

Kinematics of 90° running turns in wild mice

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Accepted 27 February 2003

Summary

Turning is a requirement for locomotion on the variable terrain that most terrestrial animals inhabit and is a deciding factor in many predator–prey interactions. Despite this, the kinematics and mechanics of quadrupedal turns are not well understood. To gain insight to the turning kinematics of small quadrupedal mammals, six adult wild mice were videotaped at 250 Hz from below as they performed 90° running turns. Four markers placed along the sagittal axis were digitized to allow observation of lateral bending and body rotation throughout the turn. Ground contact periods of the fore- and hindlimbs were also noted for each frame. During turning, mice increased their ground contact time, but did not change their stride frequency relative to straight running at maximum speed. Postcranial body rotation preceded deflection in heading, and did not occur in one continuous motion, but rather in bouts of 15–53°. These bouts were synchronized with the stride cycle, such that the majority of rotation occurred during the second half of

forelimb support and the first half of hindlimb support. In this phase of the stride cycle, the trunk was sagittally flexed and rotational inertia was 65% of that during maximal extension. By synchronizing body rotation with this portion of the stride cycle, mice can achieve a given angular acceleration with much lower applied torque. Compared with humans running along curved trajectories, mice maintained relatively higher speeds at proportionately smaller radii. A possible explanation for this difference lies in the more crouched limb posture of mice, which increases the mechanical advantage for horizontal ground force production. The occurrence of body rotation prior to deflection in heading may facilitate acceleration in the new direction by making use of the relatively greater force production inherent in the parasagittal limb posture of mice.

Key words: agility, maneuverability, moment of inertia, locomotion, running, mouse, *Mus musculus*.

Introduction

Turning is an important component of animal locomotion. Rapid turning to avoid obstacles is necessary for running through the variable terrain that most animals inhabit. Further, turning abilities may be a deciding factor in the outcome of predator–prey encounters and intraspecific competition. An animal's proficiency in turning is likely to be influenced by both its morphological configuration and behavioral repertoire. Understanding the effects of variations in these features on turning abilities requires specific knowledge of the turning process. Currently, however, the kinematics and biomechanics of running turns in quadrupeds are not well understood.

Although specific kinematics may vary in conjunction with body configuration, the mechanics of all successful running turns in which final and initial speed are the same consist of two components: (1) the center of mass must decelerate in the initial direction and accelerate in the new direction, and (2) the body must be rotated to face the new direction (Jindrich and Full, 1999). The force required to decelerate the center of mass in the original direction is equal to the decrease in momentum (mass \times change in velocity) in this direction divided by the time allotted for this deceleration. Similarly, the force required for

acceleration equals the mass multiplied by the acceleration. The torque (τ) required to rotate the body is equal to its rotational inertia (I) times the required angular acceleration (ω).

Any feature reducing rotational inertia would, therefore, reduce the torque required to achieve a given level of angular acceleration and may improve turning agility. Rotational inertia is a body's resistance to rotation about an axis. It is defined as the differential elements of a body's mass (m) multiplied by their distances from the rotational axis (r) squared ($I = \sum mr^2$) (Halliday et al., 1993). Eilam (1994) studied the kinematics of walking turns in wolves, polecats and honey badgers and found that each of these animals behaves in ways unique to its body plan to reduce the effective rotational inertia during the turn. Wolves tilt their heads down and bend laterally to reduce rotational inertia about a central turning axis, whereas long-bodied pole cats use the pelvic and pectoral girdles as two separate turning axes, and honey badgers rear up on their hindlimbs to reduce rotational inertia about the pelvic girdle (Eilam, 1994). Many possible variations also exist for running turns, and these may vary between groups of animals depending

on gait, body configuration, size, flexibility and muscular strengths. This study focuses specifically on 90° turns executed by bounding mice. It addresses whether mice behaviorally reduce their rotational inertia during turns or take advantage of the fluctuations in rotational inertia inherent to a bounding gait by rotating when it is minimized. Mice are particularly convenient subjects for kinematic analysis as their small body size allows multiple strides to be filmed from below with a single camera.

Also of interest is the effect of turning on the stride cycle. Greene and McMahon (1979) studied the gait parameters of human subjects running along paths of varying radii. They found that neither stride frequency nor step length (the distance traveled during ground contact) varied with path radius. Based on these results, and the known forces of gravity and centripetal acceleration that must be overcome to complete a turn, they made several predictions about how speed and ballistic air time should vary with path radius for humans running at maximal speed. Mice, with their very different body configuration and gait kinematics, must still overcome the same forces of gravity and centripetal acceleration to complete a turn. In this study, changes in gait parameters with path radius in mice are compared to those observed in humans and to the predictions of Greene and McMahon (1979).

A further question of this study concerns the timing of the deflection in heading of the center of mass relative to the rotation of the body axis. Jindrich and Full (1999) found that in cockroaches, the change in direction of heading led body rotation by an average of 5°. They noted that the lateral forces applied during straight-ahead running were sufficient to generate the perpendicular forces that changed the direction of heading in turns. Further, despite the greater contributions of the outside legs to turning, they found no difference in duty factors during turns. In mice, where the forelimbs are used mainly for deceleration and the hindlimbs for acceleration in straight running (Heglund et al., 1982), it was hypothesized that the forelimbs might have a greater duty factor just prior to the turn as the mouse decelerates in the original direction, and the hindlimbs might have a greater duty factor just after the turn as the mouse accelerates in the new direction. Thus, duty factors of the fore- and hindlimbs were also compared just prior to and after the center of the turn.

This paper describes the kinematics of running turns in wild mice, focussing specifically on changes in posture that influence resistance to body rotation, how gait parameters vary in running turns *versus* straight running, and the timing in deflection in heading of the center of mass relative to the rotation of the body axis. These observations suggest that for running turns in mice: (1) body rotation coincides with the portion of the stride in which rotational inertia is minimized, (2) crouched limb posture may allow relatively higher velocities to be maintained, and (3) rotating the body prior to changing the direction of heading may facilitate rapid acceleration in the new direction.

