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A comparative study of muscle activity and synergies in baboons during quadrupedal and bipedal walking and human locomotion

Abstract

Bipedal locomotion was a major functional change during hominin evolution, yet, our understanding of this gradual and complex process remains strongly debated. Based on fossil discoveries, it is possible to address functional hypotheses related to bipedal anatomy, however, motor control remains intangible with this approach. Using comparative models which occasionally walk bipedally has proved to be relevant to shed light on the evolutionary transition toward habitual bipedalism. Here, we explored the organization of the neuromuscular control using surface electromyography (sEMG) for six extrinsic muscles in two baboon individuals when they walk quadrupedally and bipedally on the ground. We compared their muscular coordination to five human subjects walking bipedally. We extracted muscle synergies from the sEMG envelopes using the non-negative matrix factorization algorithm which allows decomposing the sEMG data in the linear combination of two non-negative matrixes (muscle weight vectors and activation coefficients). We calculated different parameters to estimate the complexity of the sEMG signals, the duration of the activation of the synergies, and the generalizability of the muscle synergy model across species and walking conditions. We found that the motor control strategy is less complex in baboons when they walk bipedally, with an increased muscular activity and muscle coactivation. When comparing the baboon bipedal and quadrupedal pattern of walking to human bipedalism, we observed that the baboon bipedal pattern of walking is closer to human bipedalism for both baboons, although substantial differences remain. Overall, our findings show that the muscle activity of a non-adapted biped effectively fulfills the basic mechanical requirements (propulsion and balance) for walking bipedally, but substantial refinements are possible to optimize the efficiency of bipedal locomotion. In the evolutionary context of an expanding reliance on bipedal behaviors, even minor morphological alterations, reducing muscle coactivation, could have faced strong selection pressure, ultimately driving bipedal evolution in hominins.

Keywords: Electromyography; Evolution; Motor control; Muscle synergy; *Papio anubis.*

1. Introduction

While bipedal locomotion is seen as a major functional change during the course of hominin evolution, our understanding of the adjustments that occurred in the motor control to make bipedal walking possible for long periods of time remains very speculative (e.g., Stern and Susman, 1981; Vilensky, 1987; Dominici et al., 2011). Based on the intriguing association of anatomical traits pointing toward bipedal behavior, recent paleontological discoveries (e.g., *Orrorin tugenensis, Sahelanthropus tchadensis*) allow addressing whether bipedalism might have been habitually used very early in the hominin lineage (e.g., Senut et al., 2001; White et al., 2015; Daver et al., 2022), and also possibly before the emergence of hominins (in a few specific Miocene hominoids, i.e., 23–6 Ma, such as in *Oreopithecus bambolii* and *Danuvius guggenmosi*; Rook et al., 1999; Böhme et al., 2019). In early hominins, bipedalism might have been habitually used in combination with other locomotor modes, including (arboreal) quadrupedal behaviors (Rose, 1991; Senut, 2007; Green and Alemseged, 2012; DeSilva et al., 2018; Almécija et al., 2021; Daver et al., 2022; Meyer et al., 2023; Stamos and Alemseged, 2023; Urciuoli and Alba, 2023).

Catarrhines have a ‘quadrupedal bauplan’ generally adapted to arboreal locomotion (e.g., Cartmill, 1972; Rose, 1973; Cartmill et al., 2002; Schmitt et al., 2006; Granatosky et al., 2017; Cartmill et al., 2020). They can cope with important balance and maneuverability requirements, and they may rely on increased and continuous sensory feedback compared to other mammals (Eidelberg et al., 1981). Locomotor control has been hypothesized to be organized differently in these species compared to other mammals (Eidelberg et al., 1981; Vilensky, 1987; Courtine et al., 2005; Larson and Stern, 2007). One can also consider that non-human primates are freed, in some respects, from the (anatomical) constraints related to strict quadrupedal locomotion and coordination as they develop complex locomotor repertoires (Hunt et al., 1996). Catarrhines are also able to stand and occasionally walk bipedally (e.g., baboon: Rose, 1976; Druelle et al., 2017; chimpanzee: Stanford, 2006; Carvalho et al., 2012; Pernel et al., 2021; langur: Workmann and Schmitt, 2011; colobe: Morbeck, 1977; Gebo and Chapman, 1995; macaques: Wells and Turnquist, 2001; orangutans: Thorpe et al., 2007; and for a review, see Druelle and Berillon, 2014) despite anatomies that do not bear the skeletal traits usually understood as bipedal locomotor adaptations in hominins. Their anatomy allows bipedal walking in the so-called ‘bent-hip, bent-knee’ posture, which acknowledges that they do not use extended limb postures as observed in humans (Alexander, 2004; Hirasaki et al., 2004; Ogihara et al., 2010; Demes and O'Neill, 2013; Pontzer et al., 2014; Demes et al., 2015; Thompson et al., 2015; O'Neill et al., 2018; Blickhan et al., 2021; Thompson et al., 2021). As recently shown in a comparative study in captivity, extant catarrhines (i.e., bonobos, chimpanzees, gorillas, orangutans, hylobatids, siamangs, baboons, and mandrills in this study) are using bipedal walking for very short bouts during their daily activities (Rosen et al., 2022; see also Rose 1976; Sanford 2006; Hunt 1994; Thorpe 2007; Druelle et al. 2016), but the evolutionary transition toward habitual bipedalism obviously required a stronger involvement into this mode. As a result, such a widespread behavior observed in many extant species let us suggest that it was also the case in Miocene hominoids. The most parsimonious hypothesis remains that they were already using bipedalism, at least occasionally, which involves motor control mechanisms similar to extant non-human primate species.

