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# **Title:** Development of bipedal walking in olive baboons, *Papio anubis*: a kinematic analysis

**Short running title:** Development of bipedal walking in baboons

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## **Abstract**

**Objective:** Although extant non-human primates are not habitual bipeds, they are able to walk bipedally from an early age. In humans, children improve their walking skills through developmental processes and learning experience. In non-human primates, infants do not routinely experience bipedalism and their musculoskeletal system gradually specialises for other locomotor modes. The aim of this study is to explore the development of occasional bipedal walking in olive baboon and to test whether the postural adjustments change with age.

**Materials and Methods:** We collected kinematics and spatio-temporal parameters of bipedal gait in an ontogenetic sample of 24 baboons. Data were collected at the primatology station of the CNRS (France) and a total of 47 bipedal strides were extracted for the present analysis.

**Results:** Adults and adolescents walk bipedally in the same way, and the average kinematic pattern is similar across the age-classes. Infants walk bipedally with longer duty factor, they present larger movement amplitude of the thigh and the amplitude of the knee joint decreases with speed. In contrast, older baboons increase the amplitude of the knee and ankle joints with speed.

**Discussion:** In a non-adapted biped, the postural adjustments of bipedal walking vary with age. In infant baboons, the balance requirements are likely to be higher and these are solved by adopting a "blocking strategy". In older baboons, the postural adjustments are focused on the lower limb and the movements increase with speed. These results may echo, in some respects, the developmental sequence of the inter-segmental coordination described in the ontogeny of human locomotion.

**KEY WORDS:** Balance, Bipedalism, Coordination, Evolution, Ontogeny

## INTRODUCTION

Humans can be defined as habitually bipedal walkers and runners (e.g., Bramble & Lieberman, 2004; Harcourt-Smith, 2007; Holowka & Lieberman, 2018). As only two feet contact the ground during their locomotion, keeping balance is a challenge, and as loading is only shared between the two legs, musculoskeletal stress is high. During development, children gradually acquire independent walking (e.g., Assaiante, 1998; Hallems, D'Août, De Clercq, & Aerts, 2003; Ledebt & Bril, 2000; Van Dam, Hallems, Truijen, & Aerts, 2010; Van Dam, Hallems, Truijen, Segers, & Aerts, 2011) and their walking skills improve by repeatedly experiencing this behaviour (Adolph et al., 2012). In contrast to humans, extant non-human primates are not habitual bipeds. They commonly develop a set of locomotor skills that can be summarized into their positional repertoire (including postural and locomotor modes; Hunt et al., 1996). The locomotor skills of extant non-human primates commonly take somewhere between months and years to mature (e.g., Doran, 1992; Doran, 1997; Druelle, Aerts, & Berillon, 2016a; Dunbar & Badam, 1998; Wells & Turnquist, 2001). The developmental trajectories related to locomotion are species-specific and there is a broad diversity of positional behaviors with various degrees of specialization in adults (see Hunt, 2016, for a review). Overall, occasional bipedal walking represents a common part of the natural positional repertoire of non-human primates (Druelle & Berillon, 2014). Bipedalism can be considered a non-erratic locomotor behaviour that is commonly observed in various contexts for short bouts (e.g., Carvalho et al., 2012; Druelle, Aerts, & Berillon, 2016b; Rose, 1976; Stanford, 2006; Videan & McGrew, 2002; Wrangham, 1980). It is suggested that bipedal walking is, in some respects, "stereotyped", i.e., similar postural features are shared between species (e.g., Demes, 2011; Demes, Thompson, O'Neill, & Umberger, 2015; Pontzer, Raichlen, & Rodman, 2014). These features are the "bent-hip, bent-knee" posture, a significant protraction and reduced retraction of the hindlimbs during the movement.

Although bipedalism is occasionally performed in non-human primates, we previously hypothesized that the motor development of the main locomotor mode (for instance quadrupedal walking) may lead to an improvement of the secondary locomotor modes, such as bipedal walking (Druelle, Aerts, & Berillon, 2017a). This hypothesis is based on evidence that the rhythmic motor patterns related to locomotion are likely to share common neural control networks (e.g., Balter & Zehr, 2007; Dominici et al., 2011; Zehr, Hundza, & Vasudevan, 2009). In other words, multiple motor components can interact to mature different movement output simultaneously (Dominici et al. 2011; Ivanenko, Dominici, & Lacquaniti, 2007). Our previous results on the early locomotor development of olive baboons support this prediction because we observed that the coordination pattern during bipedal locomotion significantly improves in infant baboons (between ~6 months old and ~2 years old), while they mostly experience quadrupedal walking and only very little bipedal walking (Druelle et al., 2017a). In addition,

although adult baboons are generally less inclined to use bipedalism than infants, we have observed that when adult baboons use bipedalism, they tend to engage in it for periods of longer duration than infants do (Druelle et al., 2016b). To our knowledge, only one other research team has explored the development of occasional bipedal walking in a non-human primate species. Kimura and colleagues have provided significant work on the bipedal locomotion of chimpanzees and how it changes during development (e.g., Kimura, 1991; Kimura, 1996; Kimura & Yaguramaki, 2009). They have shown that there is an improvement in the regularity of bipedal gaits in chimpanzees during the first 3 years of life (Kimura & Yaguramaki, 2009). This occurs during the acquisition of their quadrupedal gait (Doran, 1992; Sarringhaus, MacLatchy, & Mitani, 2014). Furthermore, Kimura and Yaguramaki (2009) observed that infant chimpanzees exhibit different postures than adults, such as larger extension and range of motion of hip joints. Compared to humans, adult chimpanzees exhibit a relatively large variance, short braking duration and small energetic recovery capacities during bipedal walking (2-45%). Nevertheless, the studies on chimpanzees and baboons both point to an improvement of the bipedal walking skills in living non-human primates during development, possibly including significant changes in the kinematics and in the gait pattern. Yet, at the adult stage, the efficiency of bipedal walking in non-human primates is relatively low (Demes et al., 2015; Nakatsukasa et al., 2004, Nakatsukasa, Hirasaki, & Ogihara, 2006; Pontzer et al., 2014). From an evolutionary perspective, the question of the developmental processes of the locomotor skills remains almost entirely unexplored in hominins, certainly because juvenile fossil materials are extremely rare in early hominins (Alemseged et al., 2006). To date, it is still unclear how young hominin individuals learned to walk bipedally (but see Tardieu & Preuschoft, 1996; Tardieu, 2010). Increasing our knowledge on the ontogeny of occasional bipedal walking in non-human primates could provide new insights into the developmental trajectory of this behavior in hominins.

Baboons are clearly specialized for quadrupedal walking, yet, they are also able to suddenly raise their centre of mass relatively high above the hips and to walk on two feet on a reduced area of support (D'août, Berillon, Anvari, & Aerts, 2013). Such a transition is obviously a complex task for the neural control system (Nakajima et al., 2001; Mori, Mori, & Nakajima, 2006). Furthermore, the bipedal posture is inherently mechanically unstable compared to quadrupedalism, but the ability to maintain balance on two legs needs to be solved by the same system. Motor actions (using muscle torques) should be able to correct the perturbations encountered in this unstable posture. Gait maturity should also affect the capacity of the system to do so. As a result, in a primate species like the baboon that only occasionally uses bipedal walking, this locomotor mode should inherently represent higher demands at a younger age; even in a human that is an adapted biped, toddlers need to walk bipedally for long periods of time and they cover significant distances before being able to walk efficiently and

without falling (Adolph & Avolio, 2000; Adolph et al., 2012; Hallems, Aerts, Otten, De Deyn, & De Clercq, 2004; Ledebt & Bril, 2000). Berillon and collaborators (2010, 2011) conducted a kinematic study of bipedal walking by analysing 10 strides in an ontogenetic sample of 10 olive baboons (*Papio anubis*). Overall, they described a general gait pattern that is common to young (~6 months) and adult individuals. The bipedal gait is a compliant gait with a semiplantigrade foot posture during stance phase, a trunk that is slightly tilted forward and immobile forelimbs that are kept forward in a parasagittal plane. Beside this general pattern, they also pointed out a few variations, especially in the youngest individuals that could be related to development and maturation. Specifically, in the youngest individuals they noticed more variation in the trunk angle and a more extended foot at touchdown.

Here, we provide new information on the sagittal plane gait kinematics of bipedal walking, and its relationship to speed in a large ontogenetic sample of olive baboons, clearly separated in three age-classes from early infancy to adulthood. The aim of this study is to assess whether the kinematics change during the development of bipedal walking in a non-adapted biped species in order to estimate whether the baboons improve the way they walk bipedally. We hypothesize that the average kinematic profile and the scaled spatio-temporal parameters should vary between infant, adolescent, and adult baboons. Given the differences in both gait maturity and body proportions between the age-classes studied, we also hypothesize that speed should have a different influence on gait kinematics between these groups. Considering speed variation offers us a window to observe different control strategies, if any, in the pattern of inter-segmental coordination. By observing the developmental process of bipedal walking in baboons, we aim to test whether a non-adapted biped species changes the way it walks bipedally during development resulting in improvement of its bipedal walking skills. Second, in the evolutionary context of bipedal locomotion in hominins, studying the development of bipedalism in non-human primates and comparing it to humans offers an opportunity for us to propose new hypotheses on the pattern of locomotor learning and development in hominins. We will discuss the implications of our results for the postural movement strategies and balance control, as well as in the evolutionary context of the bipedal development in juvenile hominins.

## **Material and Methods**

### *Study site and subjects*

We sampled 24 individuals, *Papio anubis*, housed at the Primatology Station of the CNRS (Rousset-sur-Arc, France; 17 individuals are newly sampled, and 7 individuals are from Berillon et al., 2010). This research center houses and breeds several colonies of baboons in large enclosures. The individuals studied are all part of the same colony of ca. 60 individuals. In the context of the present study, we

have worked on the platform for biomechanics (Motion analysis of Primates, MAP) that is permanently installed in an outdoor enclosure and includes various devices, such as a multi-camera recording setup, force plates and EMG-equipment (for details see Berillon et al., 2011; Druelle, Supiot, Meulemans, Schouteden, Molina-Vila, Rimbaud, Aerts, & Berillon, 2021). The present work is part of a large ongoing project contributing to our knowledge about walking skills in non-human primates (e.g., Anvari et al., 2014; Berillon et al., 2010; Druelle et al., 2017; Druelle et al., 2021). The collection of the new data was performed during opportunistic recordings on the technical platform between December of 2010 and August of 2012. At the time of data collection, the colony was composed of male and female infants, adolescents and adults. An ontogenetic sample of 17 individuals aged from 6 months to 7.4 years old was selected. According to previous studies on the growth pattern of olive baboons, this species exhibits important and rapid morphological changes during the first 2 years of age (Druelle et al., 2017; Leigh, VandeBerg, Williams-Blangero, & Tardif, 2009). The morphological changes gradually slow down until approximately 6 years of age when the growth stops (females can be considered adult at 5 years old and males can be considered adult at 6.5 years old; Druelle et al., 2017). Between 3.5 and 4.5 years of age, baboons become sexually mature. Furthermore, the maturation of the neuromotor control appears to be largely complete at 3 years of age in baboons, as is also the case in other cercopithecoid species (e.g., Druelle et al., 2017; Rose 1977; Vilensky & Gankiewicz, 1990; Zeininger, Shapiro, & Raichlen, 2017; Dunbar & Badam, 1998).

