

## Hindlimb interarticular coordinations in *Microcebus murinus* in maximal leaping

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### SUMMARY

The purpose of this study was to investigate the pattern of coordinations of the hindlimb joints in the world's smallest living primate (*Microcebus murinus*). The sequencing and timing of joint rotations have been analyzed in five adult males performing maximal leaping from a take-off immobile platform to their own wooden nest. Angular kinematics of hip, knee, ankle and metatarso-phalangeal (MT) joints were deduced from high-speed X-ray films in the sagittal plane of the animals. The body mass center (BMC) of the lemurs was assimilated to their iliac crest. The maximal airborne performance of the lemurs was  $0.33 \pm 0.04$  m, which represented  $2.55 \pm 0.36$  times their snout–vent length. Take-off instant occurred  $72 \pm 7$  ms after the start of the push-off, with a BMC velocity of  $3.23 \pm 0.48$  m s<sup>-1</sup>, oriented  $55 \pm 14$  deg. with the horizontal plane. The kinematic analysis of the joints and musculo-tendon architecture of the *M. murinus* plantar flexors pointed out mechanical power amplifier mechanisms (i.e. stretch-shortening cycle of hindlimb muscles and proximo-to-distal sequence).

Key words: leaping, lemur, coordination, kinematics.

### INTRODUCTION

A common definition of jumping performance is the height reached by the body mass center (BMC) during the airborne phase, determined by the take-off velocity. Referring to Borelli's law, take-off velocity is considered as scale-independent if species are geometrically similar (Thompson, 1917). However, it has been shown that small jumpers present higher efficiency in transforming musculo-tendon energy into BMC energy (Scholz et al., 2006a). From a 'structure–function' point of view, maximum jumping performance is related to hindlimb morphology and physiology (Losos, 1990; Harris and Steudel, 2002; Toro et al., 2003), i.e. relative limb length, extensor muscle mass, body mass and percentage of fast-twitch fibers (Tihanyi et al., 1982; Bosco et al., 1983). In leaping primates, body size has a dominant influence on locomotor performance (Demes and Günther, 1989; Preuschoft et al., 1996). With increasing body size, the decreasing ratio of muscle force, available for acceleration during take-off to the body mass that has to be accelerated, dictates the proportions of the hindlimbs and then the movement pattern, i.e. thigh-powered jumpers vs foot-powered jumpers (Gebo and Dagosto, 1988). Consequently, for a given species, increasing the length of the hindlimbs should increase both the kinetic energy and potential energy of the BMC during the push-off, resulting in an increase of take-off velocity (Toro et al., 2004).

In humans, jumping performance results from complex spatio-temporal recruitment of the muscles of the lower limbs to accelerate the BMC away from its initial position (Bobbert and van Ingen Schenau, 1988; Ashby and Heegaard, 2002). When planning and executing a vertical jump, the motor system must take into account several constraints in the gravitational field. Van Ingen Schenau has demonstrated that the proximo-to-distal delay of lower limb joints extension is determined by the so-called geometrical and anatomical

constraints (van Ingen Schenau, 1989). In vertical jumping, the push-off is defined by an explosive extension of the knee joint. The more the knee approaches its maximal extension, the less the transformation of the segment angular velocity into linear velocity of BMC is effective (geometrical constraint). Furthermore, it is necessary to decelerate knee extension before its maximal extension (anatomical constraint) in order to protect this joint from any damage. Bobbert and van Ingen Schenau have shown that the sequential order of the extension of the hip, knee and ankle joints delays the negative influence of the anatomical and geometrical constraints to the last end of the push-off (Bobbert and van Ingen Schenau, 1988).

Leaping to and from trunks and branches is a pattern of locomotor behavior that commonly characterizes the repertoire of several neotropical and prosimian primates. One key question concerns the mode of interarticular coordination in jumping or leaping. Does this coordination change with the anatomical and ecological constraints? To respond to this question, it is first necessary to compare leaping performances in very differently shaped species living in completely different habitats and constructed for bipedal or quadrupedal locomotion. If the sequential order of polyarticular movements has been extensively investigated in humans, only a few numbers of data are available in the literature for prosimians and arboreal primates (Aerts, 1998). The main purpose of the present study was then to characterize hindlimb kinematics in gray mouse lemurs (Cheirogaleidae; *Microcebus murinus*; Miller 1777) to investigate if inter-joint sequences are similar to humans and non-human primates. In the case of a positive response, the question on the morphological vs ecological constraints on the mechanisms underlying these coordinations could be considered.

