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Locomotor Anatomy and Behaviour in Olive Baboons: Integrative Analysis from Early Infancy to Autonomy

François Druelle

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Universiteit
Antwerpen

Faculty of Science

Department of Biology

Laboratory of Functional Morphology

Locomotor Anatomy and Behaviour in Olive
Baboons: Integrative Analysis from Early
Infancy to Autonomy

Integratieve analyse van de vroege ontwikkeling van de
voortbeweging in de groene baviaan: anatomie en gedrag

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at the University of Antwerp

to be defended by

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Antwerpen, 2017

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Summary

The diversity of the environments in which baboons live demands specific locomotor activities (e.g. endurance walking, cliff climbing, etc.). Hence locomotor capacities and the development thereof are key to their survival. To improve our understanding of these performances and how these relate to morphology and behaviour we studied an important period of the baboons's development, i.e. the transition from the onset of independent foraging to autonomy (from 5 months to 2 years old). We conducted a longitudinal follow-up of six infant olive baboons living in captivity at the Primatology Station of the CNRS in France. We studied, in parallel, the morphometrics, the temporal kinematics and the positional behaviour of these individuals. In addition, we had the opportunity to analyse longitudinal morphometrics, collected over a seven-year period, on a large sample of captive olive baboons (30 individuals) including the male and female parents of our infants. This enabled us to describe the full morphological development of this species and to embed our sample in a larger developmental frame. Furthermore, with regard to questions on the origin of human bipedalism and the relevance of primate models, we also analysed behavioural data on bipedalism collected on a cross-sectional and ontogenetic sample of 22 baboons belonging to the same captive population.

First, our results show that the proportion of quadrupedal walking gradually increases on the expense of grasping behaviours during infancy. We observed that this pattern is highly correlated to changes in the body mass distribution, mainly at the level of the limbs where mass shifts proximally. While a more distal limb mass distribution reflects important grasping capacity for clinging onto the mother's fur, more proximal masses into the limbs are adaptive for reducing energy consumption during quadrupedal locomotion. Second, our results show that the ontogenetic changes in the pattern of body mass distribution influence bipedal walking in juveniles and adults in terms of bout duration, i.e. in individuals that possess a lighter head on a heavier trunk show longer bipedal bouts. Third, during the early period of development, young baboons improve their interlimb coordination in quadrupedal walking. We found that the intrinsic morpho-dynamics of fore- and hind limbs (at the

level of the convergence of the natural pendular period) have a significant and positive impact on this interlimb coordination pattern, thus probably facilitating, very early in development, the motor control and learning of quadrupedal walking. Finally, baboons occasionally walk spontaneously in a bipedal way and our results show that there is an improvement of the coordination of the hind limbs in this posture, coinciding to the development of interlimb coordination in quadrupedal walking. Hence, improvement of quadrupedal locomotor capacity does not exclude the development of bipedal behaviours, despite bipedal experiences remain rare in the ontogeny of baboons (<0.5% of their repertoire). This is also observed during chimpanzee ontogeny (Kimura and Yaguramaki 2009) and, therefore, sheds light on the emergence of new locomotor modes during the evolution of primates. Indeed, these results suggest a similar basic control mechanism in bipedal and quadrupedal locomotion. From an evolutionary perspective, we propose that secondary locomotor modes, such as bipedalism, experienced during infancy as by-products of locomotor development may lead to evolutionary novelties when under appropriate selective pressures.

Samenvatting

De diversiteit in leefomgeving van bavianen stelt specifieke eisen aan hun voortbeweging (bv. uithouding, rotsklimmen, etc.). Daarom zijn de locomotiecapaciteit, zowel als de ontwikkeling ervan, van groot belang voor hun overleving. Om onze inzichten in de voortbewegingsprestaties te verbeteren en om te begrijpen hoe deze prestaties relateren met de morfologie en het gedrag, bestudeerden we een belangrijke periode in de ontwikkeling van de groene baviaan, namelijk het interval tussen de aanvang van onafhankelijk foerageren tot autonomie (d.w.z. van 5 maand tot 2 jaar oud). Zes baviaanjongen werden, in het Primatologisch Station van het CNRS (Frankrijk), gedurende deze periode opgevolgd. We bestudeerden de relatie tussen morfometrie, de temporale aspecten van de gangkinematica en het positioneel gedrag van deze individuen. In aanvulling hierop werkten we mee aan een omvangrijke longitudinale morfometrische studie. Data werden over een periode van zeven jaar voor een grote groep van groene bavianen verzameld (zelfde populatie in gevangenschap; 30 individuen, inclusief de ouders van de zes jongen). Dit liet toe om de resultaten van de longitudinale studie van de vroege ontwikkeling in een ruimer ontwikkelingskader te plaatsen. Bovendien werd, in het kader van de vraag omtrent de relevantie van het gebruik van primate-modelsoorten voor onderzoek naar de origine van menselijke bipedalie, een cross-sectionele ontwikkelingsstudie op 22 bavianen uit dezelfde populatie uitgevoerd. Hiervoor werd bipedaal gedrag gekwantificeerd en geanalyseerd.

Vooreerst tonen onze resultaten hoe tijdens de bestudeerde ontwikkelingsperiode het aandeel van quadrupedaal wandelen in het positioneel gedrag gradueel toeneemt ten koste van 'grijpen'. Dit patroon is sterk gecorreleerd aan veranderingen in de massadistributie van het lichaam, voornamelijk ter hoogte van de poten, waarbij tijdens de groei de massa zich meer proximale gaat positioneren. Een meer distale pootmassa bij jongere dieren reflecteert in belangrijke mate de capaciteit van de jongen om zich vast te klampen aan de pels van de moeder. Anderzijds is een meer proximale pootmassa adaptief voor de reductie van de energieconsumptie gedurende quadrupedale locomotie. Ten tweede geven onze resultaten aan dat de ontogenetische veranderingen in het patroon van de massadistributie het bipedaal wandelen bij

juvenielen en adulten faciliteren. Dit is gereflecteerd in de duur van de periodes van bipedaal gedrag: individuen met een lichtere kop, maar zwaardere thorax wandelen bipedaal over langere tijdsintervallen. Ten derde blijkt dat bij jonge bavianen tijdens de vroege ontwikkeling de inter-poot-coördinatie van quadrupedaal wandelen verbetert. We vonden dat de intrinsieke morfo-dynamische karakteristieken van voor- en achterpoten (in termen van convergentie van de natuurlijke slingerperiode) een belangrijke positieve impact hebben op deze coördinatie en zodoende reeds zeer vroeg de motorische ontwikkeling en controle van quadrupedaal wandelen ondersteunen. Tenslotte toonden onze resultaten aan dat, samen met de ontwikkeling van de quadrupedale inter-poot-coördinatie, ook de achterpootcoördinatie tijdens het occasionele spontane bipedale wandelen verbetert. Dit wil zeggen dat ontogenetische progressie van de quadrupedale locomotiecapaciteit de ontwikkeling van bipedaal gedrag niet verhindert, ondanks het feit dat bipedalie eerder uitzonderlijk blijft tijdens de ontwikkeling van bavianen (<0.5% van het repertoire). Dit werd ook geobserveerd bij chimpansees (Kimura and Yaguramaki 2009). Dergelijke observaties kunnen worden geïnterpreteerd in de context van evolutionaire ontwikkeling van nieuwe locomotievormen bij primaten. Deze bevindingen suggereren immers een zelfde basaal controle-mechanisme voor bipedale en quadrupedale locomotie. In een evolutionair perspectief impliceert dit dat secundaire voortbewegingsmodi (zoals bv. bipedalie) die voorkomen als 'bijproduct' van de primaire locomotieontwikkeling, onder een gepaste selectieve druk kunnen leiden tot evolutionaire innovaties.

Foreword

Looking at a non-human primate in action is always fascinating. The apparent dexterity with which these animals move from the ground to the tree, from tree to tree, and how they adjust their movements on a set of various (flexible) substrates is impressive. This research work, behind its obvious biomechanical and evolutionary implications, was therefore also motivated by this amazement of nature and by the consideration of the natural spectacles to which humans are the witnesses.

General Introduction

“...*Eppur si muove*”

Galileo Galilei

The various posturo-locomotor abilities of non-human primates can be fulfilled only with the appropriate morphology (see Biewener 2003; Lécuru-Renous 1994). In other words, the morphology, via its intrinsic (neuromuscular and mechanical) properties, provides non-human primates with various posturo-locomotor capabilities. These capabilities are used daily for accessing food items, finding mates and avoiding predators. When looking closely at the diversity of these animals and the manner in which they move, it becomes obvious that locomotor performances are species-specific, and therefore, selected according to the environmental context in which they live. Firstly, the overall body shape, in parallel with size (spanning 100g to 200kg) varies greatly among non-human primates (Preuschoft et al. 1996; Fleagle 2013). Such size variability is, therefore, likely to induce constraints that differ between species. Secondly, the study of their positional repertoires, defined as the relative proportions of locomotor and postural modes (Hunt et al. 1996; Prost 1965), enables us to highlight the differences in locomotor performance. Accordingly, it has been shown that body shape is size-dependent (Kilbourne and Hoffman 2013; Preuschoft et al. 1996) and that the resulting morphological pattern is commonly adapted to the mechanical requirements related to the “preferred” locomotor mode of the species, i.e. the most adapted locomotor mode taking the environmental factors into consideration (Preuschoft 1989). Nevertheless, in the context of the diversity of the primates’ positional capacities the functional relationships between the morphological pattern and the positional repertoire need to be assessed carefully. Furthermore, how the morphological pattern may constrain, or facilitate, the most occasional components of the movement pattern is of great interest. Indeed, from an evolutionary perspective the structural variation will probably affect locomotor performance of both, preferred and occasional modes, and thus, in turn, will also affect *fitness* (Arnold 1983). Hence, knowledge about the interplay between body size, body shape and locomotion is highly valuable for a better understanding of the diversity of these species

and, when placed in their ecological context, for a better understanding of their evolution (Kilbourne and Hoffman 2013; Preuschoft 1989; Preuschoft et al. 1996; Witte et al. 1991).

The mechanics of the body and its motor control

The mechanics of the organismal system

A body possesses inherent mechanical properties. Indeed, it is composed of different segments, linked together with joints. Each segment can be described by its size (length, surface area, volume), its shape, its density, and, when considered altogether, its mass, its centre of mass, its inertia and its radius of gyration. Each joint possesses a certain number of degrees of freedom. Therefore, the “joint-segment” system can be modeled according to lever arm principles. In this respect, a body is characterised by inertial properties that reflect the resistance to linear and angular acceleration about a joint during movement. We will name these basic mechanical properties the intrinsic morpho-dynamics of the body; these properties should influence locomotor performance. With regard to, for example, animal terrestrial locomotion, this seems largely related to the principles that regulate the swing of a pendulum (Cavagna et al. 1977; Holt et al. 1990; Preuschoft et al. 1996). Indeed, on the one hand, the rise and fall of the body centre of mass within each stride of a walking gait can be modeled as an inverted pendulum (Cavagna et al. 1977). On the other hand, a limb moving forward during its swing phase can be modeled like a pendulum suspended about the proximal joint (Holt et al. 1990; Myers and Steudel 1997). Here, the performance is considered in its broadest sense, thus including different kinds and degrees of movement capacities.

Firstly, basic mechanical segmental properties may affect the level of performance via the muscular (in-)ability to perform a movement. For example, Bekoff and Trainer (1979) observed that interlimb coordination was present at birth in rats when swimming, but the ability to walk on the ground appears only after few days. Wing-flapping is present after hatching in chicks but the lift appears only after two weeks when the wing structure is effective, i.e. when the ratio of wing area to body weight is large enough (Provine 1981). In (human) toddlers, the onset of bipedal walking seems to depend, in part, on the upper body mass distribution; it is delayed in relatively top-heavy infants (Adolph et al. 1997).

Secondly, basic mechanical segmental properties may affect movement energetics, hence constraining performance. For example, it has been shown that having mass proximally concentrated in the limbs facilitates the latter's swing about their proximal joint because of the smaller moment of inertia. As a result, the muscle effort to swing the limb forward can be reduced (Myers and Steudel 1985; Preuschoft and Günther 1994; Witte et al. 1991). Kilbourne and Hoffman (2013) showed, in a sample of quadrupedal mammals varying widely in body size, that the observed positive allometry of limb length probably explains the lower values of mass-specific cost of transport in larger mammals. Indeed, long limb lengths offer the possibility to take relatively longer, but less strides, to travel a given distance. Kimura (1996) also observed that chimpanzees walk bipedally with an increase energy recovery capacity during development in part because of the relative changes in hind limb length.

Thirdly, the basic segmental properties will probably influence the pattern of kinematics. For example, infant baboons walk with relatively low stride frequencies and long stride lengths because of their distally concentrated masses into the limbs (Raichlen 2005a). In toddlers, it has been shown that there is a relationship between the morphology and the kinematics of bipedal gait. During walking, the relative step width depends on the morphology of the head and pelvis while the moment of inertia of the thorax influences hip adduction. Moreover, the range-of-motion of the trunk is limited in children with a broad pelvis. In this respect, the upper body seems to play an important role in the coordination of the walking pattern in toddlers (Van Dam et al. 2010; Van Dam et al. 2011). According to the *Support Polygon Model* (Gray 1944), the relative caudal position of the whole body centre of mass in primates would explain the preferred use of diagonal gait sequences in these species (Cartmill et al. 2002; Rollinson and Martin 1981; Young 2012; but see Young et al. 2007; Anvari et al. 2014).

Fourthly, the basic segmental properties may impact the force distribution. For example, in primates, relatively long forelimbs tend to lower the external resultant force in vertical climbing because of the lever arm lengthening. This conformation thus provides a better force-economy during this locomotor mode (Preuschoft and Witte 1991). The position of the whole body centre of mass, coupled with limb positioning, has been hypothesized to explain the weight support pattern (toward hind limb

weight bearing) in primates (Cartmill et al. 2002; Gray 1944; Raichlen et al. 2009; Rollinson and Martin 1981; but see Larson and Demes 2011; Reynolds 1985; Young 2012).

Finally, the mechanical properties of the body may also reflect other (postural) capacities than those directly related to movement. For example it has been shown that the bite force of grey mouse lemurs can be determined, in part, by head dimensions (Chazeau et al. 2013; Thomas et al. 2015). The fact that the masses are distally concentrated in the limbs of primates (zeugopodia are particularly heavy and autopodia are long and heavy) is hypothesized to be related to their important grasping capacities. These capacities allow transmitting tensile forces and rotational moments on the arboreal substrates (Preuschoft and Günther 1994).

Furthermore, these properties also represent a trade-off because of the inherent socio-ecological context in which the body is immersed including feeding strategies, predator avoidance and mating and social systems. It has been shown for example that the degree of body size dimorphism is related, in part, to male intra sexual selection in anthropoid primates (Leutenegger and Kelly 1977). Food properties seem to strongly influence hand morphologies in primates (see Pouydebat et al. 2014). Different reproductive strategies are at the origin of the bimaturism observed in male orang-utans (Banes et al. 2015). Finally, Hunt (2016) suggested that an important interspecific competition for food access led to apes evolving a larger body size to displace monkeys.

The motor control

The relationship between movement and the basic mechanical properties of the body obviously depend upon neural control mechanisms (Grillner 1985). Indeed, any muscle contraction is induced by motor neurons either via local reflex sensory feedback or higher (supraspinal) level signal processing. The coordinated motor activities, i.e. activities that retain a cyclical pattern through time, such as walking, climbing, flying, swimming, etc, are mediated by networks of neurons known as the Central Pattern Generators (CPGs). CPGs are situated in the spinal cord and characterised by rhythmic properties (Marder and Bucher 2001). Their activation mainly depends on input from supraspinal command centres in the brainstem and local sensory feedback allows modulation of

the basic motor pattern (Duysens and Van de Crommert 1998; Grillner 1985; Grillner and Jessell 2009; Pearson 2000). With regard to recent discoveries (e.g. Hägglund et al. 2013) it seems that the locomotor system in mammals is organized according to a modular neural network (Büschges and Borgmann 2013). A functional movement sequence would be controlled by a coordination of modules being dependent on the task. With respect to the high variability in motor outputs and movements generated in primates (Hunt et al. 1996), rearrangements of the spinal circuitry may have occurred during the evolution of these species toward an increase in flexibility of the modular system and less integration of the limbs. This would free the movements of the forelimbs from those of the hind limbs and would result in an increased corticospinal control of motion in these species (Dietz 2002; Eidelberg 1981; Vilensky 1987; Vilensky and Larson 1989), at least in old world monkeys and apes (Hultborn et al. 1993). While a direct cortical-motoneuronal system is premised to be present for skilled hand movements, cervical and thoraco-lumbar propriospinal systems may be coupled for locomotion (Dietz 2002). In humans, it has been shown that this neural coupling would still be present between arms and legs, as reflected in the arm swing during bipedal locomotion (Dietz et al. 2001; Zehr and Duysens 2004). This can be demonstrated via indirect evidence, for example a cyclic H response modulation (known as the Hoffmann reflex) is observed in the upper limbs during rhythmic movements of the foot (Baldissera et al. 1998; see Dietz 2002 for a review of other evidence). Furthermore, the bilateral coupling of the legs is shown to be very strong and greater than the neural coupling between the arms (Zehr et al. 2004; Zehr et al. 2003; Zehr and Duysens 2004). This is suggested to be the result of different coupling requirements; the legs should ensure balance and an efficient forward displacement during terrestrial bipedal locomotion, while the arms are specialised for independent skilled hand movements (Zehr et al. 2016; Zehr and Duysens 2004).

Toward neuro-mechanical coupling and its relationship with size

The mechanics of the body and the motor control are two separate but highly integrated components of the organism. A proper coordination and control should exploit the intrinsic dynamics (as reflected, amongst others, in the inertial properties) of the system for efficient locomotion (see

Figure A). Because the mechanical properties change with size (i.e. scaling principles apply; for a review see for instance Schmidt-Nielsen 1984) and as the size range spans three orders of magnitude in primates (see above), the potential for mechanical adaptations is extensive in these species. For example, momentum-based strategies (i.e. strategies that rely on gravity and momentum to maintain leg movements, such as the exploitation of the limbs' natural pendular period) may facilitate the control, although probably to a much lesser extent in small, short legged animals (Hooper 2012). Furthermore, according to the geometric principle of scaling and because muscle force is proportional to muscle cross sectional area, muscle force seems to vary with limb mass^{2/3}. Therefore, the ratio between the force of gravity and the restoring force generated by muscle antagonisms, ligaments and tendons (when stretched beyond rest length) is largely biased towards the gravitational force in large animals, and towards the muscle force in small animals (see Hooper 2012 for an example). As a consequence, during movement, basic mechanical segmental properties such as an appropriate position of the limb centre of mass may facilitate the neural control task. The interplay between neural control mechanisms and the basic mechanical properties of the body, therefore, appears to be largely constrained by body size (Cant 1992; Hooper 2012; Kilbourne and Hoffman 2013; Preuschoft et al. 1996). In the context of locomotor performance, a body should have both, the shape and the neural system suitable for its size. Such considerations are fundamental aspects for understanding the movement-related constraints and, therefore, the evolution of locomotor apparatus.

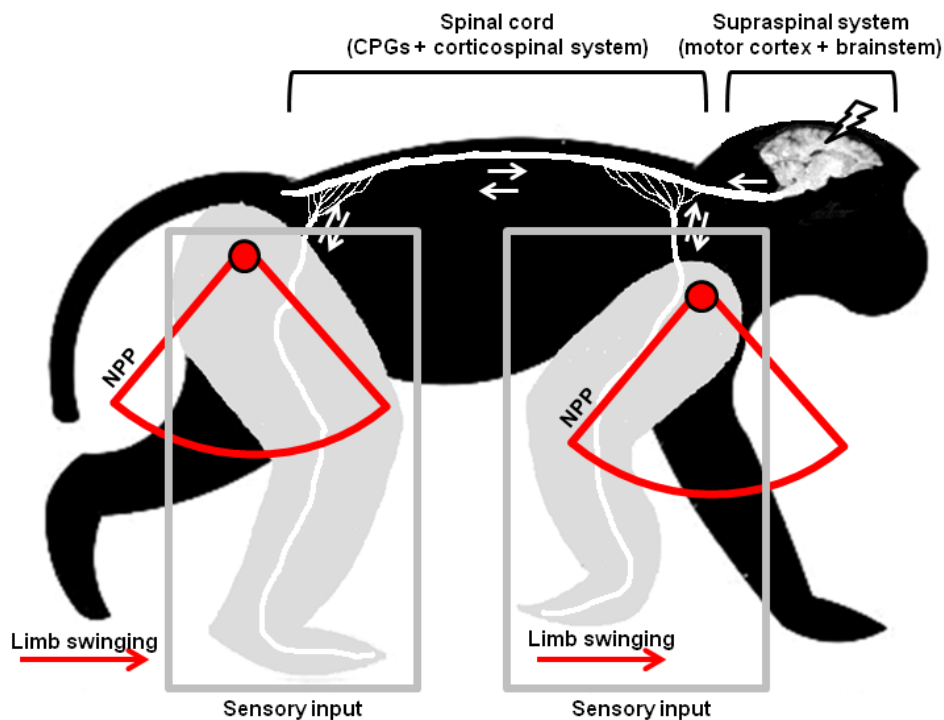


Fig. A. Schematic overview of the neuromotor control in an infant baboon walking quadrupedally and the potential coupling with limb mechanical properties. There is a simple descending supraspinal intentional drive activating the CPGs at the level of the spinal cord. These interconnected networks generate the properly coordinate motor activation of the limb muscles. The red dots represent the proximal joints about which the fore- and hind limbs swing. The red circle segments reflect the Natural Pendular Periods (NPP) of the limbs, depending on the limb intrinsic morpho-dynamics only. These mechanical properties can be used to facilitate the motor control task.

The morphological development

The phenomenon of ontogenetic allometry and its relationship with locomotor performance

Development involves size-related changes in the mechanical and physiological properties of the body. This phenomenon is known as ontogenetic allometry (Gould 1966; Thompson d'Arcy 1917). Because changes in size are likely to affect the mechanical constraints related to locomotion (see above), the pattern of allometry may be adaptive for facilitating movements during growth, i.e. from a small and light body to a

large and heavy body. Indeed, because of their immature musculoskeletal system and relatively low level of muscle force (see Grand 1977a for primates), infants may initially be limited in their locomotor performance. Nevertheless, allometric processes may enhance the movement capacities (Carrier 1996; Herrel and Gibb 2006). It has been shown that, relative to their size, infants' morphology presents anatomical mechanical advantages, thus increasing the capacity to produce force for a given amount of muscle (Carrier 1983; Young 2005). They also exhibit an important long bone cross-sectional robustness, thus increasing the safety factors, i.e. the resistance to fracture (Carrier and Leon 1990; Heinrich et al. 1999; Main and Biewener 2004; Ruff 2003; Young et al. 2010a). In consequence, these ontogenetic features may help to enhance locomotor performance in young animals. If the allometric pattern is the result of ecological constraints in part related to locomotor performance in infants, it is likely to vary according to the species, for example between precocial and altricial animals (but see Young et al. 2010a). Nevertheless, some selective pressures are likely to be shared by all species, such as the mortality risks from predation, yet the strategies may be very different between orders. For example, infant gazelles need to run for predator avoidance while the survival mode of the infant primate is clinging to the mother's fur.

A shared developmental pattern in primates?

It has been shown that primates share a common developmental pattern in terms of body shape and segment lengths (e.g. Grand 1977a; Leigh et al. 2009; Schoonaert et al. 2007; Turnquist and Wells 1994). Just after birth, individuals commonly exhibit a large head in relation to their body size, as well as large autopodia (i.e. hands and feet). Therefore, these segments show negative allometry during further development (Grand 1977a; Jungers and Fleagle 1980; Lawler 2006; Raichlen 2005b; Ravosa et al. 1993; Schoonaert et al. 2007; Turnquist and Wells 1994). The consequence of this ontogenetic pattern is a caudal shift of the body centre of mass as well as a shift of the limb centre of mass towards the proximal joint (Raichlen 2005b; Turnquist and Wells 1994). Further, it has been hypothesized that exhibiting large autopodia may be a functional adaptation enhancing grasping abilities at a young age (Jungers and Fleagle 1980; Turnquist and Wells 1994). Nevertheless, while long hands and feet would increase the span of the grip, it would also reduce the

contact pressure and thus the friction force. Therefore, the compressive force and the grasping abilities diminish. However, this strength diminution can be compensated, firstly by reducing the contact area via a reduced width, secondly by increasing both the flexor muscles in the zeugopodia (i.e. forearm and leg) and the short intrinsic muscles of the autopodia (Preuschoft 2004; Preuschoft et al. 1998; Preuschoft et al. 1996). Interestingly, the autopodia are commonly shown to be both longer and heavier at birth in primates (Schoonaert et al. 2007; Turnquist and Wells 1994). In addition, it has been shown that intrinsic proportions of autopodia (i.e. the relative length of the metapodials compared to the length of the digits) may also reflect the initially strong grasping capacities (e.g. Hamrick 2001; Young and Heard-Booth 2016). In summary, these data are all consistent with the fact that infant primates spend a substantial part of their early life using active clinging behaviours while being carried by their mother (e.g. Altmann 2001; Altmann and Samuels 1992; Anvari et al. 2014; Doran 1992b; Doran 1997; Hoff et al. 1983; Wells and Turnquist 2001). It has also been shown that infant primates exhibit a wider positional repertoire than adults, including an important proportion of climbing and suspensory behaviours (Doran 1992b; Doran 1997; Druelle and Berillon 2013; Sarringhaus et al. 2014; Wells and Turnquist 2001), making grasping capacities an important aspect of their locomotor performance, also certainly limiting the risk of falling from trees at this immature stage. Nevertheless, the hypothesis suggesting the relationship between grasping abilities and an initial functional adaptation of the autopodia and zeugopodia in primates requires further evaluation.

The form-function relationship during development and its limitations

Although size-related adaptations can be different during ontogeny and phylogeny (Biewener 1983; Main and Biewener 2004), morphological changes occurring during growth may be used as “natural experiments” for testing specific functional relationships (e.g. Raichlen 2005a; Shapiro and Raichlen 2006; Young 2005; Young 2009; Young 2012; Young et al. 2010a). Nevertheless, when testing for morphology changing with age, body size can easily be removed from the test (Hof 1996), hence just taking shape into account. However, excluding shape from the tests is impossible. Including body size inherently includes shape because an ontogenetic series implies dimensional adjustments (ontogenetic

allometry), making it difficult to assess the mechanical effect solely of body size.

In addition, more comparative ontogenetic data are required to accurately differentiate the adaptive features (in relation to their respective function) of the developmental pattern shared specifically by primates from those shared by all mammals, or even all vertebrates. Indeed, some of the previously presented trends may simply be exaptations (see Gould and Vrba 1982) of the common growth processes of vertebrates; for example the negative allometry on the size of autopodia does not seem to be unique to primates (e.g. Carrier 1983; Lammers and German 2002). In this respect, cross correlating morphological, biomechanical and behavioural data at an individual level could provide valuable insight into this topic. Furthermore, a better understanding of the growth-trajectories offers opportunities for reconstructing the evolutionary pathways of locomotor modes (Hurov 1991; Leigh 2001).

Bipedality in primates

The occasional use of bipedal behaviours in non-human primates

All non-human primates, at least our closest relatives, the Catarrhini species (see Druelle and Berillon 2014 for a review), are able to walk bipedally and to use this gait during their (daily) activities such as foraging, investigation, carrying, playing, greeting, displaying, aggressions, copulation, etc (e.g. Rose 1976; Stanford 2006; Videan and McGrew 2001). Therefore, it is commonly accepted that non-human primates are occasional bipedal walkers, while the human primate is defined as a habitual bipedal walker (e.g. Alexander 2004; Franzen et al. 2003; Multon et al. 2012).

From occasional to habitual: an evolutionary perspective

Various hypotheses have been proposed for the origin of human bipedalism. It has been suggested that bipedalism might have been an adaptation for (food) carrying (e.g. Carvalho et al. 2012; Hewes 1961), looking over tall grass in a savannah environment (Dart 1959), reaching for food (Jolly 1970), wading behaviours (e.g. Niemitz 2002; Niemitz 2010), etc (see Fleagle 2013 for a review). These hypotheses are based

on the fact that extant non-human primate species commonly practice occasional bipedalism specifically in these contexts (see Hunt 1994; Rose 1976; Stanford 2006; Wrangham 1980), yet, it also brings into question the true benefits of this occasional behaviour on individual *fitness*, i.e. for finding food, avoiding predators and finding mates. Indeed, the effects of occasional bipedal behaviours in non-human primates should be quantified to truly assess the advantages of bipedalism. Nevertheless, regarding the phylogeny of (human and non-human) primates, the previous observations indicate that habitual bipedal walking abilities emerged from a hominoid ancestor that was already capable of occasional bipedal behaviours in a terrestrial and arboreal context (e.g. Crompton et al. 2010). Therefore, while the previous functional hypotheses proposed behavioural contexts (see above) for the evolution “toward” habitual bipedalism, we suggest that, in light of our current knowledge on bipedal behaviours in Catarrhini species (Druelle and Berillon 2014), such contexts have no causal relationship with the evolution of bipedalism. Rather they are the effects of an (ancestral) ability for occasional bipedalism in these species. In this respect, bipedal behaviours might have initially been an exaptation with derived behavioural effects (those currently seen in extant non-human primates) that are likely to become advantageous for individual *fitness* (Gould and Vrba 1982); yet this still requires testing.

Furthermore, some authors aimed to identify the potential locomotor precursor of habitual bipedalism. Based on comparative models, brachiation, quadrupedal knuckle-walking and vertical climbing were all proposed as possible precursor modes for the origin of habitual bipedalism based on their kinematics and morpho-functional resemblances (e.g. Prost 1980; Richmond and Strait 2000; Tuttle 1981). Nevertheless, non-human primate models are sometimes considered as stepping stones, while they are, in fact derived, compared to our last common ancestors. Indeed, no comparative model should be considered as a “perfect stand-in”: firstly, it does not exist, secondly, further atypical models can also provide an insight, and even specifically because of their imperfect resemblance to the original form (see D’Août et al. 2014). In this context, Thorpe et al. (2007) suggested, based on the suspensory-specialised (and also highly derived) orangutan, that hand-assisted arboreal bipedality might have been the precursor of hominin bipedality because of both its similarity in kinematics and its associated ecological

benefit. However, regarding the retentive difficulties of the common questioning about why and how did habitual bipedalism evolve, the “problem” would certainly benefit from being considered from another perspective. As a result of these reflections (and according to the four questions' methodology proposed by Tinbergen 1963) a fundamental proximal question emerges: why are non-human primates, at least all Catarrhini species, able to perform occasional bipedalism? This also raises the issue about the origin of an increased flexibility of the modular neural network organization in primates (see above).

A less constrained body, in terms of its mechanical properties, may have facilitated being able to move around on two legs, while enhancing balance control and energy consumption. The knowledge acquired from studies about bipedal walking onset in modern humans (e.g. Adolph et al. 1997; Adolph et al. 2012; Hallems et al. 2004; Thelen 1985; Van Dam et al. 2010; Van Dam et al. 2011), the theoretical biomechanical reflections of Preuschoft and colleagues (e.g. Preuschoft 1989; Preuschoft 2004; Witte et al. 1991) and experimental works on non-human primates (e.g. Aerts et al. 2000; Anvari et al. 2014; Berillon et al. 2011; Berillon et al. 2010; D'Août et al. 2004; Demes 2011; Demes and O'Neill 2013; Franzen et al. 2003; Kimura 1991; Kimura and Yaguramaki 2009; Pontzer et al. 2014; Pontzer et al. 2009; Sockol et al. 2007; Tardieu et al. 1993; Thompson et al. 2015) may help to distinguish mechanical facilitators of unassisted bipedal walking. It has been hypothesized that longer hind limbs and a lower body centre of mass may have been of importance to enhance bipedal abilities in an ancestral non-human (prothominin) primate (Aerts et al. 2000; Zihlman 1996). Studies focusing specifically on morphological constraints, or morphological facilitators, of bipedal gaits in non-human primates would be of great interest for dealing with the evolutionary transition of this behaviour.

A quadrupedal model

The olive baboon

The olive baboon, *Papio anubis*, is part of the Superfamily Cercopithecoidea and of the Parvorder Catarrhini, which includes the great apes and human primates (Perelman et al. 2011). The baboon has been widely studied in its natural environment with regard to its locomotion (e.g. Hunt 1991; Hunt 1992a; Patel et al. 2013; Rose 1976; Rose 1977),

development (e.g. Altmann 2001; Altmann and Alberts 1987; Altmann et al. 1977), and socio-ecology (e.g. Altmann and Samuels 1992; Kitchen et al. 2003; Kummer 1968; Strum 2012; Strum and Western 1982). Captive populations have also been intensively used for biomedical research (see VandeBerg et al. 2009 for a review), cognition studies (e.g. Bourjade et al. 2014; Fagot and Bonté 2010; Malassis et al. 2015; Medam and Fagot 2016; Medam et al. 2016; Meguerditchian and Vauclair 2006; Meguerditchian and Vauclair 2009; Schmitt and Fischer 2009; Vauclair et al. 2005), social studies (e.g. Claidière et al. 2015; Fischer and Zinner 2011; Rowell 1966), anatomical research (e.g. Glassman et al. 1983; Glassman and Coelho 1987; Leigh et al. 2009; Love et al. 2016; Raichlen 2005b) and in biomechanics (e.g. Anvari et al. 2014; Berillon et al. 2011; Berillon et al. 2010; Raichlen 2004; Raichlen 2005a; Raichlen 2006; Shapiro and Raichlen 2005; Shapiro and Raichlen 2006).

Traditionally, four species of savannah baboons (*Papio anubis*, *P. papio*, *P. ursinus* and *P. cynocephalus*) and one species of hamadryas baboon (*P. hamadryas*) are described. Savannah baboons live in woodland savannahs, grasslands, gallery forests and even some rainforest environments. These species are highly social and live in large multi-male, multi female troops ranging from 40 to 80 individuals. Hamadryas baboons appear to live in a different socio-ecological system because of particular evolutionary contexts (see Henzy and Barrett 2003, 2005). Nevertheless, note that this taxonomic status is debated for many years and no consensus can be currently reached. For example, a recent study using mitochondrial DNA applied on 67 individuals coming from 53 sites was unable to identify the five families previously proposed (Zinner et al. 2009). Otherwise, they further support the existence of another distinct baboon species (*Papio Kindae*).

With regard to the baboon in general, infants are commonly weaned after their first year of life. They are considered infants until 2 years of age, and then juveniles until 3 years of age (see Altmann 2001). Females are considered adult at 5 years of age after a two-year period of adolescence. Males are considered to be fully adult at 7 years of age after a four-year period of adolescence. They are subjected to growth spurts and their morphological maturation is considered to follow the “typical” pattern of catarrhine primates (Leigh et al. 2009). Baboons are diurnal and mainly terrestrial during daytime. Therefore, they forage and travel

on the ground using quadrupedal locomotion (walking and running). In this respect, they are described as committed quadrupeds. Nevertheless, they commonly spend the night in trees, or on cliffs, which they can efficiently climb (Rose 1977). Their locomotor repertoire is, therefore, composed of 97% of walking, 0.7% of climbing, 0.5% of leaping and 1.6% of running (Hunt 1991). Nevertheless, careful attention should be paid to the method of observation. Indeed, the purpose of the study, and therefore the time-resolution of the observations may sometimes hide (occasional) behavioural components (Dagosto 1994; Dagosto and Gebo 1998; Doran 1992a). In fact, the adult olive baboon is also able to walk bipedally (e.g. Berillon et al. 2011; Wrangham 1980) and appears to use this gait during daily activities, but still over relatively short periods (Druelle and Berillon 2013; Rose 1976). In summary, during ontogeny, baboons undergo changes in their morphological pattern (Leigh et al. 2009; Raichlen 2005b), as well as at the level of their movement pattern (Rose 1977) and their locomotor performance is likely to be affected by growth-related changes (Patel et al. 2013; Raichlen 2005a; Shapiro and Raichlen 2006). Finally, baboons are committed quadrupedal walkers but they also practice other locomotor behaviours including occasional bipedalism, in the wild as well as in captivity (Druelle and Berillon 2013; Rose 1976).

Baboons constitute excellent models for our aims. There is certainly no resemblance between extant baboons and the last common panin/hominin ancestor (see Crompton et al. 2008), yet, understanding how a committed quadrupedal primate is able to walk bipedally may provide important insights (D'Août et al. 2014). Furthermore, the behavioural plasticity and the adaptive capacities of the baboon (see Strum 2012) make this model very relevant for a better understanding of the evolution of primates in general.

The captive environment

The Primatology Station of the CNRS (Rousset, France) houses and raises olive baboons. The animals live in enhanced parks and within their social groups. This centre provides an ideal setting for longitudinal follow-up for studying behaviour, anatomy and cognition (see Figure B). A preliminary study revealed that the captive baboons exhibit a similar positional repertoire to that observed in the wild (Druelle and Berillon 2013). The unique opportunity offered by the CNRS Primatology Station,

together with the available profound knowledge on phylogeny and biology of the olive baboon, makes this species and, more specifically, this captive group the perfect model for our aims: addressing growth-related anatomical changes in relation to locomotion in general, and bipedalism in particular.



Fig. B. The picture on the top is an overview of the park (200m²) in which the present study was conducted; various structures are laid out (see Chapter 2). The two photographs on the bottom left were taken during the morphometry protocol on anesthetized animals. The three pictures on the right-hand side show different positional behaviours voluntarily performed by baboons (vertical climbing, tripedal running and leaping).

Outline of the thesis

In this thesis, I explore the mechanical properties of the body of the olive baboon and how those influence the locomotor behaviours and the interlimb coordination. On the one hand, the objective is to assess the growth pattern of the locomotor apparatus of the olive baboon and to observe potential sex-related differences. On the other hand, the age-related morphological changes are put forward as a natural experiment for testing specific form-function relationships. Finally, the assessment of the functional changes of the baboon's morphology during development, placed in the socio-ecological context of this species, enables us to interpret the potential locomotor adaptations and their degree of evolvability (see Chapter 1 for a definition; Wagner and Altenberg 1996). Furthermore, the implication of the occasional pattern of bipedal behaviours is highlighted at all stages of this thesis because of the valuable insights into the evolution of occasional bipedality in primates, and habitual bipedality in hominins. Following this logic, I choose to arrange the chapters of my thesis according to this rather than following the chronological order of the publication.

Hence, **Chapter 1** describes the full development of the morphology of the olive baboon, from birth to adulthood, in males and females. I contributed to the recording of a large database of external measurements performed in a longitudinal manner on a captive group of multi-male, multi-female olive baboons and I analysed the full dataset. The follow-up, covering a seven-year period, provides an exhaustive picture of their growth pattern. Due to the probable (mechanical) influence of the morphological changes on the positional repertoire, we can precisely assess their relationships at an individual level in **Chapter 2**. A longitudinal sample of six infant baboons during a period of important locomotor shifts enables us to make this evaluation. Baboons are principally quadrupeds, but they also perform other locomotor modes, such as climbing, bipedalism, suspension, etc. In this respect, and with regard to our interest in bipedalism, **Chapter 3** presents a study which specifically tests the influence of the growth-related morphological changes on the practice of bipedal behaviours. To this end, we use a transversal sample of 22 individuals representing all the stages of the ontogeny.

I then address the development of the motor control via the assessment of the interlimb coordination. **Chapter 4** provides an analysis of the development of interlimb coordination of quadrupedal walking in baboons, and how this relates to the intrinsic morpho-dynamics of the body. Because it has been suggested that motor control is similar in some respects, in bipedal and quadrupedal gaits, **Chapter 5** describes the development of the hind limbs' coordination during spontaneous sequences of unassisted bipedal walking. The *Discussion* of each chapter addresses the evolutionary implications in relation to the results. The last part of this thesis draws a general conclusion on the locomotor evolution of baboons, and by extension hominoids and hominins.

Chapter 1

Segmental morphometrics of the olive baboon (*Papio anubis*): a longitudinal study from birth to adulthood

Based on: Druelle F, Aerts P, D'Août K, Moulin V, Berillon G (In press)
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The linear dimensions and inertial characteristics of the body are important in locomotion and they change considerably during the ontogeny of animals, including humans. This longitudinal and ontogenetic study has produced the largest dataset to date of segmental morphometrics in a Catarrhini species, the olive baboon. The objectives of the study were to quantify the changes in body linear and inertial dimensions and to explore their (theoretical) mechanical significance for locomotion. We took full-body measurements of captive individuals at regular intervals. Altogether, 14 females and 16 males were followed over a seven-year period, i.e. from infancy to adulthood. Our results show that individual patterns of growth are very consistent and follow the general growth pattern previously described in olive baboons. Furthermore, we obtained similar growth curve structures for segment lengths and masses, although the respective time scales were slightly different. The most significant changes in body morphometrics occurred during the two first years of life and concerned the distal parts of the body. Females and males were similar in size and shape at birth. The rate and duration of growth produced substantial size-related differences throughout ontogeny, while body shapes remained very similar between the sexes. We also observed significant age-related variations in limb composition, with a proximal shift of the centre of mass within the limbs, mainly due to changes in mass distribution and in the length of distal segments. Finally, we observed what we hypothesize to be “early biomechanical optimization” of the limbs for quadrupedal walking. This is due to a high degree of convergence between the limbs’ natural pendular periods in

infants, which may facilitate the onset of quadrupedal walking. Furthermore, the mechanical significance of the morphological changes observed in growing baboons may be related to changing functional demands with the onset of autonomous (quadrupedal) locomotion. From a wider perspective, these data provide unique insights into questions surrounding both the processes of locomotor development in primates and how these processes might evolve.

1.1 Introduction

The locomotor apparatus of animals can be considered best adapted morphologically when its size and shape are well suited to the principal mode of locomotion of the species (see Preuschoft and Günther 1994; Preuschoft et al. 1996; Witte et al. 1991). Primates are of special interest because, unlike many mammals with more specialised modes of locomotion, they adopt a variety of positional modes every day (Hunt et al. 1996) that involve a diverse range of substrate reaction forces (in terms of magnitude and direction) and moments. This is easily understood in view of the complex three-dimensional environment in which they evolve. Their locomotor apparatus should thus reflect, in some respects, an adaptive trade-off between efficiency, stability (static and dynamic), manoeuvrability, flexibility of movement, and rare but important behaviours.

It has been hypothesized that adaptations of the body to specific locomotor modes are likely to become more pronounced with development (Isler et al. 2006). This would make differential growth an important process for the locomotor transitions observed during primate ontogeny (e.g. Doran 1997; Dunbar and Badam 1998; Sarringhaus et al. 2014; Wells and Turnquist 2001). Newborn primates are unable to walk: it commonly takes several weeks to months (depending on the species) to achieve this with a semblance of interlimb coordination, and from months to years to become fully efficient and autonomous. Their locomotor development is affected by complex processes involving different factors such as neuro-muscular maturation, experience and changes in body dimensions (e.g. Adolph and Avolio 2000; Adolph et al. 2012; Garwicz et al. 2009; Kimura and Yaguramaki 2009; Nakano 1996). Adult catarrhine primates, including humans and their closest relatives, exhibit an impressive diversity in their morphometrics (i.e. linear dimensions, segmental masses, moment of inertia) in parallel with a wide diversity of locomotor modes. Yet these species appear to follow a common pattern of differential growth (Leigh et al. 2009). Consequently, studying the development of the locomotor apparatus in full is crucial to a better understanding of the ontogeny of locomotion potentially leading to specialised modes or generalized repertoires. Furthermore, such studies could improve our knowledge about the evolvability of locomotor profiles,

i.e. “the ability of random variations to sometimes produce improvement” (Wagner and Altenberg 1996).

This paper focuses on changes in morphometrics and their (theoretical) mechanical significance during the ontogeny of the catarrhine olive baboon, *Papio anubis*, based on a longitudinal study of a large sample of captive individuals. At the adult stage, baboons are specialised for quadrupedal locomotion, yet they are also capable of adopting a variety of positional modes, including bipedalism (e.g. Rose 1977). Just after birth, baboons only possess grasping abilities, but it has been shown that growing infants rapidly include quadrupedal walking and suspensory, climbing and leaping behaviour in their repertoire. As a result, infants exhibit a more diverse repertoire than adults (Druelle and Berillon 2013). Furthermore, according to previous behavioural and biomechanical observations (Altmann and Samuels 1992; Raichlen 2005a; and see Chapter 2 and 4), an autonomous locomotor profile is established in the first year of life, during which the functional demands on the limbs change in parallel with significant morphological changes. Such modifications in size and shape seem to adapt their body optimally for quadrupedal walking (Raichlen 2005b). However, potential predisposing traits in the intrinsic morpho-dynamic properties of the limbs (i.e. those morphometrics that determine the intrinsic dynamics of the limb segments) may also favour early quadrupedal locomotion (see Chapter 4). In adult baboons, it has been demonstrated that there is a divergence in mass distribution between the forelimbs and hindlimbs that creates a natural pendular period (NPP) convergence (Raichlen 2004). It has been previously argued that exhibiting good NPP convergence between the four limbs is likely to minimize muscle activity, and therefore energy expenditure, during quadrupedal locomotion (Myers and Steudel 1997; Raichlen 2004). It has further been hypothesized that the divergence in limb mass distribution might reflect the need to maintain precise grasping abilities in the hands in order to forage successfully after infants become less reliant on gripping the mother with the feet for transport (Raichlen 2005b). In this context, we have produced the largest data set of segmental morphometrics for a Catarrhini species to date and made it available for further exploration, e.g. in biomechanical studies such as (inverse) dynamic analyses of movement or musculoskeletal modelling. Based on this dataset and given that mass in newborn baboons is distally concentrated into the fore- and hindlimbs and that the body centre of

mass has a more cranial position, we first hypothesized that, during early life, the morphology must adjust rapidly in order to meet the mechanical demands of developing the locomotor repertoire. It should be noted that in baboons, this repertoire tends to be quadrupedal, but that other locomotor abilities are also present. Nevertheless, according to our recent study on the early development of quadrupedal walking in baboons (see Chapter 4), the NPP of the four limbs should be strongly convergent initially. Adult baboons are sexually dimorphic (Leigh et al. 2009) and sex-related differences have been observed in the timing and intensity of their growth patterns (Coelho 1985; Glassman et al. 1983; Glassman and Coelho 1987; Leigh et al. 2009) and in their biomechanics (see hindlimb compliance in Patel et al. 2013). With regard to morphometrics, we hypothesized that females would have a lower rate of mass gain and that this pattern would end earlier than in males.

1.2 Materials and Methods

1.2.1 Study Site and Subjects

This longitudinal study was conducted at the CNRS Primatology Station (UPS 846) at Rousset-sur-Arc, France, where approximately 300 baboons are bred and housed. From this population, we regularly measured fourteen females and sixteen males from infancy (minimum age 2 months) to adulthood; this experiment was conducted over a period of 7 years (Letter of approval MP/01/15/02/08 from the Midi-Pyrénées Region Ethics Committee, February 2008). The individuals were measured every 3 months until they were 2 years old and then every 6 months. All the individuals studied are part of the same troop and live together in a large park with various enrichments (Anvari et al. 2014; Berillon et al. 2010; Druelle and Berillon 2013; see Appendix 1.A for information on the individuals).

1.2.2 Collecting Morphometrics

Our measurement protocol allows the use of the geometric model developed by Crompton et al. (1996), as previously applied to baboons (Raichlen 2004; Raichlen 2005b). External linear measurements of the 9 body segments were taken (head - including the neck - trunk, upper arm, forearm, hand, thigh, shank, foot and tail). The landmarks used are the same as in the previous studies (see Appendix in Schoonaert et al. 2007).

The animals were anaesthetized to take the measurements (maximum duration, 20 minutes), and by convention, the limbs were measured on the left side only in order to ensure consistency between successive sessions and individuals, as well as to limit the duration of the anaesthesia. We obtained individual segment dimensions (lengths and antero-posterior and medio-lateral diameters) and estimated the inertial properties of the body segments from the model:

- segment mass, using segment average densities obtained from cadavers (Berillon et al. in prep);
- segment centre of mass (CoM), calculated from the proximal joint of the segment (from the hip joint for the trunk segment);
- segment mass moment of inertia in the sagittal (I_x) and coronal (I_y) planes; the third moment of inertia in the horizontal plane was not calculated for this study because of its low impact on locomotor mechanics (cf. Schoonaert et al. 2007). Note that the moment of inertia about the segment CoM can be found using the parallel axis theorem (see Crompton et al. 1996; Raichlen 2004)

We calculated inertial parameters for the whole body and the whole forelimb and hindlimb. Using the mathematical and geometric software *GeoGebra 5.0*, we designed free body diagrams of baboons at 2 extreme stages of their development, separately for males and females. We used a typical body posture (quadrupedal standing) observed in the wild with an average elbow joint angle of 155° and a knee joint angle of 138° for all morphotypes (see Patel et al. 2013). We calculated the position of the whole body centre of mass (BCoM) in this posture, as well as the fore- and hindlimb centre of mass (CoM1 and CoM2, respectively). The CoM position was estimated as follows (Miller and Nelson 1973):

$$COM = \frac{\sum_{i=1}^n m_i r_i}{\sum_{i=1}^n m_i}$$

Where m_i is the mass of one segment and r_i is the distance of the segment CoM from the joint of origin (e.g. hip or shoulder). Then we calculated the radius of gyration of the whole limb (RG) in the straight position. RG is a measure of overall limb mass distribution; it represents the distance of a point mass from the proximal joint that would give an equivalent inertia to the original limb. This is expressed as the square root of the whole limb's

mass moment of inertia about the proximal joint (which may be the shoulder or the hip), divided by the mass of the limb considered:

$$RG = \sqrt{\frac{I}{M}}$$

Where I is the whole limb's mass moment of inertia about the proximal joint (calculated using the parallel axis theorem; see Raichlen 2004), M is the mass of the whole limb. RG can be normalized via a percentage of limb length. The Natural Pendular Period (NPP) is a good way to represent the limb's intrinsic morpho-dynamics (Myers and Steudel 1997; Raichlen 2004; and see Chapter 4). This is calculated as follows:

$$NPP = 2\pi \sqrt{\frac{I}{M * g * COM}}$$

Where g is the gravitational constant (9.8 m.s^{-2}). We calculated the NPP of the fore- and hindlimbs for extended limbs with the hand and foot in a straight line with other segments. This procedure enables comparisons with previous studies (Myers and Steudel 1997; Raichlen 2004).

1.2.3 Statistics

In accordance with Crompton et al. (1996) and Raichlen (2004), the reliability of the external measurements procedure was assessed by calculating an estimated total body mass via the sum of the segment masses per individual. This estimated mass (y) was compared to that directly measured with an electronic scale (x) yielding an absolute error calculation:

$$\frac{|x - y|}{x} \times 100$$

In order to model individual growth patterns, we regressed each individual's absolute segmental morphometrics (length, mass, I_x , I_y) against the age at the time of measurement. Because each variable is age-dependent, we used type 1 regression models and their reliability was tested using the *Fisher test*. The slope and intercept values obtained for the significant models were used to test whether individual growth patterns followed the general pattern of growth, i.e. when all longitudinal

data are grouped together. After controlling for the normality of the sample of individual growth patterns (*Shapiro-Wilks test*), we applied the *one sample t-test* in order to assess whether the mean of the sample of individual growth patterns was equal to the mean of the general growth pattern. This analysis was done using R.2.15 software (The R Foundation, Vienna, Austria, <https://www.rproject.org/>). In order to test differences between sexes, we used the slope values and the intercept values of the individual models. Comparisons were performed with permutation tests for independent samples (StaXact 3.1 software, Cytel, Inc., Cambridge, MA).

