

Spatio-Temporal Gait Characteristics of the Hind-Limb Cycles During Voluntary Bipedal and Quadrupedal Walking in Bonobos (*Pan paniscus*)

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ABSTRACT Spatio-temporal gait characteristics (step and stride length, stride frequency, duty factor) were determined for the hind-limb cycles of nine bonobos (*Pan paniscus*) walking quadrupedally and bipedally at a range of speeds. The data were recalculated to dimensionless quantities according to the principle of dynamic similarity. Lower leg length was used as the reference length. Interindividual variability in speed modulation strategy of bonobos appears to be low. Compared to quadrupedal walking, bipedal bonobos use smaller steps to attain a given speed (differences increase with speed), resulting in shorter strides at a higher frequency. In the context of the ("hybrid") dynamic pattern approach to locomotion (Latach, 1998) we argue that, despite these absolute differences, intended walking speed is the basic control variable which elicits both quadrupedal and bipedal walking kinematics in a similar way. Differences in the initial status of the dynamic system may be responsible for the differences in step length between both gaits. Comparison with data deduced from the literature shows that the effects of walking speed on stride length and frequency are similar in bonobos, common chimpanzees, and humans. This suggests that (at least) within extant homininae, spatio-temporal gait characteristics are highly comparable, and this in spite of obvious differences in mass distribution and bipedal posture. *Am J Phys Anthropol* 111:503-517, 2000. © 2000 Wiley-Liss, Inc

Paleo-anthropologists generally agree that the development of habitual bipedalism has been a key event in human evolution (e.g., Susman, 1984; Alexander, 1992a; Fleagle, 1992; Kelly, 1992; Senut, 1992; Wood, 1992; Zihlman, 1992; Benton, 1997). At this moment, however, the fragmentary nature of the fossil and paleological records impedes the precise reconstruction of the adaptive sequence (or sequences) that led to the shift from facultative to habitual orthograde walking during the early hominid stage (Wood, 1992). Studying the locomotor performance of living primates may offer a

way out of this impasse (e.g., Foley, 1992; Potts, 1992; Hunt, 1994, 1996; Moore, 1996). Understanding the relationship between form and function in living primates seems essential in any attempt to reconstruct the locomotor behavior of extinct primates from bony remains (Fleagle, 1999, p. 325). Such "understanding" requires more

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than merely correlating design with behavior; it must include knowledge of the physiological and mechanical principles underlying the association between design and behavior. Also, because none of the extant apes can be considered a perfect model for the hominid ancestor, our approach should be comparative, and requires data from as many relevant ape species as possible (Fleagle, 1979, 1999; Fleagle et al., 1981; for debate, see Kinzey, 1987). Therefore, we are studying the mechanistic and behavioral aspects of occasional bipedal walking in extant African apes. We believe that comparisons with the kinesiology of the preferred quadrupedal gait, and with that of walking in modern humans, may point at design or behavioral constraints that have precluded habitual bipedalism in those nonhuman ape species. Insights gained in this way can facilitate the interpretation of the sparse paleontological remains of early hominids.

Biochemical evidence shows that chimpanzees are the closest relatives of the hominids (e.g., Friday, 1992; Goodman, 1992; Sibley, 1992; Wood, 1992; Borowick, 1995), making them most suitable as research subjects in the above context (cf. Sussman, 1987; Zihlman and Lowenstein, 1983; Kano, 1992; Hunt, 1994, Hunt, 1996; Moore, 1996; Zihlman, 1996). The kinesiology of locomotion has been studied extensively in the common chimpanzee *Pan troglodytes* (e.g., Jenkins, 1972; Bauer, 1977; Kimura et al., 1977, 1983; Alexander and Maloiy, 1984; Ishida et al., 1985; Kimura, 1985, 1990; Kimura, 1996; Okada, 1985; Demes et al., 1994; Reynolds, 1987; Shapiro and Jungers, 1988; Tardieu, 1990, 1991; Li et al., 1996). Apart from the data presented in Tuttle et al. (1991, 1992), however, quantitative kinesiological data for the bonobo (*Pan paniscus*), are lacking. This is unfortunate, because it has been argued that bonobos resemble the common hominoid ancestor and the early hominids more than any other African ape species in several aspects related to locomotion (body build: Zihlman, 1984; "postcranium, in particular the overall limb proportions and feet:" McHenry, 1984; see also Zihlman and Cramer, 1978; McHenry and Corruccini, 1981; Kano, 1992).

In this paper, we describe and compare stride frequency, stride length, step length, and duty factor (i.e., the spatio-temporal gait variables) of the hind limbs during voluntary bipedal and quadrupedal walking over a range of speeds. More and more it is conceived that locomotor patterns and behavior are, to a large extent, the automated expression of the intrinsic physical properties of the entire locomotor system (electrophysiological dynamics of the neuromuscular component; mechanical dynamics of the musculoskeletal and environmental component) driven by a simple, continuous command, instead of being strictly controlled in all, or many of its details (i.e., dynamic pattern approach to locomotion: e.g., Holt et al., 1990, 1991; Schöner et al., 1990; Stewart and Golubitsky, 1992; Thelen and Smith, 1994; Diedrich and Warren, 1995, 1998a,b; Stewart, 1995; Abernethy et al., 1997; Latach, 1998).¹ Clearly, independent descending control (conscious or not) can still shift the behavior of the locomotor (or any other) system away from the stable conditions, leading to alternative movement patterns. This is the "hybrid" model according to Latach (1998: p. 177–178; see Bonnard and Pailhouse, 1993; Zijlstra et al., 1995; Danion et al., 1997 for experimental studies). In the context of this ("hybrid") dynamic pattern approach to locomotion, the relationships between spatio-temporal gait characteristics and the speed of unrestrained, voluntary locomotion are assumed to be primarily molded by the integrated intrinsic "design" features (e.g., physiological, morphometrical, mechanical, or biochemical) of the locomotor system (see also Enoka, 1994; Thelen and Smith, 1994; Zernicke and Smith, 1996; McFadyen and Bélanger, 1997; Van Damme et al., 1998). Voluntary walking speed is considered the basic control variable, in the form of a simple, graded, higher-level feed-forward command (e.g., McMahan, 1984; Grillner, 1985; Latach, 1998). The advantage of this approach is that, as long as

¹ In an analogous case, Fee et al. (1998) proved that no intricate motor programs are needed to produce the acoustically complex song in zebra finches. The dynamic behavior of the syrinx changes abruptly in response to smooth continuous alterations of the pressure of the air that flows through it.

