The origin of bipedality as the result of a developmental by-product: The case study of the olive baboon (*Papio anubis*)

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A R T I C L E   I N F O

A B S T R A C T

In this paper, we point to the importance of considering infancy in the emergence of new locomotor modes during evolution, and particularly when considering bipedal walking. Indeed, because infant primates commonly exhibit a more diverse posturo-locomotor repertoire than adults, the developmental processes of locomotion represent an important source of variation upon which natural selection may act. We have had the opportunity to follow the development of locomotion in captive individuals of a committed quadrupedal primate, the olive baboon (*Papio anubis*). We observed six infants at two different stages of their development. In total, we were able to analyze the temporal parameters of 65 bipedal steps, as well as their behavioral components. Our results show that while the basic temporal aspects of the bipedal walking gait (i.e., duty factor, dimensionless frequency, and hind lag) do not change during development, the baboon is able to significantly improve the coordination pattern between hind limbs. This probably influences the bout duration of spontaneous bipedal walking. During the same developmental stage, the interlimb coordination in quadrupedal walking is improved and the proportion of quadrupedal behaviors increases significantly. Therefore, the quadrupedal pattern of primates does not impede the developmental acquisition of bipedal behaviors. This may suggest that the same basic mechanism is responsible for controlling bipedal and quadrupedal locomotion, i.e., that in non-human primates, the neural networks for quadrupedal locomotion are also employed to perform (occasional) bipedal walking. In this context, a secondary locomotor mode (e.g., bipedalism) experienced during infancy as a by-product of locomotor development may lead to evolutionary novelties when under appropriate selective pressures.

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1. Introduction

Extant primates exhibit positional repertoires with different degrees of specialization. For example, brachiation is observed in *Hylobates* (Fleagle, 1976), bipedalism in *Homo* (Witte et al., 1991; Orendurff et al., 2008; Adolph et al., 2012), quadrupedal knuckle-walking and arm-swinging in *Pan* and *Gorilla* (Doran, 1992, 1997; Remis, 1995; Sarringhaus et al., 2014), slow quadrumanous movement and arm-swinging in *Pongo* (Thorpe and Crompton, 2006),

and pronograde locomotion (arboreal and/or terrestrial quadrupedalism) in cercopithecoids (see Hunt [2016] for an overview of the locomotor adaptations in primates). These species-specific capacities are well refined at the adult stage, yet, it is generally shown that infant primates, including humans, engage in a much broader spontaneous diversity of posturo-locomotor modes than adults (e.g., Doran, 1992, 1997; Dunbar and Badam, 1998; Wells and Turnquist, 2001; Fjortoft, 2004; Druelle and Berillon, 2013; Sarringhaus et al., 2014; Zehr et al., 2016). Coordination and control of cyclical locomotor patterns relies on the activity of coupled spinal networks of neurons (Central Pattern Generators, or CPGs), driven by descending supraspinal commands and subject to sensory feedback (Grillner, 1985; Duysens and Van de Crommert, 1998;

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Pearson, 2000; Grillner and Jessell, 2009; Maes and Abourachid, 2013). Moreover, it has been suggested that these CPGs consist of independent but interconnected rhythmogenic modules that are combined depending on the specific task (Büschges and Borgmann, 2013; Hägglund et al., 2013). From this point of view, it seems conceivable that different locomotor modes may share common neural control modules (e.g., Grillner, 1985; Dietz, 2002; Zehr, 2005). The ontogenetic diversity of behaviors at an immature stage may, therefore, assist in the correct development of coordination between body parts, as well as the development of strength and balance control. However, the hypothesis that the improvement in coordination also results from better balance and strength with age cannot be excluded. In parallel to this neuromotor maturation, the mechanical properties of the locomotor apparatus (such as mass distribution, rotational inertia, segment lengths, etc.) change in such a way that the principal locomotor mode becomes optimized. In other words, the adaptations of the body for specific locomotor modes seem to become more pronounced with growth (e.g., Isler et al., 2006; Druelle et al., 2016b). In spite of these functional morphological specializations, the motor development related to the broader ontogenetic posturo-locomotor diversity may possibly lead to an improvement of the secondary locomotor modes as a kind of developmental by-product. Bipedal behavior (in posture and locomotion) in otherwise primarily quadrupedal species may be an example of this. Kimura and Yaguramaki (2009), for instance, observed an improvement in the regularity of bipedal gaits in chimpanzees during the acquisition of their (quadrupedal) locomotor skills. Furthermore, it is worth noting that, in some respects, the biomechanics of quadrupedal and bipedal locomotion are shown to be similar in chimpanzees (Pontzer et al., 2014), bonobos (Aerts et al., 2000; D'Août et al., 2004; Schoonaert et al., 2016), and baboons (Berillon et al., 2010). Aerts et al. (2000) pointed out that the basic control of walking in quadrupedal and bipedal locomotion in non-human primates is possibly identical. Interestingly, most human infants crawl during the first year of age (see Adolph and Robinson [2013] for a review). This is a form of quadrupedal walking similar, in some respects, to that of non-human primates (Patrick et al., 2009; Righetti et al., 2015). Although this locomotor mode is not an obligatory phase to achieve proper bipedal walking, it is a precursory form of mobility that appears to be functionally relevant for motor development and experience. From an evolutionary perspective, developmental by-products, when under appropriate pressure, offer opportunities for selection to produce behavioral and morphological novelties (Hurov, 1991). Such a mechanism, if shown to be present in living forms of primates, might have been one of the factors leading to the impressive diversity of locomotor adaptations observed in the hominoid lineage (Hunt, 2016), including bipedal locomotion in hominins.

