ORIGINAL PAPER

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Treadmill locomotion of the mouse lemur (*Microcebus murinus*); kinematic parameters during symmetrical and asymmetrical gaits

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Abstract

The gaits of the adult grey mouse lemur *Microcebus murinus* were studied during treadmill locomotion over a large range of velocities. The locomotion sequences were analysed to determine the gait and the various spatiotemporal gait parameters of the limbs. We found that velocity adjustments are accounted for differently by stride frequency and stride length depending on whether the animal showed a symmetrical or an asymmetrical gait. When using symmetrical gaits the increase in velocity is associated with a constant contribution of the stride length and stride frequency; the increase of the stride frequency being always lower. When using asymmetrical gaits, the increase in velocity is mainly assured by an increase in the stride length which tends to decrease with increasing velocity. A reduction in both stance time and swing time contributed to the increase in stride frequency for both gaits, though with a major contribution from the decrease in stance time. The pattern of locomotion obtained in a normal young adult mouse lemurs can be used as a template for studying locomotor control deficits during aging or in different environments such as arboreal ones which likely modify the kinematics of locomotion.

Keywords Stride frequency · Stride length · Stance duration · Swing duration · Primate

Introduction

During the last 10 years, studies on mammal locomotion have dealt with small-sized species that are commonly used in experimental biology. The grey mouse lemur (*Microcebus murinus*, Cheirogaleidae, Primates) is one of these species. It is a small nocturnal arboreal primate (60–90 g) native of Madagascar, and for which a breeding colony has been established in Brunoy (France, IBISA platform, agreement E91.114.1, DDPP Essonne) for over 50 years ago (Martin 1972). Its size, weight, and mean lifespan in captivity of 8–10 years (Perret 1997), allowed the use of this primate as a model for many types of studies in ecology and behaviour. The use of the grey mouse lemur in physiological and cognitive research for the past 12 years has shown that it is also a good model to approach the understanding of many disorders found in humans (Némoz-Bertholet and Aujard 2003;

Bons et al. 2006; Languille et al. 2012, 2015; Bertrand et al. 2013; Thomas et al. 2015). Locomotion is linked with many other vital functions and is appropriate to study 1- the adaptive responses to environmental constraints (extrinsic factor) as well as 2- the adjustments and responses to intrinsic constraints (obesity, aging, etc.). The mouse lemur has highly developed sensory modalities to ensure appropriate locomotor behaviours in the dense and three-dimensional complex forest habitat it lives in. However, as in other animals, disorders can modify this state. A decrease of motor performance, physical strength, endurance and coordination are associated to aging in humans (Lin and Woollacott 2002), and similar disorders have been documented in mouse lemurs older than 6 years (Némoz-Bertholet and Aujard 2003; Languille et al. 2012). Nonetheless, to evaluate the genuine effect of a stimulus (exogenous or endogenous) on locomotion, we need to have a standardized model of grey mouse lemur locomotion. This existing type of standardized model in mice and the derived gait measures have been largely used to identify and quantify motor function or dysfunction (Clarke and Still 1999; Herbin et al. 2004; Zumwalt et al. 2006; Wooley et al. 2009). Despite the large amount of studies on primate locomotion, only some have investigated aspects of the locomotion in the mouse lemur (Fischer et al. 2002; Schmidt

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2008; Schmitt et al. 2006; Shapiro et al. 2016). Moreover, the majority of primate locomotion studies have focused on only one type of gait, symmetrical or asymmetrical, and more specifically on the gait sequence pattern in relation to stability, substrate use, or from a comparative perspective (e.g., Stevens 2006, 2008; Higurashi et al. 2009; Carlson and Demes 2010; Young 2012). Nevertheless, none of these studies focused on the modification of kinematic parameters in relation to the symmetry *versus* asymmetry of the gait during treadmill locomotion. Moreover, animals not only appear to prefer specific gaits but they prefer certain ways of changing these gaits to increase speed (Heglund et al. 1974; Pridmore 1994; Reilly and Biknevicius 2003; Herbin et al. 2004). If individual gaits can be assumed to involve different motor patterns, it would be of interest to identify and understand how small primates control their speed in relation to the gait used. In addition, kinematic studies using high-speed filming appear to be the best non-invasive approach to correlate at the same time scale (4 ms), locomotor events and neuronal activity. The aim of this study is, first, to describe and define a model of mouse lemur treadmill locomotion to quantify the spatio-temporal gait parameters under standardized conditions. Second, we aim to define the respective contribution of the increase or decrease of these parameters to an increase in velocity or stride frequency, and third, to characterize the gait pattern in a given condition and at given age. Our results will be compared with those described in the literature, and will provide the baseline data for a subsequent kinematic studies on adaptations to different supports and aging, and their effects on kinematic in the Grey Mouse Lemur.

Materials and methods

Experimental conditions

All mouse lemurs (*Microcebus murinus*) used in this study were born in the breeding colony of Brunoy (MNHN, France; agreement n° 91.114.1, DDPP Essonne) and descend from individuals originally caught in south-western Madagascar 40 years ago. Animals are housed in large cages ($100 \times 250 \times 100$ cm) and at constant temperature (25 °C) and humidity (55%). Food (fresh fruits, milk porridge, and insects) and water were available *ad libitum*. Data were collected from eight adult males (mean age 1–3 years, mean body weight 96.8 ± 18.5 g). Analyses were made on the locomotion of untrained animals (naïve animals) on a home-made treadmill. The belt of the treadmill presents a marker each 2 cm, visible by the cameras, allowing the calculation of the distance covered during each stride. After a time of familiarization of 2 min, the animals were set on the horizontal treadmill in a Plexiglas corridor of 0.20 m wide.

