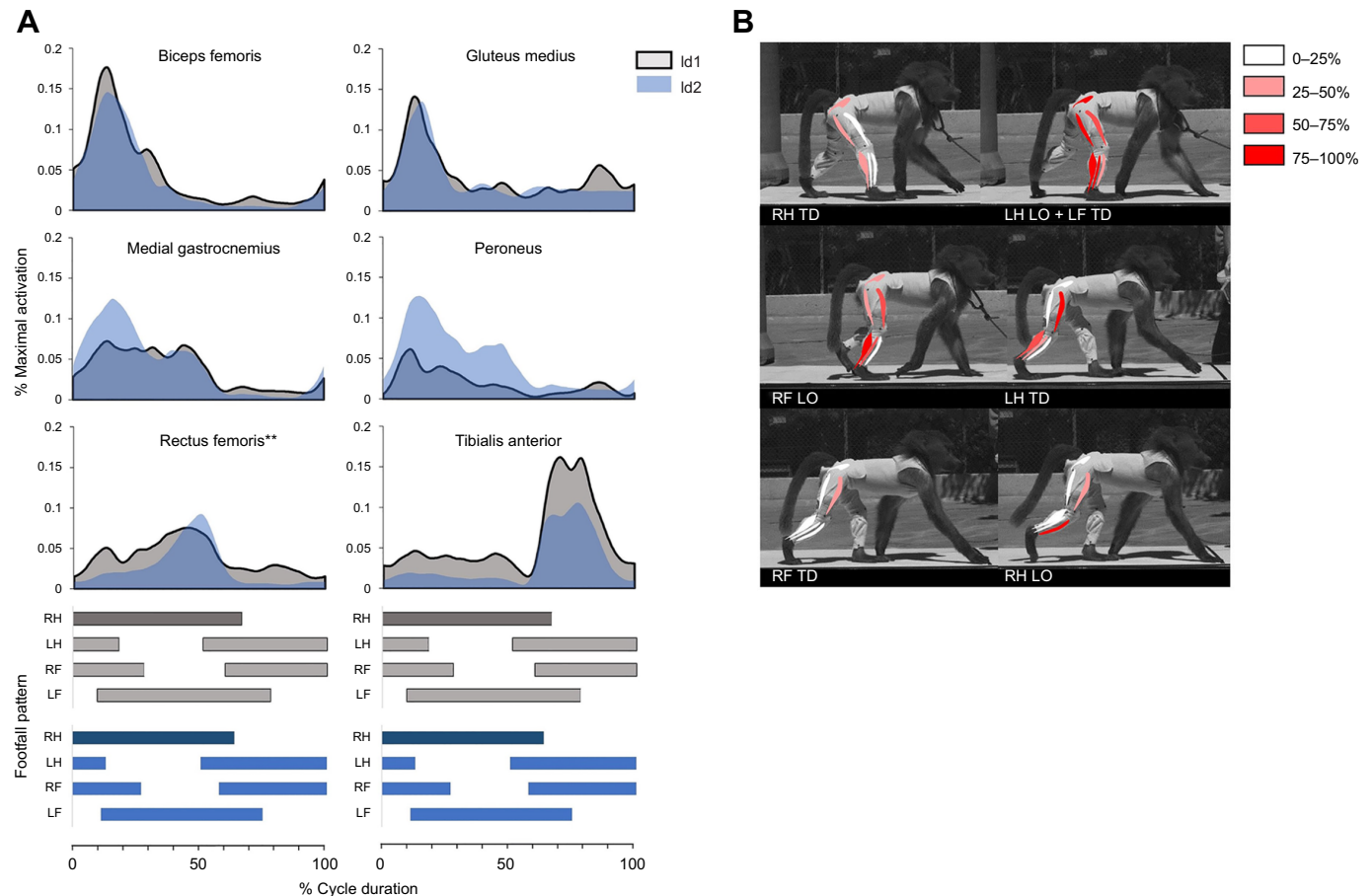
With regard to the quadrupedal strides performed on the ground and on the branch, we observed a significant difference of the activation pattern at the level of the peroneus ( $\chi^2=10.62$ , d.f.=3,  $P=0.0137$ ). While the activity of the peroneus was concentrated at the beginning of the stance phase when the baboon was walking

**Table 2. Spatio-temporal parameters of steady quadrupedal walking for diagonal sequences on the ground per individual**

Parameter	Id1 (n=12)	Id2 (n=19)	P-value
Cycle duration (s)	$0.89 \pm 0.05$	$0.95 \pm 0.03$	0.0029
Stride frequency ( $\text{s}^{-1}$ )	$1.13 \pm 0.07$	$1.05 \pm 0.04$	0.0024
Stride length (m)	$0.68 \pm 0.04$	$0.81 \pm 0.05$	0.0001
Speed ( $\text{m s}^{-1}$ )	$0.76 \pm 0.07$	$0.85 \pm 0.07$	0.0116
Duty factor (%)	$67 \pm 1$	$64 \pm 1$	0.0001
Dimensionless cycle duration	$6.98 \pm 0.39$	$7.25 \pm 0.25$	ns
Dimensionless stride frequency	$0.14 \pm 0.008$	$0.14 \pm 0.005$	ns
Dimensionless stride length	$4.22 \pm 0.26$	$4.76 \pm 0.30$	0.0004
Dimensionless speed	$0.61 \pm 0.05$	$0.66 \pm 0.05$	ns

Data are means  $\pm$  s.d. P-values compare Id1 and Id2 data (ns, not significant).





**Fig. 6. Muscular activity.** (A) Average EMG profiles of the 6 hindlimb muscles considered during steady quadrupedal walking. The activity patterns were stride normalized and averaged across 12 strides for Id1 and 19 strides for Id2. The average footfall pattern at the bottom (gait diagram) shows average stance phases (solid bars) of the right hindlimb (RH), left hindlimb (LH), right forelimb (RF) and left forelimb (LF). EMG activity was recorded on the right hindlimb (darker on the gait diagram). (B) Overview of the muscular activity of the 6 hindlimb muscles considered during the stance phase of the quadrupedal stride in Id1. The amount of muscular activity is based on the average profile observed in A and is divided into 4 levels of activation, as indicated in the key. Six events are represented: right hindlimb touch-down (RH TD), left hindlimb lift-off (LH LO)+left forelimb touch-down (LF TD), right forelimb lift-off (RF LO), left hindlimb touch-down (LH TD), right forelimb touch-down (RF TD) and right hindlimb lift-off (RH LO).

steadily on the ground, its activity was kept during the entire stance phase when walking on the branch. Furthermore, the maximal activity of the peroneus was significantly higher on the branch than on the ground (Permutation test:  $-2.858$ ,  $P=0.0022$ ). The maximal burst of activity of the rectus femoris was significantly lower on the branch (Permutation test:  $2.106$ ,  $P=0.0231$ ).