Terrestrial bipedal walking requires the central nervous system to modulate and coordinate the contraction of many muscles and greater balance adjustments are needed compared to quadrupedal walking. In a bipedal posture, the body center of mass needs to be balanced on two legs and lies above the hip joints within a small support polygon; in a quadrupedal posture, the body center of mass is positioned between four legs and anterior to the hip joints in a large support polygon (Kimura, 1996; Raichlen et al., 2009; Druelle et al., 2019). Bipedal walking in non-human primates may thus require to achieve a different muscle coordination toward higher muscle coactivation than during quadrupedal walking (Higurashi et al., 2019). In humans, a modular organization of the neuromuscular control, the so-called ‘muscle synergies’, have been suggested (Grillner, 1985; Ivanenko et al., 2004; Dominici et al., 2011; Torricelli et al., 2016) that would make this locomotor task simplified at the level of the motor control strategy (Dominici et al., 2011; Lacquaniti et al., 2012). Each synergy defines a group of coactivated muscles that are expected to work together as a single functional unit. Based on the analysis of muscle synergies, the existence of four basic activation patterns have been shown to be shared, in some respects, in rats, cats, macaques, guineafowl, and humans during walking (Dominici et al., 2011). This analysis does not contradict the potential specificities within primate neural networks but highlights the conservation of a common ancestral neural network for the execution of stepping. The application of this approach in various species and in different tasks has revealed that complex muscle patterns are commonly reconstructed with only a few muscle synergies. This approach has also been widely used for the assessment and rehabilitation of neuromotor diseases in humans (Safavynia et al., 2011; Taborri et al., 2018). Understanding the affinities between locomotor modes in primates can significantly contribute to the development of evolutionary scenarios for the transition toward locomotor specializations (e.g., Fleagle et al., 1981; Stern and Susman, 1981; Aerts et al., 2000; Berillon et al., 2011; Granatosky et al., 2016; Granatosky and Schmitt, 2019; Aerts et al., 2023). For instance, it can help to understand the link between quadrupedal and bipedal locomotion in primates in general (see Vangor and Wells, 1983; Vilensky, 1987; Shapiro and Jungers, 1994; Balter and Zehr, 2007; Zehr et al., 2009; Higurashi et al., 2019; Aerts et al., 2023) and to explore, in a comparative and evolutionary framework, what has to be resolved to specialize for bipedal locomotion (e.g., hip joint stabilization, propulsion generation, controlling the trunk position, controlling foot clearance). Therefore, understanding the motor affinities between locomotor modes in primates is likely to provide important insights into the (evolutionary) process of transitioning from a locomotor repertoire based on quadrupedalism to a repertoire based on bipedalism (e.g., Taylor and Rowntree, 1973; Foster et al., 2013; Kozma et al., 2018; Raichlen and Pontzer, 2021).

Here, we study motor control strategies through the muscle synergy theory of a quadrupedal primate, the olive baboon, *Papio anubis,* when walking quadrupedally and bipedally on the ground in comparison to those of humans. Undoubtedly, the morphology of baboons is specialized for quadrupedal walking, and their musculoskeletal system differs significantly from what is expected and observed in early hominins or Miocene apes. However, despite its specificities (see D'Août et al., 2014), this comparative model can offer valuable insights into how a quadrupedal primate naturally addresses the challenge of walking bipedally during its daily activities (e.g., Rose, 1976; Berillon et al., 2011; Druelle et al., 2022). By specifically studying baboons, along with other extant primates, we can enhance our comprehension of the intricate relationships between form and function, which encompass the intrinsic mechanisms involved in the evolutionary transition toward bipedalism. First, we hypothesize that a non-human primate with a quadrupedally-oriented locomotor repertoire should use common muscle synergies in both quadrupedal and bipedal locomotion. Nevertheless, because bipedal walking is an occasional locomotor mode in which keeping balance is a greater challenge than walking quadrupedally, a higher muscle coactivation is expected (as seen in macaques; Higurashi et al., 2019) and, hence, a less complex motor control scheme. Second, the stereotyped pattern observed in humans when walking bipedally (Dominici et al., 2011) should be shared, in some respects, with the one of the baboons walking quadrupedally, at least to deal with the major biomechanical functions inherent to walking.

2. Material and methods

2.1. Study site and subjects

The olive baboons, *Papio anubis,* were housed at the Primatology Station of the Centre National de la Recherche Scientifique (Rousset-sur-Arc, France). The experiments presented in this study were conducted inside the primatology center. All the procedures that are described in this study were evaluated by the ethical committee on animal experimentation n°14 (Projet 68-19112012, CEEA-14 Marseille) and approved by the Ministère de l'Enseignement Supérieur, de la Recherche et de l'Innovation.

