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Coordination of steering in a free-trotting quadruped

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Abstract Typically, locomotion has been studied by restricting the animal's path and/or speed, focusing on stride and step kinematics. Here we incorporate measurements of the legs and trunk in the support and swing phases, during trotting with various speeds and curvatures. This paradigm releases the animal from the confines of the treadmill and runway into the open space. The diagonal step, a new unit of locomotion, is defined by regarding the line between the two supporting diagonal legs as a frame of reference for the description of the dynamics of the virtual line between the two swinging diagonal legs. This analysis reveals that during free trotting the mouse uses three types of steps: fixating, opening, and closing steps. During progression along a straight path, the mouse uses fixating steps, in which the swinging diagonal maintains a fixed direction, landing on the supporting foreleg; during progression along a curved path the mouse uses opening and closing steps alternately. If two steps of the same type are performed sequentially, they engender an abrupt change of direction. Our results reveal how steering with the swinging diagonal, while using a virtually bipedal gait, engenders the whole repertoire of free-trotting behavior.

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Introduction

The study of locomotion is conducted in the framework of two units—the step and the stride. Studies on step structure focus on general step properties such as length and width (Ogura et al. 2001; Kiriyama et al. 2005), while studies on stride structure focus on phase relations (Domenici et al. 1998; Golubitsky et al. 1999) and footfall patterns (Hildebrand 1965, 1976, 1989). To allow a comparison within each of these units, researchers standardize the animal's movement by imposing a constraint, either on the path, (e.g., runway Cheng et al. 1997; Jamon and Clarac 1997; Hamers et al. 2001) or on path and speed, (e.g., treadmill Leblond et al. 2003; Hampton et al. 2004; Kale et al. 2004). Research on the whole range of movement the animal can perform is scarce, primarily because finding a basis for comparing different behaviors is a troublesome matter.

One way to approach this problem is to discern within the behavior a common context, isolate its units, and identify the parameters that engender the variation. For example, in his classical study of straight-path locomotion, Hildebrand (1976) described the support phase of each foot, then discerned a common context of symmetrical gaits, isolated the stride, and identified two parameters—percent of ground contact in stride and phase relationship of fore to hind feet—that engender the various symmetrical gaits. In this way he could analyze within one framework the entire array of symmetrical gaits, from trot to pace, and the whole range of speeds, from slow walking to fast running. The description of gait in terms of four binary degrees of freedom (each degree distinguishing between support and swing in each leg), has been compressed into a description in terms of two continuous degrees of freedom (% ground contact and relative phase).

A basic assumption in this type of studies is that the stride and the step are relatively fixed units. While this is valid for straight-path-constant-speed progression, it becomes problematic when applied to free locomotion. For example, when free gait consists of a mixture of straight-path, curved-path, accelerating, and decelerating steps, different splicing into strides would yield respectively different results. To study free gait, it is thus necessary to discern a context that would be common to segments of progression of various curvatures and speeds, and isolate the appropriate units and parameters.

Our observation of free locomotion in C57BL/6J mice revealed that 80% of their locomotion is performed by trotting—using alternating diagonal pairs of limbs (Fig. S1). Thus, we regard the trot as the common context, and the coupled steps of each diagonal pair as its elementary units. The trot is a 'two-beat' gait (Hildebrand 1965; Lee et al. 1999) in which each pair of diagonal legs provides a functional shift-of-weight unit, by alternating between support and swing. Therefore, we treat each two-legged swing performed on top of a two-legged support as a diagonal step and refer to it, henceforth, as a 'diagonal step' or 'step'.

Studies on quadrupeds trotting along a straight path focus on the supporting diagonals and disregard the dynamics of the swinging diagonals. Whereas this type of description is sufficient for uniform straight-path locomotion, it is not adequate for free locomotion, where the trajectory during swing is variable—an essential component of free locomotion. Because the supporting diagonal is anchored, steering must be mediated by a change of direction of the swinging diagonal.

Here, we chose to describe the trajectory of the swinging diagonal in reference to the supporting diagonal, which functions as the basis for movement and thus provides a natural momentary origin of axes (Eshkol and Harries 2001).

The path traced by a free-locomoting animal is generated by steering (shift of front) and progression (Eshkol and Harries 2001). Its analysis should, therefore, lead to an examination of the way in which shift of front is brought about. Studies addressing shift of front in a constrained setup have been performed in decapods (Domenici et al. 1998, 1999; Copp and Jamon 2001), hexapods (Jindrich and Full 1999; Durr and Ebeling 2005), quadrupeds (Eilam 1994; Kafkafi and Golani 1998), and bipeds (Courtine and Schieppati 2003; Kiriyama et al. 2005). The amount of shift of front is typically measured either cumulatively by a rotometer (Zimmerberg et al. 1986; Nielsen et al. 1999), or per time unit (Durr and Ebeling 2005). Here we define the diagonal step as a building block, and use it for parsing the continuous shift of front into amount-per-step units. This allows us to examine the relationship between stepping and shift of front.

The terms 'opening step', 'closing step', rotations around the 'inside' supporting hind leg, and around the 'outside' supporting hind leg, which were used in our lab to indicate the relationship between the direction of turning and the stepping leg (Szechtman et al. 1985; Copp and Jamon 2001) were adopted from Eshkol and Wachman (1958). Here we extend the definition of these terms to encompass the relationship between the direction of turning and the stepping diagonal. As a consequence, we can expand the common framework used for straight-path locomotion in bipeds, quadrupeds, hexapods, and octapeds (Full 1989; Dickinson et al. 2000) to also include free locomotion.

Turning has been studied in pharmacological (e.g., Szechtman et al. 1985; Cools et al. 1989; Ziegler and Szechtman 1990), genetic (e.g., Ogura et al. 2001; Pettibone et al. 2002), and neurological (e.g., Mead et al. 1996; Hampton et al. 2004) preparations. It has long been suggested that there is a considerable need for a system that cannot only quantify turns, but also characterize the way in which they are generated (Schwarting et al. 1996; Copp and Jamon 2001; Ogura et al. 2001; Walter 2003; Vidal et al. 2004). The twofold description of turning behavior in terms of shift of front and multi-limb coordination presented here could provide a solution to this need.

Materials and methods

Animals

Six female mice C57BL/6JOlaHsd were used in this study. Animals were kept in a 12:12 reversed light cycle (light 8:00 p.m.–8:00 a.m.), and housed three per cage under standard conditions of 22°C room temperature with water and food ad libitum. The animals were housed in their cages for at least 2 weeks before testing.

Setup

Mice were filmed from below at 50 half frames per second while moving freely on a glass surface in an enclosed circular arena. The arena's diameter was

80 cm, and the height of its wall was 20 cm. The glass surface was marked by grid points (2 mm × 2 mm, at 10 cm intervals) that were later used as fixed reference points for subtracting the movement of the camera. An 8 cm in diameter tube was installed in the center of the arena's roof. This tube was used to introduce the mice into the arena. A video camera (Sony 150PD), which was attached to a small trolley beneath the glass surface, was moved manually to track the mice. The apparatus was lit from below by two 250 W cold neon lights.

Procedure

Each mouse was anesthetized with isoflurane in order to apply the markers (2 mm × 2 mm stickers). The markers were placed along the midsagittal axis in five positions: (1) behind the mouth, (2) in the center of the shoulder girdle, (3) at the base of the sternum, (4) in the center of the pelvic girdle, (5) at the base of the tail. In addition, the center of each hind foot was marked with a black marker. Fore feet were tracked without the aid of markers.

Each mouse was given 5 min to recuperate, and then placed in the center tube for an additional 10-min acclimation period. After this period the tube was lifted and the mouse was released into the arena and tracked manually by the experimenter. Each mouse was filmed for 10 min after which the glass surface was cleaned with ethanol.

Data acquisition

The films were digitized using the EzVideo 1.12 software (Canopus Co., Ltd; http://www.canopus.com), which allows capturing and transferring of digital video from the camcorder to the computer. The longest sequences of continuous locomotion were selected out of each 10 min film. These sequences did not include long lingering episodes, bouts of locomotion interrupted by stops, and meddling-with-wall episodes. It should be noted that the criteria for choosing a sequence were as broad as possible so as not to limit the analysis beforehand to certain types of locomotion. For each animal, sequences were added up until they amounted to a sum total of at least 30 s; with the longest sequence lasting 22.3 s and the shortest 2.5 s. During these sequences the mice trotted at a mean speed of 25 cm/s with a lower quartile of 20 cm/s and an upper quartile of 30 cm/s. Maximal speed did not exceed 50 cm/s due to constraints imposed by arena size. The markers were tracked using the WINanalyze® (Mikromak Service) software which provided the Cartesian coordinates of the marker in reference to the moving frame. In order to subtract the movement of the camera, the grid points on the glass were also tracked and used as a fixed frame of reference. A linear transformation was used to calculate the translocation and rotation of the camera. In each frame, the five body markers and the 4 ft were tracked. In addition, the frames in which each foot established and released contact were recorded manually.