Materials and methods

Animals

Six adult wild mice *Mus musculus* L., with an average mass of 18.5±0.8 g, were used in this study. These mice were 4th and 5th generation laboratory-bred wild mice from founders caught near Gainseville, Florida. They were housed in the University of Utah Animal Care Facility from birth. Mice ranged in age from 6 to 27 months during the experiment. Although some of the mice were quite old by the end of the experiment, no significant decrease in performance, or difference in performance between old and young mice, was observed. Because two of the mice eventually escaped, only five of the mice performed trials on the straight trackway and four were used for the carpeted control runs.

Setup and procedure

Mice were videotaped from below at 250 Hz while performing 90° running turns in a 0.6 m×0.6 m L-shaped track, 10.2 cm wide, made of Plexiglas. Plexiglas was used as the running surface to allow video recording of the underside of the mouse throughout the turn. This greatly improved resolution of limb support, duty factors, stride frequency and lateral bending of the trunk. To induce mice to run, doors at either end of the trackway were opened and the mice were blown on if necessary. Runs in both directions were recorded. The Plexiglas at either end of the trackway was covered on the outside with dark-colored paper to motivate mice to run all the way to the end and to stay there until induced to run again. Each mouse made 20–30 runs on the trackway on each of 3 different days. The six fastest performances (determined by counting the number of video frames required to cover the trackway), in which the mouse made no contact with the side walls of the track, were digitized and analyzed for each mouse. Because only the fastest runs were used, all turns analyzed consisted of bounding locomotion. In the majority of trials no apparent foot slippage occurred, and those trials in which mice did slip were excluded from the analysis. Nevertheless, it seemed possible that subjects might modify their stride parameters or run more slowly, with increased caution, on the Plexiglas. To control for this possibility, the trackway was carpeted and four of the mice performed 30 control runs on each of two days. Carpeted control runs were filmed from above at 250 Hz and the fastest control run for each mouse was then analyzed and compared to experimental trials.

Stride frequency and duty factors

Stride frequency and proportion of stride time spent unsupported were compared over the two strides in the middle of the turn to those of mice running along a straight trajectory. The unsupported portion of the stride is the same as the ballistic air time referred to by Greene (1985) and encompasses both flight phases. Duty factors of the fore- and hindlimbs were compared between the first and second strides centered upon the apex of the turn, and between turns and straight runs. The apex of the turn refers to the point at which the velocity in the new direction becomes equal to that in the original direction,

i.e. when the center of mass is moving at a 45° angle relative to the initial heading. Duty factors and flight phases were determined by recording whether the hindlimbs or forelimbs were in contact with the ground for each frame of the videotape. Because the videotape was recorded at 250 Hz and contact phases ranged from 25–40 ms, whereas flight phases could be as short as 4 ms, there was some error inherent in this data. To control for this, reported duty factors were averaged over the six turns for each mouse and then over the six mice. Stride and step lengths were determined by multiplying the mean stride velocity by the stride time and total ground contact time (forelimb + hindlimb support), respectively. For measurements on the straight trajectory, five of the mice were videotaped from below at 250 Hz while they ran in a similar Plexiglas enclosure 1.22 m in length and 10.2 cm in diameter without the 90° turn. Two strides from the middle of the trackway were analyzed from six runs for each mouse. Straight runs were selected for analysis such as to obtain as wide a range of bounding speeds as possible, including the fastest straight run for each mouse.

Measurement and analysis of rotation and angle of deflection

To study rotation of the body during the turn and to measure the extent of lateral bending, it was necessary to know the angles that various ‘segments’ of the mouse’s body made with the axis of the track throughout the turn. To determine this, four black markings for digitizing were placed ventrally along the sagittal axis of the mouse in the following locations: (1) tip of chin, (2) throat, (3) caudal end of rib cage and (4) just cranial to anus. Using these markings, each mouse’s body was divided into four segments: (i) the head and neck from marking 1 to 2, (ii) the thoracic segment from marking 2 to 3, (iii) the abdomen and hindquarters from marking 3 to 4 and (iv) the postcranial body from marking 2 to 4. The angle made by each of these segments with the track axis was then calculated for each frame of the video.

To determine the extent to which head rotation preceded that of the postcranial body, the difference in angles made by each of these two segments with the track axis was measured for each frame and averaged over the two strides centered at the apex of each turn (Fig. 1A). These values were then averaged over the six turns from each mouse and the mean of these means was calculated. If the head tended to rotate prior to the body, this mean value would be significantly positive. This procedure was repeated using the upper and lower body segments to determine whether lateral bending of the trunk occurred to a significant extent.

To determine when in the stride cycle the majority of angular displacement occurred, the stride was divided into six phases: the first and second halves of forelimb and hindlimb support, flight phase 1 from hindlimb to forelimb support and flight phase 2 from forelimb to hindlimb support (see Fig. 5). The angle rotated by the head/neck and postcranial body during each of these phases was then calculated for the two strides centered at the apex of each turn. To determine the mean and maximal angles turned in bouts of rotation, it was first

necessary to locate the beginning and end of each bout. To do this angular velocity (determined from the angular displacement through the same derivation as used to determine linear velocity and explained below) was plotted over time and bouts were measured between minima. The amount of body rotation occurring in each bout was then determined by integrating the area under this curve.

The angle of deflection, described by Jindrich and Full (1999) as the angle between the instantaneous and original directions of travel of the center of mass, was also measured throughout the turn. This was calculated as the angle between a segment connecting the location of the center of mass in two consecutive video frames and the track axis. Because this measurement was subject to fluctuating error, measured values were smoothed using fourth-order central differences (Lanczos, 1956) as explained below for velocity. The extent to which body rotation preceded deflection in heading was then determined by averaging the difference between the body angle and the angle of deflection over the two strides centered at the apex of the turn.

Calculating speed

To calculate the speed of the center of mass, its location was approximated as the third marking, at the caudal end of the rib cage, based on previous measurements (Walter and Carrier, 2002). Because the actual location of the center of mass varies throughout the stride cycle, and the mouse’s skin moves relative to its body, this estimate introduces some error. To reduce this error, speed was averaged over a stride cycle. Linear velocities (V_x and V_y) in the original and new directions were calculated by first smoothing positional data using fourth-order central differences and then taking the derivatives using moving regressions (Lanczos, 1956):

$$\begin{aligned} V_x &= -2x_{-2} - x_{-1} + x_{+1} + 2x_{+2}, \\ V_y &= -2y_{-2} - y_{-1} + y_{+1} + 2y_{+2}, \end{aligned} \quad (1)$$

where x and y are the instantaneous positions of the center of mass along the x and y axes. Speed was then calculated by taking the vector sum of V_x and V_y . Walker (1998) demonstrated that this was one of the most accurate smoothing methods for the magnification level used, 0.25× (i.e. four body lengths fitted across the screen). Greater magnification was not used as this would have precluded inclusion of several strides surrounding the turn in the analysis.

