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Arboreal locomotion in rats – the challenge of maintaining stability

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SUMMARY

Arboreal locomotion has mainly been looked at to date in the context of investigations into the specialization of primates and other ‘arboreally adapted’ animals. The feat of moving on branches as small or smaller than the body’s diameter was tested in rats (*Rattus norvegicus*) as they moved on horizontal poles of different diameters. The data were compared with data pertaining to terrestrial locomotion. We investigated three-dimensional kinematics and dynamics using biplanar cineradiography with simultaneous substrate reaction force (SRF) measurements. As predicted, rats flexed fore- and hindlimbs and reduced vertical forces during pole locomotion. In addition, the orientation of the mediolateral substrate reaction force resultant (SRR) and impulses switched from lateral to medial. In order to maintain stability during arboreal locomotion, lateral spine movements increased. We propose that the combination of lateral sequence gaits, similar travel speed of the animals and similar contact times, higher or similar peak vertical forces as well as similar mediolateral impulses in forelimbs and hindlimbs are typical of clawed mammals moving on thin supports. Clawed mammals and primates share the reduction of vertical oscillations and side-to-side fluctuations, a crouched posture as well as the increase in lateral spine movements. We conclude that these features are behavioral adaptations caused by the biomechanical constraints of small branch locomotion, regardless of the way they make contact with the substrate.

Key words: arboreal, terrestrial, rat, substrate reaction force, three-dimensional kinematics, X-ray imaging.

INTRODUCTION

The basic challenge that arboreal habitats pose for the locomotor apparatus is how to prevent the animal from falling down during locomotion. Specifically, the diameter of support in relation to the animal’s body width constrains locomotor performance (Jenkins, 1974; Witte et al., 2002). Most of the studies focusing on the locomotion of arboreal mammals to date have been restricted to those animals that possess prehensile extremities (e.g. Schmitt, 1994; Schmitt and Lemelin, 2002; Schmitt, 2003c; Schmitt and Hanna, 2004; Carlson et al., 2005; Franz et al., 2005; Demes and Carlson, 2009). Prehensile extremities enable animals to generate torques around the substrate to avoid falling down by counteracting and reducing mediolateral (m-l) forces (Preuschoft, 2002). Clawed mammals, however, whose grasping abilities are either absent or reduced, are less capable of generating torques to stabilize their body against unsteadying mediolateral forces (Schmitt, 2003a; Lammers and Biknevicius, 2004).

As a consequence, the strategies for stabilization during arboreal quadrupedalism used by clawed mammals can be distinguished from those used by mammals that possess prehensile extremities. To increase stability, the latter display the following strategies during locomotion on small branches: avoidance of vertical oscillations and side-to-side fluctuations, reduction of velocity and stride frequency, and decrease in the height of proximal pivots to lower the center of mass relative to the substrate surface (Schmitt, 1994; Schmitt and Lemelin, 2002; Schmitt, 2003c; Schmitt and Hanna, 2004; Carlson et al., 2005; Franz et al., 2005; Demes and Carlson, 2009).

Studies on arboreal locomotor performance in mammals without grasping extremities are restricted to the common marmoset (*Callithrix jacchus*) (Schmitt, 2003a) and the gray short-tailed opossum (*Monodelphis domestica*) (Lammers and Biknevicius, 2004). During pole locomotion, the gray short-tailed opossum reduces the velocity and vertical substrate reaction forces it displays on the ground, in the same way as primates have been observed to do. The common marmoset, however, displays peak vertical forces and speeds during pole locomotion that do not differ greatly from those it reaches on the ground. In order to maintain stability during locomotion on small branches, *Monodelphis* exhibits similar m-l forces in both limb pairs. These forces switch from a lateral direction on the ground to a medial direction during pole locomotion. Unfortunately, the distribution of m-l forces in the common marmoset is unknown.

The combination of greater limb protraction and lower peak vertical forces in the forelimbs affords primates a higher range of motion, which has been discussed as a functional adaptation to arboreal habitats (e.g. Demes et al., 1994; Larson et al., 2000; Schmitt, 2003c; Schmidt, 2005; Hanna et al., 2006; Schmidt, 2008; Larson and Stern, 2009). Despite the appearance of greater arm protraction during small branch locomotion, the limbs of primates typically undergo a deep flexion (crouched posture) to lower the center of mass (Schmitt, 1994; Schmitt, 2003c; Franz et al., 2005). Flexed limbs are advantageous as a way of compensating for substrate irregularities. The inward rotation of the upper arm and lower leg allow the distal elements to be positioned underneath the body and thus cause an adduction of the whole extremity during the stance phase (e.g. Schmidt and Fischer, 2000; Schmitt, 2003b). However, the more adduction of the whole extremity increases, the more joint stabilization is required (Witte et al., 2002; Schmitt, 2003b). It seems likely that limb position is greatly influenced by the diameter of support, because hands and feet must be positioned underneath the trunk during locomotion on small branches. Lateral rotations of the thoracic cage and the pelvis are also clearly dependent on the diameter of support (Schmidt and Fischer, 2000; Shapiro et al., 2001; Schmidt, 2005). These authors propose that lateral rotations of the torso play a major role in increasing stride length and discuss it in terms of the evolution of primates. In clawed mammals without grasping abilities, the effects of a decreasing diameter of support on greater limb protraction, limb flexion and lateral rotations of the thoracic cage and the pelvis have never been tested.

The aim of this study is to determine the kinematic and kinetic effects of differences in the diameter of support on the locomotion of a generalized claw-bearing mammal – the rat (*Rattus norvegicus*). By comparing our own results with those of previous studies on clawed mammals and primates we seek to increase the available knowledge of general behavioral adaptations to arboreality, regardless of the way they make contact with the substrate (prehensile extremities *vs* clawed extremities).

In this study, we hypothesize that rats are not able to decrease speed substantially during pole locomotion because of their limited grasping abilities, whereas mammals that possess prehensile extremities are able to reduce velocity and increase stance durations simultaneously; rats should, however, be able to enhance dynamic stability during pole locomotion *via* speed. In order to avoid vertical oscillations and side-to-side fluctuations of the body, we hypothesize that rats adopt a more crouched posture on the poles, associated with a reduction of braking forces and vertical forces. We suppose that mediolateral forces are similar in both limb pairs, switching from medially directed forces on the ground to laterally directed ones on narrow substrates. In addition, we propose that in comparison with braking impulses, medial impulses become the main force component. We also test the hypothesis that as the diameter of support decreases, the more rats flex their limbs, preventing greater limb protraction.