TABLE 1. Individual data for the bonobos of the "Planckendael" social group

Individual (origin ¹)	Sex	Year of birth	Mass (kg)	Lower leg length (m)	Number of bouts retained for analysis	
					Bipedal	Quadrupedal
A (wild)	♀	1971	46.0	0.33		1
B (wild)	♀	1978	47.0	0.34		2
C (wild)	♀	1978	37.2	0.26	2	10
D (wild)	♂	1972	60.4	0.32	2	
E (cap.)	♂	1984	59.6	0.37		3
F (cap.)	♂	1983	26.3	0.29	3	3
G (cap.)	♂	1990	28.2	0.27	4	1
H (cap.)	♀	1993	11.6	0.22		1
I (cap.)	♂	1994	5.6	0.16	6	

¹ Wild, born in the Republic of Congo; cap. born in captivity

similar locomotor apparatuses are being compared (e.g., different modes within a species, or gaits among closely related and morphologically similar species), detailed data on the dynamics and laws of all processes underlying locomotor behavior are not required. Changes in speed modulation strategy can then be stated in terms of changes in the "integrated-design black box," in the initial dynamic state of this "black box," or in the descending modulation of that black box.

In this study, we examine how far general quadrupedal and bipedal gait characteristics exist for bonobos; how these characteristics relate to each other; and how they compare to gait characteristics for common chimpanzees and humans, deduced from data in the literature.

MATERIALS AND METHODS

The wild animal park "Planckendael" (Royal Zoological Society of Antwerp, Antwerp, Belgium) accommodates, in semi-natural circumstances, the largest social group of bonobos in the world (Van Elsacker et al., 1993). When data were collected (September 1996), the group consisted of the 9 individuals for whom relevant information is compiled in Table 1.

Lateral-view video recordings (50 Hz; Panasonic F15 S-VHS) were made when the animals were walking along a 7-m-long wall (height, 2.5 m), placed perpendicular to the camera (distance between wall and camera, 9 m) and provided with a reference grid. This wall and a water moat forced the animals to move over a strip of land with a width of 3 m in order to reach their outdoor

enclosure. Animals were habituated to the experimental conditions before data were collected.

Animals could adopt their preferred gait at any time, but bipedal walking was encouraged by permitting them to collect small food items (fruit) at the entrance of the passage to the enclosure. Video sequences were only retained for further analysis when the animals moved at a constant velocity, parallel to the reference wall (chalk lines were drawn at 0.5-m intervals, on the ground and parallel to the wall, to assess this condition). Furthermore, at least one complete stride had to be visible on the images. Table 1 shows the number of bipedal and quadrupedal walking sequences per individual that was retained for further analysis. The video sequences were provided with a time code (Panasonic AG-IA232TC-interface) and played back field by field (Panasonic AG-7350 S-VHS). For the present study, the following body points were digitized (NAC-1000 XY-coordinator): hip, knee left and right, heel left and right, and distal-most toe-tip left and right. Body markers could not be used because direct contact with the animals was not feasible.

Prior to the experiments, a planar calibration frame was recorded at the front and the back of the passage between the wall and the moat (6 and 9 m from the camera, respectively). In this way, a scaling factor could be determined at any depth of the scene (changing linearly between the calibration positions). This allowed proper scaling of the data sets, since the position of the animals could be assessed from the parallel chalk lines on the ground (see above).

Magnitude and constancy of the walking velocity were assessed from the linear regression of the horizontal hip displacement against time. The slope of the regression equals the locomotor speed, and the coefficient of determination (R^2) estimates the linearity (i.e., constant speed) of the relation. For all retained sequences, R^2 values were above 0.97. From the digitizations, we determined hind-limb stride length, stride frequency, step length, and duty factor. According to definitions by Alexander (1977a,b), stride length equals the distance travelled by the body during a complete cycle. Step length is the displacement of the body during the phase that (any part of) a particular foot touches the ground, and duty factor is the fraction of the cycle duration of such a ground-contact phase. Stride lengths were measured from time-plots of the horizontal displacement of the feet (cf. Van Damme et al., 1998). Cycle duration (i.e., 1/frequency) and contact times were determined from time-plots of the displacement of the toe and heel of a particular foot relative to the hip (cf. Van Damme et al., 1998). Duty factor was calculated as "1/contact time," and step length was obtained by multiplying contact time with locomotor speed. The independent measurement of frequency and stride length allowed evaluating the accuracy of the procedure: the slope of the regression of the product of frequency and stride length against measured speed should not differ significantly from one. Also, the intercept of this relationship should not differ from zero. These premises were confirmed by regression analysis (bipedal and quadrupedal slopes did not differ significantly from 1: both $P > 0.05$; intercepts did not differ from 0: both $P > 0.05$), indicating that our measurements were reliable.