As noted in many previous studies (e.g. Walker, 1998), there is some error inherent in positional data obtained through digitizing. Previous studies point out that this error is multiplied when taking the derivatives to obtain velocity data. With the magnification and video speed used, Walker (1998) observed the mean error in velocity derived from digitized positional data to be less than 10%, while maximum velocity values were not overestimated by more than 25% in 90% of trials.

Measurement of rotational inertia

While rotational inertia of mice in the lateral (yaw) direction

for standing/trotting postures has previously been measured (Walter and Carrier, 2002), the extent to which it varies throughout the stride cycle in bounding mice was unknown. To estimate this variation, the rotational inertia of three mice frozen in each of the following three bounding postures (9 in total) was measured: (1) with trunk and limbs maximally extended, (2) maximally flexed, and (3) midway between as in a standing posture. Rotational inertia was determined by oscillating each mouse as a pendulum about a rod passing dorsal–ventrally through its sagittal plane and timing the pendulum’s period (method described in Walter and Carrier, 2002). Each mouse oscillated about two separate axes, allowing for two separate estimations of the rotational inertia about the center of mass using the parallel axis theorem. These two estimates, which differed by less than 15% in all cases, were averaged. To account for the slight variations in mass of the nine mice, assumptions of geometric similarity were used to scale each rotational inertia value to an 18.5 g mouse. Rotational inertia values for the three mice in each posture were then averaged.

Statistical analysis

Paired Student’s *t*-tests were used to determine whether differences in velocity and gait parameters were significant between each mouse’s fastest trial turning on Plexiglas *versus* carpet, and turning *versus* straight running. *t*-tests were used to determine whether differences between the rotational inertia values for each of the three limb postures were significant. In all comparisons, parameters were assumed to be significantly different if the *P* values were less than or equal to 0.05. Student’s *t*-tests were also used to determine whether average leads in head and body angles over the deflection angle were significantly different from zero.

As it was not possible to coerce mice to run along the straight trajectory at exactly the same speeds used in turns, the

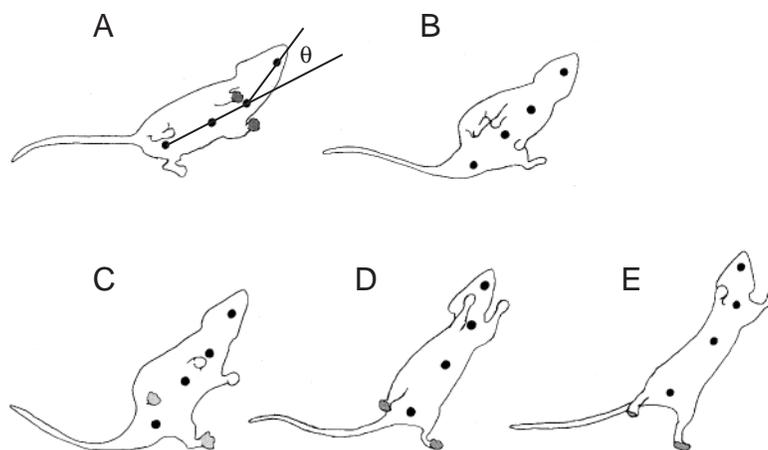


Fig. 1. A representative turn made by one of the mice. (A–E) Frames 16 ms apart. Feet in contact with the ground are shaded. Phases of the turn are described in the text. Angle θ in A is the angle by which the rotation of the head and neck precedes that of the body for that frame.

mean speeds and gait parameters of the six mice over their turns were averaged and compared to reduced major axis (RMA) regressions of the various parameters against speed. RMA regression lines (Sokal and Rohlf, 1997) were fitted to plots of stride frequency and proportion of stride unsupported *versus* straight path speed. 95% confidence intervals (Sokal and Rohlf, 1997) for means of 36 samples (turns) were also calculated.

Results

Description of turning behavior

Mice maintained their bounding gait during turns. In a typical turn (Fig. 1), a mouse planted its forefeet slightly toward the outside of the turn, began to rotate its head and neck in the turn direction (Fig. 1A), and then rotated its lower body as the hindlimbs were brought forward and planted (Fig. 1B,C). It then began accelerating in the new direction by

Table 1. Stride parameters: averages of the mean turning values from six mice and for the fastest turns and straight runs from five mice

	Mean Plexiglas turns ^a		Fastest Plexiglas turns and straight runs ^b	
	1 st stride (N=36)	2 nd stride (N=36)	Turn (N=5)	Straight (N=5)
Speed (m s ⁻¹)	1.25±0.03*	1.15±0.02*	1.29±0.06*	1.80±0.06*
Stride frequency (Hz)	12.70±0.30	12.14±0.37	13.56±1.40	13.09±1.83
Unsupported (flight phase) (% of stride time)	0.12±0.01	0.14±0.02	0.16±0.05*	0.32±0.11*
Forelimb support (% of stride time)	0.43±0.01	0.41±0.02	0.43±0.03*	0.30±0.08*
Hindlimb support (% of stride time)	0.45±0.01	0.46±0.01	0.42±0.04	0.38±0.06
Stride length (m)	0.099±0.004	0.095±0.003	0.079±0.015*	0.113±0.021*
Step length (m)	0.087±0.002*	0.081±0.001*	0.067±0.013	0.078±0.012

^aValues are means ± S.E.M.

^bValues are means ± S.D.

*Paired means are significantly different ($P \leq 0.05$).

pushing directly forward with its hindlimbs (Fig. 1D). This process, with head and body rotation synchronized to various phases of the stride cycle, continued over the two to three strides required to complete the 90° rotation (Fig. 1E).