Prior to the experiments, primates were trained using positive reinforcement techniques (Schapiro et al., 2003; Prescott and Buchanan-Smith, 2003) over a period of 18 months and the two trainers, P.M.V. and B.R., focused on the habituation and desensitization of individuals to the whole experimental setup. The initial training period took place in a spacious indoor cage, where the two individuals were paired and housed together for a duration of 18 months. During this phase, the focus was primarily on familiarizing the individuals with the presence of trainers and establishing basic behaviors such as target training and parking training. Over a span of 6 months (consisting of approximately 46 training sessions, each lasting around 30-45 minutes), the individuals progressively learned to cooperate in order to exit their enclosure while leashed, and to walk alongside the trainer using quadrupedal locomotion on the experimental setup. Subsequently, they were relocated to a larger indoor/outdoor enclosure. This training process enabled us to guide the baboons towards the technical platform for data collection. The training sessions started when the baboons were 1.5 and 2 years old. Importantly, the baboons were not specifically trained to walk bipedally. They naturally adopt this posture when the trainer provides a food reward at an elevated position, above their heads. The trainer then takes steps backward, encouraging the animals to walk on their hindlimbs until they reach the food reward. More detailed information about the training protocol is published in Druelle and Molina (2021). This training allowed us to lead the baboons to the technical platform for biomechanics (motion analysis of primates [MAP]) that is permanently installed in an outdoor enclosure of the primatology center (Berillon et al., 2011). The collection of the data presented in this study was performed during two recording sessions for individual 1 (ID1), the 31st of July 2013 and the 15th of December 2017, and one recording session for individual 2 (ID2), the 3rd of December 2013 (Druelle et al., 2021).

The human dataset comes from five healthy adult individuals of 24.6 years (SD = 0.8) on average and having a body weight of 55.6 kg (SD = 2.1) on average. We retrospectively analyzed gait data acquired at the PoliTo^{BIO}Med Lab of Politecnico di Torino (Turin, Italy) during five different recording sessions. None of the individuals had lower limb injuries or neurological or musculoskeletal disorders potentially affecting their gait performance. All the human individuals walked overground at a self-selected speed, back and forth on a 10-m straight walkway.

2.2. Data collection

Baboons Muscle activity was recorded at 2000 Hz using surface electromyography (sEMG) and a wireless Zerowire system (Aurion Srl, Milan) with the MyoResearch XP Master Edition v. 1.08.17 software (Noraxon U.S.A. Inc., Scottsdale). We focused on six hindlimb muscles that play an important role in locomotion by acting as actuators for the primary joints of the hindlimb: the hip, knee, and ankle. These specific muscles were selected due to their surface-level visibility on baboons, as previously evaluated through muscular topography assessments on olive baboon cadavers. The muscles we focused on are gluteus medius (hip extensor and rotator), biceps femoris (hip extensor and knee flexor), rectus femoris (hip flexor and knee extensor), tibialis anterior (dorsiflexion of the foot and inversion), lateral gastrocnemius (plantar flexion and knee flexion), and peroneus longus (foot eversion), all located on the right side (Swindler and Wood, 1973; Boyer et al., 2007). Baboons were instrumented during a short period of anesthesia (ca. 60 minutes) that is short and light enough to reduce the recovery period. The skin was locally prepared (shaving, cleaning, and degreasing), and the surface probes (sEMG) were taped at the level of the muscles' belly (approximately at mid-length of each muscle and electrode pairs were always positioned parallel to fibers direction; see Fig. 1). The experiments started after the baboons were totally recovered from the anesthesia (i.e., they were fully active and able to climb and run), between 60 to 90 minutes after their arrival in the enclosure. Bipedal behavior was elicited by the trainer using a food reward positioned above and in front of the animal (Fig. 2). Detailed information about the full procedure is available in Druelle et al. (2021). The movement of the animals was video captured using an integrated multicamera system (running at 200 fps, Norpix Inc.; see Berillon et al., 2011 for a general description of the experimental setup) to visually identify the locomotor events, i.e., touch-down and lift-off of the hindfeet. Surface electromyography and video recordings were synchronized using an external digital signal; in addition, a lateral video camera (running at 60 fps) was driven by the MyoResearch XP software and thus software-synchronized with the sEMG recording. We first qualitatively selected appropriate quadrupedal and bipedal strides during which the individual was walking steadily, behind the trainer, along a straight and horizontal walkway. The strides were defined from a right hindlimb touchdown to the next right hindlimb touchdown. We used the distance covered by the tip of the right foot to measure the stride length, stride duration and speed. The dataset included in the present analysis is composed of 25 quadrupedal walking strides and 18 bipedal walking strides for ID1, and 19 quadrupedal walking strides and 11 bipedal walking strides for ID2 (ID1 and ID2 are the same as in Druelle et al., 2021).

Humans Muscle activity was recorded at 2000 Hz using sEMG acquired through a multichannel acquisition system for clinical gait analysis (STEP32, Medical Technology, Turin, Italy). The probes were placed over twelve lower limb and trunk muscles of the dominant side (Fig. 1; Rimini et al., 2017) in accordance with the SENIAM recommendations for probe placement over muscles' bellies (Surface ElectroMyoGraphy for the Non-Invasive Assessment of Muscles – European concerted action in the Biomedical Health and Research Program, BIOMED II; https://www.seniam.org/). Before electrode placement, the skin was shaved and cleaned with ethyl alcohol to reduce impedance. For the sake of comparability, the following six lower-limb muscles of the dominant side (right side) were selected from the human sEMG dataset: gluteus medius, biceps femoris, rectus femoris, tibialis anterior, lateral gastrocnemius, and peroneus longus. Foot-floor contact sequences were detected through foot switches placed bilaterally beneath the heel, the first, and the fifth metatarsal head. The strides were automatically defined from a heel contact event to the next one of the same foot (Agostini et al., 2013). The walking task of the humans was synchronously video captured using an integrated camera. Detailed information about the acquisition system and the full experimental procedure are available in Rimini et al. (2017). The dataset included in the present analysis is composed of 20 bipedal walking strides per individual.

