

A comparative study of muscle activity and synergies during walking in baboons and humans

*Original*

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(Article begins on next page)

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

3

4 **Abstract**

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

30

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

32

## 33 1. Introduction

34 While bipedal locomotion is seen as a major functional change during the course of hominin  
35 evolution, our understanding of the adjustments that occurred in the motor control to make  
36 bipedal walking possible for long periods of time remains very speculative (e.g., Stern and  
37 Susman, 1981; Vilensky, 1987; Dominici et al., 2011). Based on the intriguing association of  
38 anatomical traits pointing toward bipedal behavior, recent paleontological discoveries (e.g.,  
39 *Orrorin tugenensis*, *Sahelanthropus tchadensis*) allow addressing whether bipedalism might  
40 have been habitually used very early in the hominin lineage (e.g., Senut et al., 2001; White et  
41 al., 2015; Daver et al., 2022), and also possibly before the emergence of hominins (in a few  
42 specific Miocene hominoids, i.e., 23–6 Ma, such as in *Oreopithecus bambolii* and *Danuvius*  
43 *guggenmosi*; Rook et al., 1999; Böhme et al., 2019). In early hominins, bipedalism might have  
44 been habitually used in combination with other locomotor modes, including (arboreal)  
45 quadrupedal behaviors (Rose, 1991; Senut, 2007; Green and Alemseged, 2012; DeSilva et  
46 al., 2018; Almécija et al., 2021; Daver et al., 2022; Meyer et al., 2023; Stamos and Alemseged,  
47 2023; Urciuoli and Alba, 2023).

48 Catarrhines have a ‘quadrupedal bauplan’ generally adapted to arboreal locomotion (e.g.,  
49 Cartmill, 1972; Rose, 1973; Cartmill et al., 2002; Schmitt et al., 2006; Granatosky et al., 2017;  
50 Cartmill et al., 2020). They can cope with important balance and maneuverability  
51 requirements, and they may rely on increased and continuous sensory feedback compared to  
52 other mammals (Eidelberg et al., 1981). Locomotor control has been hypothesized to be  
53 organized differently in these species compared to other mammals (Eidelberg et al., 1981;  
54 Vilensky, 1987; Courtine et al., 2005; Larson and Stern, 2007). One can also consider that  
55 non-human primates are freed, in some respects, from the (anatomical) constraints related to  
56 strict quadrupedal locomotion and coordination as they develop complex locomotor  
57 repertoires (Hunt et al., 1996). Catarrhines are also able to stand and occasionally walk  
58 bipedally (e.g., baboon: Rose, 1976; Druelle et al., 2017; chimpanzee: Stanford, 2006;  
59 Carvalho et al., 2012; Pernel et al., 2021; langur: Workmann and Schmitt, 2011; colobe:  
60 Morbeck, 1977; Gebo and Chapman, 1995; macaques: Wells and Turnquist, 2001;  
61 orangutans: Thorpe et al., 2007; and for a review, see Druelle and Berillon, 2014) despite  
62 anatomies that do not bear the skeletal traits usually understood as bipedal locomotor  
63 adaptations in hominins. Their anatomy allows bipedal walking in the so-called ‘bent-hip, bent-  
64 knee’ posture, which acknowledges that they do not use extended limb postures as observed  
65 in humans (Alexander, 2004; Hirasaki et al., 2004; Ogihara et al., 2010; Demes and O'Neill,  
66 2013; Pontzer et al., 2014; Demes et al., 2015; Thompson et al., 2015; O'Neill et al., 2018;  
67 Blickhan et al., 2021; Thompson et al., 2021). As recently shown in a comparative study in

68 captivity, extant catarrhines (i.e., bonobos, chimpanzees, gorillas, orangutans, hylobatids,  
69 siamangs, baboons, and mandrills in this study) are using bipedal walking for very short bouts  
70 during their daily activities (Rosen et al., 2022; see also Rose 1976; Sanford 2006; Hunt 1994;  
71 Thorpe 2007; Druelle et al. 2016), but the evolutionary transition toward habitual bipedalism  
72 obviously required a stronger involvement into this mode. As a result, such a widespread  
73 behavior observed in many extant species let us suggest that it was also the case in Miocene  
74 hominoids. The most parsimonious hypothesis remains that they were already using  
75 bipedalism, at least occasionally, which involves motor control mechanisms similar to extant  
76 non-human primate species.