Data preparation and analysis

The raw data obtained from the tracking system were smoothed using a specialized algorithm implemented in the stand-alone program 'SEE Path Smoother' (Hen et al. 2004), which uses the LOWESS and the Repeated Running Medians algorithms. This procedure produces reliable estimates of momentary positions and speeds during locomotion.

Trot recognition algorithm

An algorithm was developed in the Mathematica 5.1® software (Wolfram Research Inc. 2005) to locate trot bouts within the locomotion sequences, and partition them into steps (see Supplementary Material).

Calculation of shift of front

To measure the changes in direction of the whole animal, we calculated its shift of front per diagonal step. The shift of front was defined as the difference between the direction of the animal's trunk at the end and its direction at the beginning of each step. The trunk was defined as the segment that connected the point on the shoulder girdle with the point on the pelvic girdle. Note that the shift of front was not measured per frame nor with a sliding window, rather, it was partitioned into portions that were defined by the steps themselves.

Regression models

In Fig. 4a, b regression was performed separately on the positive and negative parts of each graph. The data that were included in the regression model were steps in which the shift of front was larger than the upper quartile (red clusters). By regarding only data from the upper quartile we obtained two separate clusters, without the cluster of straight steps that united them.

To compare the slopes of positive and negative changes of direction in Fig. 4d, we constructed a regression model using a dummy variable. Both shift of front and change of direction between the diagonals were taken in their absolute values with the dummy variable marking the former sign of the change of direction. In this way, we were able to check the significance of the difference between the slopes.

Results

Viewing free trotting as a progression of two lines in the plane

Figure 1 presents an example of two successive diagonal steps. The supporting diagonal, represented by a thick line, functions as the basis for movement, whereas the swinging diagonal, represented by a thin line, functions as the moving virtual limb. Since the supporting diagonal carries the weight of the body we refer to it henceforth as the heavy diagonal. Accordingly, we refer to the swinging diagonal as the light diagonal (Eshkol and Harries 2001). This allows us to regard the mouse's movement as the displacement of two lines in the plane: during each step, one line remains fixed (heavy) while the other slides along it (light).

Representing diagonal steps as two-dimensional curves

The movement of the light diagonals is visualized in Fig. 2, which presents two sequences of forward progression, one along a straight path, and another along a curved path. In this figure, the movement of the light diagonals sweeps out traces that allow us to view the unfolding of the whole movement. During progression along a straight path (Fig. 2a), the light diagonal maintains a fixed direction in relation to the heavy diagonal, landing on the heavy foreleg (i.e., the step ends when the swinging virtual limb aligns with the heavy foreleg). Upon landing, the light diagonal becomes heavy, and the heavy diagonal ends its support phase. It then becomes the new light diagonal, sweeping out an almost identical trace on the new heavy diagonal, and so forth. During progression along a curved path (Fig. 2b), the light diagonals change their direction in relation to the heavy diagonals, landing at a distance from the heavy forelegs. The figure depicts two types of traces. In steps 1, 3, and 5, the direction of the light diagonals (thin blue lines) converges toward the direction of the heavy diagonals (thick red lines), and the light diagonals land ahead of the heavy foreleg. In

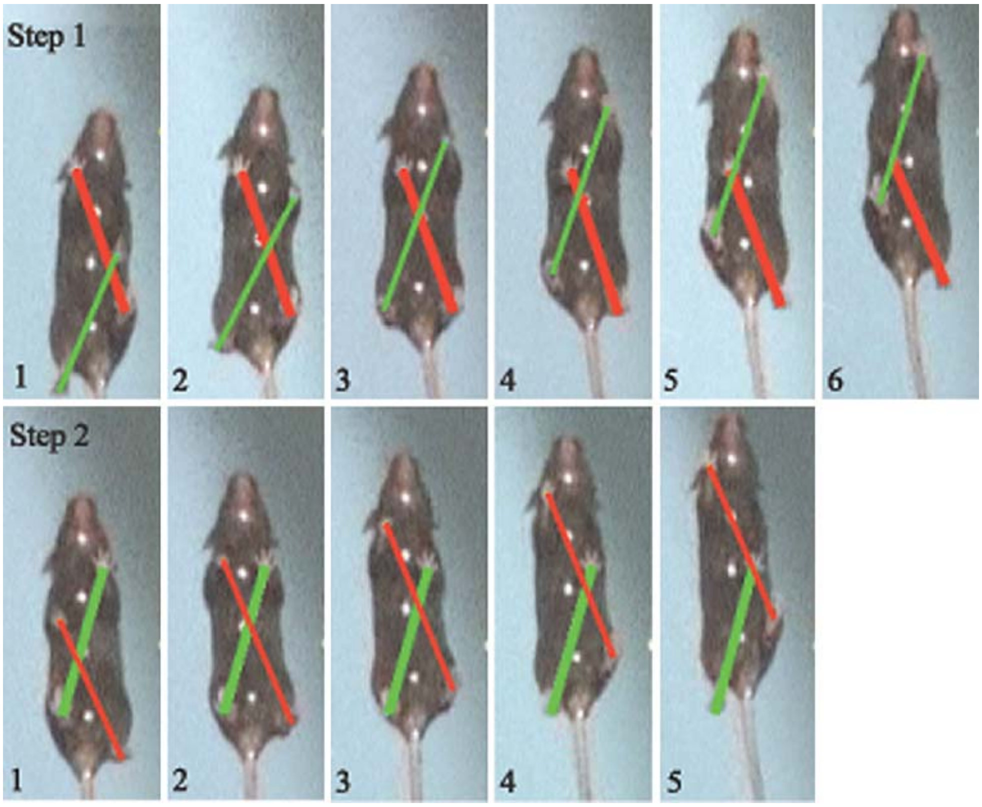

Fig. 1 A ventral frame-by-frame view (1 frame = 1/50 s) of two successive diagonal steps of a trotting C57 mouse. In each frame, the supporting (heavy) diagonal is represented by a *thick line* and the swinging (light) diagonal by a *thin line*. The *two colors* denote the two respective diagonals. In the first step, the *green diagonal* starts the swing phase at frame 1, 'slides' along the supporting *red diagonal*, and ends the swing phase on the sixth frame. In the second step the two diagonals exchange roles

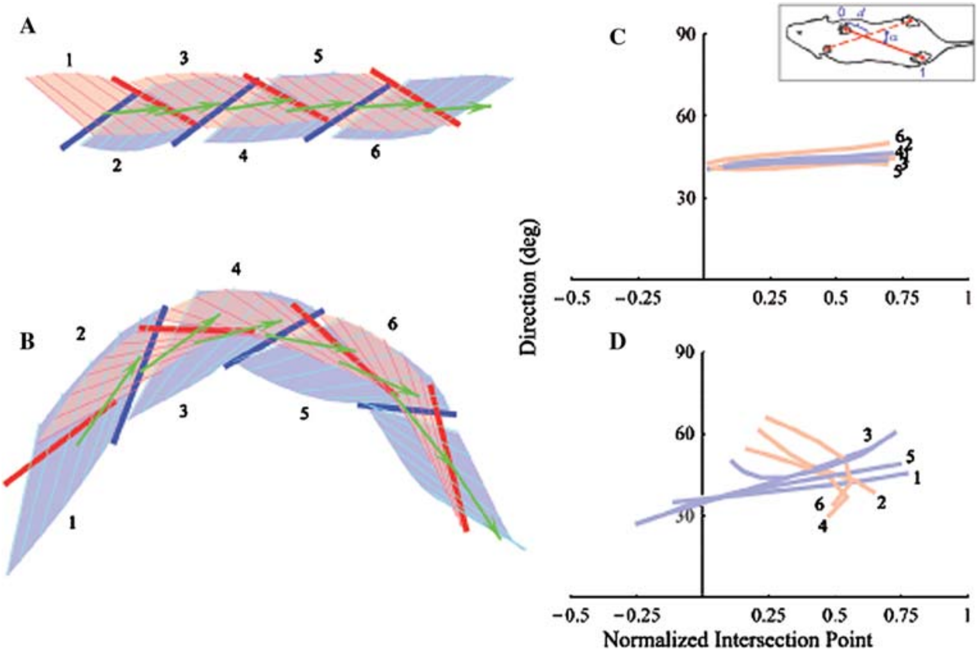

Fig. 2 The unfolding of two free-trotting sequences. Traces generated by the light diagonals during progression along a straight path (**a**), and along a curved path (**b**), and their respective two-dimensional representations (**c**, **d**). In **a**, **b** the heavy diagonals are represented by *thick lines* and the light diagonals by *thin lines*. The *numerals* designate the sequential order of the steps. The *polygons* represent the wake of the light diagonals. The different *shades of red* represent one diagonal and the *shades of blue* the other diagonal. The *green arrows* depict the animal's trunk at the end of each step. (**c**, **d**) show the two-dimensional curves of the steps depicted in **a** and **b**, with their corresponding *colors* and *numerical order* (for further explanation see text and Fig. 3). Note that similar *polygons* are represented by similar curves. Inset shows calculation method for direction (α) and normalized intersection point (d).