2.3. Muscle synergy extraction

We first visually checked the signals to ensure the absence of abnormalities and artifacts. We used MATLAB v. R2019a (The MathWorks Inc., Natick) to pre-process the sEMG signals and extract sEMG envelopes. To ensure comparable datasets, the same pre-processing steps were applied to both the baboons and the humans: band-pass filtering through a 4th order Butterworth digital filter (from 5 Hz to 500 Hz), demeaning, rectification (full-wave), low-pass filtering through a 4th order Butterworth digital filter (10 Hz). This provides an envelope of the muscular activity patterns on which we can then calculate the muscle synergies (see below).

To time-normalize the walking cycles and to avoid biases due to different stride durations, we applied a cubic spline interpolation over a time base with 600 points for the stance phase and 400 points for the swing phase. Accordingly, each stride was time-normalized to 1000-time samples. Muscle activity amplitude was normalized, per muscle, based on the maximum value observed among the gait cycles studied, separately for humans and baboons (walking quadrupedally and bipedally).

Muscle synergies were then extracted from the sEMG envelopes through the non-negative matrix factorization (NNMF) algorithm. According to the original definition by Lee and Seung (1999), the NNMF algorithm decomposes the original sEMG data in the linear combination of two non-negative matrixes: muscle weight vectors (W) and activation coefficients (C). More specifically, W are time-independent vectors that describe the contribution of each observed muscle to a specific synergy. Matrix C, instead, represents time-dependent vectors that describe the temporal modulation of the muscles enrolled in each synergy. The MATLAB function ‘nnmf’ was used to apply the NNMF algorithm and extract the muscle synergies. Detailed information about the full procedure for muscle synergy extraction is available in Ghislieri et al. (2020).

To explore the different solutions of the NNMF algorithm, the factorization process was run several times on the same sEMG envelopes, changing the factorization rank (i.e., the number of muscle synergies) between 1 and the total number of muscles acquired (i.e., 6). The selection of the optimal number of muscle synergies was performed by plotting the fraction of data variance accounted for (VAF) by the model vs. the factorization rank and by selecting the number of synergies at which the VAF curve achieves the highest curvature (Tresch et al. 2006).

Muscle synergies were then sorted in the same order for each locomotor condition and species through a k-means algorithm (MATLAB function ‘kmeans’) applied to the W matrix considering the optimal number of muscle synergies as the number of k-means clusters (Steele et al. 2015b).

To quantitatively assess the motor control strategies adopted by the central nervous system during different locomotor tasks, we calculated the fraction of data variance accounted for by the muscle synergy model considering 1 muscle synergy (called VAF1) to estimate the complexity of the original sEMG signals (Steele et al. 2015a). The VAF1 values range between 0% and 100%. When VAF1 is high, it means that a single synergy can explain most of the variance in muscle activation, which indicates a reduction in the complexity of motor control.

Moreover, the full width at half maximum (FWHM) was calculated on the activation coefficients for each stride cycle as the number of time samples exceeding half of the curve’s maximum, after subtracting the minimum within the respective stride cycle (Janshen et al., 2020; Janshen et al., 2021). This value was computed to estimate the duration of the activation of each muscle synergy. Activation coefficients characterized by long activation intervals (i.e., neural commands less selective in time) will be described by high FWHM values, while activation coefficients characterized by small activation intervals (i.e., neural commands more selective in time) will be described by low FWHM values. The generalizability of the muscle synergy model across the different species and walking conditions was assessed through the cross-variance. Cross-variance accounted for (cross-VAF) parameter was defined as in the study by Ghislieri et al. (2020). Cross-variance accounted for values range between 0% (low generalizability) and 100% (high generalizability).

2.4. Statistics

The full width at half maximum and cross-VAF are compared between species and locomotor modes using exact (nonparametric) tests: the Permutation tests for independent samples. Additionally, we employed the same tests to compare the speed and stride duration between the two baboons among the locomotor modes. We used the software for exact nonparametric inference StatXact v. 3.1 (Cytel, Inc., Cambridge). The significance threshold was set at $p < 0.05$ for the permutation tests.

3. Results

Surface electromyography signals from six muscles were recorded during terrestrial bipedal and quadrupedal walking in two female baboons and during overground bipedal walking in five healthy humans. A detailed description of the sEMG profiles obtained for individuals is provided in the Supplementary Online Material (SOM) Figures S1 (baboons) and S2 (humans; see also SOM S1). In baboons, bipedal walking generally requires higher levels of muscular activity than quadrupedal walking (Fig. 3A; SOM Fig. S1). The bursting sEMG profiles are also relatively longer in time during bipedal walking compared to quadrupedal walking. Table 1 presents the average values per individual for the speed and stride duration observed during bipedal and quadrupedal walking at comfort speed on the ground. ID1 exhibits significantly longer stride duration than ID2 when walking quadrupedally (permutation tests =-2.52, $p = 0.0097$), but the speed is not significantly different. There is no difference between the two individuals when walking bipedally.