MATERIALS AND METHODS

Animals and experimental protocol

Metric, kinematic and kinetic data were obtained from two adult female rats (*Rattus norvegicus*, Berkenhout 1769) each weighing 315 g. The Committee for Animal Research of the state of Thuringia, Germany, approved animal care and experimental procedures. Animals were motivated to move towards a box placed at the end of each track at their preferred speed. We used one terrestrial trackway and two poles with diameters of 40 and 20 mm. The latter corresponded to 50% of the diameter of the animal's body width. All supports were 200 cm long and covered with cork, which the rats were able to penetrate with their claws. A total of 137 trials at speeds between 0.29 and 1.02 m s^{-1} were observed. To rule out possible speed effects we only analyzed strides (*N*=82) with a similar range of speed on each substrate (Fig. 1; Table 1). Speed ranges from 0.6 to 0.85 m s^{-1} and averaged about 0.75±0.05 m s^{-1} on each substrate (Table 1).

X-ray motion recordings

Kinematic and metric data were obtained using biplanar X-ray imaging at the Institut für Spezielle Zoologie und Evolutionsbiologie mit Phyletischem Museum, Germany. The experimental setup consisted of the biplanar X-ray system (Neurostar, Siemens, Munich, Bavaria, Germany) and two normal light high-speed cameras (SpeedCam Visario g2, Weinberger, Nuremberg, Bavaria, Germany). Both X-ray sources were positioned at an angle of 45 deg relative to the object of interest. This position reduces distortion by enabling the X-ray amplifier to be positioned as closely as possible to the recorded animal. It also makes it possible to obtain detailed views of bony landmarks of the shoulder blade, which are often difficult to identify from the dorsoventral perspective, especially in a parasagittal position. Cineradiographic images were taken at 1000 Hz. Animals were filmed at 40 kV and 53 mA. Raw video data (vr2) were filtered (gamma correction, contrast, sharpness) and subsequently converted into the conventional audio–video–interleave format (AVI).

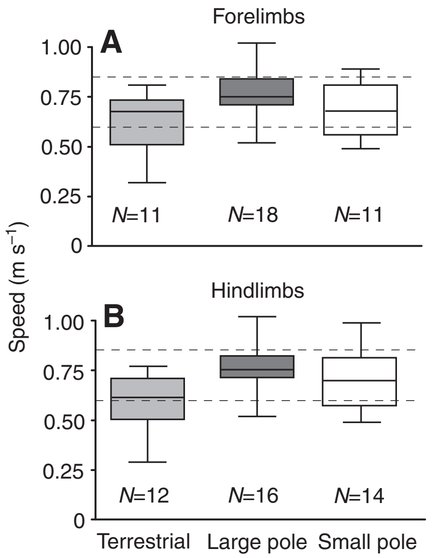

Fig. 1. Box-and-whisker plots showing the range of speed for (A) forelimbs and (B) hindlimbs for all observed trials (137 in total) during locomotion on a terrestrial substrate and two poles of 40 and 20 mm in diameter. Boxes represent 50% of data, the line within the box represents the median and each whisker corresponds to 25% of the data. Dashed lines indicate the range of speed (0.6–0.85 m s^{-1}) used for the data analysis (*N*=82). Note that there is no trial lower than 0.5 m s^{-1} during pole locomotion.

X-ray motion analysis

Motion analysis was performed using SimiMotion 3D that permits three-dimensional (3-D) calibration, the interactive digitization of previously defined bony landmarks and the calculation of joint and element angles. The *x*-axis corresponds to the direction of movement and the *y*-axis to the vertical direction. The *z*-axis was perpendicular to the *x*–*y* plane (mediolateral direction) (Wu and Cavanagh, 1995).

Landmarks used in this study included the proximal pivot of the forelimb, shoulder joint, elbow joint, wrist joint, distal tip of the third manual digit, hip joint (acetabulum), knee joint, ankle joint, metatarsophalangeal joint and the distal tip of the third pedal digit

Table 1. Means ± s.d. of speed, stance duration and duty factor for the forelimb and hindlimb during terrestrial and arboreal locomotion (large and small pole)

	Terrestrial (*N*=23)	Large pole (*N*=34)	Small pole (*N*=25)
Speed (m s^{-1}) – FL	0.72±0.05	0.77±0.04	0.74±0.07
Speed (m s^{-1}) – HL	0.71±0.04	0.77±0.04	0.73±0.06
SD (s) – FL	0.12±0.01	0.12±0.01	0.13±0.02
SD (s) – HL	0.14±0.03	0.12±0.01	0.13±0.02
S (%) – FL	46±3	55±2	61±5
S (%) – HL	50±4	54±3	57±5

FL, forelimb; HL, hindlimb; SD, stance duration; S, duty factor; *N*, the numbers of analyzed strides.

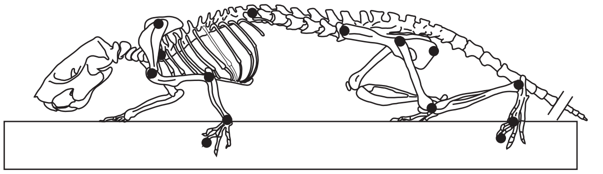

Fig. 2. Digitized skeletal landmarks (black dots) of the forelimbs, the hindlimbs and the pelvis. The proximal pivot of the forelimbs corresponds to the instantaneous center of scapular rotation (proximal end of the scapular spine).

(Fig. 2). The proximal pivot of the forelimb is the instantaneous center of scapular rotation and can be estimated to be the proximal end of the scapular spine (Jenkins and Weijs, 1979; Fischer, 1994). The thoracic cage was determined by connecting the skeletal landmarks of the thoracic vertebrae 1 and 13 that are positioned in the center of each vertebra. The position of the pelvis was determined by connecting two skeletal landmarks on the pelvis – the middle of the crista iliaca and of the tuber ischiadicum (Fig. 2).