77 Terrestrial bipedal walking requires the central nervous system to modulate and coordinate  
78 the contraction of many muscles and greater balance adjustments are needed compared to  
79 quadrupedal walking. In a bipedal posture, the body center of mass needs to be balanced on  
80 two legs and lies above the hip joints within a small support polygon; in a quadrupedal posture,  
81 the body center of mass is positioned between four legs and anterior to the hip joints in a large  
82 support polygon (Kimura, 1996; Raichlen et al., 2009; Druelle et al., 2019). Bipedal walking in  
83 non-human primates may thus require to achieve a different muscle coordination toward  
84 higher muscle coactivation than during quadrupedal walking (Higurashi et al., 2019). In  
85 humans, a modular organization of the neuromuscular control, the so-called 'muscle  
86 synergies', have been suggested (Grillner, 1985; Ivanenko et al., 2004; Dominici et al., 2011;  
87 Torricelli et al., 2016) that would make this locomotor task simplified at the level of the motor  
88 control strategy (Dominici et al., 2011; Lacquaniti et al., 2012). Each synergy defines a group  
89 of coactivated muscles that are expected to work together as a single functional unit. Based  
90 on the analysis of muscle synergies, the existence of four basic activation patterns have been  
91 shown to be shared, in some respects, in rats, cats, macaques, guineafowl, and humans  
92 during walking (Dominici et al., 2011). This analysis does not contradict the potential  
93 specificities within primate neural networks but highlights the conservation of a common  
94 ancestral neural network for the execution of stepping. The application of this approach in  
95 various species and in different tasks has revealed that complex muscle patterns are  
96 commonly reconstructed with only a few muscle synergies. This approach has also been  
97 widely used for the assessment and rehabilitation of neuromotor diseases in humans  
98 (Safavynia et al., 2011; Taborri et al., 2018). Understanding the affinities between locomotor  
99 modes in primates can significantly contribute to the development of evolutionary scenarios  
100 for the transition toward locomotor specializations (e.g., Fleagle et al., 1981; Stern and  
101 Susman, 1981; Aerts et al., 2000; Berillon et al., 2011; Granatosky et al., 2016; Granatosky  
102 and Schmitt, 2019; Aerts et al., 2023). For instance, it can help to understand the link between

103 quadrupedal and bipedal locomotion in primates in general (see Vangor and Wells, 1983;  
104 Vilensky, 1987; Shapiro and Jungers, 1994; Balter and Zehr, 2007; Zehr et al., 2009; Higurashi  
105 et al., 2019; Aerts et al., 2023) and to explore, in a comparative and evolutionary framework,  
106 what has to be resolved to specialize for bipedal locomotion (e.g., hip joint stabilization,  
107 propulsion generation, controlling the trunk position, controlling foot clearance). Therefore,  
108 understanding the motor affinities between locomotor modes in primates is likely to provide  
109 important insights into the (evolutionary) process of transitioning from a locomotor repertoire  
110 based on quadrupedalism to a repertoire based on bipedalism (e.g., Taylor and Rowntree,  
111 1973; Foster et al., 2013; Kozma et al., 2018; Raichlen and Pontzer, 2021).

112 Here, we study motor control strategies through the muscle synergy theory of a quadrupedal  
113 primate, the olive baboon, *Papio anubis*, when walking quadrupedally and bipedally on the  
114 ground in comparison to those of humans. Undoubtedly, the morphology of baboons is  
115 specialized for quadrupedal walking, and their musculoskeletal system differs significantly  
116 from what is expected and observed in early hominins or Miocene apes. However, despite its  
117 specificities (see D'Août et al., 2014), this comparative model can offer valuable insights into  
118 how a quadrupedal primate naturally addresses the challenge of walking bipedally during its  
119 daily activities (e.g., Rose, 1976; Berillon et al., 2011; Druelle et al., 2022). By specifically  
120 studying baboons, along with other extant primates, we can enhance our comprehension of  
121 the intricate relationships between form and function, which encompass the intrinsic  
122 mechanisms involved in the evolutionary transition toward bipedalism. First, we hypothesize  
123 that a non-human primate with a quadrupedally-oriented locomotor repertoire should use  
124 common muscle synergies in both quadrupedal and bipedal locomotion. Nevertheless,  
125 because bipedal walking is an occasional locomotor mode in which keeping balance is a  
126 greater challenge than walking quadrupedally, a higher muscle coactivation is expected (as  
127 seen in macaques; Higurashi et al., 2019) and, hence, a less complex motor control scheme.  
128 Second, the stereotyped pattern observed in humans when walking bipedally (Dominici et al.,  
129 2011) should be shared, in some respects, with the one of the baboons walking quadrupedally,  
130 at least to deal with the major biomechanical functions inherent to walking.