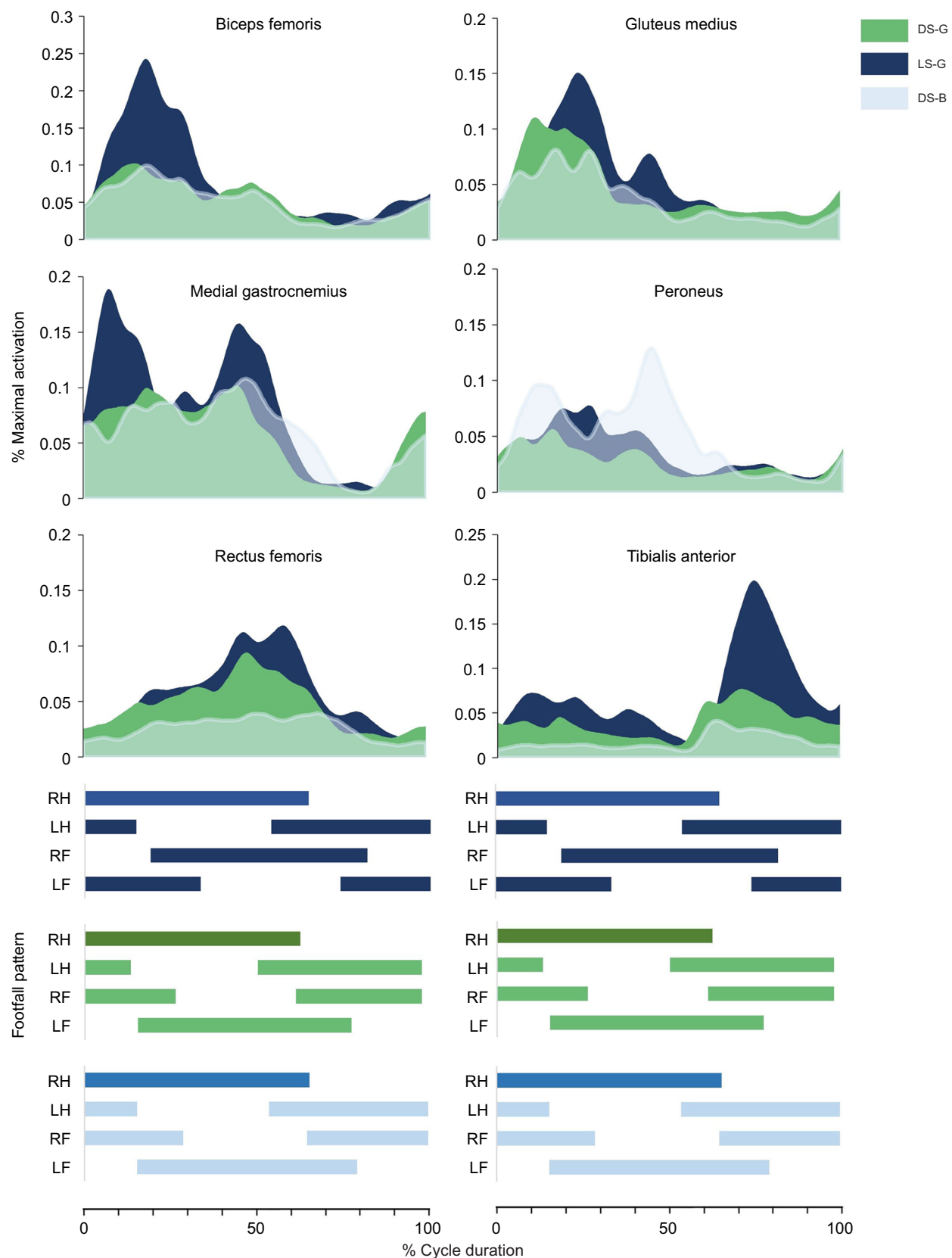
## DISCUSSION

The present study aimed to explore the quadrupedal walking pattern of baboons using different levels of analysis, via limb and body kinematics (also used to estimate the dynamics of the BCoM) and muscular activity. Overall, our study shows that the dynamics of the BCoM in a baboon walking quadrupedally on the ground using its preferred walking gait (DSDC) is effective and can be energetically

**Table 3. Spatio-temporal parameters and BCoM mechanics of steady quadrupedal walking in different substrate and gait contexts**

Parameter	DS-G ( $n=12$ )	LS-G ( $n=4$ )	DS-B ( $n=6$ )	P-value	
				DS-G vs LS-G	DS-G vs DS-B
Cycle duration (s)	$0.80 \pm 0.04$	$0.71 \pm 0.07$	$0.84 \pm 0.07$	<b>0.0209</b>	ns
Stride frequency ( $s^{-1}$ )	$1.26 \pm 0.06$	$1.44 \pm 0.15$	$1.2 \pm 0.1$	<b>0.0209</b>	ns
Stride length (m)	$0.73 \pm 0.04$	$0.71 \pm 0.05$	$0.66 \pm 0.03$	ns	<b>0.0197</b>
Speed ( $m s^{-1}$ )	$0.92 \pm 0.08$	$1.01 \pm 0.12$	$0.79 \pm 0.10$	ns	<b>0.0335</b>
Duty factor (%)	$64 \pm 2$	$65 \pm 2$	$66 \pm 2$	ns	ns
Recovery rate (%)	$42.8 \pm 9.6$	$27.9 \pm 9.8$	$32.3 \pm 8.6$	$0.0566^*$	$0.0907$
Congruity (%)	$38.7 \pm 7$	$53.6 \pm 10$	$46 \pm 12$	<b>0.0159</b>	ns
Relative amplitude	$0.86 \pm 0.26$	$0.41 \pm 0.13$	$0.78 \pm 0.27$	$0.0648$	ns
External energy ( $J kg^{-1} m^{-1}$ )	$0.33 \pm 0.08$	$0.33 \pm 0.05$	$0.36 \pm 0.10$	ns	ns

DS-G, quadrupedal walking on the ground using diagonal sequences; LS-G, quadrupedal walking on the ground using lateral sequences; and DS-B, quadrupedal walking on the branch using diagonal sequences. Significant values are indicated in bold (asterisk indicates values close to the significance threshold, i.e.  $0.05 < P < 0.1$ ).