Comparison of turns on Plexiglas with carpeted controls

The Plexiglas surface on which the mice ran had a minimal effect on speed and stride parameters. On average, mice ran only 10% faster during carpeted control runs than on Plexiglas. No significant differences were found in gait parameters including stride frequency, proportion of the stride spent unsupported, and fore- and hindlimb duty factors between the fastest carpeted and Plexiglas runs. Because the differences in speed between carpeted and Plexiglas runs, though significant, were relatively small, and there were no significant differences in other gait parameters, it seems reasonable to assume that the biomechanics and kinematics of the mice's gait were not substantially altered by the low frictional surface of the Plexiglas.

Comparison of stride parameters between turns and straight runs

Maximum speed and gait parameters did differ, however, between the fastest turns and straight runs of the mice when they ran on Plexiglas. Maximum speeds during straight runs were on average 1.37 times greater than maximum speeds over the two strides surrounding the apex of the turn, but stride frequencies did not differ significantly (Table 1). Mice spent a smaller portion of the stride period unsupported in the maximum speed turns and a greater portion supported by the forelimbs.

On average, mice had higher stride frequencies during turns than would be expected for straight runs at similar speeds (Fig. 2). The percentage of stride spent unsupported for the stride prior to the apex of the turn was not significantly different from that predicted for same speed straight runs. A slightly greater portion of the stride after the apex of the turn was spent unsupported than would be predicted for same speed straight runs (Fig. 3). Although mice ran more slowly just after the apex of turns than before, other stride parameters including proportion of stride spent unsupported, stride frequency and duty factors, did not differ between the two turning strides (Table 1).

Body rotation and rotational inertia

Postcranial body rotation did not occur in one continuous motion, but rather in bouts interspersed with periods in which little or no body rotation occurred (Fig. 4A). These bouts of increased angular velocity were synchronized with the stride cycle (Fig. 4B) and resulted in body rotations of 15–53° (Fig. 4C). Thus the total body rotation of 90° was usually completed in two or three strides. The greatest amount of body rotation occurred during the period from the second half of forelimb support to the first half of hindlimb support (Fig. 5). The rotational velocity during the intervening flight phase 2 was lower than that during the second half of forelimb support,

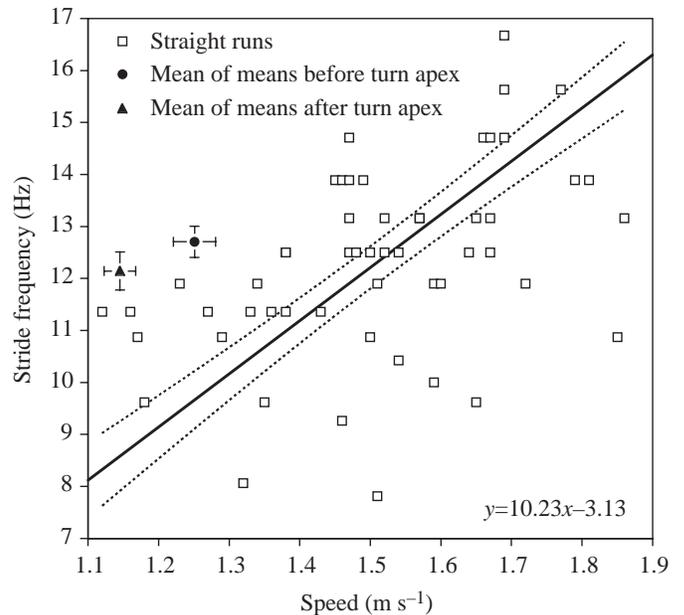


Fig. 2. Reduced major axis regression (solid line) of stride frequency and speed for 55 strides from straight runs (open squares). Broken lines show the standard errors for the regression. Superimposed are the averages of the mean stride frequencies for each of the six mice over the strides just prior to (filled circle) and after (filled triangle) the apex of each turn.