Plates were vertically adjusted to limit the path length to 0.60 m. After this period, the treadmill speed was adjusted to the chosen speed with a tachometer. Under these conditions, mouse lemurs progressed on the treadmill freely, and they were tested over a large range of treadmill speeds, from 0.15 to 1.75 m/s. Two high-speed video camera (AVT Pike-032 B/F-032C) recording at 200 frames per second were set on each side of the corridor to capture the movements of the right and left limbs. The maximum duration of a recording sequence was nine seconds and every sequence was separated by at least 5 min. Under these conditions, no signs of distress were observed in the animal during the experiments. This procedure was approved by the Ethical committee in animal experimentation "Comité Cuvier" registration number 68-023.

Kinematic variables

The characterization of the gait, as symmetrical ($-_S$) or as asymmetrical ($-_{aS}$), was defined using definitions proposed by Hildebrand (1989), established from previous papers (Hildebrand 1965, 1977; Zug 1972; Sukhanov 1974) and updated by Abourachid et al. (2007). The gaits which could not be defined as symmetrical or asymmetrical were defined as transition sequences. These transition sequences include sequences where one girdle has the limbs evenly spaced in time and the other not.

In this study, we examined several gait parameters. The diagonality in symmetrical gaits (*D*) is calculated as the percentage of the stride time which the footfall of a trailing limb is followed by the ipsilateral limb of the other girdle. We adopt the terminology of Cartmill et al. (2002) based on Hildebrand (1967), with slight deviation from the strict definition of the trot, as proposed by Nyakatura et al. (2008). Indeed we separated different gaits: lateral sequence lateral couplet LSLC ($0 < D < 25$); lateral sequence diagonal couplet LSDC ($25 < D < 45$); trot with $45 < D < 55$, diagonal sequence diagonal couplet DSDC ($55 < D < 75$); diagonal sequence lateral couplet DSLC ($75 < D < 100$). The treadmill speed and the velocity of the animal (stride length/stride time, in m/s) are generally equal, excepted during the deceleration and acceleration phases. When animal is quite stable and stays on camera screen, it moves regularly at a velocity in the range Mv-SD < velocity < Mv + SD (where Mv is the mean velocity of the sequence analyzed and SD the standard deviation of the velocity in the sequence analyzed), out of this range their strides are not homogeneous (non-regular), and were excluded from the data. During these non-regular strides the individual accelerates or decelerates and is in a permanent readjustment and does not show a regular coordination. Thus, the regular gait measures obtained at a speed characterize a global coordination and not those resulting of a deceleration at higher fixed speed or acceleration at lower

fixed speed (of the treadmill). We here used the protocol described for mice in previous papers (Herbin et al. 2004, 2006). The stride time (in s) was calculated as the time lag between two successive touch-downs of the same limb. The stride frequency SF (in Hz), was defined as the reciprocal of the stride time. The duration of the stance time S_t (in s) with the limb in contact with the ground, and the swing time S_w (in s) with the limb in flight, were measured. The duty factor DF (in %) is the fraction of the stride time (Std) when a foot is in contact with the ground. The stride length (m) was measured automatically on the frame image of the treadmill using a custom-designed software routine (*Loco.program*, was written with the open-source MATLAB functions which are available from http://www.vision.caltech.edu/bouguetj/calib_doc/), as the distance between two successive footfalls of the same foot. It was facilitated by the presence of successive marks (20-mm intervals) on the treadmill. Because these gait measures help to identify the course of the different parameters with velocity, and because we considered the animal as a single system moving in its environment, each parameter was calculated for each limb, and the mean value of the concerned parameter was calculated for each cycle. The mean and standard deviation of the parameter describe the relationship between the chosen parameter and velocity or stride frequency.

The identification of the impact of both stride frequency and stride length on velocity, and the impact of both stance time and swing time on stride frequency, were approached using stepwise regression models. As described in previous papers (Karantanis et al. 2015, 2017b), the global impact of each parameter was estimated by the R^2 of the partial correlations; the correlation between a dependent variable and its covariate, after the impact of other covariates is removed (Harrell 2001).

By contrast, the contribution of the increase (or decrease) of two parameters in the increase (or decrease) of a variable was based on the comparison of the rate of increase or decrease of each parameter in relationship with the variable. Thus, the velocity being the product of the stride frequency and stride length, the velocity rate is the sum of the SF rate ($\Delta SF/SF$) and SL rate ($\Delta SL/SL$) plus the product of SF and SL rates ($\Delta SF.\Delta SL$)/(SF.SL), the third term, always negligible, was ignored. The contribution of variation of SF (or SL) was then [$\Delta SF/ SF1$] or [$\Delta SL/SL1$]/([$\Delta SF/SF$] + [$\Delta SL/SL$]) ([] being the absolute value). The stride time "Std" (SF inverse) is the sum of stance and swing time, and then the contribution of variation of the St and Sw was $\Delta St/\Delta Std$ and $\Delta Sw/\Delta Std$ respectively. The decrease of stride time will be interpreted as an increase in stride frequency. This calculation allowed us to accurately evaluate the contribution of (1) the increase of stride frequency and stride length at a defined increasing velocity or (2) the decrease of stance time and swing at a defined increasing frequency. Consequently at

a given velocity or frequency, we can define the parameter which regulates the increase of the chosen parameter. These contributions change with the velocity or stride frequency and are different for each gait (Herbin et al. 2004).

