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EDITOR'S NOTE

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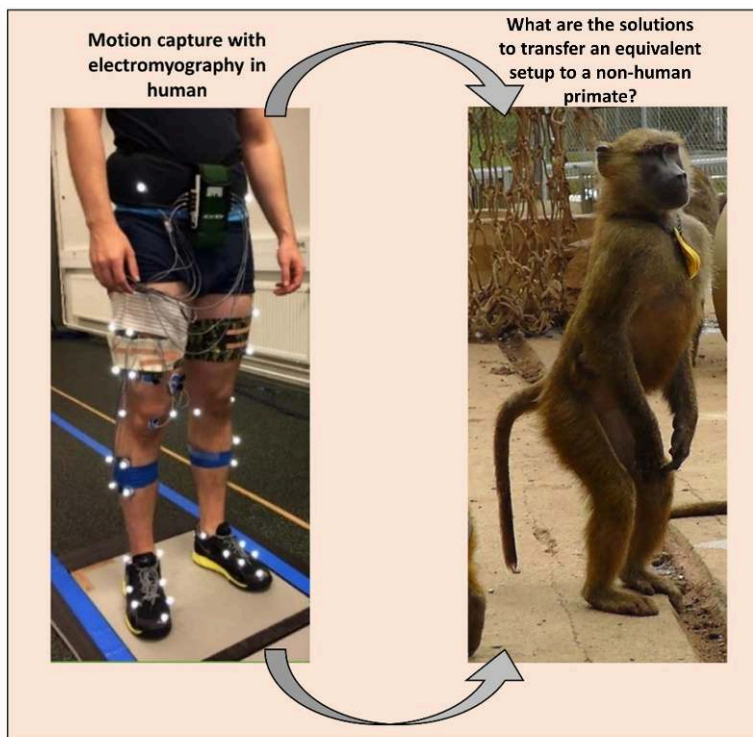
1 Introduction

- 1 The way humans walk and run bipedally is unique and this adaptation represents a key milestone in the evolutionary pathway of our lineage (Alexander, 2004; Crompton et al. 2008; Pontzer, 2017). Today, bipedal walking and running can be studied with extreme accuracy thanks to many technological developments [e.g. accelerometers, force plates, surface electromyography (EMG) electrodes, optoelectric imaging systems]. As a result, bipedalism in humans is well described biomechanically, neurologically and

physiologically (Kirtley, 2006; Winter, 2009) and these fields keep delivering fundamental findings and highly detailed results (e.g. Charles et al. 2021; Esrafilian et al. 2020; Wu et al. 2019). However, understanding the origin of habitual bipedal locomotion requires work on comparative models that are phylogenetically closely related to humans (e.g. O'Neill et al. 2018). The study of non-human primates and of the nature of their (occasional) bipedal locomotion represents a great opportunity to highlight the constraints related to this mode in non-adapted bipeds. However, studying bipedal locomotion in non-human primates using the same methodology as in humans represents a great challenge. The constraints of bringing a non-human primate into a laboratory to make it walk on a technical platform for biomechanical analysis and equipped it with sensors and markers are high, and obviously much higher than when studying humans (Fig. 1). For example, trying to make a non-human primate wear tiny infrared lights on a set of anatomical landmarks remains extremely challenging and there is always a high risk of having the expensive system destroyed by the animal.

- In this note, we propose documenting an experimental approach that aims at reaching the standards of the study of human movement in a non-human primate, the olive baboon, *Papio anubis*, thanks to the use of positive reinforcement techniques. We are applying this protocol in the context of our ongoing research work on the ontogeny of bipedal locomotion in baboons.

Figure 1



Illustrations showing a human individual equipped with a motion capture system with EMG to study knee joint loading and a baboon standing bipedally in a flexed posture. The illustration of the human individual was extracted from Esrafilian et al. (2020). The illustration on the right-hand side was taken by FD and shows a baboon raised in captivity at the primatology station of the CNRS.