131

## 132 **2. Material and methods**

### 133 *2.1. Study site and subjects*

134 The olive baboons, *Papio anubis*, were housed at the Primatology Station of the Centre  
135 National de la Recherche Scientifique (Rousset-sur-Arc, France). The experiments presented

136 in this study were conducted inside the primatology center. All the procedures that are  
137 described in this study were evaluated by the ethical committee on animal experimentation  
138 n°14 (Projet 68-19112012, CEEA-14 Marseille) and approved by the Ministère de  
139 l'Enseignement Supérieur, de la Recherche et de l'Innovation.

140 Prior to the experiments, primates were trained using positive reinforcement techniques  
141 (Schapiro et al., 2003; Prescott and Buchanan-Smith, 2003) over a period of 18 months and  
142 the two trainers, P.M.V. and B.R., focused on the habituation and desensitization of individuals  
143 to the whole experimental setup. The initial training period took place in a spacious indoor  
144 cage, where the two individuals were paired and housed together for a duration of 18 months.  
145 During this phase, the focus was primarily on familiarizing the individuals with the presence of  
146 trainers and establishing basic behaviors such as target training and parking training. Over a  
147 span of 6 months (consisting of approximately 46 training sessions, each lasting around 30-  
148 45 minutes), the individuals progressively learned to cooperate in order to exit their enclosure  
149 while leashed, and to walk alongside the trainer using quadrupedal locomotion on the  
150 experimental setup. Subsequently, they were relocated to a larger indoor/outdoor enclosure.  
151 This training process enabled us to guide the baboons towards the technical platform for data  
152 collection. The training sessions started when the baboons were 1.5 and 2 years old.  
153 Importantly, the baboons were not specifically trained to walk bipedally. They naturally adopt  
154 this posture when the trainer provides a food reward at an elevated position, above their  
155 heads. The trainer then takes steps backward, encouraging the animals to walk on their  
156 hindlimbs until they reach the food reward. More detailed information about the training  
157 protocol is published in Druelle and Molina (2021). This training allowed us to lead the baboons  
158 to the technical platform for biomechanics (motion analysis of primates [MAP]) that is  
159 permanently installed in an outdoor enclosure of the primatology center (Berillon et al., 2011).  
160 The collection of the data presented in this study was performed during two recording sessions  
161 for individual 1 (ID1), the 31<sup>st</sup> of July 2013 and the 15<sup>th</sup> of December 2017, and one recording  
162 session for individual 2 (ID2), the 3<sup>rd</sup> of December 2013 (Druelle et al., 2021).

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

170

171 *2.2. Data collection*

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

203 strides for ID1, and 19 quadrupedal walking strides and 11 bipedal walking strides for ID2 (ID1  
204 and ID2 are the same as in Druelle et al., 2021).

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

222

### 223 *2.3. Muscle synergy extraction*

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

231 To time-normalize the walking cycles and to avoid biases due to different stride durations, we  
232 applied a cubic spline interpolation over a time base with 600 points for the stance phase and  
233 400 points for the swing phase. Accordingly, each stride was time-normalized to 1000-time  
234 samples. Muscle activity amplitude was normalized, per muscle, based on the maximum value

235 observed among the gait cycles studied, separately for humans and baboons (walking  
236 quadrupedally and bipedally).

237 Muscle synergies were then extracted from the sEMG envelopes through the non-negative  
238 matrix factorization (NNMF) algorithm. According to the original definition by Lee and Seung  
239 (1999), the NNMF algorithm decomposes the original sEMG data in the linear combination of  
240 two non-negative matrixes: muscle weight vectors ( $W$ ) and activation coefficients ( $C$ ). More  
241 specifically,  $W$  are time-independent vectors that describe the contribution of each observed  
242 muscle to a specific synergy. Matrix  $C$ , instead, represents time-dependent vectors that  
243 describe the temporal modulation of the muscles enrolled in each synergy. The MATLAB  
244 function 'nnmf' was used to apply the NNMF algorithm and extract the muscle synergies.  
245 Detailed information about the full procedure for muscle synergy extraction is available in  
246 Ghislieri et al. (2020).