Analyses

The statistical significance of observed differences between the parameters was assessed comparing the regression curves using an F-test. This permits to compare the relationships between two variables in two different conditions (Motulsky and Brown 2006). The best regression curves were calculated using simple regressions from all the values (Table Curve2D, *Jandel Scientific*), and the statistical significance of each regression (best-fit value of the curve) was determined by an analysis of variance. To identify if the curves are statistically different, the regression curves where compared two by two. As in an F-test, the test compares the sum of squares and degrees of freedom for each fit. However, here the test compares, on the one hand the total of the sum of squares and the degrees of freedom from the two fits (done separately), and on the other hand the sum of square and degrees of freedom obtained by pooling the two sets of data (combined data). The F-ratio and the corresponding P value determine if the curves differ or not. All analyses were performed using Table curve (*Jandel scientific*), Prism (*GraphPad software, Inc*.), and Statistica 6.1 (*Statsoft*). The level of significance was set at 0.05.

Results

Symmetrical, asymmetrical gaits and velocity

During this study a total of 1765 sequences were analysed, among them 1291 were regular sequences, with 423 (24%) and 469 (27%) being identified as symmetrical and asymmetrical gaits respectively, and 399 (23%) being identified as transition sequences (sequence presenting only one girdle with limbs evenly spaced in time). The 474 remaining non-regular sequences (26%) and the transition sequences, too complex and too variable to be analysed here, were not taken in account in this study and will be published later.

For symmetrical gaits, the mean velocities ranged from 0.19 m/s (SD = 0.03) to 1.82 m/s (SD = 0.03); velocities ranged from 0.31 m/s (SD = 0.12) to 2.21 m/s (SD = 0.05) for asymmetrical gaits. The distribution of velocity (each 0.15 m/s) in relationship to the number of sequences showed a peak value around 0.82 m/s for symmetrical and two peaks (1.13 and 1.43 m/s) for asymmetrical gaits (Fig. 1). The distribution of the transition sequences in relation to velocity showed a first peak at 0.24 m/s corresponding to the transition between unsteady to steady locomotion. The second
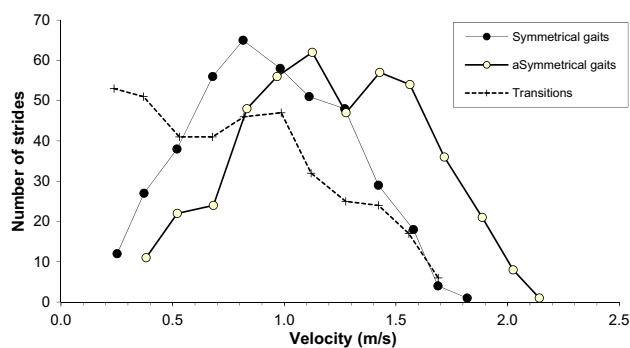
Fig. 1 Number of strides for symmetrical, asymmetrical gaits, and stride transitions in relation to mean velocity (bin of 0.15 m/s)
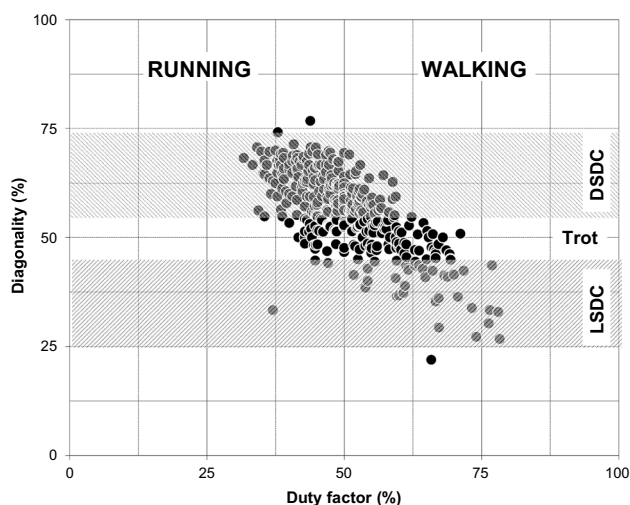
Fig. 2 Trailing forelimb duty factor plotted against diagonality in symmetrical gaits. The trot, and the DSDC are the most represented symmetrical gaits. DSDC for Diagonal sequence Diagonal couplet; LSDC for Lateral sequence Diagonal couplet. (from Cartmill et al. 2002)

peak at 0.97 m/s could correspond to the transition between symmetrical and asymmetrical gaits. After that, the number of transitions decreases until 1.69 m/s, with a plateau between 1.27 and 1.42 m/s which could correspond to transition between two different asymmetrical gaits. At velocities higher than 1.30 m/s, asymmetrical gaits are always more used than symmetrical gaits.

Diagonality and duty factor

The symmetrical gaits are equally distributed around a DF of 50%, and their diagonality ranged from 22 to 77% (Fig. 2). Trots represent 32% of the symmetrical gaits, the diagonal sequences (in which the touchdown of the contralateral forelimb follows a given hind limb) only represented by DSDC are 58%, and only 10% are lateral sequences (forelimb

follows an ipsilateral hind limb) identified as LSDC. The LSDC were found at low and high velocities, with a DF comprised between 78 and 37%, while the DSDC were observed from a DF of 59–32%. The trot appeared at a DF of 71% and were found until a DF of 35%. Only 2 lateral couplets (one LS and one DS) were identified in symmetrical gaits of the mouse lemur while moving on a treadmill. From a DF of 78 until 59.5% the LSDC and trot represent 44 and 52%, respectively ($N = 67$). The first DSDC appears at a DF of 59.4% and from this DF until a DF of 50% the gait frequencies of LSDC, trot and DCDS were 5, 37 and 58%, respectively ($N = 213$). At a DF lower than 50% the LSDC represent only 1.5%, while trot 21% and DSDC 77% ($N = 196$).