Skeletal landmarks were captured interactively in each tenth frame per plane. This corresponds to approximately ten frames during one stance phase. After spline interpolating in SimiMotion 3D between the captured skeletal landmarks in each plane, the single plane coordinates were transformed into 3-D coordinates. In order to verify the accuracy of the 3-D calibration, the calibration object was reconstructed and calculated distances between 3-D coordinates of points on the calibration object were compared (position error of max. 1 mm). Joint angles were defined anatomically with one center of rotation. Element angles were measured in relation to the substrate surface. 3-D joint angles are always the smallest angles between the elements and correspond to the flexor side of the joints investigated. Thus, 3-D joint angles can range between 0 deg and 180 deg. Two-dimensional element angles were calculated using x- and y-coordinates.

Lateral rotations of the thorax and the pelvis during stance phase were quantified by calculating the 2-D angle (x- and z-coordinates) formed by the substrate and the thoracic cage and the pelvis, respectively (Jenkins and Camazine, 1977).

The protraction angles (αPA) at touch-down were calculated by measuring the angle formed by a vertical line through the point of contact and a line connecting the proximal pivot (scapula, hip joint) with the point of contact (Schmidt, 2008).

From the y- and z-coordinates of the wrist and the shoulder joint (forelimb) and the metatarsophalangeal and hip joint (hindlimb) we determined limb abduction and adduction at touch-down, midstance and lift-off. Values below zero indicate an abducted limb and values above zero indicate an adducted limb.

The center of pressure was estimated using the y- and z-coordinates of the wrist joint (hand) and the metatarsophalangeal joint (feet) at touch-down. On the basis of the transverse positions of the hand and feet at contact (z-coordinates), we calculated the base of support (BOS), which is defined as the distance perpendicular to the trajectory of movement between limb pairs (Koopmans et al., 2007). Given that the right and left limbs were placed in a comparable way, the BOS is the sum of the distance between the center of pressure and the centroid of the substrate (pole locomotion). During terrestrial locomotion the BOS was estimated following the method proposed by Koopmans et al. (Koopmans et al., 2007).

Stance duration (SD) and duty factor (S) (Hildebrand, 1966) were also measured and calculated. A gait is classified as a walk if S is not less than 50% of the whole step cycle and as a trot if it is less than 50%. To determine the animal's average velocity, the diaphragm was digitized and plotted against time. To appreciate the variation entailed by the subjective identification of landmarks at touch-down and lift-off events, one randomly chosen sequence was independently digitized ten times. The mean digitizing error for joint and element angles was 0.9 deg. The maximum digitizing error was 1.4 deg for the calculation of the metatarsophalangeal joint. The variation in the identification of the exact touch-down and lift-off event was 10 frames (=0.01 s).

Force data acquisition

Three-dimensional substrate reaction forces (comprising an anteroposterior, mediolateral and vertical component) were measured using a force-sensitive region integrated into the middle of the pole (in this case it was 55 mm in length) or the trackway (120 mm×150 mm in size). The force-sensitive element was attached to the surface of one Kistler® force plate and separated from non-instrumented segments by 2 mm gaps. Substrate reaction forces (SRFs) were collected at 500 Hz. Analog force data were amplified (8-Channel Charge Amplifier, Type 9865, Kistler, Winterthur, Zurich, Switzerland), converted into a digital format (NI USB-6229, National Instruments, Austin, TX, USA), and recorded with LabView 8.2 (National Instruments). All data were imported and filtered in Microsoft Excel using a binomial curve fit algorithm (similar to a low-pass filter) with a window of 15 at a sampling rate of 500 Hz. In this way an average mean is taken over 0.03 s and replaces each data point. Finally, the resulting substrate reaction forces (SRFs) were calculated and normalized to the animal's body weight (BW). Kinetic data included peak vertical, braking, propulsive and mediolateral (m-l) forces and associated impulses ($BW\,s^{-1}$). The values representing m-l force directions were positive for medially and negative for laterally directed forces, regardless of which limbs generated them. SRF recordings were synchronized with cineradiographic recordings *via* a post-trigger. Only runs in which the hands and feet were placed completely on the force-sensitive element were used in the analysis.

Impulse angles in the transverse plane during ground and pole locomotion were determined at midstance (Lee et al., 2004; Demes and Carlson, 2009) and corrected to the animal's anatomical plane. Discrepancy angles were estimated following the method of Demes and Carlson (Demes and Carlson, 2009). Positive discrepancy angles characterize impulse angles directed laterally (transversal plane) to the limb.

Statistical analysis

Statistical analyses were performed using SPSS 18.0 for Macintosh. The significance level was $P<0.05$. Two-way mixed-model ANOVAs (individual, substrate, and/or limb as factors) were performed to examine the effects of different substrate diameters. The Bonferroni *post-hoc* test was used to compare substrates (terrestrial *vs* small pole, terrestrial *vs* large pole, large pole *vs* small pole).

RESULTS

Locomotor mode

Mean velocity varied between 0.29 and 1.02 $m\,s^{-1}$ across different substrates. Maximum running speed was observed on the poles (up to 1.02 $m\,s^{-1}$), minimum velocity during terrestrial locomotion (0.29 $m\,s^{-1}$). Minimum velocity during pole locomotion was 0.5 $m\,s^{-1}$. In the following, only trials at speeds between 0.6 and 0.85 $m\,s^{-1}$ were analyzed in order to avoid differences between the

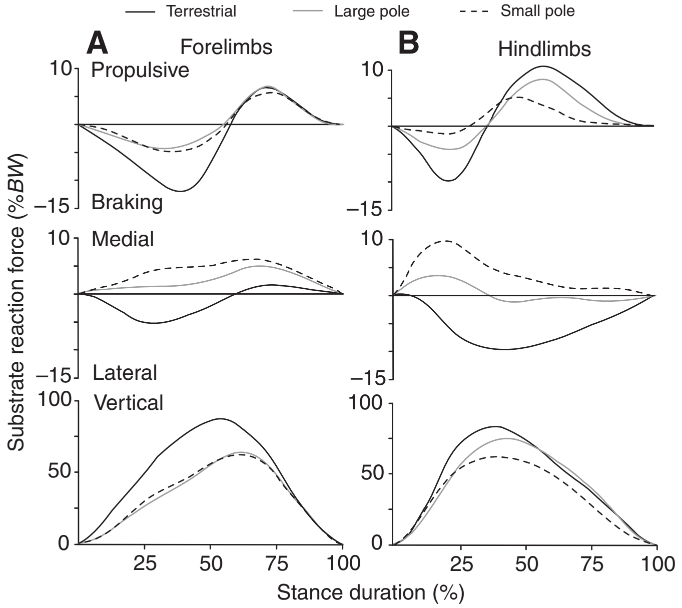

Fig. 3. Mean values of 3-D substrate reaction forces of the (A) fore- and (B) hindlimbs during stance phase.

substrates solely caused by speed (*N*=82; Fig. 1). Mean velocities, stance durations and duty factors are listed in Table 1. The rats used a trotting gait (S<50%) or a very fast walk (S=50%) during terrestrial locomotion (Table 1). During pole locomotion rats preferred exclusively a walking gait (S>50%). During terrestrial locomotion hindlimb (HL) contact times was longer than those of the forelimbs (FL; FL/HL=0.85), whereas the stance durations of the two limb pairs were similar during pole locomotion (large pole FL/HL=0.98; small pole FL/HL=0.96).

