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1 The quadrupedal walking gait of olive baboon, *Papio anubis*: an exploratory

2 study integrating kinematics and EMG

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12 ABSTRACT Primates exhibit unusual quadrupedal features (e.g. diagonal gaits, compliant walk) 13 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 14 15 necessary for balance control in unstable and discontinuous environments. In turn, the requirements 16 for mechanical stability probably conflict with the mechanical energy exchange. In order to 17 investigate these aspects, we have conducted an integrative study on quadrupedal walking in olive 18 baboon (Papio anubis) at the Primatology station of the CNRS in France. Based on kinematics, we 19 describe the centre of mass mechanics of the normal quadrupedal gait performed on the ground, as 20 well as in different gait and substrate contexts. In addition, we have studied the muscular activity of 21 six hind limb muscles using non-invasive surface probes. Our results show that baboons can rely on 22 an inverted pendulum-like exchange of energy (57% in average and the maximal observed value is 23 84%) when walking slowly (<0.9m.s⁻¹) with a tight limb phase (\approx 55%) on the ground using diagonal 24 sequence gaits. In this context the muscular activity is similar to that of other quadrupedal mammals 25 thus reflecting the primary functions of the muscles for limb movements and support. On the other 26 hand, walking on a suspended branch generates kinematic and muscular adjustments to ensure a 27 better control and to maintain stability. Finally, walking using the lateral sequence gait increases 28 muscular effort and reduces the potential for high recovery rates. The present exploratory study thus 29 supports the assumption that primates are able to make use of an inverted-pendulum mechanism on 30 the ground using the diagonal walking gait, yet a different footfall pattern and substrate appear to 31 influence muscular effort and efficiency.

32 Key words Centre of mass, Electromyography, kinematics, Locomotion, Positive reinforcement

33 INTRODUCTION

34 The origin and evolution of primates is closely related to arboreal habitats (e.g. Cartmill 1974; 35 Hamrick 2001; Toussaint et al. 2020) and many extant primates continue to live in arboreal 36 environments, or at least invest a certain amount of time foraging in the trees on thin and flexible 37 branches (Hunt 2016). Such an environment obviously implies discontinuity, variability, instability and 38 oscillations of the substrates that perturb the inherent mechanical requirements of legged 39 locomotion, i.e. propulsion, balance and stability of the walking gait. It has been shown that primates 40 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 41 42 environment (e.g. Cartmill et al. 2020; Demes et al. 1994; Druelle et al. 2020; Hunt et al. 1996; Larney 43 & Larson 2004; Larson et al. 2001; Schmitt 1999; Schmitt et al. 2006; Thorpe et al. 2007). During 44 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 45 46 shifted toward the hind limbs (see Larson 2018 for a review). These features can be integrated under 47 the compliant gait model of primate walking (Schmitt 1999). Overall, these characteristics should 48 particularly allow for control pitching, yawing and rolling moments, and limit the vertical oscillations 49 of the centre of mass, hence branch oscillation, and increase maintenance of balance (e.g. Cartmill et 50 al. 2020; Cartmill et al. 2002; Schmitt et al. 2006).

51 Parallel to these functional adjustments, the muscular activity pattern also presents specificities. EMG 52 studies on non-human primates have provided a significant knowledge about muscle basic activity 53 pattern in different locomotor modes such as climbing, brachiating and bipedal walking (e.g. Hirasaki 54 et al. 1995; Ishida et al. 1974; Jungers & Stern 1981; Stern Jr & Larson 2001; Stern & Susman 1981), 55 but the way muscle recruitment has been altered in non-human primates in relation to the arboreal 56 niche remains poorly understood (Boyer et al. 2007; Courtine et al. 2005; Larson & Stern 2009; Patel 57 et al. 2015). During primate quadrupedal walking, distal limb muscles are suggested to be under 58 higher cortical control including different speed-related modulations of the limbs compared to other 59 quadrupedal mammals (Courtine et al. 2005). The different inertial properties of non-human 60 primates compared to other quadrupeds (Grand 1977; Druelle et al. 2019) should also affect the way 61 the work is performed, and the forces transmitted. Overall, more flexible capabilities of the 62 neuromotor control are suggested in primates (Courtine et al. 2005; Jungers & Anapol 1985; Shapiro 63 et al. 1997) with the hand and the foot having distinct functional roles (Druelle et al. 2018; Hashimoto 64 et al. 2011; Lawler 2006; Patel et al. 2015). Furthermore, although the phasic recruitment of muscles 65 is generally similar to other quadrupedal mammals (Courtine et al. 2005; Higurashi et al. 2019; 66 Shapiro & Jungers 1994), specificities have been emphasized for the humeral retractors (Larson &

57 Stern 1987; Larson & Stern 1989; Larson & Stern 2007), and hip extensors might also be used for 58 different functions (Larson & Stern 2009; Reynolds 1985). As a result, primate quadrupedal control 59 and mechanics are considered particular compared to that of other (terrestrial) quadrupedal 50 mammals. However, basic biomechanical and physiological data regarding the typical quadrupedal 51 walking pattern of non-human primates is, unfortunately, non-existent. Integrative studies examining 52 the kinematics, the dynamics of the centre of mass and the muscular activity (EMG) all together are 53 very rare (see Courtine et al. 2005).