Major age-related changes in segment lengths and masses were assessed using Principal Component Analyses (PCA). The set of variables was made dimensionless before being entered into the PCA: the length variables were divided by the cube root of the total body mass measured and the segment masses were divided by the total estimated body mass (Hof 1996; Raichlen 2005b). First, the PCA allowed us to reduce the number of variables. Secondly, it allowed us to determine the most significant changes occurring in the body morphometrics during growth. Thirdly, we plotted the principal component [the interpretability of the first eigenvalue was assessed using the broken-stick method (Frontier 1976)] against age and we used a polynomial of degree n with a least-squares fit in order to accurately describe the period in which the most significant changes occur; linear models were not reliable here because of the autocorrelation of the distribution of residuals. The best fitting model is obtained when the coefficient of determination is considered high, i.e. $R^2 > 0.5$, and higher degrees do not further improve the fit (note that the end of the curve is likely to be biased because of the end of the dataset, which is why we have indicated this part with a dashed line). To estimate the developmental period when the amount of variation changes, i.e. decrease or increase in the growth rate, we calculated the second derivative of each polynomial model. A change in the sign of the second derivative curve indicates a point of inflection. The period of growth rate decrease or increase was determined from the median of the previous period, or the median between two points of inflection, or from the median of the last period (our sample stops at 7yrs for females and 8yrs for males; see Figure 1.1 for an example). We also performed a PCA, including general body morphometrics, i.e. segment lengths, segment masses and the total body mass, on 10 age-sex classes (0-6m, 1y6m-2y, 3y-3y6m,

4y6m-5y, 6y-6y6m). This analysis was added for two reasons: first, to produce general age-related baboon morphotypes (coupled body size and body shape) and show how these change; secondly, to describe general differences between males and females during ontogeny for a confirmation of our previous tests.

Furthermore, according to previous contributions showing the importance of the shape and size of limbs in locomotion (see Kilbourne and Hoffman, 2013), we specifically analyzed the relationships between whole fore- and hindlimbs in straight positions. For each variable, i.e. limb length, limb mass, limb CoM, limb moment of inertia about the proximal joint, and limb NPP, we plotted the hindlimb against the forelimb. Because the two pairs of limbs vary together with age, we modelled these relationships using the Reduced Major Axis (RMA), which is an orthogonal regression (type 2 model). The general growth pattern was thus assessed using the identity line: if the slope of the latter falls inside the confidence interval (95%) of the slope of the RMA model, this indicates a similar (isometric) growth pattern between fore- and hindlimbs. As we did for the full dataset, we validated the general growth pattern using comparisons with the mean of the sample of individual patterns (*one sample t-test* after controlling for Normality of the sample). In addition, we plotted the dimensionless CoM and the dimensionless RG (CoM and RG are normalized via a percentage of limb length) against age and used the polynomial method previously described in order to assess the transitions. The significance level is 0.05 for all tests.

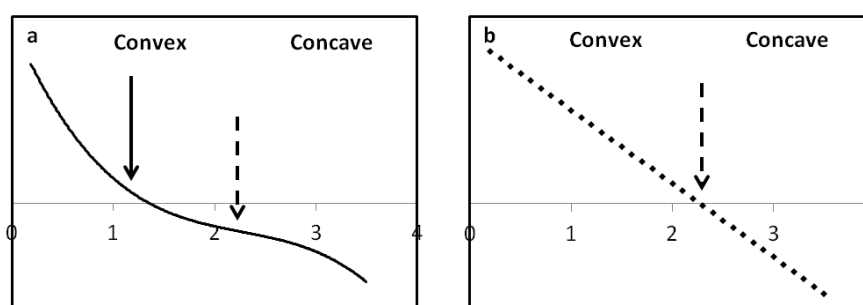


Fig. 1.1 (a) original curve, (b) curve obtained with the second derivation. The dashed arrow indicates the point of inflection of the original curve and the solid arrow indicates the median, which is used to determine the period of time during which the variation of the original curve changes, i.e. decreasing in this example.

1.3 Results

1.3.1 Validity of the Geometric Model

The total body mass estimated from the direct external measurements is very close to that measured on a scale. We obtained, for females, a mean absolute error of $4.98 \pm 1.69\%$ (mean \pm standard deviation) per individual measured and $5.16 \pm 1.3\%$ for males. These values strongly validate the reliability of the procedure and confirm the accuracy of the geometric model when applied to baboons; it was also validated previously on cadavers of different primate species using double-pendulum experiments (Crompton et al. 1996; Raichlen 2004). This geometric model makes it possible to perform *in vivo* analyses of morphological parameters, thus offering new opportunities such as longitudinal follow-up and observation, at the individual level, of performance-morphology interactions (Raichlen 2005a; Raichlen 2006; Raichlen et al. 2009; Van Dam et al. 2010; Van Dam et al. 2011; Young et al. 2007) and behaviour-morphology interactions (see Chapter 2 and 3).

1.3.2 Total Body Mass

Figure 1.2 shows that the polynomial model gives a good estimation of the increase in total body mass for female and male baboons ($R^2=0.93$ and 0.97 , respectively). We observed two points of inflection for males, indicating an increase in the rate of mass gain at around 3.3 years of age and growth ending at around 6.55 years of age. In females, the general pattern is more linear than in males. We observed one point of inflection indicating a decrease in mass gain at around 4.9 years of age. This indicates the end of growth for females (Table 1.1).

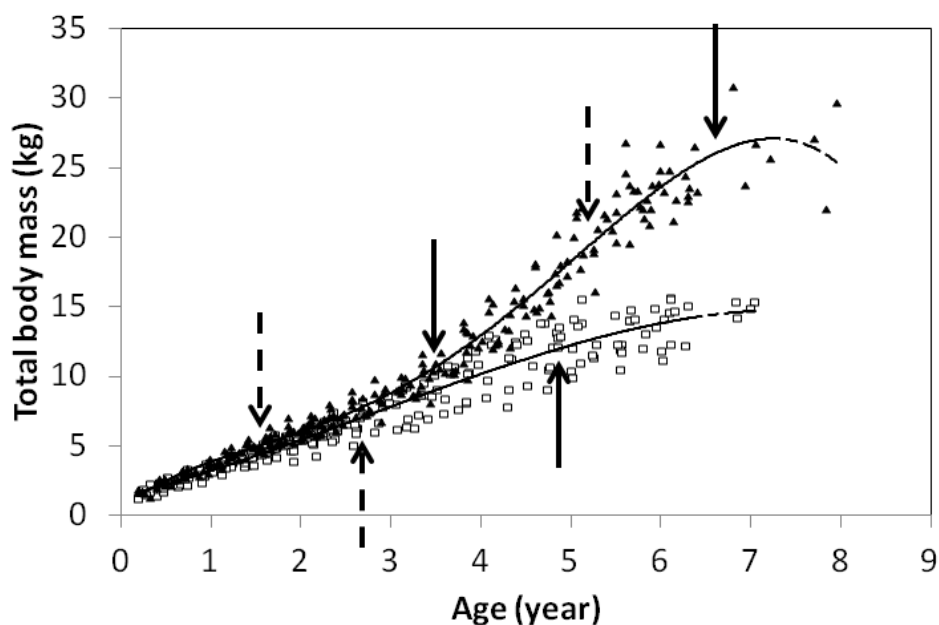


Fig. 1.2 Total body mass as a function of age for 14 female baboons (white squares) and 16 male baboons (black triangles). All longitudinal data are plotted together for each sex-class. The dashed arrow indicates the point of inflection of the original curve and the solid arrow indicates the median, which is used to determine the period of time during which the variation of the original curve changes.

TABLE 1.1 Polynomial regression models for total body mass

Sex	Polynomial equation	R^2	Point of inflection (year)	Variation in change rate (year)
Female	$-0.04x^3+0.3x^2+1.57x+1.39$	0.93	2.75	4.9
Male	$-0.04x^4+0.52x^3-1.83x^2+4.61x+0.61$	0.97	1.55 - 5.05	3.3 - 6.55

1.3.3 Individuality within the General Growth Pattern

Table 1.2 shows the absolute segment linear and inertial parameters via the slopes (a) and intercepts (b) of the linear regression models. All the models are strongly significant ($P < 0.0001$) and illustrate the general growth pattern of the olive baboon. Individual growth patterns

closely match this general pattern. In females, no significant difference was found after testing for comparisons between individual and general patterns (see Appendix 1.B). In males, we found only one significant difference for the foot mass (see Appendix 1.C).

Regarding sex-related differences during ontogeny, it is clear that males exhibit a higher growth rate in length and mass for all the segments. The intercept values were not tested for differences because the lack of measurements at birth makes the origin of the calculated models redundant (see the negative values sometimes obtained: Table 1.2). However, by taking the data from the first measurement session, i.e. when the individuals were youngest [between 2 and 5 months for males ($n=7$) and females ($n=7$)], we were able to test early sex-related differences. Only one significant difference was found: the length of the hand is longer in males than in females (79 and 74 mm, respectively, Permutation Test: -1.584 , $P=0.0061$).

TABLE 1.2 General growth pattern of the segment inertial parameters represented by linear regression model ($y=a*age+b$)

	Length (mm)		Mass (kg)		Ix (kg.mm ²)		Iy (kg.mm ²)	
	a	b	a	b	a	b	a	b
Females								
Head	10.75	114.72	0.18	0.29	1830.37	5.08	1849.83	-8.40
Trunk	33.58	233.79	1.10	0.46	74465.39	-45258.43	74056.72	-44859.45
Upperarm	16.02	102.67	0.08	0.01	829.34	-588.09	843.05	-600.66
Forearm	17.11	111.14	0.04	0.04	551.64	-266.72	550.84	-266.53
Hand	7.35	81.19	0.02	0.03	73.45	6.74	70.58	6.71
Thigh	15.82	108.61	0.17	0.05	1734.90	-1155.79	1793.15	-1200.92
Shank	15.62	111.39	0.05	0.03	641.62	-301.36	645.83	-305.03
Foot	11.46	118.61	0.03	0.05	222.34	29.11	217.17	27.98
Tail	20.92	291.90	0.03	0.05	957.71	365.70	957.71	365.70
P-value sex related								
Head	<0.0001	-	<0.0001	-	<0.0001	-	<0.0001	-
Trunk	0.0001	-	<0.0001	-	<0.0001	-	<0.0001	-
Upperarm	<0.0001	-	<0.0001	-	<0.0001	-	<0.0001	-
Forearm	0.0003	-	<0.0001	-	<0.0001	-	<0.0001	-
Hand	0.0003	-	<0.0001	-	<0.0001	-	<0.0001	-
Thigh	0.0006	-	<0.0001	-	<0.0001	-	<0.0001	-
Shank	<0.0001	-	<0.0001	-	<0.0001	-	<0.0001	-
Foot	<0.0001	-	<0.0001	-	<0.0001	-	<0.0001	-
Tail	0.0001	-	<0.0001	-	<0.0001	-	<0.0001	-
Males								
Head	16.98	109.49	0.37	0.03	5194.88	-5529.72	5263.64	-5621.16
Trunk	42.38	229.80	1.91	-0.81	162313.09	-193597.2	161090.04	-191720.7
Upperarm	20.92	96.94	0.14	-0.07	1925.15	-2410.45	1963.93	-2466.18
Forearm	21.24	106.16	0.08	-0.02	1233.91	-1423.89	1232.18	-1422.69
Hand	10.25	80.68	0.03	0.01	177.33	-126.63	169.77	-121.02
Thigh	20.15	102.29	0.30	-0.16	3861.46	-4835.30	4065.20	-5134.29
Shank	20.46	104.98	0.09	-0.02	1397.32	-1569.96	1408.82	-1586.85
Foot	15.79	115.45	0.05	0.02	464.58	-326.20	450.86	-316.19
Tail	34.13	278.38	0.06	0.01	2642.74	-2289.72	2642.74	-2289.72

1.3.4 Changes in Morphotypes (dimensionless segment lengths and masses) with Age

The PCA produces a new principal component that explains a large fraction of the variance in segment lengths: 36.12% in females and 34.7% in males; and in segment masses: 46.85% in females and 47.62% in males (the first observed eigenvalues, 3.25, 3.12, 4.22 and 4.29, respectively, always exceed the first eigenvalue provided by the broken-stick method, 2.83). Regarding segment lengths, the first dimension is compiled from the same segments for both sexes: the head (factor score (FS) female: 0.9; male: 0.86), the hand (FS female: 0.89; male: 0.84), the foot (FS female: 0.89; male: 0.84) and the tail (FS female: 0.77; male:

0.78) are positively correlated. This dimension is strongly correlated with age for females: $r=-0.89$ ($P<0.0001$) and males: $r=-0.83$ ($P<0.0001$); figure 1.3 illustrates these relationships. The 4th order polynomial gives a good estimate of growth-related changes: females: $R^2=0.9$; males: $R^2=0.86$.

Regarding segment masses, the first dimension is compiled from the same segments for both sexes: the head (FS female: 0.9; male: 0.86), the hand (FS female: 0.88; male: 0.87), the foot (FS female: 0.84; male: 0.8) and the tail (FS female: 0.75; male: 0.77) are negatively correlated with trunk mass (FS female: -0.72; male: -0.78). This dimension is strongly correlated with age for females: $r=-0.88$ ($P<0.0001$) and males: $r=-0.86$ ($P<0.0001$); figure 1.4 illustrates these relationships. The polynomial is a good estimate of these changes: females: $R^2=0.86$ (5th order polynomial), males: $R^2=0.85$ (5th order polynomial).

Using the second derivative method (see *Statistics*), we were able to detect the significant transitions in the growth patterns of segment length and segment mass (Table 1.3).

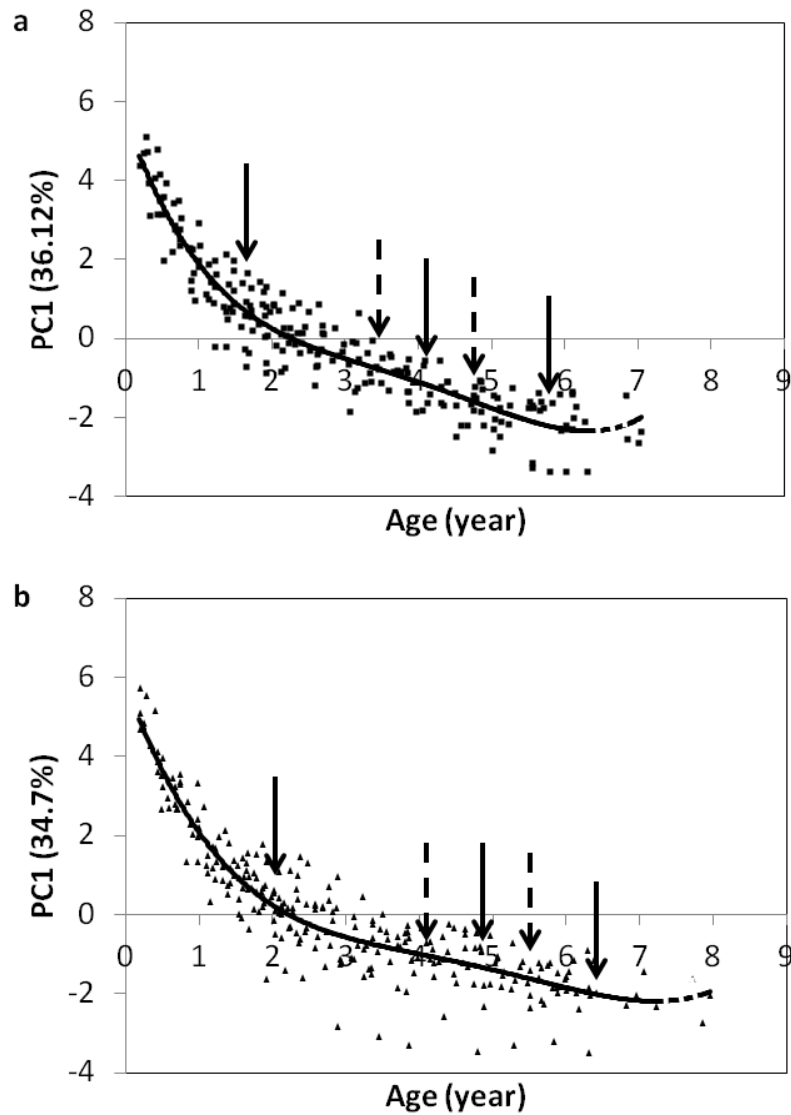


Fig. 1.3 Relationship between the projection of the individuals on PC1 (relative segment lengths) and age. (a) All females and sessions plotted together; (b) all males and sessions plotted together.

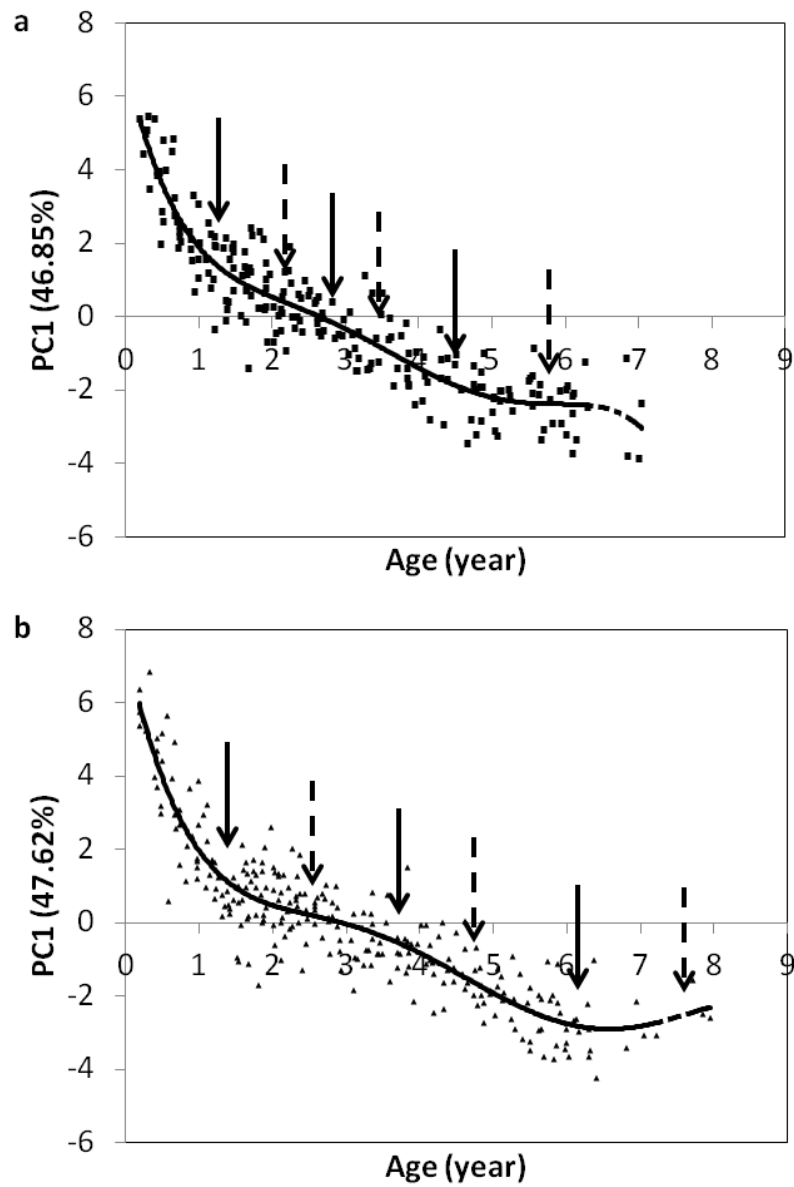


Fig. 1.4 Relationship between the projection of the individuals on PC1 (relative segment masses) and age. (a) All females and sessions plotted together; (b) all males and sessions plotted together.

TABLE 1.3 Polynomial regression models for body dimensions (dimensionless values)

Sex	Polynomial equation	R ²	Point of inflection (year)	Variation in rate of change (year)
<i>Segment lengths</i>				
Female	$0.0187x^4 - 0.3035x^3 + 1.7885x^2 - 5.16x + 5.5505$	0.9	3.35-4.75	1.65-4.05-5.9
Male	$0.0114x^4 - 0.2191x^3 + 1.5418x^2 - 5.1015x + 5.8506$	0.86	4.05-5.55	2-4.8-6.3
<i>Segment masses</i>				
Female	$-0.0106x^5 + 0.2079x^4 - 1.5057x^3 + 5.0409x^2 - 8.7328x + 6.8916$	0.86	2.25-3.55-5.95	1.1-2.9-4.75
Male	$-0.0053x^5 + 0.1313x^4 - 1.176x^3 + 4.7429x^2 - 9.2897x + 7.5563$	0.85	2.55-4.55-7.85	1.25-3.55-6.2

Segment length (Figure 1.3): In females, the greatest changes occur between birth and 1.65 yrs. The growth rate is slower between 1.65 and 4.05 yrs and accelerates between 4.05 and 5.9 yrs of age, when growth stops. In males, the greatest changes occur between birth and 2 years of age. The rate of change is slower between 2 and 4.8 yrs and accelerates between 4.8 and 6.3 yrs of age, when growth stops.

Segment mass (Figure 1.4): A similar pattern appears for segment masses, but the changes occur earlier. In females, the greatest changes occur between birth and 1.1 yrs. The rate of change is slower between 1.1 and 2.9 yrs and accelerates between 2.9 and 4.75 yrs of age, when growth stops (at 4.9 yrs for total mass gain). In males, the greatest changes occur between birth and 1.25 yrs. The rate of change is slower between 1.25 and 3.55 yrs and accelerates between 3.55 and 6.2 yrs of age, when growth stops (at 6.55 yrs for total mass gain).

Based on these changes in body morphometrics, we were able to design the two extreme morphotypes of the baboon at birth and at the beginning of adulthood. Figure 1.5 illustrates these changes and their impact on the position of the BCoM as well as CoM1 (forelimb) and CoM2 (hindlimb). During development, we clearly observed a caudal shift of the BCoM into the trunk and a proximal shift of the CoM into the fore- and hindlimbs. The PCA applied to the 10 age-related morphotypes (see *Statistics*) produced two newly composed principal components that explain a large fraction of the variance (91.72%; Table 1.4). The two eigenvalues observed exceed the eigenvalues provided by the broken-stick method (PC1: 13.50 > 2.83, PC2: 3.92 > 1.83). Therefore, the first

composed plan can be interpreted and allows general comparisons between females and males (Figure 1.6). PC1 represents age-related variations in relative segment masses (except for the shank) and shows that the most significant differences occur during the first year of life. Female morphotypes, at all stages of their development, are closer to the adult morphotype than in males. Furthermore, in females, there is no difference between morphotypes 4 and 5. According to this axis, the last two female morphotypes and the last male morphotype are very similar. PC2 represents relative limb length and total body mass. At all stages in their development, males are relatively heavier and have shorter relative limb lengths than females. In males, a significant increase in total body mass occurs in the period between morphotypes 4 and 5, which corresponds to the acceleration in mass gain described previously (see Table 1.1); this was not found in the female growth pattern.

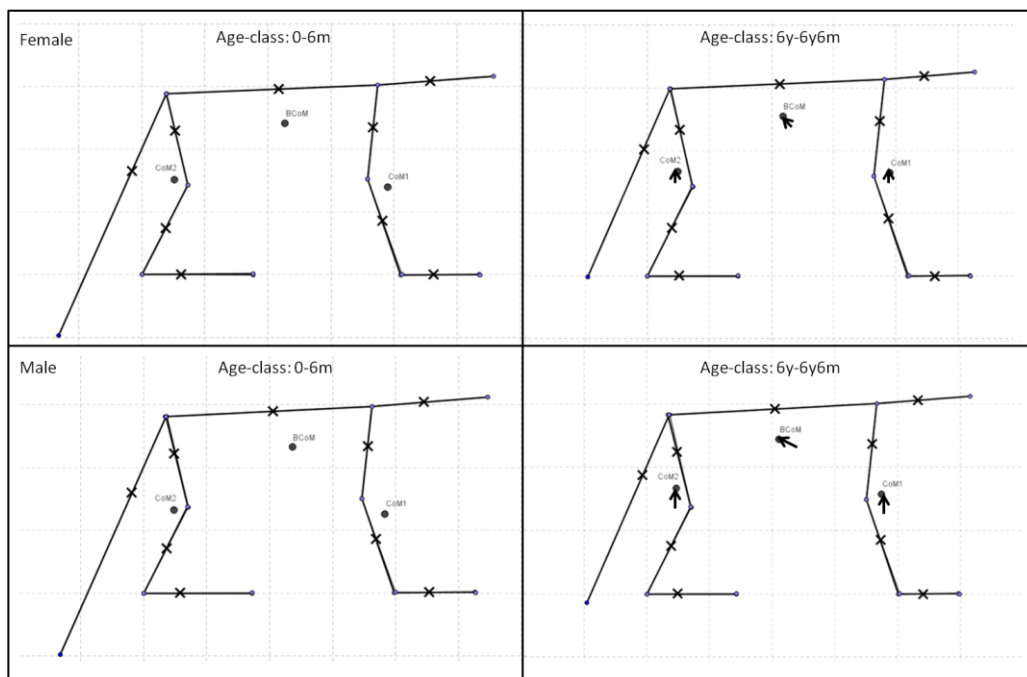


Fig. 1.5 Morphotypes of female (age-class 1, $n=12$ and age-class 2, $n=10$) and male (age-class 1, $n=13$ and age-class 2, $n=10$) baboons at two extreme stages of their ontogeny. The crosses represent the segment CoM, the small dots represent the joints between segments. All segment lengths are made dimensionless via the cube root of the total body mass.

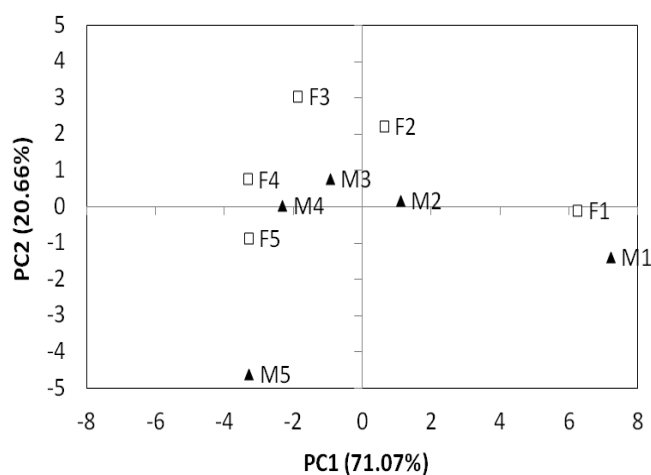


Fig. 1.6 Projection of the 10 age-sex classes on the first composed plan of the PCA applied to dimensionless values (segment lengths and masses) and total body mass. Female baboons are represented with white squares and males are represented with black triangles. Numbers indicate the stage in development, i.e. 1=0-6m, 2=1y6m-2y, 3=3y-3y6m, etc.

TABLE 1.4 Eigenvalues and eigenfactors of the PCA of morphotypes

	Dimension 1	Dimension 2
Eigenvalue	13.5	3.92
Variance (%)	71.07	20.66
	Factor 1	Factor 2
<i>Relative mass</i>		
Hand	0.9491	0.0935
Forearm	0.9747	0.0607
Upperarm	-0.9337	-0.2665
Thigh	-0.9599	-0.0151
Shank	0.5338	0.2562
Trunk	-0.979	0.0258
Head	0.9816	-0.0816
Tail	0.9626	0.1875
Foot	0.9337	0.3263
Total body mass	-0.788	-0.5466
<i>Relative length</i>		
Hand	0.9804	0.1355
Forearm	-0.5484	0.7892
Upperarm	-0.7594	0.6081
Thigh	-0.6194	0.7739
Shank	-0.3662	0.8855
Trunk	-0.5148	0.7895
Head	0.9763	-0.095
Tail	0.9127	0.3727
Foot	0.9083	0.4028

Numbers in bold indicate the main contributing factors.

1.3.5 Whole Limb Inertial Properties: Forelimb versus Hindlimb

Judging by the high values of the coefficients of determination, the limb growth pattern is well estimated by RMA models (Figure 1.7). There is no difference between the general pattern of limb growth from the full dataset and the individual pattern (Appendix 1.D and 1.E). The general patterns of growth are similar for male and female baboons (see Figure 1.3 and 1.4). Therefore, it is possible to describe a general pattern of limb growth in baboons. During ontogeny, forelimb length, from the full dataset, is always and consistently smaller than hindlimb length (slope [95% CI]: females 1.08 [1.05-1.1]; males 1.09 [1.07-1.1]). From the full dataset, the proximal shift of the CoM is more pronounced in hindlimbs than in forelimbs (slopes [95% CI]: females 0.81 [0.77-0.86]; males 0.79 [0.76-0.82]). From the full dataset, the mass and moment of inertia of the hindlimbs about the proximal joint gradually increase relatively to the forelimbs (slopes [95% CI]: 1.81 [1.76-1.87] and 1.78 [1.74-1.81], 1.50 [1.46-1.55] and 1.41 [1.38-1.44] for females and males respectively).

Regarding NPP convergence, although the coupling between forelimb and hindlimb is always close during development (Figure 1.8), the linear models show a trend towards a gradual increase in the forelimb NPP relatively to the hindlimb NPP (from the full dataset, slope [95% CI]: 0.90 [0.86-0.93] and 0.90 [0.88-0.93] for females and males, respectively). We split our sample into 1-year age-classes in order to point out the period in which the convergence of the NPP decreases. The forelimb NPP is significantly greater than the hindlimb NPP from 3 years of age onwards in females and from 1 year of age onwards in males. Therefore, convergence is optimal in young infants (see Table 1.5). Although a tendency towards more divergent NPPs is observed, this does not prevent very good convergence between both pairs of limbs at the adult stage as well (2.48% difference in females and 3.25% in males).

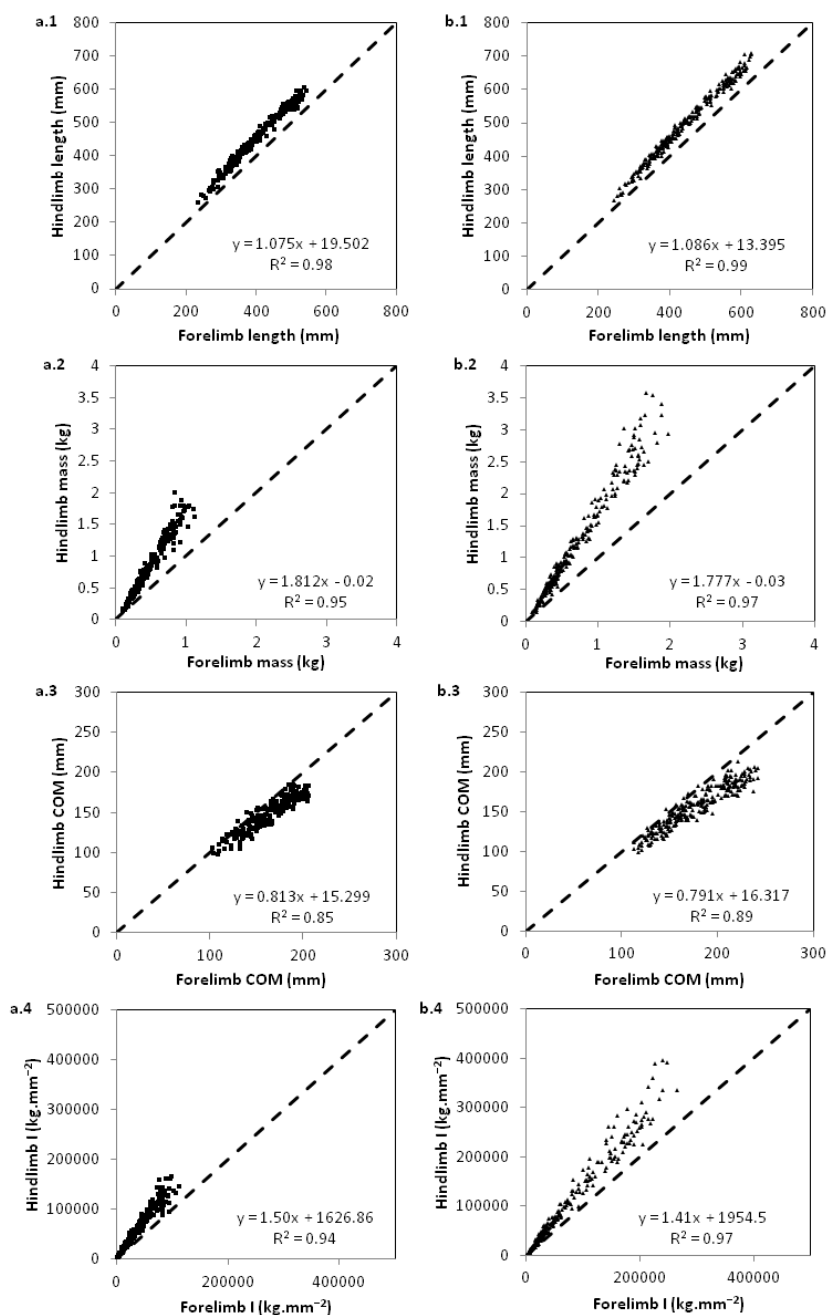


Fig. 1.7 Relationship between fore- and hindlimb length (1), Mass (2), CoM (3) and mass moment of inertia about the proximal joint (4) in female (a) and male (b) baboons. The dashed line is the line of identity ($x=y$). The linear equations represent the RMA regressions calculated with the full dataset for each variable and for each sex. The coefficients of determination indicate high reliability of the linear models in describing these relationships with age.

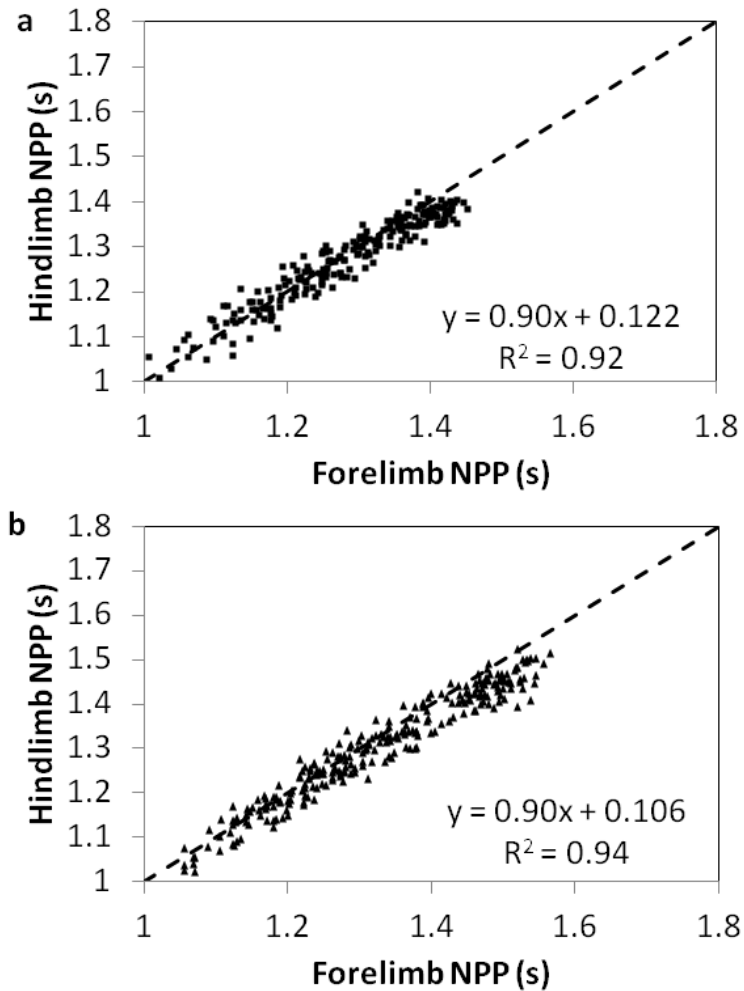


Fig. 1.8 Relationship between the NPP of the hindlimb and the NPP of the forelimb in female (a) and male (b) baboons. The dashed line is the line of identity. The linear equations represent the RMA regressions calculated with the full dataset for each variable and for each sex. The coefficients of determination indicate high reliability of the linear models in describing this relationship with age.

TABLE 1.5. Comparisons of fore- and hindlimb NPPs during baboon ontogeny

Sex	Age-class	FL Mean	HL Mean	FL-HL abs%diff	FL-HL Paired test
Female	0-1	1.11	1.11	2.56	0.7693
	1-2	1.21	1.21	1.82	0.7250
	2-3	1.28	1.28	1.66	0.3553
	3-4	1.35	1.33	1.88	0.0008
	4-5	1.38	1.36	1.99	<0.0001
	5-...	1.40	1.37	2.48	<0.0001
Male	0-1	1.12	1.11	2.18	0.0578
	1-2	1.22	1.21	2.09	0.0099
	2-3	1.30	1.28	1.91	0.0022
	3-4	1.37	1.35	2.31	0.0002
	4-5	1.45	1.42	2.63	<0.0001
	5-6	1.50	1.45	3.65	<0.0001
6-...	1.50	1.46	3.25	0.0001	

Polynomial models yield good estimates for age-related variations in CoM and RG into fore- and hindlimbs (i.e. normalized via a percentage of limb length), as seen from the high values of the coefficients of determination (Figure 1.9). Using the second derivative method (see *Statistics*), we determined the periods in which the CoM shifts proximally and RG changes in magnitude, towards a shorter radius, within the limbs (Table 1.6).

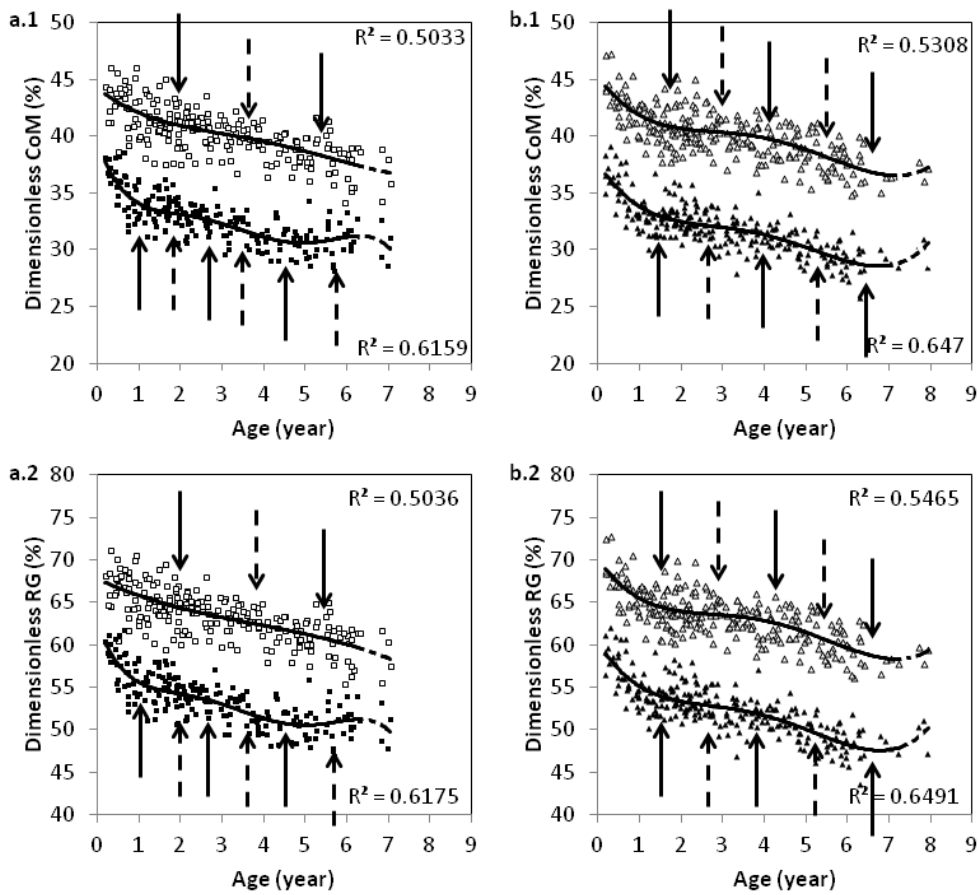


Fig. 1.9 Relationship between the position of the CoM (1) and age, and the position of the RG (2) and age in female (a) and male (b) baboons. The white colour represents the forelimb, the black colour represents the hindlimb. The polynomial models are represented in the point clouds.

TABLE 1.6. Age-related migration of the CoM and RG into the limbs

Sex	Limbs	Polynomial equation	R ²	Point of inflection (year)	Variation in rate of change (year)
<i>Centre of Mass</i>					
F	Fore	$-0.0315x^3+0.3586x^2-2.0254x+43.82$	0.50	3.75	1.85-5.4
	Hind	$-0.0183x^5+0.3393x^4-2.294x^3+7.014x^2-10.483x+39.504$	0.62	1.95-3.45-5.75	0.95-2.7-4.6
M	Fore	$0.0239x^4-0.3997x^3+2.2135x^2-5.3761x+45.38$	0.53	2.75-5.65	1.35-4.2-6.85
	Hind	$0.0277x^4-0.4423x^3+2.3898x^2-5.8444x+37.679$	0.65	2.75-5.25	1.35-4-6.65
<i>Radius of Gyration</i>					
F	Fore	$-0.0311x^3+0.356x^2-2.3023x+67.763$	0.50	3.85	1.9-5.45
	Hind	$-0.0232x^5+0.4283x^4-2.88x^3+8.7323x^2-13.111x+62.431$	0.62	1.95-3.45-5.75	0.95-2.7-4.6
M	Fore	$0.0324x^4-0.5396x^3+2.9761x^2-7.1829x+70.207$	0.55	2.75-5.55	1.35-4.15-6.8
	Hind	$0.0381x^4-0.6054x^3+3.2282x^2-7.8193x+60.294$	0.65	2.65-5.25	1.3-3.95-6.65

In females, three periods were plotted for the hindlimbs, and two periods for the forelimbs. In the hindlimbs, the greatest proximal shift of the CoM occurs between birth and 0.95 yrs. The shift continues at a lower rate from 0.95 to 2.7 yrs of age, then accelerates from 2.7 to 4.6 yrs of age, when the shift ends. In the forelimbs, the proximal shift of the CoM is close to the linear model. With the polynomial model, there is a more significant shift from birth to 1.85 yrs. This continues at a slightly slower rate from 1.85 to 5.4 yrs of age, when the shift comes to an end.

In males, three periods were plotted for hindlimbs and forelimbs. The greatest changes occur between birth and 1.35 yrs for both pairs of limbs. The shift continues at a slower rate from 1.35 to 4 yrs and 4.2 yrs for hindlimbs and forelimbs respectively, then accelerates in the hindlimbs from 4 to 6.65 yrs of age, when the shift comes to an end. In the forelimbs, it accelerates from 4.2 to 6.85 yrs of age, when it ends.

As seen in Figure 1.9, the mass is more proximally concentrated in the hindlimbs than in the forelimbs at all stages of development in both sexes. In both pairs of limbs, baboons experience a proximal migration of the CoM. The results for the RG follow those for the CoM.

1.4 Discussion

1.4.1 Growth pattern

The shapes of the growth curves for skeletal length and segment mass are very similar. Although the same number of phases (variation in rates of change) is observed for segment length and mass, the timescales vary. The greatest changes occur in the first phase, corresponding to infancy; the second involves a significant decrease in the rates of change, which speed up again in the third phase up to adulthood. Our first hypothesis was that newborn baboons would have distally concentrated limb masses and that a new morphological pattern would develop rapidly in order to meet the mechanical demands of the onset of a quadrupedally-oriented locomotor profile. Our results support this hypothesis: the greatest changes in body morphometrics occurred during the first year of life for segment mass and during the two first years for segment length. This involves a decrease in relative lengths and masses in the distal segments, i.e. the hand, foot, head and tail. From the general morphotypes, we also observed a relative increase in proximal segment masses, i.e. the thigh and upper arm, and in the trunk, as well as a relative decrease in forearm mass; no changes occurred in relative lengths for these segments. There is therefore a proximal shift of the CoM within the limbs that appears to depend mainly on the changes in relative segment masses and lengths (for autopodia); note that the CoM into each segment does not change with age. This growth pattern may be related to changes in limb functional demands because it matches the period in which baboons gradually become more active and autonomous, mainly through play and exploratory activities (Rose 1977). According to our results, the next developmental period involves changes at a slower growth rate. There is a third and final period during which the growth rate increases slightly up to the end of development. The observation of these different phases is consistent with the work of Leigh (2009), who observed the occurrence of growth spurts in baboons.

Although there are very few ontogenetic data of this kind for Catarrhini species in general, our results can nevertheless be compared with those of Turnquist and Wells (1994) for another cercopithecoid species, the rhesus macaque, and of Schoonaert et al. (2007) for a hominoid species, the chimpanzee. As previously proposed by Leigh (2009), the olive baboon's pattern of growth is similar, in some respects, to that of these two species. In macaques, the relative mass of the proximal limb segments increases while the relative masses of the distal limb segments and the head decrease. There is also a slight shift in the relative lengths of the fore- and hindlimbs in macaques, with the hindlimbs becoming relatively longer, while the slight difference in the limb lengths of baboons remains unchanged with age. Furthermore, the forearm and shank seem to remain constant throughout ontogeny in macaques, which is not the case for the relative mass of the forearm in baboons (cf. results reported here on general morphotypes). Because keeping more intrinsic muscle mass in forearms increases manual grasping abilities, this difference may be related to the fact that macaques spend more time in trees than baboons. Similarly, the growth pattern of chimpanzees (Schoonaert et al. 2007) points to a shift from distal to proximal limb mass distribution, mainly through a decrease in the relative mass of the hand and foot and an increase in the relative mass of the thigh. There is also a significant decrease in the relative head mass but no increase in the relative trunk mass. Unlike macaques and baboons, chimpanzees have longer forelimbs than hindlimbs throughout their ontogeny. Nevertheless, as in macaques, the relative mass of the forearm and shank remains constant throughout ontogeny and the upper arm does not increase in relative mass. This points to a need to maintain good grasping abilities in the hands in order to move efficiently in trees. Schoonaert et al. (2007) reported that the decrease in the relative mass of the foot and hand may be due to a decrease in dimensionless segment lengths with age. Our results also suggest this relationship because the reduction in the relative mass of autopodia (hands and feet) parallels the reduction in the relative length of these segments. Preuschoft (2004) suggested that the independence of the grip is ensured by short intrinsic muscles of the hands and feet: longer digits would therefore require stronger and heavier muscles. Although having relatively longer and/or heavier distal segments has been correlated with grasping ability (Jungers and Fleagle 1980; Lawler 2006; Raichlen 2005b; and see Chapter 2), it has also been suggested that intrinsic morphological proportions, i.e. the length of digits

relative to metapodials, may be a substantial determinant of grasping performance (Lemelin and Schmitt 2007; Young and Heard-Booth 2016). In addition, having relatively longer distal segments may also facilitate some locomotor tuning (e.g. Lawler 2006) by providing a larger area of support that potentially increases stability in quadrupedal locomotion at an early age.

1.4.2 Sex-related differences

Sex-related differences have been previously observed in the duration and rate of the growth pattern of baboons (Glassman et al. 1983; Glassman and Coelho 1987; Leigh et al. 2009). Our large ontogenetic and longitudinal sample confirms this. All the linear models based on absolute values (segment length, mass and moment of inertia) differ between males and females, which means that most sex-related differences can be directly attributed to the higher absolute segment lengths and masses in male baboons, also resulting in higher values for the moment of inertia. Nevertheless, comparing infant male and female baboons in early infancy revealed only one significant difference, in hand length. Therefore, just after birth, male and female baboons are very similar in shape and size. Regarding total body mass, a rapid increase begins at around 3 and a half years of age in males and lasts until growth ceases (at 6 and a half years), while in females no changes were observed in the rate of mass gain and growth stops earlier at around 5 years of age. However, when corrected for total body mass effect, we observed a very similar pattern of growth for both sexes. According to the PCAs, males and females undergo the same transitional periods with similar changes in relative segment masses and lengths. Nevertheless, these transitional periods always occur later in males than in females, who reach adult body dimensions at an earlier age: before 6 years of age for relative segment length and before 5 years of age for relative segment mass, while males reach adult dimensions in relative length and mass a little after 6 years of age. Regarding the proximal shift of the limb CoM, the pattern appears to be similar between sexes in the hindlimbs, but subject to different processes in the forelimbs. In females, the shift is almost linear until around 5 and a half years of age, while the proximal shift observed in males follows the typical pattern found for other body dimensions, i.e. with considerable changes initially followed by a decrease in the growth rate, and a final acceleration just before growth ceases.

1.4.3 Development of the limbs

Our results show that the forelimbs are shorter than the hindlimbs in baboons and that this relationship is consistent throughout their development. It should be noted that the decrease in the intermembral index (without the hands and feet) observed at around 5 months of age by Shapiro and Raichlen (2006) in *Papio cynocephalus* is not marked here when observing the full duration of development, but is likely to become apparent with a shorter observation window. Three aspects have been considered: (1) the difference in shape between fore- and hindlimbs relatively to limb length, (2) the impact of development on limb shape and (3) the actual difference in shape between fore- and hindlimbs, i.e. relatively to the proximal joint.

(1) Quadrupedal locomotion involves differential use of the limbs: hindlimbs are commonly used for propulsion while forelimbs are used more for braking (Demes et al. 1994). Furthermore, in primates, there is a need to maintain stronger grasping abilities in the hands than in the feet for foraging and manipulative functions (e.g. Pouydebat et al. 2014). Therefore, a disparity between mass distribution patterns in the fore- and hindlimb would reflect variations in the functional roles of the limbs during development (e.g. Patel et al. 2013; Raichlen 2005b; Rose 1977). Our results support this assumption in the sense that the CoM (linear effects) and RG (rotational effects) are always more distally positioned, relatively to limb lengths, in the forelimbs than in the hindlimbs. For example, at 3 and a half years of age, we observed that the forelimb CoM is approximately in the same relative position as the hindlimb CoM was at birth (39.92% and 39.02%, respectively in females; 40.24% and 38%, respectively in males), while the latter is more proximally concentrated (7.09% more proximal in females and 6.29% in males).

(2) Our results show that during early development, infant baboons experience a proximal shift of the CoM and RG in the fore- and hindlimbs. Regarding the kinematics of their quadrupedal walking, it has been shown that, at a very early age, infant baboons adopt longer stride lengths and lower stride frequencies because of their distally concentrated limb mass (Raichlen 2005a). Furthermore, they exhibit similar total power outputs (i.e. the sum of internal and external power) as other quadrupedal mammals developing a more proximally concentrated limb mass (Raichlen 2006). Therefore, it seems that infant baboons are using a

trade-off mechanism that adapts their kinematics to reduce the energy expenditure induced by the movement of distally heavy limbs. Nevertheless, the CoM migration found in the present study is likely to reduce the rotational inertia of distal limb segments, and therefore the energy costs of swinging limbs in adults walking quadrupedally (Wickler et al. 2004). This supports the assumption that morphological adaptations become more pronounced during ontogeny.