Substrate reaction forces

Fig. 3 shows the substrate reaction force profiles of the forelimbs and hindlimbs on each substrate. Results of the statistical analysis on SRFs are listed in Table 2. Anteroposterior forces are characterized by a decelerating impulse followed by a propulsive phase (Fig. 3). In both forelimbs and hindlimbs, rats displayed higher peak braking forces during ground locomotion than on the two poles. Propulsive forces in the forelimbs occurred in the last third of the stance phase whereas propulsive forces in the hindlimbs occurred earlier. Peak propulsive forces of both limb pairs were not affected by the diameter of support (Table 2). In contrast to the forelimbs, propulsive impulses in the hindlimbs were reduced during locomotion on the small pole.

The m-l forces were highly variable. During ground locomotion, m-l forces in the forelimbs were characterized by a lateral impulse followed by a smaller medial impulse (Fig. 3). The shift between the two components occurred at approximately 60% of stance phase and thus shortly after the anteroposterior forces cross the zero line. In the hindlimbs, however, lateral impulses dominated and no medial impulse could be detected (Fig. 3). Peak lateral forces of the hindlimbs during ground locomotion reached absolute mean values that were similar to peak medial forces during locomotion on the small pole (Fig. 3). Our results show a clear pattern correlated to the differences in the diameter of the support (Fig. 3; Table 2). Firstly, lateral impulses were reduced (relative to the ground) in the forelimbs while medial impulses become the main force component. Secondly, forces in the hindlimbs were mostly medially directed on the ground and laterally directed during pole locomotion. Thirdly, on the small pole, medial impulses were greater than the braking impulses in forelimbs and hindlimbs (Fig. 3).

Peak vertical forces are the maximum forces acting on the body, and range from 66% (small pole) to 88% (ground) of the animal's body weight (Fig. 3). Pairwise comparisons between forelimbs and hindlimbs revealed that peak vertical forces did not differ during locomotion on the ground and the small pole (ANOVA; *P*>0.05), whereas during locomotion on the large pole the hindlimbs generated higher peak vertical forces than the forelimbs (ANOVA; *P*<0.01).

Our results show that the calculated dynamic parameters were affected by substrate diameter in different ways (Table 2). Braking forces, for example, were not reduced across all substrates (*F*=13.2; significant if *F*≥19.0), but three significant differences in pairwise comparisons were found (Bonferroni *post-hoc* test), which show at least a trend towards a reduction of these forces. Peak lateral forces, however, were almost completely reduced on the poles (*F*=40.9*) whereas there was no significant difference between the two poles (*P*>0.05).

Kinematics

Lateral rotations of the thoracic cage and the pelvis

Owing to the effects of the diameter of support on the positions of forelimbs and hindlimbs at touch-down and lift-off, lateral rotation

Table 2. Results of ANOVAs performed on three-dimensional substrate reaction forces and impulses

	Forelimbs				Hindlimbs			
		P-values				*F*-values		
Variable	*F*-values	t *vs* l	t *vs* s	l *vs* s	*P*-values	t *vs* l	t *vs* s	l *vs* s
Peak vertical force	7.4	<0.001	<0.001	n.s.	1.8	n.s.	<0.001	<0.05
Peak braking force	5.6	<0.001	<0.001	n.s.	13.2	<0.001	<0.001	<0.05
Peak propulsive force	0.3	n.s.	n.s.	n.s.	0.4	n.s.	n.s.	n.s.
Peak medial force	1.5	<0.01	<0.001	<0.05	8.1	<0.05	<0.001	<0.001
Peak lateral force	7.4	<0.001	<0.001	n.s.	40.9*	<0.001	<0.001	n.s.
Vertical impulse	7.5	<0.001	<0.001	n.s.	31.1*	n.s.	<0.01	<0.05
Braking impulse	5.8	<0.001	<0.001	n.s.	7.4	<0.01	<0.001	n.s.
Propulsive impulse	0.3	n.s.	n.s.	n.s.	0.4	n.s.	<0.05	n.s.
Medial impulse	8.4	<0.01	<0.001	<0.05	27.6*	<0.05	<0.001	<0.001
Lateral impulse	5.8	<0.05	<0.01	n.s.	61.2*	<0.001	<0.001	n.s.

For the ANOVAs (*F*-values) the degrees of freedom (denominator and numerator) are 2.
Bonferroni *post-hoc* tests (*P*-values) were used to compare the substrates (t, terrestrial; l, large pole; s, small pole).
**P*<0.05.

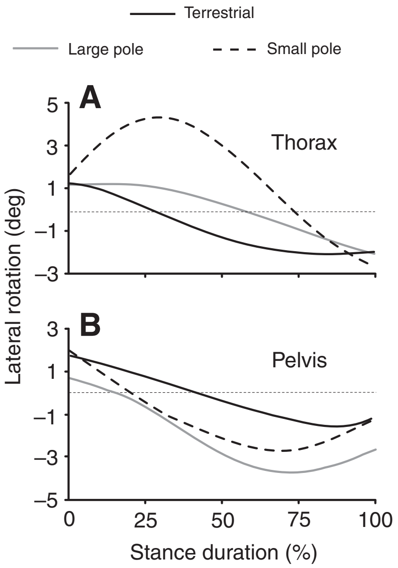

Fig. 4. Changes in the angle of lateral rotation of (A) the thoracic cage and (B) the pelvis during the stance phase on different substrates. Curves represent mean values and are related to the base of support (see text for details). Note the extent of lateral rotation in the thoracic cage in the first third of the stance phase during locomotion on the small pole and in the pelvis in the last third on both poles.