Table 1. Means and standard deviations of morphometry and kinematics data of the tested *Microcebus murinus*

Subject	Age (month)	SNV (m)	Mass (g)	Push-off time (ms)	Take-off platform to nest height (m)	$H_{\max}$ (m)	$H_{\max}/\text{SNV}$ (au)	BMC velocity at take-off ( $\text{m s}^{-1}$ )	BMC velocity vector orientation at take-off (deg.)
147HA	32	0.132	101	80	0.45	0.25	1.93	3.18	44
943FCB	24	0.127	89	60	0.54	0.33	2.60	2.62	76
101DAA	59	0.129	100	70	0.54	0.35	2.68	2.99	61
162C	12	0.123	94	74	0.54	0.35	2.82	3.88	42
179AA	12	0.131	102	74	0.54	0.35	2.70	3.47	49
Means $\pm$ s.d.	28 $\pm$ 19	0.128 $\pm$ 0.004	97 $\pm$ 6	72 $\pm$ 7	0.52 $\pm$ 0.04	0.33 $\pm$ 0.04	2.55 $\pm$ 0.36	3.23 $\pm$ 0.48	55 $\pm$ 14

SNV is the snout–vent length of the lemurs. BMC is the body mass center.  $H_{\max}$  indicates the airborne maximal height attained by the iliac crest (assimilated to BMC).

## MATERIALS AND METHODS

### Animals

The mouse lemurs of the genus *Microcebus* are the world's smallest primates and are endemic to Madagascar. *Microcebus murinus* is a nocturnal prosimian broadly distributed across the vegetated portions of the island. This arboreal primate is active at night, usually traveling along branches on all four legs, and is the most frequent leaper of the cheirogaleids (Martin, 1973; Gebo, 1987). It has developed powerful hindlimbs with opposable thumbs to climb trees and to leap to and from vertical and horizontal supports (Garbutt, 1999; Nemoz-Bertholet and Aujard, 2003). Even if they principally move in trees during the night, mouse lemurs can occasionally go on the ground to forage and to search for insects (Kappeler, 1998; Kappeler, 2000).

All experimental animals were laboratory born. Five male adult *M. murinus* were obtained from the breeding colony of the UMR 7179 (Dr M. Perret at the Département d'Ecologie et Gestion de la Biodiversité, Pr. R. Barbault, MNHN, France) (Table 1). The captive colony of gray mouse lemurs at Brunoy (MNHN, France) was established with wild-caught animals from the southwest coast of Madagascar 40 years ago (Agreement 962773). They presented no orthopedic or neurological pathologies of the anterior and posterior limbs. They were in excellent physical health and accustomed to human manipulations. The animals were maintained in metal wire mesh cages (0.55 m high  $\times$  0.60 m long  $\times$  0.70 m wide) with concrete flooring and had access to wooden nests (0.12 m high  $\times$  0.12 m long  $\times$  0.12 m wide) within the cage. Experiments were performed at the temperature corresponding to their normothermic range (18–34°C). In this range of temperatures, the animals present normal locomotor activity (Aujard and Vasseur, 2001). They were provided with water and food (fresh fruits, a milky mixture and mealworm) *ad libitum* (Genin and Perret, 2003).

### Leaping training

Three leaping sessions were devoted to acclimatize each lemur to the experimental protocol. Before and in-between each leaping trial, animals were placed in an incubator set at 24–26°C with 55% humidity for, at the most, one hour. Lemurs participated in one jump training session per day.

Animals were trained to jump inside a rectangular enclosure made of Plexiglas (1.40 m high  $\times$  0.70 m long  $\times$  0.70 m wide). Before each jump, they were taken from the incubator, placed on an immobile take-off platform and induced to jump to their own wooden nest, aimed to limit the direction and the height of each jump (Fig. 1). The nest was set at different heights (initial height: 0 m) and at a constant horizontal distance (0.40 m). Leaping height increment was fixed at 0.09 m until the animal was unable to perform the test spontaneously. Then, the increment was fixed at 0.02 m until

an approximate maximum height was achieved (i.e. the last height at which the lemur successfully made it to the landing nest). No more than 10 trials per session were allowed in order to minimize fatigue effects.

### Motion analysis

At the end of the third leaping session, each lemur was filmed in the sagittal plane at maximal leaping height (Fig. 2). Uniplanar cineradiographs were collected in lateral view at 200 frames  $\text{s}^{-1}$  (Blaser A504K camera, StadtRoda, Germany; resolution: 1280  $\times$  1024 pixels) in order to visualize joints and calculate angular excursions of the segments of the limbs. The X-ray equipment consisted of an X-ray generator (Electromed Europa 2TS, Fontenay-sous-Bois, France), an X-ray tube (Varian PG 256, Eysines, France) and an X-ray image intensifier (Thales TH9428 hp2, Neuilly-sur-Seine, France). The diameter of the X-ray images field of view was 196 mm. Distortions of the X-ray maps were corrected by reference to an orthogonal grid of steel balls (diameter 1.35 mm, with a mesh width of 17.18 mm), filmed before and after each experimental session. X-ray films were recorded on PC hard disk for further analysis. Images were calibrated, tracked and analyzed using a self-developed motion analyzer created under Matlab<sup>®</sup> 7.3.0 software (MathWorks Inc., Natick, MA, USA).