247 To explore the different solutions of the NNMF algorithm, the factorization process was run  
248 several times on the same sEMG envelopes, changing the factorization rank (i.e., the number  
249 of muscle synergies) between 1 and the total number of muscles acquired (i.e., 6). The  
250 selection of the optimal number of muscle synergies was performed by plotting the fraction of  
251 data variance accounted for (VAF) by the model vs. the factorization rank and by selecting the  
252 number of synergies at which the VAF curve achieves the highest curvature (Tresch et al.  
253 2006).

254 Muscle synergies were then sorted in the same order for each locomotor condition and species  
255 through a k-means algorithm (MATLAB function 'kmeans') applied to the  $W$  matrix considering  
256 the optimal number of muscle synergies as the number of k-means clusters (Steele et al.  
257 2015b).

258 To quantitatively assess the motor control strategies adopted by the central nervous system  
259 during different locomotor tasks, we calculated the fraction of data variance accounted for by  
260 the muscle synergy model considering 1 muscle synergy (called VAF1) to estimate the  
261 complexity of the original sEMG signals (Steele et al. 2015a). The VAF1 values range between  
262 0% and 100%. When VAF1 is high, it means that a single synergy can explain most of the  
263 variance in muscle activation, which indicates a reduction in the complexity of motor control.

264 Moreover, the full width at half maximum (FWHM) was calculated on the activation coefficients  
265 for each stride cycle as the number of time samples exceeding half of the curve's maximum,  
266 after subtracting the minimum within the respective stride cycle (Janshen et al., 2020; Janshen  
267 et al., 2021). This value was computed to estimate the duration of the activation of each muscle

268 synergy. Activation coefficients characterized by long activation intervals (i.e., neural  
269 commands less selective in time) will be described by high FWHM values, while activation  
270 coefficients characterized by small activation intervals (i.e., neural commands more selective  
271 in time) will be described by low FWHM values. The generalizability of the muscle synergy  
272 model across the different species and walking conditions was assessed through the cross-  
273 variance. Cross-variance accounted for (cross-VAF) parameter was defined as in the study  
274 by Ghislieri et al. (2020). Cross-variance accounted for values range between 0% (low  
275 generalizability) and 100% (high generalizability).

276

#### 277 *2.4. Statistics*

278 The full width at half maximum and cross-VAF are compared between species and locomotor  
279 modes using exact (nonparametric) tests: the Permutation tests for independent samples.  
280 Additionally, we employed the same tests to compare the speed and stride duration between  
281 the two baboons among the locomotor modes. We used the software for exact nonparametric  
282 inference StatXact v. 3.1 (Cytel, Inc., Cambridge). The significance threshold was set at  $p <$   
283 0.05 for the permutation tests.

284

### 285 **3. Results**

286 Surface electromyography signals from six muscles were recorded during terrestrial bipedal  
287 and quadrupedal walking in two female baboons and during overground bipedal walking in  
288 five healthy humans. A detailed description of the sEMG profiles obtained for individuals is  
289 provided in the Supplementary Online Material (SOM) Figures S1 (baboons) and S2 (humans;  
290 see also SOM S1). In baboons, bipedal walking generally requires higher levels of muscular  
291 activity than quadrupedal walking (Fig. 3A; SOM Fig. S1). The bursting sEMG profiles are also  
292 relatively longer in time during bipedal walking compared to quadrupedal walking. Table 1  
293 presents the average values per individual for the speed and stride duration observed during  
294 bipedal and quadrupedal walking at comfort speed on the ground. ID1 exhibits significantly  
295 longer stride duration than ID2 when walking quadrupedally (permutation tests  $=-2.52$ ,  $p =$   
296 0.0097), but the speed is not significantly different. There is no difference between the two  
297 individuals when walking bipedally.

298

299 *3.1. Muscle synergy model*

300 The number of muscle synergies extracted is the same between locomotor modes and  
301 species. Three muscle synergies describe the motor control strategies of baboons (during  
302 both bipedal and quadrupedal walking) and humans (Fig. 3B, C). The VAF is 92.1% (SD =  
303 2.2%) in baboons walking bipedally, 88.9% (SD = 1.5%) in baboons walking quadrupedally,  
304 and 92.2% (SD = 2.2%) in humans (walking bipedally). We ordered the synergies to obtain  
305 the best match between species and individuals and thus compare the synergies which are  
306 more alike (see below).

