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François Druelle[a,b,c], Anthony Supiot[d], Silke Meulemans[c], Niels Schouteden[c,e], Pablo Molina-Vila[b], Brigitte Rimbaud[b], Peter Aerts[c,f], Gilles Berillon[a,b]

[a]Histoire Naturelle de l'Homme Préhistorique, UMR 7194-MNHN-CNRS, Paris, France
[b]Primatology Station of the CNRS, UPS 846, Rousset-sur-Arc, France
[c]Functional Morphology Laboratory, University of Antwerp, Wilrijk, Belgium
[d]Gait and Motion Analysis Laboratory, Assistance Publique des Hôpitaux de Paris (AP-HP), Robert Debré University Hospital, Paris, France
[e]Monde Sauvage Safari Parc, Aywaille, Belgium
[f]Department of Movement and Sports Sciences, University of Ghent, Gent, Belgium

ABSTRACT Primates exhibit unusual quadrupedal features (e.g. diagonal gaits, compliant walk) compared to 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 the mechanical energy exchange. In order to investigate these aspects, we have conducted an integrative study on quadrupedal walking in 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 have studied the muscular activity of six hind limb muscles using non-invasive surface probes. Our results show that baboons can rely on an inverted pendulum-like exchange of energy (57% in average and the maximal observed value is 84%) when walking slowly (<0.9m.s^{-1}) with a tight limb phase (≈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 movements and support. On the other hand, walking on a suspended branch generates kinematic and muscular adjustments to ensure a 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 the diagonal walking gait, yet a different footfall pattern and substrate appear to influence muscular effort and efficiency.

Key words Centre of mass, Electromyography, kinematics, 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 & 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 hind limbs (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 pitching, yawing and rolling moments, and limit the vertical oscillations of the centre of mass, hence branch oscillation, and increase maintenance of balance (e.g. Cartmill et al. 2020; Cartmill et al. 2002; Schmitt et al. 2006).

Parallel to these functional adjustments, the muscular activity pattern also presents specificities. EMG studies on non-human primates have provided a 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 & Stern 1981; Stern Jr & Larson 2001; Stern & Susman 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 & 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 to other quadrupedal mammals (Courtine et al. 2005). The different inertial properties of non-human primates compared to 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 are suggested in primates (Courtine et al. 2005; Jungers & Anapol 1985; Shapiro et al. 1997) with the hand and the foot having distinct functional roles (Druelle et al. 2018; Hashimoto et al. 2011; Lawler 2006; Patel et al. 2015). Furthermore, although the phasic recruitment of muscles is generally similar to other quadrupedal mammals (Courtine et al. 2005; Higurashi et al. 2019; Shapiro & Jungers 1994), specificities have been emphasized for the humeral retractors (Larson &

Stern 1987; Larson & Stern 1989; Larson & Stern 2007), and hip extensors might also be used for different functions (Larson & Stern 2009; Reynolds 1985). As a result, primate quadrupedal control and mechanics are considered particular compared to that of other (terrestrial) quadrupedal 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 centre of mass 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 centre of mass mechanics (using kinematics) and the muscle activity of six extrinsic hind limb 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 to 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 fore- 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 voluntary 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 a 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 few strides on the ground. We thus provide a preliminary picture of the normal quadrupedal walking pattern in baboon 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 expect 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 & Schmitt 2012; Demes & O'Neill 2013). Second, we will specifically evaluate 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), while 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 centre of mass and the muscle activity together should provide an integrative picture of the quadrupedal walking pattern in baboon and how these are connected (see Courtine et al. 2005). In this context, a reduced efficiency in the mechanics of the centre of mass (for example, walking on a branch requires kinematical adjustments that tend to reduce the vertical oscillations of the centre of mass; see Gàlvez-Lòpez et al. 2011; Schmitt 1999) should match an alteration of the muscular activity toward an increased activation.

MATERIALS AND METHODS

Context of experiment, 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 (Berillon et al. *in preparation*). 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 n°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 the training was based on positive reinforcement techniques and systematic desensitization (Prescott & Buchanan-Smith 2016; Schapiro et al. 2003) and was conducted by the same two trainers, PMV and BR. 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 as target or parking training. After 6 months of training (46 sessions of training of approximately 30-45 minutes), 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), the 04/07/2013, the 31/07/2013 and the 15/12/2017, and during one recording session for individual 2

(Id2), the 03/12/2013. At the time of data collection, Id1 was 3 years old and weighed 8.14 kgs in 2013 and 7.5 years old and weighed 13.5 kgs in 2017. Id2 was 3.5 years old and weighed 8.05 kgs 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. 2017). The maturation of their neuromotor control also appears to be largely complete (see Druelle et al. 2017; 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 2000Hz using a wireless Zerowire system (Aurion Srl, Milan, Italy) with the MyoResearch XP Master Edition software (Noraxon®). We focused on 6 muscles commonly studied as actuator 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 (Figure 1). To ensure the 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 minutes); the anaesthesia was initiated with an intra-muscular injection of Ketamine (4mg/kg) and medetomidine (40µg/kg) and maintained with gas isoflurane (1%). This anaesthesia was short and light enough to shorten the recovery period using an atipamezole as antagonist. After locally shaving, cleaning and degreasing the skin, electrodes were taped at the level of the muscles' belly (approximately at mid length of each 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 to 90 minutes after their arrival in the enclosure.

Kinematics

The animals walked on a straight and horizontal calibrated walkway and on a horizontal branch (Ø 0.16 m, positioned at approximately 1m 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 per second (fps; Baumer HXC1) (see Berillon et al. 2010 for a general description of the experimental setup); synchronized recording was proceeded with Streampix 4 (by Norpix Inc.). Two cameras were laterally placed perpendicular to the walkway, to accurately record in a large field of view the main sagittal spatiotemporal 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 60fps) 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 hind limb touchdown to the next right hind limb touchdown. As we noticed some speed variation between consecutive quadrupedal strides, we calculated an acceleration/deceleration index as follows: $(average\ speed\ stride_{n+1} - average\ speed\ stride_n)/average\ speed\ stride_n$. For the present analysis, we removed the quadrupedal strides for which speed variations were above 10% between consecutive strides (note that given the small amount 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 further). Table 1 shows the dataset included in the present analysis after applying this strong selective criterion.

TABLE 1. *Studied individuals and data collected*

Individual	n/n[1]	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[2] / 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

[1]the left side of the oblique sign indicates the number of strides kept in the present analysis and the right side indicates the total number of strides recorded before applying the acceleration selection criterion (see Methods)
[2]given the small amount of data for the lateral walking gait (2 in 2013 and 2 in 2017), we have pooled these data together in the analyses

Analysis

Basic kinematics

We calculated the following spatiotemporal parameters: the cycle duration (time period between two right hind limb touchdown events), the frequency (inverse of cycle duration), the duty factor

(proportion of stance phase of the right hind limb 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 centre of mass; see below) and limb phase (time period between the right hind limb touchdown and the right forelimb touchdown relative to the cycle duration; <50% is a lateral sequence, >50% is a diagonal sequence). The spatiotemporal 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 SM and NS using the *DLTdv7* application developed in MATLAB by the T. Hendrick Lab (Figure 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 satisfactory digitization result, i.e. a smooth movement with no anomaly. Data were then filtered per stride using a 4^{th} order zero phase shift Butterworth low pass filter with a cut-off frequency of 5Hz. We then applied a cubic spline interpolation over a time base with 100 points in order to stride-normalized the individual quadrupedal cycles. Tracking the joints and body segments during the walking strides allowed us to measure 6 internal joint angles (joint extension accords 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.