### Kinematics

These films were analyzed frame-by-frame to identify previously defined skeletal landmarks (Fig. 3A): iliac crest (1), great trochanter

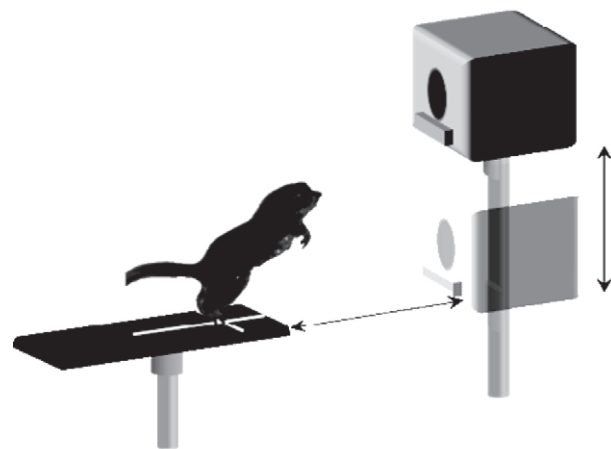


Fig. 1. Diagram of leaping platform used for filming *Microcebus murinus*. Lemurs take-off from an immobile platform and jump upwards to an adjustable nest.

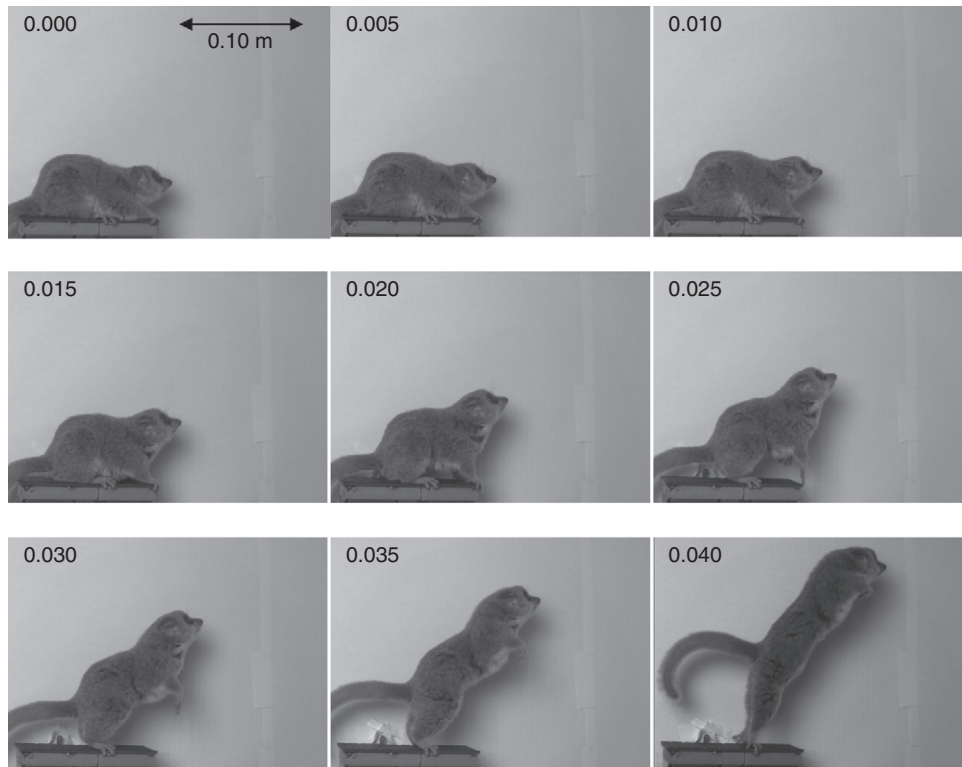


Fig. 2. Nine video frames showing the push-off phase of leaping in *Microcebus murinus*. The height reached by the animal in this trial was 0.54 m. The time code is expressed in seconds. The scale is indicated in frame 1.

(2), lateral epicondyle of the femur (3), lateral malleolus (4), tarso-metatarsal (TM) joint (5) and metatarso-phalangeal joint (MT) (6). A five rigid segments model (sacrum, thigh, lower leg, upper foot, lower foot) was obtained from the digitalization of the landmarks. From the coordinates of these markers the following articular angles were calculated: hip angle ( $\theta_H$ : 1–2–3), knee angle ( $\theta_K$ : 2–3–4), ankle angle ( $\theta_A$ : 3–4–5) and MT joint angle ( $\theta_{MT}$ : 4–5–6) (Fig. 3B). The height ( $H_{max}$ ) reached by the lemurs during the airborne phase was calculated according to free-fall Newton's law:

$$H_{max} = \frac{v_0^2 \sin^2 \phi}{2g},$$

where  $v_0$ ,  $\phi$  and  $g$  represented the BMC velocity magnitude at take-off, its orientation with the horizontal and the gravity acceleration ( $g=9.81 \text{ ms}^{-2}$ ), respectively. All velocity data were calculated through numerical derivations of positions. The BMC of the lemurs were approximated, all throughout the manuscript, to the iliac crest. It should be noted that this assumption will not report any relative segment displacement from initial position, and especially the ones of the trunk and the anterior limbs at the start of the push-off.

Interarticular coordinations were evaluated through the sequential order and timing of joint extensions. For this purpose, according to Haguenaer et al. (Haguenaer et al., 2006), the onset of each joint extension was defined when its position was 5% greater than its angular position at the start of its extension phase.

