

RESEARCH ARTICLE

Gait Characteristics and Spatio-Temporal Variables of Climbing in Bonobos (*Pan paniscus*)

KIRSTEN SCHOONAERT¹, KRISTIAAN D'AOUÏ^{1,2,3}, DIANA SAMUEL⁴, WILLEM TALLOEN⁵, SANDRA NAUWELAERTS^{1,3*}, TRACY L. KIVELL⁴, AND PETER AERTS^{1,6}

¹Laboratory for Functional Morphology, Department of Biology, University of Antwerp, Wilrijk, Belgium

²Institute of Ageing and Chronic Disease, Faculty of Health and Life Sciences, University of Liverpool, Liverpool, United Kingdom

³Centre for Research and Conservation (CRC), Antwerp, Belgium

⁴Animal Postcranial Evolution (APE) Lab, Skeletal Biology Research Centre, School of Anthropology and Conservation, University of Kent, Canterbury, United Kingdom

⁵Janssen Pharmaceutica NV of Johnson & Johnson, Turnhoutseweg, Beerse, Belgium

⁶Laboratory for Biomechanics and Motor Control of Human Movement, Department of Movement and Sports Sciences, University of Ghent, Ghent, Belgium

Although much is known about the terrestrial locomotion of great apes, their arboreal locomotion has been studied less extensively. This study investigates arboreal locomotion in bonobos (*Pan paniscus*), focusing on the gait characteristics and spatio-temporal variables associated with locomotion on a pole. These features are compared across different substrate inclinations (0°, 30°, 45°, 60°, and 90°), and horizontal quadrupedal walking is compared between an arboreal and a terrestrial substrate. Our results show greater variation in footfall patterns with increasing incline, resulting in more lateral gait sequences. During climbing on arboreal inclines, smaller steps and strides but higher stride frequencies and duty factors are found compared to horizontal arboreal walking. This may facilitate better balance control and dynamic stability on the arboreal substrate. We found no gradual change in spatio-temporal variables with increasing incline; instead, the results for all inclines were clustered together. Bonobos take larger strides at lower stride frequencies and lower duty factors on a horizontal arboreal substrate than on a flat terrestrial substrate. We suggest that these changes are the result of the better grip of the grasping feet on an arboreal substrate. Speed modulation of the spatio-temporal variables is similar across substrate inclinations and between substrate types, suggesting a comparable underlying motor control. Finally, we contrast these variables of arboreal inclined climbing with those of terrestrial bipedal locomotion, and briefly discuss the results with respect to the origin of habitual bipedalism. Am. J. Primatol. © 2016 Wiley Periodicals, Inc.

Key words: arboreal locomotion; footfall patterns; primates; biomechanics; African apes

INTRODUCTION

Understanding the origin of human bipedalism and the type of locomotion used by the pre-bipedal ancestor is an ongoing, fundamental debate in palaeoanthropology. Several hypotheses have been put forth, advocating either a primarily terrestrial origin or an arboreal origin. A terrestrial route, the “knuckle-walking hypothesis,” suggests the last common ancestor of humans and *Pan* regularly engaged in knuckle-walking, as this is the main mode of locomotion in African apes. However, morphological evidence for the relevant adaptations is sparse in the fossil record [Lovejoy et al., 2009; Richmond & Strait, 2000], and the form-function relationship of those that are present has been brought into question [Crompton et al., 2010; Inouye & Shea, 2004; Kivell & Schmitt, 2009].

There are several arboreal hypotheses for the origin of human bipedalism that hinge on the

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*Correspondence to: Sandra Nauwelaerts, Laboratory for Functional Morphology, Department of Biology, University of Antwerp, Universiteitsplein 1, 2610 Wilrijk, Belgium. E-mail: sandra.nauwelaerts@uantwerpen.be

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substantial arboreal locomotor behaviors and their associated anatomical adaptations found in all living apes [e.g., Schmitt, 2003; Susman et al., 1984; Tuttle, 1969]. For example, the “vertical climbing hypothesis” favors a climbing ancestor and centres on similarities in muscle pattern use and hindlimb position when comparing bipedalism and vertical climbing [Fleagle et al., 1981; Prost, 1980; Schmitt, 2003; Stern & Susman, 1981]. Hunt [1994] emphasises the importance of taking the arboreal ecological context into account; in keeping with this, the “arboreal orthograde” hypothesis posits that the precursor to hominin bipedalism was hand-assisted arboreal bipedalism, and those in favor of this scenario argue that it is a more parsimonious hypothesis compared to others [Crompton et al., 2008; Thorpe et al., 2007].

However, anatomical evidence alone is not sufficient to evaluate the validity of each of these hypotheses. A better comprehension of the kinematics, dynamics, and neuromechanics [see Nishikawa et al., 2007] of terrestrial and arboreal locomotion of model species (in a comparative approach), such as African apes, could provide essential additional understanding of the evolution of hominin (and hominid) locomotion [D’Août et al., 2014]. Spatio-temporal gait variables—so called collective variables—can be considered an elementary representation of the entire locomotor system, thus being useful for gaining insight into how basic neural control of movement might differ between different locomotor modes [Aerts et al., 2000; Nishikawa et al., 2007]. Aerts et al. [2000] described and compared the spatio-temporal variables (stride frequencies, stride—and step lengths, and duty factors) of the hindlimb cycles of bonobos during bipedal and quadrupedal terrestrial walking over a range of speeds. The authors showed that, despite the large quantitative differences between them, the basic aspects of hindlimb control (i.e., the modulation of the limb oscillators in relation to speed as described by the exponents of the descriptive power functions; see further) are identical in terrestrial bipedal and quadrupedal walking.

The present study adopts a similar approach, addressing the basic kinematics of bonobo arboreal locomotion. Spatio-temporal variables for the hindlimbs during quadrupedal locomotion on an arboreal support at different inclinations are examined and compared with previous results of terrestrial, level locomotion [Aerts et al., 2000]. Furthermore, as it is argued that locomotion on an arboreal substrate also affects other gait characteristics, such as symmetry, sequences used, and/or footfall patterns [e.g., Cartmill et al., 2002, 2007; D’Août et al., 2004; Hildebrand, 1967; Shapiro & Raichlen, 2005, 2006; Vilensky & Larson, 1989], these characteristics are also assessed and related to incline. Lastly, climbing steeper inclines implies a shift in arm function: to

avoid tumbling backwards, tensile arm forces are required [e.g., Cartmill, 1985; Preuschoft, 2002] while the hindlimbs remain loaded in compression. This mechanical shift in quadrupedal limb loading, which is related to body posture, may likely interact with the basic kinematical patterns. Therefore, hand posture (e.g., knuckle-walking vs. prehensile grasping) is also recorded as a qualitative proxy of this mechanical shift.