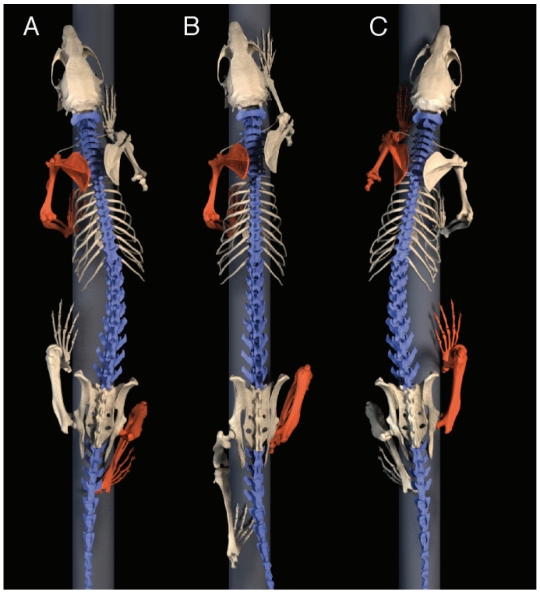

Fig. 5. Illustration of a rat walking on a pole of 20 mm in diameter at a speed of 0.6 m s^{-1} from a dorsal perspective. (A) Maximum lateral rotation of the thoracic cage and pelvis shortly after touch-down of the right forelimb and shortly before lift-off of the right hindlimb. (B) The vertebral column is nearly parallel to the direction of movement at midstance of the left forelimb and right hindlimb. (C) Maximum lateral rotation of the thoracic cage and pelvis shortly after touch-down of the left forelimb and shortly before lift-off of the left hindlimb.

of the thoracic cage and the pelvis was calculated in relation to the base of support (BOS). The timing and amplitude of the lateral rotations of the thoracic cage and the pelvis were linked to differences in the diameter of support (Fig. 4). During locomotion on the terrestrial substrate and the large pole, the thoracic cage was positioned nearly parallel to the direction of movement during the complete stance phase. By contrast, during locomotion on the small pole a lateral rotation of the thorax was observed, with a maximum rotation during the first third of the stance phase (Figs 4, 5). Lateral rotation of the pelvis was not observed during terrestrial locomotion (Fig. 4). During locomotion on both of the poles, however, maximum rotation of the pelvis was achieved during the last third of the stance phase. The thorax and the pelvis thus rotate in opposite directions during the locomotion on the small pole, causing an undulation of the spine (Fig. 5). The movements of the thoracic cage and the pelvis continued during the swing phase of the specific limb, which resulted in different positions of the thorax and the pelvis in relation to the substrate at touch-down and lift-off (Fig. 4).

Overall limb placement and position

Rats placed their forelimbs as close as possible to the top of the branch (Fig. 6). Interestingly, forelimbs and hindlimbs were spaced further from the surface of the small pole than on the large pole (Fig. 3; Table 3). According to this, rats place their limbs in a plantigrade posture on the large pole and in a digitigrade posture during locomotion on the small pole.

The BOS of the forelimbs decreased from 17±4 mm (mean ± s.d.) on the terrestrial substrate to 13±4 mm on the two poles (Table 4). During ground locomotion rats placed their feet in a semiplantigrade posture with a BOS of 34±3 mm. On the poles, however, hind paws were placed in a medially directed plantigrade or digitigrade posture in order to increase substrate contact. The first and second digits of the foot were spread, resulting in intensive contact around the substrate. Consequently, the BOS of the hindlimbs was 24±4 mm on the large pole and 17±4 mm on the small one (Table 4).

With regard to limb abduction and adduction at touch-down and lift-off, we found that in the forelimbs there was a general difference between ground and pole locomotion, with greater adduction seen on the pole regardless of the diameter of support (Fig. 7; Table 4). The hindlimbs, however, were adducted moderately during the complete stance phase on the ground and on the large pole, with much greater adduction observed on the small pole (Fig. 7; Table 4).

In terms of the protraction angle we found a trend towards greater limb protraction on the poles for both fore- and hindlimbs (Fig. 8;

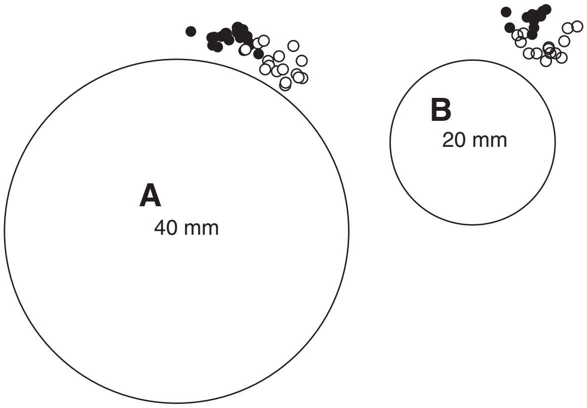

Fig. 6. Anterior view of the touch-down positions of the wrist joint (black circles) and the metatarsophalangeal joint (open circles) of all strides (N=59) relative to the substrate (A, large pole; B, small pole).

Table 3. Results of ANOVAs (*P*-values) comparing *y*- and *z*-coordinates of forelimbs and hindlimbs during locomotion on the large and small pole

	P-values
y-coordinate FL	<0.05
z-coordinate FL	n.s.
y-coordinate HL	<0.05
z-coordinate HL	n.s.

FL, forelimbs; HL, hindlimbs.

Table 4). As the diameter of support decreased the protraction angle of the forelimbs increased by about 29%, from 28 deg on the ground up to 36 deg on the small pole. Hindlimb protraction increased from 30 deg on the ground to 41 deg on the small pole – an increase of about 36%.

Element and joint angles

Rats flexed forelimbs and hindlimbs the more the diameter of support decreased, with the hindlimbs much more affected than the forelimbs (Figs 9, 10). Although greater limb flexion was associated with a decreasing diameter of support, the results were not significant between all substrates (Tables 5, 6). Elements that are in matched motion (scapula–lower arm and femur–metatarsus) were positioned more and more horizontally at touch-down. As the position of the middle elements (upper arm and lower leg) does not change, this results in stronger flexion of the limbs. Consequently, the height of the proximal pivots (scapula, hip joint) decreased, in particular in the hindlimbs (Fig. 9). At lift-off, significant differences were only observed for the upper arm and the metatarsus (Table 5).