The duty factor decreases with speed from 76.7% (SD = 9.1) and 79.5% (SD = 3.6) to 33.8% (SD = 4.8) and 23.5% (SD = 2.4) in symmetrical and asymmetrical gaits, respectively (Table 1). The decrease of the duty factor with the increasing velocity in symmetrical gaits is lower than in the asymmetrical gaits (Fig. 3). The slopes of the regressions of the duty factor of the symmetrical and asymmetrical gaits are thus significantly different ($F_{2,856} = 8.82$, $P \ll 0.001$), and this difference remains if we compare values across the same range of velocities ($F_{2,810} = 6.14$, $P = 0.002$). In addition to the results obtained for stance time and stride frequency, the stance time expressed as a percentage of the reference stride time is also different in symmetrical and asymmetrical gaits (see below).

Stride frequency and stride length

An overview of the regressions characterizing the relationship between the different parameters is provided in Table 1. Both stride frequency and stride length increased with increasing velocity (Fig. 4a, b). Thus, SF_S and SL_S increase from 2.0 Hz and 0.06 m (SD = 0.18; 0.5) to 7.9 Hz and 0.35 m (SD = 0.4; 1.75), and SF_{aS} and SL_{aS} increase from 1.7 Hz and 0.07 m (SD = 0.36; 2.4) to 8.4 Hz and 0.54 m (SD = 1.04; 2.8). The regressions of SF_S or SF_{aS} against velocity show that the difference between both gaits is not significant ($F_{2,856} = 2.31$, $P = 0.099$), and this state persists if we compare values across the same range of velocities ($F_{2,809} = 2.73$, $P = 0.065$). For SL the difference between gaits is also not significant ($F_{2,856} = 2.49$, $P = 0.083$). For asymmetrical gaits, the curves related to these parameters yield similar results. However, in symmetrical gaits, from 0.2 to 1.8 m/s the slope of the curves of SF_S is always higher than in SL_S, while in asymmetrical gaits, from 0.3 to 0.6 m/s the slope is also highest in SF_{aS}, but after, until 2.2 m/s the slopes of the both curves are not different.

The construction of the stepwise regression model, showed that in symmetrical gaits, the stride length plays a major role in the genesis of velocity ($R^2 = 78.3\%$, $F = 1453$,

Table 1 Summary of regression curve equations of the kinematic parameters analyzed in both gait

Gait	Parameters	Stride frequency	Stride length	Stance time	Swing time	Duty factor
Symmetrical	Min/max	2.0–7.9 Hz	0.06–0.32 m	0.366–0.052 s	0.213–0.058 s	33.8–76.7%
	$f(x)$	f (velocity/SF)	f (velocity/SL)	f (SF/ St)	f (SF/ Sw)	f (velocity/DF)
		$Y = 5.33x^{0.43}$	$Y = 0.19x^{0.57}$	$Y = 0.75x^{-1} - 0.05$	$Y = -0.01x + 0.16$	$Y = 46.06x^{-0.3}$
		SEa = 0.031 SEb = 0.015	SEa = 0.001 SEb = 0.016	SEa = 0.006 SEb = 0.026	SEa = 0.004 SEb = 0.001	SEa = 0.28 SEb = 0.01
		$R^2 = 0.70$, $F_{1,409} = 963$	$R^2 = 0.80$, $F_{1,409} = 1601$	$R^2 = 0.67$, $F_{1,409} = 814$	$R^2 = 0.28$, $F_{1,409} = 157$	$R^2 = 0.67$, $F_{1,409} = 836$
aSymmetrical	Min/max	1.7–8.4 Hz	0.07–0.54 m	0.473–0.042 s	0.249–0.059 s	23.5–79.5%
	$f(x)$	f (velocity/SF)	f (velocity/SL)	f (SF/St)	f (SF/Sw)	f (velocity/DF)
		$Y = 3.99x^{0.5} + 1.33$	$Y = 0.19x^{0.62}$	$Y = 0.64x^{-1} - 0.03$	$Y = -0.01x + 0.17$	$Y = 33.7x^{0.5} + 80.6$
		SEa = 0.235 SEb = 0.214	SEa = 0.002 SEb = 0.028	SEa = 0.006 SEb = 0.031	SEa = 0.004 SEb = 0.001	SEa = 1.55 SEb = 1.41
		$R^2 = 0.44$, $F_{1,447} = 349$	$R^2 = 0.57$, $F_{1,447} = 597$	$R^2 = 0.50$, $F_{1,447} = 440$	$R^2 = 0.36$, $F_{1,447} = 248$	$R^2 = 0.56$, $F_{1,447} = 569$
Comparison Sym./aSym.		=	=	≠	≠	≠
		$F_{2,856} = 2.31$, $P = 0.100$	$F_{2,856} = 2.49$, $P = 0.084$	$F_{2,856} = 5.51$, $P < 0.006$	$F_{2,856} = 10.77$, $P \ll 0.006$	$F_{2,856} = 8.82$, $P \ll 0.006$