We put forth several hypotheses regarding how bonobo gait characteristics and spatio-temporal variables will change in relation to arboreal substrate incline and between arboreal and terrestrial substrates. Firstly, it has been argued that climbing patterns generally appear to be more irregular than most other locomotor patterns used by mammals [Fleagle, 1976; Isler, 2002b, 2003]. Therefore, we hypothesize that there will be an increase in the proportion of asymmetrical footfall patterns with incline. Moreover, in accordance with the observation that “lateral-sequence” gaits are preferred in arboreal conditions, likely for increased stability [Hildebrand, 1967; Schmitt, 2003], it is predicted that the proportion of lateral-sequence gaits will also increase with incline. Secondly, given that basic hindlimb control is conserved during dramatically different modes of terrestrial locomotion in bonobos (i.e., bipedal and quadrupedal locomotion; see Aerts et al. [2000]; D’Août & Aerts [2002]), it is hypothesized that this basic control (reflected in the modulation of the limb oscillators in relation to speed) will also be retained during arboreal climbing, except for the steepest incline (90°) for which the mechanical constraints on locomotion are unavoidably altered (arm-pulling is compulsory as gravity always induces a backward moment, irrespective of the body posture). Thirdly, previous research on bonobo terrestrial locomotion suggested that the shorter stride-/step lengths and the higher stride frequencies and duty factors observed in bipedal walking relative to quadrupedal walking likely improved opportunities for balance control; thus, assuming that steeper inclines are more challenging for balance control, we predict that, at any given speed, stride-/step lengths will decrease and stride frequency and duty factor will increase with incline.

METHODS

Materials

Data were collected between 2006 and 2007. The study was conducted in accordance with the legislation of the “Federal Public Service (FPS) Health, Food Chain Safety and Environment” in Belgium, and was approved by the Ethical Committee for Animal Experiments of the University of Antwerp. Additionally, it adheres to the American Society of

Primatologists' principles for the ethical treatment of primates. To obtain climbing sequences on different slopes, an experimental set-up was constructed [Schoonaert et al., 2006] and installed inside the bonobo hall of Planckendael Zoo (Royal Zoological Society of Antwerp, Belgium). The set-up consisted of a 4 m straight pole with a diameter of 12 cm; this diameter was selected as it was large enough to accommodate the inclusion of a steel profile within it, yet small enough for the bonobos to grasp around. The slope of the pole could be varied from 0° to 90° in 15° increments. For this study, five inclinations were explored (0°, 30°, 45°, 60°, and 90°). The animals quickly habituated to the pole and climbed voluntarily on the set-up. In order to encourage them to use it more frequently, most animals were trained to follow a light spot projected by a laser pointer onto the pole; trained sequences were compared qualitatively to voluntary sequences, but showed no difference.

Lateral-view video recordings (50 Hz; temporal accuracy of ±0.02 sec) were made during quadrupedal locomotion on the pole while positioned at different inclines (see Fig. 1). A cuboid reference frame (1 m³) was filmed to allow proper scaling of the video images. Four adult individuals were studied here: three males (aged 12, 16, and 23 years) and one female (aged 11 years). The two older males were also included in the terrestrial study conducted by Aerts et al. [2000], the results of which are directly compared with the current study. Ten video sequences per individual for each substrate inclination were obtained. Each video sequence was assigned a time code (Panasonic AG-IA232TC-interface) and played back frame-by-frame; of these sequences, only those that showed steady speed were retained for further analysis (N = 189). Analysis consisted of digitizing (NAC-1000XY-coordinator) each forelimb and hindlimb's substrate contact and lift-off in a systematic way, determining the frame at which contact with



Fig. 1. Still image of the set-up, showing a bonobo climbing up the pole while it is angled at 30°.

the substrate first occurred and the frame at which the limb was fully removed. The velocity of each stride was assessed by determining the coccyx displacement over time for a complete stride cycle. The occurrence of overstriding, knuckle-walking, and prehensile grasping was qualitatively scored for all sequences.

Complete strides were classified as either a symmetrical or asymmetrical gait. A cycle was deemed symmetrical if the opposing limb's touchdown occurred between 40% and 60% of the cycle duration in order to allow comparison with Isler [2002a, 2003, 2005], though other authors have used more conservative thresholds (i.e., between 45% and 55%; Cartmill et al. [2002]); anything outside of this range was deemed asymmetrical. For further analysis, only symmetrical cycles were used. Symmetrical cycles in which ipsilateral limbs move in phase and in anti-phase are pace and trot, respectively. In between these categories, gaits were sub-divided into lateral or diagonal sequences (in accordance with Hildebrand [1967]). In a lateral-sequence gait, touchdown of the hindlimb is followed by that of the ipsilateral forelimb; in a diagonal-sequence gait, it is followed by the contralateral forelimb. Lateral- and diagonal-sequence gaits can be further sub-divided into lateral-couplet, single-foot, and diagonal-couplet gaits (see also Fig. 2).

For the symmetrical hindlimb cycles, the following gait characteristics were determined, in accordance with definitions by Alexander [1977a,b, 1992]: cycle duration (CD), duty factor (DF), contact time (CT), stride frequency (SF), stride length (SL), and step length (StL). Cycle (or stride) duration is defined

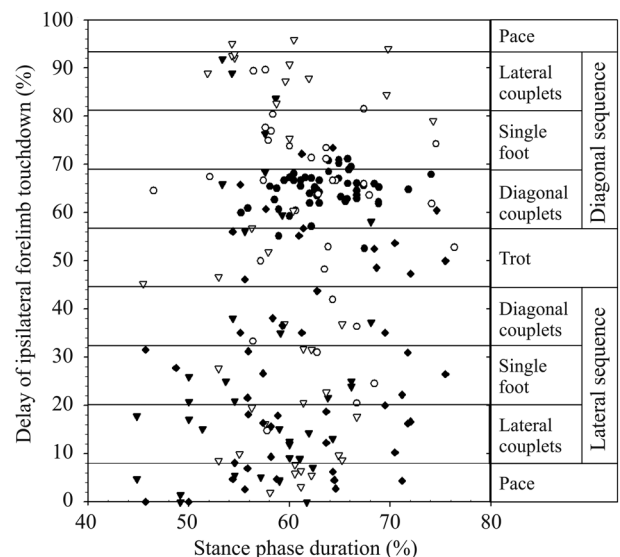


Fig. 2. Footfall patterns of symmetrical cycles during arboreal locomotion of bonobos. Footfall patterns were classified following Hildebrand [1967] for the different substrate inclines: 0° (filled circles), 30° (open circles), 45° (filled diamonds), 60° (filled triangles), and 90° (open triangles).