**Fig. 7. Average EMG profiles of the 6 hindlimb muscles considered during steady quadrupedal walking for Id1.** EMG activity was recorded in 2017 (see Table 1). The activity patterns were stride normalized and averaged across 12 strides when walking on the ground using diagonal sequences (DS-G), 4 strides when walking on the ground using lateral sequences (LS-G) and 6 strides when walking on the branch using diagonal sequences (DS-B). The average footfall pattern at the bottom (gait diagram) shows average stance phase (solid bars) of the right hindlimb (RH), left hindlimb (LH), right forelimb (RF) and left forelimb (LF). EMG activity was recorded on the right hindlimb.

efficient. In contrast, walking on a branch appears to give priority to stability, but how it affects efficiency requires further exploration. In addition, walking using the LSLC gait appears to increase muscular effort and may reduce the potential for high recovery rates in baboons. Importantly, although our study supports specific assumptions about stability and efficiency in non-human primates, further data including a larger sample size are required.

### Walking on the ground using DSDC gait

Overall, the patterns of muscular activation during steady quadrupedal walking in baboons were consistent within and between individuals (Fig. 6B shows an overview of the muscular activity pattern during quadrupedal walking). The phasic activities of the six recorded muscles are very similar to the muscular activity profile described in macaques (Courtine et al., 2005; Higurashi et al., 2019). Furthermore, despite differences in the footfall pattern between non-primate quadrupedal mammals (lateral sequences) and non-human primates (diagonal sequences), the activity pattern of the hindlimb muscles in baboons is very similar to that observed in other primates such as chimpanzees, spider monkeys, macaques and lemurs (Ishida et al., 1974; Kimura et al., 1979; Larson and Stern, 2009), as well as in dogs (Deban et al., 2012; Goslow et al., 1981) and cats (Rasmussen et al., 1978). Therefore, we can assume that the basic functions of the muscles for retracting and protracting the limbs, as well as to support the body against gravity and inertial forces are conserved across groups.

We first hypothesized that, given the ‘cursorial’ adaptations of baboons (e.g. Druelle et al., 2017a; Patel and Polk, 2010; Raichlen, 2004), they should be able to make use of an inverted pendulum mechanism when walking steadily on the ground. Our results support this hypothesis as we observed that KE and PE mainly fluctuate out of phase (congruity=39%) during normal quadrupedal walking using DSDC gaits. The recovery rates observed in baboons in this study (22–84%) cover an important range of variation compared with other specialized quadrupeds such as dogs (50–70%; Griffin et al., 2004), but these are close to the range of values available for non-human primates, such as ring-tailed lemurs and capuchin monkeys (35–71% and 11–65%, respectively) during quadrupedal walking (O’Neill and Schmitt, 2012; Demes and O’Neill, 2013). Griffin et al. (2004) developed a model showing that the pendulum-like CoM movements in quadrupedal animals are a combination of inverted pendulums around both the pectoral and pelvic girdle. These pendulums are directly influenced by the footfall pattern and body mass distribution. For example, a BCoM located at mid-trunk coupled to a forelimb that lags behind the hindlimb by 25% would result in a flat trajectory of the BCoM (Griffin et al., 2004). Baboons have a BCoM positioned at mid-trunk compared with dogs that have a cranially positioned BCoM (Druelle et al., 2019), hence baboons may rely on limb phase only to produce ‘optimal’ fluctuations of their BCoM. In the present study, we found that the ipsilateral forelimb lagged behind the hindlimb by 61% on average (minimum 54%, maximum 69%) and there was a significant relationship between recovery rate and limb phase (i.e. the lag between forelimbs and hindlimbs; see Fig. 5C). These results support the model of Griffin et al. (2004), but do not support the ‘reduced cost zone’ of 65–72% estimated recently by Miller et al. (2019) for non-human primates. However, note that, as recognized by the latter, body mass distribution can also affect the model and specific primate conformation is likely to shift the reduced cost zone of footfall timing. In addition, given the small size of our sample, our results should be carefully considered before rejecting previous assumptions.

Our results, in addition to those provided by O’Neill and Schmitt (2012) and Demes and O’Neill (2013), do not support the hypothesis of Ogihara et al. (2012) suggesting that diagonal sequence gaits impede good recovery rates in primates. The baboon appears, however, much more efficient than the macaque (Ogihara et al., 2012) when walking on the ground. As previously suggested (Druelle et al., 2016), macaques may be less equipped for quadrupedal walking than baboons. Because baboons commonly travel at least 3.5 km per day, while macaques move less than 1.5 km (Garland, 1983), the specific ecological requirements of baboons may have shaped these species into more efficient walkers (i.e. higher potential for relying on inverted pendulum strategies) than macaques. Given the ecological niche of olive baboons and their large home range (Garland, 1983; Henzi et al., 1992; Isbell et al., 1998; Pebsworth et al., 2012), they should be under strong selection for walking efficiency (Druelle et al., 2017a). This could also be the case for ring-tailed lemurs and capuchin monkeys, which both exhibit good recovery rates during quadrupedal walking (O’Neill and Schmitt, 2012; Demes and O’Neill, 2013).