#### Statistical analysis

The statistical analysis was performed on absolute data. To compare parameters characterizing the coordinations of the joints, the non-parametric Friedman test and Wilcoxon signed-rank test were successively used. Statistical significance was accepted at the  $P < 0.05$  level. In order to present mean curves, data were time normalized using a spline cubic interpolation method (Matlab<sup>®</sup> 7.3.0

software). Take-off time ended the normalization interval. The start was determined at the onset of BMC (or iliac crest) displacement.

#### RESULTS

Fig. 4A presents a typical representation of joints displacement of the right hindlimb in the sagittal plane.

Leaping performance, quantified by the maximal height attained by the lemurs between the take-off platform and the nest, was  $0.52 \pm 0.04$  m (Table 1). This performance was very consistent across all of the tested subjects. However, these data are not indicative of the real ability of the lemurs to perform maximal leaping. Indeed, they include the height between the take-off platform and the BMC of the lemurs at the instant of take-off. Moreover, the lemurs tended to grip the nest with their anterior paw before moving inside.

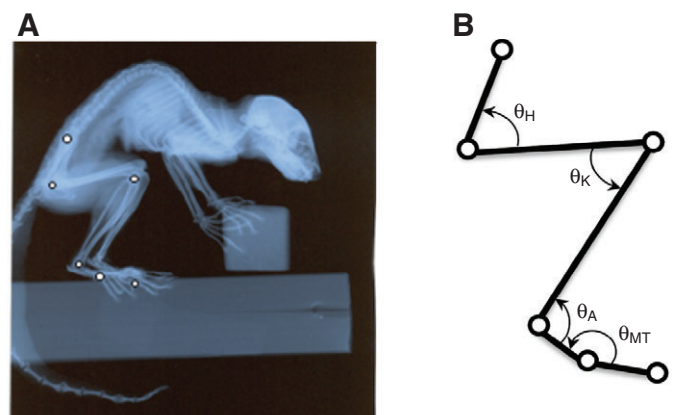


Fig. 3. (A) Skeletal landmarks on the hindlimbs of *Microcebus murinus*. (B) Segment and joint angle conventions: hip ( $\theta_H$ ), knee ( $\theta_K$ ), ankle ( $\theta_A$ ) and metatarso-phalangeal (MT) ( $\theta_{MT}$ ) joints.

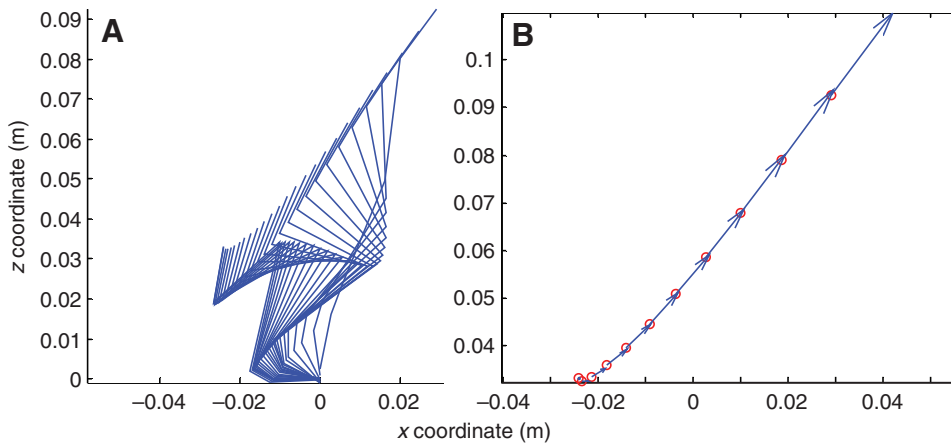


Fig. 4. (A) Mean stick diagram of the leaping push-off in *Microcebus murinus*. (B) Vector field of body mass center (BMC) (or iliac crest) velocity during push-off. Circles indicate the iliac crest positions.

Therefore, the airborne maximal height of the BMC ( $H_{\max}$ ) was calculated from BMC velocity and magnitude at the instant of take-off. This evaluated value was  $0.33 \pm 0.04$  m (Table 1) and represented  $2.55 \pm 0.36$  times the lemur's snout-vent length (SNV).

Whereas airborne leaping performance was quite similar, take-off parameters presented inter-individual variations. Take-off occurred  $72 \pm 7$  ms after the start of the push-off. At this instant, the lemur's BMC velocity, approximated to iliac crest velocity, was  $3.23 \pm 0.48$  m s<sup>-1</sup> and was oriented at  $55 \pm 14$  deg. with the horizontal plane (Table 1). Whereas the magnitude of the velocity vector increased all along the iliac crest trajectory during push-off, its orientation was reached at 20% of total push-off time and then remained constant (Fig. 4B and Fig. 5).