as the time between two initial contacts of the same limb. The duty factor is the fraction of the cycle duration that a particular limb contacts the substrate, or CT/CD. Contact time is expressed as the duration for which a limb contacts the substrate. Stride frequency is the number of strides per unit of time, or 1/CD. Stride length is defined as the distance traveled by the body's center of mass (COM) during a complete cycle, or velocity multiplied by CD. All variables were expressed as a function of walking speed (after being converted to dimensionless numbers; see below). To describe differences between arboreal and terrestrial locomotion, variables of the hindlimb cycles during terrestrial bipedal and quadrupedal walking of bonobos from Aerts et al. [2000] were included; these terrestrial data contained 17 bipedal data points from five individuals and 21 quadrupedal data points from seven individuals.

Dynamically similar locomotion can only be achieved when Froude numbers are equal [Alexander, 1992]; therefore, all spatio-temporal variables and gait velocity were made dimensionless. These size-independent measures allow comparison between different-sized individuals. The square root of the Froude number ($F = v^2 \cdot (g \cdot l)^{-1}$) was used for dimensionless velocity (DV), where v = velocity, g = gravitational acceleration, and l = a characteristic length for the locomotion type. Lower leg length (i.e., the length of the tibial segment) is used as a size determinant because it is proportional to total hindlimb length and can be estimated more reliably from the video images of individual subjects [Aerts et al., 2000; Alexander, 2004; Isler & Thorpe, 2003]. Note that zoo protocol did not allow any direct (i.e., physical) interaction with the animals, necessitating indirect estimates of this kind. Stride length was divided by lower leg length. Frequency was normalized by multiplying it with $(l/g)^{1/2}$. Duty factor is already a dimensionless variable.

Statistics

Because spatio-temporal variables tend to change exponentially with walking speed [Aerts et al., 2000], these relationships are described by power functions ($Y = 10^b \cdot DV^a$). The exponent "a" of this power function describes the relationship between velocity and a given spatio-temporal variable; the factor "b" reflects the magnitude of the given variable. Aerts et al. [2000] argued that the exponent "a" is a fundamental representation of (hind)limb control, in that it reflects the manner in which the spatio-temporal aspects of the limb oscillation, irrespective of the absolute magnitude, become modulated in relation to speed. Identical exponents "a" thus represent similar modulation/control of the limb oscillators. Effects of substrate condition on both the exponent and the factor with walking speed

were tested using a mixed model ANCOVA [Littell et al., 1996] on the log-transformed spatio-temporal variables. This was carried out separately for each variable (i.e., duty factor, step length, stride length, and stride frequency). More specifically, this mixed model ANCOVA included substrate condition, walking speed, and their interaction as fixed effects, and individual as a random effect. The latter is necessary to correct for the dependency of measurements from the same individual [Littell et al., 1996]. In addition, by modeling the individual variability, one compares the spatio-temporal variables across substrate conditions within individuals, making the tests more powerful. There were seven different substrate conditions: five arboreal conditions (0°, 30°, 45°, 60°, and 90°) and two terrestrial conditions (quadrupedal and bipedal). In the mixed model ANCOVA, estimates were obtained with restricted maximum likelihood. Additionally, the degrees of freedom were adjusted with the Satterthwaite's procedure [Satterthwaite, 1941], and the P values were corrected for multiple testing for the number of traits with the Tukey correction [Rice, 1989].

If the covariate in an ANCOVA is not centred around zero, the estimate of "b" would be the expected value of a given gait variable or a velocity equal to zero. Further, the estimated difference for "b" between substrate conditions cannot be interpreted properly if the slopes differ significantly between substrate conditions (i.e., if there is a significant interaction between substrate condition and walking speed). To resolve this problem, the intercepts are set at the mean value of the covariate by centering the covariate to have a mean of zero (achieved by subtracting the mean value of the covariate from each observation in the data); this is a standard approach in ANCOVA models [Kennedy & Gentle, 1980; Neter et al., 1996]. In this study, the estimates of "b" are the expected values of the gait variables or the average gait velocity, making its interpretation biologically relevant. All analyses and interpretations were performed on this centered data, using SAS 8.02 (SAS Institute, 1999).

RESULTS

Gait Characteristics

Table I shows the symmetrical and asymmetrical fore- and hindlimb cycles during arboreal locomotion on the pole at different inclinations. For level walking, 100% of the forelimb and hindlimb cycles are classified as symmetrical. However, there is an increase in asymmetrical gaits for the hindlimbs with increasing incline; this is also the case for the forelimbs, up to 45°. For vertical climbing, the frequency of asymmetrical gaits is intermediate between level and inclined walking. For all slope conditions (except 0°), the hindlimb cycles are more

TABLE I. Symmetry and Asymmetry of Limb Cycles and Overstriding for Different Substrate Inclines During Arboreal Locomotion in Bonobos

Slope	N	Symmetrical (%)		Asymmetrical (%)		Overstriding (%)
		Fore/hind	Fore	Hind	Fore	Hind
0°	38/52	100.0	100.0	0.0	0.0	12.0
30°	19/41	57.9	97.6	42.1	2.4	0.0
45°	24/62	50.0	96.8	50.0	3.2	0.0
60°	14/55	71.4	94.0	28.6	6.0	0.0
90°	29/47	86.2	97.9	13.8	2.1	0.0

symmetrical compared to the forelimb cycles. Furthermore, overstriding occurs in 12% of the arboreal horizontal hindlimb cycles and is not present in the other arboreal conditions.

We observed that, with increasing incline, bonobos start to use the prehensile abilities of their hands more often. While the hands always adopt a knuckle-walking posture on the horizontal pole, they gradually grip more laterally (30°, 45°, and 60°) and even around to the opposite side of the support (90°) with increasing slope incline, though it has been noted that they are still capable of knuckle-walking at 60° (Schoonaert and D'Áoût., pers. obs.). The feet, in contrast, always grab the pole between the abducted hallux and the other toes, irrespective of the incline of the pole.

The results for the symmetrical gait categories are shown in Figure 2 and Table II. The typical diagonal-sequence/diagonal-couplet gait described for terrestrial quadrupedal walking in many primates [D'Áoût et al., 2004; Hildebrand, 1967; Larson, 1998; Wallace & Demes, 2008] is also found in the 0° arboreal trials. For all other arboreal inclinations, including vertical climbing, the occurrence of all observed footfall patterns is variable. The percentage of diagonal sequences diminishes while the occurrence of trot and lateral sequences, including pace, show a tendency to increase. A relationship between these footfall patterns and velocity was not found.