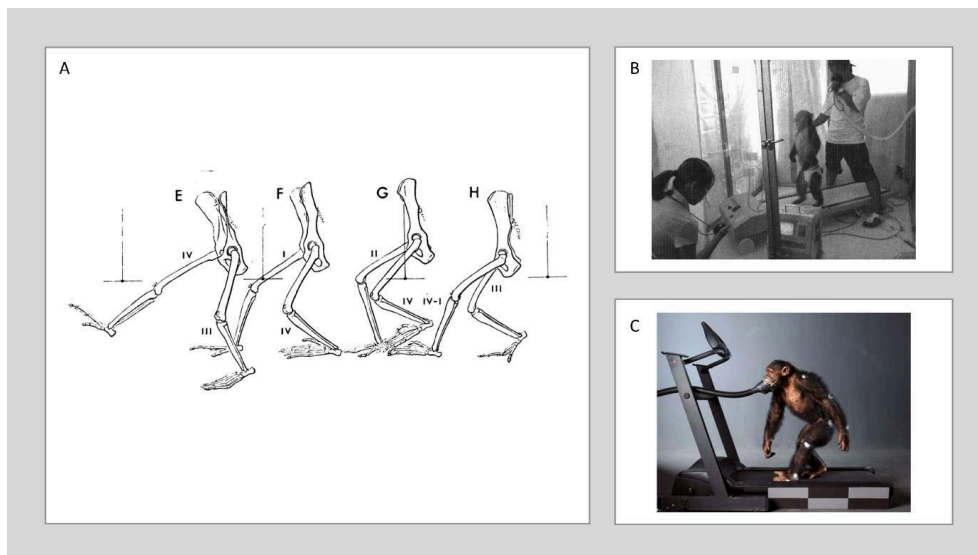
2 Basic historical elements of the study of bipedal walking in non-human primates

- 3 Locomotor resemblances and differences between human and non-human primates are of great interest in the field of palaeoanthropology. The first comparative and quantitative studies of human *versus* non-human primate bipedalism can be found in the pioneering works of Elftman and Manter (1944; 1935). In these studies, they used an advanced setup to quantify the distribution of pressure under the foot in a chimpanzee and a human walking bipedally. Forty years later, other experimental works opened new ways to explore the bipedal locomotion of non-human primates, laying the foundations of the modern comparative study of human bipedal walking (e.g. Ishida et al. 1974; Jenkins, 1972; Kimura et al. 1979; Prost, 1967; Stern & Susman, 1981; Taylor & Rowntree, 1973; Tuttle et al. 1979). These studies have highlighted both the differences and similarities between human and non-human primate bipedalism. For instance, the hyperextension of the hip at heel off and the straightened knee joint at the beginning of the stance phase are typical features of the human erect bipedalism that are not present in non-human primates (Ishida et al. 1974). Jenkins (1972) showed that, in chimpanzee, the femur is abducted and kept in a flexed position (as during quadrupedal knuckle-walking) and the movement of the pelvis is different from that of humans as it rises on the side of the swing leg (e.g. Thompson et al. 2021). There are also larger mediolateral displacements of the centre of mass in non-human primates walking bipedally compared to humans. On the other hand, Stern and Susman (1981) have shown that the role of the *gluteus medius* is the same in humans and great apes walking bipedally. Its role is to balance the side-to-side movement of the trunk at the hip during bipedal locomotion. Furthermore, Ishida et al. (1974) showed that both humans and chimpanzees present an extension of knee joint, significant activity of the *gastrocnemius* muscle, and a high peak of the vertical ground reaction force during the second phase of the stance phase.
- 4 Since then, various setups have been developed and these have opened new perspectives about our understanding of human locomotor evolution (e.g. Aerts et al. 2000; Berillon et al. 2010; D'Août et al. 2004; Hirasaki et al. 2004; Hirasaki et al. 2006; Nakatsukasa et al. 2006; O'Neill et al. 2018; Ogihara et al. 2007; Pontzer et al. 2014; Sockol et al. 2007; Thompson et al. 2021; Vereecke et al. 2006). In the literature, two main approaches can be found, the observational and experimental approaches. The observational approach concerns the studies in which the variables are not controlled. It records the behaviour of an animal when and where it happens and thus presents inherent limitations. The experimental approach aims at controlling important independent variables that can influence the dependent variable under study (e.g. bipedal kinematics, kinetics, EMG) so that the researchers can directly evaluate causes and effects (see figure 2 for examples). The experimental approach can thus open new perspectives and provide important insights into key aspects that remain difficult to study in free-ranging or uncontrolled conditions. For instance, the diversity of foot postures during bipedal walking remains poorly documented in non-human primates (but see Berillon et al. 2010; Holowka et al. 2017; Vereecke et al. 2003; Vereecke et al. 2005; Vereecke & Aerts 2008), as well as how these are affected by substrate variation. The movements of the pelvis, the lower back, the forelimbs, including hand positioning and use, are also poorly documented during bipedalism. Recent experimental studies