74 To explore the quadrupedal walking gait of non-human primates and the suggested neuromotor 75 flexibility, we conducted an integrative analysis exploring the limb kinematics, the centre of mass 76 mechanics (using kinematics) and the muscle activity of six extrinsic hind limb muscles in olive 77 baboons, Papio anubis. Baboons can be considered as (semi-)terrestrial primates as they have 78 developed a set of cursorial adaptations that mean they are more suited for terrestrial locomotion 79 and for long-distance walking. For instance, they have been shown to move between 3.6 to 9.5 km 80 per day, making them the non-human primates with the longest daily travel distance (Garland 1983); 81 their limbs are relatively extended with a digitigrade hand posture when walking, they display 82 convergent natural pendular periods of their fore- and hindlimbs and their proximal limb mass 83 distribution suggests good propulsive action capacities (Druelle et al. 2017a; Patel 2009; Patel et al. 84 2012; Raichlen 2004; Zeininger et al. 2017).

85 In this study, animals were trained to voluntary cooperate using positive reinforcement techniques. 86 Our refined experiment used surface probes (sEMG) that did not need surgical procedures. We first 87 recorded the muscular activity of two female baboons walking quadrupedally using their typical DSDC 88 gait over a flat regular ground at their voluntary walking speed. This allowed us to describe their 89 typical guadrupedal walking gait in terms of spatio-temporal parameters and muscular activity. We 90 then recorded the gait of one female baboon when walking DSDC on a suspended horizontal and 91 cylindrical substrate (branch) and while spontaneously using lateral sequence/lateral couplet (LSLC) 92 gaits for few strides on the ground. We thus provide a preliminary picture of the normal quadrupedal 93 walking pattern in baboon and its flexibility (through kinematic modulation) in the context of 94 different gait and substrate. First, and because the baboon is defined as an adapted quadrupedal 95 walker, we expect it to be able to make use of an inverted-pendulum mechanism when walking 96 steadily on the ground using its preferred walking gait (DSDC; as previously observed in ring-tailed 97 lemurs and capuchin monkeys: O'Neill & Schmitt 2012; Demes & O'Neill 2013). Second, we will 98 specifically evaluate whether the usual muscle activation pattern observed in DSDC walking is altered 99 in other gait and substrate contexts. When the baboon uses the unusual LSLC gait on the ground, 100 changes are expected in proximal muscles (i.e., in the main limb motors), while walking on a different

101 substrate, such as a branch (imposing higher balance requirements and certainly higher control),

102 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
- 104 together should provide an integrative picture of the quadrupedal walking pattern in baboon and
- 105 how these are connected (see Courtine et al. 2005). In this context, a reduced efficiency in the
- 106 mechanics of the centre of mass (for example, walking on a branch requires kinematical adjustments
- 107 that tend to reduce the vertical oscillations of the centre of mass; see Galvez-Lopez et al. 2011;
- 108 Schmitt 1999) should match an alteration of the muscular activity toward an increased activation.

109 MATERIALS AND METHODS

110 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).

118 Prior to the experiments, primates were trained over a period of 18 months and focused on the 119 habituation and desensitization of individuals to the whole experimental setup. All the training was 120 based on positive reinforcement techniques and systematic desensitization (Prescott & Buchanan-121 Smith 2016; Schapiro et al. 2003) and was conducted by the same two trainers, PMV and BR. The first 122 training period was carried out in a large indoor cage where the two individuals were pair-housed for 123 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. 124 125 After 6 months of training (46 sessions of training of approximately 30-45 minutes), individuals 126 cooperated to get out of their enclosure on a leash and to walk quadrupedally beside the trainer on 127 the experimental setup. Individuals were then moved to a bigger indoor/outdoor enclosure where 128 they could move freely. This training allowed us to lead the baboons to the technical platform for 129 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

137 Druelle et al. 2017). The maturation of their neuromotor control also appears to be largely complete

138 (see Druelle et al. 2017; Rose 1977), as has also been observed in other cercopithecoid species at this

139 age (e.g., Vilensky and Gankiewicz 1990; Zeininger et al. 2017; Dunbar and Badam 2000).

140 Data collection

141 Surface electromyography (sEMG)

142 Muscle activity was recorded at 2000Hz using a wireless Zerowire system (Aurion Srl, Milan, Italy) 143 with the MyoResearch XP Master Edition software (Noraxon®). We focused on 6 muscles commonly 144 studied as actuator of the three main joints of the hindlimb (hip, knee and ankle), and easily 145 identifiable at the surface of the skin: gluteus medius, biceps femoris, rectus femoris, tibialis anterior, 146 *gastrocnemius (medialis or lateralis)* and *peroneus longus*, of the right side (Figure 1). To ensure the 147 accurate electrode placement, the muscular topography was previously assessed on olive baboon 148 cadavers of a similar size and age that were available at the primatology station. Baboons were 149 instrumented during a short period of anaesthesia (≈60 minutes); the anaesthesia was initiated with 150 an intra-muscular injection of Ketamine (4mg/kg) and medetomidine $(40\mu g/kg)$ and maintained with 151 gas isoflurane (1%). This anaesthesia was short and light enough to shorten the recovery period using 152 an atipamezole as antagonist. After locally shaving, cleaning and degreasing the skin, electrodes were 153 taped at the level of the muscles' belly (approximately at mid length of each muscle and electrode 154 pairs and always parallel to fibre direction). We used fabric legwear and trunkwear (close-fitting 155 clothes, see Fig. 6B) to ensure a good adhesion of the equipment and to protect the electrodes. In 156 the context of the present study, we have worked on the technical platform for biomechanics 157 (Motion analysis of Primates, MAP) that is permanently installed in an outdoor enclosure of the 158 primatology centre (see Berillon et al. 2011 for details). The experiments started after the baboons 159 were totally recovered from the anaesthesia (i.e. they were fully active and able to climb and run), 160 between 60 to 90 minutes after their arrival in the enclosure.

