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Commentary

Revealing neuromuscular similarities between baboons and humans: A commentary on Druelle et al. (2024)

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We have read with great interest the insightful study by Druelle et al. (2024) on neuromuscular control during quadrupedal and bipedal locomotion in baboons with comparisons to human bipedal walking. First, we commend the authors for addressing a challenging topic and producing high-quality data that contribute to our understanding of bipedal evolution. Based on their analysis of locomotor modules, the authors speculate about the gradual and complex evolutionary shift toward habitual bipedalism. In particular in their discussion, they report an increased variability in quadrupedal as compared to bipedal gait in baboons and suggest that humans and baboons share only limited aspects of their muscle activation patterns during bipedal gait. However, in light of our previous research, we would like to propose alternative perspectives and interpretations.

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

Druelle et al. revealed that the two recorded baboons rely on similar modular control for moving bipedally and quadrupedally. Also, the authors suggest that bipedal walking in baboons exhibits reduced interindividual variability compared to quadrupedal walking. These conclusions are mainly drawn based on the similar number of muscle synergies observed and on different spatial structures (time-independent weight vectors, W), which describe the muscle contribution to specific synergies.

An issue with the comparison of synergistic structures across small groups of individuals is to know if the natural variation in synergy composition among individuals within a group can overshadow between-group difference. Indeed, synergy sets are often compared by selecting a fixed number of synergies, typically based on criteria derived from the variance-accounted-for curve. However, this curve is influenced by both structured variability (i.e., flexible recruitment of synergies adapted to task demands) and random variability (e.g., signal noise or sensorimotor fluctuations [Sylos-Labini et al., 2022]). When the selection relies on a single point of this curve, the estimated number of synergies—and thus the assessment of similarity—can be biased by the noise level, particularly in small samples (d'Avella et al., 2022). Additionally, comparisons between groups often rely on matching individual synergies (e.g., by identifying the most similar pairs across conditions or subjects). The outcome of these comparisons may vary depending on whether spatial components, temporal activations, or both are used (Martino et al., 2015), potentially leading to inconsistent interpretations. These methodological considerations highlight the importance of cautious interpretation when evaluating between-group differences in synergy structure, particularly in studies with small sample sizes.

In the case of the baboon data, visual inspection of the averaged surface electromyography (EMG) and activation coefficient (Fig. 3A and B in Druelle et al., 2024) may suggest conflicting conclusions as the greater interindividual variability of bipedal walking relative to quadrupedal walking appears evident. For example, during bipedal gait, the gluteus medius shows a shift in peak timing between individuals ID1 and ID2. Similarly, the peroneus longus and rectus femoris display different activation durations and peak amplitudes across individuals, while profiles are more consistent during quadrupedal walking. Contrary to the authors' interpretation, it could be reasonable to expect reduced variability in habitual quadrupedal walking. Indeed, motor

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expertise often leads to optimized strategies that enhance performance and reduce functional costs, as evidenced by lower variability in highly skilled movements (Fujii et al., 2009; Marineau et al., 2024). In this case, the higher variability of individual EMG data during bipedal walking may be interpreted as the reflection of the occasional nature of this gait in baboons.

The only way to address this open question would be to increase the sample size. Given the inherent variability in neuromuscular control, recruiting a larger number of baboons would likely provide a more robust evaluation of interindividual variability and strengthen conclusions regarding the similarity of modular control across different gait types.

2. Baboons and humans may share more than a few aspects of their muscle synergies

Druelle et al. (2024) highlight substantial differences between human and baboon bipedal gait and suggest that these differences stem directly from foot-ground interaction. Human bipedal locomotion is unique in the animal kingdom, requiring specific adaptations of the locomotor apparatus (Crompton et al., 1998). As illustrated in Figure 2 of Druelle et al. (2024), baboons differ from humans in bipedal gait by adopting a semiplantigrade foot posture, with no heel contact during the stance phase, and by maintaining a more crouched posture (i.e., greater knee and trunk flexion).