In this study, we selected 3 well separated age-classes in order to avoid any potential overlap in morphology (morphotype) that could arise from interindividual differences in the timing of maturation. As a result, the first age class included 7 individuals that are aged from 6 months to 1.5 years old (i.e., infants), plus 2 other individuals that are from the same age class in Berillon et al. (2010; number 854 and 632). The second age class included 6 individuals that are aged from 3 to 4 years old (adolescents), plus 4 other individuals that are from the same age class in Berillon et al. (2010; number 411, 406, 568 and 604). The last age class included 5 individuals that are older than 5 years old (adults), plus 1 other individual that is from the same age class in Berillon et al. (2010; number 606); note that the lower number of adult individuals in our sample reflects the fact that they use bipedalism less frequently than the younger ones (see Rose, 1976; Druelle & Berillon, 2013). Table 1 provides individual characteristics of the full sample. All the procedures that are described in this study were approved by the Regional Ethical Committee for animal experimentation of the Midi-Pyrénées Region (Letter MP/01/15/02/2008).

### *Data collection*

The bipedal behaviour of the olive baboons was recorded using a motion analysis system. The animals were easily video captured (see Berillon et al., 2010 for a general description of the setup); here we used an updated system with high-definition digital video camera running at 200 fps in 1280 x 800 pixel resolution (Baumer HXC13). The camera was laterally placed perpendicular to the long axis of a walkway (positioned inside the enclosure) to accurately record the main sagittal spatiotemporal and joints kinematics in a large field of view. Calibration of the field was performed using reference points on the platform. The camera was connected via a CameraLink cable to a workstation (Norpix) that enabled us to monitor and adjust various parameters such as the exposure time, the contrasts, the recording period, etc. Streampix 4.7 software (Norpix) was used to control these parameters. We collected our data opportunistically. The animals were able to walk spontaneously on the straight and horizontal calibrated walkway, during their daily activities. A lot of good sequences were collected when the baboons were carrying food items. However, given the small proportion of spontaneous bipedal walking behaviour in baboons in general (Druelle et al., 2017; Rose, 1977), we also positioned a mirror at the end of the walkway as we observed that it "stimulated" their bipedal behaviour. It increased the likelihood of recording bipedal bouts on the walkway (Table A in supplementary material describes the behavioural context of the bipedal sequences included in the current analysis). We first selected from sight appropriate bipedal sequences during which the individuals were walking steadily, along the platform, to the right or the left direction. For the sequences included in the analysis, we first calculated the following spatiotemporal parameters: the duty factor (proportion of stance phase relative to cycle duration), the stride duration (SD) and frequency (SF, i.e. the inverse of the stride duration), the stride length (SL) and the average speed ( $v$ , based on the stride duration and stride length). As the individuals vary greatly in size, we corrected for this effect by scaling the spatiotemporal parameters and the speed by following the common scaling procedures (Hof, 1996):

$$\text{Dimensionless speed} = \frac{v}{\sqrt{g \cdot l}}$$

$$\text{Dimensionless stride frequency} = \frac{SF}{\sqrt{g/l}}$$

$$\text{Dimensionless stride duration} = \frac{SD}{\sqrt{l/g}}$$

$$\text{Dimensionless stride length} = \frac{SL}{l}$$

Where  $l$  is the length of the shank length and  $g$  is the gravitational acceleration ( $9.81\text{m}\cdot\text{s}^{-2}$ ). Consistent with previous studies on primate locomotion, we used the shank length as our scaling parameter (e.g., Aerts, Van Damme, Van Elsacker, & Duchene, 2000; Berillon et al., 2010; Vereecke, D'Août, & Aerts,

2006). However, to enable us to make comparisons with the studies that used leg length as the scaling parameter (e.g., Hof, 1996), we also provide the results when we used this (i.e. length of shank and thigh together).

After recording, the digitization of the body was performed manually frame-by-frame by JÖ using the Matlab *DLTdv8* application developed by the T. Hedrick lab. Overall, 19 markers corresponding to anatomical references were positioned on the baboons (see Figure 1 and Table B in supplementary material). A bipedal stride was defined as the period between one touch-down of the reference hindlimb (i.e., the one closer to the camera) to the following touch-down of the same hind limb, thus including one stance phase and one swing phase. In total, we analyzed 40 strides separated by age class to which we added 7 strides coming from Berillon et al. (2010): 23 strides among 9 infants, 15 strides among 10 adolescents, 9 strides among 5 adults.

### *Data analysis*

Some data points were difficult to digitize properly during the full strides. This was mainly the case for the limbs positioned further from the camera because of the front limbs' movements. To correct this, we applied a general filter for missing data on our database using a piecewise linear interpolation method. The data were then filtered per stride, using a fourth order low-pass Butterworth filter with a cut-off frequency of 10Hz. We used basic trigonometry between vectors to calculate six angles in the coordinate sagittal plane per frame. The different joint angles calculated on the baboons walking bipedally are the following: the ankle, the knee, the hip and the shoulder (Figure 1). The segment angles calculated are the following: the shank, the thigh, and the trunk (Figure 1). We then applied a cubic spline interpolation over a time base with 100 points in order to stride-normalized the individual bipedal cycles for each angle. Thanks to this treatment, we were able to average the multiple strides per age-class, known as *ensemble averages*, and we could compare the strides between groups. Each angle was also characterized per stride by using two values: the mean (i.e. its central tendency) and the amplitude (i.e. range-of-motion, calculated as the difference between the maximum value and the minimum value).

To assess the out-phase movement of the forelimb relative to the hindlimb, we calculated the percentage of congruity (i.e., the phase relationship) per stride between the shoulder angle and the hip angle. We calculated this index as follows:

$$Angle\ congruity = \frac{\sum_1^{n-1} [(\widehat{Hip}_{n+1} - \widehat{Hip}_n)(\widehat{Shoulder}_{n+1} - \widehat{Shoulder}_n) > 0]}{n - 1} \times 100$$

Where  $n$  is the number of values (i.e., 100 data points after stride-normalization, see above). It measures the proportion of the gait cycle during which both angles change in phase. If the hip angle



always extends when the forelimb goes forward and always flexes when the forelimb goes backward, the angle congruity will equal 100%, suggesting a counter balancing movement of fore- and hindlimbs as observed in humans (e.g., Dietz, Fouad, & Bastiaanse, 2001; Goudriaan, Jonkers, van Dieen, & Bruijn, 2014; Killeen et al., 2017; Van de Walle et al., 2018).

### *Statistics*

After applying the size correction, all data were  $\log_{10}$ -transformed before analysis to ensure normality and homoscedasticity assumptions were met (this is controlled using *Shapiro-Wilk* tests and histograms). We applied mixed effects models in order to control for the effects of individuals. We first tested whether there is an association between the spatiotemporal parameters (i.e., dimensionless stride frequency, dimensionless stride length and duty factor; dependent variables) and the different age-classes when taking the speed effect (fixed effects) into account. To control for the interindividual variation, we included the individual effect as a random effect in the models. We used the function *lmer* (from *lme4* package) for fitting these models (the restricted maximum likelihood method was used). We used the Satterthwaite's approximation method implemented in the *lmerTest* package (Kuznetsova, Brockhoff, & Christensen, 2017) to assess the significance of the different fixed effect variables of the models (i.e., speed and age-class). We applied the same statistical procedure on the mean and amplitude of the joint and segment angles across strides, as well as on the % of divergence between the shoulder and the hip angles, thus keeping the age-classes and the dimensionless speed as fixed effects. All the statistical analyses were performed using RStudio (v1.2.5001) and the significance level was set at  $P < 0.05$ .

## **Results**

### *The spatiotemporal parameters*

Table 2 shows the spatiotemporal parameters averaged per age-class and their associated statistical results. There is no significant difference in speed and in dimensionless speed between the age-classes. The speed is significantly related to all the spatiotemporal parameters, i.e., stride frequency, stride duration, stride length and duty factor. There is a significant age effect on all the spatiotemporal parameters.

When removing the effect of size using the shank length as the scaling factor, there is no difference across age for the stride duration, stride frequency and stride length, and there is no interaction effect for these variables. There is a significant age-class effect on the duty factor and the interaction between speed and age-class is also significant ( $F=7.43$ ,  $P=0.004$ ;  $F=6.29$ ,  $P=0.005$ , respectively; Fig. 2). When applying the same tests in taking the leg length as the scaling parameter, the results are similar.

## *Kinematics*

Figure 3 and 4 show the patterns of the segment and joint angles, respectively, averaged per age-class during bipedal walking and include the  $\pm 95\%$  Confidence Interval (CI). The changes in joint and segment angles that occur during bipedal walking are very similar between the age-classes. With regard to the central tendency of the angles, we found three significant results. There is a general speed effect on the mean value of the ankle ( $F=11.22$ ,  $P=0.002$ ) and on the mean value of the thigh ( $F=4.89$ ,  $P=0.034$ ), and there is an age effect for the mean value of the shank ( $F=6.17$ ,  $P=0.017$ ; Figure 5). Table 3 summarizes the average joint and segment angles per age-class at specific instants of the bipedal gait cycle.

With regard to the range-of-motion of the angles, there is an age effect on the hip amplitude ( $F=3.58$ ,  $P=0.0499$ ) and on the thigh amplitude ( $F=4.14$ ,  $P=0.030$ ). There is a significant effect of age and of the interaction between speed and age in terms of the amplitude of the knee ( $F=6.87$ ,  $P=0.007$ ;  $F=3.69$ ,  $P=0.037$ ; respectively). There is a significant effect of speed on the shank amplitude ( $F=7.83$ ,  $P=0.009$ ; Figure 6). Table 4 summarizes the statistical results obtained for the mean and amplitude of the joint and segment angles.