Centre of mass Mechanics

The position of the body centre of mass (BCoM) can be estimated using body segment displacements and morphometrics (kinematic method; Maus et al. 2011). In 2013 and 2017, morphometrics of the studied individual (Id1) were collected using external measurements (when the individual was anesthetised). 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 weighed arithmetic mean of all segments' CoM to estimate the instantaneous position of the BCoM. By using the BCoM displacements, we estimated the variations in kinetic and potential energy during the quadrupedal strides. The kinetic energy (*KE*) is calculated as follows:

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

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

$$PE = M_b g h$$

Where g is the gravitational acceleration ($9.81\ m.s^{-2}$) and h is the height of the BCoM. The total external mass-specific mechanical energy ($W_{ext}; J.kg^{-1}.m^{-1}$) is defined as the sum of the positive increments of the total energy ($\Delta^{+}TE$) within a cycle, divided by the body mass and the stride length (SL) of the respective cycle:

$$W_{ext} = \frac{\Delta^{+}TE}{M_b SL}$$

During walking, the BCoM trajectory in relatively large animals (>1kg; 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 both 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 of recovery allows us to evaluate the efficiency of the pendular exchange of energy and is estimated as follows:

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

To evaluate the energy exchange mechanism, we calculated two parameters:

1) The relative amplitude (RA) between the kinetic and potential energy:

$$RA = \frac{\max(PE) - \min(PE)}{\max(KE) - \min(KE)}$$

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

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

Where n is the number of values (i.e. 100 data points after stride-normalization, see above). It measures the proportion of the gait cycle during which both energies 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 the supplementary material for an evaluation of different methods, Figure A). The following successive steps were applied: Band-pass 4^{th} order Butterworth filter (5Hz to 500Hz), centred, rectified (full-wave), low-pass 4^{th} order Butterworth filter (10Hz), rectified (full-wave) [*Matlab script* is available in supplementary material]. We then applied a cubic spline interpolation over a time base with 200 points in order to stride-normalized 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. Due to these treatments, we can 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; 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 (nonparametric) 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 spatiotemporal parameters (duty factor, stride length, stride duration, speed) and the CoM mechanics (%C, RA, Recovery, W_{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 (χ^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 can also 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 nonparametric inference StatXact 3.1 (Cytel, Inc., Cambridge, MA). The significance threshold was set at $P < 0.05$.

RESULTS

Average kinematics

The data used here are for Id1, 15/12/2017 (diagonal/ground n=12; Table 1).

Time plots of the hind limb and forelimb joint and segment angles are shown on the figures 3 and 4, respectively. During baboon quadrupedal walking, the hip extends gradually during the stance phase up to ~90°. It flexes rapidly during the swing phase until it reaches ~50° 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°. The swing phase is characterized by a rapid flexion of the knee up to 90° during one third of the swing phase and then by a rapid extension until reaching 140° at touch-down. The ankle shows the same pattern as the knee but is slightly delayed. The trunk angle is maintained around 3° on average and remains stable during the quadrupedal stride, the movement amplitude is ~7°. The shoulder shows a reverse pattern compared to the hip, it flexes gradually during the stance phase of the forelimb until reaching ~40° and increases during the swing phase until 80°. The range of motion of the humerus is 39° while the amplitude of the thigh (femur) is 44°. The elbow flexes during the beginning of the swing phase from ~130° to ~90° and then extends during the second part of the swing phase up to 120°. 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° to 140°. The wrist shows an extreme extension around 220° in the last third of the stance phase that precedes an important roll off before lift-off. The wrist flexes until ~100° and then extends again in preparation of touch-down at ~180°. The high wrist extension corresponds to the typical digitigrade hand posture in baboon and the wrist dorsiflexes gradually during the two third of the stance phase until reaching an extreme extension when the ipsilateral hindlimb touches down.

Average BCoM mechanics

The data used here are for Id1, 15/12/2017 (diagonal/ground n=12) and 04/07/2013 (diagonal/ground n=3).

In our sample, the recovery rates of energy are at 57% on average when the walking speed is under 0.9 $m.s^{-1}$ and tend 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 *vs* R^2=0.26 for the linear model). A broader speed range would enable confirmation of the linear or the upside-down U-shaped relationship between the recovery rates and speed in baboons. The recovery rates are significantly negatively correlated with the congruity, i.e. the more the energies are fluctuating out-of-phase, the better the recovery is (Fig. 5B). The percentage of recovery is also significantly correlated with the limb phase. A limb phase value closer to 0.55 corresponds to a higher level of recovery. There is no relationship between the recovery rates and the relative amplitude of the kinetic and potential energy.

Interindividual differences

The data used here are for Id1, 07/2013 (n=3+9) and for Id2, 12/2013 (n=19; see Table 1).

Spatio-temporal parameters Table 2 shows the average values of the spatio-temporal parameters for walking quadrupedally at comfort speed on the ground using DSDC gait per individual. The two individuals studied adjust their spatio-temporal parameters the same way according to speed (see Figure B in the supplementary material). Both individuals modulate their walking pattern by altering both their frequency and stride length. Individual 1 tends to increase walking speed mainly by increasing stride frequency (Id1: slope=0.12 ; Id2: slope=0.04), whereas individual 2 increases speed mainly by increasing stride length (Id1: slope=3.6; Id2: slope=5.7). The duty factor is significantly greater in Id1 than in Id2, although the absolute difference is small (67% and 64%, respectively, *Permutation test*: 3.538, *P*=0.0001). Within the limited speed range observed, the duty factor is not significantly related to speed for any of the individuals studied. The dimensionless stride length is longer in Id2 compared to Id1 (4.76 and 4.22, respectively, *Permutation test*: -3.108, *P*=0.0004).

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

	n=12 (Id1)		**n=19 (Id2)**		***P value***
	Mean	**SD**	**Mean**	**SD**	**Id1 *vs* Id2**
Cycle duration (s)	0.89	0.05	0.95	0.03	*0.0029*
Stride frequency (1/s)	1.13	0.07	1.05	0.04	*0.0024*

Stride length (m)	0.68	0.04	0.81	0.05	*0.0001*
Speed ($m.s^{-1}$)	0.76	0.07	0.85	0.07	*0.0116*
Dimensionless values					
Duty factor (%)	67	1	64	1	*0.0001*
Cycle duration	6.98	0.39	7.25	0.25	*ns*
Stride frequency	0.14	0.008	0.14	0.005	*ns*
Stride length	4.22	0.26	4.76	0.30	*0.0004*
Speed	0.61	0.05	0.66	0.05	*ns*

ns: not significant

Muscular activity The bursting EMG patterns are 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 evertor muscle) were active at the beginning of the stance phase. The maximum burst activity is approximately 25% of the stance phase, i.e. when the right hind limb is still in a protracted posture and when the (contralateral) left hind limb starts to swing and the left forelimb touches the ground. The *rectus femoris* (hip flexor and knee extensor) shows a reverse pattern with a burst of activity when the limb starts to be retracted, and the knee is maintained around 120°. It is approximately at 75% of the stance phase and corresponds to the (contralateral) left hind limb touching the ground. There is also a certain level of recorded activation of the *rectus femoris* in Id1, at the beginning of the stance phase, when the *gluteus medius*, the *biceps femoris* and the *gastrocnemius* are very active. The distinct activation pattern of the *rectus femoris* is the only significant difference found between the two individuals (χ^2=12, df=3, *P*=0.0069). While the activity of the muscles located in the thigh show very short bursting patterns, the burst activity of the *gastrocnemius* and *peroneus* remain active during a longer period of the stance phase, i.e. until the touch-down of the left hind limb. The *tibialis anterior* (dorsiflexion of the foot and inversion) starts its activity at the very end of the stance phase, just after the (ipsilateral) right forelimb touch-down and shows a burst of activity just after the right hind limb lift-off when the ankle is rapidly flexed. Its activity then decreases during the second period of the swing phase. There is no activity of the *gluteus medius*, *rectus femoris*, *biceps femoris*, *peroneus* and *gastrocnemius* during the swing phase, but the *biceps femoris* and *gastrocnemius* appear to start their activity at the very end of the swing phase, in preparation of the touch-down.