In recent studies, we investigated the impact of these kinematic features on human gait by asking participants to walk with altered trunk inclination (Núñez-Lisboa et al., 2024) or to walk with a semiplantigrade foot placement (Mesquita et al., 2023). We found that in both cases, participants adopted a more crouched limb configuration, characterized by greater hip, knee, and ankle flexion, and showed reduced propulsion from the trailing limb. These kinematic adaptations were accompanied by earlier and prolonged activation of distal extensor muscles (e.g., gastrocnemius) and a shift from anticipated to unanticipated step-to-step transitions, where the redirection of the center of mass occurred after foot contact rather than before. Similar results were also obtained when imposing knee flexion during the stance phase of walking (Grasso et al., 2000). For instance, the biceps femoris, typically active at the end of the swing phase in normal human gait, showed a distinct activation burst during stance. Such results suggest that at least part of the muscle activation patterns observed in baboons may arise from biomechanical constraints associated with posture and foot placement, rather than from fundamentally different control strategies.

However, the unique features of human bipedal gait develop progressively during childhood. Humans begin walking significantly later than most animals. However, precursory forms of walking emerge in early infancy, already displaying striking similarities to the mature gait observed in adulthood. Among these early forms is neonatal stepping, a behavior observed in the first weeks of life, in which newborns generate alternating leg movements when held upright with their feet touching a surface. This behavior exhibits fundamental elements of the spatiotemporal organization of mature gait (Dominici et al., 2011; Dewolf et al., 2020a, 2020b; Sylos-Labini et al., 2020). These basic motor patterns appear innate and are thought to provide a foundation upon which more refined gait emerges during development.

Later in infancy, many children exhibit what we refer to as nonindependent walking, that is, walking with bodyweight partially supported by an adult, before the fully autonomous gait is achieved. While these steps are voluntarily initiated and structurally similar to mature walking, they still differ in several respects: Infants tend to adopt a wider base of support, increased limb flexion, and a reduced use of the heel-to-toe rollover strategy. Importantly, their muscle synergies are still undergoing refinement (Sylos-Labini et al., 2022). With age and walking experience, children straighten their legs during stance and improve their exploitation of the inverted pendulum mechanism (Ivanenko et al., 2004). They progressively adopt a heel-to-toe strategy (Hallemans et al., 2006; Nuñez-Lisboa et al., 2023), which, in turn, leads to a refinement of muscle coordination (Dewolf et al., 2020a, 2020b). From this developmental perspective, if we compare baboon locomotion to human gait before these postural and coordination refinements occur, one may adopt a different view on the claim that baboons and humans share only limited aspects of their muscle synergies.

During stepping in neonates, lower-limb muscle activity is sinusoidally modulated across the gait cycle, with many extensor muscles coactivated during stance, while flexor muscles dominate during swing. Two fundamental activation patterns sufficiently reproduce the EMG profiles of all recorded muscles (Dominici et al., 2011; Sylos-Labini et al., 2022). The first pattern, occurring during stance, is triggered by limb loading, activating antigravity muscles and correlating with the knee extension in midstance (Dewolf et al., 2022). The second pattern emerges during swing, elicited primarily by limb unloading and hip extension, and is characterized by tibialis anterior activation. With age, stepping control becomes progressively refined, increasing the number of temporal patterns until an adult-like organization is achieved after independent walking is established (Sylos-Labini et al., 2020).

Druelle et al. (2024) observed in baboons a coactivation of multiple extensor muscles during stance, accompanied by tibialis anterior activity during swing. This resembles the neonatal loading response, further supported by studies on chimpanzee bipedal walking, which highlight load-related muscle activation during stance and extension torque generation at all three lower-limb joints around midstance (O'Neill et al., 2022). The similarities become even more striking when comparing muscle synergy structures in baboons and human infants before their first independent steps (10–14 months; Fig. 1). Both exhibit three synergies: The first synergy involves mainly biceps femoris and rectus femoris, the second synergy involves mainly gastrocnemius, and the third one mainly involves tibialis anterior. Such shared modular control of gait, as previously documented across species by Dominici et al. (2011), suggests the persistence of fundamental neural architectures of gait. It echoes the debated idea that 'ontogeny recapitulates phylogeny' (originally proposed by Ernst Haeckel) as early ground-stepping in humans may reflect ancestral motor patterns seen in nonhuman primates.