In this paper, we test specifically whether the development of a quadrupedally oriented locomotor profile includes the development of bipedal behaviors in a non-human primate species. The olive baboon, *Papio anubis*, is a suitable model to test this hypothesis because this species is described as a committed quadrupedal walker, yet exhibits a diversity of positional behaviors during early ontogeny, including unassisted bipedal walking (Rose, 1977; Druelle et al., 2016b). We address the following question: what are the temporal aspects of bipedal gait in infant baboons and how do these change with age? We hypothesize that (1) during development, infant baboons improve their locomotor coordination pattern when they walk bipedally, and (2) the development of coordination will be reflected in bipedal bout duration and frequency, and the proportion of spontaneous unassisted bipedal walking among all locomotor behaviors.

2. Materials and methods

2.1. Study site and subjects

This study was carried out at the CNRS Primatology Station (UPS 846) in Rousset-sur-Arc, France, and was approved by the Ethical Committee of France (Letter of approval 01946.02 from the Ethics Committee n°14). We had the opportunity to follow the development of six infants living in a large open-air enclosure together with their mothers in their social group. For details regarding the troop and study site we refer to our previous studies (e.g., Berillon et al., 2010; Anvari et al., 2014). Data were collected for each individual at two different stages of their development, enabling us to observe both quadrupedal (Druelle et al., 2017) and bipedal (this study) locomotor modes and to make comparisons between both locomotor types. At the time of the first observation session (S1, October 2013), the infants ranged from 5 to 7 months of age and had a body mass of between 1.93 and 3.1 kg. At that time, locomotor autonomy had not been acquired by any of the infant baboons. At the time of session 2 (S2, March 2015), the infant baboons ranged from 21 to 23 months of age and had a body mass of between 5.59 and 6.68 kg. At that time, locomotor autonomy was fully acquired in all subjects. Table 1 provides the individual characteristics for the six subjects involved in the present study.

2.2. Data collection

Temporal and behavioral data on bipedalism were extracted from videos recorded in the context of a longitudinal study (see Druelle et al., 2016b). A complete observation session consists of 200 min of recording for each individual using the focal sampling method (Altmann, 1974). A session covers all the daily activities of the individuals (5-min focal × 4 focal per hour × 10 h). Each focal individual was followed at a distance of 2–10 m and filmed at 30 frames per second (i.e., 30 Hz) with a handheld digital camcorder (Sanyo Xacti full HD), giving a precision of 33 ms (see also Cheyne et al., 2011; Shapiro et al., 2014).