Table 4. Results of ANOVAs performed separately on the base of support, protraction angles, limb abduction and adduction, discrepancy angles, and the substrate reaction resultant in the transverse plane

			P-values		
Variable		*F*-values	t *vs* l	t *vs* s	l *vs* s
BOS_{FL}	td	2.1	<0.05	<0.05	n.s.
BOS_{HL}	td	72.5*	<0.001	<0.001	<0.001
αLA_{FL}	td	22.7*	<0.001	<0.01	n.s.
	ms	$3.0^{\dagger}$	n.s.	n.s.	n.s.
	lo	11.2	<0.01	<0.01	n.s.
αLA_{HL}	td	28.3*	n.s.	<0.001	<0.001
	ms	9.3	n.s.	<0.01	<0.001
	lo	3.7	n.s.	<0.001	<0.01
αPA_{FL}	td	10.4	<0.01	<0.001	<0.01
αPA_{HL}	td	16.8	<0.01	<0.001	<0.05
αD_{FL}	ms	14.6	<0.001	<0.01	n.s.
αD_{HL}	ms	61.7*	n.s.	<0.001	<0.001
αIA_{FL}	ms	13.3	<0.01	<0.001	n.s.
αIA_{HL}	ms	34.4*	<0.001	<0.001	n.s.

BOS, base of support; αPA, protraction angles; αLA, limb abduction or adduction; αD, discrepancy angles; αIA, the substrate reaction resultant in the transverse plane; td, touch-down; ms, midstance; lo, lift-off; FL, forelimb; HL, hindlimb.

For the ANOVAs (*F*-values) the degrees of freedom (denominator and numerator) are 2.

Bonferroni *post-hoc* tests (*P*-values) were used to compare the substrates (t, terrestrial; l, large pole; s, small pole).

*$P<0.05$; †Non-significant pairwise comparisons are caused by the high variability.

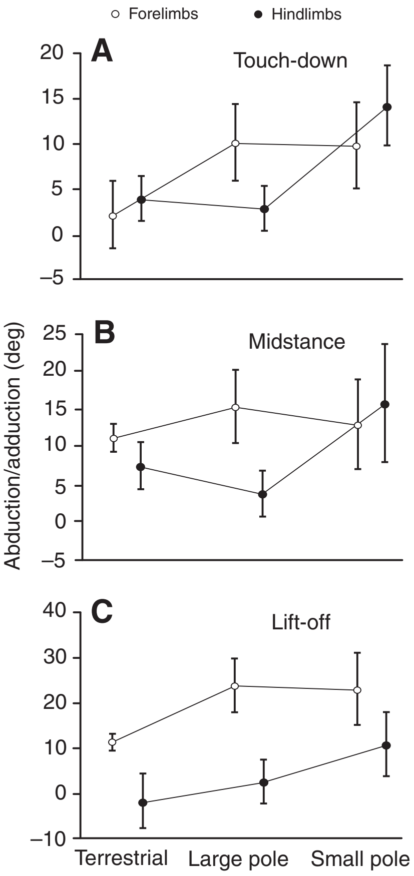

Fig. 7. Mean values (±s.d.) of the angles of abduction and adduction of the forelimbs and hindlimbs for each substrate at (A) touch-down, (B) midstance and (C) lift-off. Values near zero indicate a parasagittal limb position; values higher than zero an adducted, and values below zero an abducted limb position.

With regard to the 3-D joint angles at touch-down, we found significant differences between the substrates for the elbow joint, knee joint and ankle joint whose degree of flexion increased as the diameter of support decreased (Fig. 10; Table 6). But significant differences between the two poles were only observed for proximal joints of the forelimbs (shoulder joint, elbow joint) and hindlimbs (hip joint, knee joint) at touch-down and midstance (Table 6). Contrary to this, the distal joints of the hindlimbs (ankle joint, metatarsophalangeal joint) were affected by the substrate diameter at midstance and lift-off, and partly at touch-down too (Table 6).

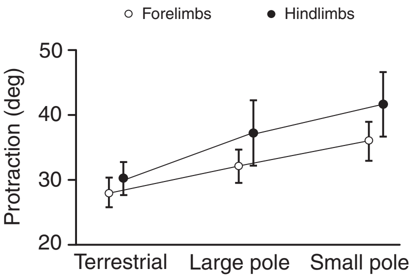

Fig. 8. Mean values (±s.d.) of protraction angles of forelimbs and hindlimbs at touch-down, for each substrate.

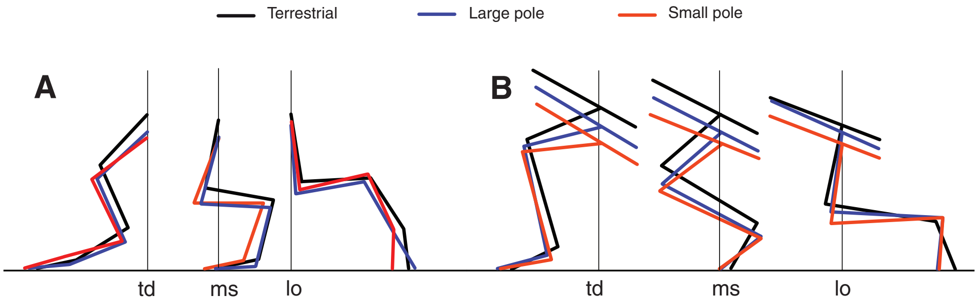

Fig. 9. Mean element angles of (A) forelimbs and (B) hindlimbs at touch-down (td), midstance (ms) and lift-off (lo) for each substrate, illustrated as stick figures considering limb proportions. From proximal to distal the elements represent the scapula, upper arm, lower arm and hand (forelimbs) and the pelvis, femur, lower leg and metatarsus (hindlimbs). Limbs are fixed vertically at the proximal pivots (scapula, hip joint).

Discrepancy angles

Both the forelimbs and the hindlimbs showed negative discrepancy angles during ground and pole locomotion (Fig. 11). The frontal resultant vector (m-l and vertical impulse) thus falls on the medial side of the limb and generated medially concave bending moments. In the forelimbs discrepancy angles differ significantly between the locomotion on the ground and the two poles (Table 4). Discrepancy angles in the hindlimbs do no differ significantly between the ground and the large pole (Table 4). As a result, differences in discrepancy angles between forelimbs and hindlimbs were greatest during locomotion on the large pole (Fig. 11).