The stride frequency, stride length and duty factor are expressed in function of velocity, and the stance time and swing time are expressed in function of stride frequency. SEa, standard error of the first coefficient; SEb, standard error of the second coefficien
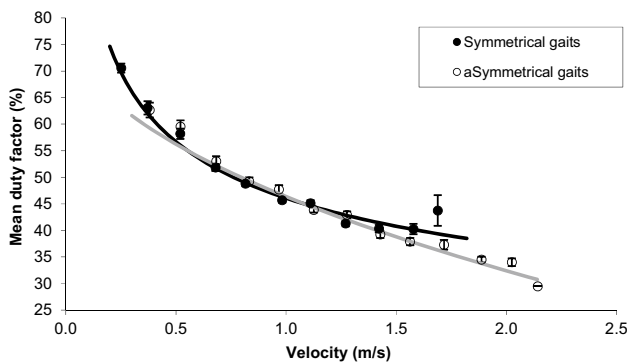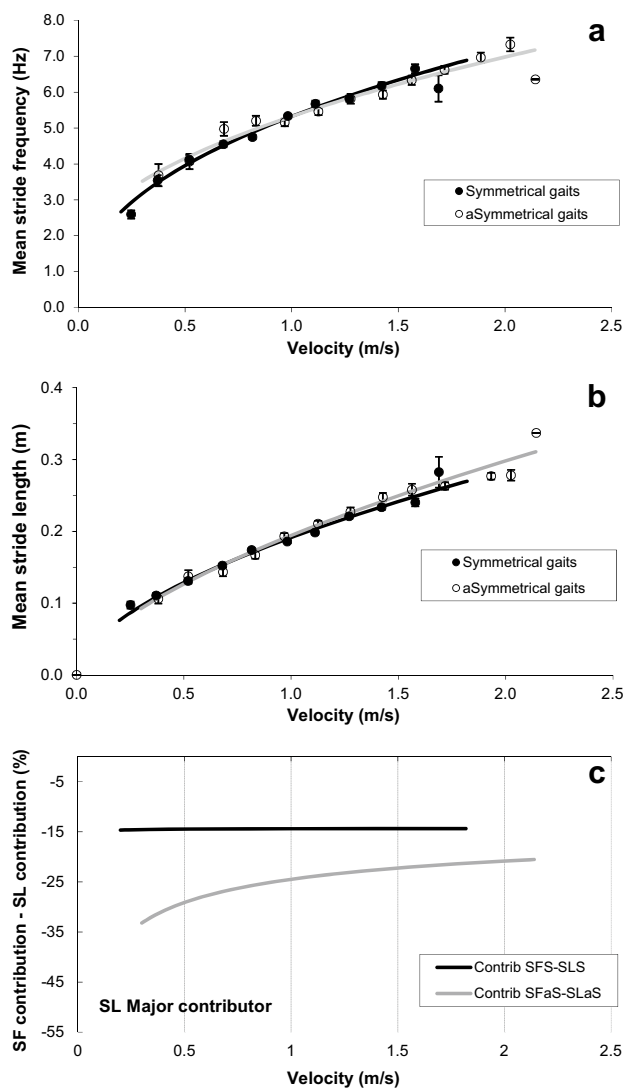

Fig. 3 Duty factor. **a** Variation in the duty factor with velocity for symmetrical and asymmetrical gaits. **b** Relationship between mean duty factor ($\pm$ SEM) and mean velocity (bin of 0.15 m/s). Both regression curves were established based on all observations for each gait ($N = 423$ for symmetrical gaits and $N = 469$ for asymmetrical gaits). *S* symmetrical gaits, *aS* asymmetrical gaits, *DF* duty factor

$p \ll 0.001$), and that the role of stride frequency was less important ($R^2 = 19.9\%$, $F = 4475$, $p \ll 0.001$). In asymmetrical gaits, the role of the stride length is lower than in symmetrical gaits, but predominant ($R^2 = 56.6\%$, $F = 578$, $p \ll 0.001$), while the role of stride frequency is a little higher ($R^2 = 39.7\%$, $F = 4628$, $p \ll 0.001$). However, as shown by the difference between the slopes of both parameters, the contribution of the increase of each parameter in the increase of velocity is different. Figure 4c presents the difference between the contribution of the increase of SF and SL with increasing velocity for each gait pattern. For

symmetrical gaits, the contribution difference of the SF-$_S$ and SL-$_S$ are independent of the velocity; with a constant and predominant contribution of the increase of the stride length (57%), the contribution of the stride frequency stays at 43% irrespective of the velocity. In asymmetrical gaits, as in symmetrical gaits, the contribution of the increase of stride length is greater than that of stride frequency, but the contribution is related to velocity. The contribution of the increase of stride length (74.8%) decreases relative to that of stride frequency until maximal speed (60% at 2.60 m/s).
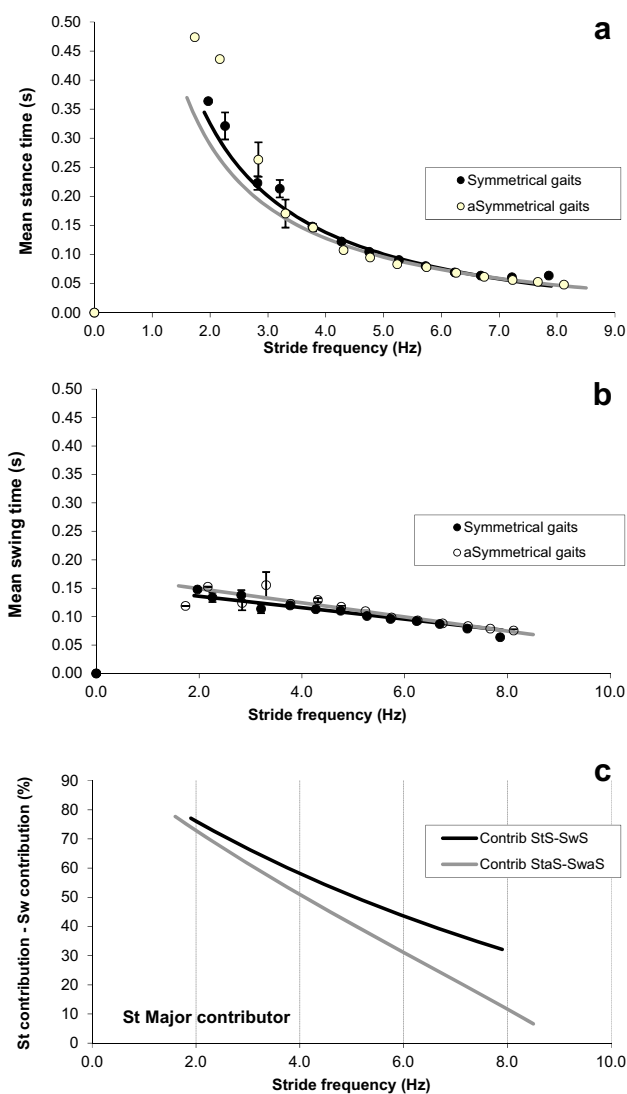
Stance time, swing time