Table 2 presents the angular data of hindlimb joints during the push-off. At the start of push-off, knee and hip initial positions were similar ( $34.38 \pm 7.45$  deg. and  $36.1 \pm 4.01$  deg., respectively) whereas MT and ankle were more extended ( $149 \pm 13.18$  deg. and  $106 \pm 16.62$  deg., respectively). The low standard deviations showed that hip values were consistent for the entire population. However, MT, ankle and knee presented small inter-individual variations, indicating low variability in initial postures of the lemurs. At take-off, joint angles for MT, ankle, knee and hip were  $170 \pm 10.31$  deg.,  $176.5 \pm 6.3$  deg.,  $165 \pm 6.88$  deg. and  $150.1 \pm 4.58$  deg., respectively. Consequently, the more proximal joints (i.e. hip and knee) were not fully extended at this instant. As indicated by standard deviations of the joints, articular angles at take-off were similar for all animals, indicating similar final postures. From these data, the calculated excursions of the joints were  $21.2 \pm 17.76$  deg.,  $71.05 \pm 16.62$  deg.,  $130.6 \pm 11.46$  deg. and  $114.02 \pm 5.16$  deg. for MT, ankle, knee and hip, respectively.

Concerning the minimal angular positions of hindlimb joints (Table 2), they all differed significantly from initial position except for the hip (Fig. 6). Indeed, they were 70%, 32% and 18% lower for MT ( $P=0.005$ ), ankle ( $P=0.037$ ) and knee joints ( $P=0.002$ ), respectively. These results underlined that joint flexions preceded their extensions during the push-off. Functionally, the extensor muscles crossing the MT and ankle presented a lengthening phase preceding a shortening one. The extension phases of the joints (70%, 32% and 18% of push-off time for MT, ankle and knee, respectively) and their amplitudes (29.25 deg., 12.61 deg. and 2.87 deg. for MT, ankle and knee, respectively) increased from proximal to distal. However, although minimal and initial positions differed, maximal and final joint angles were similar.

Mean curves of hip, knee, ankle and MT joint angle excursions over the maximal jump push-off are presented in Fig. 7. The mean

onset of the extension phases differed between the hip, knee, ankle and MT. Except hip vs knee ( $P=0.225$ ), all of the other joints extended at significantly different instances in a proximal-to-distal sequence (hip vs ankle,  $P=0.042$ ; hip vs MT,  $P=0.043$ ; knee vs ankle,  $P=0.068$ ; knee vs MT,  $P=0.043$ ; ankle vs MT,  $P=0.043$ ). Therefore, hip, knee, ankle and MT extensions began at  $16 \pm 8\%$ ,  $24 \pm 11\%$ ,  $44 \pm 25\%$  and  $72 \pm 21\%$  of total push-off phase, respectively.

## DISCUSSION

The main purpose of this study was to characterize the interarticular coordinations of the hindlimb joints during maximal leaping of the arboreal prosimian lemur *M. murinus* by analyzing the kinematic parameters. Kinematics of leaping has been studied in several vertebrates, including amphibians (Emerson, 1978; Marsh and John-Alder, 1994; Navas et al., 1999; Nauwelaerts and Aerts, 2003; Nauwelaerts and Aerts, 2006), lizards (Bels et al., 1992; Toro et al., 2003; Toro et al., 2004; Toro et al., 2006), primates (Aerts, 1998; Demes et al., 2005; Scholz et al., 2006b) and humans (Bobbert and van Ingen Schenau, 1988; van Soest et al., 1994; Jacobs et al., 1996; Selbie and Caldwell, 1996; Vanrenterghem et al., 2004). Except for humans, all of these species use quadrupedal locomotion like *M. murinus* for moving in terrestrial and arboreal habitats. Thus, it is not possible to evaluate net moment forces about hindlimb joints from force plate data as, at take-off, the two forefeet push-off first, followed by the simultaneous hindfeet (Gebo, 1987; Demes et al., 2005).

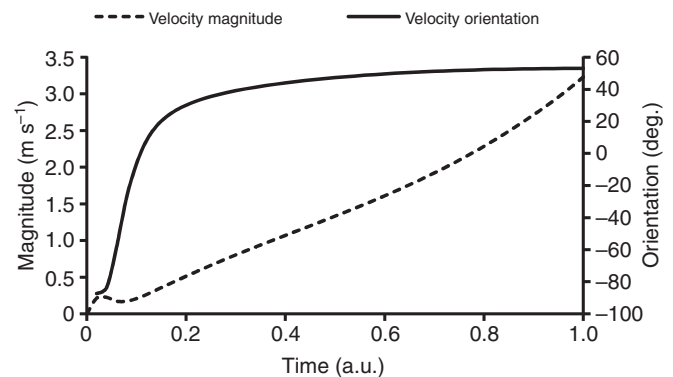


Fig. 5. Mean magnitude and orientation of body mass center (BMC) velocity vector during push-off expressed as a function of normalized push-off time.