To relate the dynamics of walking of the different-sized test subjects (see Table 1) and to allow comparison with data from man and common chimps gathered from the literature, all variables were normalized. Similar dynamic walking is achieved only when Froude numbers are equal (v^2/gl , where v = walking speed, g = gravitational acceleration, and l = an individual length characteristic for the locomotion, usually leg length; Alexander, 1992b; Zatsiorsky et al., 1994; Hof, 1996; Vaughan et al., 1997). Since precise measures of the segment

lengths of the test subjects could not be obtained (no direct interactions allowed), they had to be estimated from the video recordings. Lower leg length (in practice, the distance from knee to heel) proved to be least sensitive to digitization errors (knee and heel were easily detectable on the unmarked specimens) and is undoubtedly proportional to total hind-limb length. Therefore, we used lower leg length (i.e., knee-heel distance averaged per individual for all retained sequences) as the characteristic dimension in the normalization procedure. The square root of the Froude number is treated as a dimensionless walking speed (see, for instance, Alexander, 1992b,c; Hof, 1996; Vaughan et al., 1997). Frequency is made dimensionless by multiplying it with $(\text{lower leg length}/g)^{1/2}$ (see Alexander, 1977b; Hof, 1996; Vaughan et al., 1997). Stride length and step length were simply divided by the length of the lower leg to obtain dimensionless figures. The duty factor is a dimensionless variable as such.

We also compared our data for the bonobo with data for humans and common chimpanzees. For human walking, data were obtained from Alexander (1992c; digitized from his figure on p.39; frequencies = speed/stride length) and from Adachi et al. (1996; his Table 1). Froude numbers, frequencies, and stride lengths were (re)calculated assuming a ratio (lower leg length + foot height)/total leg length = 0.54; cf. Winter, 1990a). To our knowledge, only Alexander and Maloiy (1984; one specimen) and Reynolds (1987; two specimens) published stride lengths for a range of walking speeds for the common chimpanzee. Only the data of the latter publication could be used for comparison (see Discussion, below). Except for body mass, no morphometric data were mentioned for the two common chimpanzee specimens used in this study. Therefore, the data on body mass and hind-limb length of common chimpanzees presented by Kimura (1990, his Table 1) were regressed (log-log linear regression, $R^2 = 0.98$; $P < 0.0001$), and the resulting equation was used to estimate the hind-limb length of Reynolds' specimens. According to the X-rays presented by Jenkins (1972), lower leg length (from knee to heel as it is measured on the

TABLE 2. Spatio-temporal gait characteristics of bonobos

Individual	Velocity (m/sec)	Stride length (m)	Step length (m)	Stride frequency (1/sec)	Duty factor	Gait ¹
D	0.96	0.83	0.62	1.10	0.68	b
D	0.57	0.57	0.49	0.87	0.75	b
C	1.30	1.00	0.69	1.26	0.64	b
C	1.64	1.18	0.74	1.45	0.63	b
F	1.95	1.18	0.74	1.61	0.58	b
F	1.40	1.08	0.64	1.26	0.58	b
F	0.74	0.64	0.50	1.07	0.73	b
I	1.12	0.59	0.37	1.93	0.66	b
I	1.30	0.69	0.43	2.09	0.58	b
I	0.97	0.58	0.46	1.81	0.61	b
I	1.19	0.70	0.49	1.87	0.62	b
I	1.24	0.63	0.41	2.03	0.68	b
I	1.63	0.81	0.46	2.19	0.62	b
G	1.97	1.12	0.67	1.57	0.55	b
G	1.77	1.27	0.78	1.38	0.64	b
G	2.39	1.48	0.90	1.63	0.62	b
G	2.05	1.22	0.76	1.66	0.64	b
A	0.58	0.89	0.67	0.65	0.75	q
C	1.28	1.26	0.90	0.93	0.66	q
C	1.28	1.33	0.83	0.98	0.63	q
C	1.46	1.34	0.86	1.09	0.64	q
C	1.22	1.26	0.89	0.91	0.67	q
C	1.14	1.29	0.81	0.90	0.64	q
C	1.09	1.25	0.87	0.85	0.63	q
C	2.15	1.54	0.97	1.31	0.59	q
C	1.89	1.57	0.86	1.26	0.57	q
C	1.64	1.50	0.87	1.12	0.59	q
C	1.91	1.56	0.87	1.28	0.58	q
B	0.79	0.95	0.76	0.75	0.73	q
E	1.12	1.48	0.95	0.80	0.67	q
E	1.23	1.43	0.96	0.86	0.67	q
E	0.81	1.20	0.80	0.69	0.69	q
G	0.92	1.11	0.77	0.85	0.70	q
F	1.41	1.57	0.92	0.91	0.60	q
F	1.25	1.41	0.91	0.92	0.67	q
F	1.05	1.09	0.75	1.00	0.71	q
H	0.88	0.95	0.65	0.94	0.70	q

¹ b, bipedal; q, quadrupedal

bonobo sequences) constitutes about 50% of the total leg length (as it is for bonobos and humans) The lower leg lengths thus obtained were used to calculate dimensionless velocities and stride lengths for the common chimp (dimensionless frequencies were obtained from speed/stride length).

As bipedal running (i.e., duty factor < 0.5) by bonobos was not observed in the experiments, the analysis and discussion were limited to quadrupedal walking. Trotting and galloping were not considered.

All linear regressions (SPSS for Windows 5.0.1) were performed on \log_{10} transformed data. The relations between gait characteristics and speed were compared between locomotor modes and among species using analysis of covariance (ANCOVA; SPSS for Windows 5.0.1).

RESULTS

Bonobo gait characteristics

Table 2 presents, in absolute terms, walking velocity, stride length and frequency, step length, and duty factor for all quadrupedal and bipedal bouts mentioned in Table 1. The relationships between the spatio-temporal gait characteristics and speed are presented in Figure 1. In particular, the results for individual "I" (bipedal bouts of the smallest animal) diverge from the data of the other specimens.