### *Movement of the forelimb relative to the hind limb*

There is a no age effect and no effect of speed on the angle congruity between hip and shoulder extension, i.e. at higher speed the congruity is not significantly higher ( $F=2.88$ ,  $P=0.10$ ). The congruity values do not indicate a clear pattern of out-phase movements of the forelimbs relative to the hind limbs (infants:  $56\pm 16\%$ , adolescents:  $53\pm 11\%$ , adults:  $57\pm 7\%$ ). There is a significant age effect on the shoulder amplitude ( $F=4.98$ ,  $P=0.02$ ), toward larger amplitudes in infants compared to in adults and adolescents.

## **Discussion**

### ***Ontogenetic changes in kinematics***

We first hypothesized that the average kinematic profile and the scaled spatio-temporal parameters should vary between infant, adolescent, and adult baboons. Overall, our results depict an average profile of the kinematic parameters of the bipedal walking pattern that does not substantially change across age categories (see Fig. 3 and 4). However, interesting differences in the stance phase parameter (duty factor) and in segment angles can be depicted. When removing the effect of size, only subtle differences can be found between juveniles and older (adolescent and adult) baboons. Specifically, we observed that the stride frequency and stride length do not change during development. Infant, adolescent and adult baboons modulate their bipedal gait by altering both their

stride frequency and stride length. However, the stance phase is relatively longer in young baboons, and it is not affected by speed (the within-group correlation is not significant for infants; see Fig. 2), suggesting higher balance control requirements in young, immature, individuals. A relatively longer stance phase should indeed enhance stability and control and provides longer double limb support phases as well. Furthermore, the shank angle is lower in infants (~5° lower), mainly because it keeps a more vertical posture at touch-down (see Table 3). The infants also show a larger amplitude in the hip joint which is mainly due to the larger amplitude of the thigh segment, as the trunk pitch amplitude is not significantly different across the age classes. The higher amplitude in the hip joint has also been reported in young chimpanzees but it is not the case in young children (Kimura & Yaguramaki, 2009; Ivanenko et al., 2007). In chimpanzees, this may also be related to large movement of the thigh as the maximum forward inclination of the trunk does not vary with age, yet no information is provided on the movement amplitude of the trunk in immature chimpanzees. On contrary, in humans there is a significant hip flexion at an early stage that becomes gradually more extended. Interestingly, the amplitude of thigh movements has been shown to be relatively high in toddlers with respect to that of shank and foot movements (Ivanenko et al., 2007).

#### ***Age-related influence of speed on kinematics***

We also hypothesized that the modulation of the bipedal gait with speed is different between infants and older baboons. The mean angle value of the ankle joint in adults and adolescents gradually increases with speed, i.e., higher ankle extension, but this is not the case in infants (see Fig. 5). On contrary, the mean angle value of the thigh segment in infants gradually decreases with speed, i.e., the limb is brought less forward, but this is not the case in adults and adolescents (see Fig. 5). In addition, an important difference between infants and older baboons concerns the amplitude of the knee joint with speed. While the speed significantly affects the knee amplitude in infants towards smaller amplitudes at higher speed, the reverse pattern is observed in adults. This can be directly related to the way in which infants and older baboons modulate their bipedal gait with speed. Adults and adolescents appear to adjust their kinematics predominantly at the knee and ankle joint ("lower leg strategy"), thus increasing stride length by bringing the lower leg more forward. Infants generally exhibit higher movement amplitude of the thigh segment than older baboons. In this way, it mainly contributes to their stride length and long relative stance phase. When they walk faster, they appear to use a sort of "blocking strategy" by reducing the protraction of the thigh and the movement amplitude of the knee joint, thus keeping a long duty factor while increasing stride frequency. The kinematic variations observed in the present baboon sample may highlight different (neuromotor) control strategies related to maturity (muscle strength and coordination) and morphology (body proportions; see below).

### ***Solving the problem of balance control: the influence of body mass distribution***

Multiple options for motor control action are available to move the body effectively and to correct undesired movements (Winter 1995, 2009). Walking is a dynamic process where segmental accelerations and decelerations about joints impact the rate of change of the total angular momentum. Kinematics adjustments can, therefore, alter the change of the total angular momentum and in this way affect the stability of the body. In a bipedal posture, the balance control is inherently more challenging as the upper body needs to be stabilized above the hip. The baboons, although considered as non-adapted bipeds, are able to solve the balance control problems from an early age, as they are able to walk bipedally without falling. However, the kinematic variations observed in the present study are likely to highlight differences in the motor control strategies between infants and older baboons. On the one hand, the observation of the longer duty factor, the higher movement amplitude of the thigh and its control with speed in infants suggest an increased control of the walking pattern that is focused on the upper leg. On the other hand, the older baboons are able to smoothly adapt their movement with speed, by reducing the stance phase and increasing both stride length and stride frequency through variations of the amplitude of movement of the lower leg (knee and ankle joints), while the upper part of the leg is not affected by speed. These differences could simply arise from the differences in morphology (e.g., body proportions in toddlers; see Van Dam et al., 2010; Van Dam et al., 2011). In infant primates (including humans) the body centre of mass is positioned relatively closer to the head than in adolescents and adults (e.g., in non-human primates: Druelle, Aerts, D'Août, Moulin, & Berillon, 2017b; Grand, 1977; Turnquist & Wells, 1994; e.g., in humans: Palmer, 1944). Maintaining a relatively high centre of mass in a "bent-hip, bent-knee" posture inherently increases the gravitational moment about the hips, thus making it more challenging for the hip extensor muscles to stabilize the upper body (e.g., Preuschoft, 2004; Winter, 2009). The angle of permissible sway of the trunk must be kept small because too many oscillations of a trunk in which the centre of mass is cranially positioned would considerably increase the risk of losing balance (Winter, 2009). For example, in bipedally-trained macaques, trunk sway is very limited ( $\sim 5^\circ$ ; Hirasaki, Ogihara, Hamada, Kumakura, & Nakatsukasa, 2004). In our study, the baboons also keep a trunk relatively stable, from an amplitude of  $\sim 8^\circ$  on average in infants to an amplitude of  $\sim 5^\circ$  on average in adults, and it is not impacted by the speed of locomotion. Infant baboons are, therefore, able to stabilize their upper body during bipedal locomotion at an early age, but their balance strategy to do so is likely to be different than the one observed in older baboons. Interestingly, we observed that the amplitude of the shoulder joint angle is relatively low in baboons ( $\sim 16^\circ$  for the full ontogenetic sample, *versus*  $\sim 25^\circ$  in humans; Killeen et al., 2017) but varies significantly across age categories ( $\sim 21^\circ$  in average in infants,  $\sim 12^\circ$  in adolescents and adults). This might emphasize the search for active corrective actions from the forelimbs in infants, but

further data are required to assess this aspect. In general, there is almost no information about how the forelimbs move during bipedal walking in non-human primates (but see Tardieu, Aurengo, & Tardieu, 1993). It appears that their movement is limited in cercopithecoids compared to hominoids. Limited movement of the forelimbs has been shown to not compromise gait stability in humans (Bruijn, Meijer, Beek, & van Dieën, 2010). With regard to the out-phase movement pattern, there is no variation across the age classes in our sample, and the speed does not affect the counter balancing movement of the upper arm. The fact that the movement amplitude is low and not affected by speed has been suggested to correspond to a low level of muscular activity in humans (Goudriaan et al., 2014). However, further research including the muscular activity in non-human primates is required to better understand the dynamics of arm swinging during occasional bipedal walking in these species.

### ***Comparisons with humans***

In humans, the duration of the single-limb stance, the relative double support phase, the stride frequency and the stride length have been shown to be important determinants of a mature gait (e.g., Grieve & Gear, 1966; Ledebt & Bril, 2020; Sutherland, Olshen, Cooper, & Woo, 1980). In toddlers, a stable posture is achieved relatively rapidly, only a few weeks after the onset of independent walking (e.g., Ledebt & Bril, 2020; Schedler, Kiss, & Muehlbauer, 2019). Although this is not yet an efficient walking pattern, it represents a real improvement of the gait parameters (Ledeht & Bril, 2020). Young children have also been shown to exhibit long periods of coactivation of agonist and antagonist muscles during gait that have been related to immature balance control strategies (Berger et al., 1995; Okamoto & Kumamoto, 2001; Woollacott & Shumway-Cook, 1990). During this early period of walking the ankle muscles in humans are relatively weak (Sutherland et al., 1980). It is also only after years of practice that the fully efficient gait pattern arises in humans with adult-like joint angle patterns, reciprocal arm swinging and a mature gait (Chester, Tingley, & Biden, 2006; Halleman et al., 2004; Sutherland, 1997; Sutherland et al., 1980; Van de Walle et al., 2018). In baboons, the strategy described in young individuals (see above) reflects a more immature control for walking bipedally. The duty factor is relatively fixed and long, the stride length is likely to be controlled at the hip and the frequency varies mainly by reducing the movement amplitude at the knee joint. It is thus possible that this strategy is also related to higher coactivation of agonist and antagonist muscles in the thigh. However, it requires testing by comparing the muscle activity of young and adult baboons. Interestingly, our results on baboons may echo the developmental sequence of the inter-segmental coordination described in the ontogeny of human locomotion (see Assaiante & Amblard, 1995; Assaiante, 1998). Hip stabilization has been suggested to be the reference frame at the onset of bipedal locomotion in humans. At this stage, important co-activation patterns are observed in hip, knee and ankle muscles, hence, anticipatory postural adjustments include the whole body (Assaiante, 1998; Berger et al., 1995;

Woollacott & Shumway-Cook, 1990). This strategy has been called the "reduced damping strategy" (or the "blocking strategy") and it is an efficient and simple strategy that means that the number of degrees of freedom to be controlled can be minimized (Assaiante, 1998). In older children and adults, the activation level is lower in the hip and knee muscles, but higher at the ankle joint. Hence, the control becomes selective and relies on articulated operations that are focused on the lower leg. This developmental pattern may be suggested, in some respects, in baboons as well. In answer to the question "*do baboons improve the way they walk bipedally with age?*" it is difficult to reply at this stage of research, but it is obvious that the control strategy for walking bipedally changes with age. The ultimate goals of the musculoskeletal system are certainly to solve the control problems related to equilibrium and to be energetically efficient. The present study shows that the balance control problems are solved at an early age in baboons, yet, it is achieved with a different strategy than in adults. Moreover, a potential improvement, energetically speaking, requires further research. In chimpanzees, young individuals and adults appear to exhibit low levels of energy recovery, while adolescents (5 to 8 years of age) can show high levels of energy recovery at low speed (dimensionless speed  $\sim 0.3-0.4$ ; Kimura & Yaguramaki, 2009). But it is not clear to which anatomo-functional feature this is related.