Table 2. Means and standard deviations of initial, final, minimum, maximum and variations of angular positions (final vs initial and maximal vs minimal), in radian and degree

$\theta$	MT	Ankle	Knee	Hip
$\theta$ Initial (rad)	2.61±0.23	1.85±0.29	0.60±0.13	0.63±0.07
$\theta$ Final (rad)	2.97±0.18	3.08±0.11	2.88±0.12	2.62±0.08
$\theta$ Final – $\theta$ initial (rad)	0.37±0.31	1.24±0.29	2.28±0.2	1.99±0.09
$\theta$ Initial (deg.)	149±13.18	106±16.62	34.38±7.45	36.1±4.01
$\theta$ Final (deg.)	170±10.31	176.5±6.3	165±6.88	150.1±4.58
$\theta$ Final – $\theta$ initial (deg.)	21.2±17.76	71.05±16.52	130.6±11.46	114.02±5.16
$\theta$ Min. (rad)	2.09±0.10	1.63±0.13	0.55±0.13	0.62±0.07
$\theta$ Max. (rad)	2.97±0.18	3.09±0.10	2.88±0.12	2.63±0.08
$\theta$ Max. – $\theta$ min. (rad)	0.88±0.22	1.45±0.16	2.33±0.20	2.01±0.10
$\theta$ Initial – min. (rad)	0.52±0.29	0.22±0.20	0.05±0.02	0.01±0.03
$\theta$ Min. (deg.)	119.75±5.7	93.39±7.45	31.51±7.45	35.52±4.01
$\theta$ Max. (deg.)	170.2±10.3	177±5.73	165±6.88	150.7±4.58
$\theta$ Max. – $\theta$ min. (deg.)	50.42±12.8	83.24±8.9	133.5±11.6	115.02±6
$\theta$ Initial – min. (deg.)	29.25±16.93	12.61±11.62	2.87±1.38	0.58±1.81

MT, metatarso-phalangeal.

In 22 genera of living prosimians, only four (*Nycticebus*, *Loris*, *Perodicticus* and *Arctocebus*) do not leap at all. Moreover, Crompton and Sellers suggested that leaping was the primary predator-avoidance device in prosimian primates classed as solitary foragers, and has been adopted primarily and originally (Crompton and Sellers, 2006). Indeed, leaping is the most efficient locomotor option when the primates have to cross between trees in the canopy without unsecure climbing down to the ground and up between each tree (Günther et al., 1991) in an home range of 0.35 ha (Bennett, 2009). Leaping performance, quantified in the present study by the airborne maximal height of the lemurs, was 2.55 times their SNV length. This performance is lower than leaping specialists like *Galago senegalensis*, which are able to move their BMC over a distance equivalent to six body lengths (without tail) (Hall-Craggs, 1965). The maximal height reached in vertical leaping results from take-off velocity angle and magnitude. For performing in a similar way, different strategies can be used by the animals. Each selected strategy induces a specific slope of BMC trajectory (Crompton and Sellers, 2006). In *M. murinus*, Sellers and Crompton showed that take-off velocity angle increased from 10 deg. to 30 deg. with distance leaping from 0.25 m to 1 m (Sellers and Crompton, 1994). In the present study, these angles ranged between 42 deg. and 76 deg. These data, which can appear to be conflicting, could be explained under similar

demands. Indeed, in distance jumping, low take-off angles are required to increase the BMC velocity and induce flatter trajectories. Consequently, less time is spent in the air. When lemurs had to perform high leaping, they increased take-off angles at a mean value of 55 deg., close to the direction of the line connecting the take-off platform and the entry of the nest (52 deg.). Thus, the BMC velocity at take-off was maximal and the slope of the BMC trajectory in air was consequently flat, inducing a minimization of time spent in the air, like in distance jumping. This organization could be viewed as an adaptive strategy of escaping behavior of the lemur during anti-predator context (Göttingen, 2007). Indeed, in case of vocalization of predators (e.g. predatory birds), the lemurs spent time to stay and scan the sky to locate the predator. Then, in case of an attack, they have less time to escape. This strategy should be energetically cheaper as they have not had to react to every alarm signal and to expend high power levels of the hindlimbs' extensor at each jump (Jouffroy, 1962).

According to Bosco et al., performance in maximal vertical jump in humans is directly correlated to maximal lower limbs extensor muscles power development ability (Bosco et al., 1983). Moreover, BMC velocity at take-off is highly correlated with lower limb muscular fiber typology (Bosco and Komi, 1979) and is significantly related with the percentage of fast-twitch fibers. Compared with