steps 2, 4, and 6, the direction of the light diagonals (thin red lines) diverges from the direction of the heavy diagonals (thick blue lines), and the light diagonals land behind the heavy foreleg.

Since the heavy diagonal is the basis for movement, we calculate the light diagonal's momentary direction and position in reference to it. The direction (from hind- to foreleg) is described in terms of the deviation (in degrees) of the light diagonal from that of the heavy diagonal. The position is described in terms of the point of intersection of the light diagonal with the heavy diagonal. The position is normalized by defining the heavy foreleg as the zero point and the heavy hind leg as the unit point (see inset in Fig. 2). This is because the heavy foreleg emerged as a reference point for the landing of the light diagonal (see Sect. 'Discussion' and Fig. 2a, b). In this way the heavy foreleg becomes a point of reference, and any deviation from it is emphasized. Thus, each step is represented by a series of two-dimensional points (momentary direction and normalized momentary point of intersection; for a detailed exposition see Fig. S2). The heavy diagonal alternates between steps, imposing a respective switch in the frame of reference (Figs. 1, 2). Therefore, we also specify the heavy diagonal for each step. As will be shown later, a description in these terms, although not exhaustive, is sufficiently informative for articulating the structure of free trotting.

Figure 3a presents an example of a segment of free locomotion performed by a mouse (see supplementary data for video clip). Each step is represented by a curve, and each curve is comprised of a series of successive two-dimensional points (direction, and normalized intersection point). Because the light diagonal always moves in the direction of the heavy foreleg—defined as the zero coordinate of the x-axis—each line is generated from right to left. Therefore, the left end of a line represents the landing point in that step. The temporal order is thus represented in Fig. 3a only at the level of the single step, whereas the sequential order of the steps is absent.

Classifying diagonal steps into three types

Three main types of curves are evident in Fig. 3a: lines that are parallel to the x-axis, lines with a positive slope, and lines with a negative slope (the green colored lines, which are a subtype of the lines with a negative slope, are discussed in the explanation of example d in Fig. 7).

Lines parallel to the x-axis are also characterized by a near-zero minimal x value. The fact that the line is

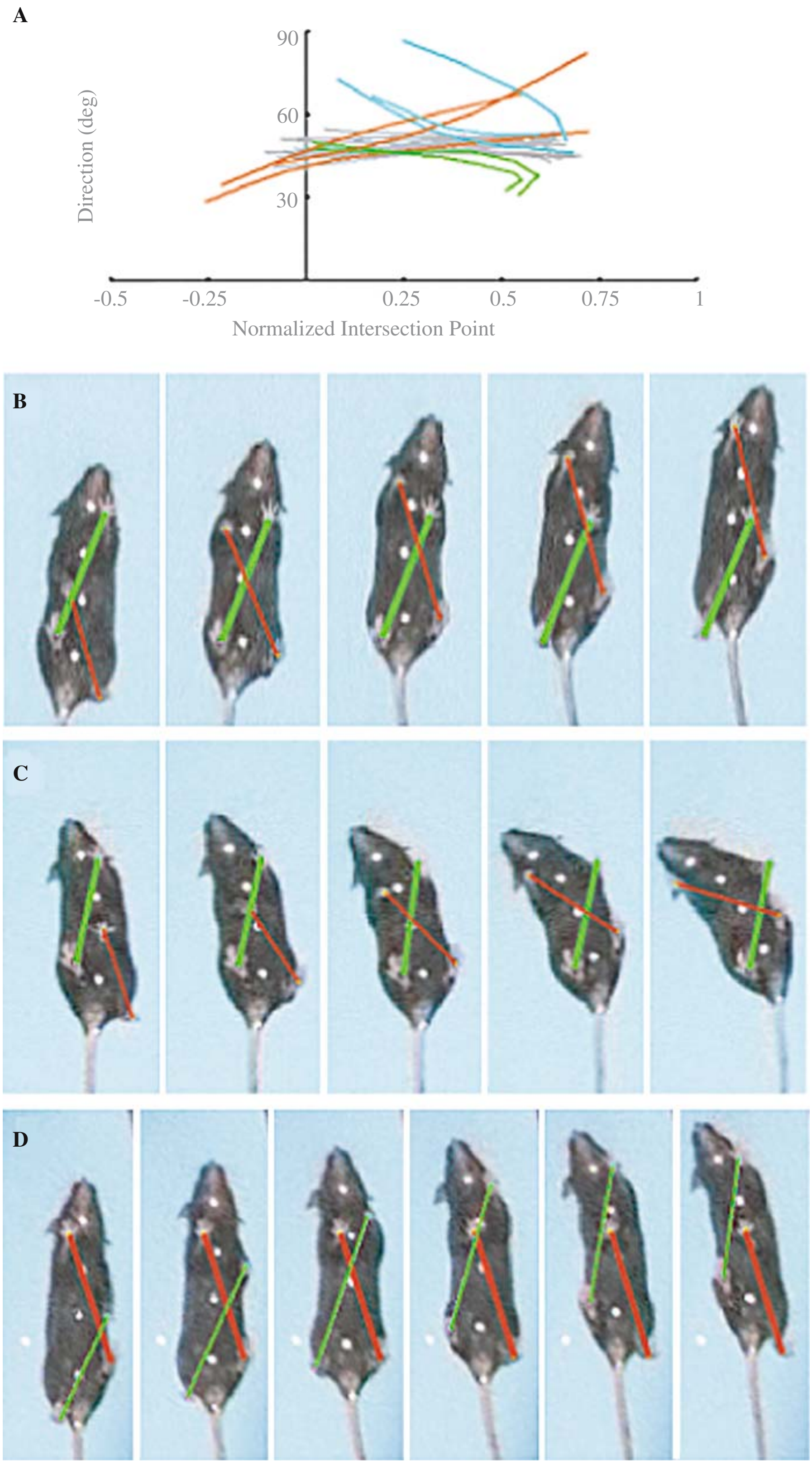

Fig. 3 **a** A two-dimensional representation of the direction of the light diagonal and the intersection point between the diagonals, in a single trot bout. Each *curve* represents a step. Each *color* denotes a specific step type: *gray*—fixating steps, *green* and *blue*—opening steps, and *orange*—closing steps. **b–d** Examples of the three step types. Each step is presented from left to right. The *thickness* and the *colors* of the *lines* are as in Fig. 1. **b** Fixating step, **c** opening step, and **d** closing step

parallel to the *x*-axis means that the direction of the light diagonal remains fixed throughout the step. A minimal *x* value near 0 means that at the end of the step the light diagonal reaches the heavy foreleg (Fig. 3b). This is the most common type of step, and we will refer to it henceforth, as a fixating step. A series of such steps is presented in Fig. 2a, with their corresponding curves in Fig. 2c.

Lines with a negative slope are also characterized by a positive minimal x value. The negative slope means that the light diagonal increases the difference between its own direction and the direction of the heavy diagonal. The positive minimal x value means that at the end of the step the light diagonal stops short of the heavy foreleg (Fig. 3c). In this type of step the direction of the light diagonal diverges from that of the heavy diagonal. Therefore, we will refer to it henceforth, as an opening step. Examples of this type are steps 2, 4, and 6, in the sequence presented in Fig. 2b, with their corresponding curves in Fig. 2d.