3. Toward evolutionary implications

While we agree with Druelle et al. (2024) on the value of studying muscle synergies in nonhuman primates to understand bipedal evolution, we believe their results highlight more similarities between humans and baboons than they suggest. Evolution does not discard ancestral traits but rather adapts them to efficiently address new challenges, supporting the idea that locomotion is built upon ancient motor primitives rather than entirely novel designs. Rather than viewing these results solely through the lens of evolutionary conservation, they can also be interpreted as evidence of shared task-dependent adaptations, that is, the emergence of similar neuromechanical solutions to the challenges of bipedal locomotion in species with distinct developmental and ecological contexts. For instance, features such as crouched limb posture, semiplantigrade foot placement, and stance-phase activation of muscles like the biceps femoris are observed both in baboon bipedalism and in early stages of human gait development. These parallels suggest that certain motor strategies may emerge

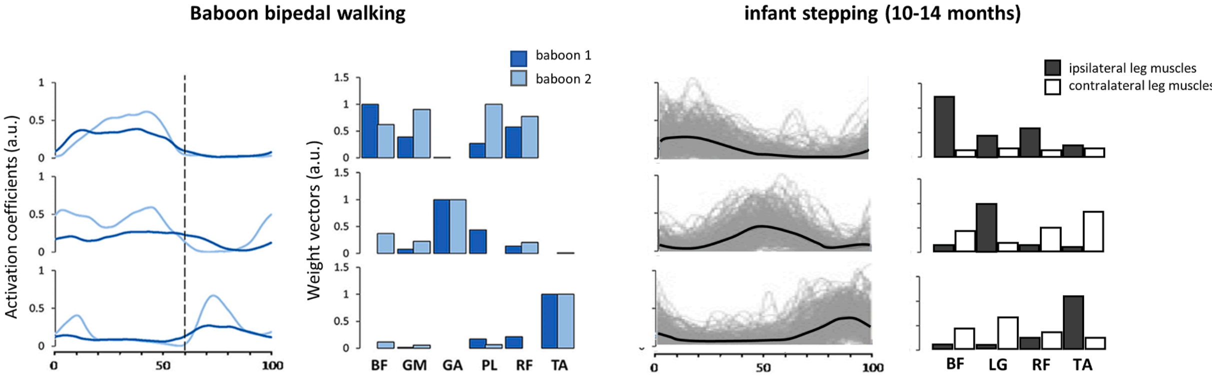

Figure 1. Comparison of the neuromuscular modules of bipedal walking in baboons (left) and supported stepping in 10- to 14-month-old infants (right). Both the average activation coefficients and the weight vectors of the three synergies extracted from EMG profiles are presented. The data from two baboon individuals (baboon 1: dark blue and baboon 2: light blue) have been redrawn from Druelle et al. (2024). The infant data have been adapted from Sylos-Labini et al. (2020). In this study, the authors computed the neuromuscular modules from four bilateral EMG recordings during treadmill stepping (ipsilateral leg muscles: dark bars; contralateral leg muscles: white bars). Abbreviations: a. u. = arbitrary units; BF = biceps femoris; EMG = electromyography; GM = gluteus medius; GA = gastrocnemius lateralis; LG = lateral gastrocnemius; PL = peroneus longus; RF = rectus femoris; TA = tibialis anterior. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

independently in response to similar biomechanical constraints, rather than reflecting direct evolutionary continuity. This perspective is supported by recent work from Núñez-Lisboa et al. (2024), which showed that adopting bent postures in human walking induces neuromechanical adjustments that resemble those observed in nonhuman primates, like greater knee flexion, lack of trailing limb propulsion, and so on. Such features mirror several aspects of baboon bipedal gait, suggesting that similar biomechanical constraints (e.g., trunk inclination and lack of heel strike) may drive analogous neuromuscular strategies despite different evolutionary histories.

While the qualitative comparison of muscle synergies between human infants and baboons provides valuable insights into shared coordination strategies during early bipedal walking, we acknowledge a key limitation: The (number of) muscles included in the synergy analysis may differ between species (Fig. 1). As such, the present comparison aims to highlight general organizational features, such as stance- vs. swing-phase activation and proximal-to-distal recruitment patterns, that may reflect common biomechanical demands or developmental principles. Future studies exploring interspecies variability in muscle synergies, particularly comparing arboreal and terrestrial species or those phylogenetically closer to humans, will further illuminate the neuromechanical adaptations shaping bipedal evolution. Investigating how different ecological niches and locomotor strategies influence neuromuscular control will be crucial in refining our interpretations of bipedal evolution. As Marcia McNutt aptly stated, “Interpretation comes and goes, but data are forever”—and the data presented by Druelle et al. (2024) provide a solid foundation for advancing this exciting field of research.

Declaration of competing interest

There is no conflict of interest.Please Check the unhandled section found

Authors contributions

Arthur H. Dewolf: Writing – review & editing, Writing – original draft, Conceptualization. **Francesco Lacquaniti:** Writing – review & editing, Writing – original draft, Conceptualization.

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