Spatio-Temporal Variables

The analyzed sequences feature a range of velocities, resulting in a large variation in spatio-temporal variables. Step length, stride length, stride frequency, and duty factor change significantly with dimensionless velocity in an exponential way (Table III). In Figure 3, the power functions of the relevant spatio-temporal variables are plotted against dimensionless velocity. According to these plots, all variables follow the same trend, irrespective

of the substrate inclination or substrate type (i.e., arboreal or terrestrial). There is an increase in stride frequency, stride length and step length, and a decrease in duty factor with increasing velocity. Even so, there are significant differences between the power functions, with respect to the exponent and/or factor, for the different substrate inclinations/types (Table IV).

As expected, *step length* increases with higher velocities ($P < 0.0001$, Fig. 3a). However, the magnitude of this increase differs significantly between the substrate conditions ($P < 0.01$, Table IV and Fig. 4). Step length generally increases more rapidly with velocity during both bipedal and quadrupedal terrestrial walking than during arboreal climbing at 30, 45 and 60 degrees. For 90°, step length was similar when compared to bipedal terrestrial walking, as illustrated in Figure 3a. Horizontal arboreal locomotion lies in between these two clusters, but does not differ significantly from bipedal and quadrupedal terrestrial walking. During horizontal quadrupedal walking (both terrestrial and arboreal), bonobos take larger steps at similar velocities when compared to arboreal inclines (except for 30°) and terrestrial bipedal walking (Table IV and Fig. 5).

The effects of substrate condition on *stride length* are almost identical to those on step length. Bonobos take larger strides when walking faster (Fig. 3b), but this increase in stride length with velocity is steeper for terrestrial walking than for inclined arboreal climbing (except for 45° and 90°, where no significant difference was found), with the horizontal arboreal substrate condition being intermediate between the arboreal inclines and the quadrupedal terrestrial substrate condition (Table IV and Fig. 4). Overall, bonobos take their largest strides during horizontal arboreal walking and their smallest strides during bipedal walking (Table IV and Fig. 5).

Stride frequency always increases with velocity ($P < 0.05$, Fig. 3c). However, the magnitude of this increase is considerably lower during bipedal terrestrial walking, though not significantly when compared to horizontal arboreal and terrestrial

TABLE II. Footfall Patterns (Given as Percentages) for Different Substrate Inclines During Arboreal Locomotion in Bonobos

Slope	N	Pace	Diagonal sequence	Trot	Lateral sequence
0°	31	0.0	93.5	6.5	0.0
30°	24	0.0	70.8	12.5	16.7
45°	24	16.7	16.7	12.5	54.2
60°	25	24.0	16.0	0.0	60.0
90°	18	44.4	5.6	16.7	33.3

TABLE III. Values for the Relationships Between the Dimensionless Variables and Dimensionless Velocity ($Y = 10^b \cdot DV^a$) for Different Substrate Inclines and Types (From Aerts et al. [2000]) During Locomotion in Bonobos

	DStL		DSL		DSF		DF	
	a	b	a	b	a	b	a	b
0°	0.307 ± 0.085	0.476 ± 0.012	0.443 ± 0.062	0.710 ± 0.013	0.514 ± 0.061	-0.821 ± 0.013	-0.162 ± 0.053	-0.232 ± 0.008
30°	0.107 ± 0.065	0.436 ± 0.012	0.387 ± 0.047	0.639 ± 0.013	0.615 ± 0.046	-0.749 ± 0.013	-0.289 ± 0.040	-0.202 ± 0.008
45°	0.168 ± 0.094	0.408 ± 0.013	0.401 ± 0.068	0.613 ± 0.013	0.598 ± 0.067	-0.722 ± 0.013	-0.225 ± 0.058	-0.205 ± 0.008
60°	0.152 ± 0.076	0.429 ± 0.011	0.359 ± 0.055	0.628 ± 0.012	0.621 ± 0.054	-0.737 ± 0.012	-0.218 ± 0.047	-0.201 ± 0.007
90°	0.228 ± 0.094	0.393 ± 0.015	0.379 ± 0.065	0.620 ± 0.014	0.583 ± 0.064	-0.738 ± 0.014	-0.197 ± 0.058	-0.236 ± 0.009
Q terr ^a	0.391 ± 0.085	0.477 ± 0.015	0.561 ± 0.070	0.663 ± 0.014	0.468 ± 0.070	-0.761 ± 0.014	-0.199 ± 0.053	-0.193 ± 0.009
B terr ^a	0.457 ± 0.079	0.369 ± 0.015	0.694 ± 0.063	0.530 ± 0.013	0.387 ± 0.062	-0.640 ± 0.014	-0.131 ± 0.049	-0.189 ± 0.009
P-value	0.0095	<0.0001	0.0008	<0.0001	0.0481	<0.0001	0.2752	<0.0001

DStL, dimensionless step length; DSL, dimensionless stride length; DSF, dimensionless stride frequency; DF, duty factor; a, the exponent of the power function; b, the factor of the power function.
^aData on terrestrial quadrupedal (Q terr) and bipedal (B terr) locomotion are from Aerts et al. [2000].

quadrupedal locomotion (Table IV and Fig. 4). Overall, stride frequency is lowest during horizontal arboreal walking and highest during terrestrial bipedal walking (Table IV and Fig. 5).

The relationship between velocity and *duty factor* does not differ between the diverse substrate conditions (Table IV, Figs. 3d and 4). However, duty factor is overall lower for a given velocity during 0° and 90° arboreal locomotion compared to all other substrate conditions (Table IV and Fig. 5).

There are two main patterns in the spatio-temporal variable results. Firstly, the four arboreal inclines and the two terrestrial locomotion types cluster together because of similar velocity-dependent changes in step- and stride-length and stride frequency, with horizontal arboreal locomotion falling in between them (Fig. 4). Secondly, step- and stride-lengths increase and stride frequencies decrease from terrestrial bipedalism, through arboreal climbing on inclines, to horizontal walking (terrestrial and arboreal) (Fig. 5).