have started to explore the movements of the trunk during bipedal walking and have revealed more flexibility than was initially predicted (Kinoshita et al. 2021; O'Neill et al. 2018; Thompson et al. 2015; Thompson et al. 2018). The study of the transitions from another locomotor mode to bipedal walking is also an area of research where there is a lack of experimental data (but see Mori et al. 2006; Nakajima et al. 2001). Studying the biomechanics of bipedalism with an experimental approach in non-human primates can allow accurately exploration of these aspects and therefore help us to better understand the evolution of the bipedal locomotor mode in primates, including hominins.

- 5 However, compared to the experimental biomechanical protocols applied in human locomotion, conducting an experiment on non-human primate locomotion represents a big challenge as it requires bringing the animal in close contact with the researchers and with fragile and expensive measurement equipment. In this context, using positive reinforcement techniques, as part of the experimental study procedure, can offer the possibility of conducting unique research protocols. Working with a cooperative animal can approach the standards of human-based studies and also direct comparisons of the data collected in humans with those collected in non-human primates. It also ensures an optimal level of the Refinement component of the "3Rs" rule (Russell & Burch, 1959).

Figure 2



The three illustrations were extracted from previously published scientific papers. (A) shows skeletal postures of a chimpanzee walking bipedally obtained from cineradiography and is after figure 1 in Jenkins (1972), (B) shows a Japanese macaque with his trainer in an experimental chamber and the illustration is after figure 2 in Nakatsukasa et al. (2004) and (C) shows a chimpanzee walking bipedally on a treadmill as part of UC Davis anthropologist Michael Sockol's research (see Sockol et al. 2007) ©Cary Wolinsky.

3 The use of positive reinforcement techniques to study bipedal walking in baboons

- 6 Movement performance is strongly influenced by several variables, such as the speed of progression and the direction of movement (e.g. Alexander, 1976; Alexander & Jayes, 1983). It is possible to apply a *post-hoc* control of these variables, but this reduces the

amount of data available for the analyses and the sampling effort needs to be enormously increased to compile enough exploitable data. Based on our experience of both, experimental and behavioural studies in olive baboons (e.g. Berillon et al. 2010; Anvari et al. 2014; Druelle et al. 2017), our team aimed at setting up an experiment on this species that makes possible to control, a priori, these variables and optimize repeatability. During the last decade, our team has implemented different training protocols based on positive reinforcement in the context of the study of locomotion in baboons, including bipedal walking. Positive reinforcement occurs when a desirable event, or stimulus, is presented because of a behaviour, hence the likelihood that this behaviour would happen again in similar conditions increases. Our goal was thus to accommodate the baboons to walk bipedally in an instrumented environment, including surface electrodes for the study of muscular activity and a treadmill. The use of such a device allowed us to control speed and direction of movement and at the same time to collect large datasets in terms of walking cycles, thus optimizing repeatability.

- 7 Here, we present the main protocol that we developed and implemented at the Primatology Station of the CNRS (UAR 846) to study bipedal and quadrupedal locomotion in olive baboons, *Papio anubis*. This protocol allows to reach the accuracy of the experimental protocols applied in humans (e.g. Berillon et al. 2013; Druelle et al. 2021). Our aim is to document the way we trained the animals using positive reinforcement techniques, as well as the amount of training necessary for baboons (and potentially for other non-human primate models) to walk bipedally and quadrupedally on a treadmill. Finally, we highlight the possibilities opened up by such an approach for the study of bipedalism in non-human primates in general. Note that according to the current international ethical regulations, the present protocol including anaesthesia of the animals cannot be implemented in apes (see the Directive 2010/63/EU of the European Parliament and of the council of 22 September 2010 on the protection of animals used for scientific purposes ; <https://eur-lex.europa.eu/legal-content/EN/TXT/HTML/?uri=CELEX:32010L0063>). The procedure described here on baboons was evaluated by ethical committees on animal experimentation and approved by the French Ministry of Higher Education and Research (Project 68-19112012, CEEA-14 Marseille, and Project APAFIS#16621-2018090509386918 v2, ethical committee n°071).
- 8 Different learning techniques, and not only positive reinforcement, were used here to train the animals to cooperate during experiments. Positive reinforcement learning paradigm, i.e., rewarding the animal when performing the desired behaviour, and systematic desensitization were the main techniques used here (Prescott & Buchanan-Smith, 2016; Schapiro et al. 2003). No coercion was used, and mistakes were ignored, not punished. The animal was always able to choose whether it was willing to participate in the training program or not (for a review of all these techniques, see Pryor, 2019). As a result, we have worked with the voluntary cooperation of the animals, thus ensuring the highest level of the Refinement component of the "3Rs" rule (Russell & Burch, 1959).