To account for the considerable size differences in the present bonobo group (see Table 1), we normalized the gait characteristics and plotted them against dimensionless speed (Fig. 2). Now the data points for individual "I" no longer stand

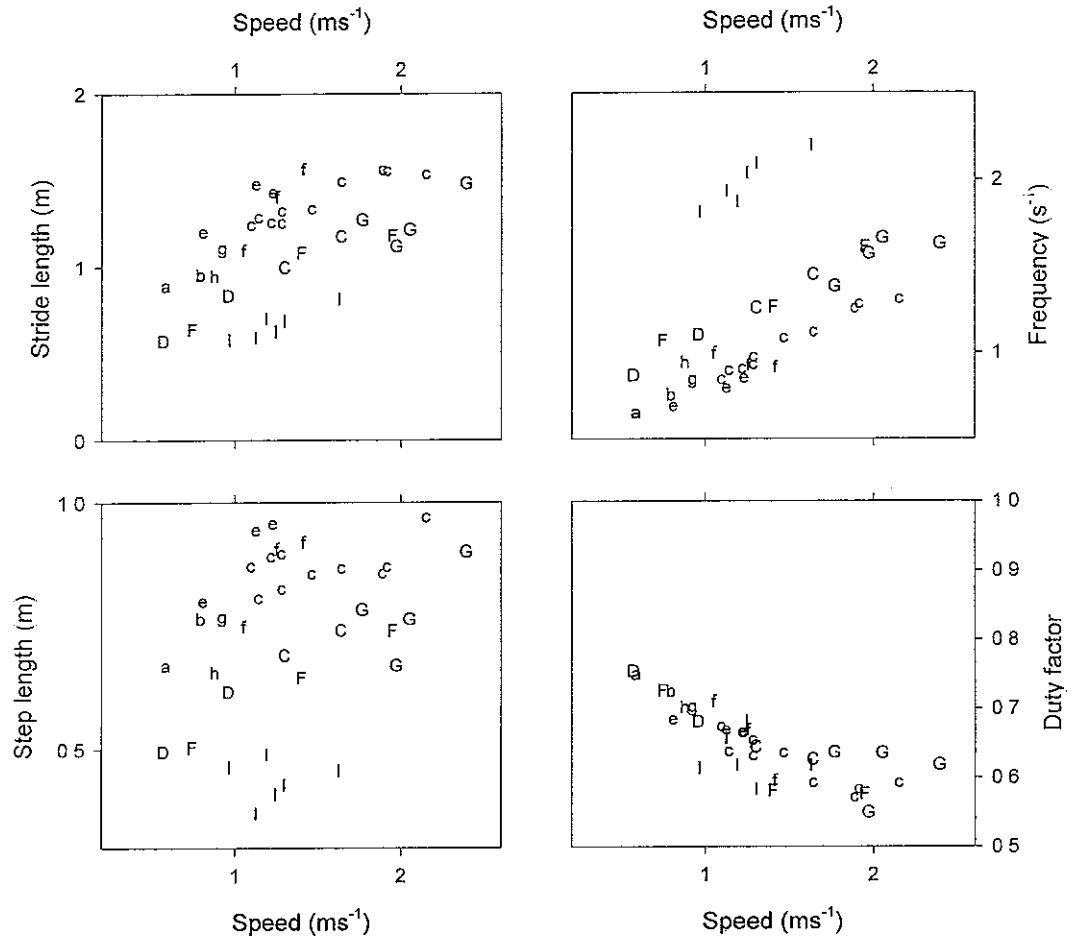


Fig. 1. Gait characteristics as a function of speed in bipedally (upper case labels) and quadrupedally (lower case labels) walking bonobos. Corresponding labels refer to the same individual (see also Table 1).

out. All relationships can be described in a highly significant way by means of a power function ($Y = 10^b \text{ speed}^a$, see Table 3; Fig. 2). For none of the variables did the exponents of the power functions (the a in the equation above) differ significantly between bipedal and quadrupedal walking (see Table 3). The factors (10^b in the above equation), however, do differ, except for the duty factor (Table 3). Thus, a bonobo walking quadrupedally takes larger strides at a lower frequency than a bonobo walking bipedally at the same speed. The relation between duty factor and walking speed does not differ between locomotor modes (Table 3; Fig. 2). Therefore, the reciprocal shifts in stride length and fre-

quency boil down to the observed differences in step length (i.e., smaller bipedal steps; see Fig. 2).

Comparison with common chimpanzees and humans

Figure 3 and Table 4 contrast bonobo walking with walking in common chimpanzees and humans. Stride lengths and frequencies were recalculated from Reynolds (1987) for chimpanzees, and from Alexander (1992b) and Adachi et al. (1996) for humans (see Material and Methods for details).

At low speeds, quadrupedal bonobos take significantly smaller strides at higher frequencies than common chimpanzees, even after normalization (Table 5; Fig. 3). How-