Lines with a positive slope are also characterized by a negative minimal x value. The positive slope means that the light diagonal reduces the difference between its own direction and the direction of the heavy diagonal. The negative minimal x value means that by the end of the step the light diagonal crosses over the heavy foreleg (Fig. 3d). In this type of step the direction of the light diagonal converges to that of the heavy diagonal. Therefore, we will refer to it henceforth, as a closing step. Examples of this type are steps 1, 3, and 5, in the sequence presented in Fig. 2b, with their corresponding curves in Fig. 2d.

The sequence of forward progression along a straight path in Fig. 2a suggests that throughout fixating steps the mouse maintains its course of progression with almost no change in the orientation of the trunk (no shift of front). On the other hand, Fig. 2b suggests that opening and closing steps are used alternately by the mouse during the performance of turns.

The relations between the step measures and per-step shift of front support classification into three step types

To study the relations between the types of steps and the amount of shift of front, we represent each line (as in Fig. 3a) by three measures that characterize it.

(1) Total change of direction performed by the light diagonal throughout the step (change of direction).
(2) Final point of intersection between the diagonals (landing intersection point).
(3) Final direction of light diagonal in reference to heavy diagonal (landing direction).

The first measure describes the amount of movement performed by the light diagonal, and the last two measures combined describe the final position of the light diagonal just before it becomes the heavy diagonal.

Shift of front is calculated for each step by subtracting the direction of the torso at the end of the step, from its direction at the beginning of the step. Thus, shift of front is measured per diagonal step; neither per frame, nor per turning bout (see Sect. 'Materials and methods').

Figure 4 presents a pair-wise scatter plot of the above three measures for all steps belonging to all mice. The color gradient represents the magnitude of per-step shifts of front, with yellow designating small shifts and dark red large shifts. Thus, each point in the figure depicts two measures of the step, and the shift of front associated with it.

An overview of all three plots reveals that the three step measures are positively correlated. In other words, the bigger is one of the measures, the bigger are the other two. For example, the larger the change of direction of the light diagonal, the more caudal is the landing intersection point, and the larger is the value of the landing direction. In addition, in all three graphs, the structure of the dependency on the positive side of the x-axis differs from the structure of the dependency on the negative side. This is reflected by the different spread and different orientation of the clusters on both sides of the y-axis, which suggest that these clusters represent two distinct populations. Finally, in all three plots there is a dark cluster on the negative side of the x-axis, a bright cluster near zero, and another dark cluster on the positive side. This implies that the negative cluster consists of closing steps with large shift of front, the central cluster consists of fixating steps with almost no shift of front, and the positive cluster consists of opening steps, again with large shift of front.

An examination of Fig. 4c, which presents the two measures used for the classification of step types, confirms that the vast majority of steps agree with our three-type classification. The yellow cluster shows that small changes of direction are associated with near-zero landing intersection points and with almost no shift of front, in accordance with the definition of fixating steps. The dark cluster in the first quadrant, similarly, shows that positive changes of direction are associated with positive landing intersection points and with a large shift of front, again in accordance with the definition of an opening step. The same applies to the dark cluster in the third quadrant and to the definition of a closing step.

Figure 4b, shows the landing direction as a function of the landing intersection point. Each point in the figure represents the posture in which the mouse concluded a step. Therefore, it can be regarded as a magnification of the left ends of the lines presented in Figs. 2c, d and 3a. To compare the relations between these two measures in the two step types, we calculated a regression line for each dark cluster (see

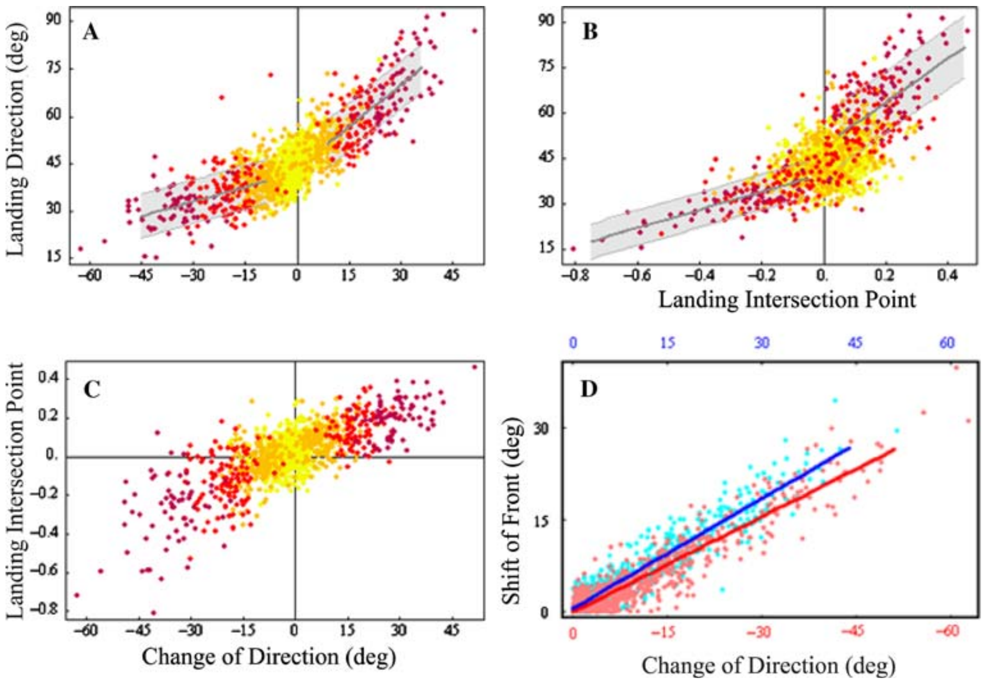

Fig. 4 A pair-wise scatter plot of the three step measures of all steps, pooled over all mice. The *color gradient* represents the magnitude of per-step shifts of front, with *yellow* representing smaller than median (3.5°) values, *orange*—values between median and upper quartile (8°), *red*—values between upper quartile and quantile 0.9 (14.2°), and *dark red*—between quantile 0.9 and maximal (38°) values. **a** Change of direction vs. landing direction, **b** landing intersection point vs. landing direction, **c** change of direction vs. landing intersection point. In (**a**) and (**b**) the *gray* areas represent the regression line ±SE of the residuals (see Sect. 'Materials and methods'). The three distinct clusters of *colored points* represent the three different step types (*yellow*—fixating steps, *red*—closing and opening steps). **d** Change of direction vs. absolute shift of front. The second quadrant is 'folded' and superimposed (in *red*) on the first quadrant (in *blue*) for comparison. As shown, the regression line of the opening steps (*blue*) is steeper, which means that for the same amount of shift of front, the mouse has to perform a bigger change in the direction of the light diagonal in closing steps

Sect. 'Materials and methods'). The slope of the regression line of the opening steps (positive side) is 1.2 (SE 0.129; R^2 0.319) and it is steeper (P-value for the difference <0.001) than that of the closing steps (negative side), which is 0.5 (SE 0.051; R^2 0.379). In addition, the spread of the points around the regression line, which reflects the strength of the correlation, is narrower (P-value for the difference <0.001, using F-test for equality of variance) in the closing steps (SD residuals 0.096) than in the opening steps (SD residuals 0.169). Finally, the range of the landing intersection point in the closing steps is twice as wide as that of the opening steps. The difference in the range of the landing intersection point implies that in opening steps, this measure is more constrained, i.e., the landing intersection point is limited in the caudal direction, presumably, by the amount of lateral bending that can be performed by the mouse. In contrast, the milder slope and the stronger correlation in closing steps imply that in this type of steps the landing direction is relatively constrained.

In Fig. 4a we plot the landing direction as a function of the change of direction of the light diagonal. The change of direction is calculated by subtracting the direction of the light diagonal at takeoff, from its landing direction. Had the takeoff and landing directions been independent, a slope of 1 would have been expected between the two measures of the graph. The regression results reveal that both slopes are smaller than 1 (P-value for positive side = 0.043, P-value for negative side <0.001), with the slope of the opening steps being closer to 1 (slope 0.87; SE 0.073; R^2 0.464; SD residuals 0.125) than that of the closing steps (slope 0.3; SE 0.052; R^2 0.176; SD residuals 0.115; P-value for the difference <0.001). These results imply that although the landing direction is constrained in both step types, the constraint is significantly stronger in the closing steps. This further supports the observation made in Fig. 4b regarding the limitation imposed on the landing direction during closing steps.