DISCUSSION

In this study we investigated the effects of substrate diameter on horizontal locomotion in rats. Our data reveal that the diameter of support has a significant influence on gaits, speeds, kinematics and dynamics. The most profound effects were observed during locomotion on the small pole, which corresponded to 50% of the diameter of the animal's body width. In numerous cases, locomotion on the large pole did not differ greatly from terrestrial locomotion.

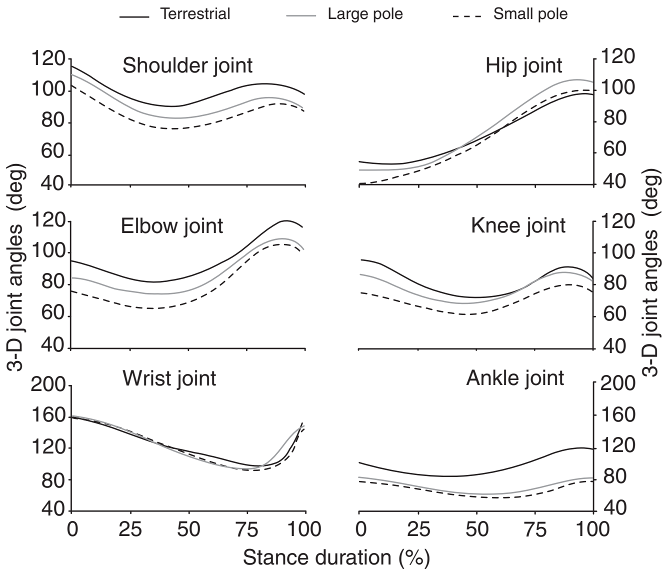

Fig. 10. Mean values of 3-D joint angular excursions during the stance phase of the fore- and hindlimbs during locomotion on different substrates.

Speed and gait adjustments

As expected, rats were not able to traverse both poles at very low speeds (Fig. 1). They used a fast walking gait with a minimum velocity of $0.5\,\mathrm{m\,s^{-1}}$ during the locomotion on the two poles. Although the lateral footfall pattern of this gait is hypothesized to be inappropriate in terms of dynamic stability for arboreal locomotion (Preuschoft, 2002), it enables the animal to increase step length and the lateral rotation of the thoracic cage and the pelvis. The in-phase gaits that normally occur at about $0.8\,\mathrm{m\,s^{-1}}$ (Gillis and Biewener, 2001) might not be feasible on small branches, yet symmetrical gaits increase lateral oscillation and therefore the risk of falling down. From this perspective it is unsurprising, then, that rats walk at a minimum velocity of $0.5\,\mathrm{m\,s^{-1}}$ on both poles. We propose that walking as fast as possible offers a compromise between

Table 5. Results of ANOVAs performed on element angles

			P-values		
Variable		*F*-values	t *vs* l	t *vs* s	l *vs* s
Scapula	td	14.6	<0.05	<0.001	<0.001
	ms	4.3	n.s.	<0.01	n.s.
	lo	2.2	n.s.	n.s.	n.s.
Upper arm	td	0.1	n.s.	n.s.	n.s.
	ms	4.4	<0.01	<0.001	n.s.
	lo	19.7*	<0.01	<0.001	n.s.
Lower arm	td	24.9*	<0.001	<0.001	<0.01
	ms	1.1	n.s.	n.s.	n.s.
	lo	0.9	n.s.	n.s.	n.s.
Hand	td	23.0*	<0.01	n.s.	<0.001
	ms	8.7	<0.001	n.s.	<0.001
	lo	10.9	<0.001	n.s.	<0.001
Pelvis	td	3.2	n.s.	n.s.	n.s.
	ms	2.5	n.s.	n.s.	n.s.
	lo	3.7	<0.05	<0.05	n.s.
Femur	td	89.1*	<0.001	<0.001	<0.001
	ms	0.9	n.s.	n.s.	n.s.
	lo	1.7	n.s.	n.s.	n.s.
Lower leg	td	1.4	n.s.	n.s.	n.s.
	ms	4.2	n.s.	<0.001	<0.05
	lo	18.5	<0.05	<0.001	<0.05
Metatarsus	td	57.8*	<0.001	<0.001	<0.05
	ms	128.2**	<0.001	<0.001	n.s.
	lo	22.7*	<0.001	<0.001	n.s.

Abbreviations: td, touch-down; ms, midstance; lo, lift-off. For the ANOVAs (*F*-values) the degrees of freedom (denominator and numerator) are 2.
**P*<0.05, ***P*<0.01.
Bonferroni *post-hoc* tests (*P*-values) were used to compare the substrates (t, terrestrial; l, large pole; s, small pole).

Table 6. Results of ANOVAs performed on three-dimensional joint angles

			P-values		
Variable		*F*-values	t *vs* l	t *vs* s	l *vs* s
Shoulder	td	13.2	n.s.	<0.001	<0.01
	ms	17.4	<0.01	<0.001	<0.05
	lo	5.2	<0.001	<0.001	n.s.
Elbow	td	26.0*	<0.01	<0.001	<0.05
	ms	37.7*	<0.01	<0.001	<0.001
	lo	5.9	<0.001	<0.001	n.s.
Wrist	td	0.7	n.s.	n.s.	n.s.
	ms	4.2	<0.01	<0.01	n.s.
	lo	1.3	n.s.	n.s.	n.s.
Hip	td	17.2	n.s.	<0.001	<0.001
	ms	4.3	n.s.	<0.05	<0.01
	lo	1.1	n.s.	n.s.	n.s.
Knee	td	24.2*	<0.01	<0.001	<0.001
	ms	10.7	n.s.	<0.01	<0.05
	lo	1.6	n.s.	n.s.	n.s.
Ankle	td	64.5*	<0.001	<0.001	n.s.
	ms	138.1**	<0.001	<0.001	n.s.
	lo	167.6**	<0.001	<0.001	n.s.
Metatarsophalangeal	td	0.7	n.s.	n.s.	n.s.
	ms	100.1**	<0.001	<0.001	n.s.
	lo	42.3*	<0.001	<0.001	n.s.

Abbreviations: td, touch-down; ms, midstance; lo, lift-off. For the ANOVAs (*F*-values) the degrees of freedom (denominator and numerator) are 2.

*$P<0.05$, **$P<0.01$.