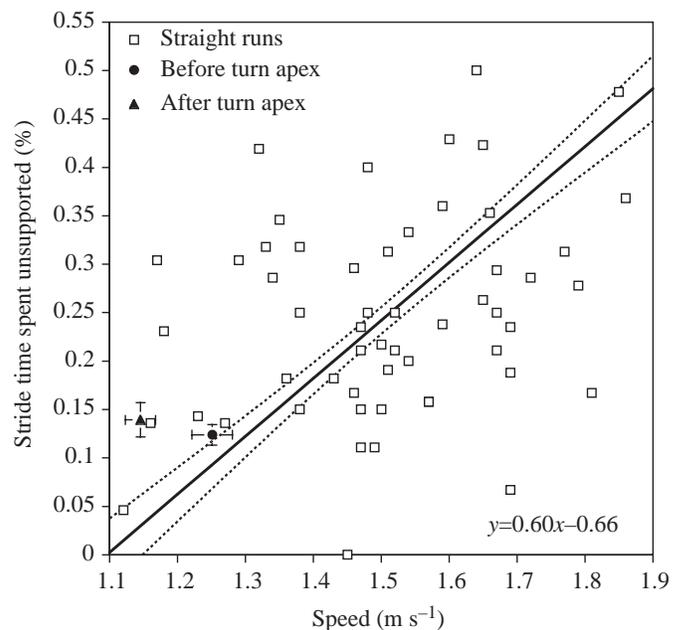
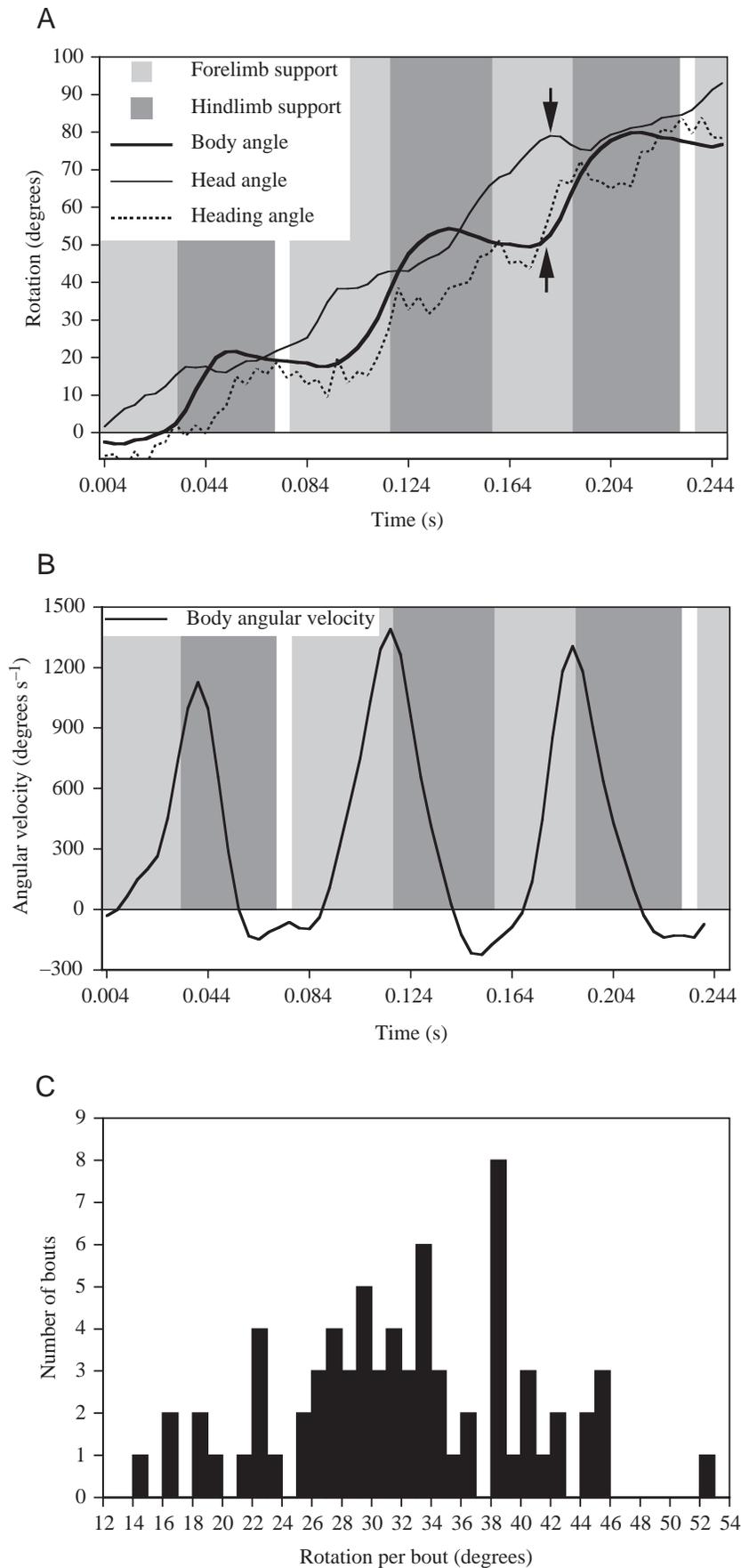


Fig. 3. Reduced major axis regression (solid line) of ballistic air time as a percentage of stride time and speed for 55 strides from straight runs (open squares). Broken lines show the standard errors for the regression. Superimposed are the averages of the mean ballistic air times for each of the six mice over the strides just prior to (filled circle) and after (filled triangle) the apex of each turn.



but not significantly different from that during the first half of hindlimb support. However, because of its short duration or absence in many of the strides, a smaller percentage of the total rotation occurred during it. The period from the end of forelimb to the beginning of hindlimb support is also the portion of the stride in which the mouse's body is maximally flexed and rotational inertia is minimized. Rotational inertia of a maximally extended 18.5 g mouse ($1.14 \times 10^{-5} \pm 4.5 \times 10^{-12}$) was 1.54 times greater than that of a fully flexed mouse ($7.41 \times 10^{-6} \pm 9.0 \times 10^{-13}$) and 1.39 times greater than that of a standing or intermediately postured mouse ($8.24 \times 10^{-6} \pm 1.0 \times 10^{-12}$). The difference in rotational inertia between flexed and intermediately postured mice was not significant.

Averaged over the two strides centered at the apex of the turn, rotation of the head/neck segment preceded that of the body by 8° and preceded the deflection of heading by 11° (Table 2). Rotation of the thoracic segment did not significantly precede that of the hindquarters. Body rotation preceded deflection of heading by an average of 3° . Thus, mice tended to rotate both their heads and trunks to face the new direction before their centers of mass began moving in this direction.

Discussion

Duty factor and stride frequency during turns versus straight running

In contrast to constant speed straight running, where the only net ground force applied over the course of a stride is a vertical force equal to the subject's weight, running along a curved trajectory requires net horizontal ground forces

Fig. 4. (A) Sample plot of rotation over time for a turn from one of the mice. Light shading represents forelimb support and dark shading hindlimb support. Thick line, postcranial body; normal line, head/neck angle; dotted line, angle of heading. The area between head and body angle traces (depicted by arrows) is the lead of the head/neck angle over the postcranial body angle. (B) Sample plot of the angular velocity of the postcranial body over time for one of the mice. Shading as in A. (C) Histogram showing the number of degrees rotated per bout for the two greatest bouts of postcranial body rotation during each turn. The angle turned per bout of rotation was determined by integrating between minima on the angular velocity over time curve in B.

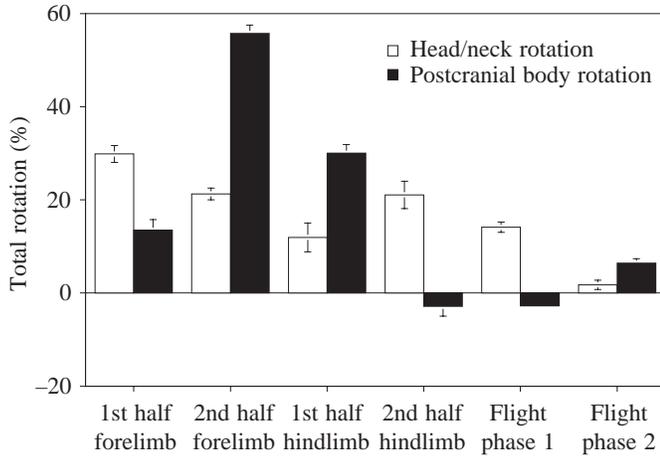


Fig. 5. Percentage of the total 90° of head/neck and postcranial body rotation that occurred during each phase of the stride cycle. Head/neck (open bars) and body (filled bars) rotation were the changes in the angles made by markings 1 and 2 and 2 and 4 with the horizontal, respectively. Flight phase 1 occurred between hindlimb takeoff and forelimb plant and flight phase 2 occurred between forelimb takeoff and hindlimb plant. Most stride cycles contained one of the two flight phases but not both. Values are means \pm S.E.M. for the six mice.