DISCUSSION

Gait Characteristics

The results of this study provide further insight into some of the distinguishing features of African ape locomotion, and of primate locomotion in general. Adult African apes typically use knuckle-walking during terrestrial quadrupedal locomotion [Doran, 1997; Tuttle, 1967] during which the hindlimb often overstrides the ipsilateral hand [D'Aouët et al., 2004; Hildebrand, 1967; Larson, 1998; Larson & Stern, 1987]. Surprisingly, we found knuckle-walking to be maintained on a horizontal arboreal support (though whether or not this is related to the diameter of the beam was not tested). This is particularly interesting because Doran [1993] found that bonobos in the wild actually exhibit palmigrade quadrupedalism more than knuckle-walking (compared to Tai chimpanzees), on substrates larger in diameter than the arboreal support used in the current study; furthermore, Doran stipulates that knuckle-walking would require an even larger substrate (i.e., greater than the 15–20 cm boughs observed during her study). That being said, the individuals presently housed at Planckendael Zoo (most of which are different to those used for the current study) also exhibit knuckle-walking on the horizontal arboreal supports in their hall, which are similar in diameter to that used in this study; thus, the pattern observed here is still maintained.

The bonobos always utilized the grasping abilities of their feet when walking on an arboreal substrate. While walking, the feet were placed with an abducted hallux, whether or not the feet were firmly grasping. This abduction of the hallux has also been observed in arboreal quadrupedal and bipedal

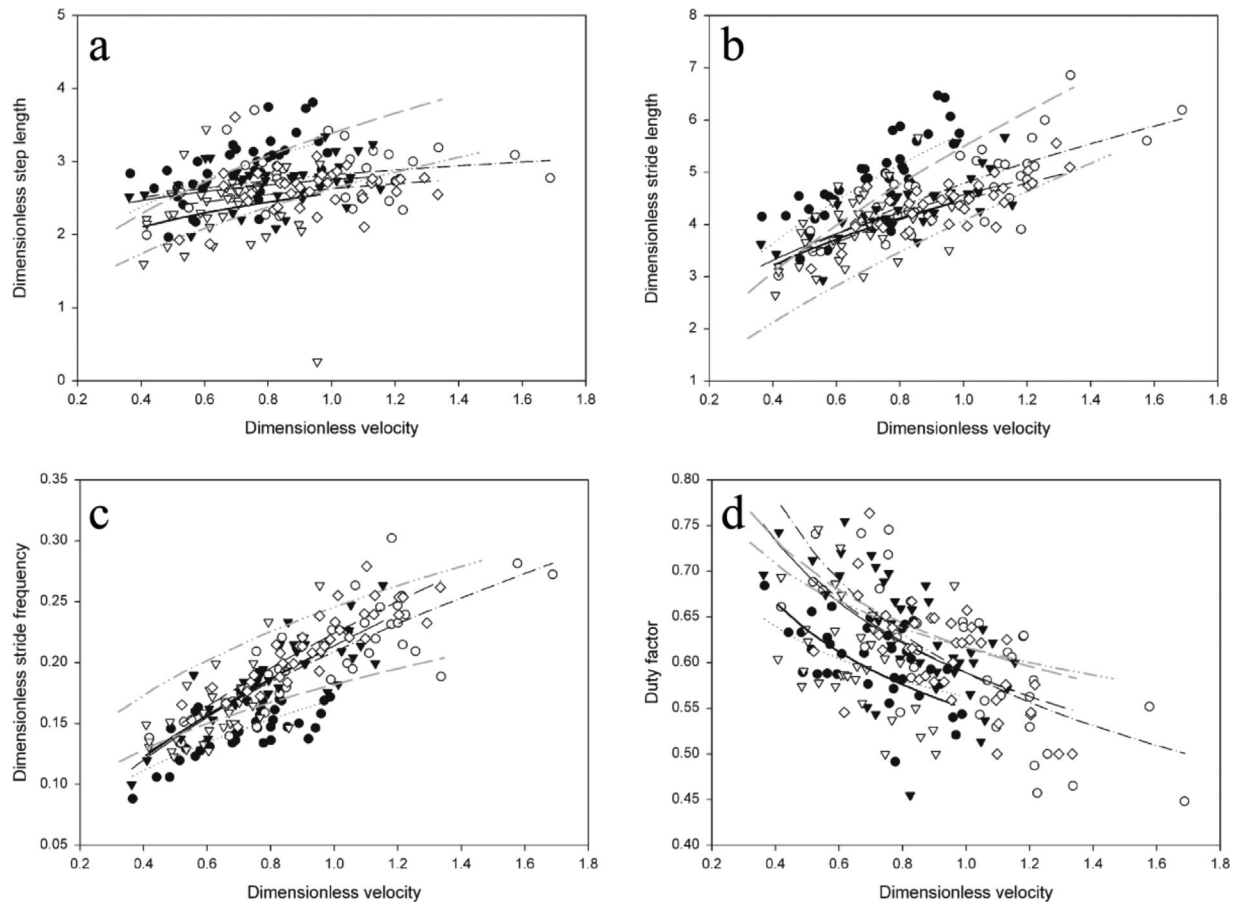


Fig. 3. Dimensionless spatio-temporal variables as a function of dimensionless velocity for the different substrate inclines: 0° (filled circles), 30° (open circles), 45° (open diamonds), 60° (filled triangles), and 90° (open triangles). Power functions are drawn for both arboreal and terrestrial (from Aerts et al. [2000]) substrate conditions: 0° (dotted line), 30° (dash-dot line), 45° (dashed line), 60° (full line), 90° (thick full line), quadrupedal terrestrial (gray dashed line), and bipedal terrestrial (gray dash-dot line).

locomotion in the wild [Susman et al., 1980], and may have an important stabilizing function, as the grip moment counters the moment acting on the body's COM. It was observed that, with increasing incline, the hands were gradually used more and more in a grasping posture. Similarly as for the feet, this may point to a greater need for stabilization (i.e., avoiding the risk of falling backwards), suggesting that maintaining balance is more challenging with increasing incline (see hypothesis 3). However, only for vertical climbing, when hands always grasped the back of the pole, can we conclude that the arms were loaded in tension. On the other inclines, the grasping hands might still exert compressive forces (as the grasping feet are obliged to do), thus, implying that hand posture cannot at all inclines be used to detect the emergence of the risk of backward tumbling. That knuckle-walking was occasionally seen even on the 60° incline may suggest that this mandatory shift in the mechanical locomotor constraints occur in bonobos only on the steepest incline (90°) (see hypothesis 2).