### Influence of different gait and substrate contexts

When walking on a branch, an inherent instability (rolling and pitching moments) is in action. Kinematical adjustments should reduce the vertical oscillations of the CoM (Gálvez-López et al., 2011; Schmitt, 1999) and in this way give priority to stability over efficiency (but see Schmitt, 2011). It has been shown that animals increase their stability on arboreal substrates through employing strategies that reduce the oscillations of their BCoM (Gálvez-López et al., 2011). However, these strategies can be of a different kind. For instance, while cats (medium sized, ~4.4 kg) make use of slower speeds and shorter swing phase durations on a narrow runway, dogs (large sized, ~28 kg) rely on high-speed locomotion and high frequency to gain dynamic stability (Gálvez-López et al., 2011). The adjustments observed in the olive baboon (13.5 kg in the present study) when walking on a (suspended, non-bending) branch are a decrease in stride length and speed, a decrease in the movement amplitude of the trunk and a trend towards a longer relative contact time. There is also an increase in ankle and wrist extension that results from a slight external rotation of the distal limb segments to fit the rounded shape of the substrate. The decrease in trunk range of motion may result in part from the shorter stride length and thus from the lower speed, as well as from the shoulder, which is kept more extended on the branch. More in-phase fluctuations of the KE and PE (congruity=46%) were also observed compared with walking on the ground. These adjustments (certainly closer to the cat strategy) reduce the vertical oscillations of the BCoM, and with the increased activity of the peroneus (increasing torque generation), meet the balance control requirements. This general strategy may reduce the possibility of relying on an efficient inverted pendulum-like exchange of energy, but we did not observe a direct significant difference in recovery rate. The baboon thus appears to adjust its movement and to increase the control in the distal segment to gain stability, but more data are required to assess how much this strategy influences efficiency. Interestingly, a previous study showed that in *Lemur catta*, walking on a raised horizontal pole does not significantly affect energetic recovery (Schmitt, 2011). Furthermore, limb interference is important during diagonal walking on the ground. The baboons move their right hindlimb on the right (or left) side of their right forelimb, while the left hindlimb moves on the right (or left) side of the left forelimb (Fig. 6B). On the branch, there is no space for limb interference and overstriding during walking, and the hindlimbs need to be

positioned behind the forelimbs at touch-down. This can also contribute to the shorter stride lengths and lower speed observed on the branch.

A study on bonobos found that when they walk on a horizontal arboreal substrate, they reduce their stance phase, take longer strides and reduce stride frequency (Schoonaert et al., 2016). This strategy appears to be very different from that used by the baboon in the present study (note that both the size of the specimens and the substrate diameter are different: 12 cm for the bonobos and 16 cm in the present study), as well as from those used by lemurs and marmosets, which all tend to decrease their speed and increase the contact time with the substrate (Franz et al., 2005; Young et al., 2016). However, we wonder whether the pole height may also be of importance. For instance, the bonobos were walking on a pole that was positioned approximately 30 cm above the ground, and hence falling was not really a risk encountered by the animals (Schoonaert et al., 2016). This emphasizes the importance of considering morphological differences and kinematic strategies coupled to risk evaluation among primates for negotiating arboreal substrates (hominoids, cercopithecoids, platyrrhines and lemuriforms all present different morphological features; Fleagle, 2013). Although balance requirements are shared between animals when walking on a horizontal branch, how these demands are met (by controlling pitching, yawing and rolling moments) can occur in very different ways, i.e. from static to dynamic stability of the BCoM. It is possible that all these strategies allow primates and other mammals to limit the vertical oscillations of the BCoM, given their respective morphology (e.g. Gálvez-López et al., 2011; Schmitt et al., 2006; Young et al., 2016).

Muscular effort is influenced by the footfall pattern (Bishop et al., 2008; Griffin et al., 2004); hence, energetic cost is probably an important factor in footfall timings (Miller et al., 2019). We hypothesized that the usual muscle activation pattern observed in diagonal gaits should be altered towards an increased activation of the proximal muscles when the baboon uses the unusual lateral gait on the ground and of the distal muscles (for increasing control) when it walks on a substrate that imposes higher balance requirements (such as a branch). First, we observed an increased activity of the biceps femoris, the gastrocnemius and the tibialis anterior when walking using LSLC gait on the ground. Second, the peroneus activity increased substantially in intensity and duration during the stance phase when walking on the branch. Generally, the peroneus is suggested to stabilize the ankle and to be an extensor and evertor of the foot. Boyer et al. (2007) suggested that the peroneus (longus) is an important muscle for positioning the foot at touchdown and for resisting inversion throughout the stance phase in primates. The activity of the peroneus observed in our study when the baboon was walking on the branch is similar to that of a lemur species walking quadrupedally on large and small poles (Boyer et al., 2007). While it is not strongly active on the ground during diagonal and lateral gaits in baboons, it appears to be specifically recruited for resisting foot inversion during the stance phase on the branch. Our kinematics support this, as we observed an increase in ankle extension (and external rotation). The more outward and everted position of the foot should ensure a better fit between the foot and the substrate, thus increasing friction and allowing transmission of the rotating moment (Lammers and Gauntner, 2008; Preuschoft, 2004).

The biceps femoris is described as a hip extensor and a knee flexor (Swindler and Wood, 1973). It is active during the initial part of the support phase. At touch-down, the limb is in a protracted position and the knee is relatively extended (~140 deg) (Larney and

Larson, 2004); the biceps femoris is, therefore, acting as a thigh (hindlimb) retractor by flexing the knee (~110 deg at midstance) and extending the hip (from 50 deg to 75 deg between touch-down and mid-stance). The fact that its activity increases substantially during lateral walking can be directly related to the higher stride frequency (relative stance phase does not change). The increase in activity of the gastrocnemius and the tibialis anterior may also result from the higher stride frequency. A faster retraction and protraction of the limb would require more muscular fibres to be active. Lateral walking also led to an increase in extension of the ankle that can be related to the increase in activity observed in the gastrocnemius and the tibialis anterior. But the functional reason for this higher extension remains elusive at this stage (note that such an ankle extension in this context also appears to be observed in capuchin monkey; see fig. 2 in Wallace and Demes, 2008). On the branch, stride length decreases as well as speed, and the activity of the rectus femoris (for controlling limb retraction) is reduced in this context.