Two anatomical constraints impose this limitation, one involving the hindquarters and one involving the forequarters. (1) Forward progression of a stepping hind leg is partly brought about by a rotation of the pelvis on the contralateral heavy hind leg, a rotation which displaces the hip joint of the stepping leg forward (Fig. 5). During the performance of an opening step, this rotation is agonistic to the direction of the turn. In the illustration presented in Fig. 5a, the mouse turns clockwise, and the pelvis also rotates clockwise. In contrast, during the performance of a closing step these two rotations are antagonistic. In the illustration presented in Fig. 5b, the mouse turns counterclockwise, but the pelvis rotates clockwise. The performance of two antagonistic rotations by a short-trunked animal limits the landing direction of the light diagonal. (2) During a closing step, the light foreleg steps in the direction of the heavy foreleg, occasionally crossing over it (Fig. 3d). The anatomical constraint on the amount of crossing over limits the landing direction of the light diagonal.

Examination of the relationship between the step measures and shift of front revealed that, out of the three measures, the change of direction of the light diagonal seems to provide the clearest partitioning of shifts of front into distinct classes (Fig. 4a–c); therefore, we will next focus on the relationship between them.

Figure 4d depicts the linear relationship between the change of direction of the light diagonal and shift of front. It is also evident that the slope on the negative side (closing steps) is milder than the slope on the positive side (opening steps). To examine this difference we reflect the data points of the closing steps on the positive side of the graph, and construct a regression model that establishes whether the difference between the regression lines of the two types of steps is statistically significant (see Sect. 'Materials and methods'). The results show that there is a strong linear connection between the two variables (R^2 0.873) and that there is a significant difference between the slopes, with the closing steps' slope being 0.516 (SE 0.007) and the opening steps' slope being 0.595 (P-value for slope coefficient of the dummy variable <0.001; SE 0.011). The meaning of this difference is that for the same amount of shift of front, the mouse has to perform a bigger change in the direction of the light diagonal in closing steps. This could be because in closing steps a larger change of direction is required to counteract the antagonistic rotation of the pelvis (as with the constraints imposed on the landing direction). Note, however, that in spite of this difference, large shifts of front are performed both with opening and closing steps (Fig. 4d).

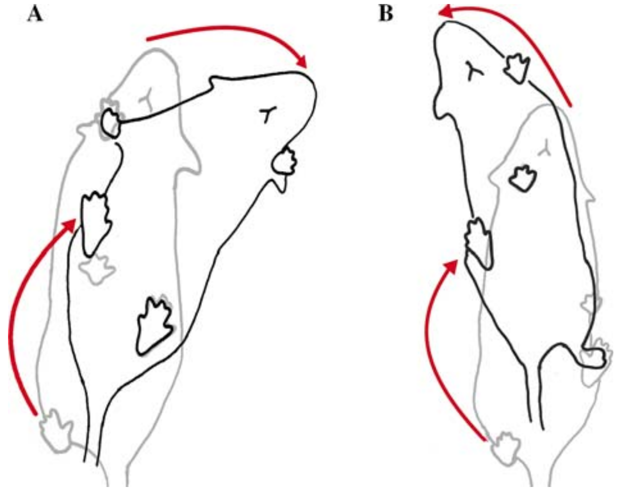

Fig. 5 The relationship between the rotation of the trunk and the rotation of the pelvis in the two step types. The illustrations depict the contours of the first (*gray*) and last (*black*) frames in an opening (**a**) and a closing (**b**) step. *Arrows* highlight the direction of rotations. As shown, during opening steps the rotations are agonistic, and during closing steps they are antagonistic

The stability of the light diagonal's characteristics during fixating steps

Having characterized the three types of steps and associating them with their respective classes of shift of front, we now pursue the opposite direction, of first characterizing quantitatively genuine classes of shift of front and only then examining the stepping types associated with them.

To obtain a genuine straight-path class and a genuine curved-path class of shifts of font we use two defining cutoff points separated by a large safety range. The value of the first cutoff point is 3.5°, which is the median of all the shifts of front recorded in this study, and the value of the second cutoff point is 9°, which is the minimal value in the dent between the two density components in Fig. 6a. The large safety range separating the two cutoff values guarantees that every step smaller than the first would belong to the straight-path class (high density—low value component), and every step bigger than the second would belong to the curved-path class (low density—high value component). Steps belonging to the range between the two cutoff points remain undefined and untreated.

The linkage between the amount of shift of front and the three step types, which is demonstrated in Fig. 4, implies that the straight-path class is comprised of fixating steps. To support the preliminary impression of the stereotypy of fixating steps we compare the variability of straight-path steps (below the 3.5° cutoff point) to that of all the other steps (above the 3.5° cutoff point). Figure 6b presents the ratio between these variabilities per mouse, for each of the three measures. A one-sided Student's t-test, examining whether the ratio differs significantly from the equal variability result of 1, reveals significant differences in

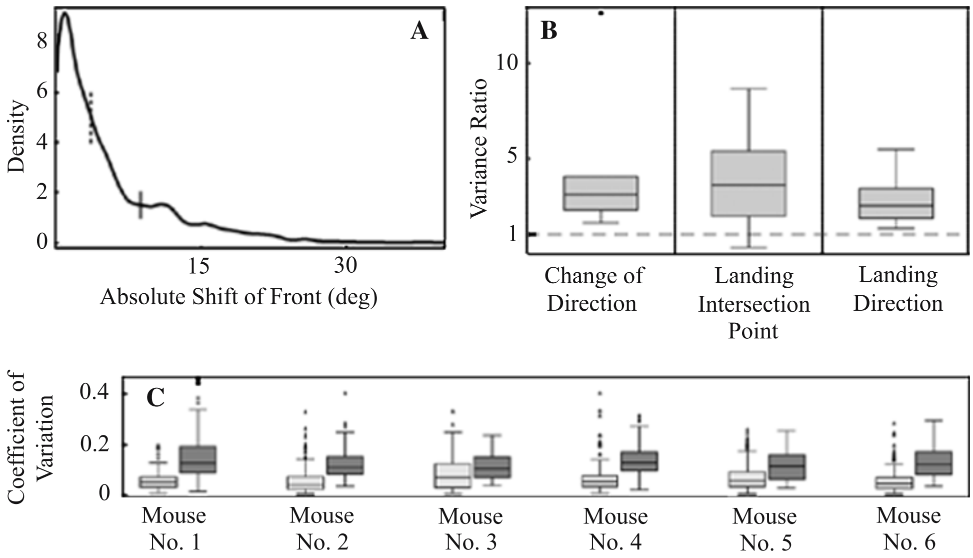

Fig. 6 **a** Density plot of absolute shift of front per step, for all steps in all mice. The *dashed vertical line* designates the threshold for straight-path steps, and the *continuous vertical line* designates the threshold for curved-path steps. **b** The variance ratio between non-straight steps and straight steps in each of the three measures. Equality of variances is designated by the *dashed line*. All three ratios are significantly higher than one, implying relative constancy during straight-path steps. **c** Boxplot summaries of the coefficients of variation of the light diagonal's direction throughout a step. Boxplots are presented for each mouse separately, comparing straight (*light gray*) vs. non-straight (*dark gray*) steps. A mixed ANOVA model reveals that the direction of the light diagonal is more stable in straight-path steps

the change of direction, landing intersection point, and landing direction (*P*-values 0.003, 0.03 and 0.003, respectively). Fixating steps are, thus, more stereotyped than all the other steps, on all three measures. In particular, the relative stereotypy in the change of direction reflects a kinematic mechanism that ensures a stability of direction throughout the step. This stability is demonstrated in Fig. 6c, which shows the coefficient of variation of the within step direction, calculated per step, for each mouse separately. The difference, evident in the figure, was found to be significant (*P*-value < 0.001), using a two-way mixed ANOVA test in which the class was a fixed factor and the mouse a mixed factor (Kafkafi et al. 2005). Thus, fixating steps involve a near zero change in direction, a relatively stable direction of the light diagonal across the step, and a close to zero shift of front per step.

How step types are concatenated to generate various paths

Having established the diagonal steps as the building blocks of free trotting, we now proceed to characterize the way in which they concatenate. We use the 9° cutoff point (Fig. 6a) to select the steps belonging to the curved-path class, and devise an algorithm to detect their sequences. The algorithm first identifies these sequences, and then adds to each its preceding step and its anteceding step. These extended sequences, if performed in succession, are joined into still longer sequences. The output of the algorithm consists of all curved-path sequences, with at most two non-curved path steps between them, leaving out all straight-path sequences.