(McMahon, 1984). Greene and McMahon (1979) studied human subjects running at maximum speeds along straight trajectories and curves of varying radii. They found that in producing the 'extra' horizontal forces necessary for turning, humans did not alter their stride frequency, but decreased the proportion of the stride spent unsupported. In mice, although stride frequency during turns was higher than in straight runs at similar speeds, it did not differ from stride frequency in straight runs at maximum speed (Fig. 2, Table 1). In contrast, turning mice did not differ significantly in the amount of time spent unsupported for the first stride of turns and straight runs at the same speed, but spent less time unsupported during turns than in straight runs at

maximum speed (Fig. 3). Thus, considering only maximal performances, mice modified their strides similarly to humans when running along curved trajectories: that is, they held stride frequency constant while decreasing the proportion of the stride spent unsupported.

Predicting relative speed from turn radius

Although the finding that the maximum speed of mice is lower in turns than in straight runs is rather intuitive, an explanation for the magnitude of the decrease in speed is not obvious. Greene and McMahon (1979) related the decrease in maximal velocity to path radius by assuming that the average total force (horizontal and vertical combined) applied during ground contact is maximized for an individual running at maximum speed. Based on this assumption, as path radius decreases and greater horizontal force is required, the average vertical force applied during ground contact must decrease proportionately. This decrease in average vertical force necessitates spending larger portion of the stride in contact with the ground at decreased radii. Greene and McMahon further assumed that stride frequency and step length at maximum speed were independent of curve radius. They thus proposed that the observed decrease in speed around curves was due to an increase in ground contact time without a corresponding increase in distance traveled during ground contact (Greene and McMahon, 1979). Greene related path radius to relative velocity through the dimensionless reciprocal Froude number (rg/v_o^2) (Greene, 1985; Fig. 6):

$$rg/v_o^2 = v_r^3 / (1 - v_r^2) \quad (2)$$

Here r is the turn radius, g the gravitational constant, v_o the subject's maximum speed on a straight trajectory, and v_r the turn speed v divided by v_o .

So are the assumptions of Greene's equation reasonable, and do they apply to mice as well as humans? The equation assumes that the vector sum of the average fore-aft, lateral and vertical forces applied during ground contact remain constant. If, however, different muscle groups that were capable of

Table 2. Average angular lead of head rotation over postcranial body rotation, upper body rotation over lower body rotation, head rotation over deflection angle, and postcranial body rotation over deflection angle

Subject	Angular lead (degrees)			
	Head versus body	Upper versus lower body	Head versus deflection	Body versus deflection
A	9.62 \pm 3.83	4.06 \pm 4.98	16.80 \pm 2.23	7.18 \pm 3.11
B	8.09 \pm 3.27	0.88 \pm 3.18	6.32 \pm 3.14	-1.77 \pm 3.19
C	11.66 \pm 2.57	2.85 \pm 1.35	14.80 \pm 5.09	3.14 \pm 5.62
D	7.25 \pm 2.29	5.97 \pm 4.06	10.17 \pm 1.98	2.92 \pm 2.45
E	8.28 \pm 4.37	0.18 \pm 5.04	11.75 \pm 7.09	3.47 \pm 6.78
F	4.59 \pm 2.31	-0.86 \pm 4.31	8.93 \pm 3.78	4.35 \pm 4.74
Mean	8.25**	2.18	11.46**	3.22*
S.E.M.	0.97	1.05	1.57	1.18

Angular measurements were averaged over the two strides best encompassing the apex of the turns. Positive values indicate that the first segment was, on average, further rotated in the turn direction.

*The mean is significantly different from zero at $P < 0.05$; ** $P < 0.001$.

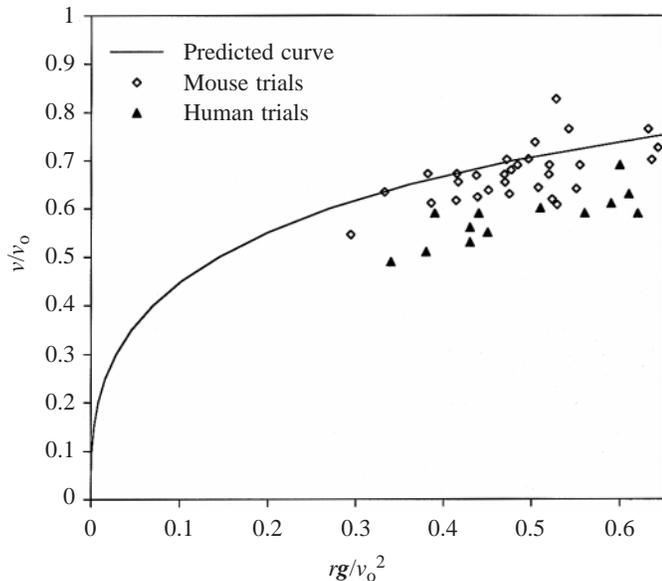


Fig. 6. A comparison of the speed–radius relationship seen in five mice with the curve predicted by Greene and McMahon (1979) and human data from Greene (1985). The dimensionless speed (v_r) is the speed of the mouse during a turn (v) divided by that mouse's maximum speed on a straight path (v_0). The reciprocal Froude number, rg/v_0^2 , is the radius (r) of the mouse's path multiplied by the gravitational constant (g) and divided by the mouse's maximum speed squared.

functioning concurrently produced these forces, one might expect the average total ground force during the stance phase of turns to be much greater. Electromyograph analyses on humans by Rand and Ohtsuki (2000) and Neptune and colleagues (1999) have in fact shown that the activity patterns of various lower limb muscle groups differ in turns from straight-ahead running. Despite this, Chang et al. (2001) measured a decrease in net ground force production during turns in humans, primarily in the inside leg. These findings are not consistent with the assumption that total force production is independent of turn radius in humans. Because ground forces were not measured in this study, it is not possible to evaluate the effects of curve radius on total ground force production in running mice. The second assumption, that stride frequency and step length are independent of path radius, was empirically demonstrated to be true for humans (Greene and McMahon, 1979). In mice, step length and stride frequency also did not differ significantly between maximum speed turns and straight runs (Table 1).