Variations around the quadrupedal gait: effects of gait and substrate

The data used here are for Id1, 15/12/2017 (diagonal/ground n=12, lateral/ground n=2, diagonal/branch n=6), and to increase the sample for the lateral walking gait, also for Id1, 04/07/2013 (lateral/ground n=2; see Table 1).

Spatio-temporal parameters and BCoM mechanics Table 3 shows the average values of the spatiotemporal 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 (1.26Hz and 1.44Hz, respectively, Permutation test: 2.193, *P*=0.0209) as well as in the % of congruity of the BCoM (38.7% and 53.6%, respectively, Permutation test: -2.272, *P*=0.0159). There is a significant difference in stride length and speed when walking on the ground compared to the branch (stride length: 0.73m and 0.66m, respectively, Permutation test: 2.277, *P*=0.0197; speed: 0.92m.s^{-1} and 0.79m.s^{-1}, respectively, Permutation test: 2.089, *P*=0.0335).

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

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

Significant values are indicated in bold

[1]values close to the significance threshold (i.e. 0.05 < *P* < 0.1) are also indicated

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

On the branch, the baboon increases the ankle extension and the range of motion of the ankle as well as the shank extension compared to the ground (ankle: 82.3° and 76.4°, respectively,

Permutation test: -3.165, *P*=0.0004; ankle ROM: 44.9° and 38.3°, respectively, *Permutation test*: -2.08, *P*=0.0339; shank: 56.6° and 53.7°, respectively, *Permutation test*: -2.79, *P*=0.0023). The range of motion of the trunk angle is reduced on the branch compared to the ground (4° and 6.3°, respectively, *Permutation test*: 2.862, *P*=0.0015). In the forelimb, the shoulder angle is kept more extended on the branch compared to the ground and the wrist is more dorsiflexed (shoulder: 58.4° and 55.3°, respectively, *Permutation test*: -2.09, *P*=0.0326; wrist: 187° and 180.8°, respectively, *Permutation test*: -2.53, *P*=0.0081). Figure C (in the supplementary material) shows the average pattern for each joint and segment angle studied in each gait and substrate context.

Muscular activity The bursting EMG profiles are very consistent across gaits and substrates (Fig. 7). There is no difference between the lateral and the diagonal sequences performed on the ground as far as the bursting EMG profiles are concerned. But the maximal burst of activity of the *biceps femoris, gastrocnemius* and *tibialis anterior* significantly increase 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 observe a significant difference of the activation pattern at the level of the *peroneus* (χ^2=10.62, df=3, *P*=0.0137). While the activity of the *peroneus* is concentrated at the beginning of the stance phase when the baboon is walking steadily on the ground, its activity is kept during all the stance phase when walking on the branch. Furthermore, the maximal activity of the *peroneus* is 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* is significantly lower on the branch (*Permutation test*: 2.106, *P*=0.0231).

DISCUSSION

The present study aims 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 efficient. On the other hand, 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 are consistent within and between individuals (Figure 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 hind limb muscles in baboons is very similar to the one observed in other primates such as chimpanzees, spider monkeys, macaques, and lemurs (Ishida et al. 1974; Kimura et al. 1979; Larson & 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 & 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 are mainly fluctuating out-of-phase (congruity = 39%) during normal quadrupedal walking using DSDC gaits. The recovery rates observed in baboon in this study (22-84%) cover an important range of variation compared to 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 the ring-tailed lemurs and the capuchin monkeys (35-71% and 11-65%, respectively during quadrupedal walking; O'Neill & Schmitt 2012; Demes & O'Neill 2013). Griffin et al. (2004) developed a model showing that the pendulum-like centre of mass movements in quadrupedal animals is a combination of both inverted pendulums around the pectoral and pelvic girdle. These pendulums are directly influenced by the footfall pattern and body mass distribution. For example, a body centre of mass 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 to 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% in average (min: 54%, max: 69%) and there is a significant relationship between the recovery rates and the limb phase (i.e. the lags between fore- and hindlimbs; see Figure 5C). These results support the model of Griffin et al. (2004), but it does 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 the 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 the ones provided by O'Neill & Schmitt (2012) and Demes & 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 the ring-tailed lemurs and the capuchin monkeys that both exhibit good recovery rates during quadrupedal walking (O'Neill & Schmitt 2012; Demes & 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. Our second hypothesis stipulated that when walking on a branch, kinematical adjustments should reduce the vertical oscillations of the centre of mass (Gàlvez-Lòpez et al. 2011; Schmitt 1999) and in this way give priority to stability upon 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 (Gàlvez-Lòpez et al. 2011). However, these strategies can be of a different kind. For instance, while cats (medium-sized, ≈4.4kg) make use of slower speeds and shorter swing phase durations on a narrow runway, dogs (large-sized, ≈28kg), on the other hand, rely on high-speed locomotion and high frequency to gain dynamic stability (Gàlvez-Lòpez et al. 2011). The adjustments observed in the olive baboon (13.5kg in the present study) when walking on a (suspended, non-bending) branch show 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 that is kept more extended on the branch. More in-phase fluctuations of the KE and PE (congruity = 46%) are also observed compared to the walk on the ground. These adjustments (certainly closer to the cat

strategy) reduce the vertical oscillations of the BCoM, and with the increase activity of the *peroneus* (increasing torque generation), meet the balance control requirements. This general strategy may reduce the possibility to rely on an efficient inverted pendulum-like exchange of energy, but we did not observe a direct significant difference in the recovery rates. 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 the efficiency. Interestingly, a previous study showed that in *Lemur catta,* walking on a raised horizontal pole does not significantly affect the energetic recovery (Schmitt 2011). Furthermore, limb interference is important during diagonal walking on the ground. The baboons move their right hind limb 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 observed that when they walk on a horizontal arboreal substrate, they reduce their stance phase, take longer strides and reduce the stride frequency (Schoonaert et al. 2016). This strategy appears to be very different from the one used by the baboon in the present study (note that both, the size of the specimens and the substrate diameter are different: 12cm for the bonobos, and 16cm in the present study), as well as from the ones used by lemurs and marmosets that 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 30cm above the ground, hence falling was not really a risk encountered by the animals (Schoonaert et al. 2016). This emphasizes the importance of considering morphological differences, 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, the ability to meet these demands (controlling pitching, yawing and rolling moments) can be performed 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. Gàlvez-Lòpez 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 the 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 increases 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 is walking on the branch is similar to the one of the 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 transmitting rotating moment (Lammers & Gauntner 2008; Preuschoft 2004).

The *biceps femoris* is described as a hip extensor and a knee flexor (Swindler & 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°) (Larney & Larson 2004), the *biceps femoris* is, therefore, acting as a thigh (hind limb) retractor by flexing the knee (≈110° at midstance) and extending the hip (from 50° to 75° 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 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 extension of the ankle that can be related to the increase 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 seems to be seen in capuchin monkey; see Figure 2 in Wallace and Demes 2008). On the branch, the stride length decreases as well as the 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 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, significant increase in muscular activity should result in 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%<LP>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 timings 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 & Daley 2007; Chadwell & Young 2015; Lammers & 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 accommodations 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 hind limbs 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 the BCoM mechanics and muscular activity). On the other hand, the diagonal walking gait does not impede good recovery rates in primates.

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FIGURE LEGENDS

Figure 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 on the picture under the schematic diagram: 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).