### ***Evolutionary perspectives***

Describing the way bipedal skills develop during ontogeny in non-adapted bipeds enables the development of new evolutionary hypotheses about the way bipedal locomotion might have developed in pre-adapted bipeds and early hominins (see Kimura & Yaguramaki, 2009). Learning to walk bipedally, i.e., solving the balance control problems, does not require walking bipedally for long period of time and distances, and appears to be proceeded early in life. The experience of (quadrupedal) walking and the onset of independent locomotion appear to be sufficient enough to be able to walk bipedally (Druelle et al., 2017). Hence, we suggest a similar process in early hominins. However, being energetically efficient represents another challenge and may require extensive experience of walking bipedally (Hallemans et al., 2004). Previous studies tend to show that bipedal walking is not more energetically demanding than quadrupedal walking in chimpanzee (Sockol, Raichlen, & Pontzer, 2007; Pontzer, Raichlen, & Rodman, 2014; Taylor & Rowntree, 1973); nevertheless, the individuals studied were regularly interacting with (bipedal) humans as they were privately owned, or trained animal actors for movies and entertainment purposes and they might have a significant experience of walking bipedally from an early age. In an evolutionary perspective, as soon as early hominins started to walk bipedally on the ground, balance was certainly not an important problem to solve, but efficient inter-segmental coordination strategies were required for walking efficiently over longer periods. Further comparative ontogenetic data such as the ones presented here

on baboons are required to tackle the question of the developmental processes of bipedal walking skills in early hominins. The present study provides a relevant comparative framework for investigating this matter.

## **Conclusion**

In this paper, kinematic and spatiotemporal parameters of bipedal gait were extracted in an ontogenetic sample of 24 baboon individuals. We investigated whether the bipedal gait pattern varies across age categories. Although the general average walking pattern is remarkably similar during ontogeny, the results show interesting age-related differences in the way baboons adjust their hind limb movements with speed. Walking bipedally for non-human primates, i.e., solving the balance control problem, does not require years of practice. The capacity to stabilise the upper body in a bipedal posture is functional very early in baboons, but the selected kinematic strategies related to speed vary with age. Our results suggest a change in the way they control and balance their posture. A more controlled bipedal posture is observed in infants ("blocking strategy"), while the adolescents and adults modulate their bipedal gait more smoothly by adjusting knee and ankle joints toward larger movement amplitude with speed. The postural adjustments thus rely on neuromotor operations that are focused on the lower limb in adolescent and adult baboons, while it is focused on the upper leg in infants. This may arise from the interaction between the ontogenetic changes in body proportions and the maturity of the musculoskeletal system.

## **Data availability statement**

All the data of the present study are available from the corresponding author upon request.

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Authors declare no competing interests.

## References

- Adolph, K. E. & Avolio, A. M. 2000 Walking infants adapt locomotion to changing body dimensions. *Journal of Experimental Psychology: Human Perception and Performance* **26**, 1148-1166.
- Adolph, K. E., Cole, W. G., Komati, M., Garciaguirre, J. S., Badaly, D., Lingeman, J. M., Chan, G. L. & Sotsky, R. B. 2012 How do you learn to walk? Thousands of steps and dozens of falls per day. *Psychological science* **23**, 1387-1394.
- Aerts, P., Van Damme, R., Van Elsacker, L. & Duchene, V. 2000 Spatio-temporal gait characteristics of the hind-limb cycles during voluntary bipedal and quadrupedal walking in bonobos (*Pan paniscus*). *American journal of physical anthropology* **111**, 503-517.
- Anvari, Z., Berillon, G., Asgari Khaneghah, A., Grimaud-Herve, D., Moulin, V. & Nicolas, G. 2014 Kinematics and spatiotemporal parameters of infant-carrying in olive baboons. *American Journal of Physical Anthropology* **155**, 392-404.
- Assaiante, C. 1998 Development of locomotor balance control in healthy children. *Neuroscience & biobehavioral reviews* **22**, 527-532.
- Assaiante, C. & Amblard, B. 1995 An ontogenetic model for the sensorimotor organization of balance control in humans. *Human movement science* **14**, 13-43.
- Balter, J. E. & Zehr, E. P. 2007 Neural coupling between the arms and legs during rhythmic locomotor-like cycling movement. *Journal of neurophysiology* **97**, 1809-1818.
- Berger, W., Trippel, M., Assaiante, C., Zijlstra, W. & Dietz, V. 1995 Developmental aspects of equilibrium control during stance: a kinematic and EMG study. *Gait & posture* **3**, 149-155.
- Berillon, G., D'Août, K., Daver, G., Dubreuil, G., Multon, F., Nicolas, G., Villetanet, B. & Vereecke, E. E. 2011 In What Manner Do Quadrupedal Primates Walk on Two Legs? Preliminary Results on Olive Baboons (*Papio anubis*). In *Primate Locomotion* (ed. L. Barrett), pp. 61-82: Springer New York.
- Berillon, G., Daver, G., D'Août, K., Nicolas, G., de la Villetanet, B., Multon, F., Digrandi, G. & Dubreuil, G. 2010 Bipedal versus Quadrupedal Hind Limb and Foot Kinematics in a Captive Sample of *Papio anubis*: Setup and Preliminary Results. *International Journal of Primatology* **31**, 159-180.
- Bramble, D. M. & Lieberman, D. E. 2004 Endurance running and the evolution of Homo. *Nature* **432**, 345-352.
- Bruijn, S. M., Meijer, O. G., Beek, P. J. & van Dieën, J. H. 2010 The effects of arm swing on human gait stability. *Journal of Experimental Biology* **213**, 3945-3952.
- Carvalho, S., Biro, D., Cunha, E., Hockings, K., McGrew, W. C., Richmond, B. G. & Matsuzawa, T. 2012 Chimpanzee carrying behaviour and the origins of human bipedality. *Current Biology* **22**, R180-R181.
- Chester, V. L., Tingley, M. & Biden, E. N. 2006 A comparison of kinetic gait parameters for 3-13 year olds. *Clinical Biomechanics* **21**, 726-732.
- D'Août, K., Berillon, G., Anvari, Z. & Aerts, P. 2013 Locomotor Versatility in Primates: Baboons Shifting to Bipedal and Tripedal Gait. In *Folia Primatologica*, vol. 84, pp. 263-263: Karger.
- Demes, B. 2011 Three-dimensional kinematics of capuchin monkey bipedalism. *American Journal of Physical Anthropology* **145**, 147-155.
- Demes, B., Thompson, N. E., O'Neill, M. C. & Umberger, B. R. 2015 Center of mass mechanics of chimpanzee bipedal walking. *American Journal of Physical Anthropology* **156**, 422-433.
- DeSilva, J. M., Holt, K. G., Churchill, S. E., Carlson, K. J., Walker, C. S., Zipfel, B. & Berger, L. R. 2013 The lower limb and mechanics of walking in *Australopithecus sediba*. *Science* **340**, 1232999.
- DeSilva, J. M., Gill, C. M., Prang, T. C., Bredella, M. A. & Alemseged, Z. 2018 A nearly complete foot from Dikika, Ethiopia and its implications for the ontogeny and function of *Australopithecus afarensis*. *Science Advances* **4**, eaar7723.
- Dietz, V., Fouad, K. & Bastiaanse, C. M. 2001 Neuronal coordination of arm and leg movements during human locomotion. *European Journal of Neuroscience* **14**, 1906-1914.



- Dominici, N., Ivanenko, Y. P., Cappellini, G., D'Avella, A., Mondì, V., Cicchese, M., Fabiano, A., Silei, T., Di Paolo, A., Giannini, C., Poppele, R. E. & Lacquaniti, F. 2011 Locomotor Primitives in Newborn Babies and Their Development. *Science* **334**, 997-999.
- Doran, D. M. 1992 The ontogeny of chimpanzee and pygmy chimpanzee locomotor behavior: a case study of paedomorphism and its behavioral correlates. *Journal of Human Evolution* **23**, 139-157.
- Doran, D. M. 1997 Ontogeny of locomotion in mountain gorillas and chimpanzees. *Journal of Human Evolution* **32**, 323-344.
- Druelle, F., Aerts, P. & Berillon, G. 2016a Effect of body mass distribution on the ontogeny of positional behaviors in non-human primates: Longitudinal follow-up of infant captive olive baboons (*Papio anubis*). *American Journal of Primatology* **78**, 1201-1221.
- Druelle, F., Aerts, P. & Berillon, G. 2016b Bipedality from locomotor autonomy to adulthood in captive olive baboon (*Papio anubis*): Cross-sectional follow-up and first insight into the impact of body mass distribution. *American Journal of Physical Anthropology* **159**, 73-84.
- Druelle, F., Aerts, P. & Berillon, G. 2017a The origin of bipedality as the result of a developmental by-product: The case study of the olive baboon (*Papio anubis*). *Journal of Human Evolution* **113**, 155-161.
- Druelle, F., Aerts, P., D'Août, K., Moulin, V. & Berillon, G. 2017b Segmental morphometrics of the olive baboon (*Papio anubis*): a longitudinal study from birth to adulthood. *Journal of Anatomy* **230**, 805-819.
- Druelle, F. & Berillon, G. 2013 Bipedal Behaviour in Olive Baboons: Infants versus Adults in a Captive Environment. *Folia Primatologica* **84**, 347-361.
- Druelle, F. & Berillon, G. 2014 Bipedalism in non-human primates: a comparative review of behavioural and experimental explorations on catarrhines. *BMSAP* **26**, 1-10.
- Dunbar, D. C. & Badam, G. L. 1998 Development of Posture and Locomotion in Free-ranging Primates. *Neuroscience Biobehavioral Reviews* **22**, 541-546.
- Goudriaan, M., Jonkers, I., van Dieën, J. H. & Bruijn, S. M. 2014 Arm swing in human walking: What is their drive? *Gait & posture* **40**, 321-326.
- Grieve, D. W. & Gear, R. J. 1966 The Relationships Between Length of Stride, Step Frequency, Time of Swing and Speed of Walking for Children and Adults. *Ergonomics* **9**, 379-399.
- Grand, T. I. 1977 Body weight: Its relation to tissue composition, segment distribution, and motor function II. Development of *Macaca mulatta*. *American Journal of Physical Anthropology* **47**, 241-248.
- Green, D. J. & Alemseged, Z. 2012 *Australopithecus afarensis* scapular ontogeny, function, and the role of climbing in human evolution. *Science* **338**, 514-517.
- Hallems, A., Aerts, P., Otten, B., De Deyn, P. P. & De Clercq, D. 2004 Mechanical energy in toddler gait A trade-off between economy and stability? *Journal of Experimental Biology* **207**, 2417-2431.
- Hallems, A., D'Août, K., De Clercq, D. & Aerts, P. 2003 Pressure distribution patterns under the feet of new walkers: the first two months of independent walking. *Foot & Ankle International* **24**, 444-453.
- Harcourt-Smith, W. E. 2007 The origins of bipedal locomotion. *Handbook of paleoanthropology* **3**, 1483-1518.
- Hof, A. L. 1996 Scaling gait data to body size. *Gait & posture* **4**, 222-223.
- Holowka, N. B. & Lieberman, D. E. 2018 Rethinking the evolution of the human foot: insights from experimental research. *The Journal of Experimental Biology* **221**, jeb174425.
- Hunt, K. D. 2016 Why are there apes? Evidence for the co-evolution of ape and monkey ecomorphology. *Journal of Anatomy* **228**, 630-685.
- Hunt, K. D., Cant, J., Gebo, D., Rose, M., Walker, S. & Youlatos, D. 1996 Standardized descriptions of primate locomotor and postural modes. *Primates* **37**, 363-387.
- Ivanenko, Y. P., Dominici, N. & Lacquaniti, F. 2007 Development of independent walking in toddlers. *Exercise and sport sciences reviews* **35**, 67-73.