3.1. Muscle synergy model

The number of muscle synergies extracted is the same between locomotor modes and species. Three muscle synergies describe the motor control strategies of baboons (during both bipedal and quadrupedal walking) and humans (Fig. 3B, C). The VAF is 92.1% (SD = 2.2%) in baboons walking bipedally, 88.9% (SD = 1.5%) in baboons walking quadrupedally, and 92.2% (SD = 2.2%) in humans (walking bipedally). We ordered the synergies to obtain the best match between species and individuals and thus compare the synergies which are more alike (see below).

The VAF1 is 74.6% (SD = 3.7%) in baboons walking bipedally, 65.3% (SD = 1.7%) in baboons walking quadrupedally, and 69.4% (SD = 2.0%) in humans (walking bipedally). According to VAF1, we can observe that the baboons walking bipedally show the least complex motor control.

3.2. Connecting the synergies in humans to potential biomechanical functions during walking

The first synergy (Syn 1) is deputed to the transition between the swing and the stance phases, particularly during the load acceptance phase. Additionally, it may contribute to decelerating the leg at the end of the swing phase. The first synergy mainly involves the gluteus medius and the rectus femoris, which act as antagonists around touch-down (Fig. 3B, C). The second synergy (Syn 2) manages the latter half of the stance phase. It is likely to be closely associated with generating propulsion and primarily involves the gastrocnemius and peroneus muscles. The third synergy (Syn 3) encompasses the coordinated action of the tibialis anterior (primarily) and biceps femoris muscles (to a lesser extent) during the swing phase and until the beginning of the stance phase. Hence, it appears to control the knee and ankle joints, as well as maintaining appropriate foot posture. While the biceps femoris contributes to knee flexion and thus prepares the limb for the load acceptance phase, the tibialis anterior muscle performs dorsiflexion of the foot and provides stability to the ankle joint during load acceptance. It is important to emphasize that determining the precise contribution of each of these muscles to the biomechanical functions proposed in this context is not a straightforward task and cannot be solely deduced from sEMG data. A careful interpretation of this relationship is imperative.

3.3. Connecting the synergies in baboons to potential biomechanical functions during walking

During bipedal walking, Syn 1 and Syn 2 are relatively alike across individuals. The first synergy involves the biceps femoris, the gluteus medius, the rectus femoris, and the peroneus longus muscles, which are generally coactivated during the stance phase. This synchronised activation likely contributes to weight-bearing and overall postural stability of the limb and body. The second synergy primarily involves the gastrocnemius muscle, exhibiting prolonged activation throughout the stance phase, as well as at the beginning and end of the swing phase. Its prominent role is likely associated with significant functions such as propulsion, ankle stabilization, and load acceptance. During quadrupedal walking, the results across individuals are similar for Syn1: it is more related to the first half of the stance phase and involves the biceps femoris, the peroneus, the gastrocnemius muscles, and, to a lesser extent the gluteus medius muscle. The contribution of these muscles during the early stance phase may be associated with load acceptance, postural stability and hindlimb retraction. The results are different between individuals for Syn 2. In ID1, it mainly involves the gastrocnemius muscle and, to a lesser extent, the rectus femoris muscle. These muscles are activated during the stance phase and towards the end of the swing phase (darker color in Fig. 3). In ID2 (lighter color in Fig. 3), Syn2 predominantly encompasses the latter half of the stance phase and mainly involves the rectus femoris muscle. In contrast, Syn 3 is very similar across individuals and locomotor modes (Fig. 3B, C). It mainly engages the tibialis anterior muscle during the swing phase, hence controlling foot dorsiflexion and potentially providing stability to the ankle joint during load acceptance.

3.4. Muscle synergy analysis

From the activation coefficients, FWHM is extracted for each muscle synergy and each stride cycle. Figure 4 represents the distributions of the FWHM values for each extracted muscle synergy across species and locomotor modes. Increased FWHM is hypothesized to be a compensatory mechanism adopted by the central nervous system to cope with internal and/or external postural instabilities. Compared to humans, the baboons walking bipedally show a significant increase in the FWHM for the two first synergies extracted (Syn 1: permutation tests = 6.453, $p < 0.0001$; Syn 2: permutation tests = 5.355, $p < 0.0001$) and a decrease of the FWHM for the third synergy (permutation tests = -4.557, $p < 0.0001$; Fig. 4). The baboons walking quadrupedally show a significant decrease of the FWHM for the first and third synergies compared to humans and an increase of the FWHM for the second synergy (Syn 1:

permutation tests = -4.922, $p = 0.0001$; Syn 2: permutation tests = 3.316, $p = 0.0007$; Syn 3: permutation tests = -3.613, $p = 0.0003$; Fig. 4). When comparing baboons walking bipedally and quadrupedally, the FWHM values are significantly higher for the two first synergies (Syn 1: permutation tests = 6.886, $p < 0.0001$; Syn 2: permutation tests = 2.439, $p = 0.0139$; Fig. 4) and significantly lower for the third synergy when walking bipedally (Syn 3: permutation tests = -2.532, $p = 0.0109$; Fig. 4).