(3) After birth, actual fore- and hindlimb CoM and RG are very similar relatively to their respective proximal joints, i.e. the shoulder and hip. However, as a result of the proximal migration of the CoM described above, the actual forelimb CoM is more distally positioned than the actual hindlimb CoM at the end of development. On this point, it appears that, at an early age, differences in fore- and hindlimb mass distribution patterns compensate for differences in fore- and hindlimb lengths by creating fore- and hindlimb NPP convergence (see Myers and Steudel 1997; Raichlen 2004). With age, there is a loss of this convergence due to changes in limb composition. Although, during walking, specific mechanisms such as limb angular excursion may actively correct potential NPP divergence in adults (hindlimb excursion is relatively greater in baboons, Larson et al. 2001), it appears that swinging a limb according to its NPP reduces muscle activity, and therefore the metabolic energy demand. In this context, good convergence between fore- and hindlimbs should facilitate limb movement because the freely chosen frequency for the four limbs would not (theoretically) require any muscle activity, making locomotion more efficient. When we considered the limbs in a straight position (which is not a behavioural posture in baboons but allows interspecies comparisons), we found that forelimbs and hindlimbs in females converge to the same NPP up to three years of age, and in males up to one year of age. After 1 year, male forelimb and hindlimb NPPs diverge significantly, i.e. the NPP of the hindlimb is always smaller than the NPP of the forelimb although their relationship remains very close (see Table 1.5). This divergence appears only after three years of age in females. Our values for adult male (Mean [95% CI]: 3.25 [1.05]) and female (2.48 [0.55]) *Papio anubis* are consistent with those found by Raichlen (2004) in adult *Papio cynocephalus* (2.35 [1.36]). Otherwise, the values we obtained for infant baboons (i.e. between 0 and 2 years of age, female: 2.11 [0.33], male: 2.13 [0.3]) are close to those obtained by Myers and Steudel (1997) for *Canis familiaris* (1.83 [1.26]). Consequently, very young baboons,

although immature in terms of neuro-muscular control and with distally heavy limbs, exhibit limb mechanical properties that should facilitate the onset of quadrupedal walking (see Chapter 4).

The findings of this study are of great interest because this biomechanical optimization (through NPP convergence) appears to predispose infant baboons for quadrupedal walking. According to Rose (1977), the first locomotor experience of infants occurs on the ground, just a few days after birth, when they squirm and tumble forwards as the hindlimbs start making propulsive movements while the forelimbs are unable to coordinate. After a few weeks, the fore- and hindlimbs seem sufficiently coordinated for quadrupedal walking. We also observed that this mode dominates their repertoire from the first locomotor stages (see Chapter 2) and is very soon performed efficiently (biomechanically speaking) (Raichlen 2006). Two important developmental processes are therefore described here: in parallel with major changes in limb shape that are related to changing functional demands, baboons exhibit “early biomechanical optimization” for quadrupedal locomotion that certainly favours a rapid developmental transition toward this mode. This is in line with a growing body of literature showing that infant primates have a musculoskeletal system characterised by a capacity for a particular type of performance that could compensate for the immaturity of the system and thus promote survival during the early stages of life (e.g. Ruff 2003; Young 2005; Young et al. 2010; Young and Heard-Booth 2016). In an evolutionary perspective, early morphological adaptation of the limbs as observed in olive baboons may point to a high degree of integration between the fore- and hindlimbs (Young et al. 2010). Such a developmental pattern (at the genotype level) is likely to be highly constrained by few possibilities for character variability, which would result in low degree of limb evolvability in baboons (Wagner and Altenberg 1996).

To summarize, the changes in limb shapes and axial body related to differential growth (allometry) are significant during the ontogeny of olive baboons and appear clearly related to changes in functional demands. Besides this growth pattern, an early morphological predisposition for quadrupedal locomotion appears to be present. Similarities with the pattern of growth of Catarrhini species can be easily described, such as the proximal shift in limb mass distribution, as well as

the caudal migration of the body centre of mass into the trunk; nevertheless, more ontogenetic data are necessary on Asian hominoids in order to confirm this Catarrhini-related growth pattern. Furthermore, the NPP convergence observed in infant baboons does not seem to be present in other Catarrhini species, at least in chimpanzees (Schoonaert et al. 2007). Such a morphological adaptation points to a high degree of locomotor specialisation for quadrupedal locomotion in baboons, which does not, however, impede their other modes of locomotion. Consequently, studying variations in the morphological development of species that are phylogenetically close appears to be important to better understand the locomotor profiles exhibited in adult extant primates and how they might evolve.

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Chapter 2

Effect of body mass distribution on the ontogeny of positional behaviours in non-human primates: Longitudinal follow-up of infant captive olive baboons (*Papio anubis*)

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The diversity of primates' positional capabilities is unique among mammals. Indeed, they exhibit a daily repertoire composed of various locomotor and postural modes that may be linked to their particular morphological pattern. Because ontogeny undergoes parallel behavioural and morphological modifications, it may be useful to investigate the biomechanical consequences of the changing body shape. We, therefore, collected accurate quantitative and longitudinal data on positional behaviours, body mass distribution patterns, activities, and environment on a sample of six infant olive baboons, *Papio anubis*. These baboons are kept at the Primatology Station of the CNRS, France, where they live within the same social group. Individual behaviours were quantified using the *focal sampling* method. The body mass distribution was estimated according to a geometric model based on direct external measurements. Multivariate analysis enabled us to analyze the interactions between the data. Our results show that body mass distribution changes together with the ontogenetic changes in positional behaviours. At an early age, individuals have distally heavy segment masses in the limbs and an important fraction of the behavioural repertoire involves efficient grasping abilities. At the end of infancy, the same individuals have relatively more mass in proximal segments of the limbs and the proportion of quadrupedal walking is significantly higher while other climbing and suspensory behaviours decreased substantially. The present study experimentally confirms the association between body mass distribution and the positional repertoire of primates. These relationships, when interpreted in

the context of basic biomechanical concepts, may improve our understanding of primate locomotion. We discuss further the implications of these functional relationships when modeling the evolutionary pathway of primates.

2.1 Introduction

In mammals, it is generally assumed that the overall morphology and body proportions are adapted to optimize their preferred locomotor mode in terms of energetics (e.g. Preuschoft and Günther 1994; Preuschoft et al. 1996; Witte et al. 1991). Nonhuman primates (NHPs) are special in this respect, because they exhibit diversified positional repertoires (i.e., multiple locomotor modes and postures, Prost 1965) that are sources of various constraints and substantial stress on the body (e.g. Hunt 1992a; Sarringhaus et al. 2014). Besides any specialisation, the morphological pattern of NHPs probably reflects trade-offs (Crompton et al. 1996; Isler et al. 2006; Schoonaert et al. 2007), thus challenging the functional interpretation of the relationships between morphology and locomotor habits. Nevertheless, establishing such relationships is essential for the interpretation of fossil taxa in primate evolution.

Body size is easily seen as a mechanical determinant of the locomotor habits for NHPs living in complex and arboreal habitats (Fleagle 2013; Fleagle and Mittermeier 1980; Napier 1967; Preuschoft et al. 1996). Body size probably affects the time spent in the trees versus the time spent on the ground (e.g. Doran 1993; Remis 1995); for example, Doran (1993) observed that, during resting activities, large (male) chimpanzees are less arboreal than smaller light weight (female) chimpanzees. It may also influence the size of the substrates used as observed in squirrel monkeys in which heavier individuals use the largest substrates (see Boinski 1989 for squirrel monkeys; and Cant 1987; Huang et al. 2015; Remis 1995 for other species), as well as the proportion of locomotor modes such as leaping, climbing, bridging, and suspensory behaviours (Cartmill and Milton 1977; Doran 1992b; 1993; 1997; Fleagle and Mittermeier 1980; Gebo 1992; Hunt 1992b; Remis 1995; Sugardjito and van Hooff 1986). However, these relationships are not always unequivocal because obvious functional disadvantages may sometimes be mitigated by other advantages. For example, it has been demonstrated that large male chimpanzees use smaller arboreal substrates than one expects based on their size, because they can, in this way, avoid the more energetically demanding vertical climbing (Hunt 1994). Similarly, when comparing macaque species, the smaller, long-tail macaque, appears to leap less frequently than the heavier, Japanese macaque, yet, the smallest species can cover longer distances in a single jump (see Chatani

2003; and Preuschoft et al. 1996 for theoretical reflection about “size threshold”).

In addition to body size, it has been suggested that other morphological parameters can predict, or at least be linked to, positional behaviours. For example, a (relatively) long tail would increase balance during quadrupedalism in the trees (e.g. Rodman 1979) and a (relatively) low intermembral index would be correlated with relatively high proportions of leaping and low proportions of suspensory behaviours (Ankel-Simons 2000; Fleagle 2013; Preuschoft et al. 1996). But also in this case the premised form-function relationships are not entirely straight forward (Anapol et al. 2005; Gebo and Chapman 1995). Previous and more recent field studies stipulate that more intricate morphological features should be taken into account for a better understanding of inter- and intra-specific positional variation (e.g. Sarringhaus et al. 2014; Schaefer and Nash 2007; Wells and Turnquist 2001). Indeed, according to biomechanical principles, segmental inertial properties (i.e., mass, position of the centre of mass and moment of inertia) probably impact the kinetics, hence the kinematics of locomotor modes (see Preuschoft et al. 1996 for concepts). For example, the relatively long natural pendular periods of the limbs observed in primates may explain their low stride frequencies when they walk quadrupedally (Raichlen 2004), and ontogenetic shifts in gait selection may be explained, in part, by the whole body centre of mass position (Young 2012). Therefore, if the inertial properties of the body influence the primates' movement dynamics, one can expect that they influence the locomotor habits (the proportion of the modes that compose their repertoire) as well. This is supported by the results of many transversal anatomical studies (Baker et al. 2011; Grand 1977a; 1977b; Isler et al. 2006; Jungers and Fleagle 1980; Raichlen 2005b; Schoonaert et al. 2007; Turnquist and Wells 1994). However, although the significance of the functional effects of inertial parameters of the body have been studied for specific locomotor modes such as leaping behaviour (e.g. Dunbar 1988; 1994), bipedalism (e.g. Kimura 1996; Nakatsukasa et al. 2006; Ogihara et al. 2012), and quadrupedalism (e.g. Dunbar 2004; Raichlen 2004, 2005b; Young et al. 2007), the significance of the functional effect of the general body mass distribution pattern (i.e. body shape) on the primate “totipotentiality” (i.e. the diversity of positional capabilities, see Prost 1965) still needs to be tested experimentally. In this respect, two hypotheses are particularly relevant for the present study. It

has been hypothesized that the mass is more proximally distributed in the limbs in NHPs that frequently move quadrupedally because of the premised mechanical advantage for pendular motion during walking (Myers and Steudel 1997; Raichlen 2004). In contrast, the limb mass would be more distally concentrated in species that frequently climb, clamber, and use suspensory behaviours due to the necessity to possess a strong musculature (located partly in autopodia, hands and feet, and partly in zygapodia, forearms and legs) for controlling manual and pedal grasping (Jungers and Fleagle 1980; Raichlen 2004, 2005a, b; Turnquist and Wells 1994; Wells and Turnquist 2001; but see comparisons between hominoids and macaques in Isler et al. 2006).

However, not only morphology affects positional behaviours. As mentioned by McGraw (1996), “understanding why animals move the way they do is a multivariate problem (p.519).” The positional repertoire of NHPs may be linked to other parameters such as the behavioural context and the physical environment (Cant 1992). For example, primates living exclusively in the highest levels of forest canopy are expected to move in a very different manner than those living mainly on the ground (e.g. in savannah habitats) due to the structure of available supports, that is, continuous versus discontinuous, horizontal versus vertical, flexible versus stiff (Fleagle 2013). Juvenile rhesus macaques, for instance, tend to use more flexible supports making them more keen to use climbing behaviours than others (Wells and Turnquist 2001). In the same manner, behavioural context probably impacts the proportion of positional behaviours, for example, traveling involves movement over relatively large distances while feeding principally involves movement from one feeding posture to another within one feeding location (Fleagle 1976). Morphology, positional behaviours, environment, and activities present a multidimensional system that requires integrative analysis at an individual level to be understood. Although the requirement for such analysis on primate locomotion (see the volume edited by Morbeck et al. 1979) has been recognized for decades, no study has succeeded in this. The difficulties of simultaneously collecting accurate morphological data in addition to behavioural and ecological data in the wild are immense (see the recent volume edited by D’Août and Vereecke 2011; and specific behavioural studies by Dagosto 1994; Dagosto and Gebo 1998) and hamper integrative approaches (see Turnquist and Wells 1994; and Wells and Turnquist 2001; however, for an attempt at integration). As an

alternative, for certain species, captive environments offer the opportunity to conduct such analysis. This is the case for olive baboons at the Primatology Station of the CNRS, where we run a long-term longitudinal and integrative study. In this context, an ontogenetic approach is particularly relevant because the observation of parallel morphological and behavioural changes during development may aid investigation into the biomechanical factors modeling body shape (Hurov 1991).

The olive baboon is a good model for our aims because this species develops relatively rapidly with important changes in both morphology and behaviour. During their first weeks of life, baboons actively and efficiently grasp their mother's fur on the belly side (Altmann 2001) and after few weeks they are gradually more frequently carried dorsally (Altmann and Samuels 1992; Anvari et al. 2014). During this early period, their positional repertoire changes dramatically from mother-dependent locomotion to autonomous locomotion, which is established at approximately 1 year of age (Altmann and Samuels 1992; Druelle and Berillon 2013; Rose 1977). Simultaneously, infant baboons (i.e. 0–2 years of age) undergo drastic changes in their pattern of mass distribution. Initially, in comparison to older individuals (i.e. juveniles and adults), they possess a relatively heavy head, a light trunk, and heavy hands and feet (see Chapter 1; Altmann et al. 1977; Leigh et al. 2009). With development, more mass becomes allocated to the proximal limb segments (Raichlen 2005a). This has been demonstrated to affect the manner in which they walk quadrupedally, that is, with gradually higher stride frequencies and shorter stride lengths, while their grasping capacities are hypothesized to decrease (Raichlen 2005b). In this context, investigating the ontogenetic shifts from an infant baboon that uses its limbs predominantly for clinging behaviours, toward an individual that uses its limbs dynamically, mainly under compressive forces and for propulsion may have important implications for our understanding of primate biology. As such, the period in which locomotor autonomy is acquired is very suitable for a longitudinal follow-up of the “morphology-behaviour” dyad within the context of activities and environment.

The purpose of this study is, therefore, to quantify the body mass distribution, the proportion of positional behaviours (including mother-dependent postures), the substrates used and the activity context during the period of acquiring locomotor autonomy. We propose to address three

hypotheses. First (Hypothesis I), according to biomechanical principles (e.g. Preuschoft et al. 1996), a more distal distribution of the limbs mass will on the one hand be related to a high proportion of behaviours that require grasping capacities such as climbing, clinging, and suspension; on the other hand, a more proximal distribution of the mass in the limbs will be related to an important proportion of pronograde behaviours such as quadrupedal locomotion. Second (Hypothesis II), following the first hypothesis and according to the growth-related changes in body mass distribution, we hypothesize that the thin and vertical structural elements of the environmental enrichment in the park will be preferred by the younger individuals (with more distally concentrated limb masses), while larger and horizontal substrates will be preferred by older individuals (with more proximally concentrated limb masses) (see also supportive evidence for this hypothesis in Dunbar and Badam 1998). Third (Hypothesis III), we hypothesize that the proportion of activities in the total repertoire is less likely to constrain, mechanically, the manner of moving more than the morphology and the environment do. Therefore, the context of the activities will be a weaker determinant of the positional behaviours performed.

2.2 Material and Methods

The present study protocol was approved by the Ethical Committee of France (Letter of approval 01946.02 from the Ethics Committee no. 14), and this research adhered to the American Society of Primatologists Principles for the Ethical Treatment of Nonhuman Primates.

2.2.1 Study site and Subjects

The study was carried out in October 2013 (session 1: S1) and in March 2015 (session 2: S2) at the Primatology Station in Rousset-sur-Arc, France (UPS 846 CNRS). The research protocol was conducted on the six infant baboons available in a colony of 60 individuals (birth rate is between 5 and 7 per year) living in an open-air enclosure (see Table 2.1 for individual characteristics). We chose this colony of baboons for several reasons: the social group is structurally similar to those observed in the wild, varied enrichment is used to enable the baboons to adopt all of the positional behaviours described in the wild (see Rose 1977; and Hunt 1992a; and Druelle and Berillon 2013 for comparisons with captive animals) and the freedom for inter individual interactions is assured.

TABLE 2.1 *Study subjects*

Name	Tatoo	Sex	Age (days)	Individual mass (kg)	Total observation time (min)	No. bouts recorded
Ilario	V908G-13C	M	216/701	3.10/6.49	200/200	2748/1895
Icono	V893E-13E	M	150/635	2.12/6.68	200/200	2513/3152
Irm	V896E-13A	F	196/681	2.44/5.87	200/200	2387/1687
Iris	V916D-13D	F	172/657	2.46/6.56	200/200	1635/2449
Ivar Jr	V894H-13A	M	147/632	2.18/6.65	200/200	1964/3305
Isabella	V896B-13E	F	181/666	1.93/5.59	200/200	2160/2989

S1 (October 2013) and S2 (March 2015) are separated by “/”

2.2.2 Morphological Data: Body Mass Distribution

Individual external linear measurements of the body segments (the head including neck, the trunk, the upper arm, the forearm, the hand, the thigh, the leg, the foot and the tail) were collected a few days prior to the sessions to collect behavioural data. Individual segmental masses were estimated following the procedure described in Druelle and colleagues (see Chapter 1); it uses external measurements according to Crompton and colleagues (1996), as well as the segmental densities available from baboon cadavers (Gilles Berillon and colleagues, unpublished manuscript). The total sum of the individual segmental masses yields an estimated individual total body mass. Figure 1 illustrates that the estimated total body mass is consistent with that directly measured with an electronic scale. The absolute error is equal to $2.96 \pm 1.6\%$ and the 99% confidence interval (CI) of the linear model is the following: slope range=0.89 - 1.01 and intercept range=-0.23 - 0.33. Because the line of identity falls inside the 99% CI of the linear model, this strongly supports the reliability of the procedure used to obtain the segmental masses.

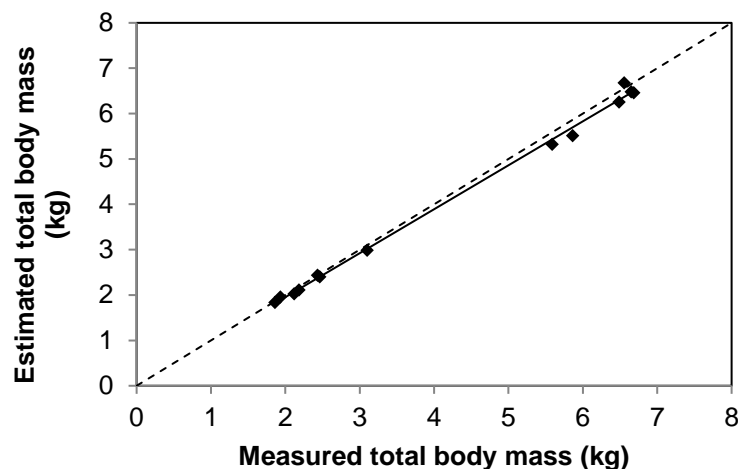


Fig. 2.1 Relationship between the total measured body mass and the total estimated body mass by the geometric model for our sample of infant olive baboons. The solid line is the least-squares regression ($y=0.9689x+0.0163$, $R^2=0.99$), the dashed line is the line of identity ($y=x$).

2.2.3 Behavioural data: positional repertoire, activity context and substrates used

Observations were quantified using *focal-animal sampling* in continuous recordings (Altmann 1974; Martin and Bateson 1993). For each individual we performed four focals per hour, each lasting five minutes; a total, 20 hours of video were recorded for each session. All of the observations were conducted between 8:00 and 18:00; this time period covers all of their daily activities. We chose focal individuals randomly each hour. All individuals were easily identified due to a hair-shave marking assigned during the morphometric recordings prior to the observations. Each focal individual was followed at a distance of 2-10 meters and filmed with a handheld digital camcorder (Sanyo Xacti full HD, frame rates: 30 fps). The continuous recording method enabled us to record frequencies and durations for each positional bout (Fleagle 1976; Fleagle and Mittermeier 1980; Doran 1992b; Martin and Bateson 1993). Moreover, this technique meant that we could observe all performed activities, even the briefest ones.

First, we used the standardized description of NHPs locomotor and postural modes provided by Hunt and colleagues (1996) to identify subtle

differences in positional behaviours of the baboons. As in the most recent studies on positional repertoires (Thorpe and Crompton 2006; Sarringhaus et al. 2014) we used modes and submodes; so that we could make future comparisons between taxa. In this context, we also labeled modes in **bold** and submodes in *italic* for the sake of clarity in the text.

Locomotion: **flexed bipedal walk** (*bipedal hop, assisted and unassisted bipedal walk*), **drop** (*bipedal drop, cling drop, forelimb-hindlimb suspensory drop, forelimb suspensory drop, hindlimb suspensory drop, quadrupedal drop and sit drop*), **inverted quadrupedal walk**, **leap**, **run** (*quadrupedal and tripedal run*), **walk** (*bound walk, crouch quadrupedal walk, quadrupedal walk and tripedal walk*), **orthograde suspensory** (*brachiate, flexed elbow forelimb swing*), **vertical ascent** (*bimanual pull-up, pulse climb, vertical climb*), **vertical descent** (*bounding descent, fire-pole slide, head-first descent, rump first descent*), **squat walk**.

Posture: **cling** (*uni or bimanual vertical cling, cling/forelimb suspend*), **forelimb-hindlimb suspend** (*contralateral forelimb-hindlimb suspend, ipsilateral forelimb-hindlimb suspend*), **hindlimb suspend**, **lie** (*back lie, cling dorsal pronograde, lateral lie, sprawl*), **orthograde forelimb suspend** (*uni or bimanual forelimb suspend, forelimb suspend/cling, forelimb suspend/squat, forelimb suspend/stand*), **orthograde stand** (*bipedal stand/forelimb suspend, assisted flexed bipedal stand, unassisted flexed bipedal stand*), **pronograde stand** (*forelimb crouch stand, full-crouch stand, hindlimb crouch stand, quadrupedal stand, tripedal stand*), **pronograde suspension** (*cling ventral pronograde, quadrumanous suspend*), **sit** (*cling dorsal orthograde, sit lie, sit-in, sit-in/cling, sit-in/out, sit-out*), **squat** (*squat, squat/cling*).

Second, we scored the general activities of the infant baboons according to the descriptions provided by Rose (1977). We described five types of activities: *Feed* during which individuals eat, transport food, peck on the ground, drink and forage in the open-air enclosure for seeds and fruits (this context is probably invariable due to the punctual distribution of the food by the caregivers of the Primatology Station). *Playing activities* during which individuals play in solitude or in active interaction with one or more conspecifics (social play); bearing, biting and following were observed but without vocal aggression or threatening behaviours which are part of the agonistic behaviours (see later). Solitary activities of an exploratory nature were also recorded in play category as in Rose (1977).

Social context during which individuals interact with one another using stereotyped grooming and greeting behaviours, friendly contacts, sexual and agonistic behaviours, but also facial and vocal contacts such as lip smacking or eyebrow raising. *Rest* characterises periods of self-grooming, sleeping and also the time spent in contact with the mother. *Travel* characterises mother-following as well as movements in the enclosure between two resting contexts.

Third, we recorded all the available structures or substrates in the park on which the infants were likely to move or to stand (16 in total): two hollow concrete pillars, a transversal bar connecting the two pillars, a suspended net, four suspended tires, a concrete walkway, a pyramid shaped with 10 stacked concrete pipes, four hollow concrete blocks, few solid concrete blocks scattered around the park, a rock fountain, the ground, the mother, the other baboons, the vertical rods from the open-air pen, the horizontal rods from the open-air pen, horizontal metal substrates in the open-air pen and finally we also considered the substrate “in the air” during the short bouts of leaping and dropping behaviours.

Sequencing and transcription were conducted using the free software of linguistic annotator, Elan 4.6.1 (Max Planck Institute for Psycholinguistics, The Language Archive, Nijmegen, The Netherlands; <http://tla.mpi.nl/tools/tlatools/elan/>), that we adapted to the goals of the present study. To accurately code the beginning and the end of the positional bouts, the activities and the substrates used, we conducted a frame by frame analysis at the transitions. A single observer (FD) conducted all the annotation work to ensure consistency.

2.2.4 Statistics

We tested each variable from our database composed of 9 body segments, 20 modes from the positional repertoire, that is, 10 locomotor modes and 10 postural modes, 5 behavioural contexts and 16 structures (substrates). All comparisons were made between the sessions 1 and 2. Because our sample size is small ($N=6$), the normality of the distribution cannot be tested. Therefore, we used two-tailed permutation tests for paired samples (StatXact® 3.1 software, Cytel, Inc., Cambridge, MA) which are the most appropriate and powerful statistical tests to use in this context.

Regarding the nature of the data, i.e., a mix of interrelated and continuous ordinal data, we used a multivariate analysis to simultaneously examine the general pattern of body mass distribution, the positional repertoire, the activities and the environment (e.g. Glassman and Coelho 1987; Jungers and Hartman 1988; Van Dam et al. 2009). Because this pattern is characterised by a subset of 50 variables, the use of a scaled Principal Component Analysis (PCA) (R 2.15.0 software, The R Foundation, Vienna, Austria, <https://www.rproject.org/>) enabled us to extract the largest contributing factors of variation in our sample of infant baboons. Furthermore, we are interested in the interactions between the various components of the locomotion. The PCA permitted us to reduce the number of dimensions and provided a full view on the interdependent variables as well as the pattern studied and how it changed; we called this new diagram the “integrative locomotor pattern”. In order to assess the variables with the largest contribution, we calculated an axis contribution value for each one (positional behaviours, activities, substrates, body mass distribution) according to the following formula:

$$\frac{\sum_{i=1}^n (x_i^2 / e)}{n} \times 100$$

Where x is the coordinate of each variable (factor score), e is the eigenvalue of the considered axis and n is the number of contributing factors, i.e. with a value above the mean.

We used the new coordinates obtained with the PCA (component scores) to test whether this global pattern of locomotion was age- and sex-dependent. Two-tailed permutation tests were used for assessing age (paired samples) and sex (independent samples) effects. In addition, the relationship between total body mass and the component scores was tested using Pearson correlation test. Statistical significance was set at $P < 0.05$ for all tests.

2.3 Results

2.3.1 Body mass distribution

We are able to describe a general growth pattern using individuals from the present sample. During infancy, the head becomes relatively lighter (mean head proportion = $18.13 \pm 2.07\%$ (S1) and $11.83 \pm 0.68\%$ (S2), Permutation test: $p=2.366$, $P < 0.05$), as well as the hands (mean

hand proportion= $2.83 \pm 0.43\%$ (S1) and $2.33 \pm 0.15\%$ (S2), $p=2.154$, $P < 0.05$), the feet (mean foot proportion= $4.64 \pm 0.35\%$ (S1) and $3.83 \pm 0.31\%$ (S2), $p=2.188$, $P < 0.05$) and the tail (mean tail proportion= $2.11 \pm 0.17\%$ (S1) and $1.75 \pm 0.09\%$ (S2), $p=2.301$, $P < 0.05$). The arms and the thighs become relatively heavier (mean arm proportion= $5.13 \pm 0.36\%$ (S1) and $6.82 \pm 0.97\%$ (S2), $p=-2.112$, $P < 0.05$; mean thigh proportion= $10.97 \pm 1.01\%$ (S1) and $13.71 \pm 1.67\%$ (S2), $p=-1.937$, $P < 0.05$) (Fig. 2.2). Individual pattern of morphological changes with age are shown in Appendix 2.A.

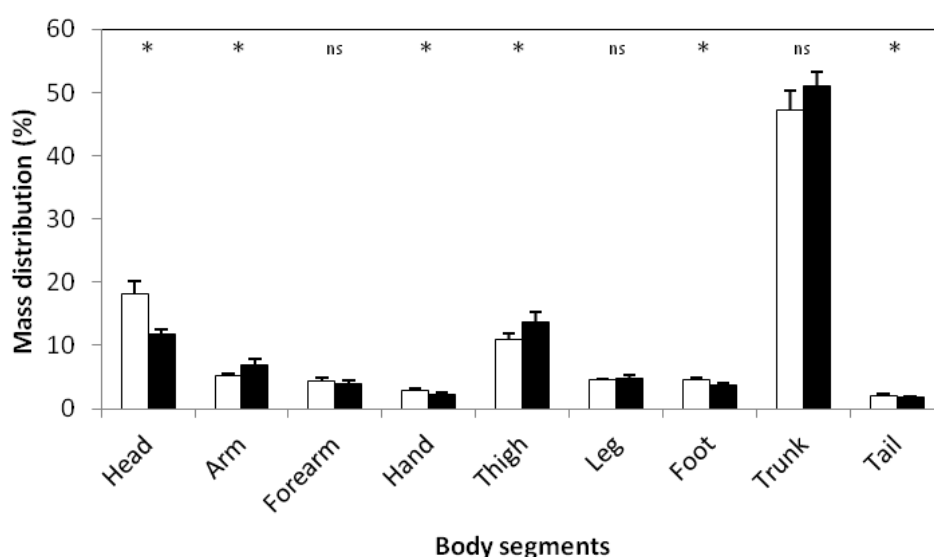


Fig. 2.2 Histogram of the average proportion of each body segment according to age-class 1= 5.8 ± 0.87 months (in white; S1) and age-class 2= 21.7 ± 0.87 months (in black; S2).

2.3.2 Positional repertoire

With regard to the general pattern, contrary to what is expected during early development, no significant change is observed in the proportion of independent locomotion (mean proportion of independent locomotion= $14.80 \pm 2.24\%$ (S1) and $20.78 \pm 4.38\%$ (S2), $p=-1.996$, $P = 0.0625$). The permutation tests reveal a general pattern of change for locomotor modes and for postures (Fig. 2.3). Infant baboons use more

pronograde walk (mean proportion= $7 \pm 1.49\%$ (S1) and $13.59 \pm 3.24\%$ (S2), $p=-2.282$, $P < 0.05$) and **squat walk** (mean proportion= $0.23 \pm 0.07\%$ (S1) and $0.75 \pm 0.34\%$ (S2), $p=-2.137$, $P < 0.05$), while they practice less climbing behaviours (**vertical ascent** mean proportion= $2.66 \pm 0.65\%$ (S1) and $1.15 \pm 0.52\%$ (S2), $p=2.337$, $P < 0.05$; **vertical descent** mean proportion= $1.22 \pm 0.35\%$ (S1) and $0.9 \pm 0.35\%$ (S2), $p=1.715$, $P < 0.05$). With regard to postural behaviours, the infants practiced less **clinging** behaviours with age (mean proportion= $1.75 \pm 0.93\%$ (S1) and $0.23 \pm 0.14\%$ (S2), $p=2.134$, $P < 0.05$). In the same manner, they practice less **forelimb-hindlimb suspension** (mean proportion= $0.11 \pm 0.12\%$ (S1) and $0.05 \pm 0.09\%$ (S2), $p=1.975$, $P < 0.05$) and **pronograde suspension** (mean proportion= $1.68 \pm 0.83\%$ (S1) and $0.57 \pm 0.43\%$ (S2), $p=2.142$, $P < 0.05$). They also **lie**, **squat** and **stand orthograde** less with development (lie mean proportion= $9.66 \pm 5.41\%$ (S1) and $1.42 \pm 1.91\%$ (S2), $p=2.096$, $P < 0.05$; squat mean proportion= $1.34 \pm 0.42\%$ (S1) and $0.61 \pm 0.23\%$ (S2), $p=2.226$, $P < 0.05$; orthograde stand mean proportion= $2.79 \pm 0.37\%$ (S1) and $1.89 \pm 0.44\%$ (S2), $p=2.15$, $P < 0.05$). For information regarding the proportion of time spent in each **mode** and the contribution of each **submode** per individual, see Appendices 2.B.1 and 2.B.2.

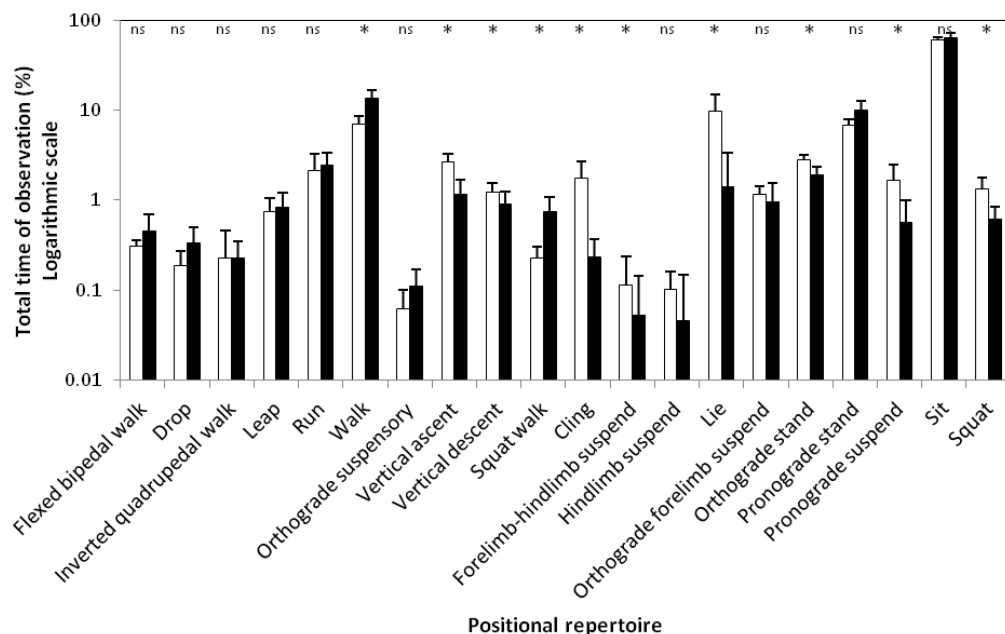


Fig. 2.3 Histogram of the average proportion of each mode in the positional repertoire for S1 (in white) and S2 (in black).

2.3.3 Activity context

Figure 2.4 shows that younger infants spend significantly more time in resting activities than older ones (mean proportion= $37.64 \pm 6.61\%$ (S1) and $13.19 \pm 3.76\%$ (S2), $p=2.313$, $P < 0.05$), while they spend less time in social behaviours (mean proportion= $2.2 \pm 1.24\%$ (S1) and $10.18 \pm 2.95\%$ (S2), $p=-2.261$, $P < 0.05$) and travelling (mean proportion= $1.44 \pm 0.92\%$ (S1) and $3.98 \pm 1.96\%$ (S2), $p=-2.182$, $P < 0.05$). As expected for early development, the proportion of social behaviours generally increases with age, while the resting context decreases. This suggests that individuals become more active and interact significantly more with their congeners. Travel increases significantly because infants are fully independent from maternal carrying by S2. Otherwise, at this early age, the general proportion of play and feeding does not change significantly. Appendix 2.C shows the age-related changes in the individual pattern of activities.

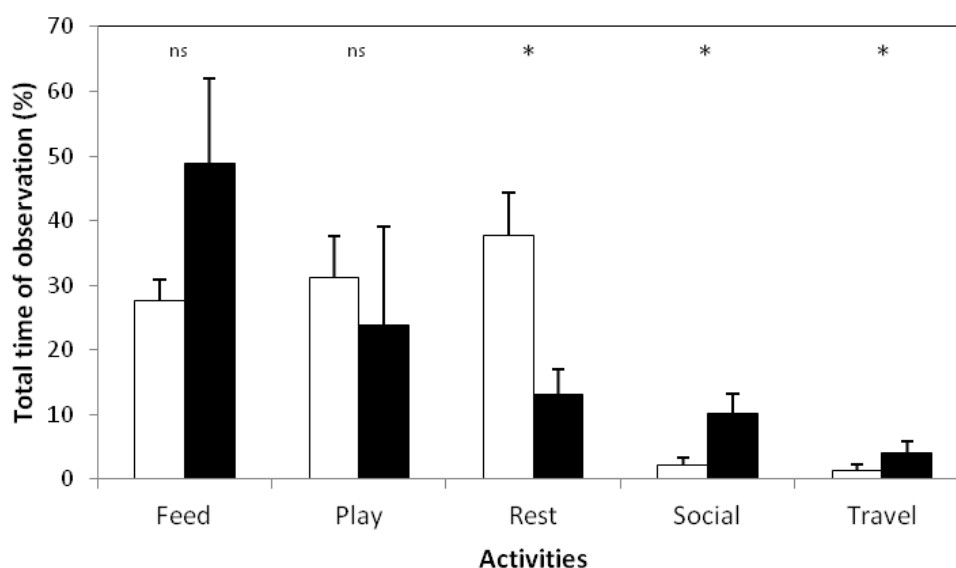


Fig. 2.4 Histogram of the proportion of each activity in which individuals were involved during the total time of observation. S1 is in white and S2 is in black.

2.3.4 Environment

Figure 2.5 shows that, with age, infant baboons changed their manner of using the available structures in the park. Infants spend significantly less time on the suspended net at an older age (mean proportion= $1.41 \pm 0.55\%$ (S1) and $0.12 \pm 0.09\%$ (S2), $p=2.265$, $P < 0.05$) as well as on the suspended tires (mean proportion= $4.3 \pm 0.89\%$ (S1) and $1.36 \pm 0.46\%$ (S2), $p=2.302$, $P < 0.05$) and pyramid (mean proportion= $10.09 \pm 2.3\%$ (S1) and $5.18 \pm 1.56\%$ (S2), $p=2.318$, $P < 0.05$). At a young age, infants also spend a substantial amount of time on their mother, which is not observed during the second recording period (mean proportion= $11.08 \pm 6.59\%$ (S1) and 0% (S2), $p=2.153$, $P < 0.05$); this suggests a full independence for foraging at this developmental stage. Finally, the time the infants are observed on the ground becomes substantial in S2 (mean proportion= $66.42 \pm 4.2\%$), although they already preferred to move on this substrate during S1 (mean proportion= $38.23 \pm 7.22\%$); there is a significant difference for the time spent on the ground between the two age-classes ($p=2.385$, $P < 0.05$). Note that, with regard to the changes previously described between S1 and S2, all individuals kept using all of the available substrates in the park, with the exception of the mother. Appendix 2.D shows individual variability in the manner in which the available substrates in the park were used.

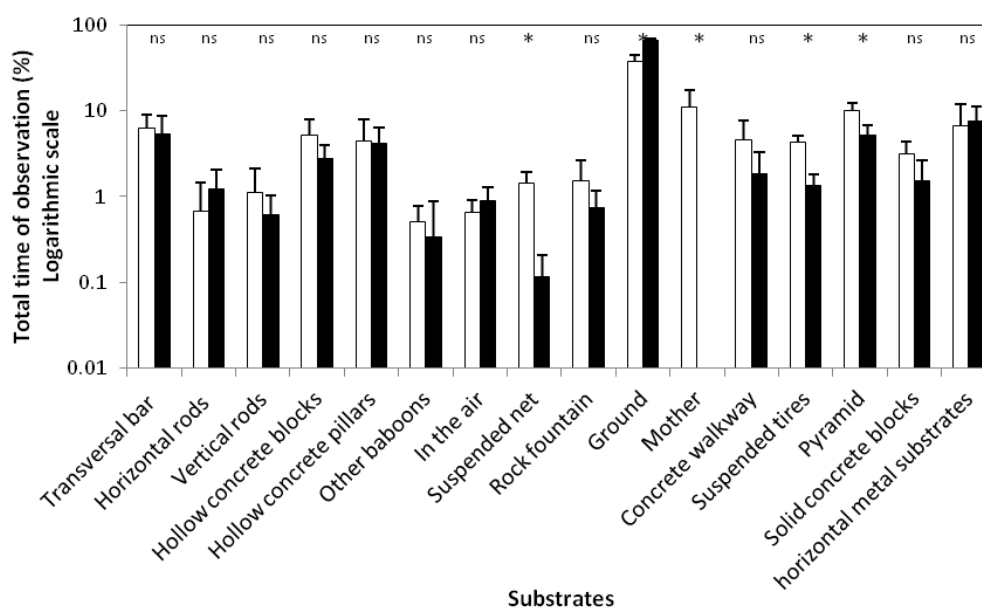


Fig. 2.5 Histogram of the average proportion of each substrate used by the individuals during the total time of observation for S1 (in white) and S2 (in black).

2.3.5 Positional behaviours within morphology-activity-environment interactions

The PCA provides three newly composed principal components which explain a high fraction of the variance (64.5%). Eigenvalues, percentages of the variance for each component and the factor scores (coordinates) for each variable on each PC-axis are indicated in Appendix 2.E. We calculated the contribution of each variable according to each principal component (PC). Figure 2.6 summarizes the main variables contributing to the axes and reports the axes contribution value for each parameter (see *Statistics* in this chapter). The PC1 is primarily determined by walking, vertical ascent, squat walking, clinging, lying, orthograde and pronograde standing, pronograde suspension and squatting postures for the positional behaviours; feeding, resting, social and travelling for the activities; suspended net, ground, mother (as a substrate), suspended tires and pyramid for the substrates; head, arm, hand, thigh, foot and tail for body mass distribution. With this axis, vertical ascent, clinging, lying, orthograde standing, pronograde suspension, squatting, resting, suspended net, mother, suspended tires, pyramid, the head segment, the

hand segment, the foot segment and the tail segment are positively correlated, while it is negatively correlated with quadrupedal walking, squat walking, pronograde standing, feeding, social, travelling, ground, the arm segment and the thigh segment. On the second axis (PC2), dropping, leaping, running, pronograde standing, playing, transversal bar, in the air, rock fountain and arm relative mass are positively correlated and it is negatively correlated with squat walking, sitting, feeding, vertical rods, horizontal metal substrates. On the third axis (PC3), inverted quadrupedal walking, orthograde suspensory, forelimb-hindlimb suspension, hindlimb suspension, orthograde forelimb suspension, horizontal rods and leg relative mass are positively correlated together, while negatively correlated with travelling. Regarding the contribution of variables, PC1 is mainly represented by positional behaviours and body mass distribution, involving a strong relationship between these two parameters as expected from our first hypothesis. PC2 is mainly represented by positional behaviours and environment and PC3 is almost exclusively represented by positional behaviours.

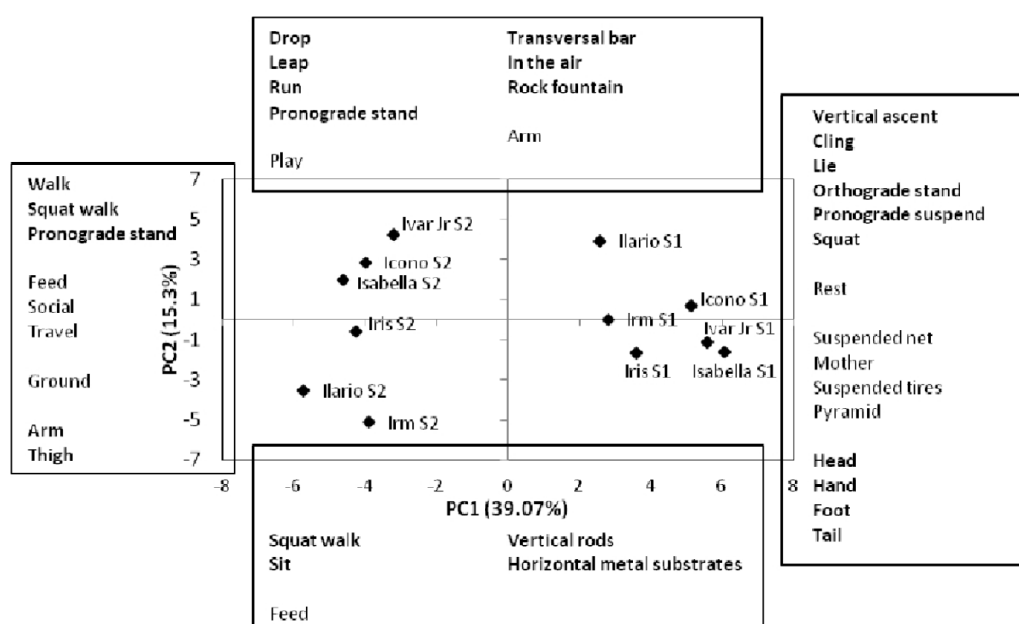


Fig. 2.6 Projection of our sample on the first composed plan of the PCA. The variables indicated on the graphic are the main contributing factors to the two axes: right and left for the x axis, up and down for the y axis. Variables in bold are part of the main parameters defined thanks to the axis contribution values.

PC1: **positional repertoire=35.82**, **morphology=24.84**, substrate=21.16, activity=18.19; PC2: **positional repertoire=49.06**, morphology=4.77, **substrate=31.47**, activity=14.7.

We tested the potential effects of age, total body mass and sex on the three axis obtained by the PCA (Table 2.2). We found a significant result with regard to the age effect on the PC1 ($p=2.425$, $P < 0.05$) as well with regard to the relationship between body mass and the PC1 (Pearson correlation test: $r=-0.97$, $P < 0.001$). Younger and lighter individuals are on the right side of the axis while the older and heavier individuals are on the left side (Fig. 2.6). No other significant results were found.

TABLE 2.2 Age, body mass and sex effects on the “integrative locomotor pattern” (PCA)

PCA dimensions	Age-class	Body mass	Sex-class
	Paired test significance	Pearson’s correlation test significance	Independent test significance
PC1 (39.07%)	0.0313	0.0002	0.9502
PC2 (15.3%)	1	0.7982	0.1688
PC3 (10.13%)	1	0.8919	0.0628

2.4 Discussion

2.4.1 Drastic changes during Infancy

The infancy of primates undergoes changes in morphology, locomotor performance, behaviour, as well as in the use of the environment and the activities performed. All of these changes happen during one of the most important transitions for survival, i.e. from an individual that is mother-dependent toward an individual capable of independent positional behaviours (e.g. Rose 1977; Wells and Turnquist 2001). The present study shows that the initiation of this ontogenetic shift occurs very early in the development of olive baboons, before five months of age (certainly as early as 1 month of age, see Rose 1977). Our results demonstrate that young infants (aged approximately 5-6 months in our sample) spend 10.86% of their time being transported by the mother (between 3.4 and 20.3% at this age in the wild; Table 5 in Rose 1977), despite the fact that they already move independently for 14.8% of their time. At 1.8 years of age, all infants are weaned and they, therefore, locomote independently for approximately 20.78% of their time; this is in line with our previous study results (20.84% in weaned infants and 22.55% in adults according to Druelle and Berillon 2013). Our study, nevertheless, observes no significant difference in the overall proportion of independent locomotor behaviours during infancy (in this case from 5 months of age to 1.8 years of age) indicating that baboons initiate independent locomotion very early on. In a more detailed manner our data show that older infants use significantly more pronograde walking (i.e. the main locomotor mode observed in adult baboons, see Hunt 1991; 1992a) than younger infants, although the latter are already able to walk quadrupedally and do so preferentially. In contrast, younger individuals practice a relatively high number of independent postural behaviours: they

cling, forelimb-hindlimb suspend, stand orthograde and squat significantly more than older infants. Therefore, the positional repertoire of young baboons, as early as 5 months of age, is composed of a substantial number of independent postures that appear to be well developed, while the independent locomotor repertoire, i.e. independent from maternal carrying, is still developing. In this respect, the manner in which infants walk quadrupedally is still different from that of the adult in terms of kinematics (Raichlen 2005b). Furthermore, it is obvious that individuals from our sample do not use locomotor behaviours in the same way as adults do: at the end of infancy, baboons are still using a substantial amount of leaping (0.84%), climbing (2.05%), suspensory (1.95%) and bipedal behaviours (2.34%) compared to adults (0.12%, 0.12%, 0.03% and 0.28%, respectively, according to Druelle and Berillon 2013), suggesting that being autonomous is different from being adult (see also Wells and Turnquist 2001; Schaefer and Nash 2007; and Sarringhaus et al. 2014 for other species).

Regarding the morphological changes, our results are in accordance with those of previous studies on baboons (see Chapter 1; Raichlen 2005a; Leigh et al. 2009) and other Catarrhini species, suggesting a common growth pattern (Grand 1977a; Turnquist and Wells 1994; Schoonaert et al. 2007). With development, the head, the hands and the feet become relatively lighter, while the upper arms and thighs, i.e. the proximal limb segments, become relatively heavier. In our sample, we also observe a significant decrease in the relative mass of the tail.

With regard to the captive environment, the manner in which our test group makes use of the substrates varies between and within individuals. The fact that infants do not exploit the park in the same manner is probably linked to social factors such as dominance rank, but data on hierarchy would be necessary to test this assumption. Nevertheless, our results demonstrate that growing infants increase the time they spend on the ground, while they spend less time on vertical, thin and discontinuous structures (suspended tires, suspended net and pyramid).

Finally, our results on activity contexts reveal that general changes occur in the time spent on social, resting and travelling activities. Growing infants significantly increase the social component; they interact more with their congeners, particularly at the level of grooming behaviours. At

the end of infancy, they also travel more, while they spend significantly less time in resting activities. We were not able to include the time spent suckling in the feeding category because this behaviour is very hard to determine visually, even on video, when infants have their head in the fur of the mother's belly (see also Rose 1977). This was, therefore, recorded as a resting activity, making the proportion of feeding slightly more important than that depicted in our analysis for the first age-class. In contrast resting activities are probably slightly less important for this age-class. Aside from this, no significant difference was observed in the amount of playing activities.

In summary, baboon's infancy is characterised by an increased proportion of quadrupedal walking at the expense of a decreased proportion of suspensory, climbing and clinging behaviours. During this period, the pattern of body mass distribution changes towards a relative increase of the mass in the proximal segments of the limbs. The end of infancy also implies moving largely on the ground and being involved in a higher proportion of interactions with other congeners, i.e. other than the mother.