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

311

312 *3.2. Connecting the synergies in humans to potential biomechanical functions during walking*

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

329

330 *3.3. Connecting the synergies in baboons to potential biomechanical functions during walking*

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

351

352 *3.4. Muscle synergy analysis*

353 From the activation coefficients, FWHM is extracted for each muscle synergy and each stride  
354 cycle. Figure 4 represents the distributions of the FWHM values for each extracted muscle  
355 synergy across species and locomotor modes. Increased FWHM is hypothesized to be a  
356 compensatory mechanism adopted by the central nervous system to cope with internal and/or  
357 external postural instabilities. Compared to humans, the baboons walking bipedally show a  
358 significant increase in the FWHM for the two first synergies extracted (Syn 1: permutation tests  
359 = 6.453,  $p < 0.0001$ ; Syn 2: permutation tests = 5.355,  $p < 0.0001$ ) and a decrease of the  
360 FWHM for the third synergy (permutation tests = -4.557,  $p < 0.0001$ ; Fig. 4). The baboons  
361 walking quadrupedally show a significant decrease of the FWHM for the first and third  
362 synergies compared to humans and an increase of the FWHM for the second synergy (Syn 1:

363 permutation tests = -4.922,  $p = 0.0001$ ; Syn 2: permutation tests = 3.316,  $p = 0.0007$ ; Syn 3:  
364 permutation tests = -3.613,  $p = 0.0003$ ; Fig. 4). When comparing baboons walking bipedally  
365 and quadrupedally, the FWHM values are significantly higher for the two first synergies (Syn  
366 1: permutation tests = 6.886,  $p < 0.0001$ ; Syn 2: permutation tests = 2.439,  $p = 0.0139$ ; Fig. 4)  
367 and significantly lower for the third synergy when walking bipedally (Syn 3: permutation tests  
368 = -2.532,  $p = 0.0109$ ; Fig. 4).

369 The calculation of the cross-VAF parameter allows us to estimate the overall effectiveness of  
370 the muscle synergy model across the different locomotor conditions and species studied.  
371 Figure 5A shows the average cross-VAF values for each condition and individual. There is a  
372 significant difference between the two baboons, i.e., the bipedal and quadrupedal patterns  
373 observed in ID1 are more similar to each other than the bipedal and quadrupedal patterns are  
374 in ID2 (permutation tests = -3.151,  $p = 0.0011$ ; Fig. 5). There is no significant difference when  
375 the two baboons are compared across the same locomotor mode, i.e., the similarity of the  
376 bipedal pattern between the two baboons is alike the similarity of the quadrupedal pattern  
377 between the two baboons. There is a significant difference between the locomotor modes for  
378 each baboon when compared to humans. Specifically, the bipedal pattern is more similar to  
379 humans than the quadrupedal pattern, and this result holds for both baboon individuals  
380 considered separately (ID1: permutation tests = 2.132,  $p = 0.0329$ ; ID2: permutation tests =  
381 4.728,  $p < 0.0001$ ; Fig. 5A) and when both individuals are analyzed as a group (permutation  
382 tests = 4.317,  $p < 0.0001$ ; Fig. 5B).

383

## 384 **4. Discussion**

### 385 *4.1. Affinities in the modular control of bipedal and quadrupedal locomotion in baboons*

386 We hypothesized that baboons, a non-adapted biped species, should rely on the same  
387 modular control of its quadrupedal locomotion for moving bipedally as humans. Our results in  
388 part support this hypothesis as few differences related to the stance phase can be  
389 emphasized. First, the baboons walking bipedally show a synergistic control with the same  
390 number of synergies as for quadrupedal walking and the synergy corresponding to the swing  
391 phase (Syn 3) is similar (in terms of both neural command and muscles' contribution) across  
392 locomotor modes. Second, the stance phase appears to be a more variable phase (Syn 1 and  
393 Syn 2). Interestingly, both baboon individuals show very similar synergies during bipedal  
394 walking suggesting that they respond in the same way to this occasional motor task. The motor  
395 control is less complex during bipedal walking (i.e., higher VAF1 values) than during the