161 Kinematics

162 The animals walked on a straight and horizontal calibrated walkway and on a horizontal branch (\emptyset 163 0.16 m, positioned at approximately 1m above the ground), where they could easily be video-164 captured using an integrated multicamera system (Norpix Inc.) with 3 synchronized HD-video cameras 165 running at 200 frames per second (fps; Baumer HXC1) (see Berillon et al. 2010 for a general 166 description of the experimental setup); synchronized recording was proceeded with Streampix 4 (by 167 Norpix Inc.). Two cameras were laterally placed perpendicular to the walkway, to accurately record in 168 a large field of view the main sagittal spatiotemporal and joints kinematics. One additional camera 169 was positioned obliquely to increase the accuracy for visually identifying the locomotor events, i.e. 170 touch-down and lift-off of the limbs. EMG and video recordings were synchronized using an external 171 digital signal; in addition, a fourth lateral video camera (running at 60fps) was driven by the 172 MyoResearch XP software and thus software-synchronized with the EMG recording.

173 We first qualitatively selected appropriate quadrupedal sequences during which the individual was 174 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 175 176 between consecutive quadrupedal strides, we calculated an acceleration/deceleration index as 177 follows: (average speed stride_{n+1} – average speed stride_n)/average speed stride_n. For the present 178 analysis, we removed the quadrupedal strides for which speed variations were above 10% between 179 consecutive strides (note that given the small amount of lateral sequences recorded (n=6), we kept 180 one stride for which the speed variation was 26% in order to keep a sample of 4 strides and, 181 therefore, use non-parametric statistics, see further). Table 1 shows the dataset included in the 182 present analysis after applying this strong selective criterion.

Individual	n/n ¹ EMG		Spatio-temporal	Kinematics	Gait type / substrate	
ID1						
04/07/2013	3/4	Х	Х	Х	Diagonal / on ground	
	2/3	Х	Х	Х	Lateral ² / on ground	
31/07/2013	9/14	Х	Х		Diagonal / on ground	
15/12/2017	12/16	Х	Х	Х	Diagonal / on ground	
	2/3	Х	Х	Х	Latera / on ground	
	6/8	Х	Х	Х	Diagonal / on branch	
D2						
03/12/2013	19/39	Х	Х		Diagonal / on ground	
¹ the left side of the c	blique sign i	ndicates t	he number of strides k	ept in the present anal	ysis and the right side	

TABLE 1. Studied individuals and data collected

¹the 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) ²given 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

183 Analysis

184 Basic kinematics

185 We calculated the following spatiotemporal parameters: the cycle duration (time period between two

186 right hind limb touchdown events), the frequency (inverse of cycle duration), the duty factor

6

187 (proportion of stance phase of the right hind limb relative to cycle duration), stride length (horizontal 188 displacement of the tip of the right foot during one stride), speed (estimated from the horizontal 189 displacement of the centre of mass; see below) and limb phase (time period between the right hind 190 limb touchdown and the right forelimb touchdown relative to the cycle duration; <50% is a lateral 191 sequence, >50% is a diagonal sequence). The spatiotemporal parameters were made dimensionless 192 using geometric scaling equations (Hof 1996) and the shank length was used as the scaling factor 193 (Aerts et al. 2000). A total of 20 anatomical reference points were digitized by SM and NS using the 194 *DLTdv7* application developed in MATLAB by the T. Hendrick Lab (Figure 2). Video footage was 195 analysed for one individual and the kinematics were therefore extracted for Id1 in different contexts 196 (see Table 1). When the tracked anatomical references were obscured by the movement of other 197 limbs, we applied a piecewise linear interpolation to add the missing datapoints. Movement patterns 198 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 4th order zero 199 200 phase shift Butterworth low pass filter with a cut-off frequency of 5Hz. We then applied a cubic spline 201 interpolation over a time base with 100 points in order to stride-normalized the individual 202 quadrupedal cycles. Tracking the joints and body segments during the walking strides allowed us to 203 measure 6 internal joint angles (joint extension accords to their increase) (Anvari et al. 2014): the 204 ankle [estimated between the foot taken as a whole (from heel to tip) and the shank segment], the 205 knee, the hip, the shoulder, the elbow and the wrist, as well as 5 external joint angles (with respect to 206 the horizontal): the shank, the thigh, the trunk, the humerus and the forearm.