With regard to the temporal data of the walking gaits, this video sampling rate has been shown to be statistically similar, via regression analysis, to 60 Hz on the same sample of baboons walking quadrupedally (see the supplementary material "30 Hz versus 60 Hz" in Druelle et al., 2017). Furthermore, we assessed measurement error based on the work of Polk et al. (2005) and tested whether the error may impact the results. All the bipedal sequences were analyzed using the video analysis software, Elan 4.6.1 (Max Planck Institute for Psycholinguistics, The Language Archive, Nijmegen, the Netherlands; http://tla.mpi.nl/tools/tlatools/elan/). We recorded the timing at touchdown and lift-off for each hind limb in each completely recorded stride. The initiation of the stance phase was assessed as the frame in which the limb came into contact with the substrate, and the initiation of the swing phase was assessed as the frame in which the limb no longer had contact with the substrate. A viewpoint from the concrete pavement in the enclosure offered us a good vantage point to identify these transitional frames. According to the annotation of the events of the footfall pattern, the following temporal parameters were calculated for each bipedal step: stance, swing, cycle duration (i.e., stance + swing phase), and hind lag duration (Fig. 1). The temporal parameters of bipedal strides were retained for the analysis only when the hands were not used for assistance (as the assisted bipedal locomotion changes balance requirements and coordination; Fig. 1A). The strides during which individuals were in transition, e.g., from quadrupedal to bipedal posture (or vice versa), were also excluded from the analysis. In total, 19 and 46 bipedal

Table 1
Study subjects.

Name	Tatoo	Sex	Age (days)[a]	Individual mass (kg)	Lower leg length (mm)	Number of bipedal bouts	Number of bipedal steps
Ilario	V908G-13C	M	216/701	3.10/6.49	110/147	9/7	6/9
Icono	V893E-13E	M	150/635	2.12/6.68	92/140	17/5	6/2
Irm	V896E-13A	F	196/681	2.44/5.87	102/152	10/20	2/12
Iris	V916D-13D	F	172/657	2.46/6.56	107/150	8/18	3/11
Ivar Jr	V894H-13A	M	147/632	2.18/6.65	105/150	5/5	1/4
Isabella	V896B-13E	F	181/666	1.93/5.59	102/148	9/24	1/8

[a] S1 and S2 are separated by "/".

steps of session 1 and session 2, respectively, were retained for analysis.

With regard to the behavioral data, the recording method enabled us to record frequencies and durations for each positional bout per individual (Druelle et al., 2016b). In the present study, we focused on the bipedal bouts.

2.3. Data analysis

As in the analysis of quadrupedal gaits in baboons (Druelle et al., 2017), we assessed the following variables: the duty factor (DF), the dimensionless frequency (dimF), the regularity of the cycle duration, the regularity of the duty factor, and the symmetry. Regularity and symmetry are measures of interlimb coordination (Fig. 1B) and, therefore, we used the methodology developed by Abourachid (2003), in which the difference between successive steps can be used to generate data for these variables. These variables are calculated as follows:

Duty factor. We calculated the duration of the stance phase relative to the cycle duration (CD) of the limb for each bipedal step. The duty factor is, by definition, a dimensionless value.

Dimensionless frequency. The frequency of each bipedal step was calculated and made dimensionless according to the dynamic similarity principle (Hof, 1996):

$$DimF = \frac{1}{CD} \times \sqrt{\frac{ll}{g}}$$

where ll is the lower leg length (in meters), g is the gravitational constant (9.8 m s^{-2}), and CD is the cycle duration (in seconds). Making use of $DimF$ enables comparisons of stride behavior of animals differing in size to be made (see for instance Aerts et al., 2000).

Regularity. We assessed the regularity between two consecutive bipedal steps using the following formula:

$$Regularity = \frac{Abs(x - y)}{x}$$

where x can be the cycle duration or the duty factor of the leading hind limb in the bipedal sequence, and y is the cycle duration or the duty factor of the contralateral hind limb. This provides information on the degree of difference between consecutive hind limb cycle durations and duty factors in a sequence: zero indicates no difference, that is, a perfect regularity with regard to the coordination pattern.

Symmetry. We considered the time lag between the touch down of both feet relative to the cycle duration of the first hind limb. This dimensionless value is expressed as a percentage. When the relative hind lag phase is 50% (see Abourachid [2003] for quadrupedal walking gaits), the gait is perfectly symmetrical. Because values can be above or below 50%, we assessed the degree of symmetry, which only considers the deviance from perfect symmetry, as:

$$Symmetry\ degree = Abs\left(\frac{HL}{CD} - 50\%\right)$$

In addition to the temporal aspects of bipedal walking gaits, we assessed three behavioral components from our longitudinal study (see Data collection): number of unassisted bipedal walking bouts, mean duration of bouts, and the proportion (i.e., frequency weighted by the duration) of unassisted bipedal walking in the positional repertoire. These variables represent the manner in which young baboons use the bipedal behavior in an activity context.