3.1 Selection of the animals

- 9 Selection of the animals for the experiments was done using a very simple "boldness test". The trainers offered treats by hand to several naive individuals in a social group. The first two females that took the food reward from the trainers' hand were selected

as study animals. A natural trend to interact with humans, as well as curious and greedy animals, represented the best option to start with. The four olive baboons that were included in the study (2 in 2013 and 2 in 2019) were housed at the Primatology Station of the CNRS (Rousset-sur-Arc, France). They spent their first year of life with their mother and within their social group. There was no direct contact with humans during this period. After the animals were weaned, they were moved from their social group and put together in a large indoor cage.

3.2 The food rewards

- 10 Several food rewards were used during the training sessions. These were fresh fruits, dried pasta and dried fruits. If available, fresh fruits (representing a healthier reward) were always preferred and attempts were made to avoid the use of sweet items. The food items were cut into small pieces to keep the animals motivated as much as possible and to avoid a rapid satiety. We rapidly noticed that each individual had its own treat preferences. As treat value increases with scarcity, we adjusted as much as possible the different types of rewards to keep animals motivated. To facilitate the learning process, we used a clicker as a "bridge" between the command and the correct behaviour, and as a secondary reinforcer (Feng et al. 2016).

3.3 Duration of the training sessions

- 11 The duration of the training sessions varied from 15 to 30 minutes per individual and per day. Animals were trained from Monday to Friday. The end of a session was determined by the motivation of the animal, i.e., a reduction in the performance of the animal, or the declining interest in the training and in the food reward. If an animal showed an aggressive behaviour toward a congener or the trainers, the training session was ended immediately.

3.4 The shaping procedure

- 12 The training process of the animals was organized step-by-step. The process of reinforcing successively and gradually approximations to a desired behaviour is called "shaping". Before the start of the shaping process, the expected behaviour, i.e., to walk, on demand, quadrupedally and bipedally on a treadmill in a specific experimental setup, was split into different phases of increasing complexity. For example, entering the experimental setup required the animals to be transferred from their enclosure to the experimental room. To do so, we first trained the animals to present their necks and collars (1), second to accept a leash (2), and third to walk side by side with the trainer (3).
- 13 During the first stages of the shaping process, we reinforced any response or behaviour that was close to the desired behaviour (e.g. presenting the neck to leashing). Once this behaviour was properly learned, we stopped reinforcing it and started to reinforce the response close to the next desired behaviour (e.g. to stay still when clipping the leash).
- 14 Below, we present the main steps of the shaping process:
 1. Systematic desensitization to the trainer - This desensitization, or counterconditioning (Schapiro et al. 2003), consists of a gradual exposure to an aversive stimulus (i.e. the close

presence to the trainer) coupled with a primary reinforcer (i.e. treats). The aim of this technique is to reduce anxiety, stress, and avoidance by gradually exposing the individual to the source of their discomfort in a thoughtfully planned way. It promotes habituation to the close proximity of the trainer and generates a great amount of positive interactions. This first training period was carried out in an indoor cage, thus allowing the trainer to come inside, in close contact, with the animals.