The stance time decreases with the increasing stride frequency from 0.366 and 0.476 s (SD = 0.118; 0.102) to 0.052 and 0.042 s (SD = 0.006; 0.003) in symmetrical and asymmetrical gaits respectively. The swing time decreases also with the increasing stride frequency from 0.213 and 0.249 s (SD = 0.054; 0.015) to 0.058 and 0.059 s (SD = 0.011; 0.011) in symmetrical and asymmetrical gaits respectively (Fig. 5a, b). As the increase in velocity depends on both spatial and temporal parameters the changes of the stance and swing time were established only in relation to the increase in stride frequency (Herbin et al. 2004). The relationship for stance and swing time against stride frequency is described in Table 1. The difference between the St-$_S$ and St-$_{aS}$ regression curve is significant ($F_{2,856} = 259$, $P = 0.004$), as is the difference of the regression curve of Sw-$_S$ and Sw-$_{aS}$ against stride frequency ($F_{2,856} = 259$, $P \ll 0.001$). These differences still exists if we compare values across the same range

Fig. 4 Stride frequency and stride length. **a** Relationship between mean stride frequency ($\pm$ SEM) and mean velocity (bin of 0.15 m/s) for symmetrical and asymmetrical gaits. **b** Relationship between mean stride length ($\pm$ SEM) and mean velocity (bin of 0.15 m/s) for symmetrical and asymmetrical gaits. **c** Difference between the contribution of the increase in stride frequency and the increase in stride length to the increase in velocity. Note the equal contribution of both variables in the increase of velocity for symmetrical gaits and the decreasing contribution of stride length for velocity increase in asymmetrical gaits. Each regression curve was established based on all observation for each gait ($N=423$ for symmetrical gaits and $N=469$ for asymmetrical gaits). *S* Symmetrical gaits, *aS* asymmetrical gaits, *SF* stride frequency, *SL* stride length

Fig. 5 Stance time and swing time. **a** Relationship between mean stance time ($\pm$ SEM) against the mean stride frequency (bin of 0.5 Hz) for symmetrical and asymmetrical gaits. **b** Relationship between mean swing time ($\pm$ SEM) and mean stride frequency (bin of 0.5 Hz) for symmetrical and asymmetrical gaits. **c** Difference between the contribution of the decrease of the stance time and the decrease of the swing time in the increase of stride frequency. Note the decreasing contribution of the stance time for both gait, however its contribution is always higher than swing time. Each regression curves were established from all the value of each gait ($N=423$ for symmetrical gaits and $N=469$ for asymmetrical gaits). *S* symmetrical gaits, *aS* asymmetrical gaits, *St* stance time, Swing time

of velocities ($F_{2,842} = 14.2$, $P \ll 0.005$). In the symmetrical gaits, at equivalent stride frequency, the stance times are longer than during asymmetrical gaits, and inversely the swing times are shorter in symmetrical gaits than asymmetrical gaits. If we compare the slopes of the correlations for each gait, we can observe that the St-$_S$ slope is higher than the Sw-$_S$ slope until 6 Hz, while the St-$_{aS}$ and the Sw-$_{aS}$

slopes is higher until 5.5 Hz. After these stride frequencies the decrease of St is not different from this of Sw.

The stepwise regression model, showed that in symmetrical gaits, the stance time plays a major role in the genesis of the stride frequency ($R^2 = 69.9\%$, $F = 937$, $p \ll 0.001$), and that the role of swing phase was much less important ($R^2 = 18.2\%$, $F = 621$, $p \ll 0.001$). In asymmetrical gaits, the impact of the stance time is lower than

in symmetrical gaits, but also major ($R^2 = 53.8\%$, $F = 519$, $p \ll 0.001$), while the role of swing phase is higher than previously ($R^2 = 30.5\%$, $F = 860$, $p \ll 0.001$). As stated above the increase of the parameters St and Sw do not contribute equally to the increase in stride frequency. The difference between the contribution of the increase of St and Sw with the increasing stride frequency in each gait pattern is shown in Fig. 5c. For both gaits the decrease of St-$_S$ contributes always more to the increase in stride frequency, with a higher contribution of the decreasing stance time in symmetrical gaits than in asymmetrical gaits (at 2 Hz the contributions of St-$_S$ and Sw-$_S$ were respectively 88–12% and 86–13% in asymmetrical gaits, and at 8 Hz the contributions of St-$_S$ and Sw-$_S$ were respectively 66–34% and 56–44% in asymmetrical gaits).

Discussion

This study reports on the spatio-temporal gait parameters of mouse lemur treadmill locomotion. We paid particular attention to an accurate description of the different variables involved in the increase of velocity for both symmetrical and asymmetrical gaits. To our knowledge, no studies in the mouse lemur, as of yet, have analysed all the variables presented here, with such a large number of data points and over this large a range of velocities. Most of studies in primates (small or large) of the last decade have analysed and detailed their locomotion using runways or poles (Demes et al. 1994; Nyakatura et al. 2008; Young 2012; Shapiro et al. 2011, 2016; Schmitt et al. 2006; Schmidt 2008), requiring in the best case, a large number of sequences to obtain a consistent number of cycles. The advantage of the treadmill is that it allowed to capture long series of cycles, during a large range of selected velocities (including maximal velocities), which allow the animal to use a large gait repertory. During a treadmill sequence, the number of cycles was greater than in a sequence obtained on a runway, and permitted to the mouse lemurs to present a succession of cycles including symmetrical and asymmetrical gaits, but also transitional cycles (23%). Consequently even if, the use of treadmill generates modifications in the natural characteristics of locomotion as an increase in stride frequency (Stolze et al. 1997; Alton et al. 1998; Herbin et al. 2007), the treadmill still is a good apparatus to quantify the different locomotor parameters (Fischer and Lehmann 1998; Herbin et al. 2004, 2007; Serradj and Jamon 2007; Bojados et al. 2013). The large data set obtained here allowed to observe that in relation to the gait type used the mouse lemur presents different strategies to increase velocity.