2.4. Statistics

The temporal and behavioral variables form, by definition (see above), two different datasets that require different statistical treatments. Different selection criterion, inherent to each analysis,
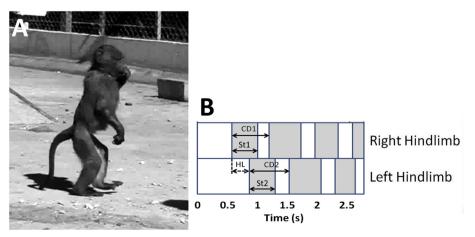

Figure 1. A) Voluntary bipedal walking in autonomous infant baboon at the CNRS Primatology Station. B) Example of a footfall sequence for bipedal gaits; gray rectangles indicate stance phases and white rectangles indicate swing phases. CD = cycle duration, St = stance phase, HL = hind lag.

also resulted in different quantities of temporal and behavioral data that could be extracted from our longitudinal study.

With regard to the temporal data, we considered the bipedal steps as the statistical units because only a limited number of bipedal steps could be extracted per individual at S1 (Table 1), making it impossible to work on the mean for an individual. Note that, with respect to our research question on bipedal walking skills in young baboons during development, bipedal steps can be considered as independent events because interlimb coordination is a recurrent control issue in each step. We compared temporal parameters, i.e., duty factor, dimensionless frequency, regularity of the cycle duration, regularity of the duty factor, and degree of symmetry, between the two sessions using exact permutation tests for independent samples. Using the equation provided by Berillon et al. (2011) on the relationship between absolute stride frequency and absolute speed for baboons walking bipedally, we could assess the speed range for the bipedal strides processed in the present study. Based on this, we were able to estimate the error range of the temporal parameters with respect to the sampling frequency (30 Hz) and speed (see Polk et al., 2005:Fig. 5). After testing for normality for each parameter in each sample at S1 and S2 (Shapiro-Wilks test), we applied a one sample t-test to assess whether the sample mean for the bipedal steps differed from the mean obtained for hind limbs in quadrupedal locomotion for the same animals at the same time points (data from Druelle et al., 2017). This method was used because the quadrupedal sample has much larger sample sizes (S1: 19 bipedal strides versus 284 quadrupedal strides; S2: 46 bipedal strides versus 585 quadrupedal strides). Therefore, the quadrupedal sample can be considered as a "population" to which the bipedal sample is compared. This analysis was carried out using the software R 2.15 (The R Foundation, Vienna, Austria, https://www.rproject.org/).

With regard to the behavioral data, individuals were considered as the statistical units. We compared behavioral parameters, i.e., bipedal frequency, mean duration, and proportion between S1 and S2, using exact permutation tests for paired samples. Age-related changes may, therefore, be highlighted. Statistical significance was set at $p < 0.05$ for all tests and permutation tests were performed using StatXact 3.1 (software, Cytel, Inc., Cambridge, MA).

3. Results

3.1. Temporal parameters with age

Using 40 h of recordings, we were able to analyze the temporal parameters of 65 bipedal steps (S1: 19, S2: 46) performed by the six individuals within our sample. In this study, ranges of absolute step frequencies are between 1.33 and 3.03 for S1 and between 0.95 and 3.70 for S2. Based on the equation provided by Berillon et al. (2011;

speed $= 0.5662 \times$ stride frequency -0.0669), speed ranges between 0.69 and 1.65 m/s at S1 and between 0.47 and 2.03 m/s at S2. With respect to these speed ranges, the measurement error is <10% for all temporal gait parameters, i.e., stride duration, stance phase duration, and swing phase duration (see Polk et al., 2005).

Table 2 presents the changes in gait temporal parameters with age. There are no significant differences between the two sessions for the dimensionless stride frequency (0.19 and 0.23, permutation test $= -1.69$, $p = 0.08$), duty factor (0.72 and 0.73, permutation test $= -0.4$, $p = 0.69$), or degree of symmetry (0.06 and 0.06, permutation test $= 0.34$, $p = 0.72$). The regularity between consecutive step cycle durations improves significantly with age, i.e., the variable approaches zero (from 0.2 to 0.09, permutation test $= 2.61$, $p = 0.01$; adding a 10% error on these two values does not affect the significance of the result). There is no significant difference for the regularity of consecutive duty factors between age classes (0.15 and 0.1, permutation test $= 0.98$, $p = 0.34$).

