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How does a mouse increase its velocity?
A model for investigation in the control of locomotion

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Abstract

We analysed treadmill locomotion of the adult SWISS-OF1 mice over a large range of velocities. The use of a high-speed video camera combined with cinefluoroscopic equipment allowed us to quantify in detail the various space and time parameters of limb kinematics. We find that velocity adjustments depend upon whether animal used a symmetrical or non-symmetrical gait. In symmetrical gaits, the increase of velocity generally results equally from an increase in the stride frequency and the stride length. On the other hand, in non-symmetrical gaits, the increase in velocity is achieved differently according to the level of velocity used. As speed increases, velocity increases first as a consequence of increased stride frequency, then as in symmetrical gaits, by an equal increase in both variables, and finally at high speed, velocity increases through increased stride length. In both symmetrical and non-symmetrical gaits, stance and swing-time shortening contributed to the increase of the stride frequency, with stance time decrease being the major contributor. The pattern of locomotion obtained in the present study may be used as a model mouse system for studying locomotor deficits resulting from specific mutations in the nervous system. *To cite this article: M. Herbin et al., C. R. Palevol 5 (2006).*

Résumé

Comment la souris augmente-elle sa vitesse ? Un modèle pour la recherche sur le contrôle moteur de la locomotion. La locomotion sur tapis roulant de la souche de souris SWISS-OF1 a été analysée à travers une large gamme de vitesses. L'utilisation de la vidéoradiographie à grande vitesse a permis de quantifier de façon très détaillée tous les paramètres de la cinématique du membre de référence. Les résultats ainsi obtenus montrent que la fréquence et l'enjambée n'interviennent pas de la même façon dans l'augmentation de la vitesse, selon l'allure utilisée. Lorsque l'animal est en allure symétrique, l'augmentation de la vitesse est généralement obtenue par une égale augmentation de la fréquence et de l'enjambée. En revanche, si la souris utilise une allure non symétrique, l'augmentation de la vitesse est obtenue différemment selon la valeur de cette dernière. L'augmentation de la vitesse est d'abord surtout assurée par une augmentation de la fréquence, puis par l'augmentation égale des deux variables et enfin surtout par l'augmentation de l'enjambée. L'augmentation de la fréquence est, en revanche, surtout assurée par une diminution de la durée du posé et cela, quelle que soit l'allure utilisée. Cette modélisation de la locomotion normale de la souris pourra être utilisée

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comme référentiel pour les études portant sur les déficits moteurs de certaines souches de souris mutantes ou transgéniques. ***Pour citer cet article : M. Herbin et al., C. R. Palevol 5 (2006)***.

1. Introduction

Locomotion takes place in the feeding behaviour and in the search for a sexual partner, and then is an essential factor in survival. The study of this complex function has been one of the major topics undertaken by É.J. Marey [32,33]. The numerous technical devices that he has brought and used, as the photographic rifle and fixed-plate chronophotograph (1882), which took images on fixed glass plates or moving celluloid film in 1891, have largely increased the precision of the analyses of motions. By the end of the 19th century, the different types of chronophotographic devices allowed recording images at speeds of 20 to 100 frames per second [34]. These technical improvements permitted a detailed analysis of the walk, run, jump, and flight. With the invention of the high-speed camera, the sampling rate increased considerably, recording events that lasted only a few milliseconds. However, this cinematographic technique provides only a silhouette that limits precise measurements of the magnitude of the motion of moving parts [31]. Walsh made for the first time (1896), an X-ray film to visualise joint movements (Walsh 1897, cit. after [41]). This new application of X-rays allowed direct visualisation of the skeleton in motion. Since this first step of the cineradiography, it has proven to be the best non-invasive approach in locomotor studies. With the invention of image intensifiers this approach has become more widespread [13,29–31]. Currently, the cinefluoroscopic equipment can be combined with high-speed video camera, that allows collection of precise data at the same timescale as neuronal activity, providing a new outlook interpretation of the locomotor behaviour [11,12].