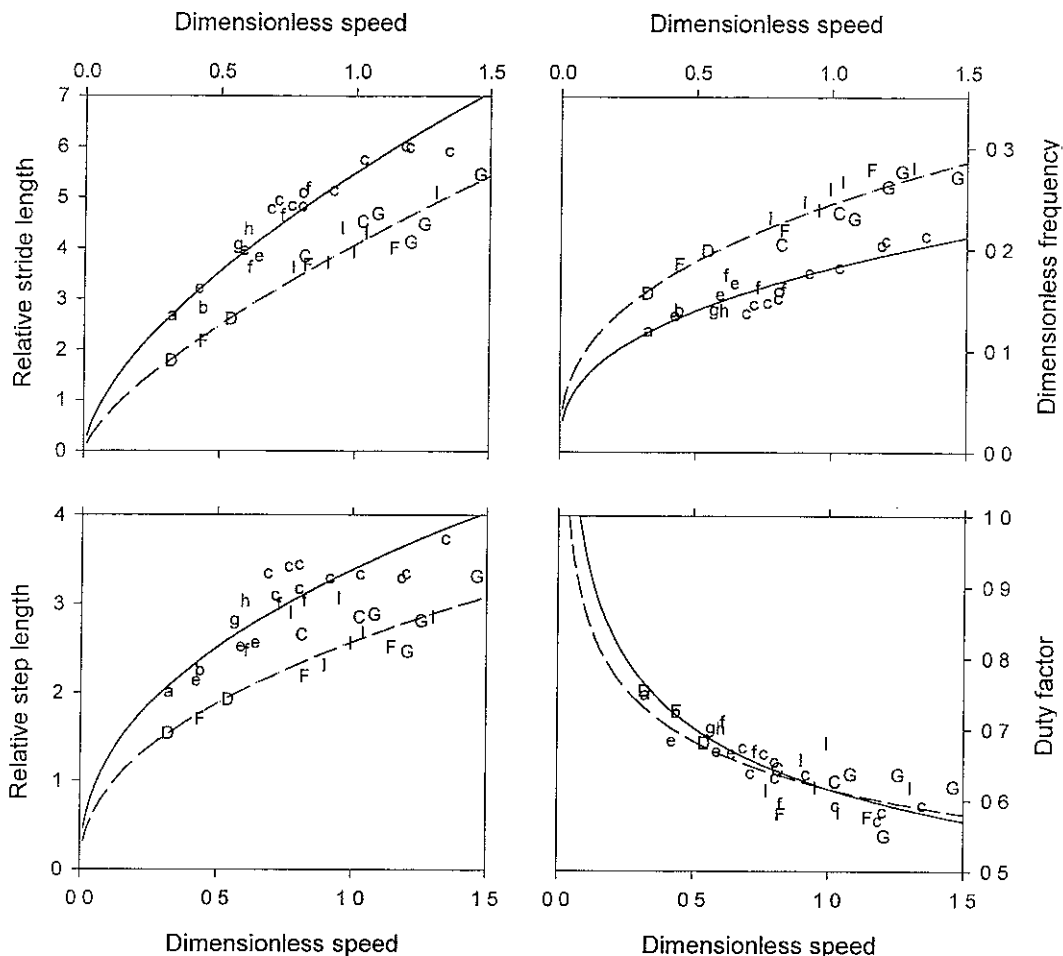


Fig 2. Dimensionless gait characteristics as a function of dimensionless speed in bipedally (upper case) and quadrupedally (lower case labels) walking bonobos. Corresponding labels refer to the same individual (see also Table 1)

TABLE 3 Parameter values ($\pm SE$) of the relations between the dimensionless variables and dimensionless speed ($Y = 10^b \cdot speed^a$) for bipedally and quadrupedally walking bonobos¹

	Bipedal		Quadrupedal		Difference between			
	a	b	a	b	Exponents (a)		Factors (b)	
					F _{1,33}	P	F _{1,34}	P
Stride length	0.71 ± 0.04	0.61 ± 0.008	0.63 ± 0.05	0.74 ± 0.10	1.66	0.26	157.87	<0.0001
Stride frequency	0.38 ± 0.03	-0.61 ± 0.006	0.38 ± 0.05	-0.74 ± 0.01	0.0007	0.98	180.0	<0.0001
Step length	0.45 ± 0.06	0.41 ± 0.010	0.43 ± 0.05	0.53 ± 0.01	0.10	0.75	67.42	<0.0001
Duty factor	-0.15 ± 0.03	-0.21 ± 0.006	-0.19 ± 0.02	-0.21 ± 0.004	1.01	0.32	0.06	0.81

¹ F-statistics and P-values denote the significance of differences between the exponents and the factors of both gaits (analysis of covariance).

ever, the difference between bonobos and chimpanzees seems to disappear at higher quadrupedal speeds (Fig. 3) In other words,

to increase speed, bonobos tend to increase quadrupedal stride length faster than common chimpanzees do