Symmetrical and asymmetrical gaits

From the lowest to the highest velocities tested here, the mouse lemur moved using symmetrical or asymmetrical gaits. The range of velocities observed on the treadmill matched the velocities registered during overground locomotion in *Microcebus* by Shapiro et al. (2016), and enclosed those used by larger Marmosets (Schmitt 2003), *Saguinus* (Arms et al. 2002), or Galagos which can run at 2.2 m/s (Crompton et al. 1993), or the lighter grey short-tailed opossum (Lammers and Zucher 2011). At the lowest velocities (until 0.85 m/s) the mouse lemur prefers to use symmetrical gaits rather than asymmetrical gaits, the ratio varying from 1.4 to 2.5. In this range of velocities, the number of transitional strides was very high and might reflect that over these velocities and on this moving support, the mouse lemur must re-adjust its motor coordination continuously to be in a comfortable posture. From 0.95 m/s until 1.25 m/s it alternates between symmetrical and asymmetrical gaits. The number of transitional strides decreased from 1.0 to 0.17 m/s. And finally, at the highest velocity, mouse lemurs only used asymmetrical gaits, the transitions between symmetrical and asymmetrical gait being stopped around 1.80 m/s. The range of velocities covered during asymmetrical gaits by our mouse lemurs on the treadmill is close to that it recorded for locomotion on a flat support by Shapiro et al. (2016). By contrast with previous studies, over all speeds covered, it appears here that mouse lemurs do not have a preference for symmetrical or asymmetrical gaits on the flat treadmill. However, if we consider non-regular sequences (81 and 244 symmetrical and asymmetrical sequences respectively) the proportion of each gait will be different, with a preference for the asymmetrical gaits (59%). The difference in the ratio could be accentuated if we assume that all sequences which were not symmetrical were "asymmetrical", including thus transition sequences in asymmetrical gaits (27 and 73% for symmetrical and non-symmetrical gaits respectively). The high proportion of transition sequences or decelerating/accelerating sequences could explain why previous studies have not found the similar use of both types of gaits on a large flat support (Shapiro et al. 2016). The other possibility could be that there was difference in the use of both gaits between treadmill and static supports. However, in a previous study on mice this was not the case. Rather, we observed an increase in the use of symmetrical gaits on the static support relative to treadmill locomotion (Herbin et al. unpublished results). Irrespective, it appears that asymmetrical gaits represent a non-negligible part of the overall gaits used by mouse lemurs, and this confirms the assumptions of previous authors (Vilensky and Patrick 1985; Young 2009), that asymmetrical gaits represent an important component of the locomotor repertoire in primates, as in other mammals.

Our significant data sample of symmetrical gaits shows that even if the mouse lemur moved on a large flat substrate, the lateral sequence gaits (LSDC) were not commonly used (10%) in contrast to diagonal sequence gaits (32%) or trots (58%). At lower velocities (DF > 72%), the individuals tend to use exclusively LSDS, and until DF = 59.5%, the walking trot (Hildebrand 1976) takes an important place (52%) in the gaits used. Since the grey mouse lemur uses DS gaits (at DF = 59.5%; mean velocity of 0.52 m/s), the gait frequency shows a concomitant decrease of the LS gaits and trot with an increase of DS gaits. At these higher walking velocities, as during the previous lower velocities, a progressive change of gait seems to take place during the trot. During the running symmetrical gaits (DF > 50%), the trot is still present but its frequency decrease as the DS (ambling) gaits increase. This proportion of trotting gaits, was not observed in previous studies in primates, which found a very low proportion (or even the absence) of trot during locomotion on different substrates (Schmitt et al. 2006; Shapiro et al. 2016). This result could be due to the fact that we allowed a deviation of ± 5% to the too strict value of 50% for trot diagonality (Nyakatura et al. 2008). But, if we applied the strict value of Cartmill et al.'s terminology (2002) the trot frequency decreases to 2%, LS increases to 21% as DS to 77% of symmetrical gaits. Yet, even with this strict definition, at walking gaits, the LS frequency will be 40%, while DS will be 57%. This shows that on a flat support there is no shift from LS to DS with the decreasing DF as previously hypothesized for small arboreal marsupials (Karantanis et al. 2015), and tends to diverge from what was expected in others marsupials (Pridmore 1994; Shapiro and Young 2010, 2014, 2016; Biknevicius et al. 2013). Nevertheless, the gait repertoire of mouse lemurs is similar to the pooled runway data of the terrestrial *Monodelphis domestica*, and of the arboreal *Caluromys philander* (Lemelin et al. 2003) or *Petaurus breviceps* (Shapiro and Young 2010). How to interpret the presences of LS, trot and DS at similar DF? Literature put forward that (1) the LS gaits are more related to terrestrial mammals (Hildebrand 1967; Demes et al. 1990; Cartmill et al. 2002; Lemelin and Cartmill 2010; Karantanis et al. 2017a), (2) that since the DS gaits are expected to increase dynamic stability and safety on narrow, declining, or swaying supports (Cartmill et al. 2007a; Schmitt et al. 2006), the DS gaits are more represented in arboreal mammals (Pridmore 1994; Cartmill et al. 2002; Schmitt and Lemelin 2002; Stevens 2008; Karantanis et al. 2015), and (3) that the DS is a trait characteristic of the locomotion of most of primates (Hildebrand 1967; Cartmill et al. 2002, 2007b; Nyakatura and Heymann 2010), and (4) that LS could represent the primitive state for primate locomotion (Schmitt 2003). Therefore, the mouse lemur, which is an arboreal specialist, did not change drastically its footfall sequence from DS to LS when moving on a large support as previously suggested for other mammals