3.2. Bipedal versus quadrupedal temporal gait parameters

Table 2 also shows comparisons between the temporal parameters of bipedal and quadrupedal gaits with age. There is no significant difference for the duty factor in bipedal or quadrupedal gaits at S1 (72 for both, t $= 0.16$, df $= 18$, $p = 0.87$), but there is a significant difference at S2 (73 and 70, respectively, t $= 2.13$, df $= 45$, $p = 0.04$; Fig. 2A). During development, the dimensionless frequency in bipedal walking is always higher than in quadrupedal walking (S1: 0.19 and 0.13, respectively, t $= 5.89$, df $= 18$, $p < 0.0001$; S2: 0.23 and 0.13, respectively, t $= 8.85$, df $= 45$, $p < 0.0001$; Fig. 2B). Because symmetry degree values are not normally distributed (Shapiro-Wilk, W $= 0.8998$, $p < 0.0001$), it was impossible, at this stage, to test for statistical differences between quadrupedal and bipedal gaits. For the same reason, it was not possible to statistically compare the regularity of cycle durations (Shapiro-Wilk, W $= 0.8944$, $p = 0.005$) and duty factors (Shapiro-Wilk, W $= 0.8463$, $p = 0.0003$) between bipedal and quadrupedal walking using the one-sample t-test (see Fig. 2).

3.3. Behavioral parameters

On average, baboons walk bipedally for significantly longer durations at the end of infancy (S2) than at the beginning of independent foraging (S1; 1.16 ± 0.2 s and 0.84 ± 0.16 s, respectively, permutation test $= -2.11$, $p = 0.03$; Fig. 3). No significant difference was observed for the proportion of bipedal walking (S1: 0.07 ± 0.03% and S2: 0.14 ± 0.1%, permutation test $= -1.4$, $p = 0.22$), nor for the number of bipedal bouts performed voluntarily (S1: 9.67 ± 3.98 and S2: 13.17 ± 8.47, permutation test $= -0.88$, $p = 0.5$).

Table 2
Temporal parameters of bipedal walking with age compared to quadrupedal walking.

	Age class	Bipedal walking[a]	Permutation test (S1 vs S2)	Quadrupedal walking	One sample t-test
Duty factor	S1	0.72 ± 0.08	ns	0.72	ns
	S2	0.73 ± 0.09		0.70	*
Dimensionless frequency	S1	0.19 ± 0.05	ns	0.13	***
	S2	0.23 ± 0.09		0.13	***
Degree of symmetry	S1	0.06 ± 0.05	ns	0.05	N/A[b]
	S2	0.06 ± 0.05		0.03	N/A
Regularity of cycle durations	S1	0.20 ± 0.09	*	0.10	N/A
	S2	0.09 ± 0.07		0.06	N/A
Regularity of duty factors	S1	0.15 ± 0.10	ns	0.08	N/A
	S2	0.10 ± 0.10		0.06	N/A

Symbol significance: *$p < 0.05$, ***$p < 0.001$.
[a] Mean ± Standard deviation.
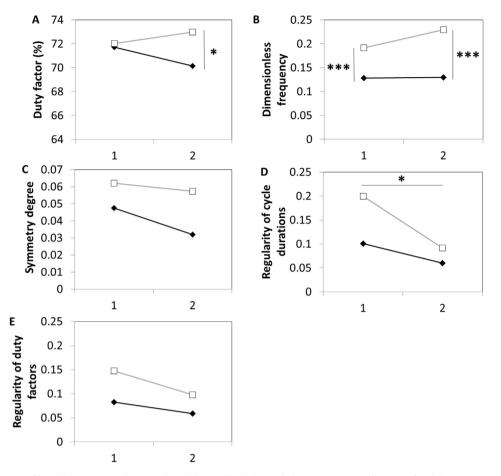[b] Not applicable because the normality of the samples for bipedal data were not obtained.

Figure 2. Temporal parameters of bipedal (white square) and quadrupedal gaits (black diamond) during voluntary walking in infant baboons at S1 and S2: A) Duty factor, B) dimensionless frequency, C) symmetry degree, D) regularity of cycle durations, E) regularity of duty factors. Symbol significance: $^*p < 0.05$, $^{***}p < 0.001$.