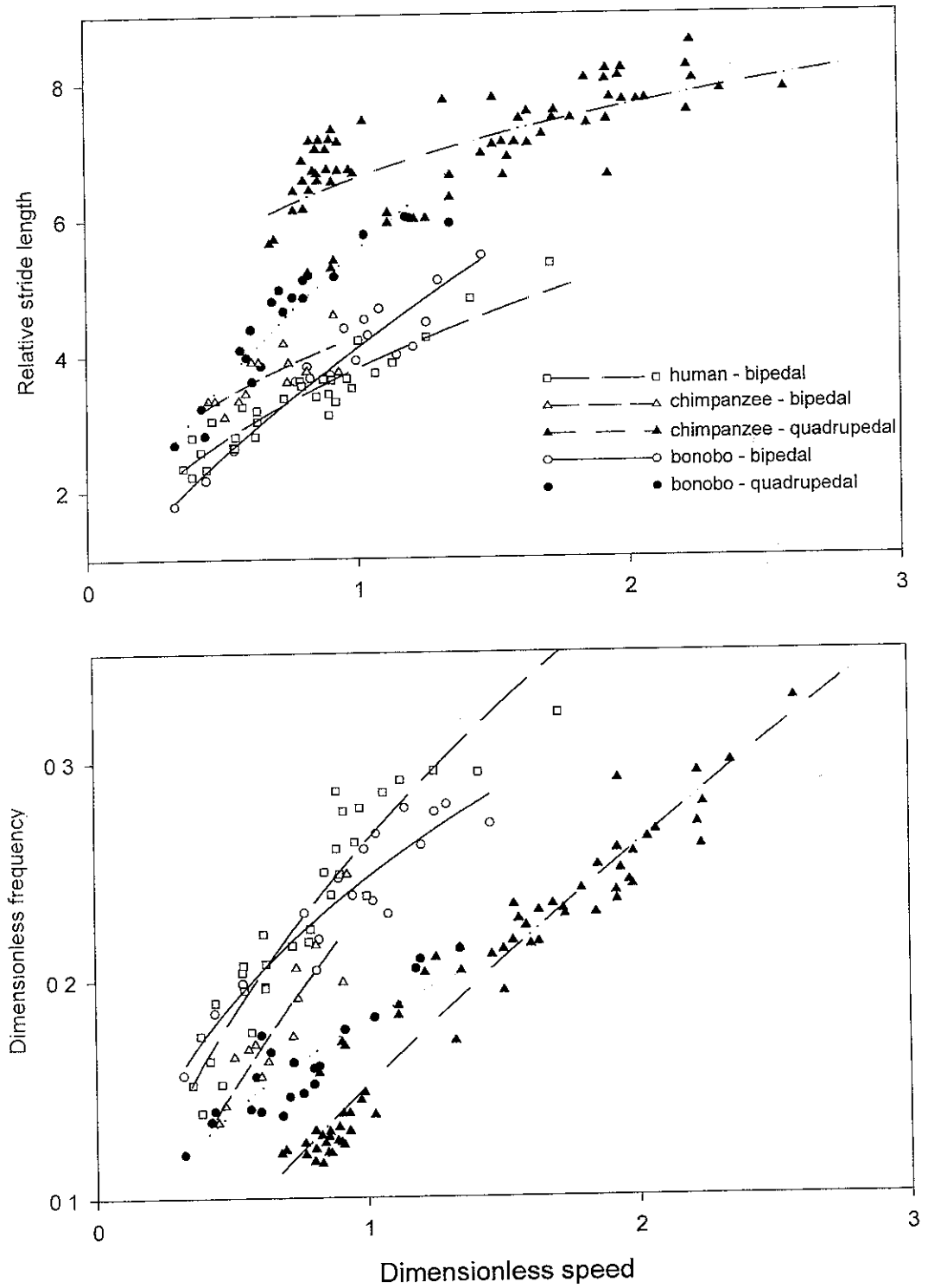


Fig. 3. Dimensionless stride length and frequency as a function of dimensionless speed in quadrupedally walking bonobos and common chimpanzees, and bipedally walking bonobos, common chimpanzees, and humans

TABLE 4. Parameter values ($\pm SE$) of the relations between dimensionless variables and dimensionless speed ($Y = 10^6 \cdot \text{speed}^2$) for common chimpanzee (Pan) and human (Homo), as recalculated from literature¹

	Bipedal		Quadrupedal	
	a	b	a	b
<i>Pan troglodytes</i>				
Stride length	0.34 \pm 0.09*	0.63 \pm 0.019*	0.21 \pm 0.025**	0.82 \pm 0.005**
Frequency	0.65 \pm 0.09**	-0.63 \pm 0.019**	0.79 \pm 0.025**	-0.82 \pm 0.005**
<i>Homo sapiens</i>				
Stride length	0.47 \pm 0.03**	0.58 \pm 0.007**	NA	NA
Frequency	0.53 \pm 0.03**	-0.58 \pm 0.007**	NA	NA

¹ See Materials and Methods. NA not applicable. * $P < 0.05$ (different from 0) ** $P < 0.001$ (different from 0)

TABLE 5. Comparison of speed modulation in the Homininae¹

	Differences between exponents		Differences between factors	
	(a)		(b)	
	F (df ₁ , df ₂)	P	F (df ₁ , df ₂)	P
Stride length BB-HB	17.50 (1, 44)	0.0001	1.3 (1, 45)	0.26
Frequency BB-HB	7.35 (1, 44)	0.009	3.11 (1, 45)	0.08
Stride length BQ-CQ	56.82 (1, 83)	<0.0001	74.82 (1, 84)	<0.0001
Frequency BQ-CQ	54.19 (1, 83)	<0.0001	76.71 (1, 84)	<0.0001
Stride length BB-CB	13.75 (1, 26)	0.001	23.36 (1, 27)	<0.0001
Frequency BB-CB	9.34 (1, 26)	0.004	110.93 (1, 27)	<0.0001
Stride length HB-CB	1.80 (1, 40)	0.19	45.12 (1, 41)	<0.0001
Frequency HB-CB	1.80 (1, 40)	0.19	45.12 (1, 41)	<0.0001

¹ BB-HB, bipedal bonobo-bipedal human; BQ-CQ, quadrupedal bonobo-quadrupedal common chimpanzee; BB-CB bipedal bonobo-bipedal chimpanzee; HB-CB, bipedal human-bipedal common chimpanzee

During bipedal locomotion, speed modulation seems similar in chimpanzees and humans, but bonobos increase stride length more and stride frequency less to obtain an equivalent change in speed (ANCOVA: comparison of exponents; see Table 5, Fig. 3). On average, however, humans and bonobos tend to have similar stride lengths and frequencies, while common chimpanzees use larger strides at lower frequencies (ANCOVA: comparison of factors; see Table 5, Fig. 3).

DISCUSSION

Gait characteristics of bonobos

In theory, any walking speed can be achieved by an infinite number of combinations of stride frequencies and stride lengths. The only boundary condition is that the product of both must match the intended speed. Despite this freedom, humans prefer specific combinations of stride frequency and length during free walking (Inman et al., 1981; Winter, 1990b; Zatsiorsky et al., 1994), most probably because energy expenditure is minimized in this way (Alexander, 1992a,c; Zatsiorsky et al., 1994; Minetti et al., 1995; Minetti and Alexander, 1997). According to the dynamic pattern ap-

proach to locomotion, a simple descending command (with an intensity directly related to intentional speed of locomotion, e.g., McMahon, 1984; Grillner, 1985; Latach, 1998), driving the intrinsic dynamic features of the locomotor system, will automatically lead to these preferred combinations of stride length and frequency.² At low speeds, both stride frequency and stride length increase (proportional to the square root of the velocity; see Table 1 in Zatsiorsky et al., 1994); at higher speeds, the stride length levels off and further velocity increase is frequency-mediated. In humans, scaling according to the principle of dynamic similarity (Alexander, 1992b; Zatsiorsky et al., 1994; Hof, 1996; Vaughan et al., 1997) effectively removes size effects and reveals a highly uniform walking pattern (e.g., Inman et al., 1981; Winter, 1990b; Skinner, 1994; Zatsiorsky et al., 1994). Of course, humans can shift their walking pattern away from the preferred step or stride length or frequency.