## Conclusion

The present study provides new exploratory data on the normal quadrupedal gait pattern in olive baboons. It is also an attempt to better understand the flexibility of the quadrupedal gait in different contexts. Baboons mainly walk quadrupedally on the ground using a DSDC gait and our evaluation of the dynamics of the BCoM using kinematics suggests that this is more efficient than walking using the LSLC gait. Also, from a motor perspective, a significant increase in muscular activity should result in a higher level of oxygen consumption. Hence, the most efficient baboon remains the one walking on the ground using DSDC gaits (potentially with a tight limb phase: 50% < limb phase < 60% and at low speed, but data from a larger speed range are required to assess how it influences the energetic recovery rates, i.e. linearly or not). Moreover, our data suggest that the use of a different walking gait, or walking on a branch, both result in less efficient forms of locomotion. Although our analysis on this aspect is preliminary, this emphasizes a possible limitation in the flexibility of the walking pattern when efficiency is the target. In other words, walking economy could be related to a stereotyped, non-flexible pattern, while gait adjustments and flexibility ensure stability in an arboreal habitat. However, further data are required to investigate this hypothesis. As recently claimed, the effect of footfall timing on mechanical stability and mechanical energy exchange on arboreal and terrestrial substrates, as well as the way these competing demands interact (Miller et al., 2019), remains poorly known. It is also possible that these two components do not have the same 'time frame', as mechanical energy exchange should occur within a stride, while mechanical stability can be performed and ensured among multiple strides (Biewener and Daley, 2007; Chadwell and Young, 2015; Lammers and Gauntner, 2008). Further integrative data including larger sample size are needed to better understand the relationships between gait adjustments, BCoM mechanics and muscular activity in non-human primates.

Overall, the quadrupedal peculiarities of primates certainly represent biomechanical adjustments to arboreal life and played a crucial role in the early differentiation of primates from other mammals. However, despite these peculiarities, they also share very similar patterns of muscle activation with other quadrupedal mammals, at least when they walk quadrupedally on the ground. This reflects the shared basic functional demands (i.e. support and propulsion) on the hindlimbs for quadrupedal locomotion in tetrapods. Finally, the diagonal gait pattern appears to be strongly implemented into the baboon neuromotor system because lateral



sequences are likely to result in a direct and significant increase of the energetic costs (at the level of BCoM mechanics and muscular activity). In contrast, the diagonal walking gait does not impede good recovery rates in primates.

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### Competing interests

The authors declare no competing or financial interests.

### Author contributions

Conceptualization: F.D., P.M., B.R., P.A., G.B.; Methodology: F.D., P.M., B.R., P.A., G.B.; Software: F.D., A.S., G.B.; Validation: F.D., A.S., S.M., N.S., G.B.; Formal analysis: F.D., A.S., S.M., N.S.; Investigation: F.D.; Resources: F.D., P.M., G.B.; Data curation: F.D., G.B.; Writing - original draft: F.D.; Writing - review & editing: F.D., A.S., S.M., N.S., P.M., P.A., G.B.; Visualization: F.D.; Supervision: F.D., P.A., G.B.; Project administration: G.B.; Funding acquisition: G.B.