2.4.2 Relationships between body mass distribution and positional behaviours

We first hypothesized that body mass distribution will adjust, in parallel, to the ontogenetic changes in positional behaviours according to biomechanical concepts (e.g. Preuschoft et al. 1996): a more distal distribution of the mass in the limbs should be related to a high proportion of behaviours that require grasping capacities such as climbing, clinging and suspension, and at the opposite, a more proximal distribution of the mass in the limbs should be related to an important proportion of pronograde behaviours loading the limbs in compression such as quadrupedal locomotion. Our results support this hypothesis. From our multivariate analysis (PCA) we observe that positional behaviours and body mass distribution are two related parameters (see PC1-axis contribution; Fig. 2.6). At an early age, individuals have relatively more mass in hands, feet, head and tail, and they use more clinging, lying (including mainly clinging dorsally to the mother; see Appendix 2.B.2) and pronograde suspension, as well as vertical ascent. All of these modes imply efficient grasping abilities hypothesized to be related to individuals with distally heavy segment masses in the limbs because of the necessity

to possess strong and heavy intrinsic muscles (Turnquist and Wells 1994; Preuschoft 2004; Raichlen 2005b). Furthermore, the first dimension of the PCA also shows that the individuals with heavy distal segments use more orthograde standing and squatting. Although these behaviours are difficult to link to the pattern of body mass distribution depicted here, having heavy hands and feet and a heavy head and a heavy tail do not impede the orthograde standing in NHPs, at least not in baboons (see Chapter 3). At the end of infancy, individuals possess relatively more mass in proximal segments of the limbs (upper arm and thigh) and they walk, stand and squat walk more. The proportion of pronograde walking doubles in the repertoire and provokes relatively more physical stress than both, pronograde standing, due to forces of acceleration and deceleration involved in locomotion, and squat walking, due to their respective proportion (S1: 6.99% versus 0.23%, S2: 13.58% versus 0.75%). Therefore, the ultimate demand on the body of the growing infant baboon seems to be related to the increasing proportion of pronograde walking (mainly composed of quadrupedal walking: S1: 87.86% and S2: 90.5%). The fact that, specifically, the mass distribution over the limb segments changes with the acquisition of this locomotor mode in the repertoire, suggests a tight functional relationship. According to biomechanics, quadrupedal walking will probably be more efficiently performed in individuals with more proximally concentrated mass into the limbs because it is the best adaptation for reducing the energy costs of swinging limbs (e.g. Myers and Steudel 1997; Raichlen 2005a). In this theoretical/mechanical framework, changes in mass distribution during infancy in olive baboons can, therefore, be interpreted as highlighting, very early on in life, a trend towards an increase of the cursorial abilities (see quadrupedalism of adult baboon in Raichlen 2004).

2.4.3 Relationships with environment and activities

Secondly we hypothesized that according to the morphological and positional variations, thin and inclined substrates should be preferred by individuals with more distally concentrated masses in the limbs while larger horizontal substrates should be preferred by individuals with more proximally concentrated masses in the limbs. Our results partially support this hypothesis. Infants with heavier distal limb segments make more use of the suspended net and tires that can be described as vertical, thin and discontinuous, and the pyramid that offers a vertical content as well as a

horizontal one and a larger substrate size. In contrast, infants with heavier proximal limb segments make more use of the ground, which can be defined as continuous, horizontal and large. Nevertheless, regarding the actual proportions, it appears that the ground is preferentially used in both age-classes, although significantly more in the second. In other words, the ground remains the substrate on which infant baboons spend most of their time at each developmental stage reported in this study, although individuals with more proximally concentrated masses in the limbs use the ground substantially more than younger individuals with less fitted limbs for quadrupedal walking. Therefore, the association between the pattern of morphology and positional repertoire seems to influence the use of the enrichments available in the park. However, because baboons appear to be committed quadrupedal walkers from an early age, this effect remains weak. These results may be of importance in the context of well-being of animals raised in captivity.

According to our third hypothesis, the development of maintenance and social activities should be the least-contributing factor (in the context of the morphological and environmental factors considered) to the “integrative locomotor pattern”. This hypothesis is supported by our PCA results. Nevertheless some relationships have been found: travelling is more associated with quadrupedal walking, and resting is associated with lying that represents mainly the proportion of time transported by the mother (88.21%; see Appendix 2.B.2). No significant differences were observed with regard to feeding contexts (see permutation tests). This context is associated with walking as well as pronograde (tripedal and quadrupedal) standing and squat walking for foraging; note that in the present captive environment squat walking is commonly observed when animals forage independently for seeds on the ground.

The two other axes of the PCA explain clearly a weaker percentage of variance, nevertheless, if they are carefully discussed, they may bring further information. The second dimension involves mainly positional behaviours and the environment with a gradient from less active individuals that primarily sit and squat walk, towards individuals using larger proportions of locomotor behaviours involving high velocity, compression and propulsion of the limbs such as running, leaping and dropping. These latter modes certainly lead to high stress for the limbs (Biewener 2003) and are associated with particular enhancements on

which individuals interact often, i.e. on the transversal bar and on the rock fountain which they use to leap and reach the bar, as well as the substrate called “in the air” (see *Material and Methods* in this chapter) because of its association with leaping and dropping behaviours. Although activities contribute less to this axis, the most active individuals spend a higher proportion of their time in playing activities. Regarding inter-individual variability in this particular context, this corresponds to interactive plays between the youngest males of our sample (from the second observational session). These individuals have relatively heavier upper arms. In addition, the PC3 is compiled of only suspensory behaviours, i.e. inverted quadrupedal walking, orthograde suspension, forelimb-hindlimb, hindlimb and orthograde forelimb suspension and these behaviours are associated with the horizontal rods from the open-air pen. It is interesting to note that individuals that practice these positional behaviours more often also possess more mass in the legs. The contribution of the morphology is low for the second and the third dimension, however, the analysis was able to emphasize these particular segments as contributing factors. In this context we suggest that (1) the practice of compressive behaviours with a high velocity content (as seen on PC2) may increase the mass in the upper arms due to the importance of being able to exert propulsive forces with the forelimbs while hindlimbs are already more efficient for propulsion (Demes et al. 1994); (2) the practice of behaviours in suspension (as seen on PC3) may increase the mass in the legs due to a higher stress on pedal grasping while manual grasping is more efficient (Raichlen 2005a). Therefore, the observations coming from PC2 and PC3 are probably the result of body plasticity (no relationship was observed with age) but this assumption requires further experiments in order to be validated.

2.4.4 Why do baboons develop the way they do?

The developmental pattern previously described can be understood in the broader natural, socio-ecological, context of the baboons' lifespan. Indeed, olive baboons principally live in savannah habitats where they travel long distances, for foraging, for hours each day (Rose 1977). To avoid predation, individuals make a particular effort to keep up with their group, which may sometimes travel rapidly. Therefore, old adults, individuals with illness and young infants (as early as by 6-7 months old) must be able to locomote efficiently (Altmann and Samuels

1992). With regard to infants, early survival is dependent on their capacity to efficiently grip their mother's fur (Altmann et al. 1977). They also need to rapidly develop an efficient mode of quadrupedal locomotion, before the cost of maternal carrying becomes too high (Altmann and Samuels 1992). In other words, locomotor autonomy causes rapid changes in the functional demands placed on the limbs and this locomotor transition is highly driven by quadrupedal locomotion. In this developmental context, the pattern of body mass distribution subtly matches with this locomotor shift.

With regards to other Catarrhini species, the locomotor transition observed in baboons appears to be similar, in some respects, to that observed in macaques (Turnquist and Wells 1994; Wells and Turnquist 2001); but adult macaques seem to be less equipped for quadrupedal walking than baboons possibly because of their higher arboreal component (Myers and Steudel 1997; Raichlen 2004). However, the locomotor shift in cercopithecoids appears to be different to that observed in the ontogeny of hominoids. Chimpanzees have been described as undergoing the most drastic locomotor transitions: infant chimpanzees, after statically clinging the mother's fur for approximately five months, exhibit a high proportion of torso-orthograde suspensory locomotion up until three years of age, before they shift towards habitual quadrupedal (knuckle-)walking (Sarringhaus et al. 2014). In mountain gorillas, relatively similar locomotor transitions occur but the adult locomotor pattern is reached more rapidly (within two years of age according to Doran 1997). In contrast, limb functional changes do not seem to be observed in orangutan (see Thorpe and Crompton 2006, but younger individuals need to be studied to conclude on this point), and a recent study further showed that infants of this species are capable, very early on, of gap crossing the way adults do (Chappell et al. 2015). Hence, primate developmental pathways are varied and are likely to reflect different selective pressures. In this context, we believe that more crossed morphological and behavioural data on distinct species of NHPs as provided in this study would enable the reconstruction of a more integrative picture of the ontogeny of the primate locomotion. Indeed, the investigation of the various developmental pathways may improve our knowledge of the evolutionary transitions toward very specialised locomotor modes, such as habitual brachiation observed in gibbon and habitual bipedalism observed in human, as well as more generalized

positional repertoires such as that observed in chimpanzee (see Hurov 1991 for a theoretical framework).

Furthermore, as shown in this study, there are biomechanical factors involved in the adaptation of body shape during ontogeny. It may improve our knowledge of how selective factors, and constraints from environments, act on NHPs morphology. Nevertheless, and as previously notified by a number of researchers (e.g. Jungers and Susman 1984), the ontogenetic changes in body proportion cannot be considered to adjust to mechanical conditions in the same way as during evolution. In other words ontogenetic extrapolation does not necessarily explain or predict the pathway of evolutionary changes, yet offers opportunities to observe possible functional relationships. Hence, more interspecific data are required in order to investigate these links in a larger framework.

To summarize, the present longitudinal study provides the first quantitative analysis for a NHP species on the full positional repertoire, combined with morphometrics, activities and environment at an individual level. Our results support the hypothesis that body mass distribution corresponds with the proportion of locomotor and postural modes according to biomechanical principles. In baboons, acquiring locomotor autonomy changes the functional role of the limbs, i.e. growing infants exhibit quadrupedal locomotion in greater proportions, while they exhibit postures that require grasping abilities in smaller proportions. This new locomotor profile also impacts the use of the structures available in the captive environment. Although we do not exclude other factors such as neural control and maturation that are known to influence, for example, the interlimb coordination (Shapiro et al. 1997) and potentially, by extrapolation, the positional repertoire, the parallel between body mass distribution and positional repertoire found in this study is obvious. As observed in other (cursorial) mammals, the pattern of body mass distribution described in these growing baboons is likely to reduce the energy costs related to their preferred locomotor mode. Infant baboons, therefore, become gradually more equipped for quadrupedal locomotion despite other positional capabilities.

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Chapter 3

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

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Objective: Despite that the biomechanics of standing and walking bipedally has been extensively studied in non-human primates, the morphological features that may constrain, or facilitate, the control of balance and thus of the spontaneous occurrence of bipedal behaviour are poorly known. We aim to test the relationship between body mass distribution and bipedal behaviour using a non-human primate species, the olive baboon, *Papio anubis*, raised in captivity.

Material and methods: We collected quantitative data on the frequency and duration of bipedalism together with morphometrics on a sample of 22 individuals. We used ontogenetic changes as a natural experiment that provides insights into the impact of morphology. Specifically we focus on 1) quantifying how body mass distribution changes from infancy to adulthood in baboons; and 2) whether the different patterns of mass distribution influence the behavioural variables, i.e., a) the frequency and b) the duration of bouts of bipedal behaviour realized in different activity contexts.

Results: With regard to assisted bipedal behaviours, the duration and frequency of bouts of standing, contrary to walking, are significantly related to age. With regard to unassisted bipedal behaviours, no correlation to age is observed; the bout duration of walking is strongly correlated to body mass and mass distribution, contrary to the frequency of walking as well as the bout duration and frequency of bipedal standing.

Discussion: Our results suggest a close relationship between the pattern of mass distribution and the mechanism of balance control in the spontaneous bipedal walking of baboons. The mechanical effects of the pattern of mass distribution on the ability to perform bipedally in extant non-human primates are discussed in the context of the evolution towards habitual bipedalism.

3.1 Introduction

Spontaneous bipedal posture and locomotion is commonly observed in free-ranging non-human primates (see Druelle and Berillon 2014 for a recent review; Hunt 1994; Rose 1976; Susman et al. 1980; Thorpe et al. 2007). Field studies have demonstrated that shifts in bipedal behaviours (locomotion and posture) occur through ontogeny, i.e. the proportion of bipedalism decreases with age which appears to be a pattern shared by the non-human Catarrhini species (Doran 1992b; Doran 1997; Druelle and Berillon 2013; Rose 1976; Sarringhaus et al. 2014; Wells and Turnquist 2001). In humans, the capacity to efficiently stand and walk bipedally increases during the normal motor development to become fully matured after approximately eight years of practice (e.g. Adolph et al. 2012; Adolph et al. 2003; Bril and Brenière 1992; Thelen 1983). Given the parallel and drastic changes in body mass distribution that occur in non-human primates (NHP) as well as in humans, it is, therefore, probable that (next to other factors such as motor control, walking experience, and environmental properties) changes in the body mass distribution will impact the capacity to move and to adopt particular postures (e.g. bipedal posture and locomotion) (Adolph and Avolio 2000; Adolph et al. 2012; Crompton 1983; Doran 1997; Dunbar and Badam 1998; Van Dam et al. 2010; Wells and Turnquist 2001). This was tested experimentally and demonstrated in humans: the pattern of mass distribution influences the kinematics and the spatio-temporal parameters of bipedal walking (Adolph and Avolio 2000; Adolph et al. 1997; Van Dam et al. 2010; Van Dam et al. 2011; Yamazaki et al. 1996). Experimental data on NHPs demonstrated the impact of segmental properties on the biomechanics of the habitual quadrupedal locomotor mode through ontogeny (e.g. Raichlen 2005a; and Shapiro and Raichlen 2006 on baboons; Young 2012 on squirrel monkeys), but no studies have explicitly tested the potential impact of segmental properties on other, less frequent locomotor behaviour, in particular on bipedalism. Our study contributes towards filling this knowledge gap, by using a cross sectional ontogenetic sample of captive olive baboons, a species that spontaneously uses bipedalism.

In modern humans, bipedalism is the habitual mode in their locomotor repertoire (e.g. Orendurff et al. 2008). However, mature locomotor patterns are only achieved after years of practice (e.g. Adolph

et al. 2003; Brenière and Bril 1998; Cavagna et al. 1983; Hallemans et al. 2004) during which the coordination of the walking pattern and the energy saving mechanisms gradually improve; i.e. step-to-step variability decreases and the straightness of the walking improves via longer step lengths, narrower step widths, less foot rotation and the inverted pendulum mechanism appears (Adolph et al. 2003; Bril and Brenière 1992; Hallemans et al. 2004; Hallemans et al. 2003; Schepens et al. 2004; Van Dam et al. 2010; Van Dam et al. 2011). This period is characterised by drastic changes in body mass distribution (Palmer 1944; Wells et al. 2002) that may impact the walking abilities. In fact, muscle strength and balance are inherent to bipedal locomotion since it involves a trade-off between the forward destabilizing propulsion of the body and the need to retain stability. Thus, such components seem to make part of the first requirements for walking onset (see Thelen 1983; Assaiante 1998). In this context, Adolph et al. (1997) observed that the onset of independent walking is delayed in top-heavy, chubby toddlers when compared to slimmer toddlers with a more homogeneous mass distribution (i.e. cylindrically-shaped according to Adolph 1997). Moreover, Adolph and Avolio (2000) observed that an experimental alteration of the body mass distribution (by putting lead weights at the shoulders) makes toddlers stagger and impacts the flexion at the knees as well as the angle of permissible sway of the trunk. Ledebt and Bril (2000) showed a parallel improvement of both the stability of the upper body and the gait parameters (i.e. step length, velocity and width) during the first weeks of independent walking. Van Dam et al. (2010; 2011) demonstrated that upper body dimensions are closely related to the kinematics and spatio-temporal parameters of walking: e.g. children with a broader pelvis undergo less movements of the thorax in the frontal plan and chubby children with long legs use a smaller step width than slimmer ones. These studies reveal an important relationship between body shape and the mechanisms of bipedal balance and walking (Preuschoft 2004; Witte et al. 1991).

In NHPs, on the contrary, the link between body mass distribution and the ontogenetic acquisition of a bipedal posture has never been tested experimentally. Yet, several field and lab studies (e.g. Doran 1993a, b; Druelle and Berillon 2013; Sarringhaus et al. 2014) suggest that morphology may impact the postural and locomotor repertoires in general (see Cant 1992 for a theoretical frame), and thus most probably the

bipedal behaviours as well. In an ontogenetic context, infants appear to be capable of bipedalism very early in their locomotor development and well in advance of achieving the adult locomotor repertoire (Rose 1976; 1977 on olive baboons; Doran 1992b; and Sarringhaus et al. 2014 on chimpanzees; Doran 1997 on gorillas; Wells and Turnquist 2001 on macaques). Furthermore, infants generally exhibit a higher proportion of bipedalism than adults (e.g. Doran 1992b; 1997; Rose 1976; Sarringhaus et al. 2014). Such a tendency has been suggested on captive bonobos and chimpanzees (Aerts et al. 2000; Videan and McGrew 2001) and recently quantified on a sample of olive baboons (Druelle and Berillon 2013). Doran (1992b; 1997) observed that locomotor activities are similar in the ontogenetic stages of chimpanzees, bonobos and gorillas for which body size is identical. Even within the adult class, body size impacts patterns of locomotor behaviour (Doran 1993b). Videan and McGrew (2002) observed, in a group of captive adult chimpanzees, that the frequency of unassisted bipedal walking decreases with body mass. Stanford (2002; 2006) reported, for an arboreal context and taking duration of bouts into account, that it is mainly adult chimpanzees that perform bipedally; however, this primarily concerns assisted bipedal standing rather than bipedal walking. Finally, Sarringhaus et al. (2014) showed in an ontogenetic sample of wild chimpanzees, based on a very precise description of the locomotor and postural repertoires, that only infants were observed walking bipedally in an unassisted manner while older individuals always walked bipedally with the assistance of the forelimbs.

Although heterogeneous, the available behavioural and morphological data suggest that morphology, at least body size, may impact bipedal behaviour in NHPs. In addition, these studies demonstrate that not only the frequency but also the duration of bipedal bouts, as well as the types of bipedalism (standing versus locomotion; assisted versus unassisted) should be taken into account to accurately investigate the potential impact of morphology on locomotor behaviours.

From the morphological point of view, morphometric studies of ontogenetic samples of NHPs demonstrated that drastic changes in body dimension and mass distribution occur with ageing. Grand (1977) and others (Jungers and Fleagle 1980; Leigh et al. 2009; Raichlen 2005b; Schoonaert et al. 2007; Turnquist and Wells 1994) described a common

trend in non-human catarrhine ontogeny: masses of the head, hands and feet decrease, hind limb mass increases, centre of mass of the limbs shifts proximally and centre of mass of the trunk shifts caudally. This pattern resembles that of humans (Palmer 1944; Wells et al. 2002); in humans, researchers (Adolph et al. 1997; 2000; Van Dam et al. 2010; 2011) have demonstrated that such changes affect balance, hence bipedal performance in terms of kinematics of the lower and upper body as well as spatio-temporal parameters (see above for details). Therefore, it can be called into question whether the changes of mass distribution over the body segments, i.e. body shape compared to overall body mass, also impact the individual's ability to stand and walk bipedally, in NHPs.

With regard to the ability to exhibit bipedalism, both in standing and locomotion, it has been argued that the shape of the upper body (i.e. relative length, width and mass distribution) impacts overall equilibrium/stability because its mass (i.e. approximately 76% of total body mass in an adult baboon) needs to be balanced at the level of the hip. This task becomes more challenging the higher the upper body's centre of mass is situated (Adolph and Avolio 2000; Ledebt and Bril 2000; Preuschoft 2004; Van Dam et al. 2010; 2011; Witte et al. 1991). Furthermore, the bent-hip bent-knee posture in bipedal NHPs increases the gravitational moment from the upper body about the hips, thus requiring higher muscle activity to stabilize the upper body (Preuschoft 2004; Winter 1995). Based on these simple biomechanics it can, therefore, be postulated that acquiring and keeping bipedal postures will be more challenging for top-heavy NHPs. Thus, regarding the natural daily life, where one can assume that neurology, metabolism, as well as behavioural and ecological contexts interact at any time on each individual in a similar manner, those individuals with a body less suitable for bipedal bouts (cf. above) can be expected to practice it for a shorter duration on average. This does not prevent top-heavy individuals from practicing bipedal bouts, yet at the expense of higher magnitudes of muscle forces to balance the torso. However, they should commonly do so over shorter periods than individuals that are morphologically best suited for such a behaviour.

Among primates, catarrhines display a huge variation in body mass distribution (e.g. Isler et al. 2006) as well as an immense diversity of locomotor modes (Hunt et al. 1996) and they all use bipedal postures (see Druelle and Berillon 2014 for a review). In other words, Catarrhines are

able to transit to bipedalism from another mode, whatever the pattern of mass distribution. On the other hand, recent pilot studies (D'Août et al. 2012; 2013) suggest that attaining bipedal balance from a quadrupedal posture may be less challenging than at first anticipated. The involved mechanism combines changes in speed and general posture and appears common to species with very different patterns of mass distribution (i.e. olive baboons, bonobos, siamangs and humans). Thus, within a single species, a change in mass distribution would probably have little impact on their ability to transit to bipedal posture. Hence the body mass distribution is a weak determinant of the observed frequency of bipedal behaviours.

Our study questions the relationship between mass distribution and the occurrence of bipedal postural and locomotor behaviours in NHPs. We focus on the ontogeny of voluntary bipedal behaviour in a cross-sectional sample of captive olive baboons, *Papio anubis*. In their natural environment, *Papio anubis* show bipedality in various contexts such as feeding, alert, friendly contacts, greeting, copulation, investigation, etc (Rose 1976). Our previous study showed that the captive environment of the study group does not affect the proportion of these behaviours (Druelle and Berillon 2013). In addition, a longitudinal morphological follow-up study provided individual morphological characteristics (see Chapter 1). We quantified individual morphological differences according to the methodology developed by Van Dam et al. (2009) on humans; this approach enabled us to characterise morphotypes thanks to a Principal Component Analysis (PCA) (see also Glassman and Coelho 1987; Jungers and Hartman 1988 in NHP) that is applied to linear morphometrics (as defined by Crompton et al. 1996). Consequently, the environmental settings of this study offer unique opportunities to investigate the relationships between a species-specific behaviour and mass distribution. The present study tests the hypothesis that the pattern of mass distribution over the body segments affects the unassisted bipedal capacities when performed in the context of daily activities. Regarding assisted bipedal behaviours the use of hands becomes a substantial component for maintaining balance and should make bipedalism easier to perform.

Based on available biomechanics insights in bipedal balance, we predict (1) that on average top-heavy individuals will stand and walk

bipedally for shorter periods. We will test this by correlating data on ontogenetic development of the locomotor repertoire and the distribution of the mass over the body segments. According to previous observations on the bipedal component in Catarrhini and available biomechanics on transition from quadrupedal to bipedal equilibrium (cf. above) we predict (2) that the patterns of mass distribution over the body segments do not impact the individual frequency in occurrence of bipedal behaviour.

3.2 Material and Methods

3.2.1 Study site and subjects

The field study was carried out at the Primatology Station in Rousset-sur-Arc, France (UPS 846 CNRS), from January to May 2012. The observations were conducted in an open-air enclosure where a troop of 60 baboons lives. We chose this troop of baboons because: the present social group is structurally similar to those observed in the wild; all ages are represented; all individuals were born in this troop. The open-air enclosure is enhanced with varied substrates (see Berillon et al. 2010; and Druelle and Berillon 2013 for further descriptions of the environment) enabling the baboons to adopt all of the positional behaviours described in the wild (Hunt 1992; Rose 1977) and providing the freedom for inter-individual interactions (Druelle and Berillon 2013). An ontogenetic sample of 22 individuals aged from 10 months to 22 years old and of both sexes was selected; all individuals studied are autonomous in terms of locomotion. Table 3.1 gives individual characteristics; this group represents one third of the total troop size. We pooled them in 5 age and sex classes, according to growth patterns of baboons (Leigh et al. 2009) and the description of the development of physical characteristics of yellow baboons (Altmann et al. 1977): male and female infants 0-2 years, juvenile females 2-5 years and juvenile males 2-7 years, adult females 5 years and more and adult males 7 years and more.

3.2.2 Morphological data

Individual external linear measurements of the 9 body segments (the head - including neck - the trunk, the upper arm, the forearm, the hand, the thigh, the leg, the foot and the tail) (see Chapter 1 and Chapter 4) enabled us to estimate individual segmental volumes according to the geometric model by Crompton et al. (1996), as it has been applied in

several other studies on human and NHPs (see Chapter 1; Isler et al. 2006; Raichlen et al. 2009; Schoonaert et al. 2007; Van Dam et al. 2009; Wall-Scheffler et al. 2006). Segmental densities were obtained from baboon cadavers (Gilles Berillon and colleagues, unpublished manuscript) enabling us to calculate segmental masses. Summed per individual, this yields an estimated total body mass. Estimated total body mass is consistent with that directly measured with an electronic scale (Fig. 3.1, $R^2 = 0.98$), proving the reliability of the procedure.

TABLE 3.1. *Study subjects*

Name	Medal	Tattoo	Sex	Age (years)	Mass (kg)	No. focal hours	No. focal days	Number in PCA
Infants								
Grant	NM ¹	V792BD	M	0.89	3.475	3.75	15	20
Goloum	NM	V894J	M	1.03	4	3.75	14	19
Granola	NM	V935I	F	1.12	2.961	3.75	15	18
Féline	1363	V936I	F	1.50	4.491	3.75	15	17
Fastoche	1364	V916K	M	1.53	5.45	3.75	14	16
Falbala	1405	V916DB	F	1.86	5.45	3.75	15	14
Fibrôme	1403	V935H	M	2.09	6.265	3.75	15	15
Juveniles								
Elvidge	1227	V893EB	F	2.98	8.57	3.75	15	5
Elfira	1326	V916I	F	3.12	8.974	3.75	15	4
Dérive	1060	V908EA	M	3.38	10.228	3.75	15	7
Désastre	884	V908J	M	3.96	13.935	3.75	15	12
Drake	852	V916H	M	3.96	13.495	3.75	15	2
Chris	854	V792BA	M	4.76	14.87	3.75	15	11
Camel	703	V916G	M	5.01	20.304	3.75	15	10
Adults								
Céline	855	V902G	F	5.23	9.956	3.75	14	13
Clara	853	V894H	F	5.33	13.815	3.75	15	3
Amélie	639	V913G	F	6.49	12.265	3.75	15	1
Voltarelle	604	V915F	F	7.54	13.8	3.75	14	6
Talia	1173	V792B	F	10.08	16.8	3.75	15	21
Jula	1278	V935	F	19	17.3	3.75	14	22
Ivar	NM	V923	M	20.09	21.3	3.75	15	8
Gaspard	NM	V905	M	21.92	24.3	3.75	15	9

¹No Medal, these individuals were identified thanks to hair-shave marking

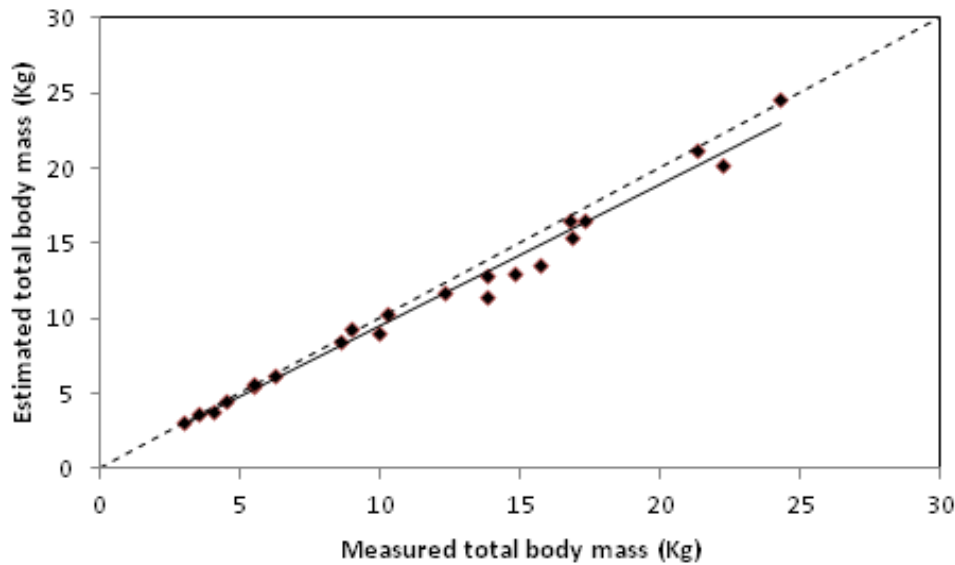


Fig. 3.1 Relationship between the total body mass measured and the total body mass estimated by the geometric model for our ontogenetic sample of captive olive baboons. The solid line is the least-squares regression ($R^2 = 0.98$; $y = 0.9402x + 0.1485$), the dashed line is the line of identity ($R^2 = 1$; $y = x$).

3.2.3 Behavioural data

In the present study we focused on bipedalism, split into the 4 sub-modes as defined by Hunt et al. (1996): unassisted flexed bipedal standing (UBS), assisted flexed bipedal standing (ABS), unassisted flexed bipedal walking (UBW) and assisted flexed bipedal walking (ABW). Observations were quantified using *focal-animal sampling* in continuous recording (Altmann 1974; Martin and Bateson 1993). By focal individual, we collected data on a 15-days period and for one 15-minutes session per day at different times of the day; in total, 82.5 hours of behaviours were recorded. All the observations were conducted between 8:00 am and 1:00 pm for all individuals; this time period has the advantage of covering different types and peaks of activities, including two food distributions: one with wheat, barley, corn, sunflower seeds, and a second with pellets (protein concentrate) or fruits and vegetables (bananas, oranges, apples, carrots and zucchini). We chose focal individuals randomly each day for each observed age group and re-equilibrate throughout the session in order to observe each individual at least two times during each food distribution, and for each hour of observation.

Each focal individual was followed at a distance of 2-10 meters and filmed with a digital camcorder (Panasonic NV-MX350 or HDC-SD90). The continuous recording method enabled us to record frequencies and durations for each positional bout (Martin and Bateson 1993); a *bout* is defined from the moment the focal individual engages in a specific posture, or a locomotor mode, until it started the next one (Fleagle 1976; Fleagle and Mittermeier 1980). Moreover, this recording technique enabled us to observe all performed postural and locomotor activities, even the briefest, such as bipedalism (Doran 1992b).

A bipedal bout is taken into consideration when it lasts longer than one second (Tourkakis 2009). This is equivalent to at least one stride when walking: average bipedal stride duration is 0.69 ± 0.16 seconds for baboons (see Table 5.3 in Berillon et al. 2010). In this analysis we considered two parameters:

- *bout frequency*, defined as the number of bouts observed per hour (i.e. hourly rate) to ensure consistency with the most recent studies in the wild (Stanford 2006) and in captivity (Videan and McGrew 2001);
- *bout duration*, defined as the duration of each bout.

Simultaneously, we scored the activities in which bipedal behaviours are performed (see Table 3.2 for description). We classified bipedal bouts inside three main behavioural contexts, 'feed', 'play' and 'social behaviours'. Obviously bipedalism may be elicited by numerous factors within each category such as food transport, two-handed gathering of food on the ground, aggression, greeting, etc (see Rose 1976), but as this is beyond the scope of the present study, this behavioural complexity is not taken into account. Sequences were analyzed by a single observer (FD) to ensure consistency. Sequencing and transcription from record to computer were performed with the software EthoLog 2.2 (Otoni 2000).

TABLE 3.2 *Main activity contexts in which bipedal behaviours have been observed*

Activity	Description
Feed	Individual eats, transports food, pecks on the ground, drinks and forages in the open air enclosure for seeds or others elements such as fruits.
Play	Interactions between conspecifics. We observe bearing, biting, following, but without vocal aggression or threatening behaviours.
Social	All interactions between individuals, including grooming, greeting behaviour, friendly contacts, sexual and agonistic behaviours, but also facial and vocal contacts such as lip smacking or eyebrow raising. Behaviours for investigation (or scanning) by individuals were also recorded in this category.

3.2.4 Statistics

The global pattern of the body mass distribution, characterised by a subset of 9 body segments, was analyzed by a scaled PCA using R software and following the principles described in Van Dam et al. (2009). This analysis enabled us to extract the largest contributing factors of variation in order to define the variance in body mass distribution of the sample. To avoid any bias due to body size, the segment mass were normalized to body mass before being entered in the PCA (see Van Dam et al. 2009; 2010).

Differences in unassisted bipedal behaviours (*frequency* and *duration*) between the three age classes (infants, juveniles and adults) were tested using analysis of covariance (ANCOVA) with total body mass as the covariate. In the absence of a normal distribution, the relationship between total body mass and bipedal variables was tested using Pearson correlation tests, while differences between age-classes with a non-parametric ANOVA (crude Monte Carlo sample size = 100,000 protocols). Differences in assisted bipedal behaviours between the three age-classes were also tested with non-parametric ANOVA. When significant results were observed, exact permutations tests were used for pair-wise post hoc analysis. The sequential method of Bonferroni-Holm was applied for all post hoc analysis; the *p-value* is adjusted by n (number of comparisons): $n.p_1$, $(n-1).p_2$, $(n-2).p_3$, and the corrected value is denoted P' (Rice 1989). Parametric tests (Shapiro-Wilk and ANCOVA) were conducted using R software and other tests (non-parametric ANOVA, permutations and

Pearson correlations) were conducted using a software of non-parametric inference, StatXact version 3.1. Pearson correlation tests were then performed to assess the relationships between morphology, i.e. using the new coordinates obtained with the PCA, and unassisted bipedal behaviours. We specifically performed these tests between the individual coordinates on the main PC axis and (1) the individual frequency (hourly rate) of unassisted bipedal walking and standing and (2) the average duration of unassisted bipedal walking and standing. Finally, as bipedal behaviours are known to be context-dependent (e.g. Hunt 1994; Tourkakis 2009) we tested whether the trends remained the same when considering the context of activity, so that we could homogenize the data. As such only the impact of morphology was assessed. Note that the sample size decreases greatly due to the separation of the behavioural contexts. Statistical significance was set at $P < 0.05$ for all tests.

3.3 Results

3.3.1 *Body mass distribution/morphotype through age*

The PCA considers all segmental masses and individuals together. The result indicates an overall pattern of variation of the body mass distribution for the entire study group. Figure 3.2 shows the projection of individuals onto the first composed plan (PC1/PC2), representing 69.86% of the total variance (44.09% for PC1 and 25.77% for PC2). Eigenvalues and eigenfactors for each variable are given in table 3.3. As a result, the right hand side of the plot characterises individuals with relatively heavier head and extremities (foot and hand) while the left hand side characterises individuals with a relatively heavier trunk. The upper part characterises individuals with relatively heavier upper arms, lower arms and thighs while the lower part characterises individuals with relatively less mass in these body segments. Along the PC1 axis, the most conspicuous trend is that infants appear to be clearly separated from the adults; juveniles are intermediate and overlap both point clouds. Along the PC2 axis, young adults and juveniles are distributed in the upper part while infants and old adults are in the lower part.

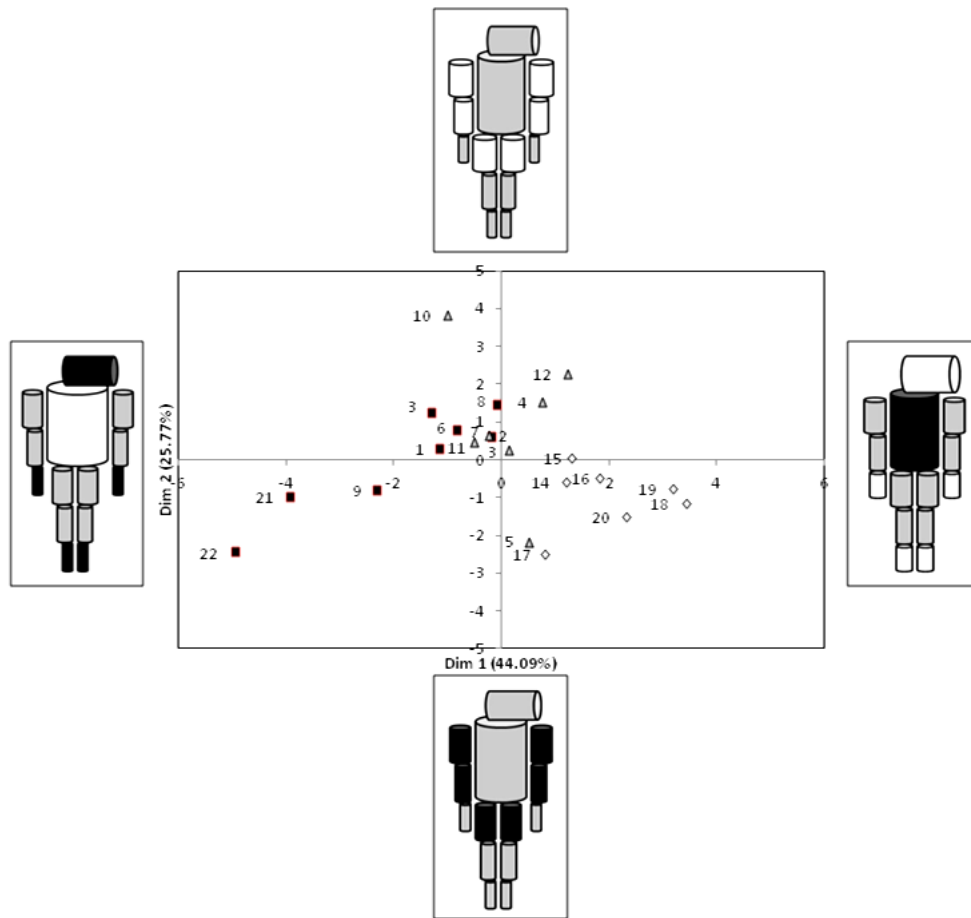


Fig. 3.2 Projection of the individuals (numbers refer to Table 3.1) onto the first composed plan of the PCA. The general plot represents the variation in body mass distribution in this sample. Symbol significance: \diamond infants; \blacktriangle juveniles; \blacksquare adults. The four extreme morphotypes obtained with the PCA are placed at each end of the axis. The segments in white and black indicate the main variables contributing to the axis. White segments are those relatively bigger and black ones are those relatively lighter.

TABLE 3.3 *Eigenvalues and eigenfactors of the PCA of individual mass of body segments*

	Dimension 1	Dimension 2
Eigenvalue	3.97	2.32
% of variance	44.09	25.77
Cumulative eigenvalue	3.97	6.29
Cumulative % of variance	44.09	69.86
	Factor 1	Factor 2
Relative head mass	0.78	-0.41
Relative trunk mass	-0.88	-0.37
Relative upper arm mass	-0.11	0.79
Relative lower arm mass	0.63	0.70
Relative hand mass	0.94	0.05
Relative thigh mass	-0.37	0.73
Relative shank mass	0.33	0.43
Relative foot mass	0.96	-0.14
Relative tail mass	0.36	-0.41

Numbers in bold indicate the main variables contributing to the axis

3.3.2 *Frequencies and durations of bipedal behaviours*

In the pooled ontogenetic sample, a total of 38.33 minutes of bipedalism have been recorded, corresponding to 767 bipedal bouts. The hourly rate of bipedalism equals 9.3, higher than what is observed in the wild for the same species (i.e. 4.15 in Rose 1976). Bipedal behaviours are primarily characterised by brief bouts of a few seconds and the main type of bipedalism performed by all age classes is the ABS. Bipedalism only occurred on the ground or on solid horizontal substrates such as concrete cylinders situated in the park.

Table 3.4 gives a detailed summary of the frequencies and durations of bipedal behaviours by age class. Differences between adults and juveniles were not observed. With regard to assisted behaviours, infants use ABS more frequently than adults ($P' = 0.005$, after Bonferroni correction). Compared to juveniles and adults, infants use ABS for shorter periods ($P' = 0.048$ and $P' = 0.032$, respectively after Bonferroni correction). Although infants tend to use ABW more frequently than the older individuals (ANOVA: $F_{3.52} = 7.287$, $P = 0.011$), no significant

difference is observed after Bonferroni corrections. No significant difference is observed concerning the duration of ABW.

With regard to unassisted bipedal behaviours, the duration of UBW was the only variable with a Normal distribution (Shapiro-Wilk, $W = 0.954$, $P = 0.515$). The ANCOVA reveals a significant relationship with the covariate, mass ($F = 6.552$, $P = 0.023$), but no differences are observed between age-classes ($F = 1.353$, $P = 0.264$). Juveniles tend to use UBS more frequently than adults and infants (ANOVA: $F_{3,52} = 6.622$, $P = 0.024$), but no differences are observed after Bonferroni correction. No difference is observed for the frequency of UBW. No difference is observed for the duration of UBS. No relationship is observed between total body mass and the frequency of UBW and UBS, neither with the duration of UBS ($r_1 = -0.19$, $P = 0.468$; $r_2 = -0.02$, $P = 0.929$, $r_3 = -0.14$, $P = 0.584$, respectively).

In summary, there are significant differences for the durations of UBW due to total body mass and the duration of ABS and the frequency of ABS due to age (see Fig. 3.3).

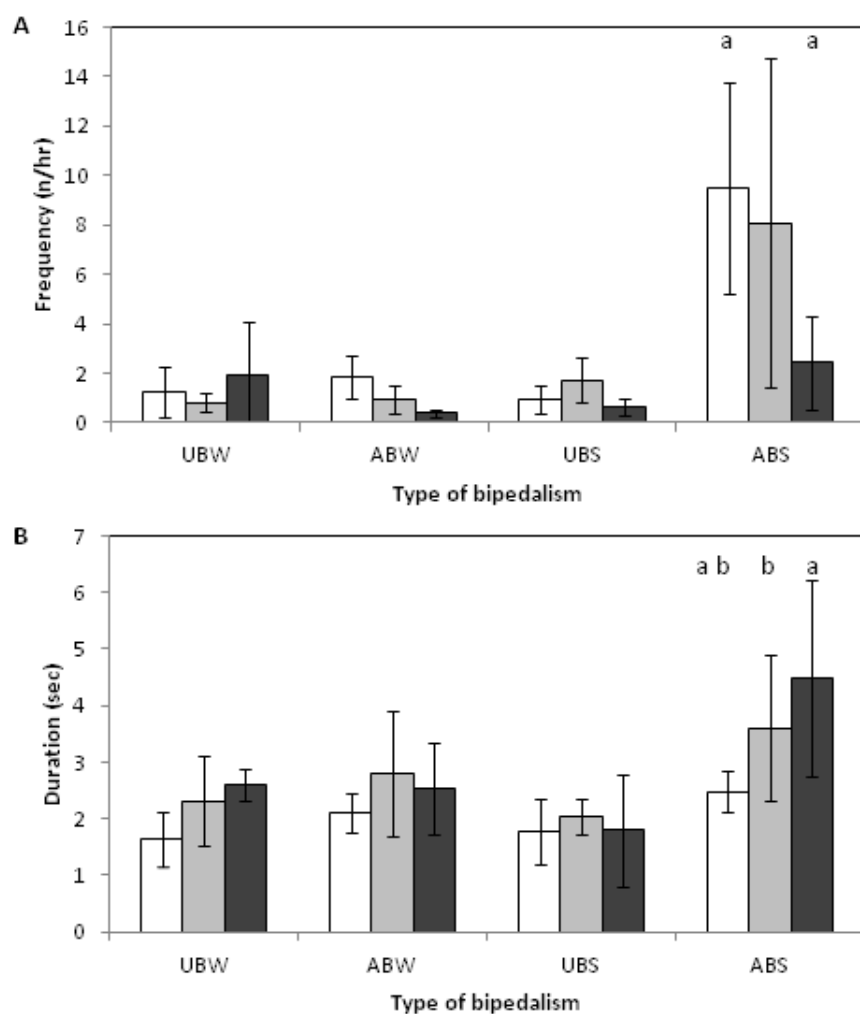


Fig. 3.3 Diagrams of bipedal frequency (A) and duration (B) according to age classes. Infants in white, juveniles in grey and adults in black. Similar letters for each type of bipedalism indicate significant differences after post-hoc analysis.

TABLE 3.4 Sum of bipedal behaviours (Mean \pm Standard deviation) performed in each age class

Type of bipedalism	Parameter	Infant	Juvenile	Adult	Statistical tests	
Walk	Unassisted	N	33	18	29	
		frequency	1.26 \pm 1.04	0.8 \pm 0.38	1.93 \pm 2.16	ANOVA + Pearson
	Assisted	Duration	1.63 \pm 0.48	2.31 \pm 0.80	2.6 \pm 0.29	ANCOVA (Mass*+Age-class)
		N	48	21	6	
		frequency	1.83 \pm 0.86	0.93 \pm 0.55	0.40 \pm 0.15	ANOVA*
		Duration	2.11 \pm 0.35	2.80 \pm 1.10	2.53 \pm 0.80	ANOVA
Stand	Unassisted	N	25	39	14	
		frequency	0.95 \pm 0.55	1.73 \pm 0.92	0.62 \pm 0.36	ANOVA + Pearson
	Assisted	Duration	1.76 \pm 0.58	2.03 \pm 0.31	1.79 \pm 1	ANOVA + Pearson
		N	249	212	73	
		frequency	9.49 \pm 4.28	8.08 \pm 6.64	2.43 \pm 1.88**	ANOVA*
		Duration	2.48 \pm 0.36	3.60 \pm 1.29*	4.48 \pm 1.74*	ANOVA*

Significantly different from infant values using pair-wise comparisons with the Sequential Bonferroni technique following significant ANOVA: * $P < 0.05$, ** $P < 0.01$

3.3.3 Morphotype vs bipedal behaviours

To identify whether the individual use of bipedalism is associated with the individual morphotype, we first plotted the coordinate of each individual on the PCA-axes and searched for correlations with the individual average bipedal variables. Correlation analysis revealed that the average duration of UBW are significantly related to the individuals' position along the first dimension of the PCA (Fig. 3.4a; $r = -0.58$, $P = 0.0155$), i.e. individuals with relatively more massive head, hands and feet practice UBW on average for shorter periods. No further significant relationships with PC1 have been found (Fig. 3.4bcd). No correlations with PC2 were found.

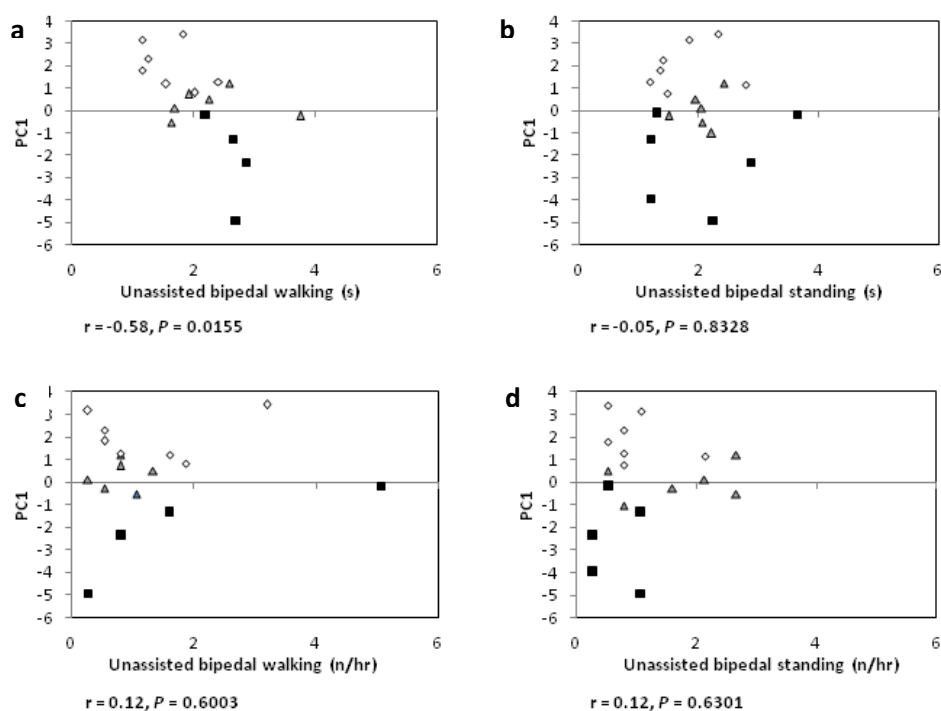


Fig. 3.4 Correlation of bipedal variables with scores for the first PC on the basis of the PCA of body mass distribution. See Fig. 3.2 for symbol significance.

3.3.4 Morphotype vs bipedalism in behavioural context

Figure 3.5 provides the individual average duration of unassisted bipedalism according to the contexts in which bipedal behaviours have been observed. With regard to UBW, a unique trend is observed irrespective of the context: the longest average UBW are observed in individuals with relatively lighter distal and cranial masses. Although similar trends are observed, no significant correlation has been found for the playing context, or for the social context, which can be due to the reduced sample size when separated into the behavioural contexts. With regard to UBS, no significant correlation between the PC1 and the average durations of bipedalism were observed.

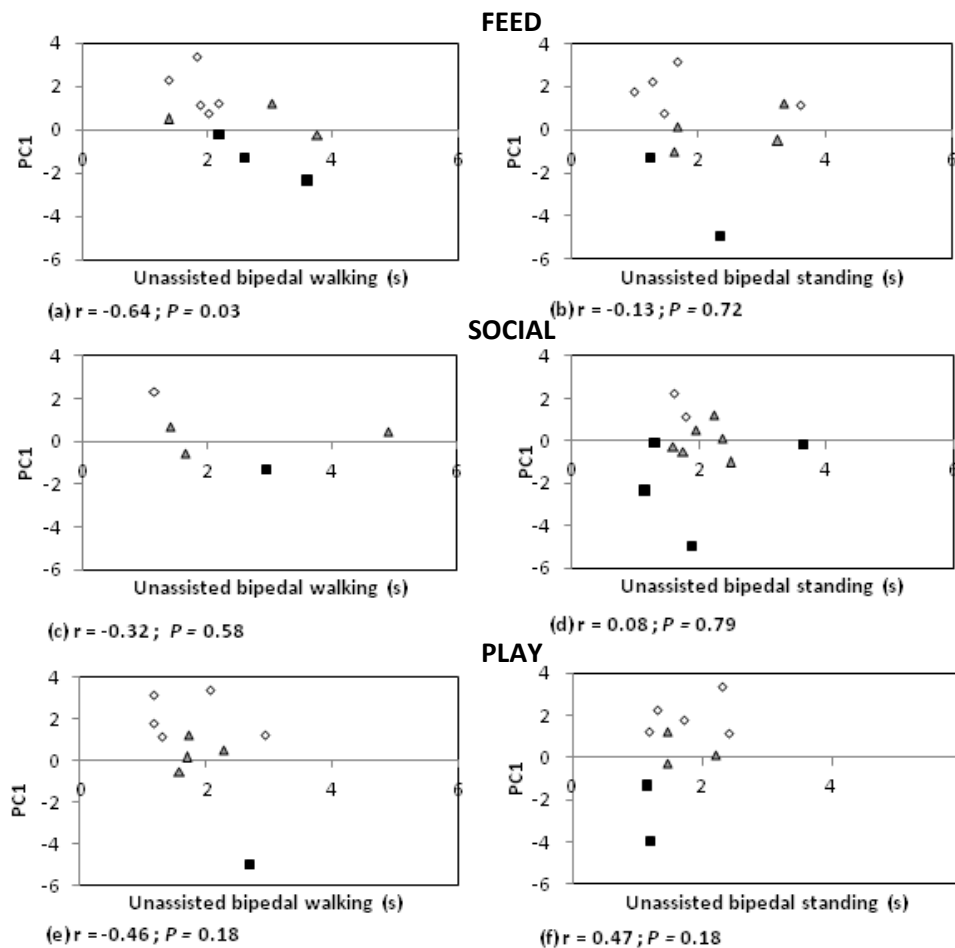


Fig. 3.5 Correlation between the PC1 coordinates and the average durations of unassisted bipedal walking (a, c, e) and standing (b, d, f) depending of the context in which bipedal bouts are performed. See Fig. 3.2 for symbol significance.