² The intrinsic features of the locomotor system include the coupled spinal neural oscillators and their peripheral connections, the musculoskeletal effectors the rest of the body, and the substrate

They do so when walking on stepping stones, when matching the cadence of an external cue (e.g., Bonnard and Pailhous, 1993; Zijlstra et al., 1995), or in unstable situations, to reduce the amplitudes of movement to feel more confident. Such shifts accord to the descending modulations of the "integrated-design black box" mentioned in the Introduction.

The bonobos used in this study also walk faster by increasing both stride frequency and length. The exponents of the power functions (Table 3) do not differ between bipedal and quadrupedal walking. In other words, if a gain in quadrupedal walking speed implies a doubling of the stride frequency, step length, or stride length, the same increase in velocity will also involve a doubling of the stride frequency (or step length, or stride length) during bipedal walking.³ This strongly suggests that the basic control of voluntary walking is equal for both locomotor modes (bipedal vs. quadrupedal) and is indeed related to the intentional speed of locomotion.

The divergence between bipedal and quadrupedal walking is further reduced by the observation that the differences in stride length and frequency merely result from differences in step length. This follows from the fact that duty factors (and hence contact-phase durations) do not differ between locomotor modes. Since stride length equals twice the step length minus the distance travelled during the double contact phase, stride lengths can only differ because step lengths differ. The argument holds also for differences in stride frequency (= velocity over stride length). The reduction of the step length during bipedal walking might represent an unconscious neuro-motoric compensation for the higher degree of instability for quadrupedally, the body is always supported by two or three legs. This agrees with the finding that, in humans, loss of confidence, as observed in impaired or elderly people, results in a reduction of the step length (Zatsiorsky et al., 1994; Grabiner, 1997; Vaughan et al., 1997). This accords

with the unconscious descending modulation of the "integrated-design black box" as mentioned in the Introduction.

Alternatively (or in addition), the smaller bipedal steps may be a mechanical consequence of the changes in body posture (i.e., altered initial state of the "integrated-design black box," cf. Introduction). The upper body is kept more erect during bipedal walking (shift from about 35° to 70° with respect to the horizontal; measured in the sagittal plane), coinciding with a steeper pelvic inclination (cf. Jenkins, 1972). Apart from a possible, direct effect on the mobility of the femur in its articulation with the pelvis, such a reorientation probably also affects muscle torques, through changes of the moment arms and the exploited regions of the length-tension and force-velocity relationships of the muscles involved. In the common chimpanzee, however, kinematical analysis showed no effect of pelvic reorientation on the movement pattern of the femur (Jenkins, 1972). Thus, bipedally, the femur ranges in a more horizontal position. The geometric consequence is that fore-aft excursions of the knee with respect to the hip are smaller than for similar femur rotations during quadrupedal walking. Obviously, this also decreases step length and must be coupled to an adjustment of the excursion of the lower leg segments. Reynolds (1987) suggested that the large quadrupedal strides of chimpanzees are needed to support most of the body weight on the hind limbs throughout a stride. To elaborate this aspect further, detailed kinematical analysis, measuring linear and angular displacements of body segments of walking bonobos will be needed.

Bonobos, like humans, seem to exhibit species-specific spatio-temporal gait characteristics. This is strongly suggested by the graphs presented in Figure 2. Ideally, an analysis of variance, with size as covariate should be carried out to compare individual spatio-temporal gait characteristics. However, such an analysis would require a sufficient number of sequences over a comparable range of velocities for all individual animals, a condition that, unfortunately, is not met by the present data set. As any interaction with the ani-

³Note, however, that absolute figures of the gait variables may differ between both locomotion modes

mals is forbidden (e.g., to induce them walking at the required speeds), it is practically impossible to collect such a data set. Nevertheless, the good fit of the regressions relating gait characteristics to speed (R^2 between 0.77–0.94), and the fact that the trials of individuals show considerable overlap along the calculated curves (Fig. 2), indicate that, at least in our bonobo group, the interindividual variability is low. This supports the assumption of a bonobo-specific style of walking.

The above conclusions imply that sexual and ontogenetic differences in locomotor patterns are small. This is particularly clear when Figures 1 and 2 are compared. In absolute terms (Fig. 1), gait characteristics of the smallest specimen (individual "I," see Table 1) diverge strongly from those of the other individuals. However, after normalization, the data for this very young animal are in line with the rest (Fig. 2; note the good fit of the regressions through the normalized data). This accords to findings in humans: when properly scaled (i.e., following the principle of dynamic similarity), there is no effect of sex (Zatsiorsky et al., 1994), and children show a mature gait from the age of 2 (Vaughan et al., 1997).

It thus seems that spatio-temporal gait variables can be reliably predicted from the regression models presented in Table 3, provided that body dimensions (*in casu* the lower leg lengths) are available.

Tuttle et al. (1991, 1992) presented stride lengths, step lengths, frequencies, and walking speeds for bipedally walking bonobos, but unfortunately data were averaged for (probably one locomotion cycle of) two individuals differing considerably in size (stature: $0.929 \text{ m} \pm 0.271 \text{ SD}$). Therefore, it is practically impossible to incorporate these data in a credible way in the present normalized data set.

Interestingly, the number of useful bipedal sequences decreased with the age of the specimens (see Table 1). This suggests that younger individuals may be more apt to walk bipedally, but the present data set is certainly too small to draw decisive conclusions in this respect.