We also observed overstriding in only 12% of horizontal arboreal trials. However, the overstriding pattern differs between arboreal and terrestrial sequences. In terrestrial locomotion, one overstriding foot may be placed medial to the ipsilateral hand ("inside foot") whereas the other may be placed lateral to the ipsilateral hand ("outside foot"). This influences the orientation of the body with respect to the direction of progression: the body is positioned obliquely, which implies that if the left foot is "inside," the longitudinal body axis will be shifted to the right [D'Aout et al., 2004]. For arboreal locomotion, animals are restricted to the more linear course of the branch and do not have the possibility of placing their feet laterally. Consequently, this study shows that when bonobos overstride during 0° arboreal locomotion this is done with one foot only, namely the "outside foot." The absence of an overstriding "inside foot" on a horizontal arboreal support is probably due to problems with stability. Just prior to foot touchdown, the foot would need to manoeuvre between the contralateral foot and the

TABLE IV. Matrix Representation of the Tukey Post-Hoc Test, Showing the Significant Differences in Exponent (Italicized, Right Side) And/or Factor (Normal, Left Side) of the Power Function Between the Hindlimb Spatio-Temporal Variables for the Different Substrate Conditions

	0°	30°	45°	60°	90°	Q terr N ^a	B terr ^a
0°		–	–	–	–	–	<i>DSL</i> **
30°	DSF*** DSL*** DF*	–	–	–	–	<i>DSL</i> * <i>DStL</i> **	<i>DSL</i> ** <i>DStL</i> ** <i>DSF</i> **
45°	DSF*** DSL*** DF** DStL**	–	–	–	–	–	<i>DSL</i> ** <i>DStL</i> * <i>DSF</i> *
60°	DSF*** DSL*** DF** DStL**	–	–	–	–	<i>DSL</i> * <i>DStL</i> *	<i>DSL</i> ** <i>DStL</i> ** <i>DSF</i> **
90°	DSF*** DSL*** DStL***	DF*	DF**	DF**	–	–	<i>DSL</i> ** <i>DSF</i> *
Q terr ^a	DSF** DSL* DF**	–	DStL**	DStL*	DF** DStL**	–	–
B terr ^a	DSF*** DSL*** DF*** DStL***	DSF*** DSL*** DStL**	DSF*** DSL***	DSL*** DStL**	DSF*** DSL*** DF***	DSF*** DSL*** DStL***	–

DStL, dimensionless step length; DSL, dimensionless stride length; DSF, dimensionless stride frequency; DF, duty factor.

*P-value between 0.05 and 0.01; **P-value between 0.01 and 0.001; ***P-value < 0.001.

^aData on terrestrial quadrupedal (Q terr) and bipedal (B terr) locomotion are from Aerts et al. [2000].

ipsilateral hand on a narrow support, thus causing an unstable cramped posture. Unlike terrestrial quadrupedalism, during horizontal arboreal quadrupedalism the body axis (crown-coccyx) is kept in line with the direction of progression. This variation in overstriding between horizontal terrestrial and arboreal substrates, as well as the absence of overstriding on inclined substrates (see Table I), further supports the premise that the pressure to maintain balance increases with incline (see hypothesis 3).

We also hypothesized that there will be an increase in the proportion of asymmetrical footfall patterns with incline. This hypothesis was only partly supported; asymmetric footfall patterns only increased for the forelimbs with increased incline (yet, not in a systematical way; see Table I). In contrast, the proportion of footfall asymmetries for the hindlimbs remained low on all inclines. This pattern likely reflects the dominance of hindlimbs in support and propulsion.

The prevailing view has been that adult non-human primates, in contrast to virtually all other quadrupeds, use diagonal-sequence symmetrical gaits almost exclusively [e.g., Cartmill et al., 2002; Hildebrand, 1967; Young et al., 2007]. When bonobos walk quadrupedally on a flat walkway, they typically use a diagonal-sequence walking gait [D'Août et al.,

2004]. This study demonstrates that this gait type is retained on an arboreal horizontal support as well. However, a review of previous studies that detail gait patterns in various primate taxa indicate that lateral-sequence gaits are more common than the aforementioned prevailing view would suggest (for an overview, see Vilensky & Larson [1989]). Indeed, with increasing incline, there is greater variation in gait patterns [Hirasaki & Matano, 1996; Prost & Sussman, 1969; Vilensky et al., 1994]. Although bonobos still use diagonal-sequence gaits on an inclined arboreal substrate, they do not do so consistently, but rather engage more in lateral-sequence gaits. Two of the possible advantages underlying this switch from a diagonal pattern to a lateral one are related to avoiding falls, a selective pressure which leads to adaptations that aid stability [Carlson & Demes, 2010]. The first is particularly applicable to this study; because the hands and feet are placed in close alignment on a narrow longitudinal support, the foot of a swing phase hindlimb would collide with the hand of the ipsilateral forelimb in the case of a diagonal footfall pattern [Hildebrand, 1967; Schmitt, 2003; Shapiro & Raichlen, 2006; Vilensky & Larson, 1989; but see Schmidt, 2005]. Secondly, in the context of a more natural setting, when a forelimb touches down on an unstable substrate, the body remains well supported given

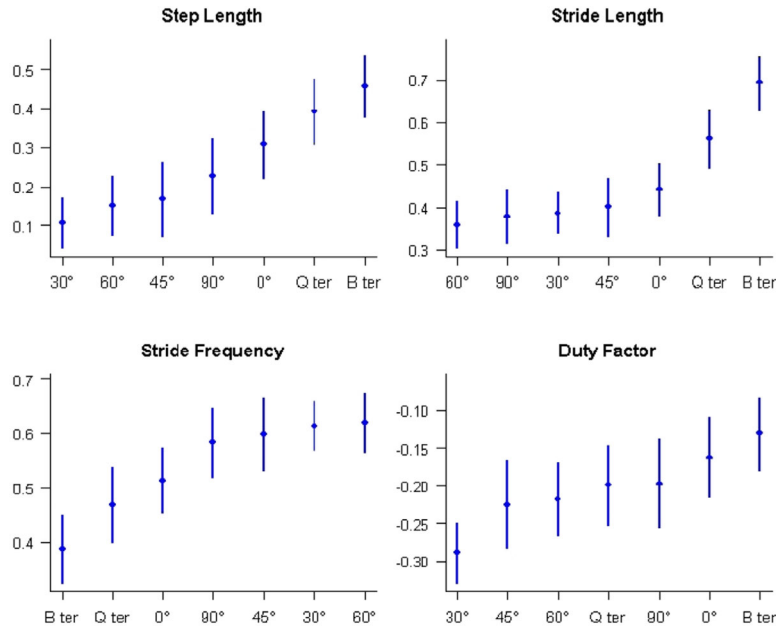


Fig. 4. Exponent of the power function (“a”) for the different spatio-temporal variables with velocity. Means and standard errors of the estimates for all substrate conditions are shown. Data on terrestrial (bipedal and quadrupedal) locomotion are from Aerts et al. [2000].

that a diagonal limb pair lies below the trunk forming a stable bipod [Shapiro & Raichlen, 2005]. Our results are in line with these assumptions; the proportion of lateral gait sequences increased with incline (except on the vertical substrate; but see below), suggesting that the need to maintain balance and stability becomes increasingly important with increasing incline (see hypothesis 1 and Table II).