Recently, the study of locomotion centred on the study of the gaits, which are defined from several spatio-temporal parameters [26]. These simple variables show that animals shift along the scale of gaits with increasing velocity. Several studies show that animals not only prefer specific gaits, but also choose certain ways of changing gait to increase speed [37]. Numerous studies on mammal locomotion deal with small mammals classically used in experimental biology. A few studies have described the general gait of small sized mammals [5,10]; see [10] for a review. However, they did not consider the problem of the symmetry versus non-symmetry of the gait, which is essential in order to make inferences about the neural coordination of locomotion [8,39]. If each type of gait (symmetrical and non-symmetrical) may involve different motor patterns, then it should be worthwhile to understand how small mammals control speed in relation to these gaits, and if symmetrical gaits are used only at slow or moderate speeds and if the non-symmetrical gaits are used at fast speeds [19,20].

Our study deals with a quantification of the kinematic parameters for each gait, and their respective contribution to increase velocity. These data, collected over a wide range of velocities and on continuous series of cycles, allow us to characterize the gait pattern in a given strain of mice, which can be compared with literature studies and exhibit some anatomical or physiological diseases in the nervous system involved in locomotion.

2. Materials and methods

Data were collected from five female *SWISS* (*OF1-ico subtype IFFA-CREDO*) mice kept in the laboratory (mean age 10 weeks, mean body weight 30 g, mean snout-vent size 9.5 cm). The mice were housed in individual cages in environmentally controlled rooms, and on a diet of rodent pellets *(ad libitum)*. These untrained animals were placed on the treadmill in a Plexiglas corridor (7-cm wide, and path length of 50 cm). The speed of the treadmill was read directly by a tachometer. A high-speed video camera (Motionscope) was run at 250 frames per second and was combined with cinefluoroscopic equipment (Philips Medical Systems). The animals were filmed in lateral view; the running corridor was set as close as possible to the input surface of the image intensifier to avoid magnification effects and loss of resolution. The use of this apparatus highly facilitated the identification of the touch down of each limb. Under these conditions, mice were tested over a large range of treadmill speed, from 13.5 cm s^{-1} to

78.3 cm s^{-1}. At least, 782 strides were selected and analysed. The instant speed of the animal (velocity) was assessed by a calculation for each stride (stride length × stride frequency, in cm s^{-1}). The deceleration and acceleration phases ($Mv - SD$ < velocity < $Mv + SD$, where Mv was the mean velocity of the sequence analysed and SD the standard deviation of the velocity in the sequence analysed), which are not homogeneous, were not analysed here. Finally, 597 regular strides were taken into consideration in this study.

The gaits were based on the definitions of Hildebrand [26], established from previous papers [22,25,40, 42]. Symmetrical gaits (-S) have the footfalls of each pair of feet (fore and hind) evenly spaced in time, the footfall of the limbs of the same pair being spaced by 50% of the reference stride. The cycles which were not identified as symmetrical were regrouped and termed as non symmetrical (-nS). To identify the type of gait, a reference stride (cycle) was selected, beginning by the movement of the forelimb [38].

The kinematic parameters analysed in this study are the same as those classically used [1,23–26]: (1) the stride time (second), calculated as the time lag between two successive touch-downs of the reference limb, (2) the stride frequency SF (hertz), defined as the reciprocal of the stride time, (3) the duration of the stance St (second) with the limb in contact with the ground, and 4) the swing time Sw (second) of limb flight, were measured; (5) the duty factor DF (percent) was the fraction of the stride time when a foot was in contact with the ground, and the stride length SL (in centimetre), as the distance between two successive footfalls of the same foot. These kinematic parameters were calculated and compared with the trailing forelimb and with the reference stride of this foot.

The method to estimate the contribution of the stride frequency and/or the stride length to increasing velocity or to estimate the contribution of the stance time and/or swing time to the increase in stride frequency was based on the comparison of the increase (or decrease) rate in each parameter with the considered variable [21]. From then on, the increase in velocity (between V_1 and V_2) was related to the sum of the increase rate of stride frequency (between corresponding SF_1 and SF_2) and the increase rate of stride length (between corresponding SL_1 and SL_2). This approach allowed a determination of the contribution of each parameter to the variable considered. The statistical significance of observed differences between the gait parameters in symmetrical and non-symmetrical gaits was assessed by comparing the regression curves using an adapted F-test [35]. Briefly, to identify if the curves were statistically differ-

ent, the regression curves were compared two by two. As in an *F*-test, the test compared the sum of square and degrees of freedom for each fit. However, here the test compared, 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 datasets (combined data). The best regression curves were calculated using simple regression from all the values (Table Curve2D, *Jandel Scientific*), and the statistical significance of each regression (best-fit value of the curve) was determined by the analysis of variance. The *F* ratio and the corresponding *P* value determine whether the curves differed or not. All analyses were also performed using Prism (*GraphPad software, Inc.*), and Statistica 6.1 (*Statsoft*) the level of significance was chosen to be 0.001.