2. "Charging the clicker" - The individuals were trained to associate the sound of the clicker to a food reward, i.e. the trainer clicked and then rewarded the animal systematically. Once the animals learn this contingency, the clicker can then be used as a "bridge" and a secondary reinforcer to precisely point the behaviour to reinforce (Feng et al. 2016; Williams et al. 2004).
3. Training some foundation behaviours - We trained the animals to give the right and left hands and the feet on demand. The teaching of these very simple four foundation behaviours have several goals. First, these interactions allow us to build up a relationship of "trust" with the animals. This enables deepening the desensitization process and accelerating the shaping process. Second, it facilitates the proper understanding of the "order-behaviour-click-reward" contingency process, thus facilitating the learning of future behaviours.
4. Parking training - We trained the animals to stand still and wait the order from the trainer before behaving. We teach this by ignoring behavioural responses that are not preceded by an order.
5. Collar presentation - We trained the baboons to present their neck and their collar with the aim of facilitating the leashing action.
6. Systematic desensitization to the carabiner and the leash - First, the animals were desensitized to be clipped with the carabiner. Second, the animals were desensitized to be clipped with the carabiner attached to the leash.
7. Training to go outside of the enclosure - Once the animals were trained to be leashed, we proposed them to go out of their enclosure. This process was performed step by step by luring the animals outside their cage. During this desensitization process, the animals could get back inside their enclosure whenever they wanted.
8. Training to walk nearby the trainer - Once the animal felt comfortable outside the cage the trainer started to walk nearby the animal until it was able to "synchronize" its walk with the speed of the trainer walk.
9. Training to walk bipedally - We did not systematically train the animals to walk bipedally, but instead to stand up on two legs for reaching the treat. Once in this position, we were keeping the treat far out of their reach to facilitate the execution of two or three complete gait cycles.
10. Desensitisation to the setup - The final training phase was the desensitization of the animals to the experimental setup, i.e., the enclosure where the experiments would be conducted. The animals were taken several times with the leash to this new enclosure where the treadmill was placed. In this environment, they could be released and fed on the treadmill in movement.
11. Training to keep walking - Once the animals accepted interaction with the trainer while walking quadrupedally on the treadmill, it was quite easy to make the animals take the treat in a bipedal posture. Our final goal was to maximize the number of bipedal gait cycles between the quadrupedal-bipedal transition phase and retrieval of the treat. We introduced the order to stand up and we increased systematically the delay between the "click" and the treat. Walking bipedally on the treadmill at different speeds was achieved in few sessions (<20) after being in contact with the device.