- Killeen, T., Easthope, C. S., Filli, L., Lörincz, L., Schrafl-Altermatt, M., Brugger, P., Linnebank, M., Curt, A., Zörner, B. & Bolliger, M. 2017 Increasing cognitive load attenuates right arm swing in healthy human walking. *Royal Society open science* **4**, 160993.
- Kimura, T. 1991 Voluntary bipedal walking of infant chimpanzees. *Human Evolution* **6**, 377-390.
- Kimura, T. 1996 Centre of Gravity of the Body during the Ontogeny of Chimpanzee Bipedal Walking. *Folia Primatologica* **66**, 126-136.
- Kimura, T. & Yaguramaki, N. 2009 Development of Bipedal Walking in Humans and Chimpanzees : A Comparative Study. *Folia Primatologica* **80**, 45-62.
- Kuznetsova, A., Brockhoff, P. B. & Christensen, R. H. 2017 lmerTest package: tests in linear mixed effects models. *Journal of Statistical Software* **82**, 1-26.
- Ledebt, A. & Bril, B. 2000 Acquisition of upper body stability during walking in toddlers. *Developmental psychobiology* **36**, 311-324.
- Leigh, S. R., VandeBerg, J. L., Williams-Blangero, S. & Tardif, S. D. 2009 Growth and Development of Baboons. In *The Baboon in Biomedical Research*, pp. 57-88: Springer New York.
- Mori, S., Mori, F. & Nakajima, K. 2006 Higher nervous control of quadrupedal vs bipedal locomotion in non-human primates; Common and specific properties. In *Adaptive motion of animals and machines*, pp. 53-65: Springer.
- Nakajima, K., Mori, F., Takasu, C., Tachibana, A., Okumura, T., Mori, M. & Mori, S. 2001 Integration of Upright Posture and Bipedal Locomotion in Non-Human Primates. In *Sensorimotor control*, vol. 326 (ed. D. R & K. AR), pp. 95.
- Nakatsukasa, M., Hirasaki, E. & Ogiwara, N. 2006 Energy expenditure of bipedal walking is higher than that of quadrupedal walking in Japanese macaques. *American Journal of Physical Anthropology* **131**, 33-37.
- Nakatsukasa, M., Ogiwara, N., Hamada, Y., Goto, Y., Yamada, M., Hirakawa, T. & Hirasaki, E. 2004 Energetic costs of bipedal and quadrupedal walking in Japanese macaques. *American Journal of Physical Anthropology* **124**, 248-256.
- Okamoto, T. & Okamoto, K. 2001 Electromyographic characteristics at the onset of independent walking in infancy. *Electromyogr Clin Neurophysiol* **41**, 33-41.
- Palmer, C. E. 1944 Studies of the center of gravity in the human body. *Child development* **15**, 99-180.
- Pontzer, H., Raichlen, D. A. & Rodman, P. S. 2014 Bipedal and quadrupedal locomotion in chimpanzees. *Journal of Human Evolution* **66**, 64-82.
- Preuschoft, H. 2004 Mechanisms for the acquisition of habitual bipedality: are there biomechanical reasons for the acquisition of upright bipedal posture? *Journal of Anatomy* **204**, 363-384.
- Reimann, H., Fetzrow, T. & Jeka, J. J. 2018 Strategies for the control of balance during locomotion. *Kinesiology Review* **7**, 18-25.
- Rose, M. 1976 Bipedal behavior of olive baboons (*Papio anubis*) and its relevance to an understanding of the evolution of human bipedalism. *American Journal of Physical Anthropology* **44**, 247-261.
- Rose, M. 1977 Positional behaviour of olive baboons (*Papio anubis*) and its relationship to maintenance and social activities. *Primates* **18**, 59-116.
- Sarringhaus, L., MacLatchy, L. & Mitani, J. 2014 Locomotor and postural development of wild chimpanzees. *Journal of Human Evolution* **66**, 29-38.
- Schedler, S., Kiss, R. & Muehlbauer, T. 2019 Age and sex differences in human balance performance from 6-18 years of age: A systematic review and meta-analysis. *PloS one* **14**, e0214434.
- Stanford, C. B. 2006 Arboreal bipedalism in wild chimpanzees: Implications for the evolution of hominid posture and locomotion. *American Journal of Physical Anthropology* **129**, 225-231.
- Stern, J. T. & Susman, R. L. 1983 The locomotor anatomy of Australopithecus afarensis. *American Journal of Physical Anthropology* **60**, 279-317.
- Sutherland, D. 1997 The development of mature gait. *Gait & posture* **6**, 163-170.
- Sutherland, D. H., Olshen, R., Cooper, L. & Woo, S. L. 1980 The development of mature gait. *J Bone Joint Surg Am* **62**, 336-353.

- Tardieu, C., Aurengo, A. & Tardieu, B. 1993 New method of three-dimensional analysis of bipedal locomotion for the study of displacements of the body and body-parts centers of mass in man and non-human primates: Evolutionary framework. *American Journal of Physical Anthropology* **90**, 455-476.
- Tardieu, C. 2010 Development of the human hind limb and its importance for the evolution of bipedalism. *Evolutionary Anthropology: Issues, News, and Reviews* **19**, 174-186.
- Tardieu, C. & Preuschoft, H. 1996 Ontogeny of the knee joint in humans, great apes and fossil hominids: pelvi-femoral relationships during postnatal growth in humans. *Folia Primatologica* **66**, 68-81.
- Turnquist, J. E. & Wells, J. P. 1994 Ontogeny of locomotion in rhesus macaques (*Macaca mulatta*): I. Early postnatal ontogeny of the musculoskeletal system. *Journal of Human Evolution* **26**, 487-499.
- Van Dam, M., Hallemans, A., Truijien, S. & Aerts, P. 2010 A cross-sectional study about the relationship between morphology and step-time parameters in children between 15 and 36 months. *Gait & posture* **32**, 400-404.
- Van Dam, M., Hallemans, A., Truijien, S., Segers, V. & Aerts, P. 2011 A cross-sectional study about the relationship between morphology and kinematic parameters in children between 15 and 36 months. *Gait & posture* **34**, 159-163.
- Van de Walle, P., Meyns, P., Desloovere, K., De Rijck, J., Kenis, J., Verbecque, E., Van Crielinge, T. & Hallemans, A. 2018 Age-related changes in arm motion during typical gait. *Gait & posture* **66**, 51-57.
- Vereecke, E. E., D'Août, K. & Aerts, P. 2006 Speed modulation in hylobatid bipedalism: A kinematic analysis. *Journal of Human Evolution* **51**, 513-526.
- Videan, E. N. & McGrew, W. C. 2002 Bipedality in chimpanzee (*Pan troglodytes*) and bonobo (*Pan paniscus*): Testing hypotheses on the evolution of bipedalism. *American Journal of Physical Anthropology* **118**, 184-190.
- Ward, C. V. 2002 Interpreting the posture and locomotion of *Australopithecus afarensis*: where do we stand? *American Journal of Physical Anthropology* **119**, 185-215.
- Ward, C. V. 2013 Postural and locomotor adaptations of *Australopithecus* species. In *The paleobiology of Australopithecus*, pp. 235-245: Springer.
- Wells, J. P. & Turnquist, J. E. 2001 Ontogeny of locomotion in rhesus macaques (*Macaca mulatta*): II. Postural and locomotor behavior and habitat use in a free-ranging colony. *American Journal of Physical Anthropology* **115**, 80-94.
- Winter, D. A. 1995 Human balance and posture control during standing and walking. *Gait & posture* **3**, 193-214.
- Winter, D. A. 2009 *Biomechanics and motor control of human movement*: John Wiley & Sons.
- Woollacott, M. H. & Shumway-Cook, A. 1990 Changes in posture control across the life span—a systems approach. *Physical therapy* **70**, 799-807.
- Wrangham, R. W. 1980 Bipedal locomotion as a feeding adaptation in gelada baboons, and its implications for hominid evolution. *Journal of Human Evolution* **9**, 329-331.
- Zehr, E. P., Hundza, S. R. & Vasudevan, E. V. 2009 The quadrupedal nature of human bipedal locomotion. *Exercise and sport sciences reviews* **37**, 102-108.
- Zeininger, A., Shapiro, L. J. & Raichlen, D. A. 2017 Ontogenetic changes in limb postures and their impact on effective limb length in baboons (*Papio cynocephalus*). *American Journal of Physical Anthropology* **163**, 231-241.

## Figure legends

**Figure 1.** Images and measurements of olive baboons walking bipedally. (A) Zoomed views of three olive baboons from the lateral camera. Each individual belongs to one of the three age-classes defined. (B) Positioning of the anatomical landmarks (the description of their osteological correspondence can be found in Table B, in supplementary material) and joint and segment angles. Segment angles (in red) are measured relative to the horizontal vector oriented in the direction of movement. Joint angles (in blue) are measured between the segments connected at the joint. For the ankle, the joint angle was measured between the shank (from the patella to the lateral malleolus) and the foot segment as a whole (from the heel to the tip of the toes). [Illustration: Céline Piret].

**Figure 2.** Spatiotemporal characteristics of bipedal walking and their relationships with speed. Following the results of the mixed effects models, a black linear regression is indicated when there is a general effect of speed only, coloured linear regressions associated with each age-class are indicated when there is both, a general interaction effect and a significant within group correlation (duty factor: infants:  $r=-0.30$ ,  $P=0.08$ ; adolescents:  $r=-0.84$ ,  $P<0.0001$ ; adults:  $r=-0.84$ ,  $P=0.0051$ ).