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### References

- Aerts, P., Van Damme, R., Van Elsacker, L. and Duchêne, V. (2000). Spatio-temporal gait characteristics of the hind-limb cycles during voluntary bipedal and quadrupedal walking in bonobos (*Pan paniscus*). *Am. J. Phys. Anthropol.* **111**, 503-517. doi:10.1002/(SICI)1096-8644(200004)111:4
- Ahn, A. N., Furrow, E. and Biewener, A. A. (2004). Walking and running in the red-legged running frog, *Kassina maculata*. *J. Exp. Biol.* **207**, 399-410. doi:10.1242/jeb.00761
- Anvari, Z., Berillon, G., Asgari Khaneghah, A., Grimaud-Herve, D., Moulin, V. and Nicolas, G. (2014). Kinematics and spatiotemporal parameters of infant-carrying in olive baboons. *Am. J. Phys. Anthropol.* **155**, 392-404. doi:10.1002/ajpa.22576
- Berillon, G., Daver, G., D'Août, K., Nicolas, G., de la Villetanet, B., Multon, F., Digrandi, G. and Dubreuil, G. (2010). Bipedal versus quadrupedal hind limb and foot kinematics in a captive sample of *Papio anubis*: setup and preliminary results. *Int. J. Primatol.* **31**, 159-180. doi:10.1007/s10764-010-9398-2
- Berillon, G., D'Août, K., Daver, G., Dubreuil, G., Multon, F., Nicolas, G., Villetanet, B. and Vereecke, E. E. (2011). In What Manner Do Quadrupedal Primates Walk on Two Legs? Preliminary Results on Olive Baboons (*Papio anubis*). In *Primate Locomotion* (ed. L. Barrett), pp. 61-62. New York: Springer.
- Biewener, A. A. and Daley, M. A. (2007). Unsteady locomotion: integrating muscle function with whole body dynamics and neuromuscular control. *J. Exp. Biol.* **210**, 2949-2960. doi:10.1242/jeb.005801
- Bishop, K. L., Pai, A. K. and Schmitt, D. (2008). Whole body mechanics of stealthy walking in cats. *PLoS ONE* **3**, e3808. doi:10.1371/journal.pone.0003808
- Boyer, D. M., Patel, B. A., Larson, S. G. and Stern, J. T., Jr. (2007). Telemetered electromyography of peroneus longus in *Varecia variegata* and *Eulemur rubriventer*: implications for the functional significance of a large peroneal process. *J. Hum. Evol.* **53**, 119-134. doi:10.1016/j.jhevol.2006.10.007
- Cartmill, M. (1974). Pads and claws in arboreal locomotion. In *Primate Locomotion* (ed. F. A. Jenkins, Jr), pp. 45-83. Academic Press.
- Cartmill, M., Lemelin, P. and Schmitt, D. (2002). Support polygons and symmetrical gaits in mammals. *Zool. J. Linn. Soc.* **136**, 401-420. doi:10.1046/j.1096-3642.2002.00038.x
- Cartmill, M., Brown, K., Atkinson, C., Cartmill, E. A., Findley, E., Gonzalez-Socoloske, D., Hartstone-Rose, A. and Mueller, J. (2020). The gaits of marsupials and the evolution of diagonal-sequence walking in primates. *Am. J. Phys. Anthropol.* **171**, 182-197. doi:10.1002/ajpa.23959
- Chadwell, B. A. and Young, J. W. (2015). Angular momentum and arboreal stability in common marmosets (*Callithrix jacchus*). *Am. J. Phys. Anthropol.* **156**, 565-576. doi:10.1002/ajpa.22683
- Courtine, G., Roy, R. R., Hodgson, J., McKay, H., Raven, J., Zhong, H., Yang, H., Tuszynski, M. H. and Edgerton, V. R. (2005). Kinematic and EMG determinants in quadrupedal locomotion of a non-human primate (Rhesus). *J. Neurophysiol.* **93**, 3127-3145. doi:10.1152/jn.01073.2004
- Crompton, R. H., Li, Y., Alexander, R. M., Wang, W. and Gunther, M. M. (1996). Segment inertial properties of primates: new techniques for laboratory and field studies of locomotion. *Am. J. Phys. Anthropol.* **99**, 547-570. doi:10.1002/(SICI)1096-8644(199604)99:4<547::AID-AJPA3>3.0.CO;2-R
- Deban, S. M., Schilling, N. and Carrier, D. R. (2012). Activity of extrinsic limb muscles in dogs at walk, trot and gallop. *J. Exp. Biol.* **215**, 287-300. doi:10.1242/jeb.063230
- Demes, B. and O'Neill, M. C. (2013). Ground reaction forces and center of mass mechanics of bipedal capuchin monkeys: implications for the evolution of human bipedalism. *Am. J. Phys. Anthropol.* **150**, 76-86. doi:10.1002/ajpa.22176
- Demes, B., Larson, S. G., Stern, J. T., Jungers, W. L., Jr., Biknevicius, A. R. and Schmitt, D. (1994). The kinetics of primate quadrupedalism: "hindlimb drive" reconsidered. *J. Hum. Evol.* **26**, 353-374. doi:10.1006/jhev.1994.1023
- Druelle, F., Aerts, P. and Berillon, G. (2016). Effect of body mass distribution on the ontogeny of positional behaviors in non-human primates: longitudinal follow-up of infant captive olive baboons (*Papio anubis*). *Am. J. Primatol.* **78**, 1201-1221. doi:10.1002/ajpa.22575
- Druelle, F., Aerts, P., D'Août, K., Moulin, V. and Berillon, G. (2017a). Segmental morphometrics of the olive baboon (*Papio anubis*): a longitudinal study from birth to adulthood. *J. Anat.* **230**, 805-819. doi:10.1111/joa.12602
- Druelle, F., Berillon, G. and Aerts, P. (2017b). Intrinsic limb morpho-dynamics and the early development of interlimb coordination of walking in a quadrupedal primate. *J. Zool.* **301**, 235-247. doi:10.1111/jzo.12423
- Druelle, F., Young, J. and Berillon, G. (2018). Behavioral implications of ontogenetic changes in intrinsic hand and foot proportions in olive baboons (*Papio Anubis*). *Am. J. Phys. Anthropol.* **165**, 65-76. doi:10.1002/ajpa.23331
- Druelle, F., Berthet, M. and Quintard, B. (2019). The body center of mass in primates: Is it more caudal than in other quadrupedal mammals? *Am. J. Phys. Anthropol.* **169**, 170-178. doi:10.1002/ajpa.23813
- Druelle, F., Aerts, P., Ngawolo, J. C. B. and Narat, V. (2020). Impressive arboreal gap-crossing behaviors in wild bonobos, *Pan paniscus*. *Int. J. Primatol.* **41**, 129-140. doi:10.1007/s10764-020-00140-z
- Dunbar, D. C. and Badam, G. L. (2000). Locomotion and posture during terminal branch feeding. *Int. J. Primatol.* **21**, 649-669. doi:10.1023/A:1005565304671
- Fleagle, J. G. (2013). *Primate Adaptation and Evolution*, 3rd edn. Academic Press.
- Franz, T. M., Demes, B. and Carlson, K. J. (2005). Gait mechanics of lemurid primates on terrestrial and arboreal substrates. *J. Hum. Evol.* **48**, 199-217. doi:10.1016/j.jhevol.2004.11.004
- Gálvez-López, E., Maes, L. D. and Abourachid, A. (2011). The search for stability on narrow supports: an experimental study in cats and dogs. *Zoology* **114**, 224-232. doi:10.1016/j.zool.2011.03.001
- Garland, T., Jr. (1983). Scaling the ecological cost of transport to body mass in terrestrial mammals. *Am. Nat.* **121**, 571-587. doi:10.1086/284084
- Goslow, G. E., Seeherman, H. J., Taylor, C. R., McCutchin, M. N. and Heglund, N. C. (1981). Electrical activity and relative length changes of dog limb muscles as a function of speed and gait. *J. Exp. Biol.* **94**, 15-42. doi:10.1242/jeb.94.1.15
- Grand, T. I. (1977). Body weight: its relation to tissue composition, segment distribution, and motor function. I. Interspecific comparisons. *Am. J. Phys. Anthropol.* **47**, 211-239. doi:10.1002/ajpa.1330470204
- Griffin, T. M., Main, R. P. and Farley, C. T. (2004). Biomechanics of quadrupedal walking: how do four-legged animals achieve inverted pendulum-like movements? *J. Exp. Biol.* **207**, 3545-3558. doi:10.1242/jeb.01177
- Hamrick, M. W. (2001). Primate origins: evolutionary change in digital ray patterning and segmentation. *J. Hum. Evol.* **40**, 339-351. doi:10.1006/jhev.2001.0467
- Hashimoto, T., Ueno, K., Ogawa, A., Asamizuya, T., Suzuki, C., Cheng, K., Tanaka, M., Taoka, M., Iwamura, Y., Suwa, G. et al. (2013). Hand before foot? Cortical somatotopy suggests manual dexterity is primitive and evolved independently of bipedalism. *Phil. Trans. R. Soc. B Biol. Sci.* **368**, 20120417. doi:10.1098/rstb.2012.0417
- Henzi, S. P., Byrne, R. W. and Whiten, A. (1992). Patterns of movement by baboons in the Drakensberg mountains: primary responses to the environment. *Int. J. Primatol.* **13**, 601-629. doi:10.1007/BF02551256
- Higurashi, Y., Maier, M. A., Nakajima, K., Morita, K., Fujiki, S., Aoi, S., Mori, F., Murata, A. and Inase, M. (2019). Locomotor kinematics and EMG activity during quadrupedal versus bipedal gait in the Japanese macaque. *J. Neurophysiol.* **122**, 398-412. doi:10.1152/jn.00803.2018
- Hirasaki, E., Kumakura, H. and Matano, S. (1995). Electromyography of 15 limb muscles in Japanese macaques (*Macaca fuscata*) during vertical climbing. *Folia Primatol.* **64**, 218-224. doi:10.1159/000156857
- Hof, A. L. (1996). Scaling gait data to body size. *Gait Posture* **4**, 222-223. doi:10.1016/0966-6362(95)01057-2
- Hunt, K. D. (2016). Why are there apes? Evidence for the co-evolution of ape and monkey ecomorphology. *J. Anat.* **228**, 630-685. doi:10.1111/joa.12454
- Hunt, K. D., Cant, J. G. H., Gebo, D. L., Rose, M. D., Walker, S. E. and Youlatos, D. (1996). Standardized descriptions of primate locomotor and postural modes. *Primates* **37**, 363-387. doi:10.1007/BF02381373
- Isbell, L. A., Pruett, J. D., Lewis, M. and Young, T. P. (1998). Locomotor activity differences between sympatric patas monkeys (*Erythrocebus patas*) and vervet