3. Results

The symmetrical and the non-symmetrical gaits represent 22.9%, and 77.1% of the total of the strides respectively. The lateral sequences (when the footfall of hind feet precedes the footfall of the ipsilateral forefeet) represent 98.6% of the symmetrical gaits and 77.7% the non-symmetrical gaits. In symmetrical gaits, 83% are moderate trot, 16% are fast trot, and 1% represents the walk. In non-symmetrical gaits, 70% are 'no-suspension-time gallops', and the rest (30%) are 'one-short-suspension-time gallops'. We have not identified clearly any bound or half-bound in the set of data. For symmetrical gaits, the velocity ranged from 20.2 to 84. 8 cm s^{-1}, while for non-symmetrical gaits the velocities ranged from 9.4 to 87.5 cm s^{-1}. In the entire velocity range, the non-symmetrical gaits were always more represented than the symmetrical gaits (Fig. 1).

3.1. Stride frequency and stride length

Variation in velocity can be induced by a change in the stride frequency or/and stride length. Fig. 2 shows that both parameters increased with the increasing velocity. In symmetrical gaits the mean stride frequency (SF) increased from 3.9 Hz (SD = 0.52) to 8.6 Hz (SD = 0.37) and the mean stride length (SL) increased from 4.7 cm (SD = 2.02) to 9.7 cm (SD = 0.37). In non-symmetrical gaits, mean SF increased from 2.4 Hz (SD = 0.43) to 8.6 Hz (SD=0.76), and mean SL increased from 3.4 cm (SD = 1.59) to 10.1 cm (SD = 0.85). The maximal SF was registered at 11.3 Hz, and the maximal SL at 11.0 cm for a velocity of 68.2 and of 85.9 cm s^{-1}, respectively. The relation-
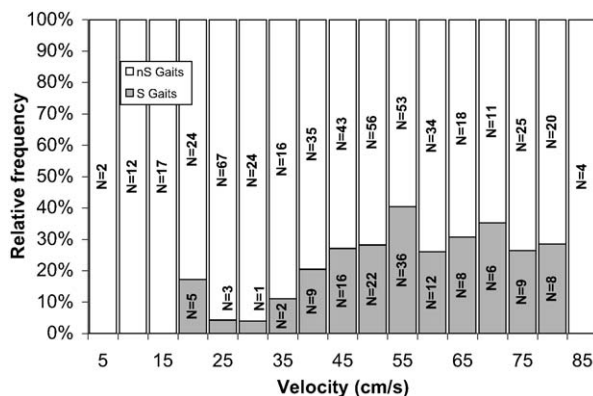
Fig. 1. Relative frequency of strides in symmetrical (S) and non-symmetrical (nS) gaits. N is the number of strides in each velocity range (bin of 5 cm s^{-1}).

Fig. 1. Fréquences relatives des cycles symétriques et non symétriques. N est le nombre de cycles dans chaque gamme de vitesse (gamme de 5 cm s^{-1}).