**Figure 3.** Mean normative sagittal joint angles (hip, knee and ankle) for each age class and the respective  $\pm 95\%$  CI. The dashed vertical line indicates the average time transition between the stance and the swing phase, and the grey surrounding surface indicates the standard deviation. The grey dashed vertical lines indicate the min-max values.

**Figure 4.** Mean normative sagittal segment angles (trunk, thigh and shank) for each age class and the respective  $\pm 95\%$  CI. The black dashed vertical line indicates the average time transition between the stance and the swing phase, and the grey surrounding surface indicates the standard deviation. The grey dashed vertical lines indicate the min-max values.

**Figure 5.** Relationships between the central tendency (mean value per stride) of the joint and segment angles with speed. The mixed effects models show that there is a significant effect of speed on the ankle joint and on the thigh segment, and there is a tendency toward a significant interaction effect between the age-classes and the speed for these angles. We applied a within group *Pearson* correlation for these angles (mean ankle: infants:  $r=0.27$ ,  $P=0.11$ ; adolescents:  $r=0.73$ ,  $P=0.0013$ ; adults:  $r=0.75$ ,  $P=0.0052$ ; mean thigh: infants:  $r=-0.35$ ,  $P=0.046$ ; adolescents:  $r=0.22$ ,  $P=0.22$ ; adults:  $r=0.53$ ,  $P=0.08$ ). The significant results of the correlation tests are indicated with the coloured linear regressions. There is also an age class effect for the mean shank angle, but no relationship with speed. A boxplot is included to visualize the age class effect for the shank and a star is provided to indicate a general age effect.

**Figure 6.** Relationships between the range-of-motion (amplitude spanned per stride) of the joint and segment angles with speed. The mixed effects models show that there is an age class effect for the hip and thigh amplitude. There is a general significant speed effect for the shank amplitude. There is a significant age effect and an interaction effect for the knee amplitude. We applied a within group *Pearson* correlation for the knee angle (infants:  $r=-0.47$ ,  $P=0.012$ ; adolescents:  $r=0.34$ ,  $P=0.11$ ; adults:  $r=0.78$ ,  $P=0.0099$ ). Boxplots are included to visualize the age class effect for the hip, knee and thigh amplitude, and a star is provided to indicate the general age effect.

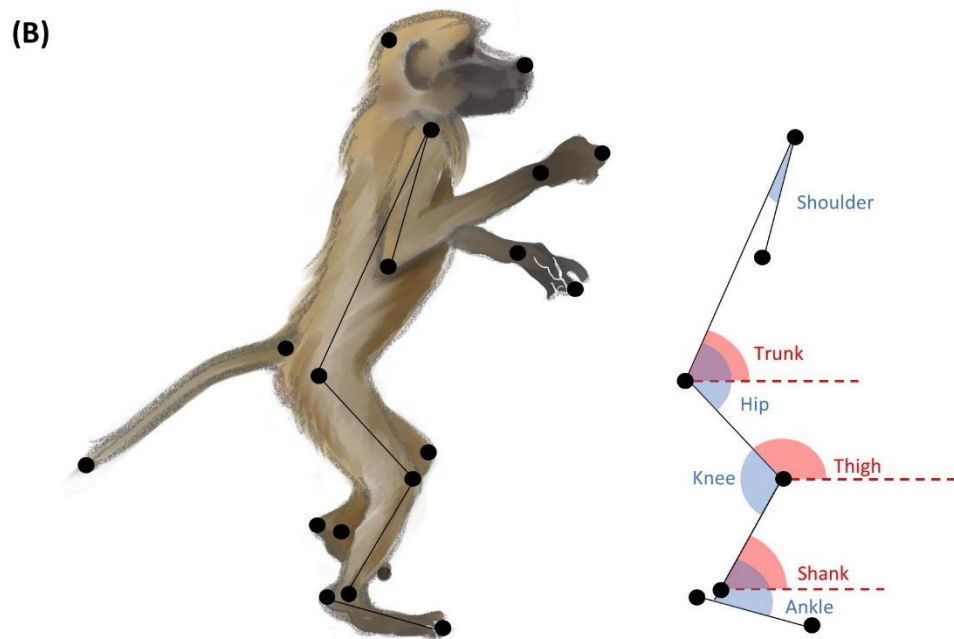
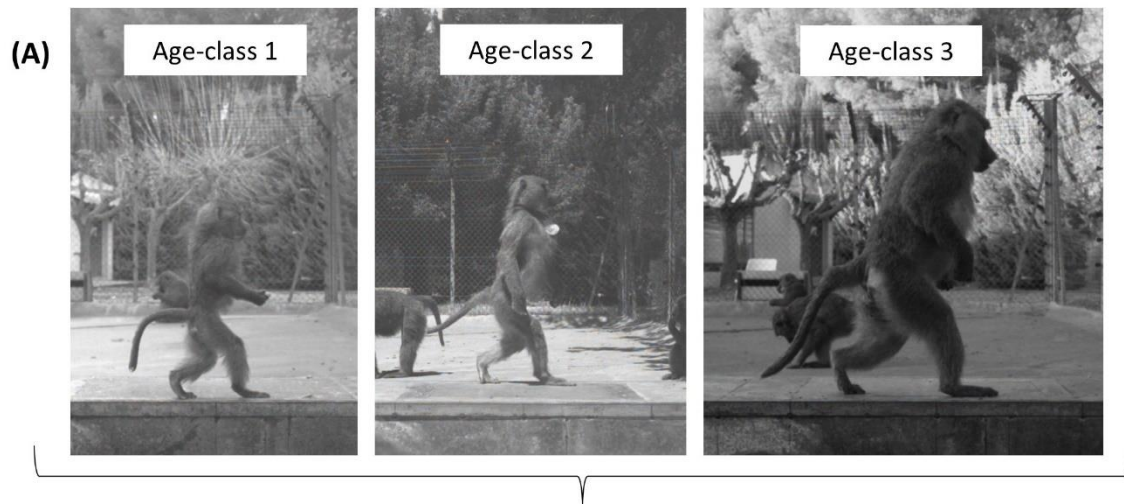