3.4 Discussion

The present study provides the first analysis correlating morphological and behavioural data on voluntary bipedalism in NHPs, using an ontogenetic sample of olive baboon. The use of captive animals offers good opportunities for both collecting morphological data and recording behaviours continuously with a high level of precision (Martin and Bateson 1993).

3.4.1 Frequency and duration of bipedalism

We recorded the individual general positional repertoire of 22 captive baboons from which we extracted proportions of the voluntary bipedal bouts. As a general result, bipedalism is mainly performed in posture, whatever the age-classes, and its occurrence varies greatly between individuals. This accords with previous studies on wild and captive olive baboons (Druelle and Berillon 2013; Hunt 1991; Rose 1976). Considering both frequency and duration of each different bipedal mode (i.e. assisted *versus* unassisted and walking *versus* standing) provides a more pertinent description of the use of bipedal behaviours in NHPs. Moreover, as a very occasional mode, bipedal walking in adults was rarely observed in previous studies (Druelle and Berillon 2013; Hunt 1991; Rose 1976); therefore, the choice of the method of data collection (e.g. sampling method, recording time, etc.) is crucial (see Dagosto and Gebo 1998; Doran 1992b). As a result, the decrease of the general proportion of bipedalism with age within the positional repertoire as previously described for olive baboons (Druelle and Berillon 2013; Rose 1976) appears to be mainly due to the decrease of the frequency of assisted bipedal standing. In addition, providing a more precise description of bipedalism is important in the context of an investigation of the morphological basis of bipedal behaviour; indeed the mechanical implications (such as stability, transition, regularity, etc.) may differ according to the type of variables we are looking for (frequency, duration, gait parameters, joint angles, etc.).

3.4.2 Ontogeny of body mass distribution

With regard to the body mass distribution, we applied a multivariate analysis according to Van Dam et al. (2009) to detect the main variance in the patterns. The distribution along the first axis (Fig. 3.2) provides a

reliable picture of the ontogenetic variation of body mass distribution in our cross-sectional ontogenetic sample. Some of the variations seem to correlate with age, at least at a general “age class” level. The PC1, in separating infants from oldest individuals, highlights the drastic changes of allometric types (see Gould 1966) during growth, with negative coefficients of allometry on the distal parts of the body, i.e. head, hand and foot, and positive coefficients of allometry on the limbs and trunk. Such allometric patterns have been widely described in Catarrhini species and have been hypothesized to be linked to the ontogenetic changes in locomotor pattern in NHPs (e.g. Grand 1977; Schoonaert et al. 2007; Turnquist and Wells 1994). At early age, the mass is more distally concentrated in the limbs because of the necessity to possess fine grasping capacities when transported by the mother (Turnquist and Wells 1994; Raichlen 2005). The growth pattern causes a proximal shift of the mass in the limbs to reduce the energy costs of swinging limbs in quadrupedal walking (Myers and Steudel 1997). Otherwise, other ontogenetic changes, such as the changes in limb dimensions in terms of relative length, may impact the manner in which these animals walk quadrupedally (Shapiro and Raichlen 2005; 2006). With respect to body mass distribution it has been proposed that a common pattern of differential growth exists in catarrhines (e.g. Grand 1977; Schoonaert et al. 2007; Turnquist and Wells 1994), including humans in some respects (Leigh 2001; Palmer 1944; Wells et al. 2002). Along PC2, individuals do not separate according to age. Both the youngest and the oldest individuals tend to have relatively less mass in the limbs than juveniles and young adults. The fact that the oldest individuals have a morphotype with less mass in the limbs; may be an effect of age due to a loss in muscular mass as it is described for humans (Bhasin et al. 2001).

3.4.3 Relationships between mass, mass distribution and bipedal behaviours

We wanted to investigate to what extent the age changes in bipedal behaviour and morphology are correlated.

With regard to body size (i.e. the total body mass), considered as a proxy for overall habitus in the ontogenetic series (i.e. implies dimensional adjustments which have important functional consequences), our results show that heavier individuals walk bipedally in an unassisted manner for significantly longer periods than lighter ones.

Besides this general trend, the pattern of body mass distribution provides additional insights into the morphological and mechanical basis for bipedal balance. We first predicted that the variation in the body mass distribution impacts the bipedal stability (see Adolph and Avolio 2000; Ledebt and Bril 2000; Winter 1995): a more cylindrically-shaped upper body (i.e. morphologies at the left end of PC1) may represent easier balance maintenance, compared to a more top-heavy body (i.e. at the right end of PC1). Our results accord partially to this prediction. We obtained a significant correlation with the average duration of bipedal walking. In addition, results show that, irrespective of the behavioural contexts (social, play and feed) in which the bipedal bouts are performed, a similar tendency is noted. However, bipedal standing does not appear to be related to the pattern of mass distribution regardless of the behavioural context. In light of these results, it is possible that the mechanisms of balance control in the flexed bipedal posture of baboons differs between standing and walking, as it is in the upright posture of humans (Assaiante 1998). Firstly, when standing bipedally, balance is reached by maintaining the centre of gravity over the supporting polygon. This limits the effect of body mass distribution in such a way that, as soon as individuals are able to raise their centre of mass to such an extent that it is positioned above the support polygon, they should not differ in their ability to keep this equilibrium in a postural context (see Winter 1995). The estimation of the position of the centre of mass based on kinematical analysis, although difficult to conduct because of the occasional character of bipedal behaviour, would enable us to challenge this assumption. Secondly, maintaining the bipedal balance during locomotion is a more complex task; it refers to dynamic processes where segmental accelerations and decelerations about joints probably alter the stability of the body in the three dimensions. In humans, the stabilization of the upper body (i.e. trunk, head and arms) appears to be fundamental for efficient bipedal walking (Ledeht and Bril 2000; Van Dam et al. 2010; Witte et al. 1991). Considering the upper body (trunk, head and arms) as one rigid segment that rotates about the hip joint, the moments acting on it will depend on the mass distribution: top-heavy configurations may impede this dynamic equilibrium more during bipedal walking (see Winter 1995). Our study demonstrates that in spite of its specialisation for quadrupedal locomotion, the mature baboons have physical characteristics, i.e. primarily light head and heavy trunk, but also relatively light hands and feet (relative to body mass), that accord to a better stability in bipedal

locomotion than in the immature baboons. Indeed, movements of relatively light cranial and distal segments will have less effect on the total angular momentum, hence the equilibrium, than movements of relatively heavy cranial and distal segments. Stabilizing the trunk seems essential when walking bipedally because too many oscillations of this body segment increases the risk of losing balance (Winter 1995; Ledebt and Bril 2000). In this context, it would be interesting to test the impact of body mass distribution on the oscillations of the upper body in baboons, and NHPs in general. Interestingly, it has been demonstrated that macaques intensively trained for bipedal walking developed a more upright and a more stable trunk than untrained individuals (Hirasaki et al. 2004). This experiment relates to important constrained and non-natural skeletal modifications (Nakatsukasa et al. 1995), such as the onset of a lordosis on the lumbar spine (Preuschoft et al. 1988), a feature that potentially minimizes the torques. Therefore, irrespective the way it is achieved, artificially by training or naturally due to changing in body mass distribution through ontogeny, the stabilization of the trunk appears to be crucial to improve the efficiency of the bipedal locomotion.

Given that all catarrhines (in their diversity of mass distribution) perform bipedal behaviours spontaneously in their daily activities and in accordance with D'Août et al. (2012; 2013) who mentioned dynamic mechanisms in the bipedal transition from quadrupedal walking, we predicted that the mass distribution should not directly impact the frequency of occurrence of bipedal behaviours. Our results confirm this prediction: no relationship was observed between the mass distribution and the bipedal frequency, for both bipedal posture and locomotion. All individuals were able to switch from any other mode within the range of the baboon's activities (e.g. sitting, climbing, quadrupedalism) to bipedalism. According to previous studies on wild catarrhines, the bipedal frequency appears to depend mainly on the ecological and behavioural context in which it is performed (Carvalho et al. 2012; Hunt 1994; Rose 1976; Stanford 2002; 2006; Thorpe et al. 2007). For example, Stanford (2006) showed that branch diameter is well correlated with the frequency of bipedal behaviour in wild chimpanzee, as well as with the duration of the bouts, although this latter correlation is weaker.

Researchers suggested that the overall goal of locomotion probably includes transporting the body with the least expenditure of

energy and the greatest stability (see Lécuru-Renous 1994). For bipedal posture and locomotion, the stabilization of the trunk, facilitated by its shape, could be one of the first mechanical requirements to enable an occasional bipedal walker to stand and walk bipedally more efficiently. A specific pattern of mass distribution, as a predisposing trait, may have played an important role in the development of bipedalism by conferring an appropriate balance without being more energy-demanding for the body. In this framework, NHPs remain relevant comparative models to provide insight into the evolution of human bipedal locomotion (D'Août et al. 2014). For example, based on the bonobo model, Zihlman (1996) proposed a prototype to reconstruct early hominin body configuration which included a lower total body centre of mass and longer and heavier hindlimbs. In this context, Tardieu (1991) and Aerts et al. (2000) previously hypothesized from their studies on bipedal locomotion of chimpanzee and bonobo that a lower total body centre of mass should add to the stability of bipedal walking. This morphological feature is supported by our data on captive olive baboons since such a body configuration enables prolonged unassisted bipedal walking. Profound mechanistic understanding of the effect of body mass distribution on the ontogenetic and evolutionary development and efficiency of bipedal performance would definitely benefit from full (neuro-)mechanical analysis (including kinematics, dynamics, energetics...) of a diversity of models and a diversity of behaviours (beyond what is presently available today). Nevertheless, careful interpretation of correlative behavioural-anatomical studies, such as the one presented here, are equally valuable and essential in revealing the key questions for further in depth analyses.

To conclude, our study demonstrates that mass distribution impacts the practice of the bipedal behaviours in NHPs. Although NHPs are all able to perform bipedal walking, the duration of the bipedal bouts is constrained by their body mass distribution making their ability to walk bipedally over long periods variable. Ontogenetic models of NHPs are relevant because they enable functional hypotheses relative to morphological and locomotor changes to be tested. Insights into the effects of the morphological ontogenetic changes in primates on their occasional bipedal behaviour may improve our understanding of the evolutionary transition toward habitual human bipedalism. However, we believe that this field of research deserves more intensive kinesiological studies. Further analyses in activity context, i.e. taking into account why

individuals stand up, and with a comparative sample, i.e. considering a wide variety of models such as catarrhine and platyrrhine, would help to assess the degree of impact of the morphotype on the practice of bipedalism. In this vein, Kimura and Yaguramaki (2009) provided the first biomechanical description of the development of bipedalism in an occasional bipedal primate, the chimpanzee. They observe that infant and adult chimpanzees walk bipedally in a different manner: infants move bipedally at high speed, while adults walk more steadily and exhibit a smaller variance in the parameters of bipedal walking. This result implies that bipedal locomotion of infants would be more energetically demanding than that of adults which appears to require a metabolic energy expenditure similar to that of quadrupedal locomotion (Pontzer et al. 2014; Sockol et al. 2007). Because NHPs do not exhibit the strong walking experience observed in human for improving bipedal locomotion (Adolph et al. 2012), the manner in which their bipedal gait changes, if it does (see Berillon et al. 2011), is probably related to their body dimensions as well as to the improvement of their main locomotor mode. More data is required on bipedal gaits during the ontogeny of NHPs to complete our understanding of the relationships between occasional and habitual locomotor behaviour. Towards this aim, we are currently conducting a longitudinal ontogenetic study that correlates morphological, biomechanical and behavioural data during the locomotor development of infant baboons in order to assess how baboons acquire, develop and refine bipedalism. Indeed, this species remains a good biological model for such a research topic because of its fast locomotor and morphological development.

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Chapter 4

Intrinsic limb morpho-dynamics and the early development of interlimb coordination of walking in a quadrupedal primate

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We question the developmental changes of the temporal aspects of quadrupedal walking and how these relate to the intrinsic morphological (size, shape) and dynamical (inertia) properties of the limbs and body. Indeed, during ontogeny of altricial species, a dependent infant develops toward autonomy. Interlimb coordination is likely to be mediated by the neurological system (central pattern generators and/or supraspinal control) whereas the mechanical parameters of limbs and body appear to influence the locomotor optimization of gaits. We studied six captive baboons at two instants in their development, when they just begin foraging independently and when they are autonomous, in order to collect, in parallel, morphometrics and temporal parameters of voluntary quadrupedal walking. The Natural Pendular Period (NPP) is put forward to represent the limb's intrinsic morpho-dynamics; the position of the body centre of mass as the morpho-dynamics of the body. The main results reveal that fore- and hindlimbs, at the level of the convergence of the NPP, have a significant and positive impact on the interlimb coordination pattern. This probably facilitates, very early in development, the control of the coordination. Nevertheless, because an improved control of the interlimb coordination points at a proceeding neuromotor maturation as well, neuromotor control appears to become gradually important relatively to the intrinsic morpho-dynamics of the limbs during infancy. These findings are of importance in the context of the evolution of the locomotor developmental processes in primates.

4.1 Introduction

Primate newborns are not able to move by themselves. The first independent behaviours involve limb movements that are poorly coordinated. However, during development, movements appear to become increasingly refined when a set of basic motor abilities required for locomotor autonomy emerges (e.g. Rose 1977; Nakano 1996; Dunbar and Badam 1998). This involves different factors such as the maturation of the muscular and nervous systems, changes in the inertial properties of the body segments and locomotor experience (e.g. Raichlen 2005; Schoonaert et al. 2007; Van Dam et al. 2010; Dominici et al. 2011; Young 2012). In this context, locomotor development may also highlight the different needs (e.g. food acquisition, predator avoidance, social interactions), linked to specific ecological niches. The study of these processes may therefore help us to better understand the evolutionary pathway of locomotor modes (Hurov 1991).

In vertebrates, locomotion has been shown to be initiated in the brainstem and follows a rostro-caudal activation of the spinal network (see Grillner et al. 2000). The control of the relative timing within and between pairs of limbs is likely to be mediated by Central Pattern Generators (CPGs) which have rhythmic properties (e.g. Grillner 1985; Pearson 2000). Nevertheless, since the experiment of Eidelberg (1981) on spinal cords of macaques, evolutionary rearrangements of the spinal circuitry have been suggested in primates, thus leaving open the debate about the implication of CPGs relatively to a supraspinal control of motion (see Vilensky and Larson 1989; Schmitt 2010). Nevertheless, the postnatal structural changes in the corticospinal system of primates have been demonstrated to contribute to improvements in motor skills (Olivier et al. 1997; Martin 2005). Furthermore, the mechanisms for neural control of locomotion do not preclude a role for morphological (mechanical) factors in the development of motor control and in the control as such (Vilensky and Patrick 1985; Shapiro et al. 1997). Indeed, the effect of the body dynamics and environment may have important implications on the resulting locomotor patterns (see Owaki et al. 2012). Regarding locomotor mechanics of walking, work must be done at each step, amongst others, to swing the limbs relatively to the body. In this regard, a limb may be considered as a pendulum with local sensory feedback functionally characterised by factors such as limb mass, position of the centre of mass

(CoM), moment of inertia or (all combined) the natural pendular period (NPP; see Methods). Because, in quadrupeds, the swing periods of the four limbs have been shown to be very similar (e.g. Alexander and Jayes 1983; Vilensky et al. 1990) and it is premised that NPP should be related to swing time for efficient locomotion (e.g. Holt et al. 1990; Myers and Steudel 1997; Raichlen 2004), it has been argued that the NPP of the four limbs should converge to each other to minimize energetic costs (Myers and Steudel 1997; Raichlen 2004). Such a convergence can also be assumed to facilitate the interlimb coordination. Moreover, it is known, according to the support polygon model, that the position of the body centre of mass (BCoM) may affect interlimb coordination as well, at the level of the limb phase (Gray 1944; Rollinson and Martin 1981; Cartmill et al. 2002). The more caudal the position of the BCoM the higher the proportion of the diagonal sequences should be in the walking gait (i.e. forelimb touchdown follows the contralateral hind limb; Hildebrand 1967; but see Young et al. 2007; Anvari et al. 2014). Taking all these arguments together, interlimb coordination could be seen as the result of interactions between control by the nervous system and the intrinsic morphological and dynamical properties (morpho-dynamics) of the musculo-skeletal systems (NPPs, BCoM, limb CoM).

Based on the Antero-Posterior Sequence concept developed by Abourachid (2003), it is possible to assess the coordination patterns during voluntary quadrupedal walking in the context of coupled neuromuscular action (initiated by an impulse from the brain, Vilensky and Larson 1989). The method, in considering the action of the forelimbs followed by the action of the hind limbs, studies whole sequences of quadrupedalism, not constrained by stride duration of a single (reference) limb (in contrast to the scheme of Hildebrand 1967).

In this framework and in order to better understand how the proper and efficient coordination patterns emerge in autonomous (adult) animals, we explored the walking gait patterns of a primate species described as a specialised quadrupedal walker, the olive baboon, *Papio anubis* (e.g. Rose 1977). This species is an interesting model for the study of coordination patterns because a large amount of information and knowledge is already available regarding the biomechanics of their quadrupedal locomotion (e.g. Larson et al. 2001; Patel et al. 2013; Raichlen 2005a; Shapiro and Raichlen 2006). Briefly, fully matured

individuals possess a good convergence of fore- and hindlimb NPPs and their quadrupedal walking gait is characterised by diagonal sequences, diagonal couplets, that is, a hindlimb touches the ground followed by the contralateral forelimb with diagonal limbs related in time as a pair. The use of the period of infancy helps to test the relationships between the morphology and the walking gait in the context of the neuromuscular maturation. Indeed, infants undergo drastic morphological changes at the level of their limb inertial properties (Raichlen 2005).

The goal of this study is therefore to explore two different instants in the development of quadrupedalism in baboons: (1) at 6 months old, infant baboons spend 11.08% of their time on their mother while they spend 7% of their time walking quadrupedally (see Chapter 2). Their locomotor autonomy is not yet acquired and their pattern of corticospinal terminals is not mature (Martin 2005). (2) At 22 months old, baboons are not observed carried by their mother anymore while they are observed walking quadrupedally for 13.59% of their time (see Chapter 2). Autonomy is fully acquired and the motor control is developed (Martin 2005). We thus propose three research questions: (1) What are the temporal aspects of quadrupedal gaits in infant baboons and how do these change with age? (2) What are the interlimb coordination patterns and how do these change? (3) How do these changes relate to the intrinsic morpho-dynamics of the limbs and body? We hypothesize that, at an early age, the changing intrinsic morpho-dynamics of the limbs and body affect the temporal parameters of gaits in the sense that changes in fore- and hindlimb CoM will impact dimensionless cycle durations and duty factors of the respective limbs (Raichlen 2005; hypothesis 1). Changes in the position of the BCoM will specifically impact limb phase (Gray 1944; Rollinson and Martin 1981; Cartmill et al. 2002; Young 2012; hypothesis 2). Variations in NPP convergence will impact interlimb coordination pattern (hypothesis 3).

4.2 Material and Methods

4.2.1 Study site and subjects

The present study was conducted at the Primatology Station of the CNRS (UPS 846 CNRS), Rousset-sur-Arc, France. This is part of a larger integrative research project on the development of locomotion in baboons (Letter of approval 01946.02 from the Ethics Committee n°14, France).

Six young baboons, housed in a large open-air enclosure with their mother and their social group, were investigated (see also Berillon et al. 2010; Anvari et al. 2014; for other protocols conducted on the same population of baboons). Data were collected for each individual at two different age-classes: at the first instant (C1) the study specimens were between 5 and 7 months old, with body masses between 1.93 to 3.1 kg; the second instant in the development (C2) came 16 months later (21 and 23 months depending the specimen) with masses between 5.59 to 6.68 kg (see Table 4.1 for individual characteristics).

TABLE 4.1 Study subjects for the two recorded sessions

Name	Sex	Age range (months)	Total body mass (kg)	Forelimb lengths TL(LL) ^b (m)	Hindlimb length TL(LL) (m)	No. of strides analyzed
Iliario (Ii)	M	6.9-7.6/23.1-23.5 ^a	3.10/6.49	0.30(0.11)/0.39(0.15)	0.34(0.11)/0.45(0.15)	56/240
Icono (Ic)	M	4.7-5.4/21-21.3	2.12/6.68	0.26(0.10)/0.37(0.14)	0.29(0.09)/0.43(0.14)	46/69
Irm (Ir)	F	6.3-7/22.5-22.8	2.44/5.87	0.27(0.10)/0.38(0.14)	0.31(0.10)/0.44(0.15)	58/89
Iris (Ii)	F	5.5-6.1/21.7-22	2.46/6.56	0.28(0.11)/0.39(0.15)	0.32(0.11)/0.46(0.15)	39/30
Ivar Jr (Iv)	M	4.7-5.1/20.9-21.2	2.18/6.65	0.28(0.11)/0.40(0.15)	0.32(0.11)/0.45(0.15)	48/102
Isabella (Is)	F	6-6.4/22-22.3	1.93/5.59	0.27(0.11)/0.37(0.14)	0.31(0.10)/0.44(0.15)	37/55

^aData from age-class 1/data from age-class 2

^bTL: total extended limb length, LL: Forearm/leg length

4.2.2 Data collection

Temporal gait data were extracted from videos recorded in the context of an *in situ* longitudinal protocol, providing also behavioural observations (see Chapter 2). Each focal individual was followed at a distance of 2-10 meters and filmed with a handheld digital camcorder (Sanyo Xacti full HD, 16X Advanced Zoom). The frame rate used in this *in situ* longitudinal analysis is a compromise between two constraints: 1) it must enable accurate temporal determination of the gaits and 2) it must enable to process a sufficient amount of records for the statistical comparisons at an individual level. To decide upon this, we first carried out a pilot study comparing the results for a sample of 24 limb phases recorded at 60 frames per second, with the same sample after the recording frequency of the sequences had been converted to 30Hz. The results obtained with the 30Hz sampling rates are strongly consistent with those obtained in 60Hz (see the supplementary material at the end of the present chapter, p.109).

All the strides recorded were on level ground and the concrete pavement of the enclosure offered a very good visibility for their assessment (see an example in Fig. 4.1). To be retained for analysis, the strides were rigorously selected according to the quality of the records, i.e. good visibility of the four limbs in movement and of the footfall pattern. Furthermore, thanks to the handheld camcorder, we were able to record the full locomotor sequences, allowing a first selection, by eye, of steady-state quadrupedal sequences. When there were at least three complete and consecutive strides initiated by a forelimb touchdown, the locomotor sequence could be further used. First and last strides of these sequences were not considered in the analysis in order to limit the effects of acceleration or deceleration linked to the transition from, or toward, another locomotor or postural mode. In each selected stride we recorded the timing at touchdown and lift-off for each limb. All the records were analyzed using the video analysis software Elan 4.6.1 (Max Planck Institute for Psycholinguistics, Nijmegen, The Netherlands). It allows a good frame by frame analysis that includes a zoom option when needed (the software is freely available to download and use from <https://tla.mpi.nl/tools/tla-tools/elan/>).

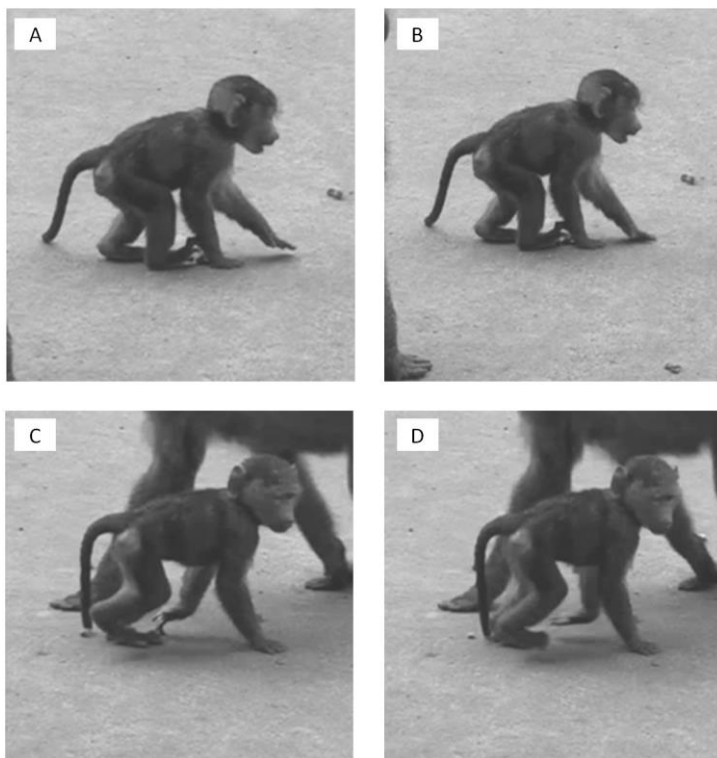


Fig. 4.1 Example of footfall measurements. A, frame before left forelimb touchdown; B, left forelimb touchdown; C, last frame before left forelimb lift-off; D, left forelimb lift-off.

Morphological data were obtained from external measurements performed on each individual under anesthesia (ketamine: 10mg/kg; limbs only measured at the left side, see Table 4.2 for the measurement protocol). As previously applied on baboons (e.g. Raichlen 2004; see Chapter 1), morphometrics and inertial properties of the body segments were estimated according to the geometric model developed by Crompton et al. (1996). The total sum of the individual segmental masses yields an estimated individual total body mass that is consistent with that directly measured with an electronic scale. The absolute error is equal to $2.96 \pm 1.6\%$ and the 99% confidence interval (CI) of the linear model is the following: slope range=0.89 - 1.01 and intercept range=-0.23 - 0.33. Because the line of identity falls inside the 99% CI of the linear model, this strongly supports the reliability of the procedure used to obtain the segment inertial properties (see Chapter 2). We calculated the position of the whole body centre of mass (BCoM; position expressed as a percentage of trunk length, with respect to the trochanter) for a body posture in which the trunk and the head are horizontal, the limbs are straight and perpendicular to the trunk, the feet and hands are positioned at 90° of the limbs and the tail is placed along the legs. We also calculated the position of the limb CoM for straight fore- and hindlimbs (expressed as a percentage of limb length, with respect to the proximal (hip or shoulder) joints). We then calculated the NPP for extended fore- and hindlimbs using the following equation (Eqn 1):

$$NPP = 2\pi \sqrt{\frac{I}{M * g * CoM}}$$

Where I is the mass moment of inertia of the whole limb about the proximal joint, M is the mass of the whole limb, g is the gravitational constant (9.8 m.s^{-2}) and CoM is the absolute distance of the centre of mass from the proximal joint. Because a limb posture changes considerably during swing, primarily due to knee and elbow flexion, we opted to calculate NPP for extended limbs as an overall representation of the morpho-dynamics of the limbs. Moreover, this enables comparison with previous studies (Myers and Steudel 1997; Raichlen 2004) where NPP was calculated in a similar way. Nevertheless, as a preliminary sensitivity analysis, we also provided limb NPPs for estimating the potential impact of a more natural posture during swing phase, that is with knee angle at 86.9° and ankle angle at 104.85° (i.e. between 119.6° and

90.1° according to Table 3 in Berillon et al. 2010), elbow angle at 120° and wrist angle at 110° (estimated from Anvari 2013). In order to compare age-classes, excluding size, dimensionless natural pendular period (dNPP) is calculated as follows (Eqn 2):

$$dNPP = \frac{NPP}{\sqrt{\frac{TL}{g}}}$$

Where TL is the total extended length of the limb considered. We estimated the convergence between fore- and hindlimbs using the absolute percentage difference (Eqn 3; Myers and Steudel 1997; Raichlen 2004):

$$NPP \text{ convergence} = \frac{abs(NPP_{fore} - NPP_{hind})}{NPP_{fore}} * 100$$

TABLE 4.2 Protocol for body segment measurements

Segment	Plan of measurement	Definition
Trunk	Length	from acromion of scapula to great trochanter
	Frontal	u_1 mediolateral armpits, u_2 mediolateral at the level of the xyphoid process, u_3 bi-trochanter
	Sagittal	v_1 claviculo-sternal thickness, v_2 xyphoid thickness, v_3 pubic thickness
Head	Length	from the back of the head to the lips
	Frontal	u_1 no measure (estimation 0.01), u_2 bi-zygomatic, u_3 mediolateral distal muzzle
	Sagittal	v_1 no measure (estimation 0.01), v_2 mandibular angle/orbit, v_3 height distal muzzle
Thigh	Length	From great trochanter to epicondyle of the femur
	Frontal	u_1 bi-trochanter divided by 2, u_2 mediolateral mid-length, u_3 bi-epicondyle
	Sagittal	v_1 anteroposterior proximal, v_2 anteroposterior mid-length, v_3 patella/knee
Lower leg	Length	From the epicondyle of the femur to lateral malleolus
	Frontal	u_1 bi-epicondyle, u_2 mediolateral mid-length, u_3 bi-malleolar
	Sagittal	v_1 patella/knee, v_2 anteroposterior mid-length, v_3 anteroposterior distal malleolus
Foot	Length	From heel (tuber calcanei) to tip of the third toe
	Frontal	u_1 bi-malleolar, u_2 mediolateral head of the metatarsals, u_3 mediolateral at the basis of the third toe
	Sagittal	v_1 anteroposterior distal malleolus, v_2 dorso-plantar head of the metatarsals, v_3 dorso-plantar at the basis of the third toe
Upper arm	Length	from acromion of scapula to epicondyle of the humerus
	Frontal	u_1 mediolateral proximal (armpit), u_2 mediolateral mid-length, u_3 bi-epicondyle
	Sagittal	v_1 anteroposterior proximal (armpit), v_2 anteroposterior mid-length, v_3 anteroposterior olecranon
Lower arm	Length	From epicondyle of the humerus to distal ulna
	Frontal	u_1 bi-epicondyle, u_2 mediolateral mid-length, u_3 mediolateral distal ulna
	Sagittal	v_1 anteroposterior olecranon, v_2 anteroposterior mid-length, v_3 anteroposterior distal ulna
Hand	Length	From distal ulna to tip of the third finger
	Frontal	u_1 mediolateral distal ulna, u_2 mediolateral head of the metacarpals, u_3 mediolateral at the basis of the third finger
	Sagittal	v_1 anteroposterior distal ulna, v_2 anteroposterior head of the metacarpals, v_3 anteroposterior at the basis of the third finger
Tail	Length	from tail basis to tip
	Circumference	proximal, mid-length and distal circumference

u indicate diameters in the frontal plane and v indicate diameters in the sagittal plane. Three diameters are typically measured for each body segment, one proximal, one at mid-length and one distal.

4.2.3 Data analysis

For each complete quadrupedal stride we assessed three aspects: the *interlimb regularity*, the *symmetry* and the *limb phase*. All these temporal variables are aspects of limb movement coordination, therefore, considering those together allows establishing a level of coordination pattern.

Interlimb regularity Theoretically, limbs can be considered independent from each other. In other words, each limb may be subjected to its own

“clock”. Therefore, in each stride recorded, we first considered limbs separately. We calculated for each limb, the cycle duration, i.e., sum of the duration of the stance and swing phases (CD), as well as the limb duty factor, i.e., duration of the stance phase relative to the limb cycle duration (DF). We used the following notations: F1: first forelimb in the sequence of the stride, i.e., the reference limb, F2: contralateral forelimb, H1: ipsilateral hindlimb relative to F1, H2: contralateral hindlimb (see Fig. 4.2). We then calculated the ‘absolute percentage deviation’ (*abs%dev*) in order to estimate the difference between the limbs inside each stride recorded (Eqn 4):

$$abs\%dev = \frac{Abs(x - y)}{x} * 100$$

Where x can be the CD, or the DF, of the reference limb (F1) and y is the CD, or the DF, of the limb compared (F2, H1, H2). We also applied this formula between the two hindlimbs, i.e., x represents H1 and y represents H2. We then calculated a *mean* and a *standard deviation* (s.d.) of these absolute % deviations for each individual per session. The *mean* provides the degree of difference inside the strides recorded for each individual: *index of discordance*; zero indicates no discordance, i.e., limb-clocks of the pair considered are equal. The *standard deviation* provides the variability of the *index of discordance*, called *index of dispersion*; zero indicates no dispersion.

Symmetry and limb phase Following the Antero-Posterior Sequence method (Abourachid 2003), we considered the relative phasing, or time lags, between the limbs. Thus, we used the notations as applied in this study: Fore Lag (FL): time lag between the footfall of F2 and F1 relatively to the CD of F1; Hind Lag (HL): time lag between the footfall of H2 and H1 relatively to the CD of H1; Pair Lag (PL): time lag between the footfall of F1 and H1 relatively to the CD of F1 (see Fig. 4.2). Theoretically, a perfect time symmetrical gait is established when FL and HL values equal 0.5; for this study, a tolerance of ± 0.05 is allowed to define strides as symmetrical (see Abourachid 2003). Regarding limb phase, a lateral sequence is established when PL value is larger than 0.5 and a diagonal sequence is established when PL value is smaller than 0.5. Per individual, symmetry and limb phase are expressed as proportions of the total number of strides (cf. Table 4.1).

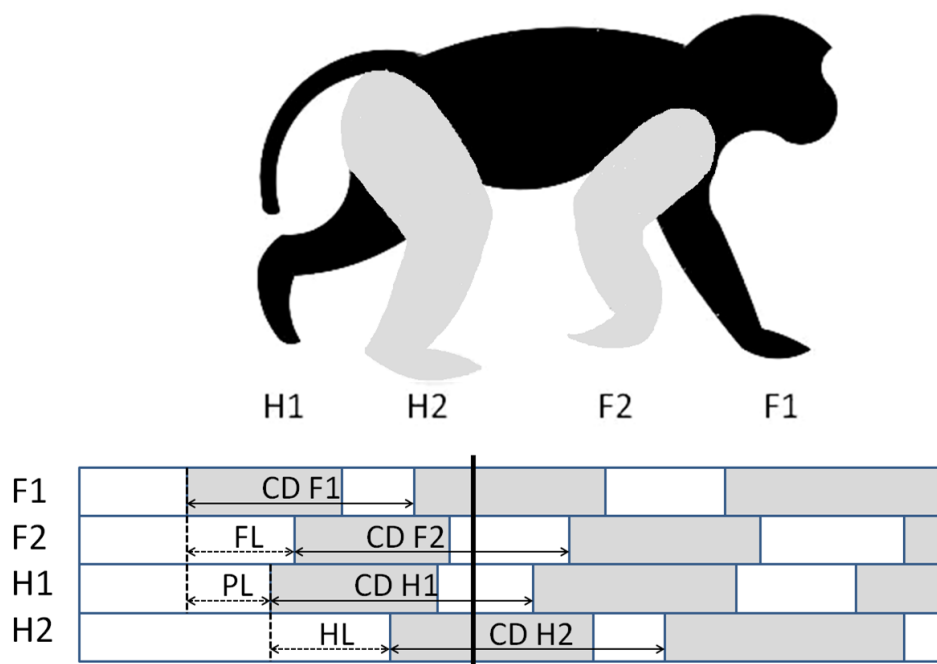


Fig. 4.2 Typical footfall sequence of an infant baboon walking quadrupedally (real data, coming from Iris). The grey square show the stance phases and the white ones the swing phases. The vertical solid line indicates the position of the frame (baboon image above) during the quadrupedal sequence. See the text for abbreviations significance.

Because of the hand-held moving camera used for the recordings, we were not able to calibrate efficiently the volume of the enclosure. As a result, neither spatial variables of the quadrupedal gaits (step and stride lengths), nor walking velocity could be calculated. Nevertheless, temporal gait variables, as defined above, are most of often velocity-dependent (see Alexander and Jayes 1983; Hof 1996). Indeed, when baboons walk, they commonly increase their speed by increasing linearly their stride frequency (and stride length) (Berillon et al. 2011; Raichlen 2005), as it is the case in other primates (e.g. Aerts et al. 2000) and animals in general (e.g. Ahn et al. 2004; Biewener 2003). Therefore, a linear relationship exists between stride frequency and speed, and according to this knowledge, the formula of the dimensionless stride frequency allows an estimation of the speed while removing size effect (Eqn 5):

$$\dim F = F * \sqrt{LL/g}$$

Where F is the mean frequency (i.e., the inverse of the CD) of the four limbs for a stride and LL is the length of the leg (see Aerts et al. 2000; Berillon et al. 2011). Note that our frequency is calculated as the mean of the four limbs, while our value of cycle duration was assessed for each limb separately. The results prove that identical relative speed ranges are used in C1 and C2 (see results) meaning that the locomotor velocity cannot confound the comparison of the datasets.

4.2.4 Statistics

Comparisons in morphometrics were conducted between the two sessions using exact permutation tests for paired samples. Because our sample size is small ($n=6$), the normality of the distribution cannot be tested making permutations an appropriate and powerful statistical test to use herein. The convergence between fore- and hindlimb NPPs was estimated using Reduced Major Axis (RMA) regression and the significance of the slope was assessed with the 95% confidence interval (95% CI) overlapping 1, i.e., the identity line ($x=y$). We compared direct and dimensionless temporal parameters between age-classes using exact permutation tests for paired samples.

Because differential capabilities of fore- and hindlimbs have been described in very young baboons with an initially more apparent coordination and controlled application of power in the hindlimbs (Rose 1977), Friedman test is used to assess differences in *index of discordance* between limb CDs and DFs, as well as the *index of dispersion*, in each session (C1 and C2). When significant, we applied Permutation tests with the sequential Bonferroni correction because of the 6 possible multiple comparisons between the limbs (Rice 1989). We then applied a Principal Component Analysis (PCA) on the 11 variables representing interlimb coordination, i.e., *interlimb regularity* (8 variables; 4 couples for CD and DF each), *symmetry* (2 variables; Absolute*(FL-50%) and Absolute*(HL-50%)) and *limb phase* (1 variable; PL-50%) in order to draw a global coordination pattern of the manner in which young baboons walk quadrupedally. Such an analysis, by reducing the number of dimensions via intercorrelated variables, enables depicting the most significant changes among and between individuals. We used the broken-stick

method (see Frontier 1976; and Jackson 1993 for comparisons with other methods) to assess interpretable eigenvalues.

In order to test specific relationships between morphometrics and temporal parameters of gaits (see hypotheses) we used partial correlations that enable to remove age effect. All the tests were performed using *R 2.12.0* and *StatXact 3.1*. Statistical significance was set at $P < 0.05$ for all tests.

4.3 Results

4.3.1 Morphometrics during development

Table 4.3 shows morphometrics of the baboons studied at two different periods of their development. At an early age, the body CoM is positioned more cranially than at the end of infancy (Permutations: 2.406, $P = 0.0313$). The results also show a significant difference between the position of the forelimb CoM in the two age-classes (Permutations: 2.147, $P = 0.0313$): it shifts proximally. No age-related variations are observed for the position of the CoM into the hindlimbs (Permutations: 1.576, $P = 0.0625$). The fore- and hindlimb dNPPs do not change between ages (Permutations: 2.087, $P = 0.0625$ and 1.752, $P = 0.0625$, respectively), nor the NPP convergence (Permutations: 1.58, $P = 0.125$). Figure 4.3 and the result of the RMA regression demonstrate a strong convergence between fore- and hindlimb NPPs along the developmental period studied. Comparing the NPP values for straight limbs with those of the “estimated natural posture” (ENP, see Method), we observe a decrease forelimb NPP by 7.5% at both age-classes (ENP, C1: 0.99s and C2: 1.14s) and a decrease hindlimb NPP by 14.5% at both age-classes (ENP: 0.92s at C1 and 1.06s at C2). In this posture the NPP convergence is 7.21 at C1 and 7.1 at C2.

TABLE 4.3 Morphometrics of the studied subjects

ID	Session	Forelimb NPP (s)	Hindlimb NPP (s)	Forelimb dNPP	Hindlimb dNPP	NPP convergence	Trunk CoM (%)	Hindlimb CoM (%)	Forelimb CoM (%)
II	1	1.12	1.12	6.42	5.99	0.21	60.12	33.51	42.09
	2	1.26	1.27	6.29	5.90	0.87	53.17	32.67	39.65
Ic	1	1.03	1.00	6.32	5.87	2.52	63.95	32.18	41.09
	2	1.18	1.20	6.06	5.74	1.44	55.57	30.74	35.84
Ir	1	1.05	1.06	6.33	5.95	1.03	59.99	33.26	41.44
	2	1.24	1.26	6.33	5.96	1.32	55.71	33.49	41.22
Ii	1	1.07	1.09	6.35	6.00	1.52	59.88	34.32	42.29
	2	1.25	1.26	6.25	5.80	0.32	52.75	31.77	39.09
Iv	1	1.10	1.08	6.53	6.02	1.78	61.36	34.08	44.89
	2	1.27	1.27	6.25	5.92	0.14	55.18	32.84	38.82
Is	1	1.07	1.10	6.49	6.20	3.02	60.78	37.25	43.70
	2	1.21	1.20	6.19	5.68	0.64	54.52	28.80	37.76

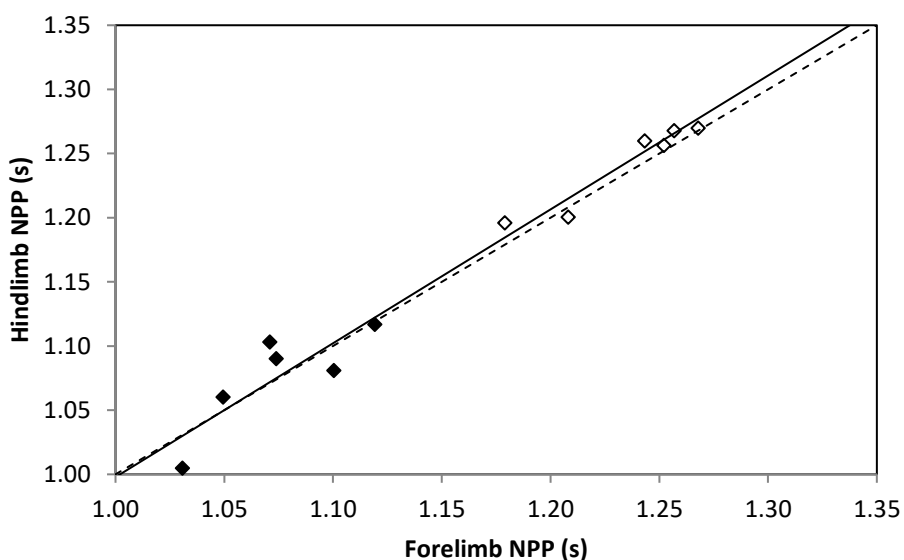


Fig. 4.3 Relationship between the NPP of the hindlimb and the NPP of the forelimb in the sample of baboons at both ages (C1 in black and C2 in white). The solid line represents the RMA regression, i.e., the convergence between the fore- and hindlimb NPPs ($R^2=0.97$, $y=1.0432x-0.0453$). The broken line is the line of identity. The 95% CI [0.92-1.18] of the RMA slope overlaps with 1, therefore indicating a strong convergence of the limb NPPs.

4.3.2 Quadrupedal gait

Speed proxy Regarding our dimensionless frequency value based on the mean frequency of the four limbs, the results do not show significant differences in the magnitude (C1: 0.13 and C2: 0.13, Permutations: -1.863, $P=0.0938$), nor in the variability (C1: 0.03 and C2: 0.02, Permutations: 1.655, $P=0.125$). This indicates that, for this sample and relatively to their size, baboons walk quadrupedally in the same ranges of speed and with the same variation within this range.

Basic temporal data Table 4.4a presents individual mean and standard deviation (s.d.) of cycle durations and swing durations for each limb in the quadrupedal sequences recorded and table 4.4b presents dimensionless cycle duration and duty factor. CDs and swing durations increase significantly between age-classes for the four limbs (CDs: Permutations: F1: -2.244, $P=0.0313$; F2: -2.270, $P=0.0313$; H1: -2.314, $P=0.0313$; H2: -2.357, $P=0.0313$; swing durations: Permutations: F1: -2.311, $P=0.0313$; F2: -2.411, $P=0.0313$; H1: -2.214, $P=0.0313$; H2: -2.392, $P=0.0313$), however, the dimensionless CDs (1/limb specific $dimF$) decrease significantly (Permutations: F1: 2.038, $P=0.0313$; F2: 2.102, $P=0.0313$; H1: 2.092, $P=0.0313$; H2: 2.137, $P=0.0313$; cf. Raichlen 2005). The variability of the dimensionless CDs is identical in both age-classes for all limbs, except for the H2 (Permutations: 2.044, $P=0.0313$). DFs do not change significantly neither in magnitude (Mean) and variability (s.d.) between age-classes. As dimensionless swing time equals 1-DF, the same conclusions can be drawn for swing time.

We test the relationship between the limb NPPs and the mean swing phases. Although it is obvious that the limb NPPs (divided by 2) do not match to the mean durations of swing phases, there is a significant positive correlation between both at C1 (Forelimb: Pearson: $r=0.68$, $P=0.0123$; Hindlimb: Pearson: $r=0.6$, $P=0.04$), no correlation has been observed at the instant of C2 (Forelimb: Pearson: $r=0.51$, $P=0.0961$; Hindlimb: Pearson: $r=0.39$, $P=0.2019$).

TABLE 4.4a Temporal data (Mean and s.d.) of studied subjects, direct measurements

ID	Age-class	Cycle duration (s)							
		F1		F2		H1		H2	
		Mean	s.d.	Mean	s.d.	Mean	s.d.	Mean	s.d.
Ivar Jr	1	1.01	0.18	0.99	0.20	0.97	0.16	0.95	0.19
	2	1.04	0.14	1.04	0.14	1.04	0.13	1.04	0.15
Icono	1	0.82	0.17	0.84	0.20	0.81	0.18	0.80	0.20
	2	0.91	0.13	0.90	0.14	0.90	0.11	0.91	0.15
Ilario	1	0.91	0.14	0.91	0.12	0.90	0.14	0.90	0.13
	2	0.98	0.13	0.99	0.13	0.99	0.14	0.99	0.13
Isabella	1	0.79	0.16	0.81	0.17	0.79	0.18	0.81	0.18
	2	0.95	0.12	0.95	0.14	0.95	0.12	0.95	0.12
Iris	1	0.81	0.15	0.80	0.15	0.80	0.15	0.80	0.17
	2	0.90	0.18	0.87	0.19	0.87	0.19	0.87	0.19
Irm	1	0.81	0.14	0.80	0.15	0.79	0.16	0.78	0.17
	2	0.94	0.18	0.94	0.16	0.94	0.16	0.94	0.17
Mean	1	0.86	0.16	0.86	0.17	0.84	0.16	0.84	0.17
	2	0.95	0.14	0.95	0.15	0.95	0.14	0.95	0.15
Paired permutation test Significance		-2.244	0.698	-2.27	0.905	-2.314	1.144	-2.357	1.444
		0.0313	0.5	0.0313	0.4375	0.0313	0.375	0.0313	0.25
		Swing duration (s)							
Ivar Jr	1	0.27	0.07	0.26	0.06	0.23	0.05	0.24	0.07
	2	0.30	0.05	0.29	0.05	0.30	0.05	0.31	0.08
Icono	1	0.23	0.06	0.23	0.06	0.23	0.06	0.22	0.08
	2	0.27	0.04	0.27	0.05	0.26	0.06	0.26	0.11
Ilario	1	0.25	0.06	0.24	0.04	0.23	0.04	0.24	0.05
	2	0.28	0.06	0.28	0.04	0.30	0.07	0.29	0.06
Isabella	1	0.24	0.07	0.25	0.06	0.23	0.07	0.25	0.09
	2	0.29	0.03	0.28	0.06	0.29	0.04	0.29	0.04
Iris	1	0.24	0.04	0.24	0.05	0.24	0.04	0.24	0.04
	2	0.27	0.03	0.28	0.06	0.25	0.04	0.28	0.06
Irm	1	0.23	0.05	0.24	0.05	0.23	0.07	0.23	0.05
	2	0.30	0.07	0.29	0.04	0.27	0.04	0.28	0.06
Mean	1	0.24	0.06	0.24	0.05	0.23	0.05	0.24	0.06
	2	0.28	0.05	0.28	0.05	0.28	0.05	0.29	0.07
Paired permutation test Significance		-2.311	1.3	-2.411	1	-2.214	0.5774	-2.392	-0.4685
		0.0313	0.3125	0.0313	0.625	0.0313	1	0.0313	0.7813

TABLE 4.4b Temporal data (Mean and s.d.) of studied subjects, dimensionless measurements

ID	Age-class	Dimensionless cycle duration							
		F1		F2		H1		H2	
		Mean	s.d.	Mean	s.d.	Mean	s.d.	Mean	s.d.
Ivar Jr	1	9.73	1.78	9.54	1.98	9.33	1.55	9.17	1.82
	2	8.37	1.1	8.42	1.16	8.43	1.04	8.44	1.22
Icono	1	8.46	1.78	8.71	2.05	8.39	1.88	8.3	2.06
	2	7.58	1.07	7.55	1.13	7.5	0.93	7.59	1.24
Ilario	1	8.59	1.28	8.54	1.16	8.52	1.36	8.47	1.26
	2	8.03	1.02	8.07	1.05	8.07	1.12	8.05	1.07
Isabella	1	7.74	1.56	7.91	1.64	7.78	1.75	7.91	1.79
	2	7.72	0.98	7.72	1.12	7.74	1.01	7.73	0.95
Iris	1	7.79	1.41	7.62	1.45	7.67	1.44	7.61	1.58
	2	7.24	1.45	7.05	1.52	7.07	1.55	7.04	1.56
Irm	1	7.93	1.33	7.85	1.5	7.74	1.58	7.63	1.7
	2	7.55	1.43	7.58	1.29	7.51	1.28	7.56	1.36
Mean	1	8.37	1.52	8.36	1.63	8.24	1.59	8.18	1.7
	2	7.75	1.18	7.73	1.21	7.72	1.16	7.74	1.23
Paired permutation test Significance		2.038	1.767	2.102	1.856	2.092	1.924	2.137	2.044
		0.0313	0.125	0.0313	0.0625	0.0313	0.0625	0.0313	0.0313
		Duty Factor (%)							
Ivar Jr	1	73	5	74	6	76	6	75	6
	2	71	5	72	4	71	3	71	5
Icono	1	71	7	72	5	71	6	72	7
	2	70	5	70	6	71	7	71	10
Ilario	1	71	8	74	5	74	4	73	6
	2	71	6	71	5	70	5	70	5
Isabella	1	69	7	69	6	71	6	68	9
	2	69	4	70	7	69	4	69	4
Iris	1	69	5	70	5	70	5	69	5
	2	69	6	67	6	70	5	67	6
Irm	1	71	6	69	7	70	8	70	7
	2	68	5	68	5	70	5	70	6
Mean	1	71	6	71	5	72	6	71	7
	2	70	5	70	5	70	5	70	6
Paired permutation test Significance		1.604	1.606	1.89	0.3015	1.64	1.225	1.616	0.6489
		0.25	0.1875	0.0938	1	0.25	0.3125	0.1875	0.6563

Significant *P-values* are indicated in bold

Interlimb regularity within the quadrupedal strides Figure 4.4 shows the interlimb regularity of quadrupedalism in our sample using the *index of discordance* and the *index of dispersion*. In the younger baboons (C1), there is a difference in the *index of discordance* for the CD (Friedman test: 13.4, $P=0.0006$), as well as for the *index of dispersion* for the CD (Friedman test: 15, $P=0.0001$), but no significant differences remain after Bonferroni corrections. When baboons are slightly older (C2), there is a difference in the *index of discordance* for the CD (Friedman test: 13.2, $P=0.0007$) and the DF (Friedman test: 10.6, $P=0.0073$), as well as in the *index of dispersion* for the CD (Friedman test: 8.6, $P=0.0292$). Again no significant differences remain after Bonferroni corrections.