Bonobos are not the only primates to engage in lateral-sequence gaits. Other studies observed such gaits on terrestrial substrates in juvenile baboons [Shapiro & Raichlen, 2005], capuchin monkeys [Carlson & Demes, 2010; Wallace & Demes, 2008] and squirrel monkeys [Vilensky et al., 1994]; on horizontal arboreal supports in macaques [Dunbar & Badam, 2000] and the common

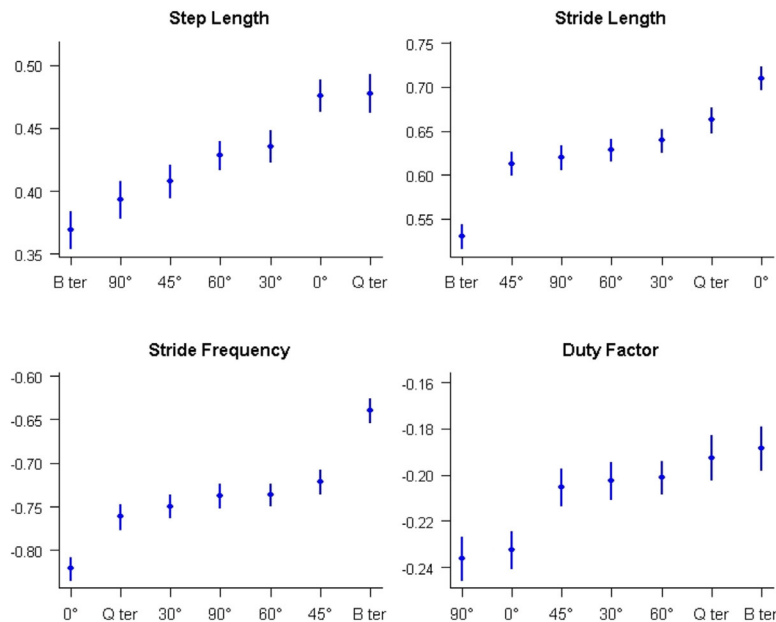


Fig. 5. Factor of the power function (“b”) for the different spatio-temporal variables. Means and standard errors of the estimates for all substrate conditions are shown. Data on terrestrial (bipedal and quadrupedal) locomotion are from Aerts et al. [2000].

marmoset [Schmitt, 2003]; on inclined and/or declined arboreal supports in sugar gliders (a relevant marsupial study; Shapiro & Young [2010]) and tamarins [Nyakatura et al., 2008; Nyakatura & Heymann, 2010]; and, albeit less pronounced, on flat inclined supports in New World Monkeys [Prost & Sussman, 1969] and some species of strepsirrhines [Stevens, 2003], and for vertical climbing in hominoids [Isler, 2003], and macaques [Hanna & Schmitt, 2011]. Still, the fact that bonobos can use either gait pattern on inclines may reflect the plasticity of this feature.

Effects of Substrate *Inclination* on Spatio-Temporal Variables

Spatio-temporal variables on different inclinations, from horizontal arboreal walking to vertical climbing, were evaluated to find out how they were affected by substrate inclination. Despite the wide range of inclinations, we found that each variable followed a trend in relation to speed modulation strategies: higher speeds were obtained by increasing step- and stride-length and stride frequency and decreasing duty factor in a similar manner, irrespective of the degree of inclination. These relationships are described by power functions (Table III). As argued above, the exponent “a” represents the modulation/control of the limb oscillators. It was hypothesized (hypothesis 2) that this basic mode of control would be shared on all inclines, except during vertical climbing. The results generally support this hypothesis; the exponents did not differ significantly across inclines, but they also did not differ on the vertical substrate either. This strongly suggests that the manner in which the spatio-temporal aspects of the limb oscillation are modulated in relation to speed, irrespective of the absolute magnitude of these aspects, is conserved on all inclines.

However, the above conclusions do not preclude differences in the magnitude of the spatio-temporal variables. A bonobo walking on a horizontal arboreal support takes larger steps and strides at a lower frequency and duty factor (the latter, however, being similar for 0° and 90°) than a bonobo climbing on inclined substrates at the same speed. There are no gradual changes in spatio-temporal variables with increasing incline; rather, results for all inclines are clustered together (except for duty factor, where the 90° incline differs from the other inclines). Other studies addressing the effects of substrate inclination report a similar change in stride frequency and duty factor (Nakano [2002] for the Japanese macaque; Lammers [2004] for a non-primate: the gray short-tailed opossum). Stevens [2003] found shorter stride durations in lemurids on inclines, but no consistent pattern of hindlimb duty factors was evident. In humans, higher stride frequencies and smaller step lengths occur during uphill walking

[Diedrich & Warren, 1998]. In the latter case, it could be argued that the sloping substrate provides a physical constraint (and thus an early mechanical stop) for the swinging leg, resulting in shorter steps; in contrast, while locomoting on a narrow (arboreal) substrate, the leg can—and does—swing freely next to and below the substrate. To meet the higher demands for dynamic stability when performing on narrow inclined supports, bonobos may obtain better control by combining higher stride frequencies with reduced step- and stride-lengths at any given speed (see hypothesis 3). At the same time, duty factor increases; this implies long relative contact phases with the arboreal substrate at higher frequencies, thus allowing for more accurate equilibrium corrections if necessary. Interestingly, the vertical condition, with low duty factors, is an exception. Perhaps the fact that the body is mainly suspended from above in this condition poses fewer stability and propulsion-related demands on the hindlimbs.