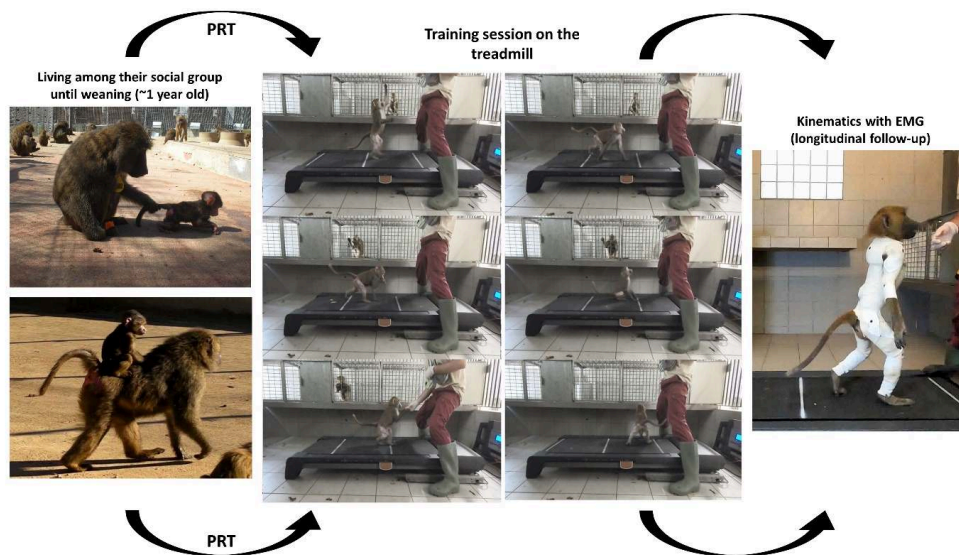
TABLE 1

| Timetable | Environment of the animals | Procedure |
|-----------------|--------------------------------|--|
| 04/2018-03/2019 | Large enclosure | Socially housed (no direct contact with humans) |
| 03/2019 | Large enclosure | " <i>Boldness test</i> " to select individuals |
| 01/04/2019 | Indoor cage | Selected individuals are socialized |
| 17/04/2019 | Indoor cage | First training session (start of the shaping procedure): Systematic desensitization, parking training, training foundation behaviours, etc. <i>68 training sessions</i> |
| 10/07/2019 | Large indoor/outdoor enclosure | Individuals are moved to a larger enclosure |
| 12/07/2019 | Large indoor/outdoor enclosure | First training session with the treadmill |
| 22/07/2019 | Large indoor/outdoor enclosure | Id1 walks on the treadmill at the 4th training session |
| 02/08/2019 | Large indoor/outdoor enclosure | Id2 walks on the treadmill at the 12th training session |
| | | <i>57 training sessions</i> (reinforcing the shaping procedure and the treadmill training) |
| 23/09/2019 | | End of the training after a total of 125 sessions |

Training schedule for the two individuals trained in 2019 using positive reinforcement technique

- 15 The aforementioned protocol was applied to two female individuals in 2013 (trained by PMV) and two others in 2019 (trained by FD). Table 1 and figure 3 show the general work flow of this protocol, from birth of the animals to the first experiments. As far as the individuals trained in 2019 are concerned, one individual made her first bipedal steps during the second session in contact with the treadmill device, and the first bipedal behaviour occurred at the 4th session. We have estimated at 75 minutes the time this female spent walking on the treadmill before the experiments (15 sessions of 5 minutes in average). The second female needed 12 sessions to accept walking on the treadmill. We have estimated that she spent 40 minutes on the treadmill before the start of the experiments. In total, after 23 weeks of training, including 125 sessions (for both individuals), the baboons were properly trained, and the experiments could start. The first session of data collection took place the 24th of October 2019 and allowed us to collect 3D kinematics of bipedal walking. The second session of data collection took place on the 28th and 29th of November and allowed us to collect data on the muscular activity during bipedal and quadrupedal walking using surface probes. No specific training was done for the instrumentation of the animals. Before the EMG experiments, the individuals were anesthetized to allow us to locally shave, clean and degrease the skin and to ensure accurate electrode placement (see Druelle et al. 2021). In summary, accurate 3D kinematics and EMG data of the hindlimb and back muscles were collected in these young baboons, while controlling the direction and speed of the animals using a treadmill device.

Figure 3



Workflow of the training process using Positive Reinforcement Techniques (PRT), from birth to the first experimental work including kinematics and EMG on bipedal walking. The pictures on the left-hand side show the early life of the baboons living in their social group at the primatology station of the CNRS. The pictures in the middle are examples of the variability of postures adopted by a young female olive baboon, Ophélie (Id1), when moving on a treadmill during a training session of ~5 minutes. The picture on the right-hand side shows a baboon equipped with surface electrodes walking bipedally on a treadmill during a session of data collection.

4 Conclusion and perspectives

- 16 In the present report, we have shown that a few minutes, spread over a relatively small amount of training sessions, are needed to make a pronograde non-human primate (the olive baboon) accept walking bipedally on a treadmill at different speeds. The treadmill is a very relevant device to use for collecting accurate and reproducible biomechanical data of primate locomotion. While Tuttle et al. (1979) noted already in 1979 that the methods of recording and analysing data in animal experimentation differ between studies and may hinder the interpretation of the dissimilarities between the results to functional aspects, this observation appears to remain true today. Conducting experimental studies in which the training is used and documented may already yield valuable insight into future studies about primate locomotion. The unique nature and the accuracy of the data collected in these setups make it highly relevant and valuable for our understanding of bipedal locomotion in non-human primates and it helps reach the standards of the study of human movement. Based on these biomechanical data and the fossil record, new modelling approaches can now propose simulations of extinct species (e.g. DeSilva et al. 2013; Nicolas et al. 2007). Going further into our understanding of the bipedal behaviour in our closest relatives also requires collecting accurate 3D kinematics (Demes, 2011; Kinoshita et al. 2021; O'Neill et al. 2018; Thompson et al. 2021; Vereecke et al. 2006) and to test how their bipedal walking pattern is likely to be affected by the speed of progression and variations in the substrate. In this context, appropriate refinement procedures such as the one presented here can significantly facilitate the work with these animals (see also other examples; Foster et al. 2014).