Because the Froude number (v_0^2/rg) is dimensionless, Greene's equation should be equally applicable to animals of all sizes. The radii required for similar inverse Froude numbers are proportionately smaller in smaller animals because their maximum speeds are lower. For an inverse Froude number of 0.5, Greene's human subjects used a radius of 3.1 m, which was approximately 20 times larger than the average radius for mice (0.153 ± 0.005 m; mean \pm S.E.M., $N=5$). In other words, because the humans and mice were running along curves of

equivalent radii for their maximum speed, their speeds should have been affected to the same extent.

The speeds of human subjects running along curves of various radii, showed close agreement with Greene and McMahon's prediction at larger radii, but fell below the predicted curve at reciprocal Froude numbers <1 (Greene, 1985; McMahon, 1984). For reciprocal Froude numbers from 0.3–0.65, human velocities fell below the curve by an average of 17% whereas mice velocities, on average, fell below the curve by only 3.9% (calculated from Greene, 1985; Fig. 6). Thus at these small Froude numbers, mice were able to run closer to their maximum speeds than humans.

It is possible that being quadrupedal *versus* bipedal confers some advantage in turning. The bounding gait used by the mice places outside and inside limbs in contact with the ground simultaneously. Thus if mice exhibited the same decrease in force production by the inner legs as do humans (Chang et al., 2001), it might be partially ameliorated by the concurrent force production of the outside legs. Alexander (2002) suggested that at very small radii humans might run slower than predicted by Greene and McMahon because they are limited by friction rather than their muscular ability to produce force.

Biewener (1983) suggested that the crouched posture of small quadrupedal mammals might increase their maneuverability by increasing the summed length of their limb segments relative to their hip or shoulder heights. This would allow them to exert ground forces over a longer contact period. Another possible advantage of the crouched posture in turning is the mechanical advantage at the limb joints in applying horizontal ground forces. Whereas an upright posture confers a much greater mechanical advantage in producing the vertical ground reaction forces needed to counteract gravity (Biewener, 1989), it decreases the mechanical advantage for horizontal ground forces (Fig. 7). For instance, when humans perform running turns, much of the deflection in linear momentum is produced by braking and medio-lateral forces of the vastus medialis and other thigh muscles of the outer leg (Rand and Ohtsuki, 2000). Given the long lever arm of the nearly straight lower limb and the very short lever arm of the muscles' insertions in humans, these muscles are clearly operating at a very low mechanical advantage (Fig. 7). In contrast, mice, with their crouched posture, would be likely to apply the necessary horizontal forces at a much greater mechanical advantage, thereby giving them an advantage in turns of smaller radii. Greene and McMahon's over-prediction of human performance at smaller radii may be because their estimate does not account for the difference in mechanical advantage at which horizontal and vertical forces are produced. This possibility is supported by the improved turning performance of humans along banked curves observed by Greene (1987). A banked surface would allow a runner to apply part of the horizontal ground force through the same mechanism and mechanical advantage through which vertical force is normally applied. In mice, the more comparable mechanical advantage for horizontal and vertical force production might contribute to the closer

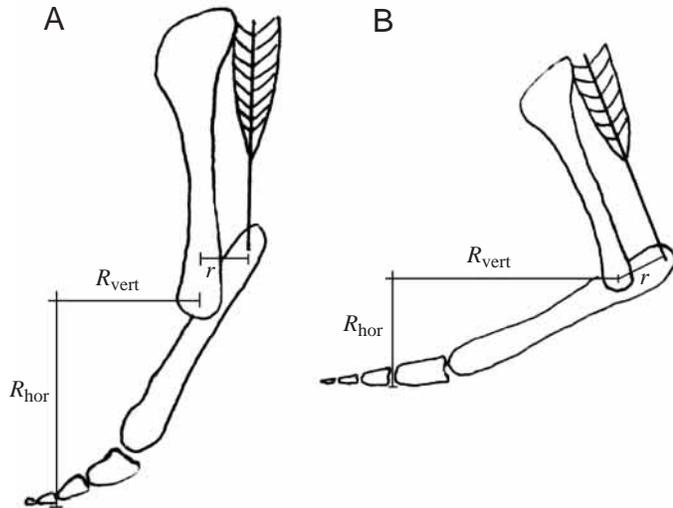


Fig. 7. Comparison of the effective mechanical advantage for horizontal *versus* vertical force production in crouched and upright postures. Biewener (1989) defines effective mechanical advantage as the ratio of the muscle moment arm (r) to the moment arm of the ground reaction force (R). For a crouched posture, the horizontal moment arm (R_{hor}) is smaller relative to the vertical moment arm (R_{vert}) than for an upright posture. This means that for a crouched posture the effective mechanical advantage for horizontal force production is greater relative to that for vertical force production than for a more upright posture.

agreement of their performance with Greene's prediction at smaller radii.

Duty factor compared between strides of the turn

There is a division of labor in mammals in which the forelimbs are primarily used for deceleration and hindlimbs are primarily used for acceleration (Heglund et al., 1982). Because of this, it seemed likely that mice might have a longer forelimb support phase in the stride prior to the apex of the turn, when more deceleration in the original direction is likely to occur, and a longer hindlimb support phase in the stride just after the apex, when more acceleration in the new direction is likely to occur. Although there was a trend in this direction (Table 1), there were no significant differences in forelimb and hindlimb support phase lengths between the two strides. Force plate data during running turns would be of great interest, as it would allow more exact timing of force application by the limbs involved.

Turning mice rotate when rotational inertia is minimized

Turning mice rotated their body axes in a series of discrete bouts of 15–53°, interspersed with periods where no rotation occurred (Fig. 4A). These bouts of angular rotation generally coincided with the end of forelimb support and the beginning of hindlimb support (Fig. 5). This suggests a division of labor in which the forelimbs provide more of the torque to rotate the body, after which the hindlimbs are used to accelerate the body in the new direction.