ship between stride frequency or stride length and velocity is shown in Fig. 2. The relationship between stride frequency and velocity was significantly different between both gaits ($F_{2.593} = 10.87$, $P \ll 0.001$). The difference persists if we compare values across the same range of velocities ($F_{2.558} = 14.9$, $P \ll 0.001$). By contrast the relationship between stride length and velocity was the same in both gaits ($F_{2.593} = 5.77$, $P > 0.001$). In symmetrical gaits, the SF and SL correlation curves show that there is an equal increase in both variables with velocity (Fig. 2A). The slope of each curve was very close for a given velocity. At 20 cm s^{-1}, the slopes of the curves were respectively 0.143 and 0.144 for SF-S and SL-S, and decrease respectively to 0.05 and 0.047 at 85 cm s^{-1} (around –65%). In non-symmetrical gaits, the correlation curves yield different results (Fig. 2B). The slope of SF correlation curve shows approximately the same decrease as SF and SL in symmetrical gaits, while the slope of the SL correlation curve shows a lower decrease (–50%), from 0.124 to 0.064, for the same velocities. Thus, it is clear that the two variables do not contribute equally to the increase in velocity, and the contribution of the variables is not the same for each gait. For symmetrical gaits, from 20 to 85 cm s^{-1}, the contributions of the SF and SL were almost the same (Fig. 2C). The SF contribution was a little higher than SL contribution between 20 to 49 cm s^{-1}, with a maximal difference around 14% at 20 cm s^{-1}. At highest velocity, the contribution of SF and SL were the same ($\leq 10\%$). For the non-symmetrical gaits, from 10 to 29 cm s^{-1}, the contribution of the stride frequency was predominant in the increase of velocity. At 15 cm s^{-1}, the SF contribution was predominant and equal to 65%. In the range of 29 to 68 cm s^{-1} SF and SL equally

contributed to velocity increase. Finally, above 68 cm s^{-1}, SL was the major contributor to velocity increase, with a maximal contribution (57.4%) at 88 cm s^{-1}.

3.2. Stance time and swing time

The variation in stride frequency can be induced by a change in the stance time or/and swing time. The stance time and the swing time decrease with increasing stride frequency (Fig. 3). In symmetrical gaits the mean stance time (St) decreased from 0.212 s at 3 Hz to 0.049 s (SD = 0.006) at 8.4 Hz, and the mean swing time (Sw) decreased from 0.124 s to 0.071 s (SD = 0.006) at the same stride frequencies (Fig. 3A). In non-symmetrical gaits, the mean stance time and the mean swing time decreased respectively from 0.412 s (SD = 0.045) and 0.112 s (SD = 0.023) at 1.9 Hz to 0.052 s and 0.036 s at 11.4 Hz (Fig. 3B). In the range between 1.9 Hz and 5 Hz, the decrease of St was higher than the decrease of Sw, and at a higher stride frequency the decrease of both parameters was very similar. As stated above, the parameters St and Sw do not contribute equally to the increase in stride frequency. Fig. 3C shows the contribution of St and Sw to the increasing stride frequency in each gait pattern. In the symmetrical gaits, in the range of 3 to 8 Hz, the decrease of St contributed predominantly to the increase in stride frequency, with a contribution ranging from 78% to 55%. In non-symmetrical gaits up to 9 Hz, the St contribution was the major factor in the increase in stride frequency. From 9 Hz to 11.5 Hz, the contributions of the decreases of St and Sw were equal.
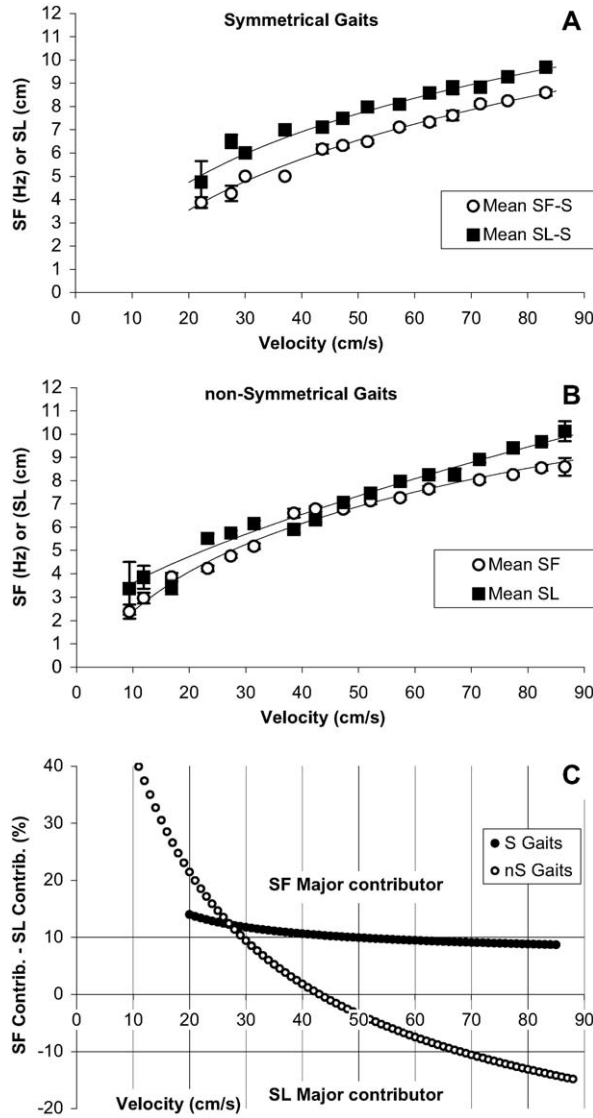
Fig. 2. Stride frequency and stride length. (**A**) Relationship between mean stride frequency (± standard error around the mean value, SEM), or mean stride length (± SEM) and mean velocity (bin of 5 cm s^{-1}) for symmetrical gaits. (**B**) Relationship between mean stride frequency (± SEM) or mean stride length and mean velocity (bin of 5 cm s^{-1}) for non-symmetrical gaits. (**C**) Difference between the contribution of the increase of the stride frequency and the increase of stride length in the increase of velocity. The dotted line represents a variation of 10% around 0 where the contribution of each variable is equal to 50% (more or less 5%). Each regression curves were established from all the value of each gait ($N = 137$ for symmetrical gait and $N = 460$ for non-symmetrical gait). S, symmetrical gaits; nS non-symmetrical gaits; SF, stride frequency; SL stride length.