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

Figure 3. Average hind limb joint and segment angles (± 95% Confidence Interval) for Id1, during quadrupedal walking (DSDC) at comfort speed (~0.92m.s^{-1}), including the average footfall pattern. The joint and segment angles are measured on the right side. The average footfall pattern at the bottom (gait diagram) shows average stance phases (solid bars) of the right hind limb (RH), left hind limb (LH), right forelimb (RF) and left forelimb (LF). The right hind limb is the limb of reference. It is darker on the gait diagram and the stance phase is indicated on the graphs with a light background.

Figure 4. Average forelimb joint and segment angles (± 95% Confidence Interval) for Id1, during quadrupedal walking (DSDC) at comfort speed (~0.92m.s^{-1}), including the average footfall pattern. The joint and segment angles are measured on the right side. The average footfall pattern at the bottom (gait diagram) shows average stance phases (solid bars) of the right hind limb (RH), left hind limb (LH), right forelimb (RF) and left forelimb (LF). The right forelimb is the limb of refence. It is darker on the gait diagram and the stance phase is indicated on the graphs with a light background.

Figure 5. Influence of various walking variables on the recovery rates during quadrupedal locomotion. A significant relationship is found between speed and the recovery rates (A), the congruity of the fluctuations of kinetic and potential energy and the recovery rates (B) and the diagonality and the recovery rates (C), but not between the relative amplitude of the fluctuation of kinetic and potential energy and the recovery rates (D).

Figure 6. (a) Average EMG profiles of the 6 hind limb muscles considered during steady quadrupedal walking. The activity patterns are stride-normalized and averaged across 12 strides for Id1 (grey) and 19 strides for Id2 (blue). The average footfall pattern at the bottom (gait diagram) shows average stance phases (solid bars) of the right hind limb (RH), left hind limb (LH), right forelimb (RF) and left forelimb (LF). The EMG activity was recorded on the right hind limb (darker on the gait diagram). (b) Overview of the muscular activity of the 6 hind limb 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 in 4 levels of activation. Six events are represented: Right Hind limb Touch-Down (RH TD), Left Hind limb Lift-Off (LH LO) + Left Forelimb Touch-Down (LF TD), Right Forelimb Lift-Off (RF LO), Left Hind limb Touch-Down (LH TD), Right Forelimb Touch-Down (RF TD) and Right Hind limb Lift-Off (RH LO).

Figure 7. Average EMG profiles of the 6 hind limb muscles considered during steady quadrupedal walking for Id1 (recorded in 2017, see Table 1). The activity patterns are stride-normalized and averaged across 12 strides when walking on the ground (green), 4 strides when walking using lateral sequences (dark blue) and 6 strides when walking on the branch (light blue). The average footfall pattern at the bottom (gait diagram) shows average stance phases (solid bars) of the right hind limb (RH), left hind limb (LH), right forelimb (RF) and left forelimb (LF). The EMG activity was recorded on the right hind limb.