- monkeys (*Cercopithecus aethiops*): implications for the evolution of long hindlimb length in Homo. *Am. J. Phys. Anthropol.* **105**, 199–207. doi:10.1002/(SICI)1096-8644(199802)105:2<199::AID-AJPA7>3.0.CO;2-Q
- Ishida, H., Kimura, T. and Okada, M. (1974). Patterns of bipedal walking in anthropoid primates. In *Proceedings of the 5th congress of the International Primatological Society*, 1974, pp. 287–301. Japan Science Press.
- Jungers, W. L. and Anapol, F. C. (1985). Interlimb coordination and gait in the brown lemur (*Lemur fulvus*) and the talapoin monkey (*Miopithecus talapoin*). *Am. J. Phys. Anthropol.* **67**, 89–97. doi:10.1002/ajpa.1330670203
- Jungers, W. L. and Stern, J. T. (1981). Preliminary electromyographical analysis of brachiation in gibbon and spider monkey. *Int. J. Primatol.* **2**, 19–33. doi:10.1007/BF02692297
- Kimura, T., Okada, M. and Ishida, H. (1979). Kinesiological characteristics of primate walking: its significance in human walking. In *Environment, Behavior, and Morphology: Dynamic Interactions in Primates* (ed. M. E. Morbeck, H. Preuschoft and N. Gombert), pp. 297–311. Fischer.
- Lammers, A. R. and Gauntner, T. (2008). Mechanics of torque generation during quadrupedal arboreal locomotion. *J. Biomech.* **41**, 2388–2395. doi:10.1016/j.jbiomech.2008.05.038
- Larney, E. and Larson, S. G. (2004). Compliant walking in primates: elbow and knee yield in primates compared to other mammals. *Am. J. Phys. Anthropol.* **125**, 42–50. doi:10.1002/ajpa.10366
- Larson, S. G. (2018). Nonhuman primate locomotion. *Am. J. Phys. Anthropol.* **165**, 705–725. doi:10.1002/ajpa.23368
- Larson, S. G. and Stern, J. T. (1987). EMG of chimpanzee shoulder muscles during knuckle-walking: problems of terrestrial locomotion in a suspensory adapted primate. *J. Zool.* **212**, 629–655. doi:10.1111/j.1469-7998.1987.tb05961.x
- Larson, S. G. and Stern, J. T. (1989). The role of propulsive muscles of the shoulder during quadrupedalism in vervet monkeys (*Cercopithecus aethiops*). *J. Mot. Behav.* **21**, 457–472. doi:10.1080/00222895.1989.10735494
- Larson, S. G. and Stern, J. T. (2007). Humeral retractor EMG during quadrupedal walking in primates. *J. Exp. Biol.* **210**, 1204–1215. doi:10.1242/jeb.002337
- Larson, S. G. and Stern, J. T., Jr. (2009). Hip extensor EMG and forelimb/hind limb weight support asymmetry in primate quadrupeds. *Am. J. Phys. Anthropol.* **138**, 343–355. doi:10.1002/ajpa.20935
- Larson, S. G., Schmitt, D., Lemelin, P. and Hamrick, M. (2001). Limb excursion during quadrupedal walking: how do primates compare to other mammals? *J. Zool.* **255**, 353–365. doi:10.1017/S0952836901001455
- Lawler, R. R. (2006). Sifaka positional behavior: ontogenetic and quantitative genetic approaches. *Am. J. Phys. Anthropol.* **131**, 261–271. doi:10.1002/ajpa.20430
- Maus, H.-M., Seyfarth, A. and Grimmer, S. (2011). Combining forces and kinematics for calculating consistent centre of mass trajectories. *J. Exp. Biol.* **214**, 3511–3517. doi:10.1242/jeb.057422
- Miller, C. E., Johnson, L. E., Pinkard, H., Lemelin, P. and Schmitt, D. (2019). Limb phase flexibility in walking: a test case in the squirrel monkey (*Saimiri sciureus*). *Frontiers in Zoology* **16**, 5. doi:10.1186/s12983-019-0299-8
- Ogihara, N., Makishima, H., Hirasaki, E. and Nakatsukasa, M. (2012). Inefficient use of inverted pendulum mechanism during quadrupedal walking in the Japanese macaque. *Primates* **53**, 41–48. doi:10.1007/s10329-011-0265-3
- O'Neill, M. C. and Schmitt, D. (2012). The gaits of primates: center of mass mechanics in walking, cantering and galloping ring-tailed lemurs, *Lemur catta*. *J. Exp. Biol.* **215**, 1728–1739. doi:10.1242/jeb.052340
- Patel, B. A. (2009). Not so fast: speed effects on forelimb kinematics in cercopithecine monkeys and implications for digitigrade postures in primates. *Am. J. Phys. Anthropol.* **140**, 92–112. doi:10.1002/ajpa.21039
- Patel, B. A. and Polk, J. D. (2010). Distal forelimb kinematics in *Erythrocebus patas* and *Papio anubis* during walking and galloping. *Int. J. Primatol.* **31**, 191–207. doi:10.1007/s10764-010-9394-6
- Patel, B. A., Larson, S. G. and Stern, J. T. (2012). Electromyography of wrist and finger flexor muscles in olive baboons (*Papio anubis*). *J. Exp. Biol.* **215**, 115–123. doi:10.1242/jeb.063107
- Patel, B. A., Wallace, I. J., Boyer, D. M., Granatosky, M. C., Larson, S. G. and Stern, J. T. (2015). Distinct functional roles of primate grasping hands and feet during arboreal quadrupedal locomotion. *J. Hum. Evol.* **88**, 79–84. doi:10.1016/j.jhevol.2015.09.004
- Pebsworth, P. A., Morgan, H. R. and Huffman, M. A. (2012). Evaluating home range techniques: use of Global Positioning System (GPS) collar data from chacma baboons. *Primates* **53**, 345–355. doi:10.1007/s10329-012-0307-5