Figure 7 presents six prototypic examples of the ways in which curved-path sequences are generated. In each example, the *x*-axis represents the temporal order of steps, and the *y*-axes the values of the four step measures. It should be noted that in this figure, shift of front is represented in terms of both magnitude and direction (left, positive; right, negative). Example 7a depicts the simplest sequence, which consists of a single curved-path step, in this case a closing step, preceded and followed by a fixating step. The sequence in example 7b is comprised of two curved-path steps, again, preceded and followed by a fixating step. This sequence illustrates how a continuous shift of front in one direction (red line) is composed of two opposing-but-complementary curved-path steps. The first is an opening step, with a positive change of direction (blue), a positive landing intersection point (green), and a landing direction (cyan) that diverges positively from the typical straight-path value (dashed gray line). The second is a closing step, with a negative change of direction, a negative landing intersection point, and an almost typical straight-path value of the landing direction. Note that the linkage between the measures' values in this and all the other examples coincides with the definition of the

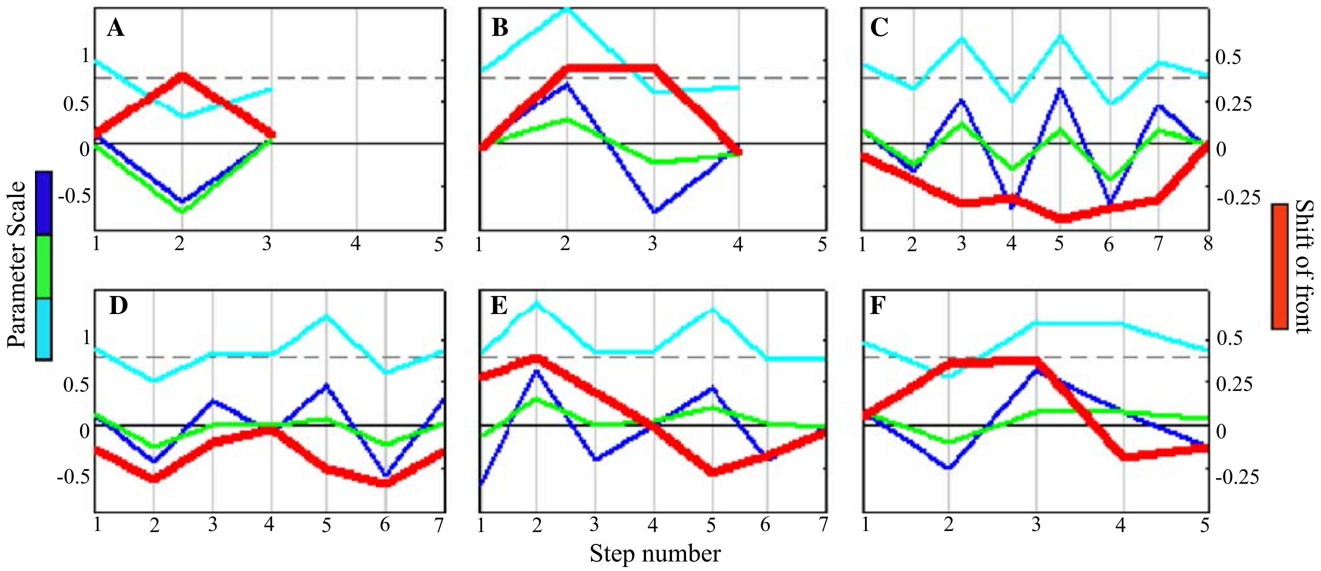

Fig. 7 Six prototypical examples of bouts of progression along a curved path. The *x-axis* represents the successive steps that make up each bout. The *left y-axis* represents the change of direction (*blue*), the landing intersection point (*green*), and the landing direction (*cyan*). The *right y-axis* represents the amount of shift of front in each step (*red*). The *dashed line* denotes the median landing direction of all straight-path steps, and is used as a reference for the landing direction line. Note that the parameters characterizing each step are plotted on the *vertical gray line* denoting that step. The examples show either a single bout of increasing length (**a**–**c**) or two bouts sequences (**d** and **e**) in which alternate concatenation of opening and closing steps generates a continuous shift of front in the same direction. Example f presents a sequence in which the performance of two successive opening steps (# 3 and # 4) causes an abrupt change in shift of front direction

step types (text related to Fig. 3). Example 7c presents an even longer sequence, comprised of six curved-path steps. To generate a continuous shift of front in the same direction, the mouse concatenates opening and closing steps in an alternate manner. This is reflected in the alternation of the three step measures around the typical straight-path values. In example 7d the curved-path sequence is performed in two bouts separated by a single fixating step (step # 4).

The third step in this example constitutes a subtype of opening steps, which are used to ‘reset’ the diagonals into a straight-path posture. As shown, the shift of front is relatively small in this step, but still within the range of curved-path steps. Its change of direction is positive, indicating that it is an opening step. Yet, its landing intersection point and landing direction show values that are typical of fixating steps. This means that the final posture of the mouse in this step is similar to the final posture in fixating steps, a posture which is accompanied by a straight body. By performing this subtype, the mouse concludes a part of the turn, and straightens. The straightening, which constitutes a pause in the curved-path sequence, is followed by the performance of either a curved-path or a fixating step (as in this example). This subtype is also presented in Fig. 3a (green curves).

Example 7e also consists of two bouts separated by a fixating step, but in this case they are performed in opposite directions, as implied by the switch of the shift of front (red line) from positive (left) to negative (right) values. Steps # 3 and # 6 in the sequence are additional examples of straightening steps, in this case of closing steps. Finally, example 7f presents a sequence in which the switch from positive to negative shift of front is not mediated by a fixating step. This is accomplished by the performance of two successive opening steps (# 3 and # 4). The performance of an opening step followed by an opening step, or a closing step followed by a closing step characterizes all instances involving a direct switch in the direction of shift of front. In contrast, the performance of a closing step followed by an opening step, or vice versa, characterizes all instances involving a continuous shift of front in the same direction.

Discussion

Straight-runway walking versus traveling in a natural environment

Treadmills and straight runways have been useful for focusing on footfall patterns, and on step kinematics of individual appendages (e.g., Herbin et al. 2004; Ganor and Golani 1980; Leblond et al. 2003). Progression at a constant speed and progression along a straight path are, however, more the exception than the rule for animals traveling through natural environments, whereas knowledge of how animals move in the real world, involving temporally varying and spatially complex paths, is critical to understanding locomotor performance (Dickinson et al. 2000). In the present study we obtain such knowledge by a novel method of articulating locomotion. First, we track the parts of the trunk and the feet, during the support and the swing phases, in the course of progression with various speeds, along paths of varying curvature. Then we measure the behavior in relation to selected origins of axes that compress the apparent variability into relatively simple constructs that highlight its intrinsic structure.

Coordinate systems and origins of axes for free trotting

Having designed an algorithm that captures trotting sequences, we find that the trot is the primary gait used by C57 mice, and that this gait is maintained over a wide range of curvatures and speeds. The apparent variability in the movement of the swinging limbs is diminished once the supporting diagonal is used as a frame of reference. Anchoring the supporting foreleg as an origin of axes, allows a compressed description of the trajectory traced by the swinging diagonal. Viewing the data from that perspective yields three types of steps, whose concatenation engenders all the path forms captured in all the mice by the trotting algorithm.

Free trotting is generated by concatenating three types of diagonal steps

Once highlighted, the three diagonal step types can be readily discerned, even by an untrained observer, explicating the way in which the animal steers. Opening, closing, and fixating steps are performed when the swinging diagonal, respectively, diverges, converges, or maintained fixed in relation to the supporting diagonal. Each of these types is characterized by several, distinct, kinematic properties (Fig. 3).

Reducing degrees of freedom as a means for simplifying locomotion

The necessity of reducing the number of degrees of freedom during the performance of a complex movement has long been recognized. This recognition has lead Bernstein (Bernstein 1967) to define coordination as the ‘process of mastering redundant degrees of freedom’. A clear example for the use of this coordination principle is found in the movement of the octopus’s arm. During fetching, the octopus articulates its unsegmented arm into three temporarily rigid segments thus reducing the hyper redundant number of degrees of freedom (Sumbre et al. 2005).

It has long been noted that during straight-path locomotion two-, four-, six-, and eight-legged animals can reduce the number of degrees of freedom by trotting, i.e., using two sets of propulsive virtual limbs one after the other (Full 1989; Blickhan and Full 1993; Dickinson et al. 2000). The set can differ in the number of legs used, one for a human, two per diagonal for a dog, three per tripod for a cockroach, and four per set for a crab, but the ground-reaction force patterns are remarkably similar (Blickhan and Full 1993).