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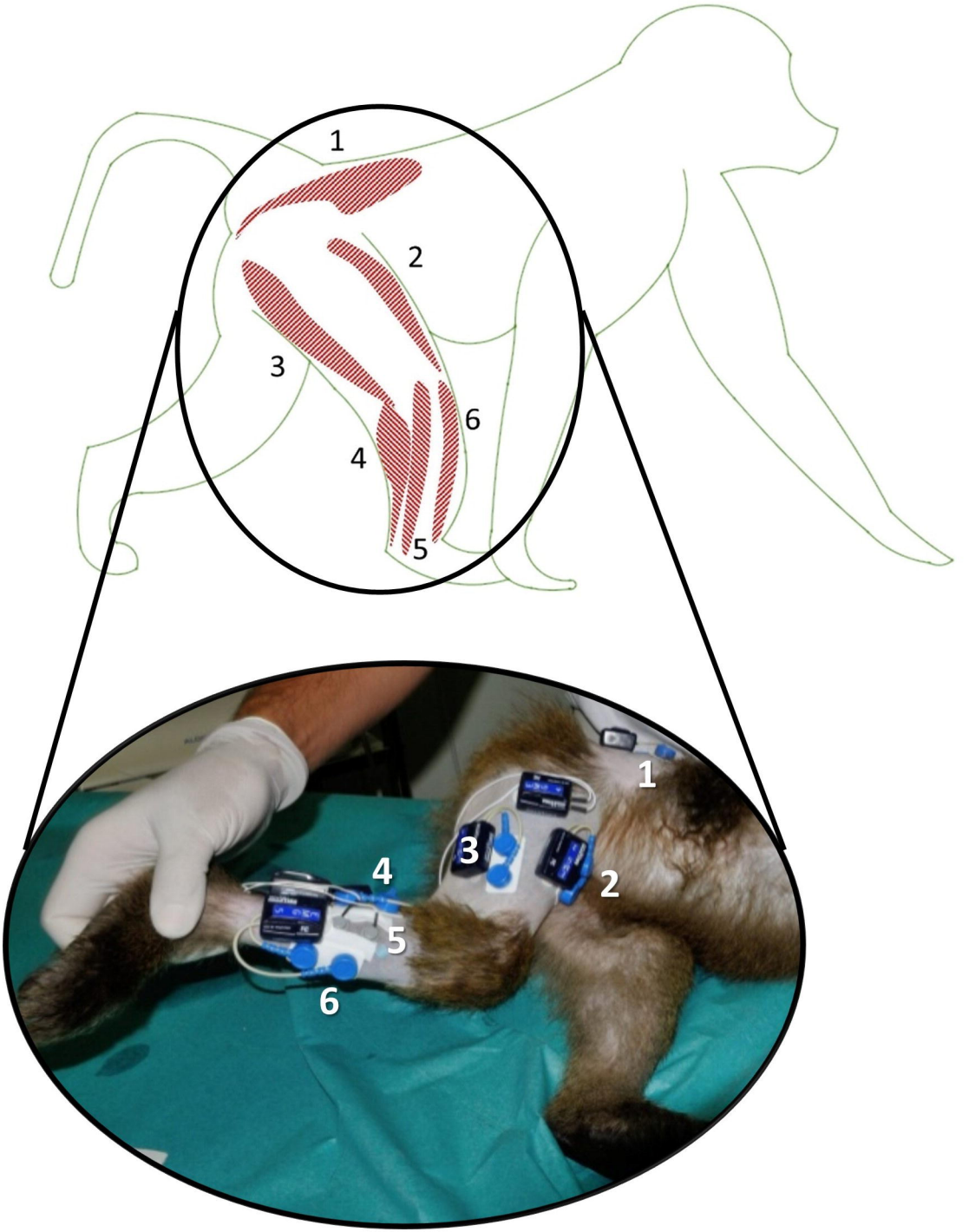
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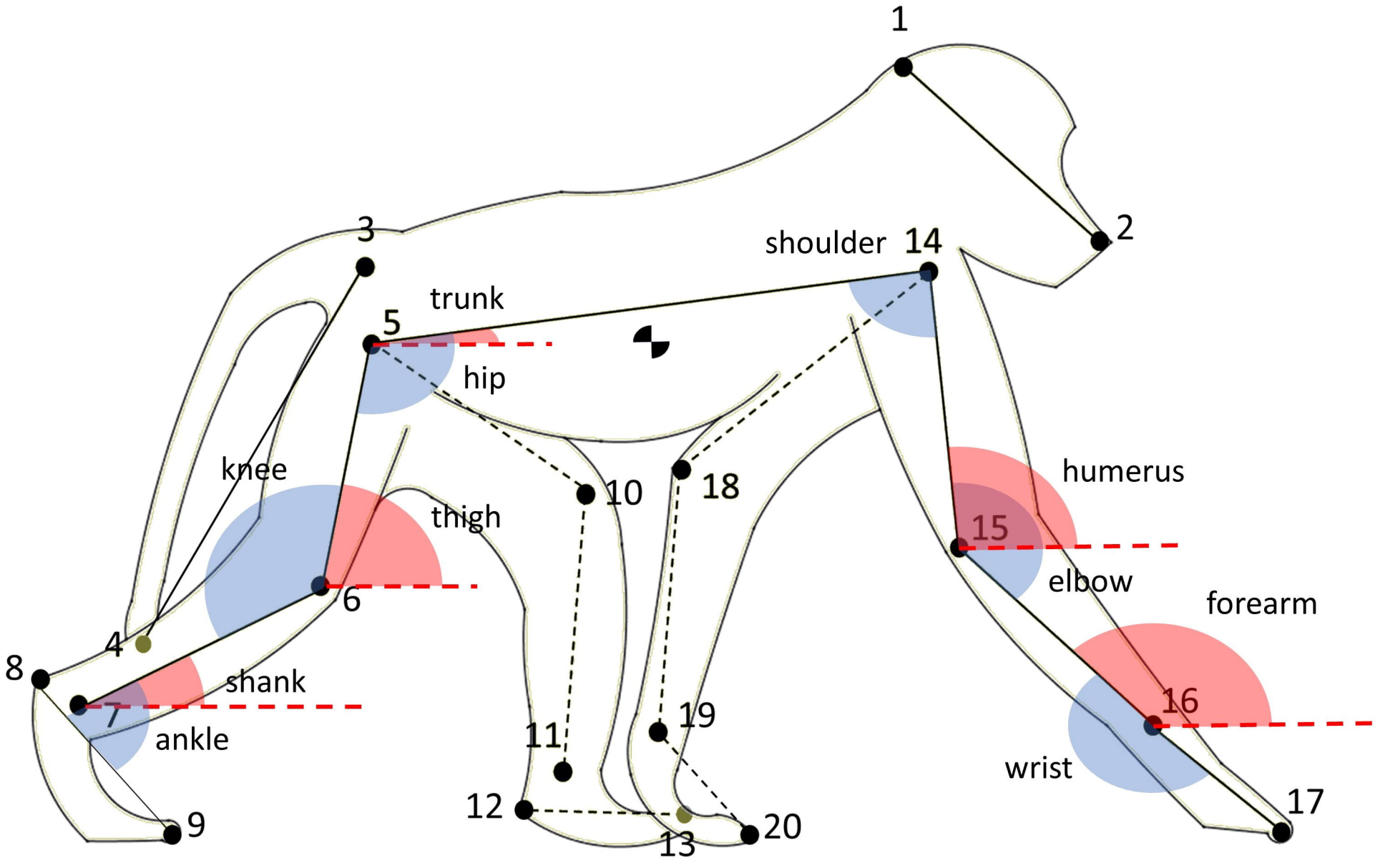
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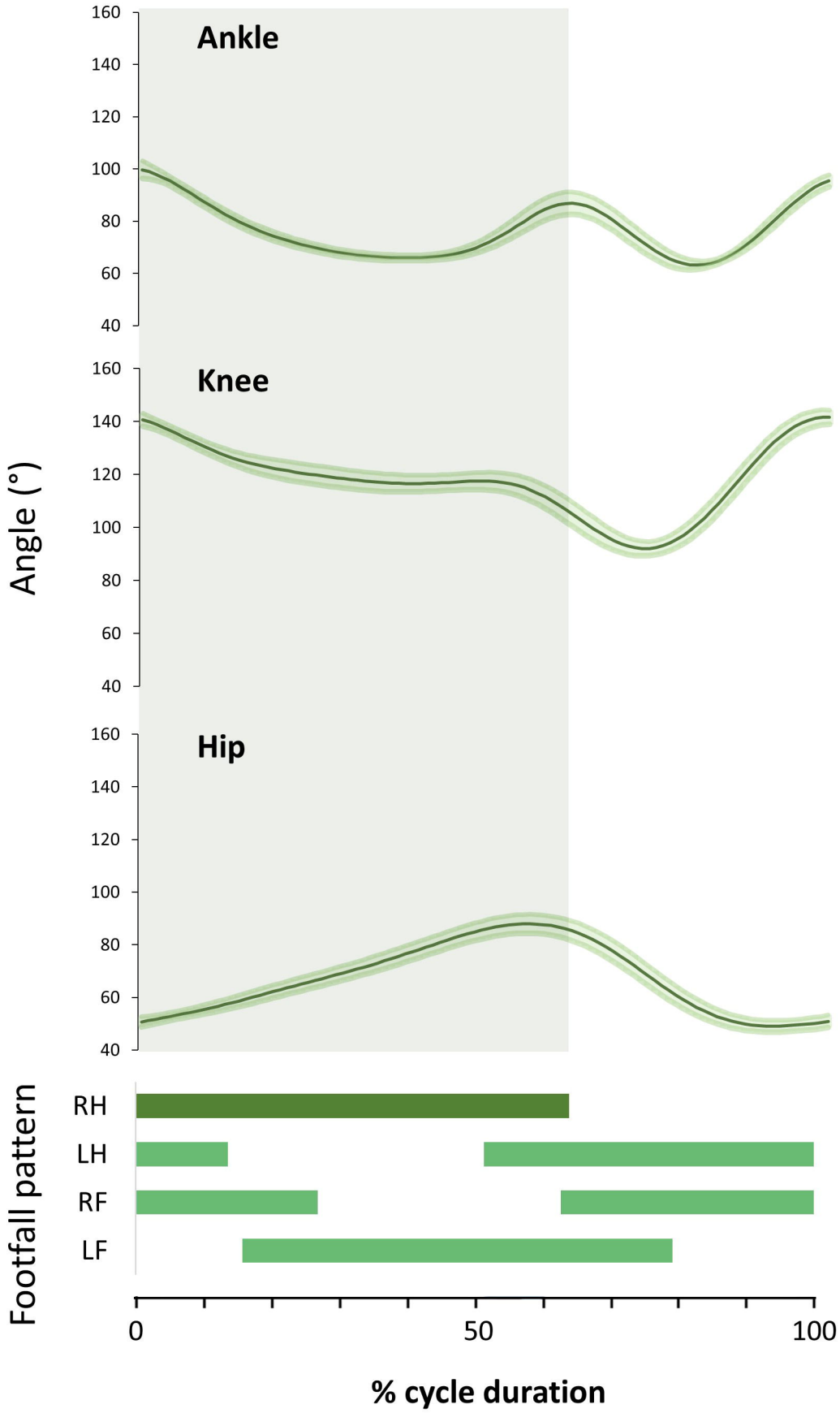
Ankle
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Angle (°)