Effects of Substrate *Type* on Spatio-Temporal Variables

It was also hypothesized that the basic pattern of limb modulation [Aerts et al., 2000] would be conserved across both terrestrial and arboreal substrates (with the exception of the vertical substrate; but see above). This hypothesis was only partly supported. Comparisons with previous results for bipedal terrestrial locomotion [Aerts et al., 2000] show that almost all exponents differ to those for the arboreal substrates. Furthermore, stride- and step-length modulation during quadrupedal terrestrial locomotion differs when compared to some of the arboreal inclines (see Table IV). These results were unexpected because of (1) the established identical modulation control for bipedal and quadrupedal terrestrial locomotion (see Table IV and Aerts et al. [2000]) and (2) the similarity in limb modulation across all of the arboreal inclines. However, taken together, this suggests that the established differences likely reflect very subtle functional shifts. Although stride frequency and step- and stride-length always increase with velocity, there are differences in the magnitude of increase between terrestrial locomotion (both bipedal and quadrupedal) and arboreal inclined locomotion. For terrestrial locomotion, bonobos prefer to take larger steps and strides to increase walking speed, while for arboreal locomotion bonobos exhibit higher stride frequencies.

Spatio-temporal variables of arboreal horizontal walking were compared with those of terrestrial quadrupedal walking in order to quantify specifically the effects of substrate type (narrow arboreal support vs. flat walkway). None of the variable exponents differed significantly between 0° arboreal locomotion and terrestrial quadrupedal locomotion. Nevertheless, a bonobo walking quadrupedally on a horizontal

arboreal support takes larger strides at a lower frequency and lower duty factor than a bonobo walking on a flat terrestrial substrate at the same speed. All things being equal, a lower duty factor should decrease stability. However, this effect may be outweighed by their ability to grasp around the arboreal support, which can be assumed to increase stability when compared to a flat (terrestrial) substrate. Therefore, bonobos on an arboreal substrate may be capable of meeting their stability and propulsive requirements despite exhibiting a small duty factor.

Vertical Climbing

Contrary to our expectations (hypothesis 2), vertical climbing does not differ from the other inclines in terms of basic limb modulation. Apparently, the mechanical shift in locomotor constraints imposing altered limb use does not affect this aspect of control, again pointing at the presence of a conserved fundamental pattern.

In vertical climbing, hindlimb duty factor is significantly lower (for a given speed) than in the other substrate conditions (except for horizontal arboreal walking). In order to generate the same vertical impulse (force-time integral) in the direction of travel, there are two basic options: either the hindlimb force should increase considerably, or (part of) the impulse should be generated by the forelimbs. The latter possibility is not consistent with the hypothesis that vertical climbing is pre-adaptive for terrestrial bipedalism. If the forelimbs were contributing toward the impulse, this would mean that bonobo vertical climbing differs from spider-monkey climbing during which the forelimbs are used to keep the body close to the substrate (rather than for generating propulsion), which could strengthen the hindlimb muscles that are important in bipedal locomotion [Hirasaki et al., 2000]. However, quantifying the magnitude and orientation of substrate reaction forces of the forelimb is needed to resolve this issue.

The only previously published spatio-temporal data on vertical climbing in hominoids, including bonobos, are from Isler [2002a,b, 2003, 2005]; Isler & Thorpe [2003]. These authors studied climbing on a rope, as opposed to a stiff beam (as in this study); therefore, a comparison of our spatio-temporal variables with theirs may yield good insight into the impact of arboreal substrate type on vertical climbing gait. Isler [2002a] found that bonobo climbing was more diverse compared to gorillas, in terms of speed and gait patterns. Compared with other hominoids, however, the climbing kinematics of bonobos and gorillas were more similar to each other than to those of orangutans and gibbons [Isler, 2005]. As with our study, they found quite variable footfall patterns in bonobos climbing on a vertical rope;

however, our data show lower mean duty factors and higher relative climbing speeds compared to rope climbing [Isler, 2003]. On the other hand, relative stride lengths are much larger in bonobos climbing a vertical pole compared to bonobos climbing a rope. Combined, these results suggest that climbing on a highly compliant substrate, like a rope, poses a higher locomotor challenge than climbing on a rigid support.

Implications for the Evolution of Hominin Bipedalism

In the context of arboreal hypotheses on the origins of hominin bipedalism, one might predict arboreal kinematics to resemble terrestrial bipedal kinematics, though differences do not necessarily reject that hypothesis. In line with this, the similarity in limb modulation between all arboreal inclines but the differences between arboreal and terrestrial substrates may offer further insight into these origins. Aerts et al. [2000] and Nishikawa et al. [2007] argued that similarities in step- and stride-length and stride frequency (irrespective of their actual magnitudes) relative to locomotor speed, suggested that the basic aspects of limb control (i.e., at the supraspinal level; see Fig. 16 in Nishikawa et al. [2007]) for quadrupedal and bipedal terrestrial locomotion were similar. Applying this rationale to the current results leads to the conclusion that the same may hold true for horizontal quadrupedal arboreal locomotion: limb modulation generally did not differ significantly from that observed for terrestrial locomotion. This pattern changes, however, when considering inclined arboreal locomotion. Although the exponents of the aforementioned variables in relation to speed seem to cluster mutually over all inclinations, they do differ significantly from those observed in, primarily, terrestrial bipedal locomotion (except for step length for 90°). It should be mentioned that kinematic features are unlikely to mirror motor patterns perfectly. However, they are a good proxy in situations where data can only be collected in a strictly non-invasive fashion, as is the case in the present study (for instance, the option of using electromyography on bonobos in a zoo is not practical, ethical, or legal).

Taken together, these results might point to differences in basic limb control between horizontal and inclined (arboreal) locomotion, rather than between terrestrial and arboreal substrates. In this respect, and only relying on spatio-temporal aspects of locomotion, this and the previously mentioned studies on bonobo locomotion [Aerts et al., 2000; Nishikawa et al., 2007] seem to support an origin of bipedalism from horizontal quadrupedalism, regardless of whether it is terrestrial or arboreal. Full dynamical analysis of arboreal and terrestrial

primate behavior is required to gain more conclusive insights into which of these habitual bipedalism originated from.

CONCLUSION

The results of this study show that there are differences in the gait characteristics and spatio-temporal variables of bonobos with increasing arboreal substrate inclination. The hands gradually shift from a knuckle-walking posture to a grasping posture, primarily to maintain stability; this is further aided by the grasping abilities of the feet, crucial to which is the abduction of the hallux. A rise in incline is also met with a rise in the occurrence of lateral-sequence gaits, perhaps to prevent falls and limb collisions. With respect to spatio-temporal variables, there is no progressive change with increasing incline; rather, they cluster together—the exception being duty factor on the 90° incline. The pattern of speed modulation for these variables is comparable between the horizontal arboreal condition and the terrestrial quadrupedal condition; this suggests a similarity in the motor control for both. In the context of the evolution of bipedalism, the similarities in speed modulation between the horizontal arboreal condition and the terrestrial quadrupedal condition point to an origin from horizontal quadrupedalism, irrespective of whether the substrate is arboreal, or terrestrial.

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