4. Discussion

In our sample of baboons, no age-related differences were found at the level of the basic temporal aspects of bipedal walking. There is no change in the duty factor, nor in the dimensionless frequency during infancy. According to a previous study involving an onto-genetic series of olive baboons, it seems that the duty factor and dimensionless frequency remain constant across the lifespan (Berillon et al., 2011). Nevertheless, compared to quadrupedal walking, i.e., the locomotor mode for which the morphology of the
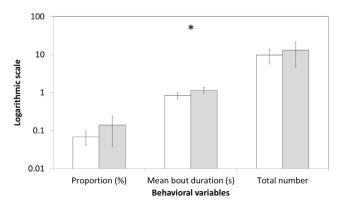

Figure 3. Mean values of the behavioral parameters of voluntary bipedal walking in our sample of infant baboons. S1 is represented with a white bar, S2 is represented with a gray bar. See Figure 2 for symbol significance.

adult baboon seems to be optimized (Druelle et al., 2016b), the bipedal duty factor remains larger at the older age. This may result from the fact that quadrupedal performance improves with age (Druelle et al., 2017), while we can expect the requirement for balance control when walking bipedally (upright trunk posture) to remain equally high at all ages. Thus, keeping relatively long stance phases probably provides longer double limb support phases that in turn enhances stability and control. Furthermore, the dimensionless frequency of hind limbs is greater during bipedal walking compared to quadrupedal walking for the two developmental stages studied. This conforms to previous results in olive baboons (Berillon et al., 2010), as well as in bonobos (Aerts et al., 2000; D'Août et al., 2004), and suggests an alternative dynamic mechanism for keeping balance (higher frequencies provide more frequent opportunities to correct balance perturbations). However, in baboons, unlike in very young chimpanzees, no high-speed bipedal locomotion was observed (dimensionless frequency: 0.19 for young baboons and 0.29 for young chimpanzees, recalculated from Table 3 in Kimura and Yaguramaki [2009]). Terrestrial bipedal walking in baboons was previously interpreted as a non-erratic locomotor mode, which is performed in a "stereotyped" manner from the very beginning of their life (Berillon et al., 2010). With respect to the consistency of the duty factor and the dimensionless frequency values found herein with age, our results support this description.

We hypothesized that during development, the coordination pattern should improve when infant baboons walk bipedally. Our results support this hypothesis. During bipedal locomotion, the

regularity between cycle durations of sequential hind limb movements increases substantially with age. This occurs in parallel to the improvement of the interlimb coordination pattern of quadrupedal walking. Nevertheless, infant baboons only occasionally experience bipedal locomotion (mainly during playing and feeding activities; Rose, 1976; Druelle et al., 2016b), whereas they constantly experience quadrupedal walking. Therefore, this result suggests a basic mechanism of control in bipedal and quadrupedal locomotion equivalent to that seen in bonobos (Aerts et al., 2000; D'Août et al., 2004; Schoonaert et al., 2016), macaques (Nakajima et al., 2004), and humans (Dietz, 2002; Michel et al., 2008; Zehr et al., 2009). Furthermore, it also suggests that quadrupedal locomotion does not constrain the development of bipedal locomotion in non-human primates. In other words, non-human primates probably employ the same neural networks used for quadrupedal locomotion for (occasional) bipedal walking. The modular neural networks may simplify muscle control via muscle synergies (Lacquaniti et al., 2012). In this respect, the same modular controllers of the rhythm-generating neural network may produce the muscular activity in both quadrupedal and bipedal locomotion. Interestingly, we were not able to find any bipedal sequences longer than two steps in younger baboons (aged approximately six months old), while we found and analyzed sequences consisting of up to five steps in the same individuals one and a half years later.

This brings us to our second hypothesis, that is that the development of coordination should be reflected in the behavioral parameters of spontaneous unassisted bipedal walking. We observed a significant increase in the duration of bipedal walking bouts, but not in the frequency and proportion (i.e., weighted frequency). During bipedal locomotion, upper body mass needs to be balanced at the hip while forward propulsion destabilizes the body. Retaining trunk stability requires muscle strength. In this context, the duration of bipedal walking bouts may be used as a proxy for the capacity to keep bipedal balance (see also Druelle et al., 2016a). At an early age, an improvement of the coordination pattern through the regularity of consecutive cycle durations is, therefore, likely to impact the duration of bipedal walking bouts, but not the frequency of bipedal behaviors.