Figure 1

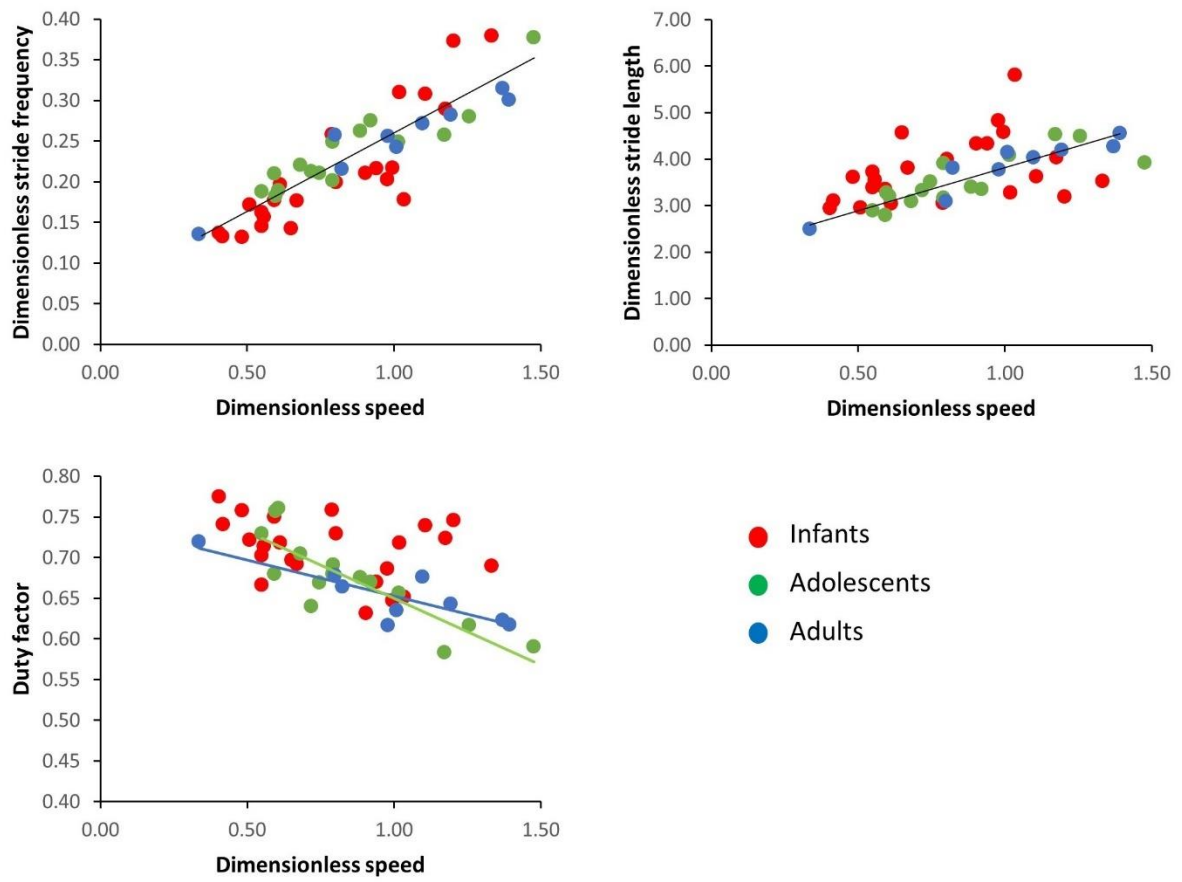
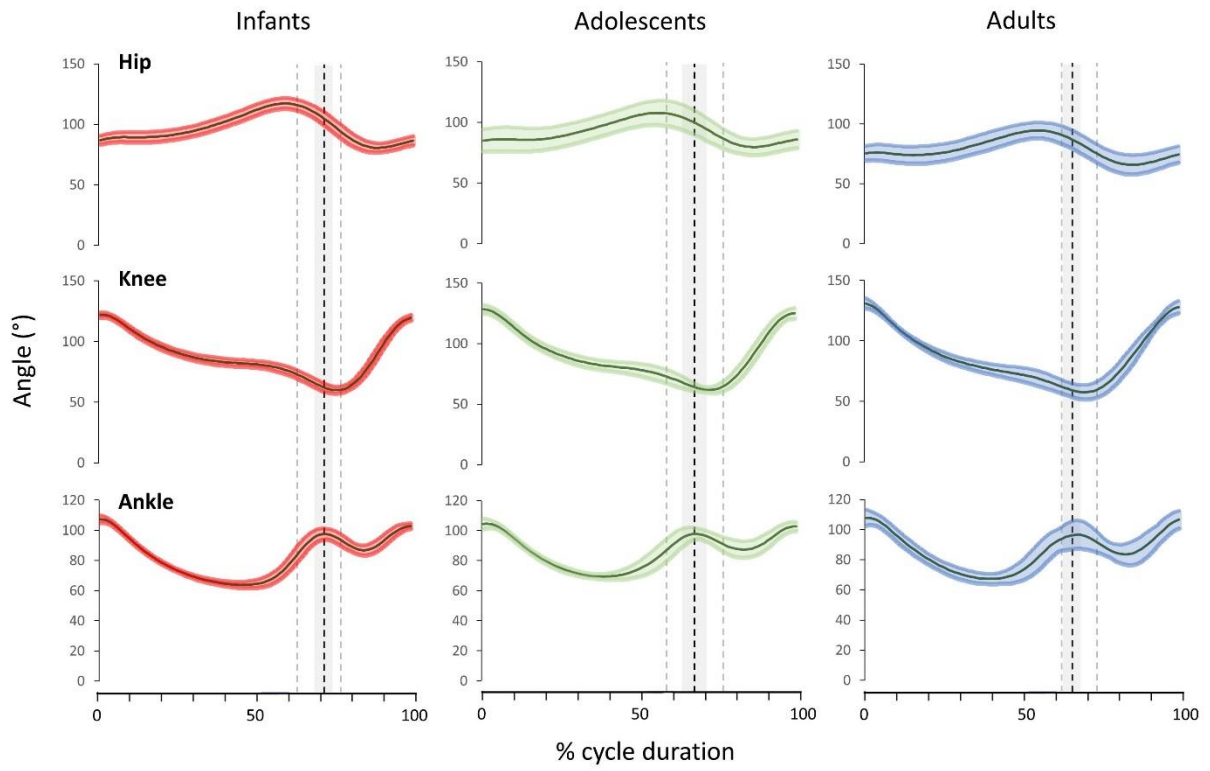
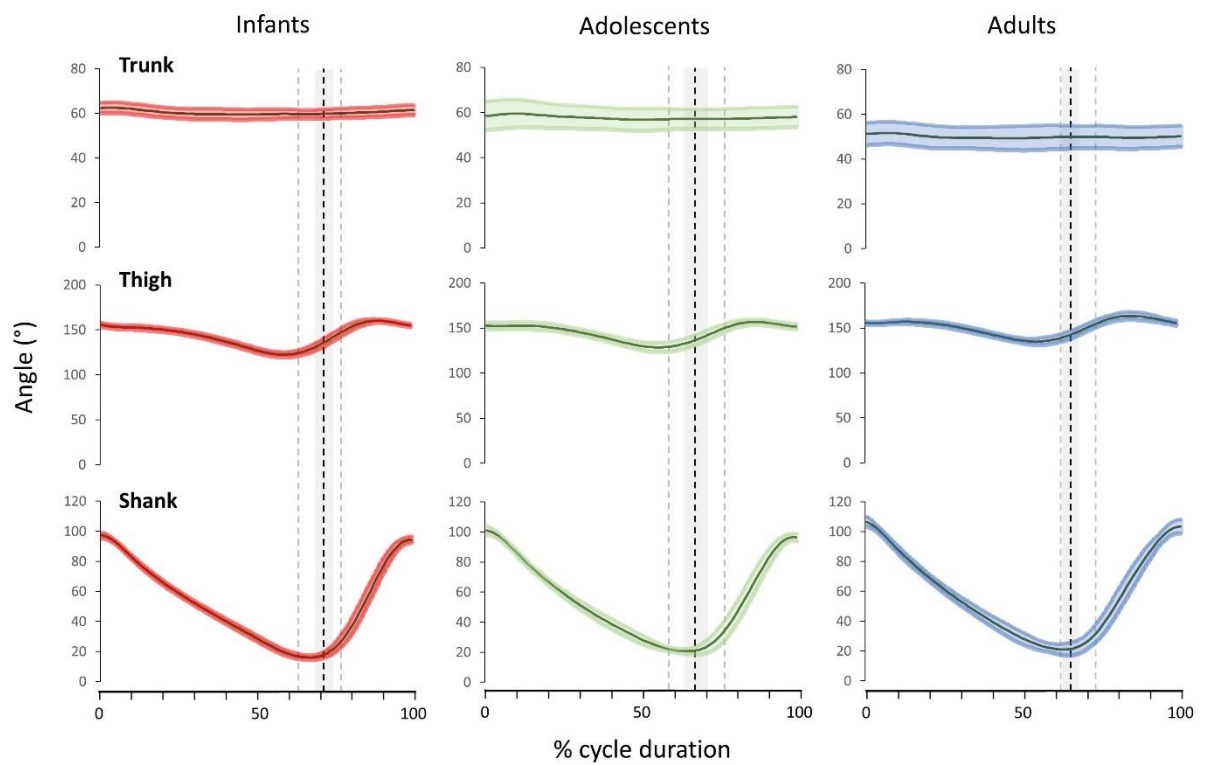