207 Centre of mass Mechanics

208 The position of the body centre of mass (BCoM) can be estimated using body segment displacements 209 and morphometrics (kinematic method; Maus et al. 2011). In 2013 and 2017, morphometrics of the 210 studied individual (Id1) were collected using external measurements (when the individual was 211 anesthetised). The geometric model of Crompton et al. (1996) was used to estimate the body 212 proportions (segment volume and length) as well as the position of the segment's CoM (i.e. head, 213 trunk, arm, forearm, hand, thigh, shank, foot and tail). Based on these data, we calculated the 214 weighed arithmetic mean of all segments' CoM to estimate the instantaneous position of the BCoM. 215 By using the BCoM displacements, we estimated the variations in kinetic and potential energy during 216 the quadrupedal strides. The kinetic energy (KE) is calculated as follows:

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

217 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

218 velocity in the fore-aft direction. The potential energy (*PE*) is calculated as follows:

$$PE = M_b gh$$

219 Where g is the gravitational acceleration (9.81 m.s^{-2}) and h is the height of the BCoM. The total 220 external mass-specific mechanical energy $(W_{ext}; J. kg^{-1}. m^{-1})$ is defined as the sum of the positive 221 increments of the total energy $(\Delta^+ TE)$ within a cycle, divided by the body mass and the stride length 222 (SL) of the respective cycle:

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

223 During walking, the BCoM trajectory in relatively large animals (>1kg; Reilly et al. 2007) generally 224 follows an inverted pendulum movement. In this context, PE and KE fluctuate out-of-phase and 225 energy exchange between PE and KE is possible. During the rise of the BCoM, energy is converted 226 from KE to PE, while during the fall PE is converted back into KE. If the amplitudes of both energy 227 fluctuations are very similar and they fluctuate perfectly out-of-phase, there will be an optimal 228 energy recovery via the inverted pendulum mechanism (i.e. 100% recovery). Hence, the percentage 229 of recovery allows us to evaluate the efficiency of the pendular exchange of energy and is estimated 230 as follows:

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

231 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 PEand KE:

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

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.

239 sEMG

240 We first visually checked the signals to ensure the absence of abnormalities and artefacts. We used 241 MATLAB (R2019a) to analyse, filter and create an envelope of the EMG signals (see the 242 supplementary material for an evaluation of different methods, Figure A). The following successive steps were applied: Band-pass 4th order Butterworth filter (5Hz to 500Hz), centred, rectified (full-243 244 wave), low-pass 4th order Butterworth filter (10Hz), rectified (full-wave) [Matlab script is available in 245 supplementary material]. We then applied a cubic spline interpolation over a time base with 200 246 points in order to stride-normalized the individual guadrupedal cycles. This provides an envelope of 247 the muscular activity pattern on which we then applied different statistical analyses (see below). Each 248 individual muscle amplitude was also normalized per day of experiment based on the maximum peak 249 contraction value of the set of quadrupedal walking sequences. Due to these treatments, we can 250 average the multiple strides per individual.

251 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}).

266 In order to evaluate potential differences between the walking contexts, we divided the EMG signals 267 into 4 phases of equal duration, representing 25% of the cycle duration. The numerical integration of 268 these different phases allowed us to estimate the proportion of EMG activation per phase and its 269 distribution across phases. We conducted a Chi-square test of independence (χ^2) to assess whether 270 there is a significant relationship between the distribution of the activation pattern between

9

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.

278 RESULTS

279 Average kinematics

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

281 Time plots of the hind limb and forelimb joint and segment angles are shown on the figures 3 and 4, 282 respectively. During baboon quadrupedal walking, the hip extends gradually during the stance phase 283 up to ~90°. It flexes rapidly during the swing phase until it reaches ~50° and remains in a constant 284 position at the end of the swing phase just before the foot touches the ground and while the knee is 285 extending. The knee starts flexing slowly during the stance phase and reaches a plateau around mid-286 stance, but the flexion increases rapidly just before lift-off when the ankle is rapidly extending from 287 65° to 90°. The swing phase is characterized by a rapid flexion of the knee up to 90° during one third 288 of the swing phase and then by a rapid extension until reaching 140° at touch-down. The ankle shows 289 the same pattern as the knee but is slightly delayed. The trunk angle is maintained around 3° on 290 average and remains stable during the quadrupedal stride, the movement amplitude is ~7°. The 291 shoulder shows a reverse pattern compared to the hip, it flexes gradually during the stance phase of 292 the forelimb until reaching ~40° and increases during the swing phase until 80°. The range of motion 293 of the humerus is 39° while the amplitude of the thigh (femur) is 44°. The elbow flexes during the 294 beginning of the swing phase from ~130° to ~90° and then extends during the second part of the 295 swing phase up to 120°. It increases slowly during the stance phase, but it reaches a plateau around 296 mid-stance, as also observed in the knee. The end of the stance phase is characterized by an 297 extension of the elbow from 130° to 140°. The wrist shows an extreme extension around 220° in the 298 last third of the stance phase that precedes an important roll off before lift-off. The wrist flexes until 299 ~100° and then extends again in preparation of touch-down at ~180°. The high wrist extension 300 corresponds to the typical digitigrade hand posture in baboon and the wrist dorsiflexes gradually 301 during the two third of the stance phase until reaching an extreme extension when the ipsilateral 302 hindlimb touches down.

303 Average BCoM mechanics

The data used here are for ld1, 15/12/2017 (diagonal/ground n=12) and 04/07/2013 (diagonal/ground n=3).