Fig. 2. Fréquences et enjambées. (**A**) Relation entre la fréquence moyenne (± SEM), ou l'enjambée moyenne (± erreur standard autour de la moyenne, SEM) et l'augmentation de la vitesse moyenne (gamme de 5 cm s^{-1}) dans les allures symétriques. (**B**) Relation entre la fréquence moyenne (± SEM), ou l'enjambée moyenne (± SEM) et l'augmentation de la vitesse moyenne (gamme de 5 cm s^{-1}) dans les allures non symétriques. (**C**) Différence entre la contribution de l'augmentation de la fréquence et de l'augmentation de l'enjambée dans l'augmentation de la vitesse. Les pointillés représentent une variation de 10% autour de 0, traduisant une contribution égale à 50% de chaque variable (plus ou moins 5%). Dans chaque type d'allure, les courbes de régression ont été établies à partir de la totalité des cycles ($N = 137$ pour les allures symétriques, $N = 460$ pour les allures non symétriques). S, allures symétriques ; nS, allures non symétriques ; SF, fréquence ; SL, enjambée.

4. Discussion

The present study reports the spatial and temporal parameters involved in mouse locomotion. Particular attention was paid to an accurate description of the variables involved in the increase of velocity in the symmetrical and non-symmetrical gaits. Surprisingly, few studies in mice have analysed these variables over a large
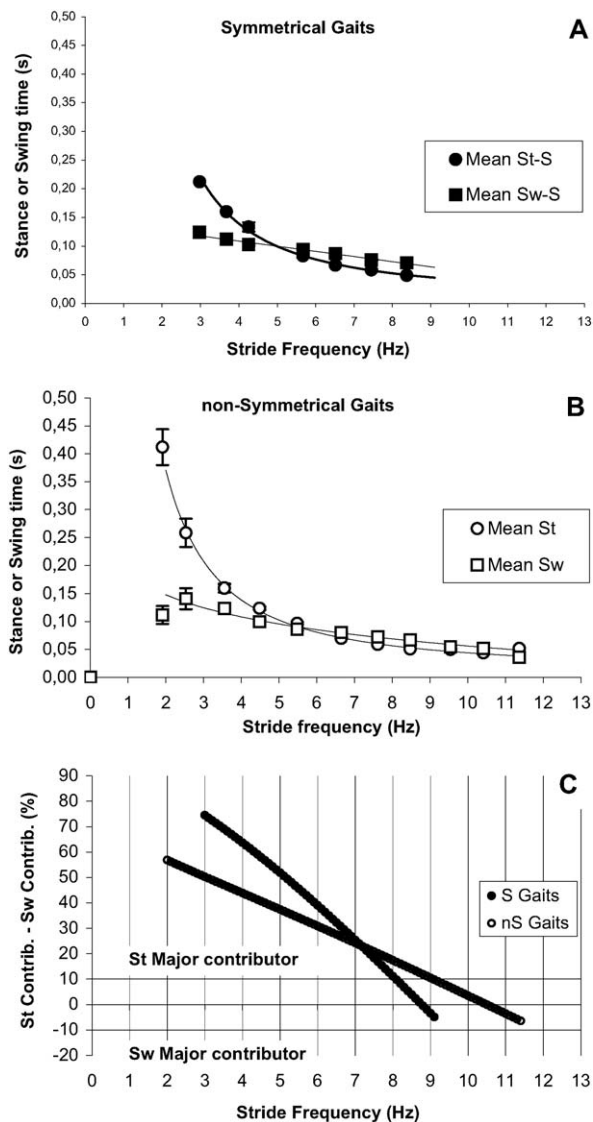
Fig. 3. Stance time and swing time. (**A**) Relationship between mean stance time (± SEM) and mean swing time and mean stride frequency (bin of 1 Hz) for symmetrical gaits. (**B**) Relationship between mean stance time (± SEM) and mean swing time and mean stride frequency (bin of 1 Hz) for non-symmetrical gaits. (**C**) Difference between the contribution of the decrease of the stance time and the decrease of swing time in the increase of stride frequency. The dotted line represents a variation of 10% around 0 where the contribution of each variable is equal to 50% (more or less 5%). Each regression curve was established from all the values of each gait ($N = 137$ for symmetrical gait and $N = 460$ for non symmetrical gait). S, symmetrical gaits; nS non-symmetrical gaits; St, stance time; Sw, swing time.