Figure 2



**Figure 3**



**Figure 4**

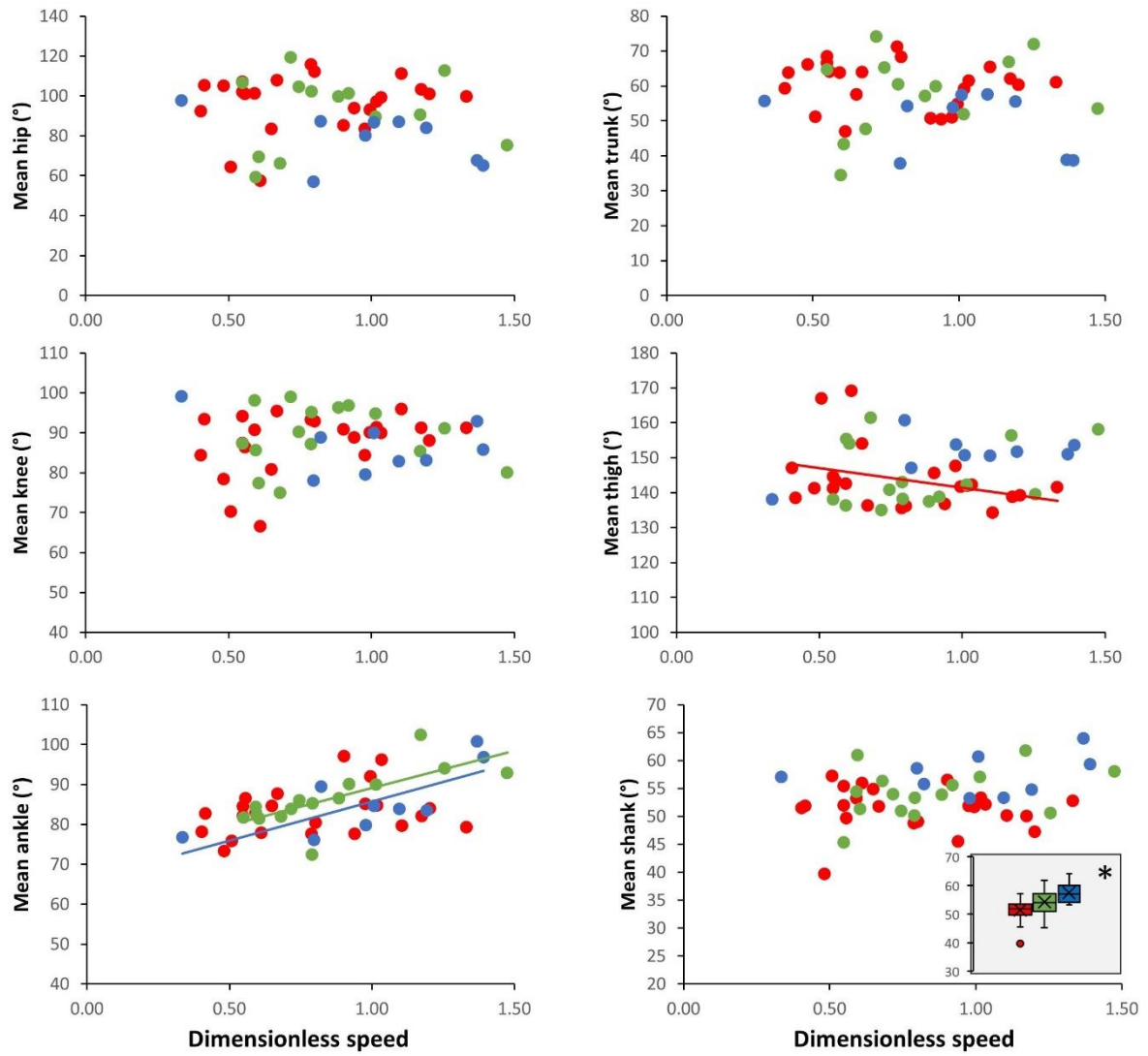


Figure 5



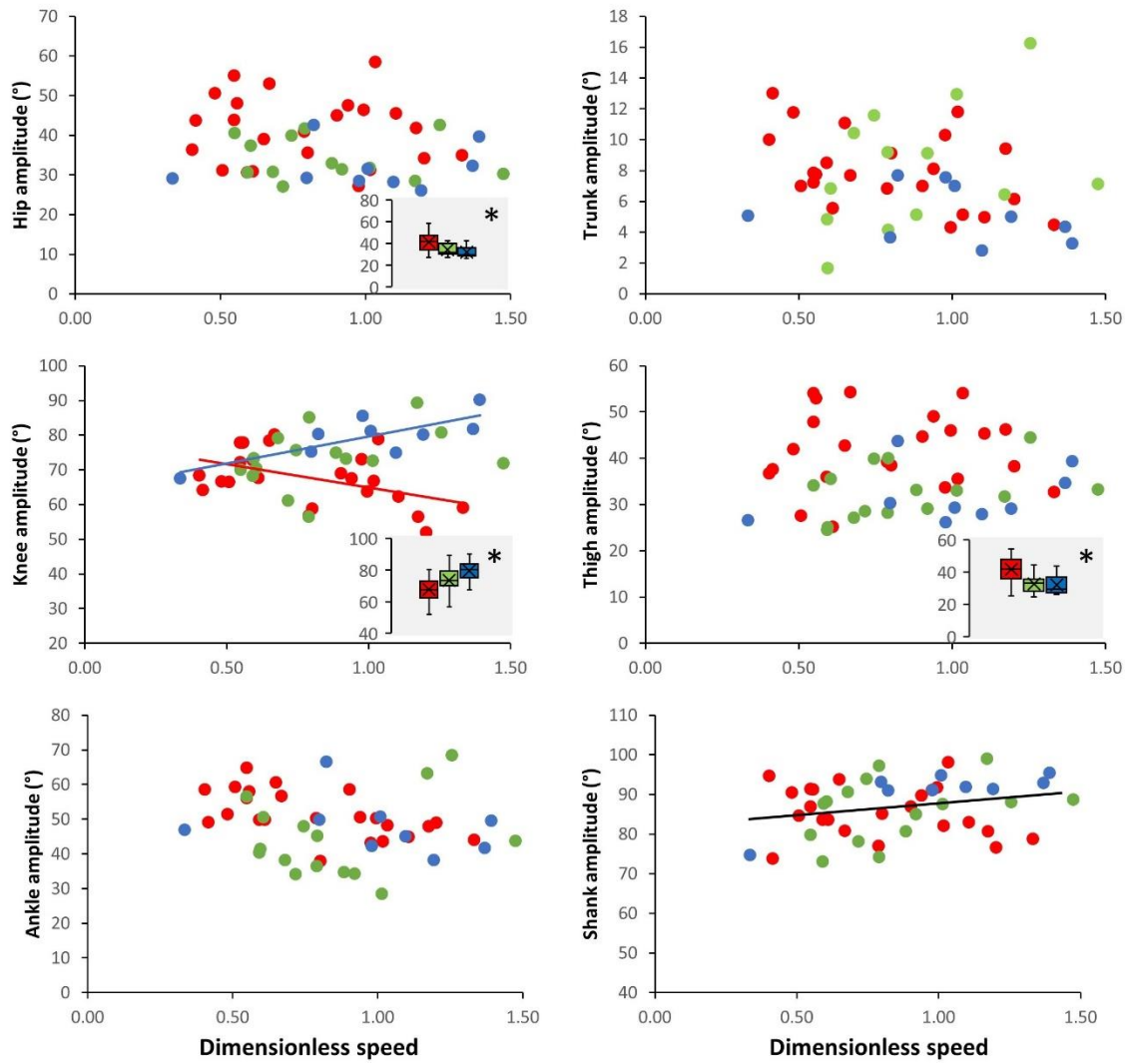


Figure 6

**TABLE 1.** Characteristics of the three age classes

	<b>Age class 1 (infant)</b>		<b>Age class 2 (adolescent)</b>		<b>Age class 3 (adult)</b>	
	<b>Mean</b>	<b>min-max</b>	<b>Mean</b>	<b>min-max</b>	<b>Mean</b>	<b>min-max</b>
<b>Age (year)</b>	0.93	0.5-1.58	3.58	3.14-4.1	6.68	5.39-7.4
<b>Body mass (kg)</b>	3.3	2.3-5.4	10.22	7.3-12.5	13.9	10.9-15.5
<b>N (individuals)</b>	9		10		5	
<b>Sex*</b>	4f, 5m		7f, 3m		5f	
<b>Number of strides</b>	23		15		9	

\*f: female; m: male

TABLE 2. Spatio-temporal parameters of steady bipedal walking per age-class

	Infant (n=21)		Adolescent (n=11)		Adult (n=8)		Speed effect		Age effect		Interaction effect	
	Mean	SD	Mean	SD	Mean	SD	F value	P value	F value	P value	F value	P value
<b>Cycle duration (s)</b>	0.57	0.13	0.60	0.09	0.58	0.12	117.55	<b>&lt;0.0001</b>	14.39	<b>0.0002</b>	2.42	ns
<b>Stride frequency (1/s)</b>	1.93	0.50	1.74	0.26	1.83	0.28	115.42	<b>&lt;0.0001</b>	14.52	<b>0.0001</b>	2.48	ns
<b>Stride length (m)</b>	0.44	0.07	0.65	0.09	0.72	0.08	27.33	<b>&lt;0.0001</b>	14.30	<b>0.0002</b>	2.42	ns
<b>Speed (m.s<sup>-1</sup>)</b>	0.86	0.27	1.14	0.30	1.36	0.30	N/A	N/A	2.05	ns	N/A	N/A
<b>Dimensionless values (shank length = scaling factor)</b>												
<b>Duty factor</b>	0.71	0.03	0.67	0.04	0.65	0.03	33.82	<b>&lt;0.0001</b>	7.43	<b>0.004</b>	6.29	<b>0.005</b>
<b>Cycle duration</b>	5.20	1.25	4.36	0.66	4.18	0.81	110.67	<b>&lt;0.0001</b>	0.84	ns	1.22	ns
<b>Stride frequency</b>	0.21	0.06	0.24	0.04	0.25	0.04	106.24	<b>&lt;0.0001</b>	0.77	ns	1.42	ns
<b>Stride length</b>	3.77	0.55	3.53	0.44	3.82	0.47	28.53	<b>&lt;0.0001</b>	0.87	ns	1.04	ns
<b>Speed</b>	0.79	0.24	0.85	0.21	1.00	0.24	N/A	N/A	0.15	ns	N/A	N/A
<b>Dimensionless values (shank + thigh length = scaling factor)</b>												
<b>Duty factor</b>	0.71	0.03	0.67	0.04	0.65	0.03	32.24	<b>&lt;0.0001</b>	8.29	<b>0.002</b>	5.92	<b>0.007</b>
<b>Cycle duration</b>	3.70	0.90	3.11	0.46	2.94	0.54	109.89	<b>&lt;0.0001</b>	0.06	ns	1.43	ns
<b>Stride frequency</b>	0.30	0.08	0.33	0.05	0.36	0.05	110.17	<b>&lt;0.0001</b>	0.06	ns	1.41	ns
<b>Stride length</b>	1.90	0.27	1.80	0.24	1.90	0.24	30.16	<b>&lt;0.0001</b>	0.04	ns	1.22	ns
<b>Speed</b>	0.56	0.17	0.61	0.16	0.71	0.17	N/A	N/A	0.11	ns	N/A	N/A

**TABLE 3.** Mean ( $^{\circ}$ ) and standard deviation (SD) of joint and segment angles at specific instants of the bipedal gait cycle per age-class

	Infant		Adolescent		Adult	
	Mean	SD	Mean	SD	Mean	SD
<b>Joint angles</b>						
<b>Ankle</b>						
Initial foot contact	107.46	6.25	104.44	7.06	107.87	8.13
Mid stance	66.92	3.94	69.95	3.23	68.79	5.69
Toe off	97.17	10.11	97.68	8.79	96.28	14.27
Mid swing	86.95	8.87	87.46	10.81	83.56	10.69
Final foot contact	102.78	5.10	102.77	6.18	106.57	8.94
<b>Knee</b>						
Initial foot contact	121.83	5.98	128.49	7.16	131.04	6.70
Mid stance	84.93	7.45	83.59	8.08	80.40	5.97
Toe off	63.67	8.99	65.19	7.59	59.44	8.64
Mid swing	77.74	11.59	80.85	13.64	79.95	12.30
Final foot contact	119.51	6.30	124.95	9.07	127.86	7.84
<b>Hip</b>						
Initial foot contact	86.95	9.37	85.05	17.34	75.63	9.72
Mid stance	97.74	11.31	94.68	15.88	81.21	11.23
Toe off	106.31	13.64	100.63	18.89	87.51	11.76
Mid swing	81.36	10.60	80.04	12.20	66.33	12.50
Final foot contact	86.51	9.55	85.91	13.30	74.56	10.67
<b>Segment angles</b>						
<b>Shank</b>						
Initial foot contact	97.33	4.68	101.14	5.76	106.57	5.40
Mid stance	46.85	4.28	45.89	6.29	48.62	4.92
Toe off	17.13	4.59	20.84	4.71	21.69	6.92
Mid swing	56.87	15.08	57.02	14.69	63.11	11.73
Final foot contact	94.48	5.23	96.51	5.09	103.48	7.25
<b>Thigh</b>						

Initial foot contact	155.50	5.68	152.65	7.78	155.53	3.30
Mid stance	141.92	6.90	142.30	7.27	148.21	4.68
Toe off	133.45	11.11	135.65	11.30	142.25	6.98
Mid swing	159.00	7.41	156.17	6.65	163.17	6.66
Final foot contact	154.97	4.45	151.56	6.42	155.62	4.32
<b>Trunk</b>						
Initial foot contact	62.45	5.90	58.51	11.62	51.17	7.68
Mid stance	59.66	6.11	57.65	9.07	49.42	7.31
Toe off	59.76	4.89	57.09	7.88	49.76	7.78
Mid swing	60.48	5.54	57.38	8.37	49.50	7.57
Final foot contact	61.48	5.68	58.02	8.33	50.18	7.29
<b>Shoulder</b>						
Initial foot contact	-8.59	9.24	-8.39	8.71	-3.54	14.91
Mid stance	-1.74	10.05	-4.39	10.19	0.07	13.22
Toe off	-1.46	12.87	-6.87	10.34	-3.84	12.51
Mid swing	-4.68	10.17	-7.43	8.87	-5.58	11.47
Final foot contact	-8.33	9.21	-8.83	7.12	-8.23	10.43

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**TABLE 4.** *Statistical results of the mixed effects models applied on the mean and amplitude of the joint and segment angles*

	Speed effect		Age effect		Interaction effect	
	F value	P value	F value	P value	F value	P value
<b>Mean</b>						
<b>Ankle</b>	11.22	<b>0.002</b>	1.57	ns	2.62	<i>0.089</i>
<b>Knee</b>	2.99	ns	0.03	ns	1.30	ns
<b>Hip</b>	1.27	ns	1.60	ns	0.25	ns
<b>Shank</b>	1.16	ns	6.17	<b>0.017</b>	0.91	ns
<b>Thigh</b>	4.89	<b>0.034</b>	1.43	ns	2.67	<i>0.083</i>
<b>Trunk</b>	0.03	ns	2.78	<i>0.087</i>	1.71	ns
<b>Shoulder</b>	0.01	ns	0.20	ns	0.02	ns
<b>Amplitude</b>						
<b>Ankle</b>	0.62	ns	0.77	ns	1.40	ns
<b>Knee</b>	1.78	ns	6.87	<b>0.007</b>	3.69	<b>0.037</b>
<b>Hip</b>	0.03	ns	3.58	<b>0.0499</b>	0.24	ns
<b>Shank</b>	7.83	<b>0.009</b>	0.61	ns	2.14	ns
<b>Thigh</b>	2.29	ns	4.14	<b>0.03</b>	0.15	ns
<b>Trunk</b>	0.64	ns	1.95	ns	0.82	ns
<b>Shoulder</b>	0.84	ns	4.98	<b>0.019</b>	1.41	ns

Significant results are indicated in bold and results that are close from the significant threshold are indicated in italic.

"ns" indicates a result that is not significant.