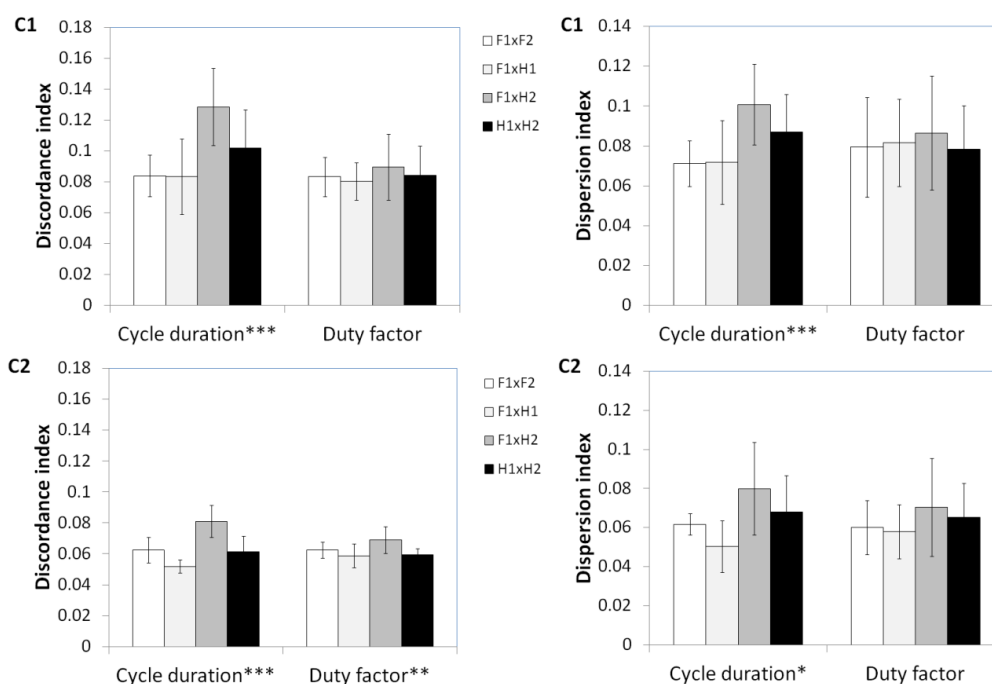


Fig. 4.4 Evaluation of the coordination (discordance and dispersion indices) within the quadrupedal stride at each developmental stage (C1 and C2 separately). The significant level obtained with Friedman test is noticed with stars: $P < 0.05^*$, $P < 0.01^{**}$, $P < 0.001^{***}$.

Interlimb regularity between age-classes Table 4.5 shows comparisons of the regularity between age-classes. The results indicate significant differences in the *index of discordance* for the CD between F1 and F2, F1 and H1, F1 and H2, as well as for the DF between F1 and F2. The discordance is always smaller for individuals of age-class 2. There are also significant differences in the *index of dispersion* of the CD between H1 and H2, as well as for the DF between F1 and H1. The dispersion is always greater in individuals of age-class 1. These results indicate clearly that, when infant baboons become older, the interlimb regularity of their quadrupedal gaits becomes better.

TABLE 4.5 Differences in interlimb regularity between age-classes

	Age-class 1	Age-class 2	Permutation	Significance
Index of discordance				
<i>Cycle duration</i>				
F1xF2	0.08	0.06	1.93	0.0313
F1xH1	0.08	0.05	2.01	0.0313
F1xH2	0.13	0.08	2.10	0.0313
H1xH2	0.1	0.06	1.99	0.0625
<i>Duty factor</i>				
F1xF2	0.08	0.06	2.15	0.0313
F1xH1	0.08	0.06	2.16	0.0625
F1xH2	0.09	0.07	1.54	0.125
H1xH2	0.08	0.06	1.94	0.0625
Index of dispersion				
<i>Cycle duration</i>				
F1xF2	0.07	0.06	1.37	0.25
F1xH1	0.07	0.05	1.57	0.0938
F1xH2	0.1	0.08	1.48	0.0625
H1xH2	0.09	0.07	1.62	0.0313
<i>Duty factor</i>				
F1xF2	0.08	0.06	1.49	0.1563
F1xH1	0.08	0.06	2.00	0.0313
F1xH2	0.09	0.07	1.72	0.2813
H1xH2	0.08	0.07	1.14	0.2813

Numbers in bold indicate significant differences between sessions

Symmetry and limb phase with age Although figure 4.5 shows a trend toward an increase proportion of the symmetry with age, there are no significant differences between age-class 1 and 2 (FL: 63% and 79%, respectively, Permutations: -1.86, $P=0.0625$; HL: 62% and 77%, respectively, Permutations: -1.84, $P=0.0938$; FL+HL: 43% and 63%, respectively, Permutations: -2.00, $P=0.0625$). The results show a significant increase of the proportion of diagonal sequences with age (C1: 82% and C2: 98%, Permutations: -2.04, $P=0.0313$).

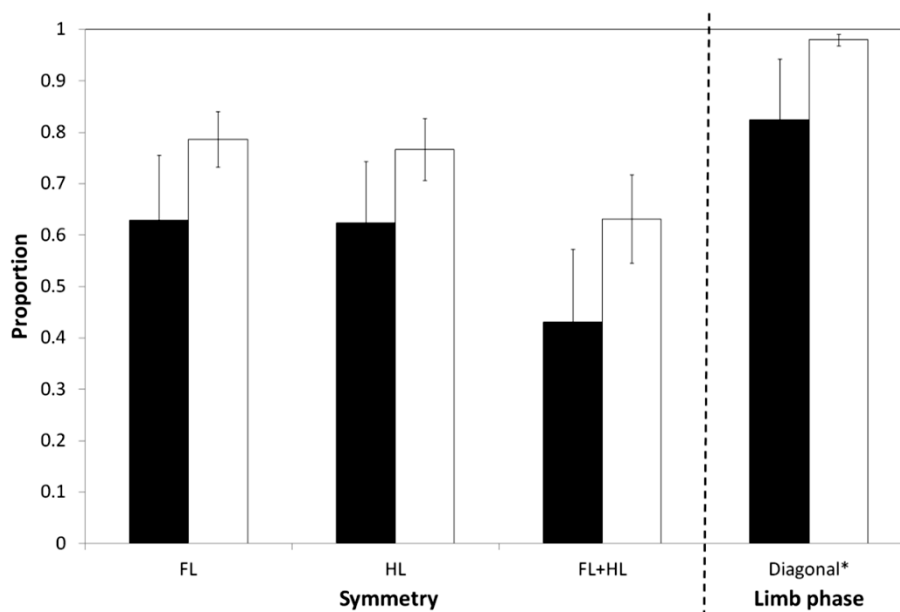


Fig. 4.5 Histogram of the proportion of symmetrical and diagonal gaits during C1 (in black) and C2 (in white).

Interlimb coordination pattern The PCA applied on the 11 variables representing the temporal aspects of interlimb coordination retained 7 variables as the most contributing factors providing thus a full description of the quadrupedal gait in baboons and how it changes (see Fig. 4.6a for the projection of the quadrupedal strides on the first composed plan). The first observed eigenvalue is the only one that exceeds eigenvalues provided by the broken-stick method ($3.58 > 3.02$, Frontier 1976), making the PC1 interpretable in the frame of our study. Younger individuals (C1) are on the right hand side of axis 1 (Fig. 4.6b) and exhibit less regularity for the CD between the forelimbs, as well as for the CD between F1 and H1, F1 and H2, H1 and H2, and for the DF between F1 and H1, and F1 and H2. Older individuals (C2) are on the left hand side of axis 1, and they show a better symmetry between the forelimbs (see Table 4.6 for eigenvalue and eigenfactors of the PC1). Therefore the first axis of our analysis is very relevant for describing the interlimb coordination pattern of quadrupedalism in our sample.

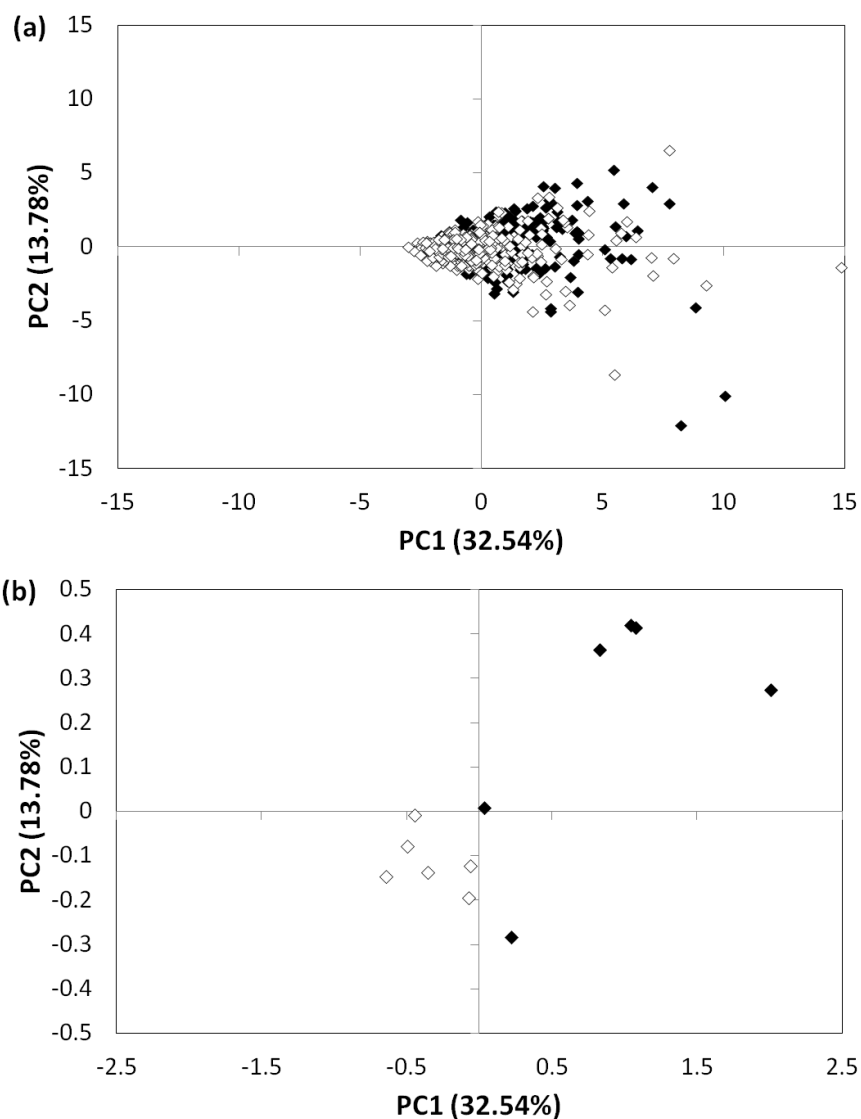


Fig. 4.6 (a) Projection of the quadrupedal strides onto the first composed plan of the PCA. (b) Projection of the individuals onto the first composed plan of the PCA. The axis 1 represents the pattern of interlimb coordination in our sample (see Table 6 for contributing variables). The axis 2 does not represent an interpretable axis (variance explained 13.78%); C1 is represented with black diamonds and C2 with white diamonds.

TABLE 4.6 *Eigenvalue and eigenfactors of the PC1 of individual parameters of quadrupedal gaits*

Eigenvalue	3.58
% of variance	32.54
Factor scores	
CD F1F2	0.63
CD F1H1	0.61
CD F1H2	0.73
CD H1H2	0.58
DF F1F2	0.56
DF F1H1	0.58
DF F1H2	0.63
DF H1H2	0.51
Fore lag	0.63
Hind lag	0.43
Pair lag	0.22

Numbers in bolds indicate the main contributing factors

4.3.3 Morphometrics versus quadrupedal gaits

Table 4.7 shows the relationships between the manner in which young baboons walk quadrupedally and the intrinsic morpho-dynamics of their body. It appears that interlimb regularity (estimated via the PC1 coordinates of each individual) is significantly influenced by the convergence of the NPP in the sense that better is the convergence, better is the coordination. No significant results were observed regarding limb phase and dimensionless parameters of quadrupedal gaits.

TABLE 4.7 *Partial correlation, age removed*

	r	Statistic	P-value
<i>Hypothesis 1</i>			
CoM Forelimb x dimCD F1	0.28	0.88	0.3767
CoM Forelimb x dimCD F2	0.25	0.77	0.4417
CoM Hindlimb x dimCD H1	-0.08	-0.25	0.8034
CoM Hindlimb x dimCD H2	-0.01	-0.03	0.9728
CoM Forelimb x DF F1	-0.03	-0.1	0.9216
CoM Forelimb x DF F2	-0.02	-0.07	0.9452
CoM Hindlimb x DF H1	0.05	0.16	0.8700
CoM Hindlimb x DF H2	-0.26	-0.81	0.4186
<i>Hypothesis 2</i>			
BCoM x PL	0.16	0.49	0.6241
BCoM x %diagonal	-0.27	-0.84	0.3997
<i>Hypothesis 3</i>			
NPP convergence x PC1	0.68	2.75	0.006

Significant *P-values* are indicated in bold

4.4 Discussion

We will address the questions posed in the introduction.

(1) *What are the temporal aspects of quadrupedal gaits in infant baboons and how do these change with age?*

Absolute CDs increase, yet when excluding size (i.e., considering dimensionless CDs) there is a decrease in the CD. This conforms to Raichlen's findings (2005), nevertheless, while he attributed the decrease in dimensionless CD to the reduced inertial properties of the limbs, we were not able to find any relationship at this level. Note that we see only a proximal shift in the CoM of the forelimbs (see Table 4.3) and the dimNPPs (representing size-independent overall inertial properties) do not change between age-classes. Our sample is also covering a later period of baboon's infancy what suggests a more mature neuromuscular control (Martin 2005), thus potentially limiting relationships between kinematics and limb mass distribution. Furthermore, a portion of this control seems to be already established, in some respect, in younger individuals because (1) the variability of the dimensionless CDs do not change between the age-classes (but for H2) and (2) the overall stance and swing proportions of the locomotor cycles (DF and dimensionless swing time) remain identical over the size classes. Our first hypothesis is

therefore not validated here, at least over the age range sampled in this study.

(2) What are the interlimb coordination patterns and how do these change?

Thanks to the PCA, we were able to describe a general pattern of coordination for the quadrupedal gaits. There is a gradient from young individuals that walk with a weak coordination of the limbs, i.e. high interlimb irregularities, to older individuals that walk with a better coordination. Rose (1977) described differential capabilities of the fore- and hindlimbs in very young olive baboons (during the first months of age), suggesting initially a better coordination and control of power in the hindlimbs compared to the forelimbs. In our study, that considers older individuals (from 5 to 23 months), there is no indication for specific limb pairs being better coordinated than others (see Fig. 4.4). Nevertheless, when looking at age effects, we observe a significant improvement in the regularity of the CDs for all pairs of limbs (according to PC1), but for the pair of hindlimbs (according to paired permutation tests on the *discordance index*; Table 4.5). Regarding the *discordance index* of DFs, we only observe a significant decrease between age-classes for the forelimbs, and the symmetry becomes better for the forelimbs only (according to PC1). This could be explained by the fact that coordination between hindlimbs is already established at a young age as suggested by Rose (1977), indeed. Furthermore, as shown by Shapiro and Raichlen (2006), infant baboons use already preferentially diagonal sequences at 5 months of age (82% in our sample) and our results demonstrate that this preference is even more marked at the end of infancy (98%). Taken together, our results demonstrate that, even after beginning foraging independently, young baboons still further improve their quadrupedal interlimb coordination pattern.

(3) How do these changes relate to the intrinsic morpho-dynamics of the limbs and body?

Increased proportion of diagonal sequences appears with age in our sample. Although this is suggested to be linked to a more caudal position of the BCoM (e.g. Gray 1944; Rollinson and Martin 1981; Cartmill et al. 2002), our results do not allow to conclude on this point (see also Young et al. 2007; Anvari et al. 2014), despite the fact that the study

specimens exhibit a more caudal BCoM position at C2 mainly due to a lighter head, relatively (see Chapter 1). Our second hypothesis is therefore not validated and again, this seems to suggest that intrinsic morpho-dynamics may be less determinative than neuromotor control in the developmental emergence of diagonal sequences in quadrupedal walking (Vilensky and Larson 1989).

NPPs are introduced in the study as a representation of the overall inertia of the swinging limbs. As a preliminary exploration, we looked at the NPP in an “estimated natural posture” and found that natural limb flexion during swing phase may reduce limb NPPs by 7.5% for forelimbs and 14.5% for hindlimbs. These values are consistent with those estimated by Raichlen (2004). Furthermore, we found that the NPP convergence is likely to be altered at some point, yet, further precise explorations at the level of limb kinematics during swing phases need to be conducted. If these intrinsic limb morpho-dynamics are determinative in the control of the swing phase, one should expect a relationship between NPP and swing phase duration (yet, not necessarily a perfect match between half the NPP and the swing time; see Turvey et al. 1988; Holt et al. 1990). This relationship is found for all limbs at the first age-class, but is absent at the older age. Still, the interlimb coordination improves from C1 to C2. This confirms that at C1 neuromotor control is not fully mature making the intrinsic morpho-dynamics of the limbs an important determinant of the interlimb coordination pattern. Then, the control gradually becomes mature, and fully mature at C2, therefore important relatively to the intrinsic morpho-dynamics of the limbs. On the other hand, it is remarkable that partial correlations highlight convergence between NPPs of fore- and hindlimbs as strongly related to the interlimb coordination. It is very probably that this convergence facilitates the control of the coordination as mediated by the neuromuscular system. Therefore this result confirms our third hypothesis about the impact of limb morpho-dynamics on the mechanics of quadrupedal interlimb coordination in baboons. Maybe, NPP convergence of the limbs also minimizes costs of transport in quadrupeds, as argued by Myers and Steudel (1997) and Raichlen (2004). Obviously, these explanations are not mutually exclusive, as simplification of the control and reduction of energy expenditure may have gone hand in hand when driving the evolution of this developmental convergence. Anyway, an improved

control of the interlimb coordination points at a proceeding neuromotor maturation, which is obviously reflected in the age effect (see PCA).

In conclusion, while the control of the limbs is in progress through the gradual expression of the corticospinal system (Martin 2005), interlimb coordination of quadrupedal walking appears to be (initially) facilitated by intrinsic limb morpho-dynamics making it an important determinant in the process of quadrupedal learning. This finding highlights the specific needs related to the baboon's socio-ecological niche (e.g. Rose 1977; Altmann and Samuels 1992). Altmann and Samuels (1992) suggested that although it may be more energetically-demanding for the mother through lactation, an early acquisition of locomotor skills in infant baboons should favor its survivorship. Indeed, female baboons usually resume sexual cycling 12 months after they gave birth (e.g. Altmann and Samuels 1992; Strum and Western 1982) implying that by this time their infant would be able to locomote efficiently on the ground in order to keep following their group. In this context, other intrinsic limb morpho-dynamics are likely to be found in other primate species with different needs. These are important to study in order to reconstruct the evolutionary pathway of locomotor modes.

Acknowledgments We thank all the team of the animals' keepers of the Primatology station of the CNRS for their assistance during the collection of the data, as well as Romain Lacoste and Sandrine Melot, Cristina Caballero and Pablo Molina Vila, the two permanent veterinarians, the temporary veterinarian (at the time of the study) and the well-fare manager, respectively. We also would like to thank Naina Shakirova, Master student, for all the time she spent digitizing the quadrupedal sequences, as well as Raoul Van Damme for discussions on the statistics. We thank two anonymous reviewers for useful comments on earlier versions of this manuscript. All authors contributed to the conceptualization of the study. G.B. provided the financial and material resources. F.D. conducted the experiments and analyzed the experimental data. F.D. and P.A. interpreted the results and drafted the first version of the manuscript. All authors revised the manuscript. This work was supported by the UPR 2147 of the CNRS and the University of Antwerp.

Supplementary material

Raw temporal parameters (i.e. 24 swing and 24 stance phases durations) measured on the original 60Hz recordings as well as on the converted 30Hz sequences were compared in order to evaluate the impact of the frame rate on the gait temporal description used in this study. We regressed the limb phases durations of both samples (60Hz *versus* 30Hz) against each other. The line of identity ($x=y$) is included in the confidence interval of the slope, what indicates statistically identical results for both phases. For the swing and stance phases, the slopes equal respectively 0.98 (confidence interval 95% [0.76, 1.19], $r^2=0.8$) and 0.98 (confidence Interval 95% [0.93, 1.03], $r^2=0.99$). This indicates that 30Hz sampling rates are sufficiently high for the purpose of the study to decide unambiguously about the frames at which touchdown and lift-off occur and to assess the footfall pattern in young primates. This conforms to the methods used in previous contributions to that field (e.g. Nakano 1996; Shapiro et al. 2014; Webb and Sparrow 2007). We thus decided to proceed with recording at 30Hz enabling us to reduce considerably the digitization and data handling time for each sequence without impacting the quality of the dataset, but at the same time to increase the studied sample for statistical comparisons between age classes and individuals.

Chapter 5

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

Based on: Druelle F, Aerts P, Berillon G (In revision) *Journal of Human Evolution*

In this paper we point out 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 represent important sources of variation upon which natural selection may act. In France, at the Primatology Station of the CNRS, we had the opportunity to follow the development of locomotion in a committed quadrupedal primate, the olive baboon. Six infants were observed 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 behavioural components. Our results show that, while the basic temporal aspects of the bipedal walking gaits (i.e. duty factor, dimensionless frequency and hind lag) do not change during development, the baboon significantly improves the coordination pattern between hind limbs. This is likely to influence the bout duration of spontaneous bipedal walking. At the same developmental stage the inter limb coordination in quadrupedal walking is improved and the proportion of quadrupedal behaviours increases significantly. Therefore, the quadrupedal pattern of primates does not impede the realization of bipedal behaviours. Furthermore, the neural networks for quadrupedal locomotion seem to be employed in non-human primates for the elaboration of (occasional) bipedal walking. These results thus point to an equal basic mechanism of control in bipedal and quadrupedal locomotion. In this context, we suggest that 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.

5.1 Introduction

Extant primates exhibit positional repertoires with different degrees of specialisation. 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 *Panins* and *Gorillins* (Doran 1992, 1997; Remis 1995; Sarringhaus et al. 2014), slow quadrumanous 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, elicit 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). With regard to the fact that the rhythmic motor patterns related to locomotion are likely to share common central neural control mechanisms (e.g. Grillner 1985; Dietz 2002; Zehr 2005), such an ontogenetic diversity of behaviours at an immature stage may assist the proper development of coordination between body parts, as well as of strength and balance control. Parallel to this neuromotor maturation, the mechanical properties of the locomotor apparatus change, in the sense that optimal morphometrics (such as mass distribution, rotational inertia, segment lengths...) required for the principal locomotor mode become more pronounced with growth (e.g. Isler et al. 2006; see Chapter 2 and 4). In spite of these functional morphological specialisations, the motor development related to the broader ontogenetic posturo-locomotor diversity may possibly lead to improvement of secondary locomotor modes as a kind of developmental by-products. The bipedal behaviour (in posture and locomotion) in otherwise primarily quadrupedal species may be an example of this. Kimura and Yaguramaki (2009), for instance, observed an improvement of the regularity of bipedal gaits in chimpanzees during the acquisition of their (quadrupedal) locomotor skills. Furthermore, it is worth noting that biomechanics of quadrupedal and bipedal locomotion have been shown to be similar, in some respects, 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 at a possibly equal basic control of walking in

quadrupedal and bipedal locomotion in non-human primates. Interestingly and regarding a broader context, most human infants are observed crawling during the first year of age (see Adolph and Robinson 2013 for a review). This is a form of quadrupedal walking very similar 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, experience and exploratory activities (Adolph and Robinson 2013).

In an evolutionary perspective, developmental by-products, under appropriate (ecological) pressures, offer opportunities for the selection of behavioural and morphological novelties (Hurov 1991). Such a mechanism, if shown to be present in living forms of primates, might have been one of the motors for the impressive diversity of locomotor adaptations observed in the Hominoid lineage (Hunt 2016), including the bipedal locomotion in hominins.

In this paper, we want to test specifically whether the development toward a quadrupedally-oriented locomotor profile includes the development of bipedal behaviours in a non-human primate species. For this aim, the olive baboon, *Papio anubis*, is an ideal model because this species is described as a committed quadrupedal walker, yet exhibiting a diversity of positional capacities during early ontogeny, including unassisted bipedal walking (Rose 1977; see Chapter 2). We address the following question: What are the temporal aspects of bipedal gaits in infant baboons and how do these change with age (for quadrupedal gaits Chapter 4)? We hypothesize that (1) during development, infant baboons improve the coordination pattern when they walk bipedally; (2) the development of coordination will be reflected in the behavioural parameters (i.e. bipedal bout duration and frequency, and the proportion of bipedal behaviours) of spontaneous unassisted bipedal walking.

5.2 Material and Methods

5.2.1 Study site and subjects

The study was carried out at the CNRS Primatology Station (UPS 846) in Rousset-sur-Arc, France and was approved by the Ethical Comity of France (Letter of approval 01946.02 from the Ethics Committee n°14).

We had the opportunity to follow the development of the olive baboon in studying six infants living in a large open-air enclosure with their mother and in their social group. For details regarding the troop and study site we refer to our previous works (e.g. Berillon et al. 2010; Anvari et al. 2014). Data were collected for each individual at two different instants of their development, allowing observations of both quadrupedal (see Chapter 4) and bipedal (this study) locomotor modes and thus comparisons. At the time of the first session of observation (S1, October 2013), the locomotor autonomy of infant baboons was not yet acquired, ranging from 5 to 7 months in age and from 1.93 to 3.1kg in body mass. At the time of session 2 (S2, March 2015) the autonomy was fully acquired, the infant baboons ranging from 21 to 23 months in age and from 5.59 to 6.68kg in body mass. Table 5.1 gives the individual characteristics for the six infant baboons involved in the present study.

TABLE 5.1 *Study subjects*

Name	Tatoo	Sex	Age (days)	Individual mass (kg)	Lower leg length (mm)
Ilario	V908G-13C	M	216/701 ¹	3.10/6.49	110/147
Icono	V893E-13E	M	150/635	2.12/6.68	92/140
Irm	V896E-13A	F	196/681	2.44/5.87	102/152
Iris	V916D-13D	F	172/657	2.46/6.56	107/150
Ivar Jr	V894H-13A	M	147/632	2.18/6.65	105/150
Isabella	V896B-13E	F	181/666	1.93/5.59	102/148

¹S1 and S2 are separated by “/”

5.2.2 Data collection

Behavioural and temporal data on bipedalism were extracted from videos recorded in the context of a longitudinal protocol (see Chapter 2). Each focal individual was followed at a distance of 2-10 meters and filmed at 30 frames per second with a handheld digital camcorder (Sanyo Xacti full HD), thus allowing a precision of 33ms (see also Cheyne et al. 2011; Shapiro et al. 2014). This frequency has been shown to be statistically similar to 60Hz on the same sample of baboons (see the supplementary material in Chapter 4). Note that the minimum stride duration observed for bipedal walking is 510ms according to Berillon et al. (2011), therefore

the resolution used herein is largely sufficient to assess the temporal aspects of gait. A complete session of observation consists of 200 minutes of continuous recording for each individual and covers all the daily activities of the individuals (5-min focal x 4 focal per hour x 10 hours). All the bipedal sequences were digitized using video analysis software, Elan 4.6.1. The temporal parameters of bipedal strides were retained for the analysis when there was no assistance of the hands (Figure 5.1A). Strides during which individuals are in transition, e.g. from quadrupedal to bipedal posture (or vice versa), were excluded from the analysis. 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 contacted the substrate and the initiation of the swing phase was assessed as the frame in which the limb no longer contacted the substrate. The concrete pavement of the enclosure offered a good visibility for the assessment of these transitional frames.

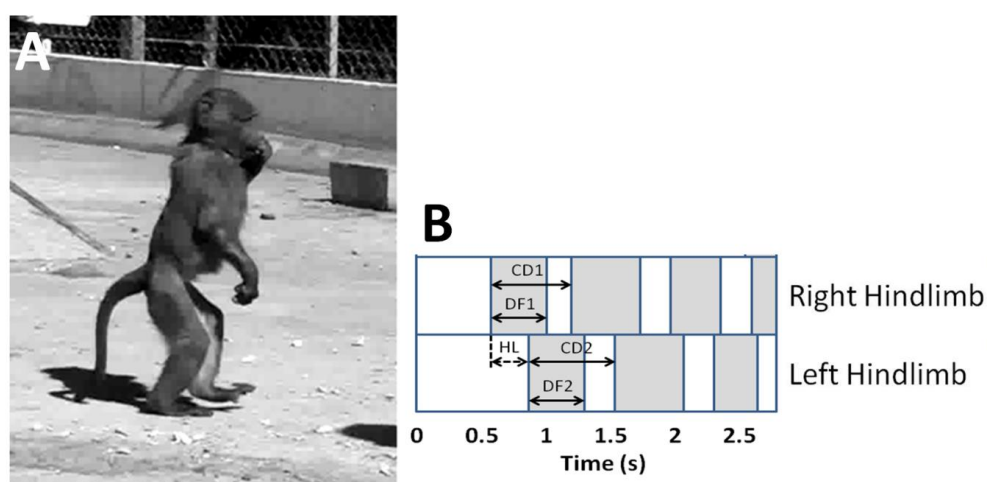


Fig. 5.1 (A) Voluntary bipedal walking in autonomous infant baboon at the CNRS Primatology Station. (B) Example of a footfall sequence for bipedal gaits, grey squares indicate stance phases and white squares indicate swing phases; CD: cycle duration, DF: duty factor, HL: hind lag.

5.2.3 Data analysis

For each complete stride we assessed four temporal components: the duty factor (DF), the dimensionless frequency (dimF), the regularity (for the cycle duration and duty factor) and the symmetry; regularity and symmetry are aspects of limb movement coordination (Figure 5.1B).

Duty factor We calculated the duration of the stance phase relatively to the cycle duration (CD) of the limb considered for each bipedal step. The duty factor is thus by definition a dimensionless value given in percentage.

Dimensionless frequency The frequency of each bipedal step considered in our analysis is calculated and made dimensionless according the dynamic similarity principle (Alexander and Jayes 1983):

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

Where l is the lower leg length (in meter) g is the gravitational constant (9.8 m.s^{-2}) and CD the cycle duration (in s). Making use of $DimF$ enables comparison of stride behaviour of animals differing in size (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 first hind limb considered 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 regarding the coordination pattern.

Symmetry We considered the time lag between the hind limb footfall relatively to the cycle duration of the first hind limb. This dimensionless value is given in percentage and a perfect symmetrical gait is established when the relative hind lag phase is 50% (see Abourachid 2003 for quadrupedal walking gaits). Because values can be above or below 50%,

we assessed the degree of symmetry, which only considers the deviance from the perfect symmetry, as follows:

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

We also assessed three behavioural components from the full follow-up: 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.

5.2.4 Statistics

Because a smaller amount of temporal data could be extracted from our follow-up compared to the behavioural ones, we applied two different statistical treatments for the two kinds of datasets.

Regarding the temporal components, the bipedal steps were considered as the statistical units. Comparisons in temporal parameters, i.e. duty factor, dimensionless frequency, regularity, and symmetry, were conducted between the two sessions using exact permutation tests for independent samples. Furthermore, after controlling for Normality of each parameter in each sample at S1 and S2 (*Shapiro-Wilks test*), we applied the *one sample t-test* in order to assess whether the sample of bipedal steps was different to the mean obtained for hind limbs in quadrupedal locomotion (data from Chapter 4). This alternative method is used because sample size differences are too important for allowing direct comparisons between samples. This analysis was done using the software R 2.15 (The R Foundation, Vienna, Austria, <https://www.rproject.org/>).

Regarding the behavioural components, individuals were considered as the statistical units. Comparisons in behavioural parameters, i.e. bipedal frequency, duration and proportion, were conducted between S1 and S2 using exact permutation tests for paired samples.

Any age-related changes may therefore be highlighted. Statistical significance was set at $P < 0.05$ for all tests and permutation tests were performed using StaXact 3.1 (software, Cytel, Inc., Cambridge, MA).

5.3 Results

5.3.1 Temporal parameters with age

In 40 hours of recordings, we were able to analyze the temporal parameters of 65 bipedal steps (S1: 19 and S2: 46) performed by the six individuals of our sample. Table 5.2 presents the changes in the temporal parameters of gait with age. There are no significant differences between the two sessions for the dimensionless stride frequency (0.19 and 0.23, permutation test=-1.685, $P=0.0835$), the duty factor (0.72 and 0.73, permutation test=-0.3995, $P=0.6901$) and the degree of symmetry (0.06 and 0.06, permutation test=0.3441, $P=0.7221$). The regularity between consecutive cycle durations increases significantly with age, i.e. it becomes closer to zero (from 0.2 to 0.09, permutation test=2.61, $P=0.0114$). There is no significant difference for the regularity of consecutive duty factors between age classes (0.15 and 0.1, permutation test=0.9845, $P=0.3442$).

TABLE 5.2. Temporal parameters of bipedal walking with age, compared to quadrupedal walking

	Age class	Bipedal walking	Permutation test (S1 vs S2)	Quadrupedal walking	One sample t-test
Duty factor	S1	0.72±0.08 ¹	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 ²
	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

¹Mean±Standard deviation

²Not applicable because the normality of the samples for bipedal data were not obtained

5.3.2 Bipedal versus quadrupedal temporal parameters

Table 5.2 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 and quadrupedal gaits

at S1 (72% for both, $t=0.1627$, $df=18$, $P=0.8726$) but there is a significant difference at S2 (73% and 70%, respectively, $t=2.1305$, $df=45$, $P=0.0386$; Fig. 5.2A). During development, the dimensionless frequency in bipedal walking is always higher than in quadrupedal walking (S1: 0.19 and 0.13, respectively, $t=5.8879$, $df=18$, $P<0.0001$; S2: 0.23 and 0.13, respectively, $t=8.8514$, $df=45$, $P<0.0001$; Fig. 5.2B). Because hind lag values are not *normally* distributed it was impossible to test for statistical differences between quadrupedal and bipedal gaits. Qualitatively, however, the symmetry in bipedal walking does not seem as good as in quadrupedal walking and the degree of symmetry diverges more from zero during bipedal gaits (Fig. 5.2C). For the same reason it was not possible to compare statistically the regularity of cycle durations and duty factors between bipedal and quadrupedal walking using the *one-sample t-test*. Nevertheless, judging figure 5.2D and 5.2E, a similar tendency toward an increase of the regularity with age is observed, i.e. values become closer to zero.

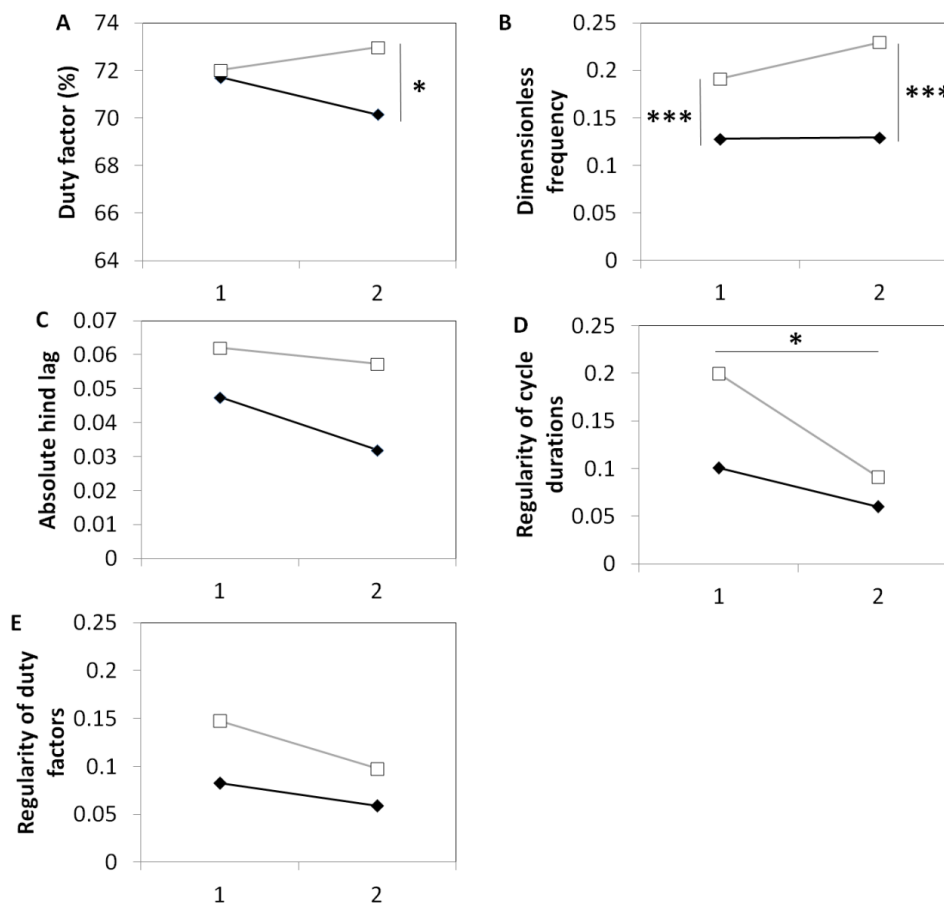


Fig. 5.2 Temporal parameters of bipedal (white square) and quadrupedal gaits (black diamond) during voluntary walking in infant baboons at S1 and S2: (A) DF, (B) DimF, (C) absHL, (D) ratio of CD, (E) ratio of DF. Symbol significance: * $P < 0.05$, *** $P < 0.001$.

5.3.3 Behavioural parameters

Figure 5.3 shows that, at the end of infancy (S2), baboons perform bipedally on significantly longer durations in average than at the beginning of independent foraging (S1) ($1.16 \pm 0.2s$ and $0.84 \pm 0.16s$, respectively, permutation test = -2.114 , $P = 0.0313$). No significant difference is observed for the proportion of bipedal walking (S1: $0.07 \pm 0.03\%$ and S2: $0.14 \pm 0.1\%$, permutation test = -1.4 , $P = 0.2188$), neither for the number of bipedal bouts performed voluntarily (S1: 9.67 ± 3.98 and S2: 13.17 ± 8.47 , permutation test = -0.8773 , $P = 0.5$).

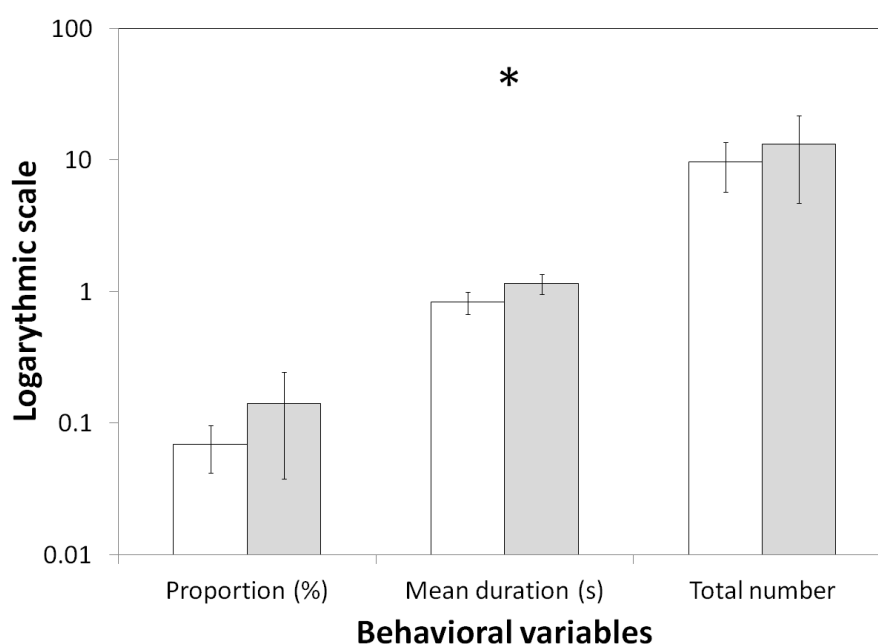


Fig. 5.3 Mean values of the behavioural parameters of voluntary bipedal walking in our sample of infant baboons. S1 is represented with a white bar, S2 is represented with a grey bar. See figure 5.2 for symbol significance.

5.4 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 ontogenetic series of olive baboons, it seems that duty factor and dimensionless frequency remain constant across lifespan as well (Berillon et al. 2011). Nevertheless, when compared to quadrupedal walking, that is the locomotion for which the baboon's adult morphology is the best adapted (see Chapter 1, 2 and 4), the duty factor becomes significantly larger in bipedal walking than in quadrupedal walking. This may be the result of greater balance requirements in bipedal posture throughout ontogeny compared to quadrupedalism. Indeed, keeping relatively long stance phases is likely to afford longer overlapping periods of limb support, therefore enhancing stability. 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 provides more frequent opportunities to correct balance perturbations). However, in baboons no high-speed bipedal locomotion as that described in very young chimpanzees 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 interpreted as a non-erratic locomotor mode (Berillon et al. 2010). Our results confirm this description because baboons walk bipedally in a stereotyped manner from the very beginning of their life.

We first hypothesized that during development of infant baboons the coordination pattern should improve when they 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, while infant baboons strongly experience quadrupedal walking, the bipedal locomotion is only occasionally performed (see Chapter 2). Therefore, this result points to an equal basic mechanism of control in bipedal and quadrupedal locomotion as also suggested 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 suggests that quadrupedal locomotion is not exclusive of a bipedal development in non-human primates. In other words, the neural networks for quadrupedal locomotion seem to be employed in non-human primates for the elaboration of (occasional) bipedal walking. Interestingly, we were not able to find any bipedal sequences longer than two steps in younger baboons (aged around six months old), while we found and analyzed sequences composed as far as five steps in the same individuals one and a half year later. This brings us to our second hypothesis, that is, the development of coordination should be reflected in the behavioural 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, the upper body

mass needs to be balanced at the hip while forward propulsion destabilizing the body. Retaining this 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 Chapter 3). 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 behaviours.

Regarding the chimpanzee, Kimura and Yaguramaki (2009) demonstrated that the steadiness of bipedal walking increases significantly from two years old. In chimpanzee, this age corresponds to a shift in terms of autonomy and in the proportion of use of quadrupedal locomotion, i.e. from around 10% of its locomotor repertoire (the rest is mainly composed of orthograde behaviours, i.e. climbing, bipedalism and suspension) before 2 years old to around 70% after two years old (percentages are estimated from Figure 1 in Doran 1992). Although this species exhibits a different locomotor repertoire than the one of the committed quadrupedal baboon (Hunt 1992), it is obvious that the maturation of its preferred locomotor mode, that is terrestrial and arboreal quadrupedal (knuckle-)walking (Sarringhaus et al. 2014), also corresponds to a development of bipedal abilities. Although unassisted bipedal walking possesses its unique and proper features, the development of quadrupedal walking appears to improve bipedalism in Cercopithecoids and Hominoids, i.e. Catarrhini species which are the closest relatives of man. Replaced in the continuum of movements that characterises locomotor repertoires of primates (see Thorpe and Crompton 2006 for theoretical reflections), the development of coordinates limb movements in quadrupedalism, through the development of central neural motor control, is likely to be equally significant for other modes, at least for bipedal walking. While toddlers learn walking bipedally by experiencing specifically the bipedal behaviour (Adolph et al. 2012), infant baboons and chimpanzees improve their bipedal walking skills by experiencing multiple locomotor modes, and specifically quadrupedal walking. The secondary locomotor modes experienced during infancy as a by-product of locomotor development may thus lead to evolutionary novelties when under proper selective pressures. Here we pointed out to the importance of considering infancy and the developmental processes in the potentiality of the emergence of

new locomotor modes, including bipedalism. Indeed, infancy is likely to afford opportunities to generate novel, and exaptive, responses to the environment (e.g. Greeno 1994; Hurov 1991). In this context, we propose that occasional bipedalism would be a by-product of the developmental pathways among Catarrhini species, making this behaviour an exaptation with various effects that can be currently observed in these species, such as food-carrying, investigation, etc (e.g. Rose 1976; Hunt 1994; Carvalho et al. 2012).

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 the early hominin species (see Crompton et al. 2008 for a review). The neural coupling between arms and legs observed in humans strongly suggests that the bipedal locomotor CPGs evolved from the quadrupedal networks (Dietz 2002; Zehr et al. 2009; Zehr et al. 2016). In this respect, our results support the idea that the use of bipedal walking in pre-hominids was not exclusive of quadrupedal displacements. In a recent work, authors proposed that the particular morphological characteristics found within the same species, *Ardipithecus ramidus*, suggest that bipedal and quadrupedal behaviours were both possible in significant proportion (White et al. 2015). Therefore, relying on 1) the mechanism of developmental by-products presents (at least) in Catarrhini species and 2) appropriate inter individual morphological variations (e.g. at the level of the body mass distribution pattern, see Chapter 3), it is very probable that a more habitual practice of bipedal behaviours, through their gradual implementation, emerged in the context of the last common ancestor of panins and hominins. Once this resulted bipedalism was embedded in the regular locomotor repertoire, further evolution towards habitual bipedalism might have become more probable.

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Conclusions and Future directions

In this thesis I have merged behaviour, biomechanics and anatomy in order to propose an integrative and understandable picture of the locomotor development in a Cercopithecoid primate, the olive baboon. This approach also enables us to address evolutionary matters because the locomotor capacities of baboons and their development are key to their survival. Moreover, the influence of environmental factors on the locomotor apparatus is obviously a fundamental parameter of the system as well (Cant 1992). This component cannot be assessed in a captive environment compared to fieldwork in natural environments. Studies in the wild, however, face not insubstantial difficulties when dealing with the morphological parameters. Therefore, the behaviour may be considered as the keystone between both approaches. Hence, in our study, the integration of the knowledge provided by previous fieldwork studies on olive baboons is crucial in order to reconstruct the biology of this species and to provide a relevant picture of their evolution. Thus, I also aim to consider my results in the broader socio-ecological context of the baboon living in the wild.

Furthermore, growth-related morphological changes have offered “natural experiments” for the assessment of specific functional relationships. The present research project also aimed to address the biomechanical and behavioural issues regarding the evolution of primate locomotor systems in general. To my knowledge, this is the first integrative and longitudinal study conducted on the locomotion of a non-human primate species during its development.

The functional development of the olive baboon

Morphology-(performance)-behaviour

Our first aims were to precisely describe the morphological growth pattern of the olive baboon and to subsequently test the functional relationships of these changes. We found that sex-related morphotypes are very similar at birth. The males become rapidly larger than females, both in weight and linear dimensions. Nevertheless, the changes in shape

follow a common pattern between sexes. While infants have large and heavy distal segments, i.e. hands, feet, head and tail, adults have heavier proximal segments, i.e. trunk, thigh and upper arm. Looking at the general development, two life history periods undergo particularly significant rates of change: from birth to 2 years of age, and from 3 years to adulthood. Furthermore, we observed that infants exhibit very convergent natural pendular periods between fore- and hind limbs that decreases gradually during development (see Chapter 1). At this stage, we have hypothesized that this convergence would be an adaptation for facilitating early quadrupedal walking. Then, with regard to the positional repertoire, we found that the initial morphotype, in terms of body mass distribution, and the direction of the shifts can be explained according to the biomechanical principles related to grasping on the one hand, and quadrupedalism on the other hand. Indeed, based on the biomechanical theory, the initial morphotype seems to reflect relatively good grasping abilities during the period in which infant baboons often cling, climb and suspend. Then, an increase specialisation of the mechanical properties for quadrupedal locomotion parallels a substantial increase of the proportion of quadrupedal walking (see Chapter 2). Yet it is worth noting that, throughout development, quadrupedal walking remains proportionally the most important locomotor mode. As a result of the changing morphotype, we also observed that a heavy head on a light trunk as seen in infants constrains the ability to walk bipedally for long periods, while the relatively lighter head and the heavier trunk of juveniles and adults facilitate its practice during daily activities (see Chapter 3). The pattern of body mass distribution, therefore, influences the practice of unassisted bipedal walking in baboons. Nevertheless, given our present results and the fact that infants perform bipedally (while standing and during locomotion) for a greater proportion of time than adults (Druelle and Berillon 2013), the frequency of appearance of this mode does not seem to be constrained by morphology.

Morphology-performance-(behaviour)

According to the integrative framework proposed by Arnold (1983), the observed correlations between morphology and behaviour probably depend on performance. The morphology is the framework for movement capacities, and the latter may be employed more or less frequently, during variable time intervals. In this context, the interlimb coordination of

quadrupedal walking was put forward as an estimation of the maturation of neuromotor control. Interestingly, we observed that both, age and the “fore-hind-convergence” of the limbs’ natural pendular period have significant and positive influences on the interlimb coordination pattern. Because these effects do not interact with each other, it is very likely that two parallel factors are in action for quadrupedal learning in baboons, i.e. neuromuscular maturation and development of appropriate mechanical properties (see Chapter 4). These results, therefore, support the proposed hypothesis about the presence of early optimization of the limbs in baboon (see Chapter 1). They also support the observation of the important proportion of quadrupedal walking at an early age (see Chapter 2) making the functional link between morphology, performance and behaviour, as proposed in the previous theoretical framework (Arnold 1983). This convergence thus represents an adaptation for facilitating learning processes related to quadrupedal walking. Indeed, an early acquisition of (quadrupedal) locomotor skills in young baboons should favour their survivorship (Altmann and Samuels 1992). Finally, we found that there is a parallel improvement in the coordination of the hind limbs during unassisted bipedal walking, while basic temporal parameters (frequency and duty factor) do not change with age. Bipedal walking, therefore, is performed in a stereotypical manner during the development of baboons, yet the capacity to move forward in this posture improves. This is also reflected in the increased duration of bipedal walking bouts. In this respect, we proposed that the improvement of the occasional bipedal pattern, considered as a secondary locomotor mode, could be the result of developmental by-products related to the development of quadrupedal walking in primates, at least in Catarrhini species (see Chapter 5). It supports the idea of an equal basic neural control when walking in these postures.