- 17 In addition, positive reinforcement methods can allow electromyographic studies. These can also provide important insights into primate locomotion, by providing unique perspectives for our understanding of human bipedal evolution (Higurashi et al. 2019; Stern & Susman, 1981). However, setting such experiments is dramatically challenging due to constraints related to legislation (country-related), technical material and behaviour of the animal (e.g. stress management). For instance, surgical/insertion procedures are commonly needed in order to insert the electrodes into the focal muscles (e.g. Boyer et al. 2007; Courtine et al. 2005; Higurashi et al. 2019; Stern & Susman, 1981). This invasive procedure could be a source of veterinary problems, disturb the normal walking patterns and bring inherent replicability problems. With regard to surface electrodes, low intra-operator repeatability and inter-operator reproducibility have been emphasised in humans for the collection of high-quality EMG signals for gait analysis (see Agostini et al. 2020, for a review). As a consequence, this field certainly suffers from a great diversity of methodological approaches and varied experimental conditions, which make the data heterogeneous and difficult to compare quantitatively. As also pointed out in humans (Agostini et al. 2020), there is a clear lack of normative data for what concerns the general muscular activity pattern during walking in non-human primates. For instance, muscle activation is obviously modulated by the speed of locomotion (Courtine et al. 2005), yet, this information has been regularly missing in the primate literature about muscle activity, and more generally in kinematics and kinetic studies. The use of trained individuals to walk at constant speed using a treadmill device clearly solve this issue.
- 18 To conclude, non-human primates have been increasingly studied in their natural environment, as well as in captive settings, for various purposes within the fields of (palaeo)anthropology, neuroscience, ethology, psychology, evolutionary biology, etc. Here, we have focused on the study of locomotion, and more specifically on the experimental study of bipedal locomotion in the context of evolutionary biology and palaeoanthropology. There is no doubt that studying bipedal behaviour in non-human primates can help us to better understand the evolutionary transition toward habitual bipedalism in hominins. Nevertheless, a full understanding of the acquisition of a habitual bipedal gait requires the study of bipedal walking in a broad range of non-human primates at various and finer levels. In our opinion, studies including cooperative animals that can freely move and accept wearing specific material is one of the most valuable experimental tools for filling this gap of knowledge over the next decades.

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Conflict of Interest

20 The authors declare that they have no competing interests.

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ABSTRACTS

To date, the use of positive reinforcement techniques to study locomotion in non-human primates remains poorly developed. However, using cooperative animals that can freely move in experimental setup allows us to collect valuable and relevant data and makes these repeatable and comparable between species. Based on the current knowledge and our experience, we present an experimental approach that aims at reaching the standards of the study of human movement in a non-human primate, the olive baboon, *Papio anubis*, thanks to the use of positive reinforcement techniques. This report documents the training protocol that we set up at the Primatology station of the CNRS (France). We further elaborate on the importance of conducting such experiments for a better and finer understanding of the bipedal behaviour in non-human primates. Experimental studies including cooperative animals that can freely move are likely to represent valuable experimental tools to fill important gaps of knowledge in the study of locomotion in general, and in the study of the acquisition of habitual bipedal walking in hominins.

À ce jour, l'utilisation de techniques dites de renforcement positif pour étudier la locomotion des primates non humains reste peu développée. Cependant, l'utilisation d'animaux coopératifs qui peuvent se déplacer librement dans une configuration expérimentale nous permet de collecter des données précieuses et pertinentes, les rendant ainsi reproductibles et comparables entre les espèces. Sur la base des connaissances actuelles et de notre expérience, nous présentons ici une approche expérimentale qui vise à atteindre les standards de l'étude du mouvement humain chez un primate non humain, le babouin olive, *Papio anubis*, grâce à l'utilisation de techniques de renforcement positif. Ce rapport documente le protocole d'entraînement que nous avons mis en place à la Station de Primatologie du CNRS (France). Nous développons également l'importance de mener de telles expériences pour une meilleure compréhension du comportement bipède chez les primates non humains. Les études expérimentales qui incluent des animaux coopératifs pouvant se déplacer librement sont susceptibles de représenter des outils expérimentaux précieux pour combler d'importantes lacunes dans les connaissances sur la locomotion en général, et en particulier sur l'acquisition de la marche bipède habituelle au sein de la lignée humaine.

INDEX

Mots-clés: Locomotion, Evolution, Bipédie, Entraînement au clicker, *Papio anubis*

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