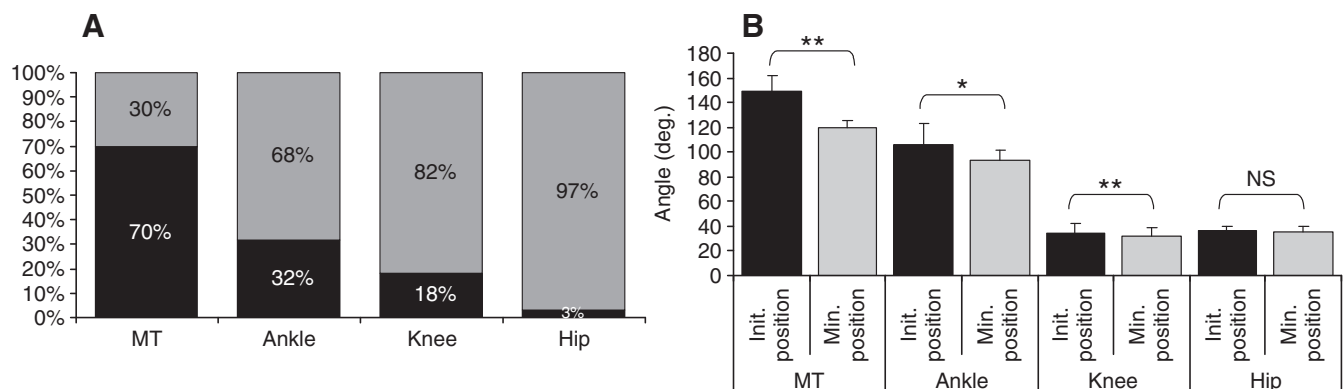


Fig. 6. (A) Flexion (black) and extension (gray) phases for hindlimb joints expressed as a function of normalized push-off time. (B) Mean and standard deviation values for the initial and minimum angular joint positions. \* $P < 0.05$ ; \*\* $P < 0.01$ ; NS, not significant.

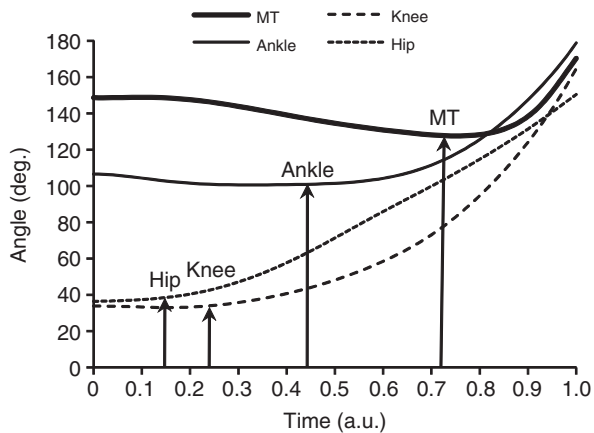


Fig. 7. Mean excursions of the hindlimb joints as a function of normalized push-off time. Arrows on the horizontal axis indicate the beginning of extension phases for knee, ankle and metatarso-phalangeal (MT) joints.

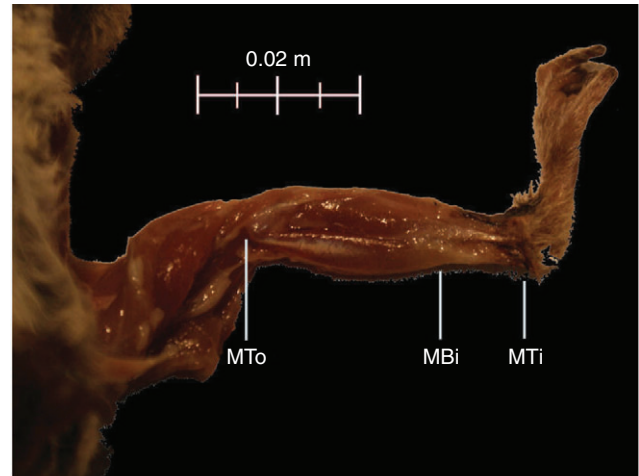


Fig. 8. Dissection showing the medial view of the left hindlimb in *Microcebus murinus*. The hamstrings were totally excised to discover the m. gastrocnemius medialis origin (MTo) on the medial femoral condyle. MTi = musculo-tendon insertion on the calcaneum. MBI = m. gastrocnemius medialis muscle belly insertion on the Achilles tendon.

other primates, *M. murinus* is considered to be a jumper, although this lemur is not able to reach the equivalent performance of pure jumpers such as *Galago*. This is consistent with their hindlimb muscle typologies, which contain a higher percentage of slow-twitch fibers than *Galago* (Edgerton et al., 1975) but lower than other primates (Petter and Jouffroy, 1993). Moreover, m. vasti medialis and lateralis presented more than 95% of fast-twitch fibers in *Microcebus*, indicating a specific adaptation for explosive ballistic movements. In addition to fiber typology, hindlimb musculo-tendon architecture is involved in power development ability (Alexander, 1993). So, long and compliant tendons of the plantar flexors (i.e. m. soleus and m. gastrocnemii) in humans (Kurokawa et al., 2001) allowed maximum jumping performance (Bobbert, 2001). For example, gorillas present a ratio of muscle fascicle length to muscle-tendon unit length equal to 1 (Payne et al., 2006), as their locomotion consists mainly in terrestrial quadrupedalism (Berge, 1991) with few rebounds. The anatomical study of the hindlimb of *M. murinus* enables the evaluation of their ability to leap as was previously performed by Payne et al. (Payne et al., 2006), i.e. the ratio of muscle belly length to total muscle-tendon unit length. After dissection of one hindlimb of *M. murinus* (Fig. 8), the measured muscle belly and musculo-tendon lengths were 2.4 and 3.4 cm, respectively. Consequently, the ratio was equal to 0.7. This value is similar to the one of gibbons (Payne et al., 2006), characterized as one highly arboreal ape. This relatively high ratio should indicate a low ability to store energy (Biewener and Roberts, 2000). It should be compensated, like in the great ape, by the high magnitude of compliance in branches, resulting in a net loss of energy to locomotor supports (Alexander, 1991). However, a specific study on the anatomical and histochemical characteristics of the triceps surae in *Micocebus*, i.e. muscle tendon and belly areas and muscle fascicle characterizations, seemed necessary to infer on the ability of *Microcebus* to leap.