306 In our sample, the recovery rates of energy are at 57% on average when the walking speed is under 307 0.9 m.s⁻¹ and tend to decrease at higher speed (Fig. 5A). Note, that although we provided a linear 308 regression model for this relationship, a second-degree polynomial might be a better fit for the data 309 $(R^2=0.34 vs R^2=0.26$ for the linear model). A broader speed range would enable confirmation of the 310 linear or the upside-down U-shaped relationship between the recovery rates and speed in baboons. 311 The recovery rates are significantly negatively correlated with the congruity, i.e. the more the 312 energies are fluctuating out-of-phase, the better the recovery is (Fig. 5B). The percentage of recovery 313 is also significantly correlated with the limb phase. A limb phase value closer to 0.55 corresponds to a 314 higher level of recovery. There is no relationship between the recovery rates and the relative 315 amplitude of the kinetic and potential energy.

316 Interindividual differences

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

318 Spatio-temporal parameters Table 2 shows the average values of the spatio-temporal parameters for 319 walking quadrupedally at comfort speed on the ground using DSDC gait per individual. The two 320 individuals studied adjust their spatio-temporal parameters the same way according to speed (see 321 Figure B in the supplementary material). Both individuals modulate their walking pattern by altering 322 both their frequency and stride length. Individual 1 tends to increase walking speed mainly by 323 increasing stride frequency (Id1: slope=0.12; Id2: slope=0.04), whereas individual 2 increases speed 324 mainly by increasing stride length (Id1: slope=3.6; Id2: slope=5.7). The duty factor is significantly 325 greater in Id1 than in Id2, although the absolute difference is small (67% and 64%, respectively, 326 Permutation test: 3.538, P=0.0001). Within the limited speed range observed, the duty factor is not 327 significantly related to speed for any of the individuals studied. The dimensionless stride length is 328 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 (ld1)		n=19	P value	
	Mean	SD	Mean	SD	ld1 vs ld2
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

329 **Muscular activity** The bursting EMG patterns are very consistent between the two individuals (Fig. 6). 330 The gluteus medius (hip extensor and rotator muscle), the biceps femoris (hip extensor and knee 331 flexor), the gastrocnemius (ankle extensor muscle) and the peroneus (foot evertor muscle) were 332 active at the beginning of the stance phase. The maximum burst activity is approximately 25% of the 333 stance phase, i.e. when the right hind limb is still in a protracted posture and when the (contralateral) 334 left hind limb starts to swing and the left forelimb touches the ground. The rectus femoris (hip flexor 335 and knee extensor) shows a reverse pattern with a burst of activity when the limb starts to be 336 retracted, and the knee is maintained around 120°. It is approximately at 75% of the stance phase 337 and corresponds to the (contralateral) left hind limb touching the ground. There is also a certain level 338 of recorded activation of the rectus femoris in Id1, at the beginning of the stance phase, when the 339 gluteus medius, the biceps femoris and the gastrocnemius are very active. The distinct activation 340 pattern of the rectus femoris is the only significant difference found between the two individuals 341 (χ^2 =12, df=3, P=0.0069). While the activity of the muscles located in the thigh show very short 342 bursting patterns, the burst activity of the gastrocnemius and peroneus remain active during a longer 343 period of the stance phase, i.e. until the touch-down of the left hind limb. The tibialis anterior 344 (dorsiflexion of the foot and inversion) starts its activity at the very end of the stance phase, just after 345 the (ipsilateral) right forelimb touch-down and shows a burst of activity just after the right hind limb 346 lift-off when the ankle is rapidly flexed. Its activity then decreases during the second period of the 347 swing phase. There is no activity of the gluteus medius, rectus femoris, biceps femoris, peroneus and 348 gastrocnemius during the swing phase, but the biceps femoris and gastrocnemius appear to start 349 their activity at the very end of the swing phase, in preparation of the touch-down.

350 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).

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354 Spatio-temporal parameters and BCoM mechanics Table 3 shows the average values of the 355 spatiotemporal parameters for walking quadrupedally on the ground using diagonal sequences (DS-356 G), for walking quadrupedally on the branch using diagonal sequences (DS-B) and for walking 357 quadrupedally on the ground using lateral sequences (LS-G). We observed a significant difference in 358 stride frequency (and duration) between diagonal and lateral gaits (1.26Hz and 1.44Hz, respectively, 359 Permutation test: 2.193, P=0.0209) as well as in the % of congruity of the BCoM (38.7% and 53.6%, 360 respectively, Permutation test: -2.272, P=0.0159). There is a significant difference in stride length and 361 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, 362 363 Permutation test: 2.089, P=0.0335).

	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

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

Significant values are indicated in bold

¹values 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).

369 On the branch, the baboon increases the ankle extension and the range of motion of the ankle as 370 well as the shank extension compared to the ground (ankle: 82.3° and 76.4°, respectively, 371 Permutation test: -3.165, P=0.0004; ankle ROM: 44.9° and 38.3°, respectively, Permutation test: -2.08, 372 P=0.0339; shank: 56.6° and 53.7°, respectively, Permutation test: -2.79, P=0.0023). The range of 373 motion of the trunk angle is reduced on the branch compared to the ground (4° and 6.3°, 374 respectively, Permutation test: 2.862, P=0.0015). In the forelimb, the shoulder angle is kept more 375 extended on the branch compared to the ground and the wrist is more dorsiflexed (shoulder: 58.4° 376 and 55.3°, respectively, Permutation test: -2.09, P=0.0326; wrist: 187° and 180.8°, respectively, 377 Permutation test: -2.53, P=0.0081). Figure C (in the supplementary material) shows the average 378 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).