Answering the research questions and addressing biological hypotheses

I started the present project aiming to assess the functional relationships between the morphological pattern and the positional repertoire in the context of the diversity of primates’ positional capacities. Thereafter, I questioned how the morphological pattern may constrain, or facilitate, the most occasional components of the movement pattern in these species. In the frame of the study results presented in this thesis,

several ways to comply with the previous objectives can be put forward. Indeed, the integrative character of our research work enables us to test, based on a “natural experiment”, functional hypotheses proposed in a broader biological context, including the evolution of animals and their biomechanics.

First, it has been previously hypothesized that biological systems tend to self-optimize, in terms of energy consumption, with age (see Holt et al. 1990; Isler et al. 2006). This is supported by the results obtained from our longitudinal sample of 6 infant baboons that show a functional relationship between body mass distribution and the positional repertoire. Indeed, based on the biomechanical principle stipulating that limbs with proximally concentrated masses facilitate movement, it seems that limb growth-related changes observed in baboons follow this tendency (see also the transversal studies from Turnquist and Wells 1994; Wells and Turnquist 2001 on macaques).

Second, according to previous ontogenetic studies (e.g. Lawler 2006; Young 2005; Young and Heard-Booth 2016) musculoskeletal growth is allometric in ways that increase locomotor performance and promote survival during immaturity (see for a review Herrel and Gibb 2006). Our results support this hypothesis: the limbs' natural pendular period convergence observed in infant baboons allows an early improvement of the interlimb coordination pattern during quadrupedal walking. Furthermore, this early optimization of the limbs may be of importance for the good energy recovery observed in young baboons (on 3 individuals in longitudinal follow-up, Raichlen 2006). Note that this character may also be representative of a primitive form. Early adapoid primates were probably arboreal quadrupedal generalists (e.g. Ni et al. 2013; Rose et al. 2009), thus potentially also exhibiting a strong NPP convergence of the limbs. Nevertheless, in this context, the fact that this characteristic remains present in young baboons, but for example not in hominoid species (see Chapter 4), still suggests an important adaptive feature for quadrupedal walking on which natural selection keeps acting.

Third, the gait selection hypothesis proposed in the frame of the *Support Polygon Model* (Cartmill et al. 2002; Gray 1944) was not validated in the context of a previous study on infant-carrying in female baboons (Anvari et al. 2014). Our results do not support this hypothesis

either. Indeed, when removing the age effect, we were unable to find any relationship between the caudal shift of the whole body centre of mass and the increase proportion of the diagonal sequences during quadrupedal walking. According to our study, this seems to be the result of neuromaturational processes rather than an effect of the changing mechanical properties of the body.

Fourth, Raichlen (2005a) proposed, based on a longitudinal sample of 4 infant baboons, that limb mass distribution would affect the kinematics of quadrupedal walking in the way that proximally concentrated limb masses would increase the relative limb frequency, and vice versa. Although we observed a decrease of the mean dimensionless cycle durations for each limb with age, we did not find any relationship between stride durations and limb COM. In this context, it is worth noting that limb mass distribution does not change in the hind limbs of our sample and that the coefficients of correlation between limb COM and kinematics are close to zero. There is a proximal shift of the mass in the forelimbs and the coefficients of correlation are around 0.25 (but not significant). Nevertheless, Raichlen (2005a) cautiously proposed, slight changes in the kinematics as a result of the morphological changes. Therefore, considering the full development of baboons (see Chapter 1), it is possible that our longitudinal sample represents a period (from 6 to 22 months) in which only slight morphological changes occur, therefore, we were unable to observe the anticipated effect. Indeed, the general growth pattern depicts an important proximal shift of limb mass from birth to 11 months old in females and until 16 months old in males, potentially greatly reducing the limb COM difference between baboons at 6 months old and 22 months old.

Fifth, previous studies on primate bipedal behaviours proposed an equal basic control of walking in quadrupedal and bipedal locomotion (Aerts et al. 2000; D'Août et al. 2004). Studies on humans (e.g. Dietz 2002; Zehr et al. 2009) support this hypothesis. The fact that we observed an improvement of hind limb coordination during unassisted bipedal walking in infant baboons while they have very little experience of bipedal walking, but they strongly experience quadrupedal walking, also supports this hypothesis. Indeed, the modular neural network may simplify muscle control, via a muscular activation in synergy (Zelik et al. 2014). In this respect, the same modular controllers of the rhythm-generating neural

network may produce the muscular activity in both quadrupedal locomotion and bipedal locomotion in primates.

Regarding the addressed and supported hypotheses, it seems that key adaptations for movement performance in baboons in particular, and in primates in general, must be found in the mechanical properties of the limbs. The limb mass distribution probably reflects a gradient from grasping to cursorial capabilities in primates. The intrinsic limb morphodynamics probably enable momentum-based strategies during walking thus enhancing locomotor control. Furthermore, a fundamental aspect of (primate) locomotion illustrated by our results is the continuous nature of some positional modes (see Thorpe and Crompton 2006). Indeed, while it has been shown that the kinematics of some modes may be very similar (e.g. Berillon et al. 2011; Berillon et al. 2010; D'Août et al. 2004; Fleagle et al. 1981; Pontzer et al. 2014; Schoonaert et al. 2016), an equal motor control, at the level of its intrinsic modular neural system organization, may be a more determinative aspect of the locomotor continuity. In other words, locomotor modes that are based on the same motor control may be more easily interchangeable, during evolution, than modes that look kinematically similar but have a different (neural) basis. Quadrupedal and bipedal walking are thus closely related locomotor modes in terms of their neuromotor control as shown by our study of the coordination pattern. Therefore, experiencing and learning one mode may enhance the capacity to perform the other one. In this respect, a morphological pattern, even though presenting specialised traits, will probably also corresponds to positional capacities in addition to those expected on the basis of this morphology, at least in primates.

Implications for primate evolution

The results of our research show an important (mechanical) integration of the limbs in baboons, which probably decreases the possibility of substantial genetic variations between the limbs. Indeed, the strong convergence between the fore- and hind limbs' natural pendular periods in newborn seems to be an important adaptation for their survivorship (in both cases, i.e. if this character was maintained from primitive form or derived). Furthermore, fore- and hind limbs undergo a parallel development that appears to be highly synchronised (see Chapter 1). The degree of evolvability of the limbs (i.e. "the ability of random

variations to sometimes produce improvement” according to Wagner and Altenberg 1996) in baboons seems, therefore, to be very low. On the contrary, it has been shown that there is a reduced integration between the limbs in humans and apes in comparison to quadrupedal monkeys (Young et al. 2010b). This reduced integration, by enhancing the evolvability of the limbs, might have been a strong determinant of the multiple locomotor adaptations observed in hominoids compared to cercopithecoids (see Hunt 2016; Schmitt 2010 for reviews). In this respect, the proposed equal basic control of walking in quadrupedal and bipedal locomotion, coupled with a reduced integration of the limbs may have facilitated the evolution toward habitual bipedalism. Indeed, Young and colleagues (2010b) proposed that the effect of a selection for limb functional dissociation may have resulted in evolutionary “experimentations”. Although evolutionary “experimentations” do not seem probable in the context of the evolutionary processes, the secondary locomotor modes experienced during primate infancy (see Chapter 5) may have provided a “fertile soil” to develop evolutionary novelties related to locomotion. If so, developmental by-products under proper selective pressures might have led protohominins towards a more habitual practice of bipedal behaviours.

Regarding the evolutionary pathway of the morphological pattern, a reduced integration of the limbs may have allowed a lengthening of the hind limbs relative to the forelimbs. Then, biomechanical reasons (constraints) might have provoked an elongation of the trunk in hominins. Indeed, such an elongation should have offered the mass moment of inertia required to stabilize the upper body against the movements of longer and heavier limbs (Preuschoft 2004; Witte et al. 1991). From this point of view it is interesting to note that the upper body, in terms of its shape, seems to be an important determinant for both bipedal walking onset (Adolph et al. 1997) and the bipedal kinematics in humans (Van Dam et al. 2010; Van Dam et al. 2011). Furthermore, a substantial morphological modification resulting from bipedal training in a non-human primate species appears at the level of the trunk. A lordosis emerges in the lumbar spine, in response to the mechanical constraints imposed by the gravitational moment in this posture. Hence, the torque generated by gravity on the upper body, as well as the bending moment along the trunk, are limited. Consequently, the muscular torques required to keep an upright posture are potentially reduced (Preuschoft et al. 1988).

Based on the process of “bipedalization” previously described by Rose (1991), our view is that bipedal behaviours may have gradually replaced quadrupedal behaviours, while the frequency of climbing, leaping and suspensory activities remained unchanged in the first hominins. Firstly, the evolutionary history of hominins suggests a (terrestrial) quadrupedal phase prior to the adoption of habitual bipedalism (Gebo 1996; see also White et al. 2015). Secondly, climbing, leaping and suspensory activities enable the exploitation of the arboreal environment that certainly remained an important ecological niche for the first hominins (potentially for feeding strategies and predator avoidance) (e.g. Crompton 2016; Hunt 2016; Senut 2016). Further studies are required to assess the neurological coupling between quadrupedalism and bipedalism, and potentially with the other “arboreal” modes. Nevertheless, if the modular strategies relying on neural primitives are shared between bipedal and quadrupedal tasks, it would have greatly reduced the “cost” of the transition between the two locomotor modes.

While the study of human morphology easily interprets human body shape as an adaptive system to bipedal performances for endurance walking and running (Bramble and Lieberman 2004; Multon et al. 2012; Witte et al. 1991), the impressive locomotor capacities that are developed by our athletes and the new evidence of arboreal competences in humans show a broad picture of what humans and their locomotor performances are (e.g. Kraft et al. 2014). Indeed, most of us live in modern cities, i.e. with a high level of technology for commuting. As such, samples of individuals living in these modern societies represent a derived stage that is certainly not the best model for understanding our locomotor performance and evolution (e.g. Orendurff et al. 2008). However, in less technological societies, the plasticity of our developmental morphology may lead us to impressive and diverse locomotor abilities related to tree climbing that would probably be valuable for survivorship (Kraft et al. 2014; Venkataraman et al. 2013). Note that human infants playing in natural environments practice various locomotor modes and further develop their locomotor performance (e.g. Fjortoft 2004; Pellegrini et al. 2007). Such observations remind us that human species belong to the primate order which is characterised by impressive posturo-locomotor capacities including climbing and suspensory behaviours. Therefore, in a broader context, the acceptance of multiple locomotor capabilities in human would help us reconsider our own

evolution. Moreover, the impressive diversity of locomotor patterns observed in the few hominoid species compared to (quadrupedal) monkeys means that the context of the emergence of hominoids and its diversification is crucial to understand the evolution of protohominins (Young et al. 2010b). Based on these considerations, it can be argued that the evolutionary shift that occurred between 30 and 20 million years ago in primates (Raaum et al. 2005; Stevens et al. 2013; Zalmout et al. 2010) leading to the emergence of the Cercopithecoids' lineage and of the Hominoids' lineage, is probably a very important milestone for the evolutionary transition toward brachiation, suspensory behaviours, quadrupedal knuckle-walking, and bipedalism. As a consequence, the study of primate locomotion is still highly valuable to gain insight into the locomotor evolution of man.

From primates to robots: Rethinking the shape

With regards to human technological advances coming from biomimicry (e.g. Ijspeert 2014), studying locomotor performances of primates seems particularly relevant as input for more applicable research domains such as bipedal locomotion modeling and simulation (e.g. D'Août et al. 2014; Nicolas et al. 2007; Ogihara and Yamazaki 2001; Sellers et al. 2005; Sellers et al. 2003; Wang et al. 2003) and (humanoid) robot designing (e.g. Chestnutt et al. 2005; Collins et al. 2001; Spenko et al. 2008). Indeed, a better understanding of these mechanisms may highly simplify the motor control of autonomous machines while moving in complex and diverse environments (Hooper 2012). Thus, robots, like animals, should exploit the intrinsic dynamics of the mechanical system (i.e. gravity, inertia, visco-elastic properties) rather than working against these (e.g. Alexander 1991; Cavagna et al. 1977; Seok et al. 2013). In this context, while legged locomotion represents certainly the best adaptation for moving on all kinds of substrates in animals, it is interesting to point that all the rovers sent to the planet Mars, such as Opportunity, Spirit and Curiosity have wheels but not limbs. This demonstrates the difficulty to provide strength, stability, maneuverability, movement flexibility and energy recovery in legged robots (e.g. Collins et al. 2001; Hutter et al. 2013; McGeer 1990; Owaki et al. 2012; Seok et al. 2015). Yet, this observation is also very stimulating for future research. It demonstrates that movement exploration is a fascinating area of research which is still at an early stage. The potentiality of applications from these

studies therefore remains highly relevant (D'Août et al. 2014; Ijspeert 2014). As an example, it is commonly hypothesized that maneuverability would be advantageous in unpredictable environments, and that gaining maneuverability is done at the expense of (static) stability in animals, thus suggesting a tradeoff effect (Biewener 2003; Huang and Ahmed 2011). Indeed, stability is defined as the capacity to recover from perturbations during movement (Bruijn et al. 2013), and maneuverability is defined as the capacity to change movement direction and speed (Biewener 2003). However, in the dynamic system which characterises primate locomotion, i.e. numerous movements in an arboreal environment with a discontinuity and variability of substrates, stability and maneuverability should both be maximized rather than representing a trade-off (see Sefati et al. 2013). As it is shown in the present thesis and in other numerous papers (e.g. Adolph and Avolio 2000; Myers and Steudel 1985; Preuschoft et al. 1998; Preuschoft and Witte 1991; Preuschoft et al. 1996; Raichlen 2005a; Raichlen et al. 2009; Shapiro and Raichlen 2006; Van Dam et al. 2010; Witte et al. 1991; Young et al. 2007), the structural properties and morphology definitely contribute to these mechanical requirements. Nevertheless, regarding, for example, all the debates surrounding the peculiarities of quadrupedal walking in primates (i.e. the large angular excursion, the weight-bearing support biased towards the hind limbs, the compliant walking, the relatively long and low frequency strides, the diagonal sequences) and their biomechanical reasons (for reviews see Larson 1998; Schmitt 2010), it is clear that we still have a lot to learn about primates, in terms of what governs their locomotor pattern and, in this context, how they manage stability and maneuverability. The study of the locomotion of primates may, therefore, be valuable for functionally designing our machines, including robots (e.g. Owaki et al. 2012).

Future directions

Dealing with the dynamic interactions between morphology, performance and behaviour in primates may lead to various projects in the field, or in the laboratory (see for example Morbeck et al. 1979). What follows (as examples) are two lines of thought for such future projects:

First, as a result of this research work and given very relevant recent reviews (Crompton et al. 2008; Crompton et al. 2010; Hunt 2016), the evolutionary shift at the origin of Cercopithecoids and Hominoids

seems to be a fundamental milestone for understanding the evolutionary past of living humans. Because one of the fundamental aspects of primate locomotion is their capability to exploit arboreal and terrestrial environments, a gradual increase in body size in stem hominoids, for example in *Proconsul* (see Rafferty et al. 1995; Rose 1993; Ward 1993), might have provoked important changes in the mechanical constraints related to movements in the trees, i.e. stability and maneuverability. As a consequence, this might have opened the way toward new locomotor strategies via, for example, a selection for a reduced integration of the limbs (Young et al. 2010b). Because the physical properties of the environment and their interplay with the body size probably influences the locomotor strategies to maintain stability and maneuverability (Cant 1992), I will address these relationships in the context of the largest extant (quadrupedal) Cercopithecoid, the (male) *Mandrillus sphinx*. My aim is to use this comparative model further to address how an increasing body size may influence primate locomotor evolution in (dense) forest habitats, and thus the emergence of stem hominoids. In this respect, innovative fieldwork studies, yet with their own limitations, provide the ideal framework for such a project (Schmitt 2011).

Second, I am also very intrigued by grasping capacities in infants and juveniles and what may enhance these capacities. Inspired by a recent paper dealing with the ontogeny of the intrinsic hand and foot proportions in capuchin monkey (Young and Heard-Booth 2016), I concluded that cross correlating behavioural and osteological data would be very interesting to test these functional relationships. Indeed, it has been hypothesised that grasping capacities depend upon various physical properties, yet, cross data are missing to validate these hypotheses. Furthermore, as previously observed (see Chapter 3 and Chapter 5) some behavioural variables (such as bout duration) may be used as proxy for testing locomotor capacities. In the context of the present thesis, the primatology station of the CNRS gave me the opportunity to regularly collect radiographs on the longitudinal sample of the six infant baboons. Therefore, the exploitation of this material facilitates correlation analyses to identify grasping capacities at the level of the osteo-behavioural interface.

Overall conclusion

From an ontogenetic perspective, our data showed that quadrupedal walking is the principal locomotor mode used from early life to adulthood in baboons. Nevertheless, its proportion of use significantly increases during infancy at the expense of grasping behaviours. We demonstrated that this pattern is highly correlated to changes in the morphotype of baboons. While limb mass is initially more distally distributed, reflecting important grasping capacities for clinging to the mother's fur, the proximal shift of the mass into the limbs at the later stage appears to be adaptive for reducing energy consumption during quadrupedal locomotion. During this transitional period, young baboons are also improving their interlimb coordination during quadrupedal walking. We found that there is an early optimization of the limbs at the level of the intrinsic morpho-dynamics which has a significant and positive impact on this interlimb coordination pattern, thus probably facilitating, very early in development, the control of the coordination as well as the initiation of quadrupedal walking. Interestingly, baboons voluntarily use bipedal walking and this ability goes hand-in-hand with the development of interlimb coordination in quadrupedal walking. Hence, improvement of quadrupedal locomotor capacity does not exclude development of bipedal behaviour. Furthermore, it seems highly likely that the neural networks for quadrupedal locomotion are also employed for occasional bipedal walking in baboons. Finally, based on mechanical principles, the morphotype of juvenile and adult baboons also appears to be less constraining than the morphotype of infants for performing bipedally.

From an evolutionary perspective, the functional development of the baboon's morphology reflects adaptations related to its socio-ecological context. Our results also highlight mechanisms that may be shared by all primates, therefore aiding the reconstruction of the origin of locomotor modes in general, and bipedalism in particular. Indeed, the process of the secondary locomotor modes resulting from developmental by-products questions the emergence of new locomotor modes in primates. This further supports the importance of considering the development in the context of the evolutionary processes and supports the idea of a continuum between different locomotor modes at the level of the neural control. In this respect, a repertoire where bipedal balance gradually became more important during evolution could have originated

from a repertoire where quadrupedal balance was initially the most important. Finally, the results about the constraints related to the morphological pattern are very relevant in the context of the morphological variations on which natural selection may act. In this respect, an increase of the inertia of the trunk may have facilitated the duration of bipedal behavioural bouts in protohominins.

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List of Publications

Research Articles:

Druelle F, Aerts P, and Berillon G. In revision. 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*

Druelle F, Aerts P, D'Août K, Moulin V, and Berillon G. In press. Segmental morphometrics of the olive baboon (*Papio anubis*): a longitudinal study from birth to adulthood. *Journal of Anatomy*

Druelle F, Berillon G, and Aerts P. Early view. Intrinsic limb morphodynamics and the early development of interlimb coordination of walking in a quadrupedal primate. *Journal of Zoology* doi:10.1111/jzo12423

Druelle F, Aerts P, and Berillon G. 2016. 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(11):1201-1221

Druelle F, Aerts P, and Berillon G. 2016. 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(1):73-84.

Druelle F, and Berillon G. 2014. Bipedalism in non-human primates. A cross review of behavioral and experimental explorations on catarrhines. *Bulletins et Mémoires de la Société d'Anthropologie de Paris* 26(3-4):111-120.

Druelle F, and Berillon G. 2013. Bipedal Behaviour in Olive Baboons: Infants versus Adults in a Captive Environment. *Folia Primatologica* 84(6):347-361.

Popular Science Articles:

- Berillon G, Cazeau C, and Druelle F.** 2016. Bipédie chez les primates. *Revue du Podologue* 12(68): 13-15.
- Druelle F, and Berillon G.** 2015. Tous Bipèdes! *Pour la Science*, Dossier n°86: 32-36.

Abstracts (conference proceedings):

- Druelle F, Aerts P, and Berillon G.** 2017. De la distribution des masses au répertoire positionnel: Modèle primate et perspectives paléanthropologiques. *1842^{èmes} journées de la Société d'Anthropologie de Paris (Paris, France)*. **Oral presentation**
- Druelle F, Berillon G, and Aerts P.** 2016. The interplay between morphology and locomotion during the development of olive baboons (*Papio anubis*): Implications for the evolution of primate locomotion. *Zoology meeting (Antwerpen, Belgium)*. **Oral presentation**
- Druelle F, Aerts P, and Berillon G.** 2016. Développement posturo-locomoteur du babouin olive. Approche intégrative longitudinale et implications évolutives chez les primates. *29^{ème} colloque de la Société Francophone De Primatologie (Paimpont, France)*. **Oral presentation (awarded)**
- Druelle F, Berillon G, and Aerts P.** 2016. Primate infancy and the mechanics of quadrupedal development. *Society for Experimental Biology meeting (Brighton, England)*. **Oral presentation**
- Druelle F, Aerts P, and Berillon G.** 2016. What can we learn from the study of the locomotor development of non-human catarrhines about the evolutionary pathway toward habitual bipedalism? *Young Natural History Scientists meeting (Paris, France)*. **Poster**
- Druelle F, Berillon G, and Aerts P.** 2015. Give me your shape and I will tell you how you move: A case study of the ontogeny of the olive

baboon. *Meeting of the International Interdisciplinary Thematic Network (RTP-I), CNRS (Rousset, France)*. **Poster**

Druelle F, Aerts P, and Berillon G. 2015. Does Mass Distribution Reflect the Manner in which Primates Move? An Integrative Study Using the Baboon as a Model. *6th congress of the European Federation for Primatology (Roma, Italy)*. *Folia Primatologica* 86(4): 273-274. **Oral presentation**

Druelle F, Aerts P, and Berillon G. 2014. From the zoo to the field: Development of a new method using photogrammetry. *7th annual CRC Zoo Research Symposium (Antwerpen, Belgium)*. **Oral presentation**

Druelle F, Aerts P, and Berillon G. 2014. Que peut-on apprendre du développement locomoteur des catarrhiniens? Approche intégrative de la bipédie chez le babouin olive élevé en captivité. *27^{ème} colloque de la Société Francophone De Primatologie (Poitiers, France)*. **Oral presentation**

Druelle F, and Berillon G. 2013. La bipédie chez les primates non-humains: Approche comportementale et morphologique au cours du développement du babouin olive, *Papio anubis*. *43^{ème} colloque de la Société Française pour l'Etude du Comportement Animal (Dijon, France)*. **Oral presentation**

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Druelle F, and Berillon G. 2013. La bipédie dans le répertoire locomoteur du babouin olive (*Papio anubis*) captif, de la naissance à l'adulte. Etude transversale et impact possible de la morphologie. *1838^{èmes} journées de la Société d'Anthropologie de Paris (Paris, France)*. **Poster**

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Appendices

Model of Crompton and colleagues (1996)

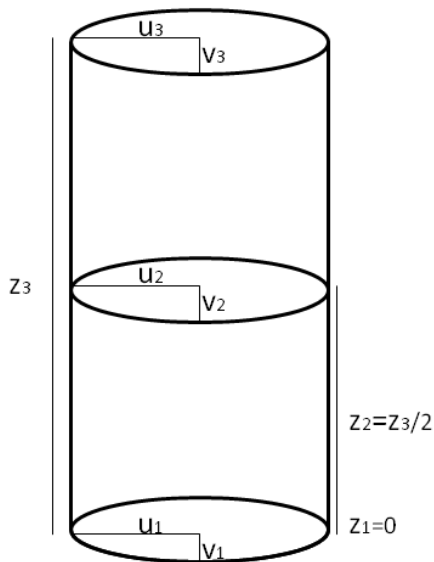


Fig. I Model for a column with an elliptical basis. “z” represents lengths, “u” and “v” represent radii in two different planes (mediolateral and anteroposterior).

Figure I shows the column-shaped model which is applied on each body segment. The three cross sections are an ellipse where z is the height of the given cross section. Thus the respective axes are:

$$u = \begin{cases} u_1 = \sqrt{a \times z_1^2 + b \times z_1 + c} \\ u_2 = \sqrt{a \times z_2^2 + b \times z_2 + c} \\ u_3 = \sqrt{a \times z_3^2 + b \times z_3 + c} \end{cases} \quad \text{and} \quad v = k \times u$$

↓

$$u_1^2 = a \times z_1^2 + b \times z_1 + c$$

$$u_2^2 = a \times z_2^2 + b \times z_2 + c$$

$$u_3^2 = a \times z_3^2 + b \times z_3 + c$$

From these equations, we calculate the determinant $A (\neq 0)$ as follows:

$$\det A = \begin{pmatrix} z_1^2 & z_1 & 1 \\ z_2^2 & z_2 & 1 \\ z_3^2 & z_3 & 1 \end{pmatrix}$$

$$\det A = 1 \times (z_1^2 \times z_2 - z_2^2 \times z_1) - 1 \times (z_1^2 \times z_3 - z_3^2 \times z_1) + 1 \times (z_2^2 \times z_3 - z_3^2 \times z_2)$$

We can calculate the three components a , b and c , extracted from the first equations, as follows:

$$A \begin{pmatrix} a \\ b \\ c \end{pmatrix} = \begin{pmatrix} u_1^2 \\ u_2^2 \\ u_3^2 \end{pmatrix} \Leftrightarrow \begin{pmatrix} a \\ b \\ c \end{pmatrix} = A^{-1} \times \begin{pmatrix} u_1^2 \\ u_2^2 \\ u_3^2 \end{pmatrix}$$

$$a = \frac{\det \begin{pmatrix} u_1^2 & z_1 & 1 \\ u_2^2 & z_2 & 1 \\ u_3^2 & z_3 & 1 \end{pmatrix}}{\det A}$$

$$a = \frac{[(u_1^2 \times z_2 - u_2^2 \times z_1) - (u_1^2 \times z_3 - u_3^2 \times z_1) + (u_2^2 \times z_3 - u_3^2 \times z_2)]}{\det A}$$

$$b = \frac{\det \begin{pmatrix} z_1^2 & u_1^2 & 1 \\ z_2^2 & u_2^2 & 1 \\ z_3^2 & u_3^2 & 1 \end{pmatrix}}{\det A}$$

$$b = \frac{[(z_1^2 \times u_2^2 - z_2^2 \times u_1^2) - (z_1^2 \times u_3^2 - z_3^2 \times u_1^2) + (z_2^2 \times u_3^2 - z_3^2 \times u_2^2)]}{\det A}$$

$$c = \frac{\det \begin{pmatrix} z_1^2 & z_1 & u_1^2 \\ z_2^2 & z_2 & u_2^2 \\ z_3^2 & z_3 & u_3^2 \end{pmatrix}}{\det A}$$

$$c = \frac{[u_1^2(z_1^2 \times z_2 - z_2^2 \times z_1) - u_2^2(z_1^2 \times z_3 - z_3^2 \times z_1) + u_3^2(z_2^2 \times z_3 - z_3^2 \times z_2)]}{\det A}$$

Then, the segment mass is calculated as follows:

$$\text{Segment mass} = \frac{1}{6} \rho \pi L k (3bL + 6c + 2aL^2)$$

Where ρ is the density, L is the segment length and k is the mean of the ratios of the two radii: $\frac{v_1}{u_1}, \frac{v_2}{u_2}, \frac{v_3}{u_3}$

The segment centre of mass is calculated as follows:

$$\text{Segment center of mass} = \frac{1}{2} \times \frac{3aL^2 + 6c + 4bL}{2aL^2 + 6c + 3bL}$$

Chapter 1

Appendix 1.A *Subjects information*

Female (n=14)			Male (n=16)		
Subject	Min-Max Age (y:year, m:month)	No. recorded sessions	Subject	Min-Max Age (y:year, m:month)	No. recorded sessions
V913G	1y7m-6y3m	12	V908H	1y6m-6y1m	12
V935E	1y8m-6y3m	12	V894G	1y7m-6y3m	12
V936F	1y4m-6y0m	12	V902F	1y8m-6y3m	12
V915G	1y4m-6y0m	12	V937E	1y6m-6y1m	12
V936G	0y2m-6y1m	17	V916F	1y1m-6y3m	15
V902G	0y4m-6y0m	17	V896G	1y4m-5y11m	13
V908I	0y5m-6y1m	17	V935F	0y6m-4y8m	13
V894H	0y6m-6y1m	16	V916G	0y5m-6y1m	17
V792BB	0y3m-7y0m	19	V792BA	0y2m-6y4m	18
V916DA	0y5m-5y2m	17	V894I	0y2m-7y8m	20
V916I	0y2m-4y0m	14	V896BB	0y3m-7y10m	20
V993EB	0y3m-6y9m	18	V908EA	0y5m-7y2m	19
V936H	0y3m-6y10m	18	V908J	0y2m-7y11m	21
V908GA	0y3m-7y0m	19	V935G	0y4m-6y0m	17
			V916H	0y2m-5y11m	19
			V908K	0y3m-6y9m	17

Appendix 1.B.1 Individual growth pattern of the segment lengths represented by linear regression model ($Y=a*age+b$) in females

	Hand		Forearm		Upperarm		Thigh		Shank		Trunk		Head		Tail		Foot		
	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b	
V913G	4.67	88.48	13.77	122.97	16.57	106.18	11.12	121.82	12.26	120.75	31.01	258.58	6.94	122.91	21.67	302.74	8.66	125.61	
V935E	5.15	88.20	11.41	131.31	12.08	121.71	9.18	137.90	11.13	128.95	26.48	258.05	9.64	120.61	16.53	321.71	7.50	133.13	
V936F	5.61	89.12	15.74	113.73	14.67	106.97	13.25	117.52	12.87	120.18	28.48	252.86	10.04	116.76	16.53	307.21	9.42	128.50	
V915G	5.26	81.79	12.88	115.53	11.86	112.32	11.75	121.28	12.19	119.26	24.70	251.08	8.51	117.09	12.36	272.43	7.78	121.48	
V936G	7.56	79.25	19.36	104.29	17.51	95.09	16.12	103.71	16.67	104.08	39.33	205.38	11.27	109.12	25.12	258.29	12.76	111.84	
V902G	7.26	73.88	17.42	102.65	15.48	96.99	17.05	99.45	16.72	99.40	36.15	196.77	10.29	109.21	18.23	234.55	11.80	106.59	
V908I	7.25	86.03	16.87	115.59	14.95	116.39	14.96	119.56	15.69	120.80	35.29	245.41	10.10	123.09	27.14	325.59	11.05	125.48	
V894H	7.33	85.49	19.59	110.43	14.91	113.33	18.96	108.42	17.78	109.82	29.33	248.35	12.96	109.32	25.46	318.23	13.09	119.49	
V792BB	7.28	83.20	15.86	114.84	13.23	107.99	15.14	111.27	13.81	116.23	30.46	254.17	11.05	117.82	19.94	292.44	10.74	122.45	
V916DA	8.82	76.10	20.41	101.43	19.14	92.94	20.64	98.04	20.47	101.66	43.03	225.47	11.68	110.80	33.01	263.20	14.30	108.63	
V916I	12.19	76.58	25.29	102.55	22.79	93.33	22.58	101.22	22.24	103.50	43.50	222.96	14.93	112.21	43.30	287.04	19.30	112.96	
V993EB	8.78	76.18	17.31	109.63	16.72	94.52	15.41	102.79	15.33	107.74	34.65	240.99	11.63	114.79	25.28	290.90	12.20	115.98	
V936H	8.14	81.34	17.69	111.97	15.95	100.15	15.56	103.49	15.53	111.41	27.46	226.79	10.37	116.64	4.47	305.39	12.19	119.10	
V908GA	8.15	79.58	18.36	110.04	18.28	97.75	17.88	103.68	17.31	110.19	39.88	221.20	11.78	111.43	24.57	289.53	12.27	118.18	
Mean	7.39	81.80	17.28	111.92	16.01	103.98	15.69	110.73	15.71	112.43	33.55	236.29	10.80	115.13	22.40	290.66	11.65	119.24	
SD	1.93	5.10	3.46	8.27	2.89	9.45	3.67	11.42	3.18	8.79	6.19	19.93	1.91	4.93	9.27	26.14	3.00	7.61	
Shapiro-Wilk (Normal distribution test)																			
Obs Test Stat	0.91	0.94	0.96	0.92	0.95	0.92	0.99	0.88	0.96	0.96	0.94	0.90	0.96	0.92	0.96	0.95	0.91	0.99	
P-value	0.14	0.42	0.71	0.22	0.59	0.23	0.98	0.07	0.64	0.62	0.45	0.13	0.75	0.20	0.68	0.57	0.16	0.99	
Comparison with the global pattern																			
FULL DATASET																			
Obs Test Stat	7.35	81.19	17.11	111.14	16.02	102.67	15.82	108.61	15.62	111.39	33.58	233.79	10.75	114.72	20.92	291.90	11.46	118.61	
P-value	0.07	0.45	0.19	0.36	-0.01	0.52	0.89	0.69	0.11	0.44	-0.02	0.47	0.10	0.31	0.60	-0.18	0.24	0.31	
FULL DATASET																			
Obs Test Stat	0.94	0.66	0.85	0.73	0.99	0.61	-0.14	0.50	0.91	0.67	0.99	0.65	0.92	0.76	0.56	0.86	0.81	0.76	

Appendix 1.B.2 Individual growth pattern of the segment masses represented by linear regression model ($y=a*age+b$) in females

	Hand		Forearm		Upperarm		Thigh		Shank		Trunk		Head		Tail		Foot		
	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b	
V913G	0.01	0.03	0.04	0.05	0.08	0.01	0.12	0.09	0.04	0.03	0.98	0.48	0.14	0.33	0.03	0.04	0.03	0.04	
V935E	0.01	0.04	0.03	0.07	0.06	0.05	0.14	0.12	0.04	0.05	1.07	0.93	0.15	0.38	0.03	0.05	0.02	0.07	
V936F	0.01	0.03	0.04	0.03	0.07	-0.01	0.14	0.08	0.04	0.05	1.00	0.50	0.18	0.27	0.03	0.06	0.03	0.03	
V915G	0.01	0.03	0.03	0.05	0.06	0.03	0.14	0.05	0.04	0.04	0.90	0.33	0.14	0.27	0.02	0.06	0.02	0.04	
V936G	0.01	0.02	0.04	0.03	0.07	0.00	0.14	0.04	0.05	0.02	1.04	0.30	0.16	0.27	0.03	0.03	0.03	0.04	
V902G	0.01	0.02	0.04	0.02	0.06	0.02	0.13	0.02	0.05	0.01	0.85	0.13	0.15	0.27	0.02	0.03	0.03	0.03	
V908I	0.02	0.03	0.04	0.05	0.08	0.06	0.21	0.06	0.06	0.04	1.26	0.59	0.19	0.32	0.05	0.06	0.04	0.06	
V894H	0.02	0.02	0.05	0.04	0.08	0.03	0.21	-0.03	0.06	0.01	1.07	0.53	0.20	0.31	0.04	0.06	0.03	0.05	
V792BB	0.02	0.03	0.05	0.04	0.09	0.01	0.18	0.07	0.05	0.04	1.15	0.74	0.19	0.33	0.03	0.07	0.03	0.05	
V916DA	0.02	0.02	0.06	0.01	0.07	0.01	0.18	0.01	0.05	0.02	1.24	0.34	0.18	0.27	0.04	0.04	0.03	0.04	
V916I	0.02	0.02	0.06	0.02	0.10	0.00	0.25	-0.03	0.07	0.02	1.27	0.37	0.23	0.25	0.05	0.04	0.05	0.03	
V993EB	0.02	0.02	0.05	0.03	0.08	0.02	0.16	0.07	0.05	0.04	1.24	0.45	0.21	0.29	0.04	0.05	0.03	0.05	
V936H	0.02	0.03	0.04	0.04	0.08	0.01	0.16	0.04	0.05	0.04	0.94	0.57	0.17	0.30	0.03	0.06	0.03	0.05	
V908GA	0.02	0.02	0.05	0.03	0.10	-0.02	0.19	0.01	0.05	0.03	1.38	0.19	0.20	0.26	0.03	0.05	0.03	0.05	
Mean	0.02	0.03	0.04	0.04	0.08	0.02	0.17	0.04	0.05	0.03	1.10	0.46	0.18	0.29	0.03	0.05	0.03	0.05	
SD	0.00	0.01	0.01	0.02	0.01	0.02	0.04	0.04	0.01	0.01	0.16	0.21	0.03	0.04	0.01	0.01	0.01	0.01	
Shapiro-Wilk (Normal distribution test)																			
Obs Test Stat	0.94	0.95	0.93	0.98	0.94	0.96	0.94	0.97	0.95	0.95	0.96	0.97	0.95	0.92	0.97	0.97	0.76	0.95	
P-value	0.39	0.58	0.32	0.91	0.46	0.68	0.45	0.78	0.50	0.54	0.71	0.84	0.50	0.20	0.84	0.86	0.00	0.46	
Comparison with the global pattern																			
FULL																			
DATASET	0.02	0.03	0.04	0.04	0.08	0.01	0.17	0.05	0.05	0.03	1.10	0.46	0.18	0.29	0.03	0.05	0.03	0.05	
Obs Test Stat	0.26	-0.05	0.18	0.16	0.06	0.06	0.31	-0.24	0.20	0.07	0.01	0.10	0.11	0.01	0.45	-0.75	N/A	-1.08	
P-value	0.80	0.96	0.86	0.87	0.95	0.95	0.77	0.82	0.85	0.94	0.99	0.92	0.91	0.99	0.66	0.47	N/A	0.30	

Appendix 1.B.3 Individual growth pattern of the segment inertia (X axis) by linear regression model ($Y=a*age+b$) in females

	Hand		Forearm		Upperarm		Thigh		Shank		Trunk		Head		Tail		Foot		
	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b	
V913G	68.54	7.33	530.31	-361.87	995.19	-1234.26	1139.86	-687.89	551.89	-430.71	79415.18	-74746.62	1371.00	278.65	1157.12	-410.96	203.54	-63.95	
V935E	60.72	31.72	445.46	-38.76	821.01	-702.68	1557.63	-737.61	569.91	-201.83	78633.40	-54881.08	1675.09	226.88	972.77	261.02	186.96	77.74	
V936F	69.66	2.59	525.56	-490.73	781.66	-885.36	1654.90	-1387.88	575.18	-298.72	71144.64	-56757.96	1952.13	-696.86	784.02	437.57	255.56	-138.05	
V915G	45.89	22.18	383.27	-163.27	586.11	-347.58	1407.39	-1040.63	544.91	-310.32	56735.08	-47172.26	1393.10	-86.57	373.09	529.64	159.93	-5.49	
V936G	60.67	10.07	435.49	-160.27	767.74	-551.63	1346.82	-686.76	545.76	-232.34	64816.56	-37803.35	1534.71	88.31	794.80	-10.16	247.98	-40.25	
V902G	53.44	-5.06	425.13	-250.49	547.35	-390.73	1325.58	-1075.63	551.06	-419.75	47443.51	-37895.74	1386.03	115.79	390.73	142.37	163.38	-6.40	
V908I	86.18	12.81	542.27	-131.17	909.97	-299.86	2232.80	-1246.81	819.21	-254.28	93963.02	-58083.69	2035.04	239.60	1871.12	142.99	296.74	2.54	
V894H	89.02	-1.51	683.43	-415.68	869.45	-504.06	2522.84	-2466.20	758.06	-531.33	68430.55	-30544.78	2185.03	-275.66	1409.68	306.89	239.31	6.21	
V792BB	68.91	28.87	627.41	-276.79	862.64	-530.54	1941.80	-1215.59	689.57	-277.91	78913.86	-26302.40	2069.92	138.55	832.74	809.05	222.24	84.37	
V916DA	77.21	-8.95	610.32	-426.78	809.56	-634.84	1831.19	-1425.66	666.51	-365.67	82811.31	-49220.09	1691.03	84.84	1181.65	-151.87	206.38	-3.50	
V916I	107.12	-16.05	691.50	-296.34	991.96	-608.12	2332.24	-1481.37	766.64	-332.56	66616.89	-19025.73	2138.46	11.37	1698.54	-80.95	391.43	-75.85	
V993EB	95.85	-18.82	647.65	-381.34	835.02	-554.69	1595.49	-882.45	604.62	-189.85	89397.13	-53444.12	2215.18	-130.23	1295.43	26.57	246.28	58.75	
V936H	76.81	15.35	530.23	-93.51	838.00	-609.26	1680.62	-1060.19	667.92	-288.83	52985.62	-23432.73	1789.83	210.04	452.95	873.82	246.47	37.20	
V908GA	84.69	-7.17	696.87	-404.80	1104.04	-916.16	2104.19	-1533.25	763.32	-394.41	104708.38	-81838.68	2168.89	-428.72	1034.01	314.97	216.99	42.77	
Mean	74.62	5.24	555.35	-277.99	837.12	-626.41	1762.38	-1209.14	648.18	-323.47	73929.65	-46510.66	1828.96	-16.00	1017.76	227.93	235.23	-1.71	
SD	16.91	15.88	106.35	141.72	147.57	248.35	415.39	462.58	97.77	96.35	16100.21	18629.02	319.82	283.47	458.87	357.81	58.86	62.29	
Shapiro-Wilk (Normal distribution test)																			
Obs Test Stat	0.99	0.97	0.93	0.95	0.94	0.91	0.96	0.87	0.88	0.96	0.99	0.96	0.89	0.87	0.97	0.98	0.89	0.95	
P-value	0.99	0.83	0.30	0.54	0.43	0.16	0.75	0.04	0.06	0.75	0.98	0.72	0.08	0.05	0.71	0.92	0.09	0.59	
Comparison with the global pattern																			
FULL DATASET	73.45	6.74	551.64	-266.72	829.34	-588.09	1734.90	-1155.79	641.62	-301.36	74465.39	-45258.43	1830.37	5.08	957.71	365.70	222.34	29.11	
Obs Test Stat	0.26	-0.35	0.13	-0.30	0.20	-0.58	0.25	N/A	0.25	-0.86	-0.12	-0.25	-0.02	N/A	0.49	-1.44	0.82	-1.85	
P-value	0.80	0.73	0.90	0.77	0.85	0.57	0.81	N/A	0.81	0.41	0.90	0.81	0.99	N/A	0.63	0.17	0.43	0.09	

Appendix 1.B.4 Individual growth pattern of the segment inertia (y axis) by linear regression model ($y=a*age+b$) in females

	Hand		Forearm		Upperarm		Thigh		Shank		Trunk		Head		Tail		Foot		
	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b	
V913G	65.40	8.86	528.76	-358.81	1008.07	-1246.02	1183.30	-1246.02	-726.49	554.53	-431.78	79303.43	-74605.10	1381.27	277.68	1157.12	-410.96	198.85	-62.35
V935E	58.40	31.04	444.27	-37.06	831.29	-705.72	1610.61	-705.72	-777.57	574.17	-205.61	78134.82	-54144.33	1697.71	229.71	972.77	261.02	183.33	72.76
V936F	66.55	4.53	525.18	-490.33	792.60	-899.39	1686.01	-899.39	-1395.65	578.15	-300.37	70583.90	-56039.35	1968.83	-702.26	784.02	437.57	260.32	-136.52
V915G	43.85	22.44	381.96	-162.05	593.87	-353.44	1447.40	-353.44	-1081.54	548.07	-313.86	56318.29	-46452.82	1399.86	-81.06	373.09	529.64	155.40	-4.65
V936G	58.51	9.89	435.02	-160.05	781.43	-565.67	1384.96	-565.67	-710.29	549.10	-234.91	64421.83	-37442.93	1553.45	75.77	794.80	-10.16	243.57	-40.82
V902G	51.55	-5.24	424.79	-250.69	554.92	-397.01	1358.77	-397.01	-1100.96	553.93	-423.00	47349.93	-37780.98	1387.65	130.95	390.73	142.37	159.47	-5.95
V908I	82.45	12.51	541.83	-131.65	924.67	-306.94	2337.45	-306.94	-1333.92	825.74	-259.12	93228.59	-57305.01	2054.76	231.78	1871.12	142.99	290.29	-0.14
V894H	85.86	-0.92	682.04	-414.90	882.81	-513.77	2616.13	-513.77	-2568.50	763.02	-536.67	68155.85	-30162.38	2207.84	-303.61	1409.68	306.89	232.97	7.16
V792BB	66.21	28.08	627.09	-277.29	882.25	-548.82	2007.17	-548.82	-1256.59	695.21	-283.46	78612.86	-26231.00	2099.04	116.13	832.74	809.05	216.71	82.87
V916DA	74.07	-8.64	608.97	-425.84	820.18	-643.98	1885.58	-643.98	-1466.60	670.46	-368.62	82470.19	-48951.44	1714.86	67.48	1181.65	-151.87	200.15	-3.07
V916I	103.52	-15.98	690.62	-296.28	1007.42	-619.41	2398.07	-619.41	-1520.15	770.54	-334.72	65168.91	-18634.35	2169.37	-9.04	1698.54	-80.95	381.30	-73.12
V993EB	91.34	-17.55	647.23	-382.41	849.23	-567.38	1656.01	-567.38	-924.96	609.31	-194.88	88914.61	-52981.84	2246.14	-166.98	1295.43	26.57	240.31	57.42
V936H	74.49	14.06	529.21	-93.48	853.05	-625.16	1734.75	-625.16	-1100.87	672.39	-291.77	52644.92	-23155.14	1806.80	186.07	452.95	873.82	241.21	35.95
V908GA	81.42	-6.84	695.56	-404.13	1122.80	-935.05	2175.69	-935.05	-1589.57	767.45	-397.95	103944.91	-81234.68	2188.27	-438.51	1034.01	314.97	211.62	41.75
Mean	71.69	5.45	554.47	-277.50	850.33	-637.70	1820.14	-637.70	-1253.83	652.29	-326.91	73518.07	-46080.10	1848.28	-27.56	1017.76	227.93	229.68	-2.05
SD	16.29	15.45	106.29	141.69	150.33	250.17	433.57	250.17	477.88	98.59	96.19	15976.76	18533.58	326.62	285.64	458.87	357.81	57.49	60.82
Shapiro-Wilk (Normal distribution test)																			
Obs Test Stat	0.99	0.96	0.93	0.95	0.94	0.91	0.96	0.96	0.86	0.88	0.96	0.98	0.96	0.89	0.88	0.96	0.98	0.90	0.95
P-value	0.99	0.74	0.30	0.55	0.43	0.16	0.68	0.68	0.03	0.06	0.69	0.98	0.71	0.09	0.06	0.71	0.92	0.10	0.58
Comparison with the global pattern																			
FULL DATASET	70.58	6.71	550.84	-266.53	843.05	-600.66	1793.15	-600.66	-1200.92	645.83	-305.03	74056.72	-44859.45	1849.83	-8.40	957.71	365.70	217.17	27.98
Obs Test Stat	0.25	-0.31	0.13	-0.29	0.18	-0.55	0.23	-0.55	N/A	0.25	-0.85	-0.13	-0.25	-0.02	-0.25	0.49	-1.44	0.81	-1.85
P-value	0.80	0.76	0.90	0.78	0.86	0.59	0.82	0.59	N/A	0.81	0.41	0.90	0.81	0.99	0.81	0.63	0.17	0.43	0.09

Appendix 1.C.1 Individual growth pattern of the segment lengths represented by linear regression model ($y=a*age+b$) in males

	Hand		Forearm		Upperarm		Thigh		Shank		Trunk		Head		Tail		Foot		
	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b	
V908H	8.21	83.04	20.27	103.36	19.65	98.92	17.84	104.90	19.45	104.29	39.54	246.81	16.69	103.83	35.09	275.82	15.35	110.98	
V894G	10.40	83.51	20.98	114.11	19.21	104.84	20.51	107.76	21.86	103.48	45.44	207.18	18.05	109.59	40.16	284.48	16.32	118.01	
V902F	7.30	84.14	18.08	113.27	19.75	104.39	17.21	112.37	17.97	108.54	41.83	213.05	17.41	101.60	23.26	194.01	14.02	113.95	
V937E	8.02	87.58	21.64	106.35	19.19	102.76	16.74	117.49	18.39	110.56	40.66	239.61	16.34	108.03	34.63	270.03	15.02	118.45	
V916F	8.31	87.34	18.03	111.01	16.47	111.39	16.12	120.21	17.96	110.47	37.81	253.06	16.79	106.74	31.20	289.01	13.52	120.37	
V896G	10.32	86.35	20.77	112.21	21.37	98.03	22.17	100.79	22.17	105.93	45.00	229.35	18.70	105.34	39.06	297.57	15.36	124.71	
V935F	10.02	78.33	24.27	101.13	20.76	107.54	20.47	102.90	20.76	105.54	39.36	240.17	14.13	113.30	36.85	270.88	15.87	114.47	
V916G	11.72	79.38	21.48	109.88	22.43	97.62	21.42	103.24	23.03	102.43	45.69	223.44	18.68	110.24	40.35	300.94	16.57	117.35	
V792BA	10.89	80.31	21.37	111.06	22.28	91.76	20.31	104.64	21.66	106.88	48.38	216.74	16.77	111.20	24.57	285.87	16.76	114.39	
V894I	9.87	79.08	20.79	101.96	20.27	95.52	19.81	97.24	19.10	101.96	40.58	235.15	16.97	114.18	35.50	269.49	15.67	116.53	
V896BB	9.06	76.29	20.66	102.57	19.04	92.61	18.43	100.20	19.25	101.49	37.32	217.18	15.91	107.23	32.08	262.68	14.59	108.16	
V908EA	11.05	77.39	21.93	108.19	21.43	93.73	19.44	103.00	20.96	105.68	43.50	232.52	16.21	106.78	35.46	275.79	15.89	114.58	
V908J	10.38	85.32	19.77	113.99	20.84	99.59	20.24	103.90	21.12	110.54	37.43	233.79	16.45	115.18	36.14	293.44	15.42	122.76	
V935G	10.56	77.71	22.61	97.30	22.96	86.00	19.46	95.44	21.58	99.04	44.05	228.48	18.75	108.24	37.04	272.37	16.97	111.05	
V916H	12.39	80.26	24.03	101.48	22.63	96.31	22.46	98.88	23.43	100.18	48.90	226.28	18.67	110.47	43.07	279.07	17.79	113.32	
V908K	12.64	77.65	23.53	97.56	24.53	87.92	24.71	90.80	24.19	95.90	51.83	214.39	18.72	102.71	39.03	263.90	17.59	110.65	
Mean	10.07	81.48	21.26	106.59	20.80	98.06	19.83	103.98	20.81	104.56	42.96	228.58	17.20	108.42	35.22	274.08	15.79	115.61	
SD	1.56	3.82	1.81	5.84	1.95	6.95	2.26	7.65	1.95	4.31	4.39	12.85	1.32	3.97	5.36	24.28	1.19	4.54	
Shapiro-Wilk (Normal distribution test)																			
Obs Test Stat	0.96	0.92	0.95	0.92	0.98	0.99	0.98	0.94	0.95	0.96	0.95	0.98	0.90	0.98	0.90	0.98	0.90	0.98	
P-value	0.68	0.15	0.52	0.15	0.91	0.99	0.89	0.40	0.55	0.70	0.47	0.95	0.08	0.93	0.09	0.00	0.96	0.83	
Comparison with the global pattern																			
FULL DATASET	10.25	80.68	21.24	106.16	20.92	96.94	20.15	102.29	20.86	104.18	42.38	229.80	16.98	109.49	34.13	278.38	15.79	115.45	
Obs Test Stat	-0.46	0.84	0.05	0.29	-0.25	0.64	-0.56	0.89	-0.11	0.35	0.53	-0.38	0.68	-1.08	0.81	-0.71	0.01	0.14	
P-value	0.65	0.42	0.96	0.77	0.81	0.53	0.58	0.39	0.91	0.73	0.61	0.71	0.51	0.30	0.43	0.49	0.99	0.89	