A reduction in the number of degrees of freedom has also been demonstrated in studies on curved-path locomotion. For example, flies (Strauss and Heisenberg 1990) maintain an alternating tripod gait at high speeds (alternating triangles of first and last leg on one side and middle leg on contralateral side) in which the supporting tripods retain their shape through varying curvature levels (Strauss and Heisenberg 1990). Similarly, in ants there is a coordination of alternating tripods in a wide variety of speeds and path curvatures (Zollikofer 1994). Speed is regulated by the distance between consecutive supporting tripods, and curvature is regulated by the angle between the tripods and the central body axis, but the shape of tripods is unaffected, neither by speed nor by curvature. In both flies and ants, tripods are the fixed building blocks of the gait: changes in the animal’s trajectory are brought about by changes in the parameters which regulate the relations between them.

While all the above studies focus on the supporting limbs (propulsive set), this study adds a description of the steering mechanism by depicting the dynamics of the swinging set. There is an analogy between the results obtained for the hexapodal gaits and those obtained for the trotting mouse. The two supporting tripods correspond to the alternating heavy diagonals. The distance between consecutive supporting tripods corresponds to the shift of the intersection point along the heavy diagonal, and the angle between the tripods and body axis correspond to the change of direction between the diagonals.

An analogy also holds between curved-path bipedal locomotion and curved-path quadrupedal trot. Several studies examining turning behavior in humans identify diverging and converging steps (Eshkol and Wachman 1958; Andrews et al. 1977; Hase and Stein 1999). Eshkol refers to them as ‘opening’ and ‘closing steps’, the terminology we adopted in the present study. If we regard the heavy diagonal as analogous to the supporting bipedal foot, and the light diagonal as analogous to the swinging bipedal foot, then the correspondence between quadrupedal and bipedal step types becomes

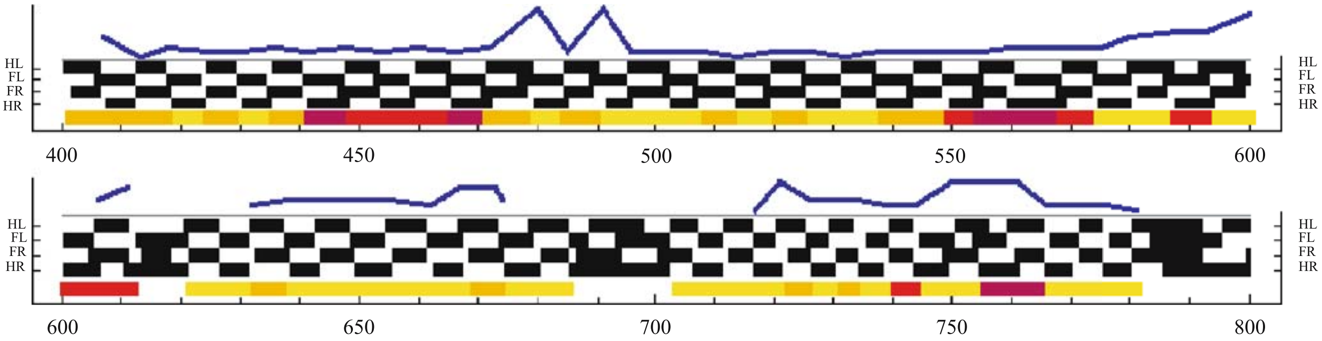

Fig. 8 The predominance of trot in a wide context of speeds and curvatures. This plot depicts a selected sequence of 8 s performed by a specific mouse. *Black rectangles* represent frames in which the corresponding foot was in contact with the ground. The *color gradient* represents the magnitude of per-step shifts of front as in Fig. 4. *White* represents frames which were not recognized by the algorithm as trotting steps. The *blue line* represents trot variability (see Sect. 'Calculation of trot variability' in Supplementary Material). The predominance of the checkerboard pattern implies the use of the trot gait throughout different speeds (*length of black rectangles*), and different curvatures (*yellow* and *red bars*). Note that there is no direct correlation between trot variability, curvature, and/or speed

evident. Similarly, fixating steps are analogous to bipedal straight-path steps, since in both cases the light limb maintains its direction in relation to the base of support. Opening, closing, and fixating steps are produced from a common pattern by using different parameters, thus generating straight or curved paths. An analogous generative rule has been found in the production of straight and curved paths in bipedal human locomotion (Courtine and Schieppati 2004).

Is swing phase similar during free locomotion in all virtually bipedal animals?

Trot is typically described as a 'two-beat' gait consisting of two functional steps (Hildebrand 1965; Lee et al. 1999) performed over a wide range of speeds (Herbin et al. 2004) in the transition between diagonal walk and gallop (Farley and Taylor 1991). In C57 mice progressing in speeds of up to 50 cm/s this gait constitutes the main mode of locomotion (see also Lepicard et al. 2006), being used in a wider context than previously considered (Figs. 8, S1). Previous studies highlighted the essential similarity in the behavior of the supporting limbs during straight-path locomotion in all the animals that use two alternating propulsive sets. Here, we highlight the similarity in the behavior of the swinging limbs during curved-path locomotion. We expect that the described regularities in the dynamics of the swinging limbs would also apply in bipeds, quadrupeds, hexapods, and octapeds.

Using the supporting foreleg as an origin of axes for measurement

A recent study on the ontogeny of locomotion in small mammals showed that, regardless of age, foreleg landing occurred at a highly standardized position below the eye (Schilling 2005). This position remains stable even during exaggerated lateral head movements (Kafkafi et al. 1996). Furthermore, deprivation of visual input from forepaw during the sensitive developmental period resulted in deficits in guided placing (Hein 1974). These findings support our choice of the heavy foreleg as the normalizing zero point. It is tempting to speculate that the location of foreleg landing is noted by the animal, recorded in its memory, and subsequently used as a reference point. The regularity in the relationship between this reference point and the landing of the light diagonal could mean that the position of this virtual limb is also monitored by the animal.

Non-trivial representations of movement in the CNS?

Studies on the neuronal control of locomotion in normal animals and in mice with mutations directed at specific populations of spinal cord motor circuitry show a correlation between spinal activity and basic kinematic parameters such as speed (Gosgnach et al. 2006), left–right alternation (Kullander et al. 2003; Lanuza et al. 2004), and flexor–extensor phase relations (Yakovenko et al. 2005). The evidence presented in this study suggests that in addition to the search for such basic parameters it might be profitable to search for non-trivial representations of movement in the CNS (e.g., Bosco et al. 2005).

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References

Andrews JR, McLeod WD, Ward T, Howard K (1977) The cutting mechanism. Am J Sports Med 5(3):111–121

Bernstein N (1967) The co-ordination and regulation of movements. Pergamon, Oxford

Blickhan R, Full RJ (1993) Similarity in multilegged locomotion: bouncing like a monopode. J Comp Physiol A 173:509–517

Bosco G, Eian J, Poppele RE (2005) Kinematic and non-kinematic signals transmitted to the cat cerebellum during passive treadmill stepping. Exp Brain Res 167(3):394–403

Cheng H, Almstrom S, Gimenez-Llort L, Chang R, Ove Ogren S, Hoffer B, Olson L (1997) Gait analysis of adult paraplegic rats after spinal cord repair. Exp Neurol 148(2):544–557

Cools AR, Scheenen W, Eilam D, Golani I (1989) Evidence that apomorphine and (+)-amphetamine produce different types of circling in rats. Behav Brain Res 34(1–2):111–116

Copp NH, Jamon M (2001) Kinematics of rotation in place during defense turning in the crayfish *Procambarus clarkii*. J Exp Biol 204(Pt 3):471–486

Courtine G, Schieppati M (2003) Human walking along a curved path. II. Gait features and EMG patterns. Eur J Neurosci 18(1):191–205

Courtine G, Schieppati M (2004) Tuning of a basic coordination pattern constructs straight-ahead and curved walking in humans. J Neurophysiol 91(4):1524–1535

Dickinson MH, Farley CT, Full RJ, Koehl MA, Kram R, Lehman S (2000) How animals move: an integrative view. Science 288(5463):100–106

Domenici P, Jamon M, Clarac F (1998) Curve walking in freely moving crayfish (*Procambarus clarkii*). J Exp Biol 201(Pt 9):1315–1329

Domenici P, Schmitz J, Jamon M (1999) The relationship between leg stepping pattern and yaw torque oscillations in curve walking of two crayfish species. J Exp Biol 202(Pt 22):3069–3080