392 DISCUSSION

393 The present study aims to explore the quadrupedal walking pattern of baboons using different levels 394 of analysis, via limb and body kinematics (also used to estimate the dynamics of the BCoM) and 395 muscular activity. Overall, our study shows that the dynamics of the BCoM in a baboon walking 396 quadrupedally on the ground using its preferred walking gait (DSDC) is effective and can be 397 energetically efficient. On the other hand, walking on a branch appears to give priority to stability, but 398 how it affects efficiency requires further exploration. In addition, walking using the LSLC gait appears 399 to increase muscular effort and may reduce the potential for high recovery rates in baboons. 400 Importantly, although our study supports specific assumptions about stability and efficiency in non-401 human primates, further data including a larger sample size are required.

402 Walking on the ground using DSDC gait

403 Overall, the patterns of muscular activation during steady guadrupedal walking in baboons are 404 consistent within and between individuals (Figure 6B shows an overview of the muscular activity 405 pattern during quadrupedal walking). The phasic activities of the six recorded muscles are very 406 similar to the muscular activity profile described in macaques (Courtine et al. 2005; Higurashi et al. 407 2019). Furthermore, despite differences in the footfall pattern between non-primate guadrupedal 408 mammals (lateral sequences) and non-human primates (diagonal sequences), the activity pattern of 409 the hind limb muscles in baboons is very similar to the one observed in other primates such as 410 chimpanzees, spider monkeys, macaques, and lemurs (Ishida et al. 1974; Kimura et al. 1979; Larson & 411 Stern 2009), as well as in dogs (Deban et al. 2012; Goslow et al. 1981) and cats (Rasmussen et al. 412 1978). Therefore, we can assume that the basic functions of the muscles for retracting and 413 protracting the limbs, as well as to support the body against gravity and inertial forces are conserved 414 across groups.

415 We first hypothesized that, given the "cursorial" adaptations of baboons (e.g. Druelle et al. 2017a; 416 Patel & Polk 2010; Raichlen 2004), they should be able to make use of an inverted-pendulum 417 mechanism when walking steadily on the ground. Our results support this hypothesis as we observed 418 that KE and PE are mainly fluctuating out-of-phase (congruity = 39%) during normal guadrupedal 419 walking using DSDC gaits. The recovery rates observed in baboon in this study (22-84%) cover an 420 important range of variation compared to other specialized quadrupeds such as dogs (50-70%; Griffin 421 et al. 2004), but these are close to the range of values available for non-human primates, such as the 422 ring-tailed lemurs and the capuchin monkeys (35-71% and 11-65%, respectively during quadrupedal 423 walking; O'Neill & Schmitt 2012; Demes & O'Neill 2013). Griffin et al. (2004) developed a model 424 showing that the pendulum-like centre of mass movements in guadrupedal animals is a combination 425 of both inverted pendulums around the pectoral and pelvic girdle. These pendulums are directly 426 influenced by the footfall pattern and body mass distribution. For example, a body centre of mass 427 located at mid-trunk coupled to a forelimb that lags behind the hindlimb by 25% would result in a flat 428 trajectory of the BCoM (Griffin et al. 2004). Baboons have a BCoM positioned at mid-trunk compared 429 to dogs that have a cranially positioned BCoM (Druelle et al. 2019), hence baboons may rely on limb 430 phase only to produce "optimal" fluctuations of their BCoM. In the present study, we found that the 431 ipsilateral forelimb lagged behind the hindlimb by 61% in average (min: 54%, max: 69%) and there is a 432 significant relationship between the recovery rates and the limb phase (i.e. the lags between fore-433 and hindlimbs; see Figure 5C). These results support the model of Griffin et al. (2004), but it does not 434 support the "reduced cost zone" of 65-72% estimated recently by Miller et al. (2019) for non-human 435 primates. However, note that, as recognized by the latter, body mass distribution can also affect the 436 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 consideredbefore rejecting previous assumptions.

439 Our results, in addition to the ones provided by O'Neill & Schmitt (2012) and Demes & O'Neill (2013), 440 do not support the hypothesis of Ogihara et al. (2012) suggesting that diagonal sequence gaits 441 impede good recovery rates in primates. The baboon appears, however, much more efficient than the 442 macaque (Ogihara et al. 2012) when walking on the ground. As previously suggested (Druelle et al. 443 2016), macaques may be less equipped for quadrupedal walking than baboons. Because baboons 444 commonly travel at least 3.5 km per day, while macagues move less than 1.5 km (Garland 1983), the specific ecological requirements of baboons may have shaped these species into more efficient 445 446 walkers (i.e. higher potential for relying on inverted-pendulum strategies) than macaques. Given the 447 ecological niche of olive baboons and their large home range (Garland 1983; Henzi et al. 1992; Isbell 448 et al. 1998; Pebsworth et al. 2012), they should be under strong selection for walking efficiency 449 (Druelle et al. 2017a). This could also be the case for the ring-tailed lemurs and the capuchin monkeys 450 that both exhibit good recovery rates during quadrupedal walking (O'Neill & Schmitt 2012; Demes & 451 O'Neill 2013).