Comparisons with common chimpanzees and humans

Despite the many publications dealing with locomotion in the common chimpanzee, only two studies (Alexander and Maloij, 1984; Reynolds, 1987) related spatio-temporal gait characteristics to walking speed in this species. Kimura (1990) presented individual cycle duration (= 1/frequency) and stride length for 7 specimens ranging from about 1–19 years old, but, unfortunately, the data were averaged over a range of speeds and to our knowledge, the original data were not published. Tuttle et al. (1992) also presented spatio-temporal information on bipedal gait in chimpanzees, but they averaged data from 2 adults and 8 young animals, which differ considerably in size. In Alexander and Maloij (1984), relative stride length is related to Froude number for one specimen. However, the hip height, used to normalize the data, is not mentioned in the text, precluding recalculation of the data for comparison with the bonobo data set. According to Figure 2 in Alexander and Maloij (1984), stride lengths of the two available bipedal walking bouts of about identical speed do not seem to differ from the quadrupedal stride length at the same speed. This seems to contrast with the data recalculated from Reynolds (1987). Many studies of human walking suffer the same illness: the gait characteristics presented are averages for a range of speeds or for a group of test persons, or are reported for preferred speeds only (e.g., see Inman et al., 1981; Winter, 1990b; Zatsiorsky et al., 1994). Therefore, we had to restrict our comparison to the data presented by Reynolds (1987) on common chimpanzees and by Alexander (1992b) and Adachi et al. (1996) on humans. Note, however, that lower leg length was used to normalize the data sets. In addition, it should be kept in mind that the data by Reynolds (1987) on the common chimpanzee were obtained from two individuals only, with bipedal and quadrupedal tests carried out at different ages (and size; see Materials and Methods).

When walking slowly on four legs, bonobos take significantly smaller strides at higher frequencies than common chimpan-

zees, likely because angular excursions of the bonobo's legs are smaller. This might conform to the hypothesis formulated by Reynolds (1987) that large quadrupedal strides are required to support most of the body weight on the hind limbs (see above; see also Demes et al., 1994). Since the relative mass contribution of the hind legs is higher in bonobos than in common chimpanzees (Zihlman, 1984; Preuschoft et al., 1998), the body center of mass will be situated closer to the hip joint, thus requiring smaller angular excursions for weight bearing by the hindlimbs during quadrupedal walking.

Because of the limited information available on bipedal walking in the common chimpanzee (13 bouts from 2 specimens), the biological significance of the interspecific differences in gait characteristics reported remains unsettled. Perhaps the most realistic and important conclusion from Figure 3 is that the spatio-temporal characters of bipedal walking are very similar for humans, common chimpanzees, and bonobos. Indeed, at a dimensionless speed of 1 (about the average of the speed range in bonobos and humans), stride lengths and frequencies of common chimpanzees and humans differ by only 5% and 7%, respectively, from those of bonobos (calculated from the equations presented in Tables 3 and 4). This is much less than, for instance, the difference in stride length between quadrupedal and bipedal walking (in bonobos, 35%; in common chimpanzees, 55%). The apparent similarity of the relationship between dimensionless stride length (and frequency) and dimensionless speed in humans, common chimpanzees, and bonobos confirms the statement by Reynolds (1987) that "walking stride length of bipedal primates including humans only differs from other mammals because of limb length differences." Tuttle et al. (1991, 1992) also argued that gait characteristics like stride and step length are conservative within humans and great apes.

Common chimpanzees, bonobos, and modern humans differ considerably in body proportions (relative leg masses, muscularization, distribution of mass over the leg segments; Zihlman, 1984; Kano,

1992; Preuschoft et al., 1998) and in posture (erect vs. bent-hip/bent-knee walking; e.g., Crompton et al., 1998; Li et al., 1996). However, our results suggest that these differences do not greatly affect the overall dynamics of the oscillating legs (reflected in the spatio-temporal gait characteristics) during bipedal walking. In other words, spatio-temporal gait characteristics of bipedal walking in extant homininae are mainly determined by linear leg dimensions (cf. the present normalization), irrespective of the inertial properties of leg segments (mass, mass distribution) and irrespective of leg posture.

Therefore, we speculate that the spatio-temporal characteristics of bipedal strides in extinct hominids (like *Australopithecus*) matched those of similarly sized chimpanzees, or modern humans, walking at dynamically equivalent speeds (in this case, lower leg length should be used to assess similarity in size; cf. Materials and Methods). This corroborates the conclusion of Reynolds (1987) that angular excursions at the hip of the hominids that made the Laetoli footprints "were similar to that of modern humans, bipedal non-human primates, as well as mammals in general." In this case, stride lengths likely scale to limb length, indeed (cf. the present findings). Tuttle et al. (1991, 1992) also suggested that gait characteristics of the Laetoli hominids highly resembled those of humans and great apes. Jungers (1982; p. 677), on the other hand, argued that "the relatively short hind limb of Lucy implies substantial kinematic differences in bipedal gait from the modern condition." He reached this conclusion by direct morphometric comparison with a modern human of similar body mass (a pygmy of 27–30 kg), but with proportionally longer legs. Indeed, to obtain equivalent strides, Lucy would have had to walk with larger angular excursions (different kinematics). However, such an increase in angular excursions is not needed to obtain equivalent dimensionless stride lengths (stride lengths expressed in terms of limb lengths; cf. the dynamic similarity principle). Therefore, the assertion by Jungers (1982) does not contradict the present hypothesis on the

conservative nature of spatio-temporal gait characteristics.

Still, changes in segmental mass will lower the position of the center of gravity of the body. The fractional contribution of the hind leg mass in total body mass varies from 18% in the common chimpanzee, to 24% in the bonobo, to 30% in modern humans (Zihlman, 1984; Preuschoft et al., 1998). A lower center of gravity should add to the stability of (and probably to the confidence in) erect bipedal behavior. This agrees with the observation that bonobos might engage more in bipedalism than common chimpanzees (Susman et al., 1980; but see Doran, 1993: "aided arboreal bipedalism" is more frequent in common chimpanzees). According to Zihlman (1984), the general mass distribution (arms vs. legs vs. head/trunk) of *Australopithecus* is close to that of modern humans (Fig 11 in Zihlman, 1984). Maybe the coincident gain in stability was a prerequisite for the further evolution towards erect habitual bipedal locomotion in humans.

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