With regard to the chimpanzee, Kimura and Yaguramaki (2009) demonstrated that the steadiness of bipedal walking increases significantly from two years of age. In chimpanzees, this age corresponds to a shift in terms of autonomy and in the proportion of utilization of quadrupedal locomotion, i.e., from approximately 10% of its locomotor repertoire (the rest is mainly composed of orthograde behaviors, i.e., climbing, bipedalism, and suspension) before 2 years of age to approximately 70% after two years of age (percentages are estimated from Doran, 1992:Fig. 1). Although this species exhibits a different locomotor repertoire than that of the committed quadrupedal baboon (Hunt, 1992), it appears that the maturation of its preferred locomotor mode, i.e., terrestrial and arboreal quadrupedal knuckle-walking (Sarringhaus et al., 2014), corresponds to the development of its bipedal abilities. Although unassisted bipedal walking possesses unique features, the development of quadrupedal walking correlates with an improvement in bipedalism in cercopithecoids and hominoids. With regard to the continuum of movements that characterizes the locomotor repertoires of primates (see Thorpe and Crompton [2006] for theoretical reflections), the development of coordinated limb movements in quadrupedalism, through the development of central neural motor control, is probably equally significant for other modes, or at least for bipedal walking. While human toddlers learn to walk bipedally by strongly experiencing bipedal behavior (Adolph et al., 2012) among a set of various movements such as reaching and crawling (e.g., Corbetta and Bojczyk, 2002; Adolph and Robinson, 2013; Righetti et al., 2015), infant baboons and chimpanzees improve their bipedal walking skills by experiencing multiple locomotor modes, but primarily quadrupedal

walking. Further studies are required to assess the neurological coupling between quadrupedalism and bipedalism, as well as with the other (arboreal) modes. However, it is reasonable to hypothesize that sharing neural primitives for bipedal and quadrupedal tasks could simplify the switch between the two locomotor modes. This in turn suggests that the secondary locomotor modes experienced during infancy as a by-product of locomotor development may facilitate the evolution of novel locomotor modes, because infancy may provide opportunities to generate novel responses to the environment (e.g., Hurov, 1991; Greeno, 1994). Our results (and others from chimpanzees [Kimura and Yaguramaki, 2009]) suggest that occasional bipedalism may be considered as a developmental by-product. In this context, this behavior could have resulted, at the adult stage, in various advantages for food-carrying, investigation, displaying, etc. (e.g., Rose, 1976; Hunt, 1994; Carvalho et al., 2012) that might have led to the evolution of habitual bipedalism in hominins (see Fleagle [2013] for a review).

Based on fossil discoveries and the study of extant (human and non-human) primates, various models of locomotion have been proposed for the last common ancestor of panins and hominins, as well as for early hominin species (see Crompton et al., [2008] for a review). Nevertheless, the neural coupling between arms and legs observed in humans strongly suggests that the bipedal locomotor CPGs evolved from quadrupedal networks; in other words, cervical and thoraco-lumbar propriospinal systems were initially coupled for locomotion (Dietz, 2002; Zehr et al., 2009, 2016). In this respect, our results support the idea that a more habitual bipedal walking (in early hominins) could have originated from a repertoire that included quadrupedal displacements and, therefore, did not require the development of a novel neural patterning network to achieve bipedal behavior. Recently, White et al. (2015) proposed that the particular morphological characteristics found within *Ardipithecus ramidus* suggest that bipedal and quadrupedal behaviors were both possible in significant proportion. Therefore, given 1) the mechanism of developmental by-products present in catarrhine species and 2) appropriate inter-individual morphological variations (e.g., at the level of the body mass distribution pattern, Druelle et al., 2016a), it is possible that the habitual practice of bipedal behaviors gradually emerged in the last common ancestor of panins and hominins. Once bipedalism formed part of the regular locomotor behavioral repertoire, further evolution towards habitual bipedalism would have "only" required selection for morphological changes increasing locomotor efficiency. To summarize, our results underscore the importance of considering infancy and the developmental processes in understanding the emergence of new locomotor modes, including bipedalism.

Acknowledgments

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