452 Influence of different gait and substrate contexts

453 When walking on a branch, an inherent instability (rolling and pitching moments) is in action. Our 454 second hypothesis stipulated that when walking on a branch, kinematical adjustments should reduce 455 the vertical oscillations of the centre of mass (Galvez-Lopez et al. 2011; Schmitt 1999) and in this way 456 give priority to stability upon efficiency (but see Schmitt 2011). It has been shown that animals 457 increase their stability on arboreal substrates through employing strategies that reduce the 458 oscillations of their BCoM (Gàlvez-Lòpez et al. 2011). However, these strategies can be of a different 459 kind. For instance, while cats (medium-sized, ≈ 4.4 kg) make use of slower speeds and shorter swing 460 phase durations on a narrow runway, dogs (large-sized, ≈28kg), on the other hand, rely on high-speed 461 locomotion and high frequency to gain dynamic stability (Galvez-Lopez et al. 2011). The adjustments 462 observed in the olive baboon (13.5kg in the present study) when walking on a (suspended, non-463 bending) branch show a decrease in stride length and speed, a decrease in the movement amplitude 464 of the trunk and a trend towards a longer relative contact time. There is also an increase in ankle and 465 wrist extension that results from a slight external rotation of the distal limb segments to fit the 466 rounded shape of the substrate. The decrease in trunk range of motion may result in part from the 467 shorter stride length and thus from the lower speed, as well as from the shoulder that is kept more 468 extended on the branch. More in-phase fluctuations of the KE and PE (congruity = 46%) are also 469 observed compared to the walk on the ground. These adjustments (certainly closer to the cat

470 strategy) reduce the vertical oscillations of the BCoM, and with the increase activity of the *peroneus* 471 (increasing torque generation), meet the balance control requirements. This general strategy may 472 reduce the possibility to rely on an efficient inverted pendulum-like exchange of energy, but we did 473 not observe a direct significant difference in the recovery rates. The baboon thus appears to adjust its 474 movement and to increase the control in the distal segment to gain stability, but more data are 475 required to assess how much this strategy influences the efficiency. Interestingly, a previous study 476 showed that in Lemur catta, walking on a raised horizontal pole does not significantly affect the 477 energetic recovery (Schmitt 2011). Furthermore, limb interference is important during diagonal 478 walking on the ground. The baboons move their right hind limb on the right (or left) side of their right 479 forelimb, while the left hindlimb moves on the right (or left) side of the left forelimb (Fig. 6b). On the 480 branch, there is no space for limb interference and overstriding during walking and the hindlimbs 481 need to be positioned behind the forelimbs at touch-down. This can also contribute to the shorter 482 stride lengths and lower speed observed on the branch.

483 A study on bonobos observed that when they walk on a horizontal arboreal substrate, they reduce 484 their stance phase, take longer strides and reduce the stride frequency (Schoonaert et al. 2016). This 485 strategy appears to be very different from the one used by the baboon in the present study (note that 486 both, the size of the specimens and the substrate diameter are different: 12cm for the bonobos, and 487 16cm in the present study), as well as from the ones used by lemurs and marmosets that all tend to 488 decrease their speed and increase the contact time with the substrate (Franz et al. 2005; Young et al. 489 2016). However, we wonder whether the pole height may also be of importance. For instance, the 490 bonobos were walking on a pole that was positioned approximately 30cm above the ground, hence 491 falling was not really a risk encountered by the animals (Schoonaert et al. 2016). This emphasizes the 492 importance of considering morphological differences, kinematic strategies coupled to risk evaluation 493 among primates for negotiating arboreal substrates [hominoids, cercopithecoids, platyrrhines and 494 lemuriforms all present different morphological features (Fleagle 2013)]. Although balance 495 requirements are shared between animals when walking on a horizontal branch, the ability to meet 496 these demands (controlling pitching, yawing and rolling moments) can be performed in very different 497 ways, i.e. from static to dynamic stability of the BCoM. It is possible that all these strategies allow 498 primates and other mammals to limit the vertical oscillations of the BCoM, given their respective 499 morphology (e.g. Gàlvez-Lòpez et al. 2011; Schmitt et al. 2006; Young et al. 2016).

500 Muscular effort is influenced by the footfall pattern (Bishop et al. 2008; Griffin et al. 2004), hence 501 energetic cost is probably an important factor in footfall timings (Miller et al. 2019). We hypothesized 502 that the usual muscle activation pattern observed in diagonal gaits should be altered towards an 503 increased activation of the proximal muscles when the baboon uses the unusual lateral gait on the 504 ground and of the distal muscles (for increasing the control) when it walks on a substrate that 505 imposes higher balance requirements (such as a branch). First, we observed an increased activity of 506 the biceps femoris, the qastrocnemius and the tibialis anterior when walking using LSLC gait on the 507 ground. Second, the peroneus activity increases substantially in intensity and duration during the 508 stance phase when walking on the branch. Generally, the *peroneus* is suggested to stabilize the ankle 509 and to be an extensor and evertor of the foot. Boyer et al. (2007) suggested that the peroneus 510 (longus) is an important muscle for positioning the foot at touchdown and for resisting inversion 511 throughout the stance phase in primates. The activity of the *peroneus* observed in our study when 512 the baboon is walking on the branch is similar to the one of the lemur species walking quadrupedally 513 on large and small poles (Boyer et al. 2007). While it is not strongly active on the ground during 514 diagonal and lateral gaits in baboons, it appears to be specifically recruited for resisting foot inversion 515 during the stance phase on the branch. Our kinematics support this, as we observed an increase in 516 ankle extension (and external rotation). The more outward and everted position of the foot should 517 ensure a better fit between the foot and the substrate, thus increasing friction and allowing 518 transmitting rotating moment (Lammers & Gauntner 2008; Preuschoft 2004).