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Footfall pattern
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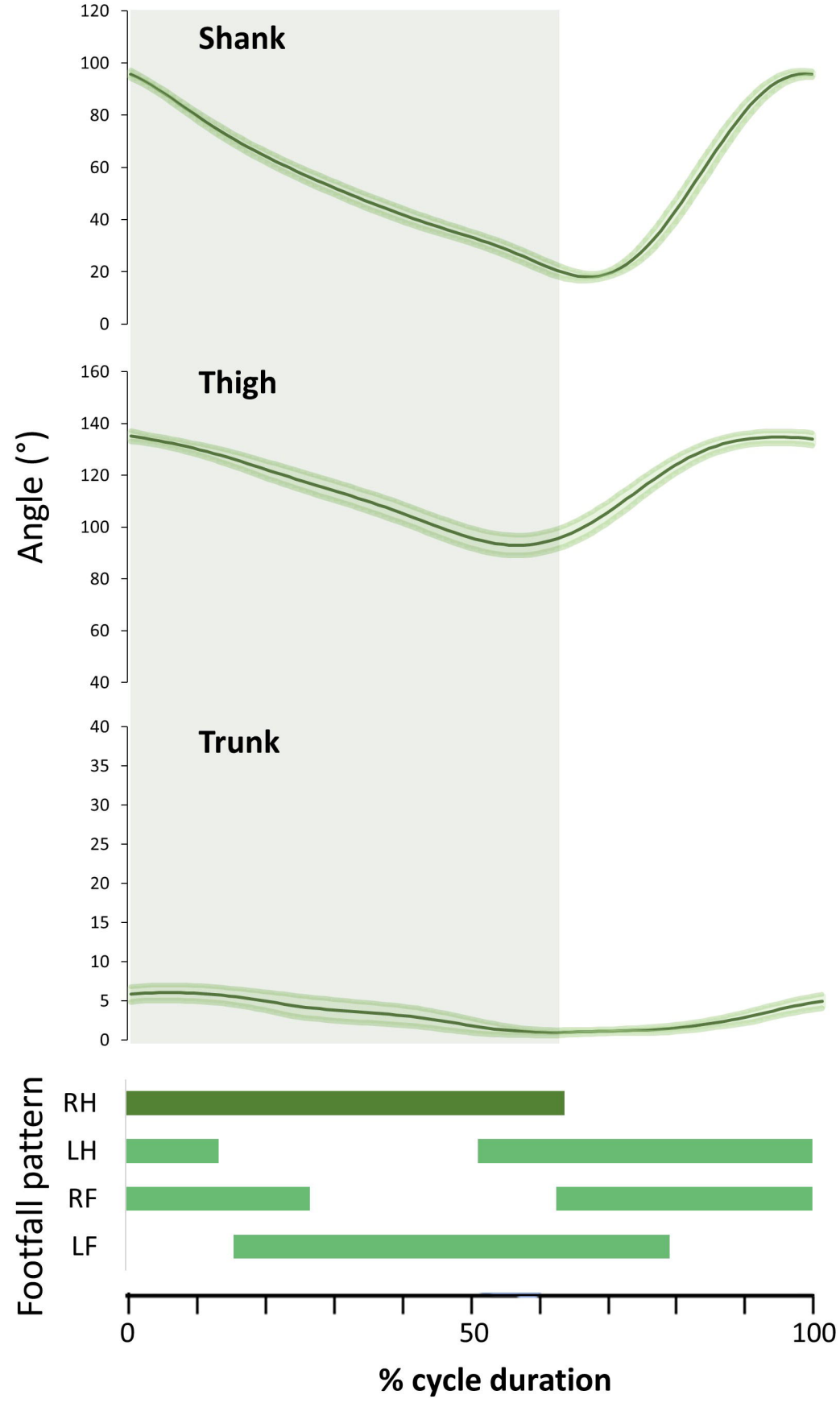
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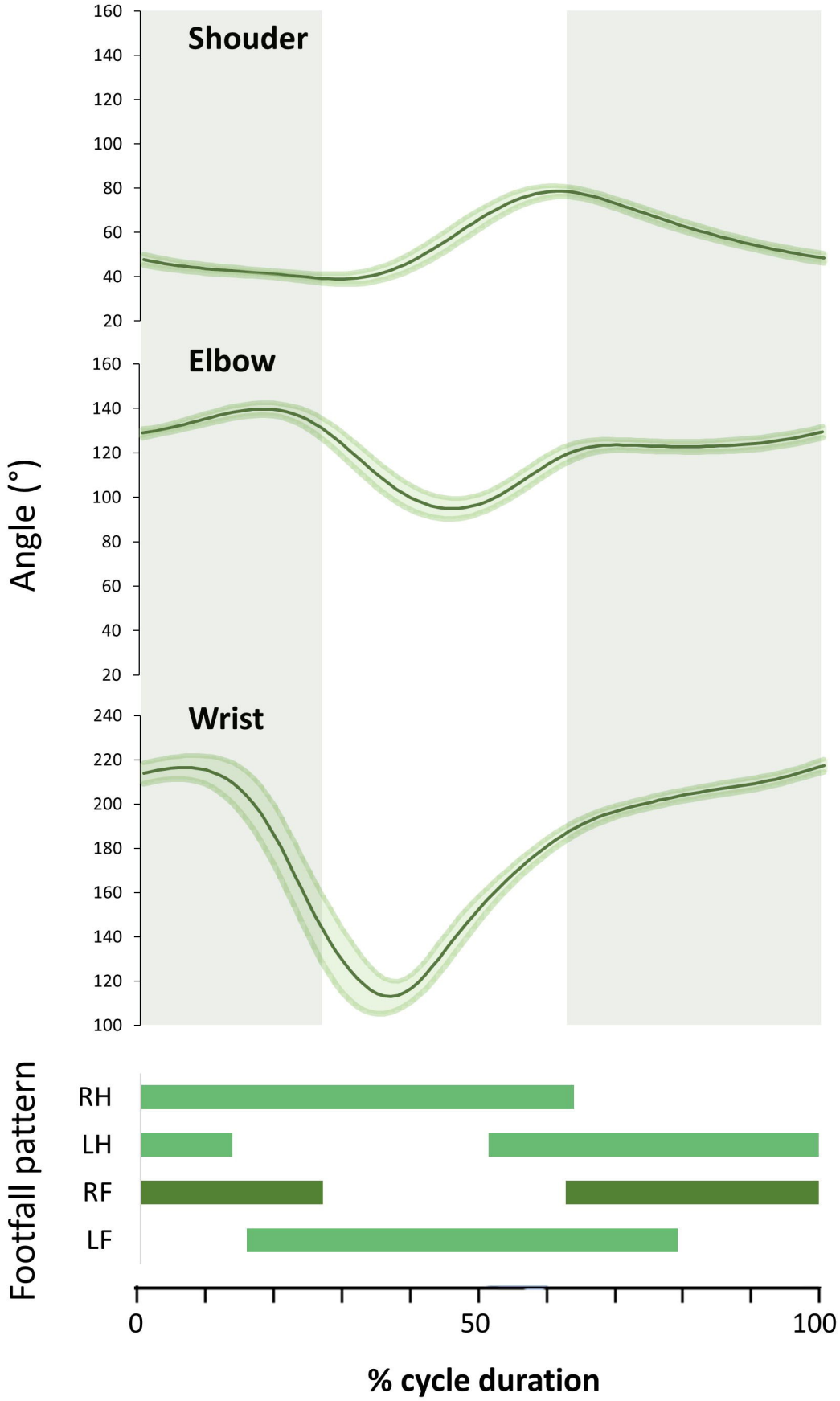
Shouder
Elbow