The calculation of the cross-VAF parameter allows us to estimate the overall effectiveness of the muscle synergy model across the different locomotor conditions and species studied. Figure 5A shows the average cross-VAF values for each condition and individual. There is a significant difference between the two baboons, i.e., the bipedal and quadrupedal patterns observed in ID1 are more similar to each other than the bipedal and quadrupedal patterns are in ID2 (permutation tests = -3.151, $p = 0.0011$; Fig. 5). There is no significant difference when the two baboons are compared across the same locomotor mode, i.e., the similarity of the bipedal pattern between the two baboons is alike the similarity of the quadrupedal pattern between the two baboons. There is a significant difference between the locomotor modes for each baboon when compared to humans. Specifically, the bipedal pattern is more similar to humans than the quadrupedal pattern, and this result holds for both baboon individuals considered separately (ID1: permutation tests = 2.132, $p = 0.0329$; ID2: permutation tests = 4.728, $p < 0.0001$; Fig. 5A) and when both individuals are analyzed as a group (permutation tests = 4.317, $p < 0.0001$; Fig. 5B).

4. Discussion

4.1. Affinities in the modular control of bipedal and quadrupedal locomotion in baboons

We hypothesized that baboons, a non-adapted biped species, should rely on the same modular control of its quadrupedal locomotion for moving bipedally as humans. Our results in part support this hypothesis as few differences related to the stance phase can be emphasized. First, the baboons walking bipedally show a synergistic control with the same number of synergies as for quadrupedal walking and the synergy corresponding to the swing phase (Syn 3) is similar (in terms of both neural command and muscles' contribution) across locomotor modes. Second, the stance phase appears to be a more variable phase (Syn 1 and Syn 2). Interestingly, both baboon individuals show very similar synergies during bipedal walking suggesting that they respond in the same way to this occasional motor task. The motor control is less complex during bipedal walking (i.e., higher VAF1 values) than during the quadrupedal progression and the activation coefficients show a longer period of activation (i.e., higher FWHM values) during the stance phase, thus supporting our prediction of more coactivated muscles in this locomotor mode, as previously observed in macaques (Higurashi et al., 2019). Bipedal walking remains an occasional locomotor mode in baboons and macaques and keeping balance is likely to represent a greater challenge than walking quadrupedally. A longer period of muscle coactivation during the stance phase can help in this task as it would benefit in stabilizing the degrees of freedom at the hip and knee joints (see also Druelle et al., 2022). Third, with regard to quadrupedal walking, it appears that one synergy (Syn 2) shows clear differences between individuals, while the other two synergies (Syn 1 and Syn 3) are very similar. The difference thus arises from a neural command covering the stance phase for ID1 (Syn 2, dark color) in which the gastrocnemius muscle contributes significantly (as during bipedal walking), while the equivalent neural command for ID2 (Syn 2, light color) is focused on the second half of the stance phase and mainly involves the rectus femoris muscle. Interindividual variability of the sEMG profiles can be expected according to various parameters, such as differences in body built and inertial properties as well as differences in motivation during the experimental sessions (see Winter and Yack, 1987; Courtine et al., 2005). Also, we observed significant differences in the stride duration between individuals during quadrupedal walking, thus pointing out to different speed-related strategies (see also Druelle et al., 2021). Individual 1 exhibits shorter stride duration (i.e., higher stride frequency) than ID2 while moving at the same speed. In addition, an important flexibility of the neuromotor control has been suggested in primates as it allows to cope with the different substrates encountered during daily activities, such as the ground, trees, and cliff faces. Development and individual experiences can also play a significant role for building up locomotor strategies. A flexible nature of the neuromotor command during quadrupedalism would fit with the tight evolutionary relationship of primates in general, and baboons in particular, with the complex arboreal environment (Vangor and Wells, 1983; Vilensky, 1987; Vilensky and Larson, 1989; Young, 2012; Chadwell and Young, 2015; Patel et al., 2015; Young et al., 2016; Druelle et al., 2021). Interestingly, Syn 1 in quadrupedal walking presents the lowest FWHM values (see Fig. 4), thus suggesting that the early period of the stance phase (potentially related to the stability of foot positioning and the load acceptance function) is particularly effective in baboons. In summary, occasional bipedal walking in baboons elicits remarkably similar synergies, as they respond to the same challenging mechanical requirements. However, when it comes to habitual quadrupedal walking, we can expect to observe more interindividual variations. This variation arises not despite their specialization but rather because of it as they are much more experienced in practicing this mode.