519 The biceps femoris is described as a hip extensor and a knee flexor (Swindler & Wood 1973). It is 520 active during the initial part of the support phase. At touch-down, the limb is in a protracted position 521 and the knee is relatively extended (≈140°) (Larney & Larson 2004), the biceps femoris is, therefore, 522 acting as a thigh (hind limb) retractor by flexing the knee (≈110° at midstance) and extending the hip 523 (from 50° to 75° between touch-down and mid-stance). The fact that its activity increases 524 substantially during lateral walking can be directly related to the higher stride frequency (relative 525 stance phase does not change). The increase activity of the *gastrocnemius* and the *tibialis anterior* 526 may also result from the higher stride frequency. A faster retraction and protraction of the limb 527 would require more muscular fibres to be active. Lateral walking also led to an increase extension of 528 the ankle that can be related to the increase activity observed in the gastrocnemius and the tibialis 529 anterior. But the functional reason for this higher extension remains elusive at this stage (note that 530 such an ankle extension in this context also seems to be seen in capuchin monkey; see Figure 2 in 531 Wallace and Demes 2008). On the branch, the stride length decreases as well as the speed and the 532 activity of the rectus femoris (for controlling limb retraction) is reduced in this context.

533 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 537 the dynamics of the BCoM using kinematics suggests that this is more efficient than walking using the 538 LSLC gait. Also, from a motor perspective, significant increase in muscular activity should result in 539 higher level of oxygen consumption. Hence, the most efficient baboon remains the one walking on 540 the ground, using DSDC gaits (potentially with a tight limb phase: 50%<LP>60% and at low speed, but 541 data from a larger speed range are required to assess how it influences the energetic recovery rates, 542 i.e., linearly or not). Moreover, our data suggest that the use of a different walking gait, or walking on 543 a branch, both result in less efficient forms of locomotion. Although our analysis on this aspect is 544 preliminary, this emphasizes a possible limitation in the flexibility of the walking pattern when 545 efficiency is the target. In other words, walking economy could be related to a stereotyped, non-546 flexible pattern, while gait adjustments and flexibility ensure stability in an arboreal habitat. However, 547 further data are required to investigate this hypothesis. As recently claimed, the effect of footfall 548 timings on mechanical stability and mechanical energy exchange on arboreal and terrestrial 549 substrates, as well as the way these competing demands interact (Miller et al. 2019) remains poorly 550 known. It is also possible that these two components do not have the same "time-frame" as 551 mechanical energy exchange should occur within a stride, while mechanical stability can be 552 performed and ensured among multiple strides (Biewener & Daley 2007; Chadwell & Young 2015; 553 Lammers & Gauntner 2008). Further integrative data including larger sample size are needed to 554 better understand the relationships between gait adjustments, BCoM mechanics and muscular 555 activity in non-human primates.

556 the guadrupedal peculiarities of primates certainly represent biomechanical Overall. 557 accommodations to arboreal life and played a crucial role in the early differentiation of primates from 558 other mammals. However, despite these peculiarities, they also share very similar patterns of muscle 559 activation with other quadrupedal mammals, at least when they walk quadrupedally on the ground. 560 This reflects the shared basic functional demands (i.e. support and propulsion) on the hind limbs for 561 quadrupedal locomotion in tetrapods. Finally, the diagonal gait pattern appears to be strongly 562 implemented into the baboon neuromotor system because lateral sequences are likely to result in a 563 direct and significant increase of the energetic costs (at the level of the BCoM mechanics and 564 muscular activity). On the other hand, the diagonal walking gait does not impede good recovery rates 565 in primates.

566

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575

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 refere. 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). 601 Figure 6. (a) Average EMG profiles of the 6 hind limb muscles considered during steady quadrupedal 602 walking. The activity patterns are stride-normalized and averaged across 12 strides for Id1 (grey) and 603 19 strides for Id2 (blue). The average footfall pattern at the bottom (gait diagram) shows average 604 stance phases (solid bars) of the right hind limb (RH), left hind limb (LH), right forelimb (RF) and left 605 forelimb (LF). The EMG activity was recorded on the right hind limb (darker on the gait diagram). (b) 606 Overview of the muscular activity of the 6 hind limb muscles considered during the stance phase of 607 the quadrupedal stride in Id1. The amount of muscular activity is based on the average profile 608 observed in (a) and is divided in 4 levels of activation. Six events are represented: Right Hind limb 609 Touch-Down (RH TD), Left Hind limb Lift-Off (LH LO) + Left Forelimb Touch-Down (LF TD), Right 610 Forelimb Lift-Off (RF LO), Left Hind limb Touch-Down (LH TD), Right Forelimb Touch-Down (RF TD) and 611 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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