Fig. 3. Durée du posé et durée du levé. (**A**) Relation entre la durée moyenne du posé (± SEM), ou durée moyenne du levé (± SEM) et l'augmentation de la fréquence moyenne (gamme de 1 Hz) dans les allures symétriques. (**B**) Relation entre la durée moyenne du posé (± SEM), ou durée moyenne du levé (± SEM) et l'augmentation de la fréquence moyenne (gamme de 1 Hz) dans les allures non symétriques. (**C**) Différence entre la contribution de la diminution de la durée du posé et la diminution de la durée du levé dans l'augmentation de la fréquence. Les pointillés représentent une variation de 10% autour de 0, traduisant une contribution égale à 50% de chaque variable (plus ou moins 5%). Dans chaque type d'allure, les courbes de régression ont été établies à partir de la totalité des cycles ($N = 137$ pour les allures symétriques, $N = 460$ pour les allures non symétriques). S, allures symétriques ; nS, allures non symétriques ; St, durée du posé ; Sw, durée du levé.

range of velocities in relationship to the type of gaits. It is not easy to impose a velocity on a mouse, and to have a consistent number of strides even by using a treadmill. This use of a treadmill presents advantages to produce a

consistent number of readily quantifiable homogeneous sequences, and can be compared with studies that have analysed kinematics variables involved in the locomotion.

4.1. Gait patterns

Our results show that the adult mice used different patterns to increase velocity, whether or not it was a symmetrical gait. The gait repertoire was close to those described in the literature for mice, although we never observed on treadmill a half-bound, bound, or typical gallop pattern [19,26,28]. Gaits consisted of a typical trot, fast trot (running trot of Parchman et al. [36]), and a large range of non-symmetrical gaits. In symmetrical gaits, from 20 to 85 cm s^{-1}, the mice mostly used a moderate trot, which changed to a fast trot with increasing speed. The slowest gaits were non-symmetrical gaits usually part of exploratory behaviour. As speed increased, from 20 to around 90 cm s^{-1}, the mice switched to a transverse gallop with a short suspension time in a gathered position. As stated above, the typical gallop, with a medium or a long suspension time, was never completely achieved, because the mouse was not able to maintain this gait for much more than one or two successive strides. However, it is clear that mice use symmetrical and non-symmetrical gaits throughout the same range of velocities. Consequently, our results do not confirm the 'breakpoint' from which mice switch from symmetrical to non-symmetrical gait [19,20]. Even if there is a genuine relationship of stride frequency or body mass against velocity, the transitional velocity that these authors have determined from their formula cannot be applied, and our data rather come within the scope of the '*continuum* of gaits' [25], a *continuum* which exists in each gait over a large range of velocities.