At the end of forelimb support and the beginning of

hindlimb support, when the majority of body rotation occurs, the mouse has reached a maximum in sagittal bending. The appendages and caudal region are located most closely to the turning axis, such that the rotational inertia is only 65% of that when the mouse is fully extended (Fig. 6). Thus the torque required to rotate the mouse's body at a given angular acceleration is 35% less than would be required if the mouse were to rotate during the period of maximum extension. Having a phasic stride cycle that includes periods of increased and decreased rotational inertia is a novelty of the bounding gait of quadrupedal mammals and might explain the discontinuous body rotation observed in mice. In cockroaches, where rotational inertia varies little over the stride cycle, body rotation is less abrupt (Jindrich and Full, 1999).

Rotation of the head and neck was smoother than rotation of the body, showing less variation in angular velocity within a given turn (Fig. 5). Head rotation occurred early in the forelimb duty phase and preceded the sharper rotations of the body axis as well as the deflection in heading (Table 2). Many studies on walking turns in humans have similarly found head rotation to precede body rotation and deflection in heading (e.g. Grasso et al., 1996, 1998; Patla et al., 1999; Imai et al., 2001; Hollands et al., 2001). Hollands and colleagues (2001) suggested that, through neurons which fire selectively based on head orientation, turning head to the new travel direction could be used by the CNS as an allocentric reference frame to reorient the body. Turning the sensory organs to face the new direction first would also increase the time available for the both humans and mice to perceive the environment they must navigate through. This extra reaction time is likely to be important in a flight situation. In portions of some mice turns, head and body rotation appear to be out of phase. This may be advantageous as it would reduce the maximum torque required at a given instant.

Lateral bending might allow axial muscles to aid the appendicular skeleton in creating the torque necessary for rotation by bending and straightening the body. In contrast, if the body were held laterally rigid, although axial muscle activity would be required to maintain this rigidity, appendicular muscles would have to create more of the torque through concentric contractions. Rotation of the thoracic region, however, did not precede that of the abdominal region (Table 2), suggesting that lateral bending did not occur to a significant extent. It is also possible, however, that periods in which thoracic rotation preceded that of the hindquarters occurred, but were approximately equal to periods in which rotation of the hindquarters preceded that of the thoracic region. In this case, although a significant amount of lateral bending may have occurred, the average lead of the thoracic region would be insignificant.

Eilam (1994) described three possible methods of behaviorally reducing rotational inertia: bending the body, rearing up on one set of limbs, and rotating about multiple axes. Although mice did not rear up or bend laterally, the sagittal bending of their bounding gait did tend to bring the trunk and limb mass closer to the rotational axis during the periods of

maximal body rotation. Further, the early rotation of the head may have allowed it to be rotated about a more proximal axis than the rest of the body.

Body rotation precedes deflection of heading angle in mice

Jindrich and Full (1999) describe the angle of deflection as the difference between the direction in which the center of mass is traveling at a given instant and its original direction. This deflection in heading must be created by ground forces that are perpendicular to the original direction. These ground forces could be generated by an animal facing the original direction applying medio-lateral forces, or by an animal that has already rotated to face the new direction applying forces parallel to its body axis. In cockroaches, where rotation of the fore-aft axis lags an average of 5° behind the angle of heading (Jindrich and Full, 1999), medio-lateral ground forces are applied to change heading. In mice, however, rotation of the body axis led the angle of heading by an average of 3.2° (Table 2). Rotating the body before deflecting the heading of their center of mass would allow mice to use forces applied parallel to their body axis to change their heading. This difference makes sense given the differences in limb configuration and running gait between mice and cockroaches. The parasagittal limb posture and bilaterally symmetrical gait of bounding mice yields reduced leverage for lateral force production. In contrast, the sprawled posture and alternating tripod gait of cockroaches is much more conducive to generating lateral force. Compared to the changes in heading seen in mice (Fig. 4A), the changes in heading observed by Jindrich and Full in cockroaches were much more abrupt (1999). In fact, Jindrich and Full (1999) mention that the lateral force impulses applied by a cockroach during straight-ahead running are sufficient to generate the perpendicular forces observed in turning. The fact that mice rotate into the new turn direction earlier in the turn also makes sense, in that mice may be using distant visual cues to a greater extent to enable them to maneuver through the terrain.

Conclusions

Both overall agility and ideal kinematics for a running turn are highly dependent on the body form and gait parameters of the subject organism. Mice in trotting postures have higher rotational inertia about their turning axis than a similarly massed human would have. Further, the fluctuations in rotational inertia over their bounding stride cycle are likely to be much greater than those seen in running humans or cockroaches. Given this, it makes sense that body rotation in mice is more phasic, and synchronized to a greater degree with a particular phase of the stride cycle. Mice also differ from cockroaches and humans in their relative abilities and mechanical advantages in producing vertical, horizontal and lateral forces. Whereas cockroaches, with their sprawled posture, generate sufficient lateral forces in straight-ahead running to deflect the heading of their center of mass during turns (Jindrich and Full, 1999), the parasagittal limb posture of mice yields less lateral force production. Thus it makes sense

that mice tend to rotate before deflecting their heading, allowing them to use forces applied parallel to the body axes to accelerate in the new direction. Finally, the crouched posture of mice compared to humans increases their mechanical advantage in horizontal force production. This may explain why mice are able to maintain a relatively higher speed while running along a curved path than can humans.

List of symbols

g	gravitational constant
I	rotational inertia
M	body mass
r	moment arm of muscle
R	moment arm of ground reaction force
R_{hor}	horizontal moment arm
R_{vert}	vertical moment arm
r	rotational axis
V_x	velocity in x direction
V_y	velocity in y direction
v_0	maximum speed on a straight trajectory
ν	turn speed
ν_r	ν/v_0
x	instantaneous position of center of mass along x -axis
y	instantaneous position of center of mass along y -axis
∞	angular acceleration
τ	torque
g	gravitational constant

I would like to thank David Carrier for his support throughout this study and for his comments on this manuscript. I thank Dennis Bramble, Stephen Deban and David Lee for technical assistance. I thank Patrick Willems and Norman Heglund for helpful comments and use of their computers, and Linda Morrison for help in obtaining and working with mice. Two anonymous reviewers also provided helpful comments.

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