- Prescott, M. J. and Buchanan-Smith, H. M. (2016). *Training Nonhuman Primates Using Positive Reinforcement Techniques: A Special Issue of the Journal of Applied Animal Welfare Science*, Psychology Press.
- Preuschoft, H. (2004). Mechanisms for the acquisition of habitual bipedality: are there biomechanical reasons for the acquisition of upright bipedal posture? *J. Anat.* **204**, 363–384. doi:10.1111/j.0021-8782.2004.00303.x
- Raichlen, D. A. (2004). Convergence of forelimb and hindlimb natural pendular period in baboons (*Papio cynocephalus*) and its implication for the evolution of primate quadrupedalism. *J. Hum. Evol.* **46**, 719–738. doi:10.1016/j.jhevol.2004.04.002
- Rasmussen, S., Chan, A. K. and Goslow, G. E., Jr. (1978). The cat step cycle: electromyographic patterns for hindlimb muscles during posture and unrestrained locomotion. *J. Morphol.* **155**, 253–269. doi:10.1002/jmor.1051550302
- Reilly, S. M., McElroy, E. J. and Biknevicius, A. R. (2007). Posture, gait and the ecological relevance of locomotor costs and energy-saving mechanisms in tetrapods. *Zoology* **110**, 271–289. doi:10.1016/j.zool.2007.01.003
- Reynolds, T. R. (1985). Mechanics of increased support of weight by the hindlimbs in primates. *Am. J. Phys. Anthropol.* **67**, 335–349. doi:10.1002/ajpa.1330670406
- Rose, M. D. (1977). Positional behaviour of olive baboons (*Papio anubis*) and its relationship to maintenance and social activities. *Primates* **18**, 59–116. doi:10.1007/BF02382953
- Schapiro, S. J., Bloomsmith, M. A. and Laule, G. E. (2003). Positive reinforcement training as a technique to alter nonhuman primate behavior: quantitative assessments of effectiveness. *J. Appl. Anim. Welf. Sci.* **6**, 175–187. doi:10.1207/S15327604JAWS0603\_03
- Schmitt, D. (1999). Compliant walking in primates. *J. Zool.* **248**, 149–160. doi:10.1111/j.1469-7998.1999.tb01191.x
- Schmitt, D. (2011). Translating Primate Locomotor Biomechanical Variables from the Laboratory to the Field. In *Primate Locomotion* (ed. K. D'Août and E. E. Verecke), pp. 7–27. New York: Springer.
- Schmitt, D., Cartmill, M., Griffin, T. M., Hanna, J. B. and Lemelin, P. (2006). Adaptive value of ambling gaits in primates and other mammals. *J. Exp. Biol.* **209**, 2042–2049. doi:10.1242/jeb.02235
- Schoonaert, K., D'Août, K., Samuel, D., Talloen, W., Nauwelaerts, S., Kivell, T. L. and Aerts, P. (2016). Gait characteristics and spatio-temporal variables of climbing in bonobos (*Pan paniscus*). *Am. J. Primatol.* **78**, 1165–1177. doi:10.1002/ajp.22571
- Shapiro, L. J. and Jungers, W. L. (1994). Electromyography of back muscles during quadrupedal and bipedal walking in primates. *Am. J. Phys. Anthropol.* **93**, 491–504. doi:10.1002/ajpa.1330930408
- Shapiro, L. J., Anapol, F. C. and Jungers, W. L. (1997). Interlimb coordination, gait, and neural control of quadrupedalism in chimpanzees. *Am. J. Phys. Anthropol.* **102**, 177–186. doi:10.1002/(SICI)1096-8644(199702)102:2<177::AID-AJPA3>3.0.CO;2-W
- Stern, J. T., Jr. and Larson, S. G. (2001). Telemetered electromyography of the supinators and pronators of the forearm in gibbons and chimpanzees: implications for the fundamental positional adaptation of hominoids. *Am. J. Phys. Anthropol.* **115**, 253–268. doi:10.1002/ajpa.1080
- Stern, J. T. and Susman, R. L. (1981). Electromyography of the gluteal muscles in *Hylobates*, *Pongo*, and *pan*: implications for the evolution of hominid bipedality. *Am. J. Phys. Anthropol.* **55**, 153–166. doi:10.1002/ajpa.1330550203
- Swindler, D. R. and Wood, C. D. (1973). *Atlas of Primate Gross Anatomy*. Krieger Publishing Company.
- Thorpe, S. K. S., Crompton, R. H. and Alexander, R. M. (2007). Orangutans use compliant branches to lower the energetic cost of locomotion. *Biol. Lett.* **3**, 253–256. doi:10.1098/rsbl.2007.0049
- Toussaint, S., Llamasi, A., Morino, L. and Youlatos, D. (2020). The central role of small vertical substrates for the origin of grasping in early primates. *Curr. Biol.* **30**, 1600–1613.e3. doi:10.1016/j.cub.2020.02.012
- Vilensky, J. A. and Gankiewicz, E. (1990). Effects of growth and speed on hindlimb joint angular displacement patterns in vervet monkeys (*Cercopithecus aethiops*). *Am. J. Phys. Anthropol.* **81**, 441–449. doi:10.1002/ajpa.1330810313
- Wallace, I. J. and Demes, B. (2008). Symmetrical gaits of *Cebus apella*: implications for the functional significance of diagonal sequence gait in primates. *J. Hum. Evol.* **54**, 783–794. doi:10.1016/j.jhevol.2007.10.008
- Young, J. W., Stricklen, B. M. and Chadwell, B. A. (2016). Effects of support diameter and compliance on common marmoset (*Callithrix jacchus*) gait kinematics. *J. Exp. Biol.* **219**, 2659–2672. doi:10.1242/jeb.140939
- Zeininger, A., Shapiro, L. J. and Raichlen, D. A. (2017). Ontogenetic changes in limb postures and their impact on effective limb length in baboons (*Papio cynocephalus*). *Am. J. Phys. Anthropol.* **163**, 231–241. doi:10.1002/ajpa.23201