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Angle (°)
Footfall pattern
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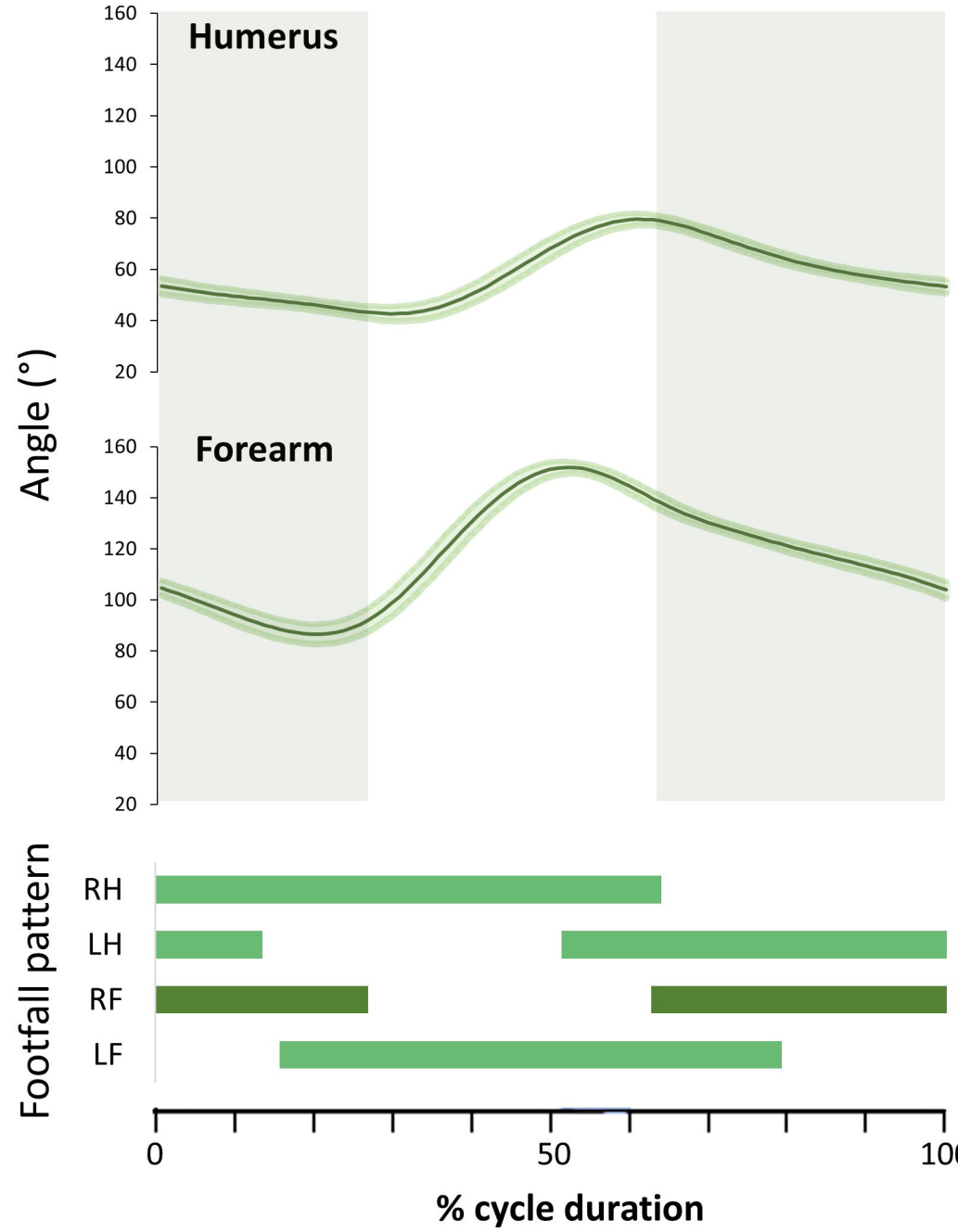
Humerus
Forearm
Angle (°)
Footfall pattern
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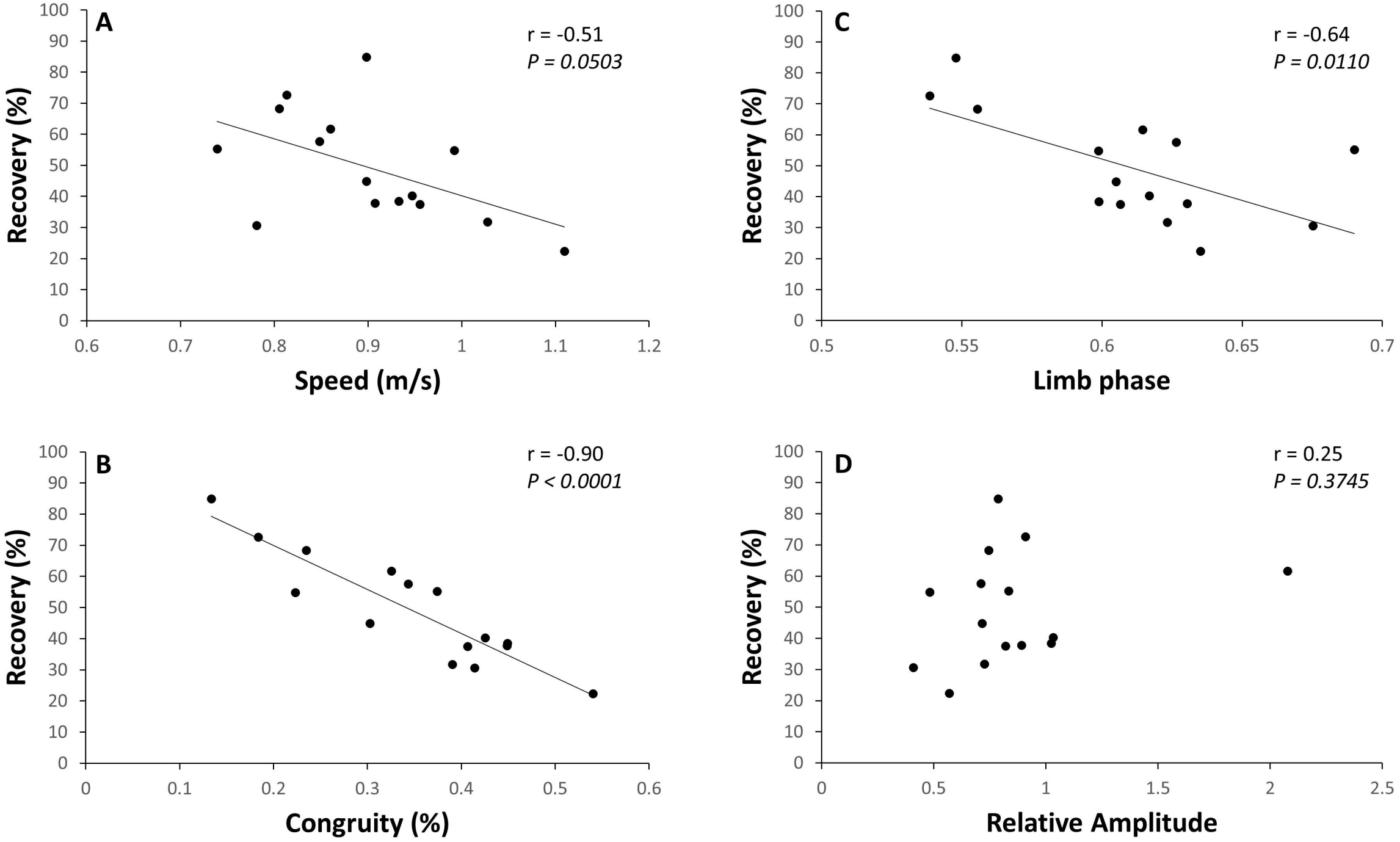
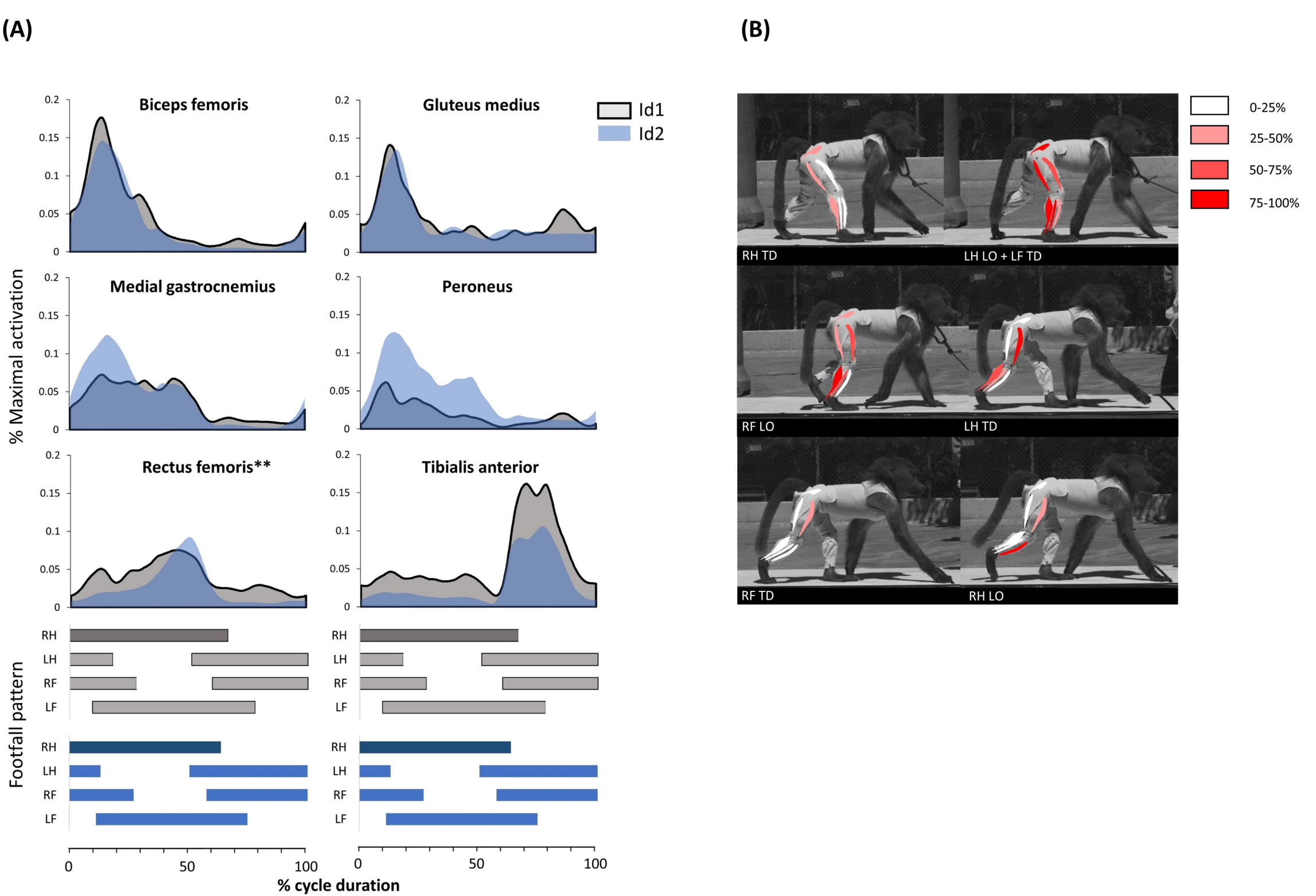