396 quadrupedal progression and the activation coefficients show a longer period of activation  
397 (i.e., higher FWHM values) during the stance phase, thus supporting our prediction of more  
398 coactivated muscles in this locomotor mode, as previously observed in macaques (Higurashi  
399 et al., 2019). Bipedal walking remains an occasional locomotor mode in baboons and  
400 macaques and keeping balance is likely to represent a greater challenge than walking  
401 quadrupedally. A longer period of muscle coactivation during the stance phase can help in this  
402 task as it would benefit in stabilizing the degrees of freedom at the hip and knee joints (see  
403 also Druelle et al., 2022). Third, with regard to quadrupedal walking, it appears that one  
404 synergy (Syn 2) shows clear differences between individuals, while the other two synergies  
405 (Syn 1 and Syn 3) are very similar. The difference thus arises from a neural command covering  
406 the stance phase for ID1 (Syn 2, dark color) in which the gastrocnemius muscle contributes  
407 significantly (as during bipedal walking), while the equivalent neural command for ID2 (Syn 2,  
408 light color) is focused on the second half of the stance phase and mainly involves the rectus  
409 femoris muscle. Interindividual variability of the sEMG profiles can be expected according to  
410 various parameters, such as differences in body built and inertial properties as well as  
411 differences in motivation during the experimental sessions (see Winter and Yack, 1987;  
412 Courtine et al., 2005). Also, we observed significant differences in the stride duration between  
413 individuals during quadrupedal walking, thus pointing out to different speed-related strategies  
414 (see also Druelle et al., 2021). Individual 1 exhibits shorter stride duration (i.e., higher stride  
415 frequency) than ID2 while moving at the same speed. In addition, an important flexibility of the  
416 neuromotor control has been suggested in primates as it allows to cope with the different  
417 substrates encountered during daily activities, such as the ground, trees, and cliff faces.  
418 Development and individual experiences can also play a significant role for building up  
419 locomotor strategies. A flexible nature of the neuromotor command during quadrupedalism  
420 would fit with the tight evolutionary relationship of primates in general, and baboons in  
421 particular, with the complex arboreal environment (Vangor and Wells, 1983; Vilensky, 1987;  
422 Vilensky and Larson, 1989; Young, 2012; Chadwell and Young, 2015; Patel et al., 2015;  
423 Young et al., 2016; Druelle et al., 2021). Interestingly, Syn 1 in quadrupedal walking presents  
424 the lowest FWHM values (see Fig. 4), thus suggesting that the early period of the stance  
425 phase (potentially related to the stability of foot positioning and the load acceptance function)  
426 is particularly effective in baboons. In summary, occasional bipedal walking in baboons elicits  
427 remarkably similar synergies, as they respond to the same challenging mechanical  
428 requirements. However, when it comes to habitual quadrupedal walking, we can expect to  
429 observe more interindividual variations. This variation arises not despite their specialization  
430 but rather because of it as they are much more experienced in practicing this mode.