4.2. Kinematic parameters

Kinematic studies that have been performed on small rodents have been mostly done on the rats, and few on mice. However, the few existing ones can be compared with the present data. The most detailed analyses in mice were done using footprints on a track, with older mice of the same strain. These confirm that gait variables show a consistent relationship over a large extent of velocities [5,6].

In mice as in the other mammals, the increasing velocity is achieved from a dual mechanism: increase in stride frequency and stride length. As previously described, both parameters increase with increasing velocity. The range of stride frequencies are in agreement with those previously reported in a mouse on a treadmill, 0.333–0.121 s [19,28], or on a track, 0.423–0.167 s [6]. However, if our corresponding velocity values are consistent with those of Clarke and Still [6], they do not fit with those of Heglund and co-workers [19,20], who nevertheless also used a treadmill in their studies. This difference could be due to the fact that they did not take into account the occurrence of a different relationship between the stride frequency and velocity with the two types of gaits. The stride length and the corresponding velocity in the present analysis do not correspond with those found in the previous study [6]. The data in the literature are higher than those that we have registered, and could result from the fact that the mouse moved on a track and not on a treadmill [9]. However, our study shows that both parameters contribute to increasing velocity, but are not the same in each gait type. In the symmetrical gait, the contribution of stride frequency is slightly equal to the stride length in increasing velocity (Fig. 2), while in non-symmetrical gaits, from the lowest to the highest velocities, the contribution of stride frequency is less and less marked, and at the higher velocities, the increase of velocity is achieved principally by the increase in stride length, even if the stride frequency still increases (Fig. 2). Previous studies in rodents have shown the same tendency, namely that velocity increase is primarily due to increased stride length, while stride frequency remains nearly constant [4,6,19]. However, previous studies never discriminated the type of gait analysed, and thus obtained results probably based on the more represented type of gait, which is generally the non-symmetrical one (here around 70%).

The increase of the stride frequency is achieved from a dual mechanism of decrease in stance time and swing time. Previous studies have already proposed that the contribution of the swing time is important in increasing stride frequency [3,18,27]. The present results confirm this contribution of swing time. Indeed, the decrease in stance time is the major contributor, except at the highest stride frequencies, where the increase of stride frequency is achieved by an equal contribution of both parameters. Even if the constant decrease in the swing time is less pronounced than in the stance time, its contribution is always significant in the modulation of the stride frequency (Fig. 3).

This separate analysis of the two types of gaits brings a new perspective to the contribution of each variable and its efficiency in the increase in velocity and stride frequency (Fig. 4). The above results enable us to formulate the hypothesis that in both gaits, when contribution of the stance time is less than around 67% in the increase in stride frequency, thus the increase in stride frequency cannot be the major contributor to the increase in velocity. However, from this limit to 48%, in the symmetrical gaits, the increase in stride frequency
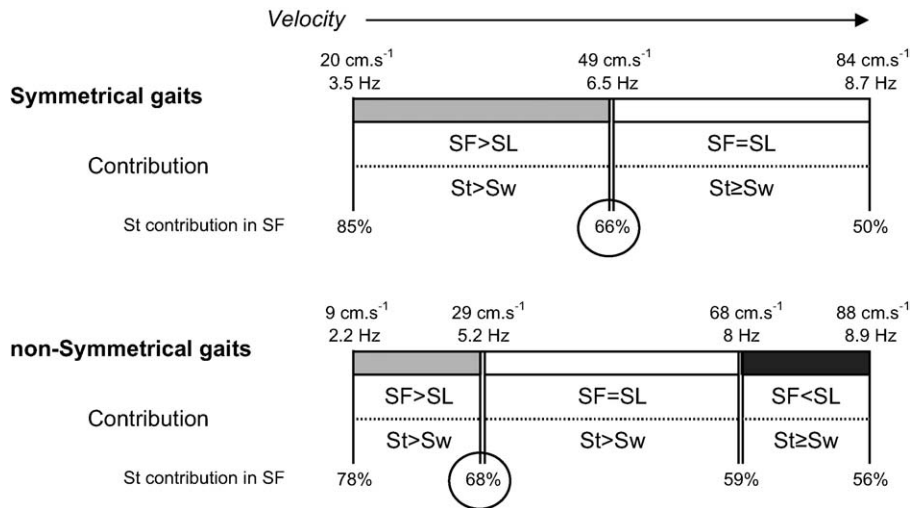
Fig. 4. Relationship between each contribution with increasing velocity. First, the figure shows the contribution of stride frequency compared to the contribution of stride length in the increasing velocity, and second the figure shows the contribution of stance time compared to the contribution of swing time in the increase of corresponding stride frequency. SF, stride frequency; SL, stride length; St, stance time; Sw, swing time; St contribution, contribution of the decrease of stance time in the increase of stride frequency.