A
r = -0.51
P = 0.0503
Recovery (%)
Speed (m/s)
B
r = -0.90
P < 0.0001
Recovery (%)
Congruity (%)
C
r = -0.64
P = 0.0110
Recovery (%)
Limb phase
D
r = 0.25
P = 0.3745
Recovery (%)
Relative Amplitude


(A)
(B)
Biceps femoris
Gluteus medius
Medial gastrocnemius
Peroneus
Rectus femoris**
Tibialis anterior
Id1
Id2
% Maximal activation
0.2
0.15
0.1
0.05
0
Footfall pattern
RH
LH
RF
LF
0
50
100
% cycle duration
RH TD
LH LO + LF TD
RF LO
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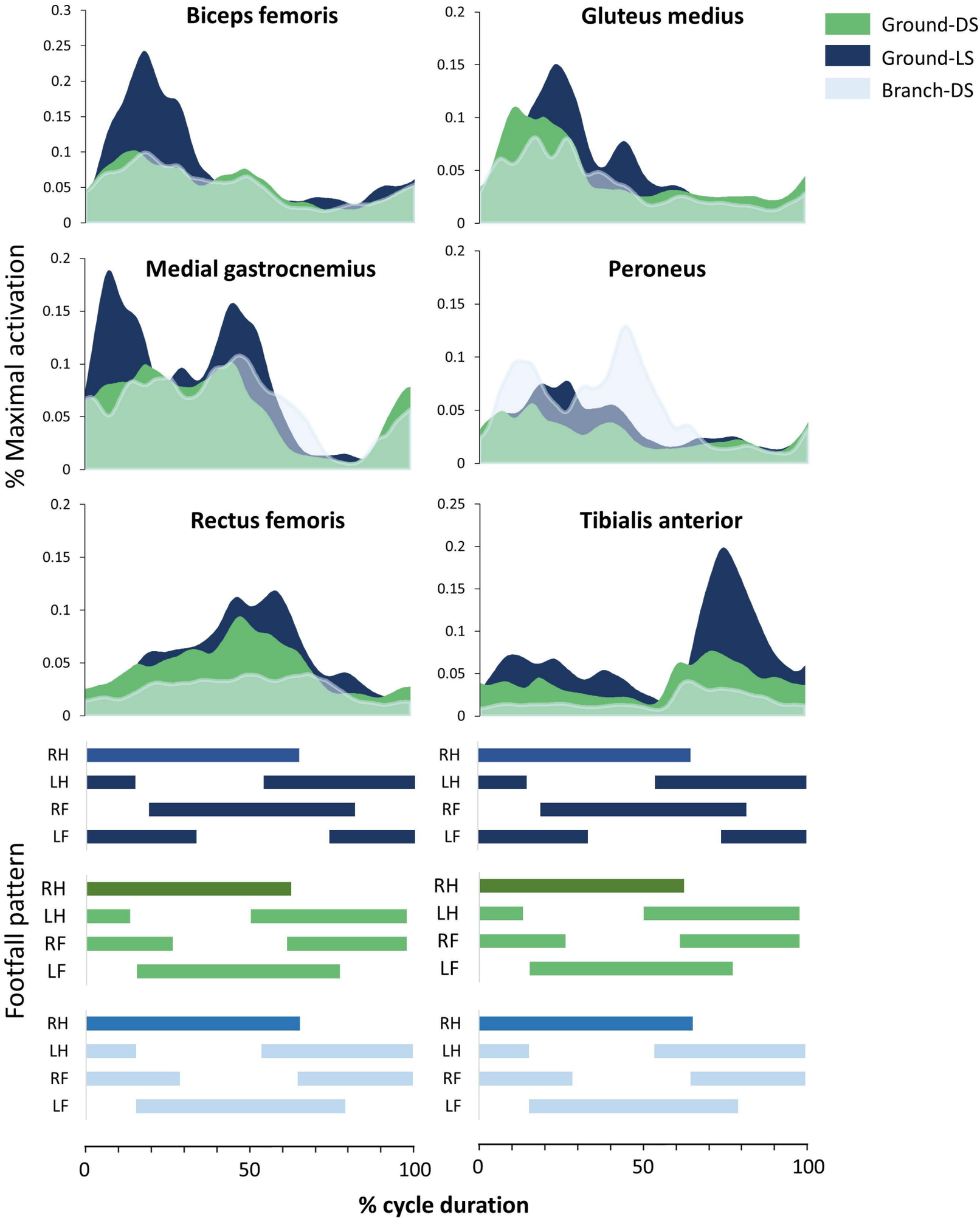
RF TD
RH LO
0-25%
25-50%
50-75%
75-100%


Biceps femoris
Gluteus medius
Medial gastrocnemius
Peroneus
Rectus femoris
Tibialis anterior
Ground-DS
Ground-LS
Branch-DS
% Maximal activation
Footfall pattern
RH
LH
RF
LF
0
50
100
% cycle duration