(Lemelin et al. 2003; Wallace and Demes 2008). The use of LS footfall sequences is still rare. It was demonstrated that the use of the treadmill creates a visual-motor conflict for the individual when it moves on this type of support (Grillner 1981; for review see; Herbin et al. 2007), yet, the mouse lemur seems to move easily on the flat treadmill belt. Despite this unnatural support could be perceived as unsafe and unstable, and could induce a more frequent use of more stabilizing DS gaits.

Temporal and spatial parameters

Whatever the gaits used, the parameters analysed during this study are speed-dependent. As was described previously for mice in the same conditions, stride frequency and stride length increased with increasing velocity (Herbin et al. 2007). The lack of data on spatio-temporal gait parameters in other small primates on the same support prevents us from comparing our data to others, but it is interesting to note that range of stride frequencies in the mouse lemur is close to that observed for mice on the same support (Herbin et al. 2004, 2006). Due to their larger size, the stride lengths of the mouse lemurs were longer than those of mice, and consequently permitted to this small primate to attain higher velocities.

The increase in velocity is achieved by a dual mechanism of an increase in stride frequency and stride length (Fig. 4). In both gaits, the stride length has a major impact on velocity, the stride frequency playing a secondary role. The same tendency has been observed in other primates and arboreal mammals (Larson et al. 2000, 2001), and could be explained by the fact that an arboreal primate must assure its stability by increasing the parameters which promote secure grasping by a farther reach of the limbs (Demes et al. 1994). However the regulation of the increase of the velocity is not ensured by the same parameter. In symmetrical gaits, contributions of the increase of both parameters were independent of the animal's velocity, with always a SL contribution 14% higher than the SF (Fig. 4c). This corresponds to an increase in the stride length which is higher than the increase in stride frequency irrespective of the velocity. For asymmetrical gaits, the tendency was different, and if the increase of velocity was also obtained by the dual effect of an increase in stride frequency and in stride length, the regulation is dependent on the velocity. Indeed, with increasing velocity (from 0.29 to 1.08 m/s) the contribution of the increase in stride length decreases (from 75 to 62%). From a velocity of 1.08 m/s the contribution of the increase in stride length stayed around 62%. Consequently in asymmetrical gaits, even if the impact of the stride length is modulated by the stride frequency, it remains the major regulator of the increase of velocity. As in symmetrical gaits, this higher contribution of the increase of stride length could serve a reduction of the oscillations

and could thus endorse a more continuous and safer progression along unsafe or unstable substrates such as narrower arboreal supports. If we compare those results with those of mice in same conditions (Herbin et al. 2004), we can observe that during symmetrical gaits the increase in velocity was obtained by a constant pattern of the contribution of both stride length and frequency independent of the velocity, while in asymmetrical gaits the pattern of the contribution of length and frequency changes with velocity.

The increasing stride frequency is also achieved by a dual mechanism of a decrease in both stance time and swing time (Fig. 5). During symmetrical gaits at the equivalent stride frequency the stance times were longer than during asymmetrical gaits, and inversely the swing times were shorter. These results are not surprising and are in the accordance with the fact that during asymmetrical gaits, such as gallop, half bound, or bound, the contact duration with the support is shorter than during walking or trotting. The duty factor confirmed this tendency and at equivalent velocities was always shorter during asymmetrical gaits. However, irrespective of the gait used, the increase in stride frequency was always provided predominantly by a decrease in stance time relative to swing time, even if the contribution of the decrease in stance is higher during symmetrical than asymmetrical gaits. Previously we have shown in mice under the same conditions, a similar pattern. This did not prevent that there was a real impact and contribution of the decrease of the swing time in the increase of stride frequency as it was previously observed for other species (Halbertsma 1983; Vilensky and Patrick 1985; Clarke 1991; Herbin et al. 2004, 2007).

This type of analysis of the metric parameters in relation to gaits brings a new perspective on the understanding of the impact and the contributions of each variable and their efficiency in the regulation of the velocity. Like in rodents, the results for this small arboreal primate show that there was a dual implication of temporal and spatial parameters (stride frequency and stride length) in the increase in velocity (Camargo et al. 2015; Karantanis et al. 2017a, b). The prediction that during walking velocities the majority of primates and small non-cursorial mammals increase velocity by only changing their stride frequencies was not confirmed here for mouse lemurs (Fischer et al. 2002; Schilling and Fischer 1999; Schmidt 2008). This difference could be due to the larger range of velocities tested, or the fact that previous studies examined only symmetrical gaits where the spatial parameters (step length and body progression during the contact phase) are not modified to increase velocity (Schmidt 2008).

The treadmill allowed to test the complete performance of the grey mouse lemur including high velocity sequences. The fact that we used a flat treadmill, an unnatural support for mouse lemurs, does not allow us to speculate on whether the strategy described here is characteristic of arboreal mammals, but permits to separate a mouse pattern and a mouse lemur pattern on the same treadmill support. Even if the natural gait of the mouse lemurs is modified by the use of a treadmill, the results are consistent: all stride characteristics can be quantified precisely and can be easily reproduced. This locomotion model established for a group of young adult grey mouse lemurs should be considered as a baseline for future studies aiming to evaluate the effects of age, or changes in body weight. Finally, our data are of interest for studies aiming to evaluate how different locomotor supports impact gait metrics during locomotion.

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