Appendix 1.C.2 Individual growth pattern of the segment masses represented by linear regression model ($y=a*age+b$) in males

	Hand		Forearm		Upperarm		Thigh		Shank		Trunk		Head		Tail		Foot		
	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b	
V908H	0.04	-0.01	0.08	-0.03	0.14	-0.12	0.26	-0.19	0.08	-0.04	2.00	-1.63	0.33	-0.11	0.08	-0.04	0.06	0.00	
V894G	0.04	0.00	0.10	-0.06	0.14	-0.12	0.33	-0.28	0.09	-0.05	2.26	-2.49	0.45	-0.26	0.08	-0.04	0.07	-0.02	
V902F	0.03	0.01	0.08	-0.08	0.13	-0.11	0.28	-0.27	0.08	-0.06	2.11	-2.39	0.35	-0.16	0.05	-0.02	0.06	-0.01	
V937E	0.03	0.01	0.09	-0.05	0.17	-0.18	0.32	-0.31	0.08	-0.04	2.10	-1.74	0.40	-0.18	0.07	-0.03	0.06	0.01	
V916F	0.03	0.02	0.07	0.00	0.11	-0.03	0.33	-0.27	0.08	-0.02	1.87	-1.03	0.38	0.00	0.06	0.00	0.05	0.03	
V896G	0.03	0.02	0.08	-0.03	0.16	-0.13	0.36	-0.32	0.10	-0.05	2.26	-1.98	0.37	-0.06	0.07	-0.01	0.06	0.02	
V935F	0.03	0.02	0.06	0.01	0.10	0.01	0.21	-0.04	0.06	0.02	1.43	0.19	0.25	0.24	0.05	0.02	0.04	0.02	
V916G	0.04	0.01	0.08	-0.01	0.17	-0.10	0.34	-0.19	0.10	-0.03	2.06	-0.84	0.40	0.03	0.08	0.01	0.06	0.02	
V792BA	0.03	0.01	0.07	0.01	0.14	-0.07	0.28	-0.08	0.08	0.00	1.95	-0.76	0.38	0.05	0.05	0.02	0.05	0.03	
V894I	0.03	0.01	0.09	-0.03	0.14	-0.05	0.28	-0.07	0.09	-0.01	1.77	-0.37	0.40	0.04	0.07	0.02	0.06	0.03	
V896BB	0.03	0.02	0.08	-0.02	0.13	-0.06	0.25	-0.08	0.08	-0.03	1.66	-0.61	0.34	0.07	0.07	0.00	0.04	0.03	
V908EA	0.03	0.01	0.09	-0.03	0.15	-0.11	0.36	-0.24	0.10	-0.03	1.90	-0.84	0.36	-0.02	0.06	0.01	0.05	0.02	
V908J	0.03	0.03	0.08	0.02	0.14	-0.03	0.34	-0.11	0.10	0.00	1.88	-0.20	0.38	0.10	0.06	0.03	0.06	0.05	
V935G	0.03	0.01	0.08	-0.03	0.15	-0.09	0.31	-0.18	0.08	-0.01	2.07	-1.04	0.36	0.07	0.07	0.00	0.06	0.01	
V916H	0.04	0.01	0.09	-0.01	0.14	-0.04	0.32	-0.14	0.10	-0.03	2.13	-0.78	0.39	0.12	0.07	0.01	0.06	0.03	
V908K	0.04	0.01	0.08	-0.02	0.16	-0.09	0.30	-0.11	0.10	-0.04	2.03	-0.86	0.37	0.04	0.07	-0.01	0.05	0.03	
Mean	0.03	0.01	0.08	-0.02	0.14	-0.08	0.30	-0.18	0.09	-0.03	1.97	-1.08	0.37	0.00	0.06	0.00	0.05	0.02	
SD	0.00	0.01	0.01	0.03	0.02	0.05	0.04	0.09	0.01	0.02	0.22	0.76	0.04	0.13	0.01	0.02	0.01	0.02	
Shapiro-Wilk (Normal distribution test)																			
Obs Test Stat	0.93	0.96	0.95	0.97	0.96	0.97	0.96	0.92	0.93	0.97	0.93	0.94	0.89	0.96	0.94	0.95	0.94	0.90	
P-value	0.25	0.64	0.47	0.75	0.71	0.88	0.56	0.20	0.21	0.75	0.27	0.35	0.06	0.72	0.40	0.42	0.37	0.07	
Comparison with the global pattern																			
FULL DATASET	0.03	0.01	0.08	-0.02	0.14	-0.07	0.30	-0.16	0.09	-0.02	1.91	-0.81	0.37	0.03	0.06	0.01	0.05	0.02	
Obs Test Stat	1.20	0.70	0.84	-0.31	0.10	-1.12	0.46	-0.85	-0.98	-1.17	1.07	-1.44	-0.03	-1.05	2.07	-2.14	2.57	-0.43	
P-value	0.25	0.50	0.41	0.76	0.92	0.28	0.65	0.41	0.34	0.26	0.30	0.17	0.98	0.31	0.06	0.05	0.02	0.67	

Appendix 1.C.3 Individual growth pattern of the segment inertia (X axis) represented by linear regression model ($y=a*age+b$) in males

	Hand		Forearm		Upperarm		Thigh		Shank		Trunk		Head		Tail		Foot		
	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b	
V908H	181.25	-220.59	1241.06	-1950.94	1962.82	-3370.40	3265.59	-5339.01	1222.78	-1816.17	169712.69	-276009.99	4452.42	-6745.20	3268.81	-4539.19	503.18	-619.32	
V894G	251.09	-324.08	1551.18	-2653.01	2019.85	-3406.65	4915.71	-8830.46	1753.34	-2931.26	206221.56	-404176.21	6828.58	-11608.24	3921.93	-6160.47	642.21	-874.36	
V902F	149.44	-172.24	1194.22	-2156.46	1866.32	-3168.90	3510.00	-6333.53	1331.07	-2243.23	179964.71	-354834.14	5003.31	-8469.47	934.34	-1422.68	469.96	-615.43	
V937E	154.39	-118.92	1434.02	-2462.56	2471.36	-4580.54	3924.22	-6556.74	1264.21	-1792.38	180934.07	-295516.07	5260.25	-8057.03	2711.12	-3767.30	539.26	-655.49	
V916F	142.84	-85.17	1010.17	-1291.05	1425.86	-1648.20	4171.95	-6382.43	1280.42	-1664.10	163406.21	-232956.74	5318.32	-6960.53	2476.25	-2609.91	417.35	-355.96	
V896G	176.91	-145.27	1272.08	-1794.14	2134.31	-3398.45	5035.13	-8420.73	1860.12	-2860.36	205631.46	-349189.65	5562.85	-7995.52	3423.19	-4289.80	540.92	-523.71	
V935F	130.24	-76.15	807.63	-712.56	1236.50	-955.41	2283.53	-2098.13	811.90	-581.72	102870.30	-79644.98	2609.47	-831.68	1762.13	-998.86	314.11	-158.27	
V916G	209.30	-173.44	1276.84	-1312.79	2180.72	-2543.85	4342.05	-5083.43	1556.42	-1697.44	169583.11	-189957.38	5838.22	-5763.36	3643.29	-2892.00	480.89	-287.26	
V792BA	166.02	-100.68	1117.49	-1050.12	1931.58	-2161.38	3582.78	-3692.94	1226.17	-1071.82	177669.25	-199533.34	5240.18	-4750.90	1671.60	-793.50	409.86	-193.98	
V894I	173.73	-110.13	1357.26	-1449.69	1965.77	-2250.00	3349.64	-3432.53	1279.39	-1280.73	149132.81	-142612.65	6054.89	-5921.08	2815.43	-1999.27	518.87	-280.38	
V896BB	125.32	-69.04	1112.70	-1187.86	1656.11	-2006.75	2969.28	-3202.47	1241.09	-1438.74	123040.69	-137678.56	4681.80	-4498.95	2482.19	-1987.66	362.39	-200.74	
V908EA	170.27	-122.83	1562.55	-1889.21	2041.52	-2678.62	4556.60	-5932.82	1596.18	-1751.14	166571.39	-190162.85	4881.05	-5402.31	2586.60	-2216.24	455.58	-372.69	
V908I	205.35	-79.96	1287.76	-1079.19	2092.62	-2177.20	4906.58	-5546.57	1759.57	-1510.33	156804.48	-147252.65	5759.74	-5043.80	2972.97	-1809.19	522.63	-220.56	
V935G	158.47	-101.62	1093.96	-1167.80	1933.48	-2366.93	3336.31	-3879.29	1170.96	-1152.99	169393.39	-191025.76	4987.93	-4406.85	2557.19	-1987.22	446.99	-305.63	
V916H	232.25	-149.73	1301.55	-1209.60	1835.35	-1835.56	3880.05	-4021.32	1597.80	-1594.89	186495.72	-193661.09	5442.78	-4224.23	2937.30	-2099.16	454.97	-199.53	
V908K	233.69	-185.82	1185.80	-1234.44	2330.79	-2797.38	4128.40	-4635.23	1704.97	-1967.70	195520.91	-214767.48	5332.38	-5276.25	2855.96	-2483.77	475.87	-269.59	
Mean	178.78	-139.73	1237.89	-1536.34	1942.81	-2584.14	3884.86	-5211.73	1416.03	-1709.69	168934.55	-22436.22	5203.39	-5997.21	2688.77	-2628.51	472.19	-383.31	
SD	37.76	65.90	192.87	549.87	308.56	866.68	767.61	1847.96	282.14	604.93	27253.78	89046.26	896.46	2384.90	756.38	1416.32	77.05	210.43	
Shapiro-Wilk (Normal distribution test)																			
Obs Test Stat	0.95	0.87	0.97	0.92	0.94	0.97	0.97	0.97	0.93	0.94	0.92	0.94	0.88	0.94	0.95	0.90	0.97	0.87	
P-value	0.42	0.02	0.78	0.16	0.39	0.81	0.79	0.76	0.23	0.40	0.17	0.37	0.04	0.40	0.51	0.08	0.86	0.03	
Comparison with the global pattern																			
FULL DATASET	177.33	-126.63	1233.91	-1423.89	1925.15	-2410.45	3861.46	-4835.30	1424.25	-1623.53	162313.09	-193597.24	5194.88	-5529.72	2642.74	-2289.72	464.58	-326.20	
Obs Test Stat	0.15	N/A	0.08	-0.82	0.23	-0.80	0.12	-0.81	-0.12	-0.57	0.97	-1.41	N/A	-0.78	0.24	-0.96	0.39	-1.09	
P-value	0.88	N/A	0.94	0.43	0.82	0.44	0.90	0.43	0.91	0.58	0.35	0.18	N/A	0.45	0.81	0.35	0.70	0.29	

Appendix 1.C.4 Individual growth pattern of the segment inertia (y axis) represented by linear regression model ($y=a^*age+b$) in males

	Hand		Forearm		Upperarm		Thigh		Shank		Trunk		Head		Tail		Foot		
	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b	a	b	
V908H	170.66	-204.37	1238.96	-1947.34	1997.52	-3436.78	3430.57	-5645.97	1233.78	-1837.18	169041.58	-274879.63	4480.64	-6788.02	3268.81	-4539.19	487.37	-599.18	
V894G	240.74	-309.82	1548.80	-2649.77	2055.41	-3472.63	5215.28	-9483.00	1770.89	-2967.22	205101.17	-401862.06	6954.27	-11868.16	3921.93	-6160.47	622.45	-846.24	
V902F	143.64	-165.96	1191.14	-2150.92	1897.39	-3229.99	3646.67	-6606.15	1339.84	-2260.67	178402.82	-351089.56	5079.35	-8615.64	934.34	-1422.68	453.69	-590.58	
V937E	147.02	-110.74	1435.93	-2467.64	2531.62	-4705.20	4111.88	-6933.33	1274.61	-1811.72	179456.67	-292458.94	5345.24	-8219.24	2711.12	-3767.30	526.56	-642.73	
V916F	135.04	-76.93	1008.47	-1289.38	1452.48	-1688.40	4425.37	-6870.60	1293.40	-1686.95	161724.38	-229927.96	5399.48	-7063.53	2476.25	-2609.91	403.17	-345.22	
V896G	169.82	-139.21	1269.29	-1787.92	2172.82	-3460.00	5288.70	-8885.04	1873.97	-2883.36	204400.84	-346723.27	5609.20	-8059.04	3423.19	-4289.80	523.35	-508.30	
V935F	124.86	-72.82	806.34	-710.98	1249.87	-963.85	2365.79	-2187.75	816.38	-585.76	102440.52	-79148.45	2646.98	-869.48	1762.13	-998.86	306.29	-154.36	
V916G	199.26	-164.06	1273.79	-1309.96	2240.13	-2626.06	4553.79	-5363.19	1569.11	-1714.28	168404.66	-188131.27	5902.14	-5839.55	3643.29	-2892.00	464.74	-273.84	
V792BA	159.43	-96.78	1116.56	-1050.06	1969.12	-2209.06	3735.49	-3864.38	1232.96	-1079.43	176726.40	-198109.39	5320.42	-4845.29	1671.60	-793.50	399.56	-189.00	
V894I	165.54	-104.12	1356.14	-1449.66	2007.13	-2303.50	3533.28	-3634.78	1293.06	-1298.77	148188.70	-141355.23	6166.82	-6074.70	2815.43	-1999.27	502.91	-268.81	
V896BB	119.36	-65.25	1111.88	-1188.30	1694.72	-2065.02	3118.17	-3386.58	1249.90	-1452.24	122049.32	-136462.01	4751.03	-4577.86	2482.19	-1987.66	351.01	-193.12	
V908EA	163.65	-118.61	1558.94	-1866.09	2081.48	-2741.20	4826.28	-6336.37	1608.44	-1769.62	165340.66	-188374.07	4938.74	-5464.27	2586.60	-2216.24	444.62	-366.52	
V908J	197.89	-79.44	1286.17	-1078.90	2132.94	-2221.05	5219.24	-5968.97	1774.30	-1529.86	155200.48	-145420.06	5827.65	-5119.65	2972.97	-1809.19	507.22	-215.86	
V935G	151.50	-96.64	1093.46	-1168.42	1969.77	-2415.51	3528.48	-4132.66	1179.26	-1162.93	167900.39	-188883.82	5025.61	-4454.85	2557.19	-1987.22	435.21	-297.90	
V916H	222.83	-143.81	1298.50	-1207.70	1866.40	-1869.24	4060.22	-4240.17	1611.47	-1612.06	185336.73	-192135.48	5513.13	-4307.30	2937.30	-2099.16	439.73	-189.95	
V908K	225.14	-179.84	1183.53	-1233.37	2379.48	-2860.77	4312.68	-4856.30	1719.17	-1988.60	193692.92	-212169.26	5371.01	-5305.18	2855.96	-2483.77	464.22	-263.56	
Mean	171.02	-133.03	1236.12	-1534.78	1981.14	-2641.77	4085.74	-5524.70	1427.54	-1727.54	167713.01	-222945.65	5270.73	-6091.99	2688.77	-2628.51	458.26	-371.57	
SD	36.53	62.80	192.64	549.46	318.52	888.34	824.55	1981.45	285.00	611.14	27067.88	88470.25	914.31	2429.89	756.38	1416.32	74.54	204.09	
Shapiro-Wilk (Normal distribution test)																			
Obs Test Stat	0.94	0.87	0.97	0.92	0.95	0.97	0.96	0.97	0.93	0.95	0.92	0.88	0.94	0.95	0.90	0.97	0.87	0.87	
P-value	0.37	0.02	0.77	0.15	0.42	0.80	0.68	0.79	0.24	0.41	0.19	0.36	0.04	0.39	0.51	0.08	0.87	0.03	
Comparison with the global pattern																			
FULL DATASET	169.77	-121.02	1232.18	-1422.69	1963.93	-2466.18	4065.20	-5134.29	1435.88	-1640.67	161090.04	-191720.68	5263.64	-5621.16	2642.74	-2289.72	450.86	-316.19	
Obs Test Stat	0.14	N/A	0.08	-0.82	0.22	-0.79	0.10	-0.79	-0.12	-0.57	0.98	-1.41	N/A	-0.78	0.24	-0.96	0.40	-1.09	
P-value	0.89	N/A	0.94	0.43	0.83	0.44	0.92	0.44	0.91	0.58	0.34	0.18	N/A	0.45	0.81	0.35	0.70	0.29	

Appendix 1.D Individual linear regression models (RMA) in female baboons

	Forelimb x Hindlimb		Length (mm)		NPP (s)		I (kg.mm ⁻²)		COM (mm)	
	a	b	a	b	a	b	a	b	a	b
V913G	1.36	0.07	0.92	77.00	0.81	0.22	1.09	6849.06	0.75	22.91
V935E	1.86	-0.04	1.03	41.91	0.86	0.17	1.43	4743.94	0.74	27.46
V936F	1.75	0.07	1.00	53.15	1.01	-0.03	1.54	3687.94	0.97	-13.85
V915G	1.94	-0.04	1.05	39.06	0.84	0.20	1.63	1006.29	0.79	20.86
V936G	1.77	0.00	1.05	22.34	0.96	0.06	1.64	365.85	0.93	-0.01
V902G	1.92	-0.05	1.14	-8.43	0.93	0.08	1.67	-1759.33	0.87	7.29
V908I	2.20	-0.14	1.06	28.45	0.81	0.24	1.77	-1545.52	0.74	31.45
V894H	2.07	-0.15	1.19	-28.59	0.89	0.12	1.59	-4275.73	0.77	18.64
V792BB	1.76	0.00	1.09	15.40	0.98	0.03	1.62	-928.59	0.96	-8.45
V916DA	1.79	-0.01	1.15	-2.36	0.95	0.06	1.50	2320.13	0.82	14.93
V916I	1.94	-0.06	1.07	23.73	0.87	0.17	1.68	9.16	0.78	24.86
V993EB	1.66	0.03	1.02	37.47	0.82	0.22	1.28	5874.37	0.71	30.47
V936H	1.75	-0.01	1.05	25.37	0.98	0.01	1.53	482.36	0.91	0.11
V908GA	1.68	0.02	1.08	20.95	0.90	0.11	1.38	3024.32	0.81	12.88
Mean	1.82	-0.02	1.06	24.68	0.90	0.12	1.52	1418.16	0.82	13.54
SD	0.20	0.07	0.07	26.31	0.07	0.09	0.18	3161.11	0.09	14.51
Shapiro-Wilk (Normal distribution test)										
Obs Test Stat	0.95	0.92	0.96	0.97	0.94	0.95	0.92	0.98	0.91	0.94
P-value	0.55	0.21	0.61	0.85	0.38	0.55	0.20	0.96	0.14	0.35
Comparison with the general pattern										
FULL DATASET	1.81	-0.02	1.08	19.50	0.90	0.12	1.50	1626.86	0.81	15.30
Obs Test Stat	0.17	-0.09	-0.86	0.74	0.04	-0.06	0.52	-0.25	0.59	-0.45
P-value	0.87	0.93	0.41	0.47	0.97	0.95	0.61	0.81	0.56	0.66

Appendix 1.E Individual linear regression models (RMA) in male baboons

	Forelimb x Hindlimb											
	Mass (kg)		Length (mm)		NPP (s)		I (kg.mm ⁻²)		COM (mm)			
	a	b	a	b	a	b	a	b	a	b	a	b
V908H	1.53	0.04	1.10	6.83	0.89	0.13	1.24	8107.63	0.81	16.58		
V894G	1.85	-0.03	1.15	-18.68	1.03	-0.08	1.52	-3150.16	0.92	-11.36		
V902F	1.75	-0.03	1.08	12.80	0.93	0.08	1.40	3458.54	0.79	18.78		
V937E	1.58	0.03	1.04	37.57	0.85	0.19	1.22	13370.56	0.72	35.24		
V916F	2.21	-0.25	1.11	9.31	0.78	0.28	1.62	-1992.89	0.68	40.37		
V896G	1.97	-0.09	1.14	-4.88	1.00	0.00	1.79	-6936.13	0.93	-2.84		
V935F	1.72	-0.05	1.04	23.10	0.85	0.16	1.24	2352.34	0.71	28.10		
V916G	1.71	-0.03	1.10	6.38	0.95	0.05	1.41	2986.39	0.89	3.32		
V792BA	1.64	0.05	1.08	18.17	0.89	0.13	1.33	6179.17	0.81	13.22		
V894I	1.63	0.04	1.07	19.28	0.89	0.12	1.29	5202.53	0.75	22.02		
V896BB	1.67	0.01	1.07	18.43	0.88	0.14	1.39	1787.44	0.76	21.78		
V908EA	1.87	-0.01	1.04	31.87	0.84	0.16	1.30	4313.59	0.72	19.80		
V908J	1.99	-0.10	1.12	3.31	0.87	0.14	1.55	-2588.18	0.74	24.11		
V935G	1.69	0.02	1.04	34.56	0.86	0.16	1.25	5401.64	0.71	26.30		
V916H	1.81	-0.08	1.09	9.03	0.89	0.11	1.36	1137.59	0.79	16.04		
V908K	1.62	0.05	1.09	10.04	0.95	0.05	1.42	1212.66	0.85	6.49		
Mean	1.77	-0.03	1.08	13.57	0.90	0.11	1.39	2552.67	0.79	17.37		
SD	0.18	0.08	0.03	14.50	0.06	0.08	0.16	4860.44	0.08	13.43		
Shapiro-Wilk (Normal distribution test)												
Obs Test Stat	0.92	0.85	0.95	0.97	0.95	0.94	0.90	0.98	0.93	0.97		
P-value	0.18	0.02	0.50	0.73	0.44	0.36	0.08	0.93	0.25	0.82		
Comparison with the general pattern												
FULL DATASET	1.78	-0.03	1.09	13.39	0.90	0.11	1.41	1954.50	0.79	16.32		
Obs Test Stat	-0.33	N/A	-0.67	0.05	0.20	0.18	-0.36	0.49	-0.20	0.31		
P-value	0.74	N/A	0.51	0.96	0.84	0.86	0.72	0.63	0.84	0.76		

Chapter 2

Appendix 2.A Individual body mass distribution (%)

Segments	Session	Individual						Mean	SD
		Ilario	Icono	Irm	Iris	Ivar Jr	Isabella		
Head	October 2013	17.72	22.25	17.15	16.56	17.94	17.17	18.13	2.07
	March 2015	11.64	12.61	12.37	11.33	10.83	12.22	11.83	0.68
	% diff	34.29	43.33	27.88	31.58	39.64	28.84		
Arm	October 2013	5.60	5.44	5.19	5.04	4.93	4.61	5.13	0.36
	March 2015	6.10	8.21	5.65	6.28	7.49	7.21	6.82	0.97
	% diff	-8.92	-51.01	-8.89	-24.60	-52.03	-56.51		
Forearm	October 2013	3.62	4.60	4.40	5.01	5.02	4.13	4.46	0.54
	March 2015	3.40	4.21	4.63	3.72	4.05	3.58	3.93	0.45
	% diff	6.26	8.53	-5.04	25.76	19.34	13.45		
Hand	October 2013	2.83	2.85	2.39	2.62	3.63	2.64	2.83	0.43
	March 2015	2.40	2.25	2.16	2.26	2.58	2.32	2.33	0.15
	% diff	15.23	21.16	9.68	13.68	28.89	12.28		
Thigh	October 2013	11.10	11.98	11.37	11.42	10.89	9.05	10.97	1.01
	March 2015	12.92	14.07	11.67	15.26	12.41	15.92	13.71	1.67
	% diff	-16.36	-17.48	-2.61	-33.70	-13.96	-75.91		
Leg	October 2013	4.76	4.37	4.43	4.93	4.35	4.13	4.50	0.29
	March 2015	5.00	5.26	3.99	5.54	4.54	4.05	4.73	0.64
	% diff	-4.99	-20.32	9.76	-12.17	-4.28	1.96		
Foot	October 2013	4.80	4.24	4.17	4.70	4.94	5.00	4.64	0.35
	March 2015	4.22	3.46	3.97	3.93	3.98	3.45	3.83	0.31
	% diff	12.19	18.52	4.85	16.40	19.38	31.10		
Trunk	October 2013	47.50	42.21	48.98	47.63	45.87	51.16	47.23	3.03
	March 2015	52.55	48.32	53.86	49.94	52.29	49.41	51.06	2.15
	% diff	-10.62	-14.49	-9.96	-4.84	-13.98	3.42		
Tail	October 2013	2.07	2.06	1.92	2.08	2.42	2.10	2.11	0.17
	March 2015	1.79	1.61	1.71	1.74	1.83	1.85	1.75	0.09
	% diff	13.52	21.86	11.07	16.46	24.51	12.13		

Numbers in bold indicate % difference for individuals that do not follow the common pattern of changes observed in the sample.

Appendix 2.B.1 Proportion of locomotor behaviors, mode and submode per individual (%)

Modes	Session	Individual						Mean	SD
		Ilario	Icono	Irm	Iris	Ivar Jr	Isabella		
LOCOMOTION	October 2013	18.24	15.82	15.43	11.64	13.64	14.06	14.80	2.24
	March 2015	21.57	21.83	15.08	16.12	26.37	23.74	20.78	4.38
	% diff	-18.23	-37.98	2.26	-38.47	-93.35	-68.89		
Flexed bipedal walk	1	0.37	0.35	0.33	0.22	0.28	0.28	0.30	0.06
	2	0.30	0.23	0.37	0.37	0.54	0.91	0.45	0.25
<i>bipedal hop</i>	1	15.85	19.99	13.48	14.41	11.80	7.16	13.78	4.27
	2	4.14	10.55	9.40	4.49	8.43	3.80	6.80	3.00
<i>assisted bipedal walk</i>	1	61.06	49.16	62.83	66.17	74.90	70.52	64.11	8.90
	2	69.91	72.54	30.81	47.89	83.63	64.62	61.57	19.07
<i>unassisted bipedal walk</i>	1	23.09	30.86	23.69	19.42	13.31	22.32	22.11	5.74
	2	25.95	16.91	59.79	47.62	7.94	31.58	31.63	19.28
Drop	1	0.32	0.18	0.23	0.19	0.08	0.14	0.19	0.08
	2	0.15	0.44	0.12	0.38	0.43	0.49	0.33	0.16
<i>bipedal drop</i>	1	5.19	0.00	4.14	0.00	0.00	2.70	2.01	2.34
	2	6.07	2.04	0.00	6.73	5.80	1.77	3.73	2.81
<i>cling drop</i>	1	35.34	21.18	42.95	18.65	17.14	24.32	26.60	10.30
	2	3.18	14.75	4.38	11.97	6.22	19.66	10.03	6.52
<i>forelimb-hindlimb suspensory drop</i>	1	0.00	0.00	0.00	0.00	0.00	2.40	0.40	0.98
	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>forelimb suspensory drop</i>	1	18.32	9.88	19.22	16.27	23.43	10.21	16.22	5.32
	2	56.65	49.99	37.96	47.61	46.77	29.19	44.69	9.69
	1	0.00	0.00	3.77	8.94	6.86	1.80	3.56	3.69
<i>hindlimb suspensory drop</i>	2	3.47	1.39	0.00	1.60	4.25	0.00	1.78	1.76
<i>quadrupedal drop</i>	1	30.62	41.65	18.80	30.02	28.57	45.35	32.50	9.61
	2	27.17	25.76	34.67	12.77	23.05	30.07	25.58	7.43
<i>sit drop</i>	1	10.53	27.29	11.11	26.12	24.00	13.21	18.71	7.89
	2	3.47	3.18	22.99	17.05	12.15	18.25	12.85	8.14
Inverted quadrupedal walk	1	0.08	0.07	0.18	0.69	0.14	0.20	0.23	0.23
	2	0.03	0.27	0.14	0.32	0.33	0.28	0.23	0.12
Leap	1	1.25	0.65	0.82	0.52	0.44	0.83	0.75	0.29
	2	0.45	1.17	0.30	0.92	1.10	1.12	0.84	0.38
Run	1	4.44	1.97	1.67	1.35	1.62	1.86	2.15	1.14
	2	1.55	3.00	1.10	2.39	3.01	3.43	2.42	0.92
<i>quadrupedal run</i>	1	94.77	96.22	95.87	87.22	99.09	94.20	94.56	3.97
	2	97.39	98.26	94.93	93.23	96.86	91.31	95.33	2.68

<i>tripedal run</i>	1	5.23	3.78	4.13	12.78	0.91	5.80	5.44	3.97
	2	2.61	1.74	5.07	6.77	3.14	8.69	4.67	2.68
Walk	1	8.74	7.94	7.70	5.36	7.14	5.03	6.99	1.48
	2	16.57	13.77	10.99	9.13	17.68	13.37	13.58	3.23
<i>bound walk</i>	1	3.26	5.17	4.46	8.77	1.93	5.75	4.89	2.34
	2	0.78	1.75	0.82	2.12	3.14	1.79	1.73	0.88
<i>crouch quadrupedal walk</i>	1	1.40	1.40	2.18	3.63	5.00	2.00	2.60	1.43
	2	1.01	3.17	0.60	1.86	3.41	1.95	2.00	1.12
<i>quadrupedal walk</i>	1	89.65	89.27	88.64	83.98	91.47	84.14	87.86	3.09
	2	92.25	90.74	92.85	89.01	89.94	88.22	90.50	1.81
<i>tripedal walk</i>	1	5.69	4.15	4.72	3.63	1.60	8.11	4.65	2.17
	2	5.96	4.34	5.73	7.01	3.51	8.04	5.77	1.67
Orthograde suspensory	1	0.10	0.02	0.10	0.08	0.02	0.05	0.06	0.04
	2	0.09	0.04	0.07	0.20	0.14	0.15	0.11	0.06
<i>brachiate</i>	1	7.79	0.00	0.00	0.00	0.00	0.00	1.30	3.18
	2	0.00	0.00	14.03	2.63	10.85	7.60	5.85	5.89
<i>flexed elbow forelimb swing</i>	1	92.21	100	100.00	100.00	100.00	100.00	98.70	3.18
	2	100.00	100.00	85.97	97.37	89.15	92.40	94.15	5.89
Verical ascent	1	1.97	2.99	2.75	2.02	2.53	3.69	2.66	0.64
	2	0.69	1.27	0.53	0.93	1.67	1.79	1.15	0.52
<i>bimanual pull-up</i>	1	11.49	11.74	10.70	14.54	14.54	5.74	11.46	3.24
	2	10.49	19.68	7.83	10.09	27.72	3.73	13.25	8.81
<i>pulse climb</i>	1	15.95	10.91	17.45	10.71	10.24	12.45	12.95	3.03
	2	23.82	26.60	21.35	16.63	26.15	21.67	22.70	3.69
<i>vertical climb</i>	1	72.57	77.35	71.85	74.75	75.21	81.82	75.59	3.63
	2	65.69	53.72	70.82	73.28	46.13	74.60	64.04	11.60
Verical descent	1	0.67	1.25	1.45	0.98	1.24	1.68	1.21	0.35
	2	0.55	1.08	0.47	0.78	1.22	1.32	0.90	0.35
<i>bounding descent</i>	1	30.18	23.13	19.97	17.97	22.93	32.56	24.46	5.74
	2	30.35	40.98	29.39	32.41	34.35	37.10	34.10	4.37
<i>fire-pole slide</i>	1	6.26	4.08	2.78	0.00	0.00	13.20	4.39	4.94
	2	1.31	0.69	7.49	8.21	2.52	6.39	4.43	3.31
<i>head-first descent</i>	1	24.71	29.55	18.93	19.88	33.10	13.53	23.28	7.26
	2	50.39	36.56	42.51	23.38	33.42	31.36	36.27	9.34
<i>ru/np-first descent</i>	1	38.85	43.24	58.32	62.16	43.97	40.71	47.87	9.82
	2	17.95	21.77	20.62	36.00	29.71	25.15	25.20	6.67
Squat walk	1	0.27	0.33	0.18	0.21	0.12	0.26	0.23	0.07
	2	1.19	0.57	1.00	0.69	0.22	0.87	0.75	0.34

Grey highlight indicates the most commonly used submode for each mode category in session 1 and 2. Modes are labeled in bold.

Appendix 2.B.2 Proportion of postural behaviors, mode and submode per individual (%)

Modes	Session	Individual						Mean	SD
		Ilario	Icono	Irm	Iris	Ivar Jr	Isabella		
POSTURE	October 2013	81.76	84.18	84.57	88.36	86.36	85.94	85.20	2.24
	March 2015	78.43	78.17	84.92	83.88	73.63	76.26	79.22	4.38
	% diff	4.07	7.14	-0.41	5.07	14.74	11.27		
Cling	1	1.71	1.01	2.01	0.76	1.57	3.39	1.74	0.93
	2	0.08	0.34	0.05	0.32	0.23	0.38	0.23	0.14
<i>uni and bimanual vertical cling</i>	1	87.97	96.46	87.33	84.51	93.84	100.00	91.69	6.01
	2	100.00	85.83	62.50	70.30	63.66	85.58	77.98	14.89
<i>cling/forelimb-suspend</i>	1	12.03	3.54	12.67	15.49	6.16	0.00	8.31	6.01
	2	0.00	14.17	37.50	29.70	36.34	14.42	22.02	14.89
Forelimb-hindlimb suspend	1	0.02	0.01	0.06	0.31	0.21	0.08	0.11	0.12
	2	0.00	0.00	0.00	0.23	0.06	0.02	0.05	0.09
<i>contralateral forelimb-hindlimb suspend</i>	1	0.00	0.00	0.00	23.56	0.00	0.00	3.93	9.62
	2	0.00	0.00	0.00	38.55	0.00	0.00	6.42	15.74
<i>ipsilateral forelimb-hindlimb suspend</i>	1	100.00	100.00	100.00	76.44	100.00	100.00	96.07	9.62
	2	0.00	0.00	100.00	61.45	100.00	100.00	60.24	48.99
Hindlimb suspend	1	0.00	0.14	0.15	0.07	0.15	0.10	0.10	0.06
	2	0.00	0.02	0.00	0.26	0.00	0.00	0.05	0.10
Lie	1	3.46	17.51	4.91	7.40	10.80	13.71	9.63	5.39
	2	0.62	0.92	0.10	1.22	5.23	0.42	1.42	1.91
<i>back lie</i>	1	5.76	1.12	3.59	5.00	2.52	0.68	3.11	2.05
	2	10.63	19.01	15.12	12.03	36.89	7.14	16.80	10.63
<i>cling dorsal pronograde</i>	1	78.72	87.51	90.56	81.07	93.74	97.68	88.21	7.31
	2	0.00	0.00	0.00	0.00	19.62	0.00	3.27	8.01
<i>lateral lie</i>	1	15.17	11.37	2.24	11.02	3.29	1.22	7.39	5.85
	2	80.07	59.10	84.88	72.27	38.05	76.49	68.48	17.30
<i>sprawl</i>	1	0.34	0.00	3.61	2.92	0.45	0.41	1.29	1.55
	2	9.30	21.89	0.00	15.69	5.45	16.37	11.45	8.04
Orthograde forelimb suspend	1	1.31	0.90	0.97	1.63	1.03	1.06	1.15	0.27
	2	0.31	0.95	0.61	2.02	1.08	0.72	0.95	0.59
<i>forelimb suspend (uni or bimanual)</i>	1	48.02	80.01	57.03	50.17	53.65	48.91	56.30	12.09
	2	47.91	64.41	50.70	52.97	64.37	59.76	56.69	7.14
<i>forelimb suspend/cling</i>	1	40.99	1.06	27.79	27.94	31.37	25.48	25.77	13.28
	2	26.28	10.63	8.84	24.25	21.26	13.82	17.51	7.38
<i>forelimb suspend/squat</i>	1	10.43	8.04	8.49	10.54	13.64	20.47	11.93	4.63
	2	20.10	15.87	20.53	13.55	13.73	17.71	16.92	3.05
<i>forelimb suspend/stand</i>	1	0.57	10.90	6.70	11.35	1.34	5.14	6.00	4.58
	2	5.70	9.09	19.93	9.24	0.64	8.72	8.89	6.33

Orthograde stand	1	2.73	3.27	3.14	2.67	2.63	2.26	2.78	0.37
	2	1.36	2.34	1.85	1.37	2.31	2.12	1.89	0.44
<i>(bipeda)stand/ forelimb-suspend</i>	1	5.23	2.06	0.00	5.39	2.27	24.89	6.64	9.17
	2	0.00	3.43	1.17	3.62	2.59	9.41	3.37	3.27
<i>assisted bipedal stand</i>	1	92.30	95.78	94.26	91.58	96.62	69.62	90.03	10.18
	2	99.50	92.22	93.10	84.08	94.35	80.96	90.70	6.89
<i>unassisted bipedal stand</i>	1	2.24	1.76	4.29	3.03	1.11	3.23	2.61	1.14
	2	0.50	4.36	5.73	11.95	2.67	9.20	5.74	4.23
<i>hand bipedalism</i>	1	0.22	0.39	1.45	0.00	0.00	2.26	0.72	0.93
	2	0.00	0.00	0.00	0.35	0.38	0.43	0.19	0.21
Pronograde stand	1	8.27	6.13	7.56	5.94	7.70	5.28	6.81	1.19
	2	9.70	10.25	6.87	8.24	14.58	10.10	9.96	2.61
<i>forelimb crouch stand</i>	1	5.03	8.49	2.24	8.54	8.20	4.95	6.24	2.58
	2	8.55	22.22	11.62	21.30	11.06	20.54	15.88	6.11
<i>full-crouch stand</i>	1	25.47	20.31	11.95	31.29	29.64	30.09	24.79	7.47
	2	24.09	16.83	14.05	23.34	14.03	11.99	17.39	5.14
<i>hindlimb crouch stand</i>	1	19.02	18.30	17.44	11.02	12.53	14.96	15.55	3.26
	2	5.17	10.68	6.11	9.67	6.25	8.81	7.78	2.24
<i>quadrupedal stand</i>	1	29.76	35.39	28.46	30.50	26.82	28.36	29.88	2.98
	2	32.15	22.80	37.42	13.36	31.42	30.94	28.02	8.57
<i>tripedal stand</i>	1	20.72	17.50	39.92	18.64	22.81	21.65	23.54	8.25
	2	30.04	27.47	30.80	32.33	37.25	27.72	30.94	3.60
Pronograde suspension	1	1.00	2.98	0.66	1.97	1.99	1.46	1.68	0.83
	2	0.08	0.62	0.28	0.84	1.24	0.35	0.57	0.43
<i>cling ventral pronograde</i>	1	48.79	88.44	47.61	38.24	77.59	69.15	61.64	19.69
	2	0.00	0.00	0.00	0.00	7.91	0.00	1.32	3.23
<i>quadumanous suspend</i>	1	51.21	11.56	52.39	61.76	22.41	30.85	38.36	19.69
	2	100.00	100.00	100.00	100.00	92.09	100.00	98.68	3.23
Sit	1	61.69	50.39	63.63	66.36	59.45	56.48	59.66	5.67
	2	65.93	61.93	74.69	68.59	48.32	61.23	63.45	8.89
<i>cling dorsal orthograde</i>	1	1.72	5.02	0.08	2.87	0.46	3.23	2.23	1.86
	2	0.00	0.00	0.00	0.00	0.00	0.24	0.04	0.10
<i>sit lie</i>	1	0.72	0.00	0.08	1.49	0.16	0.45	0.48	0.56
	2	0.13	0.00	0.00	0.31	0.50	0.00	0.16	0.21
<i>sit-in</i>	1	90.79	86.63	96.94	89.22	88.86	82.38	89.14	4.81
	2	93.30	98.59	92.52	95.09	89.89	94.45	93.97	2.90
<i>sit-in/cling</i>	1	1.63	5.77	1.86	5.75	9.49	13.47	6.33	4.55
	2	4.94	0.38	4.43	2.88	3.35	2.91	3.15	1.59
<i>sit-in/out</i>	1	2.13	1.23	0.61	0.53	0.67	0.34	0.92	0.66
	2	1.62	0.38	1.50	0.99	3.28	1.41	1.53	0.97
<i>sit-out</i>	1	3.01	1.35	0.42	0.14	0.36	0.14	0.90	1.13
	2	0.01	0.65	1.55	0.72	2.98	0.99	1.15	1.03
Squat	1	1.44	1.54	1.37	1.11	0.66	1.91	1.34	0.42
	2	0.34	0.78	0.47	0.78	0.43	0.88	0.61	0.23
<i>squat</i>	1	71.65	92.29	67.34	94.76	72.12	74.55	78.79	11.68
	2	93.22	71.56	48.74	40.92	75.36	44.64	62.41	20.81
<i>squat/cling</i>	1	28.35	7.71	32.66	5.24	27.88	25.45	21.21	11.68
	2	6.78	28.44	51.26	59.08	24.64	55.36	37.59	20.81
Carried by congeneres	1	0.15	0.32	0.08	0.12	0.16	0.17	0.17	0.08
	2	0.00	0.00	0.00	0.00	0.12	0.00	0.02	0.05
Fall	1	0.02	0.04	0.05	0.02	0.04	0.08	0.04	0.02
	2	0.00	0.03	0.00	0.02	0.06	0.06	0.03	0.03

Grey highlight indicates the most widely used submode for each mode category in session 1 and 2. Modes are labeled in bold.

Appendix 2.C Individual activity (%)

Activity	Session	Individual						Mean	SD
		Ilario	Icono	Irm	Iris	Ivarjr	Isabella		
Feed	October 2013	24.75	25.11	31.29	31.52	27.98	24.78	27.57	3.21
	March 2015	51.32	43.17	58.38	60.02	25.13	55.49	48.92	13.12
	% diff	-107.33	-71.91	-86.57	-90.42	10.19	-123.95		
Play	October 2013	43.37	32.42	29.67	26.66	29.06	25.67	31.14	6.45
	March 2015	13.35	37.12	7.01	17.93	47.38	19.65	23.74	15.34
	% diff	69.22	-14.49	76.38	32.76	-63.02	23.46		
Rest	October 2013	27.76	36.69	33.73	39.52	41.08	47.08	37.64	6.61
	March 2015	17.28	11.92	17.53	7.56	11.90	12.93	13.19	3.76
	% diff	37.75	67.52	48.04	80.86	71.04	72.54		
Social	October 2013	1.47	4.23	3.01	2.17	0.92	1.37	2.20	1.24
	March 2015	10.51	5.33	13.16	12.52	11.37	8.18	10.18	2.95
	% diff	-616.39	-25.89	-336.78	-477.22	-1133.37	-494.90		
Travel	October 2013	2.64	1.54	2.29	0.13	0.95	1.10	1.44	0.92
	March 2015	7.54	2.46	3.92	1.97	4.22	3.76	3.98	1.96
	% diff	-185.20	-59.46	-71.17	-1394.18	-342.11	-242.72		

Numbers in bold indicate % difference for individuals that do not follow the common pattern of changes observed in the sample.

Appendix 2.D Proportion of time spent on the available substrates per individual (%)

Substrates	Session	Individual						Mean	SD
		Ilario	Icono	Irm	Iris	Ivar Jr	Isabella		
Transversal bar	October 2013	8.11	6.01	10.73	6.30	3.07	3.53	6.29	2.87
	March 2015	3.45	9.42	2.10	2.36	9.92	4.53	5.30	3.50
	% diff	57.42	-56.69	80.47	62.58	-222.85	-28.22		
Horizontal rods	October 2013	0.54	0.00	0.58	2.14	0.08	0.74	0.68	0.77
	March 2015	0.21	0.95	0.90	2.70	1.36	1.28	1.23	0.82
	% diff	60.31	-100.00	-54.57	-26.07	-1655.19	-74.07		
Vertical rods	October 2013	0.75	0.55	1.24	0.64	0.38	3.07	1.11	1.00
	March 2015	0.92	0.14	1.12	0.59	0.14	0.81	0.62	0.41
	% diff	-21.37	75.25	9.67	7.92	63.45	73.76		
Hollow concrete blocks	October 2013	10.20	5.54	2.32	6.00	3.52	3.43	5.17	2.83
	March 2015	2.38	0.99	3.35	4.32	3.37	2.29	2.78	1.15
	% diff	76.65	82.14	-44.34	27.98	4.18	33.41		
Hollow concrete pillars	October 2013	0.79	0.25	6.70	3.30	9.10	6.81	4.46	3.57
	March 2015	1.24	6.69	1.94	5.21	5.84	4.17	4.18	2.18
	% diff	-57.76	-2616.88	70.97	-57.92	35.77	36.85		
Other baboons	October 2013	0.25	0.56	0.50	0.98	0.47	0.26	0.50	0.27
	March 2015	0.05	0.07	0.00	0.00	1.28	0.30	0.28	0.50
	% diff	80.56	87.90	100.00	100.00	-173.44	-15.99		
In the air	October 2013	1.11	0.61	0.73	0.53	0.37	0.64	0.66	0.25
	March 2015	0.47	1.16	0.35	1.00	1.12	1.31	0.90	0.40
	% diff	57.61	-89.54	52.43	-89.36	-206.50	-104.53		
Suspended net	October 2013	1.39	1.33	2.27	0.85	1.78	0.86	1.41	0.55
	March 2015	0.00	0.16	0.00	0.22	0.16	0.04	0.10	0.10
	% diff	100.00	87.94	100.00	73.95	90.85	95.08		
Rock fountain	October 2013	3.46	0.93	1.65	0.12	1.92	1.04	1.52	1.14
	March 2015	0.49	1.49	0.53	0.84	0.83	0.25	0.74	0.43
	% diff	85.91	-59.77	67.98	-599.68	56.60	75.73		
Ground	October 2013	43.90	43.21	35.10	35.02	45.41	26.72	38.23	7.22
	March 2015	70.96	67.53	71.27	64.90	62.15	61.72	66.42	4.20
	% diff	-61.66	-56.29	-103.05	-85.34	-36.88	-130.95		
Mother	October 2013	4.32	19.95	4.68	8.37	11.45	17.72	11.08	6.59
	March 2015	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	% diff	100.00	100.00	100.00	100.00	100.00	100.00		
Concrete walkway	October 2013	6.19	0.68	2.11	6.34	3.44	9.07	4.64	3.11
	March 2015	2.91	0.62	0.83	0.40	3.65	2.78	1.86	1.40
	% diff	52.94	8.96	60.63	93.71	-5.85	69.39		
Suspended tires	October 2013	5.28	3.83	4.06	4.47	5.22	2.94	4.30	0.89
	March 2015	0.47	1.67	1.44	1.36	1.71	1.52	1.36	0.46
	% diff	91.12	56.42	64.60	69.67	67.25	48.30		
Pyramid	October 2013	8.51	8.78	10.50	11.07	7.69	14.01	10.09	2.30
	March 2015	2.68	5.38	5.70	7.23	4.21	5.86	5.18	1.56
	% diff	68.47	38.68	45.74	34.73	45.22	58.21		
Solid concrete blocks	October 2013	4.63	4.42	2.67	1.85	3.28	1.91	3.13	1.21
	March 2015	1.28	0.95	0.84	1.75	0.61	3.63	1.51	1.11
	% diff	72.26	78.42	68.42	5.46	81.54	-89.68		
horizontal metal substrates	October 2013	0.58	3.36	14.15	12.02	2.82	7.45	6.73	5.44
	March 2015	12.48	2.78	9.63	7.13	3.63	9.52	7.53	3.76
	% diff	-2044.76	17.17	31.97	40.64	-28.88	-27.80		

Numbers in bold indicate individuals for which the trend is different from the rest of the sample.

Appendix 2.E Eigenvalues and eigenfactors of the PCA of individual parameters of locomotion

	Dimension 1	Dimension 2	Dimension 3
Eigenvalue	19.54	7.65	5.07
% of variance	39.07	15.3	10.13
Cumulative eigenvalue	19.54	27.19	32.26
Cumulative % of variance	39.07	54.37	64.5
Factor scores			
<u>Positional behavior</u>			
Flexed bipedal walk	-0.403	0.3595	-0.1015
Drop	-0.5435	0.7597	0.2425
Inverted quadrupedal walk	0.009	0.0769	0.8242
Leap	-0.1714	0.8954	0.0972
Run	-0.1867	0.8607	-0.0966
Walk	-0.8233	0.2639	-0.3458
Orthograde suspensory	-0.5557	0.2199	0.482
Vertical ascent	0.8771	0.2003	-0.0638
Vertical descent	0.5372	0.3155	0.0593
Squat walk	-0.7978	-0.4412	-0.2387
Cling	0.8044	0.0268	-0.0762
Forelimb-hindlimb suspend	0.3207	-0.2014	0.8314
Hindlimb suspend	0.3799	-0.1717	0.5305
Lie	0.8538	0.0056	-0.0928
Orthograde forelimb suspend	0.2378	0.2362	0.8664
Orthograde stand	0.7509	0.3819	-0.1495
Pronograde stand	-0.6322	0.5744	-0.1192
Pronograde suspend	0.7708	0.1315	0.1259
Sit	-0.3681	-0.631	0.2475
Squat	0.7511	0.1708	0.0278
<u>Activity</u>			
Feed	-0.803	-0.4093	0.1619
Play	0.3355	0.8628	-0.0433
Rest	0.9497	-0.2296	-0.0731
Social	-0.8603	-0.2048	0.0514
Travel	-0.7396	-0.1138	-0.5345
<u>Substrate</u>			
Transversal bar	0.0917	0.7096	-0.0574
Horizontal rods	-0.3556	0.0498	0.9029
Vertical rods	0.3661	-0.4005	-0.0998
Hollow concrete blocks	0.4298	0.2304	0.0632
Hollow concrete pillars	0.1594	0.1273	0.3155
Other baboons	0.2531	0.2182	0.1572
In the air	-0.3908	0.8404	0.1588
Suspended net	0.7745	-0.0679	-0.1398
Rock fountain	0.3756	0.4628	-0.2808
Ground	-0.9258	-0.0557	-0.1443
Mother	0.634	-0.108	0.0353
Concrete walkway	0.5322	0.0409	0.053
Suspended tires	0.8707	0.1925	0.0426
Pyramid	0.8244	-0.0863	0.3172
Solid concrete blocks	0.5369	0.3121	-0.2373
Horizontal metal substrates	-0.1924	-0.6059	0.1886

Body mass distribution

Head	0.9069	0.0315	-0.1914
Arm	-0.7624	0.5438	-0.0139
Forearm	0.5899	-0.2907	0.1909
Hand	0.7065	0.1059	-0.1635
Thigh	-0.7684	0.2486	0.2472
Leg	-0.3238	0.1691	0.4946
Foot	0.801	-0.2294	-0.0147
Trunk	-0.6194	-0.3262	-0.012
Tail	0.858	-0.0331	-0.0456