4.2. Baboons and humans share only a few aspects of their muscle synergies

Since bipedalism and quadrupedalism represent the habitual locomotor mode of humans and baboons, respectively, and a (neuromotor) relationship between the two locomotor modes has been previously established (Aerts et al., 2000; D'Août et al., 2004; Balter and Zehr, 2007; Zehr et al., 2009; Berillon et al., 2011; Higurashi et al., 2019; Aerts et al., 2023), we hypothesized that the patterns observed in humans should be shared, in some respects, with the ones of the baboons walking quadrupedally. Our results partially support this hypothesis. Although the number of synergies is alike, the shape of the neural commands and the muscle contributions show significant variations between the two species. The most similar synergy is the one activated during the swing phase (Syn 3), where the tibialis anterior (greater extent) and the biceps femoris (lesser extent) muscles contribute significantly in humans, while the tibialis anterior is the main contributor to this synergy in baboons (as commonly observed in quadrupedal mammals; Rasmussen et al., 1978; Kimura et al., 1979; Vilensky, 1987). It is worth noting that the important differences observed can also directly result from the way the two species touch the ground, i.e., semi-plantigrady in baboons with no heel contact during the stance phase (Berillon et al., 2010) *versus* plantigrady in humans with a clear heel-strike at touch-down (see Oku et al., 2021 for explorations of this influence in macaques). For instance, this clear kinematic difference makes the biceps femoris muscle working in a very different way in baboons compared to humans, i.e., initiating its activity just before touch-down in baboons and during all the stance phase, while it is primarily active at the end of the swing phase during the transition between the swing and the stance phase in humans. Furthermore, we observe that baboons' bipedal walking is more similar to human bipedal walking than baboon quadrupedal walking is to human walking (see cross-VAF analyses). Interestingly, the swing phase appears to require less muscle activity in baboons walking bipedally compared to humans (FWHM values are significantly lower in baboons for the synergy related to the swing phase). The swing phase is managed in a relatively simple and efficient way in baboons. Therefore, concerning the possible biomechanical functions related to the stance phase, i.e., load acceptance, weight-bearing and propulsion, it appears plausible that they could constitute the foremost mechanical prerequisites for a baboon engaged in bipedal walking, as opposed to focusing on foot clearance and positioning. Interestingly, the recent study by O'Neill et al. (2022) on the three-dimensional joint mechanics during bipedal walking of the chimpanzee (another non-adapted biped) draws similar conclusions. They showed that during the stance phase, significant differences in work and power output exist between chimpanzees and humans, while the human limb structure does not specifically reduce positive work and power during limb swing. Additionaly, their results reveal a shift of positive mechanical work and power output toward the distal joints in humans during the stance phase, contrasting with the more proximal distribution of limb work in bipedal chimpanzees. Although the angle of attack differs between the study of O'Neill et al. (2022) and this study and despite the data sources differ (inverse dynamics and EMG), both findings highlight the most significant distinctions between an adapted and a non-adapted biped at the stance phase level.

4.3. Toward evolutionary implications

In sum, a quadrupedally-adapted non-human primate does not control its bipedal and quadrupedal locomotion the same way that an adapted biped controls its bipedal locomotion. From an evolutionary perspective, this observation may imply that important rearrangements of the muscle coordination occurred during hominin evolution. Whether these changes can be attributed to shifts in neuromotor control, variations in musculoskeletal structure associated with adopting an upright posture, or a combination of both, remains an open question (e.g., Goto et al., 2023). Although a non-adapted biped can walk bipedally, this mode requires increased muscular activity and muscle coactivation to respond to an increased loading regime as well as to control its impaired balance. Similar observations have been made in macaques when walking quadrupedally and bipedally on a treadmill (Higurashi et al., 2019) and in other non-human primates (Ishida et al., 1974; Stern and Susman, 1981; Vangor and Wells, 1983). These observations are particularly relevant in the context of the process of the evolutionary transition toward bipedalism, as they highlight some possible mechanical requirements that could be refined to improve bipedal locomotion in non-adapted bipeds (see also O'Neill et al., 2022). In a baboon model, from the muscular perspective, the stance phase poses significant challenges compared to humans. In humans, the contribution of the rectus femoris, gluteus medius and biceps femoris is reduced during this phase, corresponding to a minimal amount of positive mechanical work performed at the hip (O'Neill et al., 2022). Although the morphology of a baboon differs considerably from that of early hominins or Miocene apes, the mechanical requirements during bipedal walking should be similar. Indeed, despite ensuring the basic mechanical requirements of propulsion, balance, and stability for bipedal walking, these functions are not efficiently guaranteed. As a result, even slight morphological changes that reduce muscle coactivation could have faced strong selection pressure in early hominins where bipedal locomotion played a greater role in their positional repertoire than in extant non-human primate species (e.g., Rose, 1991; Daver et al., 2022).

Interestingly, the early hominin fossil record provides evidence of subtle and gradual morphological changes. For instance, a combination of features such as anteroposterior curvature, subtrochanteric platymeria, the presence of a calcar femorale, thicker cortical bone laterally and in general proximally, and potential anteversion of the femoral neck have been identified in the femoral shaft of *Sahelanthropus tchadensis* and could be related to a greater reliance on bipedal locomotion (Daver et al., 2022; contra opinion expressed by Macchiarelli et al., 2020). Similarly, the derived nature of the proximal femur of O*rrorin tugenensis* characterized by traits such as a spherical head and a long neck, has been noted (Senut et al., 2001; Pickford et al., 2002; Richmond and Jungers, 2008; Almécijà et al., 2013; but find controversial aspects in Gibbons 2002; Ohman et al. 2005; Kuperavage et al., 2010). Additionally, the broad and sagittally facing iliac blades of *Ardipithecus ramidus* represent further morphological traits possibly associated with the refinement of bipedal movement and the ability to withstand higher and more repetitive compressive forces on the ground, thus possibly by reducing the coactivation of hamstring, quadriceps and gluteus muscles (Lovejoy et al., 2009). Interestingly, O'Neill et al. (2022) suggest a greater dependence on non-muscular tissues for mechanical energy dissipation during hominin evolution. This would directly contribute to fatigue resistance during more extended periods of bipedal walking.

In any case, the activation of muscles plays a pivotal role in determining an organism's movement abilities, influencing factors such as range of motion, energy expenditure, and work and power output. Reviving a fossil in terms of its movement necessitates the development of appropriate musculoskeletal models, involving the skeletal structure and the attached muscles (e.g., Wang et al., 2004; Wiseman, 2023; O'Neill et al., in press). However, having a model in place does not grant the individual the ability to move; a comprehensive theory of motor control is also required. This involves understanding the coordinated activation of muscles, including muscle synergies in adapted and non-adapted bipeds, to approach optimal motor control strategies. This understanding is particularly important in early hominins, where a locomotor repertoire with a greater reliance on bipedal behaviors is considered.