The BMC trajectory analysis all through the push-off indicated that its angle at take-off was already reached at 20% of the push-off duration. The displacement of the hindlimb in lemurs is organized at the very beginning of the push-off to orientate the BMC velocity in an efficient way. Thus, from 20% to the end of the push-off, BMC displacement was only devoted to its linear acceleration,

for maximizing its velocity at take-off instant. The production of this launching ramp resulted from specific coordination of hindlimb joints. Indeed, all involved joints are moving through rotations. Thus, every point belonging to the rotated segment describes a circle around the moving joint. When more than one joint rotates simultaneously in a monotonic way or in phase (i.e. the initialization and ending of all joint displacements occur at the same time), the free extremity of the system describes a concave trajectory, which is the result of the combination of all joint rotations. Consequently, the system is unable to produce any linear trajectory of the BMC. However, if all joint rotations occur successively, the free extremity or the BMC of the moving system could describe a flatter trajectory than in the precedent case (Legreneur and Creveaux, 2009). MT, ankle and knee displacements were not strictly monotonic as they presented extension preceding flexion phase. Despite the problem of formally evaluating the effect of these movements on BMC trajectory, it should be reasonable to assume that these joints, in regards to their flexion amplitudes, could not modify the global linear kinematics of the BMC induced by proximo-to-distal sequence of the hindlimb joints. It should be noted that this linearization should occur for any kind of the sequential order of the joint displacements. This is consistent with our results. Indeed, interarticular coordination analysis in *Microcebus* pointed out a sequential organization of hindlimb joints from the hip to MT (i.e. hip extension preceded knee, ankle and MT extensions), resulting in a linear displacement of the BMC (or iliac crest). Furthermore, as previously observed in bonobo (Scholz et al., 2006b), *Galago* (Aerts, 1998), *Rana esculenta* (Nauwelaerts and Aerts, 2003) and humans (Haguenaer et al., 2006), this temporal organization was always a proximo-to-distal sequence. Then, besides BMC trajectory linearization, the sequence should be a by-product of the functional compromise between minimizing the angular velocities of segments to keep the shortening velocities of the muscles low and maximizing them to optimize the vertical velocity of BMC (Bobbert and van Soest, 2001).

Leaping techniques had become very stereotyped by the time each lemur had reached its maximal performance. It consisted of a very deep crouch at the start of the push-off, the knee and the hip being maximally flexed (34.39 deg. and 36.1 deg., respectively), and the

ankle and MT relatively extended (106 deg. and 149 deg., respectively). But, at take-off, all joints did not reach their maximal extension. Consequently, the lemurs did not use the total joint angular range of motion to maximally accelerate their BMC. Similar behavior is observed in human jumping, according to anatomical constraint. Indeed, it is necessary to reach zero angular velocity of hindlimb joints as they are at maximal extension, in order to preserve their physical integrity. It is therefore necessary to take-off before maximal extension to keep velocity of the BMC around its maximal value at this instant.

Regarding joint amplitudes, hip and knee seemed to have the main propulsive role in force production with no significant flexion phases. Thus, the agonistic muscles crossing these joints could potentially act concentrically through all of the push-off. Hip amplitude was smaller than that of the knee. This result could be interpreted under the assumption of a BMC velocity orientation role of the trunk. The extension of the ankle and MT joints was preceded by high flexion phases in duration and amplitude. Functionally, it seemed that the monoarticular extensor actuators crossing these joints would produce strength through a stretch-shortening cycle as in *Anolis* (Toro et al., 2006). This strength can lead to an increase in power by storing elastic potential energy in muscle during lengthening (Alexander and Bennet-Clark, 1977). This mechanism could compensate the loss of force induced by the limited range of motion of ankle and MT joints, and potentially be used as a mechanical power amplifier (Aerts, 1998).

In conclusion, prosimians *M. murinus* presented highly stereotyped interarticular coordinations of the hindlimb in maximal leaping characterized by a proximo-to-distal pattern. The primary function of this sequence was to orientate BMC velocity at the very beginning of the push-off and accelerate it all along its trajectory for maximizing its magnitude at take-off. This mechanism could contribute to power amplification with countermovement. However, any data cannot help us to evaluate the respective contributions of these mechanisms. The proximo-to-distal sequence was observed previously in humans (Bobbert and van Ingen Schenau, 1988) and in some tetrapods (Aerts, 1998; Nauwelaerts and Aerts, 2003; Scholz et al., 2006b). Their highly different ecological constraints, usual modes of locomotion (bipedal vs quadrupedal) and morphologies indicate that such a pattern could be only interpreted through mechanical constraints, which seem to be conservative through vertebrates (i.e. gravitational, anatomical and geometrical).

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