432 *4.2. Baboons and humans share only a few aspects of their muscle synergies*

433 Since bipedalism and quadrupedalism represent the habitual locomotor mode of humans and  
434 baboons, respectively, and a (neuromotor) relationship between the two locomotor modes has  
435 been previously established (Aerts et al., 2000; D'Août et al., 2004; Balter and Zehr, 2007;  
436 Zehr et al., 2009; Berillon et al., 2011; Higurashi et al., 2019; Aerts et al., 2023), we  
437 hypothesized that the patterns observed in humans should be shared, in some respects, with  
438 the ones of the baboons walking quadrupedally. Our results partially support this hypothesis.  
439 Although the number of synergies is alike, the shape of the neural commands and the muscle  
440 contributions show significant variations between the two species. The most similar synergy  
441 is the one activated during the swing phase (Syn 3), where the tibialis anterior (greater extent)  
442 and the biceps femoris (lesser extent) muscles contribute significantly in humans, while the  
443 tibialis anterior is the main contributor to this synergy in baboons (as commonly observed in  
444 quadrupedal mammals; Rasmussen et al., 1978; Kimura et al., 1979; Vilensky, 1987). It is  
445 worth noting that the important differences observed can also directly result from the way the  
446 two species touch the ground, i.e., semi-plantigrady in baboons with no heel contact during  
447 the stance phase (Berillon et al., 2010) *versus* plantigrady in humans with a clear heel-strike  
448 at touch-down (see Oku et al., 2021 for explorations of this influence in macaques). For  
449 instance, this clear kinematic difference makes the biceps femoris muscle working in a very  
450 different way in baboons compared to humans, i.e., initiating its activity just before touch-down  
451 in baboons and during all the stance phase, while it is primarily active at the end of the swing  
452 phase during the transition between the swing and the stance phase in humans. Furthermore,  
453 we observe that baboons' bipedal walking is more similar to human bipedal walking than  
454 baboon quadrupedal walking is to human walking (see cross-VAF analyses). Interestingly, the  
455 swing phase appears to require less muscle activity in baboons walking bipedally compared  
456 to humans (FWHM values are significantly lower in baboons for the synergy related to the  
457 swing phase). The swing phase is managed in a relatively simple and efficient way in baboons.  
458 Therefore, concerning the possible biomechanical functions related to the stance phase, i.e.,  
459 load acceptance, weight-bearing and propulsion, it appears plausible that they could constitute  
460 the foremost mechanical prerequisites for a baboon engaged in bipedal walking, as opposed  
461 to focusing on foot clearance and positioning. Interestingly, the recent study by O'Neill et al.  
462 (2022) on the three-dimensional joint mechanics during bipedal walking of the chimpanzee  
463 (another non-adapted biped) draws similar conclusions. They showed that during the stance  
464 phase, significant differences in work and power output exist between chimpanzees and

465 humans, while the human limb structure does not specifically reduce positive work and power  
466 during limb swing. Additionally, their results reveal a shift of positive mechanical work and  
467 power output toward the distal joints in humans during the stance phase, contrasting with the  
468 more proximal distribution of limb work in bipedal chimpanzees. Although the angle of attack  
469 differs between the study of O'Neill et al. (2022) and this study and despite the data sources  
470 differ (inverse dynamics and EMG), both findings highlight the most significant distinctions  
471 between an adapted and a non-adapted biped at the stance phase level.

472

#### 473 *4.3. Toward evolutionary implications*

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

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

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

526

#### 527 4.4. *Potential limitations and conclusions*

528 The study presented here poses several inherent challenges as conducting motor control  
529 analysis on non-human primates involves striking a delicate balance between the scientific  
530 inquiry, animal welfare considerations, accessibility to the animals and statistical  
531 requirements. Regarding our experimental protocol on baboons, we have tried to refine it as

532 much as possible to minimize the duration of the anesthesia required for skin preparation and  
533 electrode positioning. Furthermore, with regard to baboon morphology, the accessibility of the  
534 muscles from the skin using surface probes differs significantly from that of humans. The  
535 smaller size of baboons compared to humans introduces inherent spatial limitations when  
536 positioning the surface probes. Therefore, we were only able to select six muscles that are  
537 accessible from the skin in baboons. Although in muscle synergy analyses, the outcomes of  
538 non-negative matrix factorization can be sensitive to the number of muscles considered  
539 (Steele et al., 2013), previous studies based on five and six muscles have successfully applied  
540 muscle synergy analyses, yielding results comparable to studies that utilized a larger muscle  
541 set (Steele et al., 2015b; Kim et al., 2018; Steele et al., 2019; Hu et al., 2019; Oudenhoven et  
542 al., 2019; Vandekerckhove et al., 2020). Essential aspects of the muscle synergy analysis  
543 thus appear to remain consistent across studies using different number of muscles. Therefore,  
544 focusing on 6 muscles that contribute to crucial flexion and extension movements of the  
545 hindlimb (agonist and antagonist muscles acting on the ankle, knee and hip) represents a  
546 compromise that enables us to work effectively with baboons and to perform a comprehensive  
547 muscle synergy analysis that can be meaningfully compared to human data. Nevertheless,  
548 gathering data from a broader set of muscles would undoubtedly enables a more  
549 comprehensive muscle synergy analysis, shedding further light on the shared characteristics  
550 and distinctions between bipedal and quadrupedal locomotion. The cross-VAF, overall  
551 commonalities, and differences between baboons and humans might be further refined with  
552 additional muscle data. Specifically, decomposing the general EMG signal into more than  
553 three synergies could provide additional insights.

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

563

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565

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581

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913

914 **Figure captions**

915

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

920

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

924

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

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

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

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