Durr V, Ebeling W (2005) The behavioural transition from straight to curve walking: kinetics of leg movement parameters and the initiation of turning. J Exp Biol 208(Pt 12):2237–2252

Eilam D (1994) Influence of body morphology on turning behavior in carnivores. J Mot Behav 26(1):3–12

Eshkol N, Harries JG (2001) EWMN Part I. The Movement Notation Society, Israel

Eshkol N, Wachman A (1958) Movement notation. Weidenfeld & Nicholson, London

Farley CT, Taylor CR (1991) A mechanical trigger for the trot–gallop transition in horses. Science 253(5017):306–308

Full RJ (1989) Mechanics and energetics of terrestrial locomotion: from bipeds to polypeds. In: Wieser W, Gnaiger E (eds) Energy transformations in cells and organisms. Thieme, Stuttgart, pp 175–182

Ganor I, Golani I (1980) Coordination and integration in the hindleg step cycle of the rat: kinematic synergies. Brain Res 195(1):57–67

Golubitsky M, Stewart I, Buono PL, Collins JJ (1999) Symmetry in locomotor central pattern generators and animal gaits. Nature 401(6754):693–695

Gosgnach S, Lanuza GM, Butt SJ, Saueressig H, Zhang Y, Velasquez T, Riethmacher D, Callaway EM, Kiehn O, Goulding M (2006) V1 spinal neurons regulate the speed of vertebrate locomotor outputs. Nature 440(7081):215–219

Hamers FP, Lankhorst AJ, van Laar TJ, Veldhuis WB, Gispen WH (2001) Automated quantitative gait analysis during overground locomotion in the rat: its application to spinal cord contusion and transection injuries. J Neurotrauma 18(2):187–201

Hampton TG, Stasko MR, Kale A, Amende I, Costa AC (2004) Gait dynamics in trisomic mice: quantitative neurological traits of Down syndrome. Physiol Behav 82(2–3):381–389

Hase K, Stein RB (1999) Turning strategies during human walking. J Neurophysiol 81(6):2914–2922

Hein A (1974) Prerequisite for development of visually guided reaching in the kitten. Brain Res 71(2–3):259–263

Hen I, Sakov A, Kafkafi N, Golani I, Benjamini Y (2004) The dynamics of spatial behavior: how can robust smoothing techniques help? J Neurosci Methods 133(1–2):161–172

Herbin M, Gasc JP, Renous S (2004) Symmetrical and asymmetrical gaits in the mouse: patterns to increase velocity. J Comp Physiol A 190(11):895–906

Hildebrand M (1965) Symmetrical gaits of horses. Science 150(697):701–708

Hildebrand M (1976) Analysis of tetrapod gaits: general considerations and symmetrical gaits. In: Herman RM, Grillner S, Stein PS, Stuart DG (eds) Neural control of locomotion. Plenum, New York, pp 203–236

Hildebrand M (1989) The quadrupedal gaits of vertebrates. Bioscience 39:766–776

Jamon M, Clarac F (1997) Variability of leg kinematics in free-walking crayfish, *Procambarus clarkii*, and related inter-joint coordination. J Exp Biol 200(Pt 8):1201–1213

Jindrich DL, Full RJ (1999) Many-legged maneuverability: dynamics of turning in hexapods. J Exp Biol 202(Pt 12):1603–1623

Kafkafi N, Golani I (1998) A traveling wave of lateral movement coordinates both turning and forward walking in the ferret. Biol Cybern 78(6):441–453

Kafkafi N, Levi-Havusha S, Golani I, Benjamini Y (1996) Coordination of side-to-side head movements and walking in amphetamine-treated rats: a stereotyped motor pattern as a stable equilibrium in a dynamical system. Biol Cybern 74(6):487–495

Kafkafi N, Benjamini Y, Sakov A, Elmer GI, Golani I (2005) Genotype–environment interactions in mouse behavior: a way out of the problem. Proc Natl Acad Sci USA 102(12):4619–4624

Kale A, Amende I, Meyer GP, Crabbe JC, Hampton TG (2004) Ethanol's effects on gait dynamics in mice investigated by ventral plane videography. Alcohol Clin Exp Res 28(12):1839–1848

Kiriyama K, Warabi T, Kato M, Yoshida T, Kokayashi N (2005) Medial–lateral balance during stance phase of straight and circular walking of human subjects. Neurosci Lett 388(2):91–95

Kullander K, Butt SJ, Lebret JM, Lundfald L, Restrepo CE, Rydstrom A, Klein R, Kiehn O (2003) Role of EphA4 and EphrinB3 in local neuronal circuits that control walking. Science 299(5614):1889–1892

Lanuza GM, Gosgnach S, Pierani A, Jessell TM, Goulding M (2004) Genetic identification of spinal interneurons that coordinate left–right locomotor activity necessary for walking movements. Neuron 42(3):375–386

Leblond H, L'Esperance M, Orsal D, Rossignol S (2003) Treadmill locomotion in the intact and spinal mouse. J Neurosci 23(36):11411–11419

Lee DV, Bertram JE, Todhunter RJ (1999) Acceleration and balance in trotting dogs. J Exp Biol 202(Pt 24):3565–3573

Lepicard EM, Venault P, Abourachid A, Pelle E, Chapouthier G, Gasc JP (2006) Spatio-temporal analysis of locomotion in BALB/cByJ and C57BL/6J mice in different environmental conditions. Behav Brain Res 167(2):365–372

Mead L, Hargreaues E, Galea L (1996) Sex difference in rodents spontaneous activity levels. In: Sanberg P, Ossenkopp KP, Kavaliers M (eds) Motor activity and movement disorders: research issues and applications. Humana, Totowa, pp 111–140

Nielsen DM, Crosley KJ, Keller RW Jr, Glick SD, Carlson JN (1999) Rotation, locomotor activity and individual differences in voluntary ethanol consumption. Brain Res 823(1–2):80–87

Ogura H, Aruga J, Mikoshiba K (2001) Behavioral abnormalities of Zic1 and Zic2 mutant mice: implications as models for human neurological disorders. Behav Genet 31(3):317–324

Pettibone DJ, Hess JF, Hey PJ, Jacobson MA, Leviten M, Lis EV, Mallorga PJ, Pascarella DM, Snyder MA, Williams JB, Zeng Z (2002) The effects of deleting the mouse neurotensin receptor NTR1 on central and peripheral responses to neurotensin. J Pharmacol Exp Ther 300(1):305–313

Schilling N (2005) Ontogenetic development of locomotion in small mammals—a kinematic study. J Exp Biol 208(Pt 21):4013–4034

Schwarting RKW, Fornaguera J, Huston JP (1996) Automated video-image analysis of behavioral asymmetry. In: Sanberg P, Ossenkopp KP, Kavaliers M (eds) Motor activity and movement disorders: research issues and applications. Humana, Totowa, pp 141–174

Strauss R, Heisenberg M (1990) Coordination of legs during straight walking and turning in *Drosophila melanogaster*. J Comp Physiol A 167(3):403–412

Sumbre G, Fiorito G, Flash T, Hochner B (2005) Neurobiology: motor control of flexible octopus arms. Nature 433(7026):595–596

Szechtman H, Ornstein K, Teitelbaum P, Golani I (1985) The morphogenesis of stereotyped behavior induced by the dopamine receptor agonist apomorphine in the laboratory rat. Neuroscience 14(3):783–798

Vidal PP, Degallaix L, Josset P, Gasc JP, Cullen KE (2004) Postural and locomotor control in normal and vestibularly deficient mice. J Physiol 559(Pt 2):625–638

Walter RM (2003) Kinematics of 90 degrees running turns in wild mice. J Exp Biol 206(Pt 10):1739–1749

Wolfram Research Inc. (2005) Mathematica. Wolfram Research Inc., Champaign

Yakovenko S, McCrea DA, Stecina K, Prochazka A (2005) Control of locomotor cycle durations. J Neurophysiol 94(2):1057–1065

Ziegler MG, Szechtman H (1990) Relation between motor asymmetry and direction of rotational behaviour under amphetamine and apomorphine in rats with unilateral degeneration of the nigrostriatal dopamine system. Behav Brain Res 39(2):123–133

Zimmerberg B, Riley EP, Glick SD (1986) Differential effects of prenatal exposure to alcohol on activity and circling behavior in rats. Pharmacol Biochem Behav 25(5):1021–1025

Zollikofer C (1994) Stepping patterns in ants—influence of speed and curvature. J Exp Biol 192(1):95–106