4.4. *Potential limitations and conclusions*

The study presented here poses several inherent challenges as conducting motor control analysis on non-human primates involves striking a delicate balance between the scientific inquiry, animal welfare considerations, accessibility to the animals and statistical requirements. Regarding our experimental protocol on baboons, we have tried to refine it as much as possible to minimize the duration of the anesthesia required for skin preparation and electrode positioning. Furthermore, with regard to baboon morphology, the accessibility of the muscles from the skin using surface probes differs significantly from that of humans. The smaller size of baboons compared to humans introduces inherent spatial limitations when positioning the surface probes. Therefore, we were only able to select six muscles that are accessible from the skin in baboons. Although in muscle synergy analyses, the outcomes of non-negative matrix factorization can be sensitive to the number of muscles considered (Steele et al., 2013), previous studies based on five and six muscles have successfully applied muscle synergy analyses, yielding results comparable to studies that utilized a larger muscle set (Steele et al., 2015b; Kim et al., 2018; Steele et al., 2019; Hu et al., 2019; Oudenhoven et al., 2019; Vandekerckhove et al., 2020). Essential aspects of the muscle synergy analysis thus appear to remain consistent across studies using different number of muscles. Therefore, focusing on 6 muscles that contribute to crucial flexion and extension movements of the hindlimb (agonist and antagonist muscles acting on the ankle, knee and hip) represents a compromise that enables us to work effectively with baboons and to perform a comprehensive muscle synergy analysis that can be meaningfully compared to human data. Nevertheless, gathering data from a broader set of muscles would undoubtedly enables a more comprehensive muscle synergy analysis, shedding further light on the shared characteristics and distinctions between bipedal and quadrupedal locomotion. The cross-VAF, overall commonalities, and differences between baboons and humans might be further refined with additional muscle data. Specifically, decomposing the general EMG signal into more than three synergies could provide additional insights.

The exploration of the muscle synergies related to bipedal locomotion in a quadrupedal non-human primate can be a relevant and complementary approach to tackle the mechanisms of the gradual and complex evolutionary shift toward habitual bipedalism in hominins. A better understanding of the neuromotor circuitry, through muscle synergies, and how it is likely to be connected to the different biomechanical functions during locomotor modes among and between primate species is required. This study, while informative, has necessitated speculation in this regard. Consequently, future studies on the muscular activity of non-human primates are promising to propose a refined scenario, including the neuromotor control, for the evolution of bipedalism in hominins.

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Figure captions

Figure 1. The images depict the placement of sEMG probes on a human subject (lateral, back and front) and a baboon individual, providing visual reference for electrode positioning. Abbreviations: BF = biceps femoris; GM = gluteus medius; GA = lateral gastrocnemius; PL = peroneus longus; RF = rectus femoris; TA = tibialis anterior.

Figure 2. Illustration stills of diverse bipedal postures adopted by Id1 and Id2 during data collection at the CNRS primatology station's biomechanics technical platform. The animals moved forward, guided by the trainer holding a food reward.

Figure 3. A) Average (±95% confidence intervals) surface electromyography (sEMG) profiles of the six hindlimb muscles considered for the human sample (five subjects) during bipedal walking (green) and the two baboon individuals (ID1: dark colors, ID2: light colors), during quadrupedal walking (brown) and bipedal walking (blue). The activity patterns were stride-normalized to 1000-time samples (represented from 0% to 100% of the gait cycle) and averaged across strides. Surface electromyography activity was recorded on the right hindlimb. B) Average (± SD) activation coefficients of the three synergies extracted from sEMG profiles in five human subjects (green) and activation coefficients from sEMG profiles in two baboons (ID1: dark colors, ID2: light colors) when walking quadrupedally (brown) and bipedally (blue). The dashed vertical line indicates the transition from the stance to the swing phases and it is positioned at 60% following stance and swing normalization. C) Average (± SD) weight vectors in humans and individual weight vectors in baboons are represented, respectively. Abbreviations: a. u. = arbitrary units; BF = biceps femoris; GM = gluteus medius; GA = lateral gastrocnemius; PL = peroneus longus; RF = rectus femoris; TA = tibialis anterior.

Figure 4. Boxplots of full width at half maximum (FWHM) values for each extracted muscle synergy across species and locomotor modes. Box shows 25th and 75th percentiles with median; whiskers are minimum and maximum values. The comparison of each synergy (Syn) with its respective synergy number across species and locomotor modes is significant.

Figure 5. A) Average cross-variance accounted for (cross-VAF) values (means and SD) for each condition and each baboon individual. Higher values indicate conditions that are more alike to each other. Comparison is shown between baboon individuals 1 (ID1) and 2 (ID2) in green, between locomotor modes within individuals in yellow, between ID1 and humans in blue, and between ID2 and humans in brown. B) Comparison between humans as a group

and baboons as a group with bipedal baboons and humans in dark blue and quadrupedal baboons and humans in brown. Note that due to the variability between the two baboon individuals, averaging their EMG signals generally results in higher cross-VAF values. Asterisk indicates a significant difference: single asterisk stands for $p < 0.05$; double asterisk stands for $p < 0.01$; triple asterisk stands for $p < 0.001$. Abbreviations: Bip = Bipedal walking; Quad = Quadrupedal walking.