Fig. 4. Relation entre chaque contribution dans l'augmentation de la vitesse. La figure montre premièrement la contribution de la fréquence, comparée à celle de l'enjambée dans l'augmentation de la vitesse, et deuxièmement la contribution de la durée du posé, comparée à celle du levé dans l'augmentation de la fréquence correspondante. SF, fréquence ; SL, enjambée ; St, durée du posé ; Sw, durée du levé ; St contribution, contribution de la diminution de la durée du posé dans l'augmentation de la fréquence.

still achieved an equal contribution with the stride length, while in non-symmetrical gaits, when contribution of the stance time is less than around 59% in the increase in stride frequency; the increase in stride frequency becomes the minor contributor to the increase in velocity. This pattern is partly in agreement with the approach previously described in the mouse [6]. The major difference with our results is that the respective variable contributions, especially the contribution of stance time, do not change in direct relationship with the velocity, but primarily with the type of gait, and lastly with velocity.

4.3. Motor controls of gaits

The kinematic results obtained in this study suggest that stride frequency and stride length increase differently as a function of the gait used. A shortening in duration of the support phase (stance time) and of the swing time, leads to the increase in frequency. On the other hand, the increase in stride length is achieved by an increase in vertical and horizontal impulse transmitted by the limb during the support phase [5,16,28]. However, the required forces and the amplitude of the stride length, to be effective, must be exerted during an adequate stance time or swing time, and the shortening of each step of the stride must be achieved by a definite

control. As previously described, "the motor pattern of intact animals more or less accurately reflects the organization of the spinal central pattern generators (CPGs) which give rise to them" [7]. Each characteristic of the stride phases is then the consequence of the specific neuronal pathways activated during a definite gait [2]. The present results show that in symmetrical and non-symmetrical gaits, the increase in velocity is not achieved with the same strategy. In the symmetrical gaits, the increases in the rate of the stride frequency and stride length with increasing speed are almost equal, while in the non-symmetrical gaits the increase of these rates are not equal and could result from a different motor control pathway. The hypothesis that limbs at the same speed could be coordinated in different ways, despite the fact that no change occurs in the alternation between limbs of the same pair, has been already suggested [16,24,25], but to our knowledge, this hypothesis has not been further investigated. Generally, the control of locomotion is rarely studied in relation to the symmetry or non-symmetry of the gait [14], but only in relation to velocity changes [15,17]. This control of locomotion by the central nervous system (CNS) in an accelerative phase should increase the descending drive on the CPGs, which should lead to an increased extensor output and secondarily to a tendency to increase the frequency [15]. This neuronal pattern should

be adapted to the new context, since the frequency and amplitude do not progress equally in both types of gaits. The above general pattern could be available to control the symmetrical gaits, but should be reassessed for the non-symmetrical gaits. The differences in speed increase suggest that the control may be implied by another or a more complex pathway.

The available pool of mouse locomotor deficits provides useful resource to investigate the nervous control of the locomotion, and could enable us to elucidate this speculative aspect of the nervous control in relationship with the gait. Even if the natural gait of the mouse is modified by the use of a treadmill, the results are consistent; all the characteristics of the stride can be quantified accurately and can be easily reproduced. The use of recorded high-speed images combined with cinefluoroscopic equipment yields much data on the succession of cycles within the time scale required by neurophysiology. Both patterns described above, may be similar for several mammals and valid on any ground surface. Moreover, the locomotion model established in a specific strain of normal mouse should be adequate to identify the effects of some motor nervous-related mutations on the locomotion, or to evaluate the actual impact of a neuropharmacological treatment in locomotor recovery after experimental lesions.

Acknowledgements

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