Bonferroni *post-hoc* tests (*P*-values) were used to compare the substrates (t, terrestrial, l, large pole, s, small pole).

morphological constraints (e.g. lack of prehensile feet) and the need to remain dynamically stable.

Dynamic consequences

The reduction of peak vertical forces (pVF) is typical of animals moving on narrow branches (Schmitt, 1994; Schmitt and Lemelin, 2002; Schmitt, 2003c; Lammers and Biknevicius, 2004; Schmitt and Hanna, 2004; Franz et al., 2005). Unlike in the case of primates, the ratio between pVF and the contact times of the fore- and hindlimbs were similar on the small pole in rats (Fig. 3). We suppose that the equality of weight distribution between the fore- and hindlimbs during the locomotion on the small pole increases the stability of the body as a whole.

Other mammals without grasping extremities or with reduced grasping extremities, such as the gray short-tailed opossum (*Monodelphis domestica*) and the common marmoset (*Callithrix jacchus*) respectively, carry more weight on their forelimbs (Lammers and Biknevicius, 2004; Schmitt, 2003a). The woolly opossum (*Caluromys philander*) generates higher pVF on its hindlimbs (Schmitt and Lemelin, 2002). Unfortunately, the comparability of these studies is dubious in terms of the diameter of support. These diameters range from 7 mm (*Caluromys*) to more than 20 mm (*Monodelphis*, *Callithrix*). Support diameter influences the gait chosen by the animal, and with it the velocity and ultimately the transmitted pVF (e.g. Schmitt, 1994; Schmitt, 2003c; Stevens, 2003; Schmitt and Hanna, 2004; Franz et al., 2005; Stevens, 2008). Thus, it is possible that the high velocities observed in *Monodelphis* and *Callithrix* were the result of the diameter of the pole (Schmitt, 2003a; Lammers and Biknevicius, 2004) in contrast to *Caluromys* that was able to encompass the 7 mm branches (Schmitt and Lemelin, 2002). It is probable that *Caluromys* is constrained to increase speed above a certain diameter too.

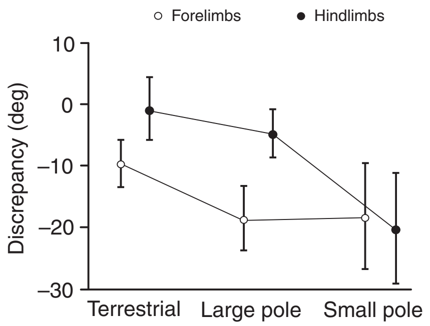

Fig. 11. Mean values (±s.d.) of discrepancy angles at midstance in fore- and hindlimbs for each substrate (see text for details).

As predicted, rats usually reduced braking forces during pole locomotion relative to terrestrial locomotion (Fig. 3; Table 2). The decrease in peak braking forces is a distinctive characteristic of arboreal locomotion and can be attributed to the greater level of limb flexion involved in movement on arboreal supports (Lammers and Biknevicius, 2004). Unlike in the case of *Monodelphis* (Lammers and Biknevicius, 2004), rats exhibit higher velocities during pole locomotion (Fig. 1). In addition to greater limb flexion, rats minimize possible oscillation in the direction of movement by using inside rotations of the forelimbs and hindlimbs at touch-down (Fig. 5). By doing this, peak braking forces and braking impulses are reduced whereas medial impulses are increased (Fig. 3; Table 2). Presumably, mammals lacking prehensile feet place their limbs in the same way.

This assumption is supported by one of the most pronounced results of this study – the shift from medially directed substrate reaction forces on the ground (subject pushed laterally) to laterally directed ones on the pole (Fig. 3). This corresponds to previous studies (Schmitt, 1994; Schmitt, 2003a; Lammers and Biknevicius, 2004; Carlson et al., 2005). Primates experience higher m-l forces during locomotion on flat surfaces as a result of higher velocities and the associated need to avoid slipping. However, their prehensile hands and feet enable them to grasp and thus to generate torques around the arboreal substrate (Preuschoft, 2002). Lemurids, for example, center their foot on the pole so that their hallux and opposing digits fall on the opposite side (Carlson et al., 2005). This position allows them to apply medially or laterally directed forces. Contrary to this, lemurids placed their hands as close as possible on the top and side of the branch as observed in rats (see below). By doing this, they generate medial forces applied more consistently in one direction (Carlson et al., 2005). Therefore, reduced m-l forces are probably linked to the minimization of side-to-side fluctuations of the center of mass (CoM) over arboreal substrates (Carlson et al., 2005). The magnitude of the transverse SRF in the spider monkey and the baboon, for instance, decreased by up to 30% on arboreal substrates. In order to compensate for their lack of grasping ability, rats rely on fore- and hindlimbs with equal functionality during locomotion on the small pole (e.g. similar stance durations and transmitted forces). In addition, contralateral limbs (e.g. the left forelimb and right hindlimb) exert m-l forces in opposite directions and 'grip' the arboreal substrate in the way observed in *Monodelphis* (Lammers and Biknevicius, 2004). Consequently, medial impulses were found to be greater than braking impulses during walking on the small pole in forelimbs and hindlimbs (Fig. 3).

Effects of substrate diameter on kinematics

During locomotion on both poles rats placed their forelimbs as close as possible on the top and side of the branch (Fig. 6). This position allowed them to generate the medially directed pressure that is necessary to avoid slipping. Observations, still images and drawings from previous studies support the assumption that this strategy is not restricted to mammals lacking grasping extremities [p. 271 in Carlson et al. (Carlson et al., 2005); p. 444 in Schmitt (Schmitt, 1994); p. 254 in Schmidt (Schmidt, 2000); p. 4326 in Lammers and Biknevicius (Lammers and Biknevicius, 2004); p. 6 in Schmidt (Schmidt, 2005)]. The hindlimbs, however, are positioned in a medial direction and towards the sides rather than the top of the branch (Fig. 6). The advantages of this are threefold. Firstly, pad contact (especially of the tarsal pads) is increased. During ground locomotion rats place their feet in a semiplantigrade posture. The interdigital pads have substrate contact in the early stance phase (Clarke, 1992). On the poles, a substrate contact starts at touch-down and ends in the late stance phase. Increasing the area of contact results in a stabilized foothold on small substrates. Secondly, placing their hind paws in a medial direction enables rats to 'grasp' branches despite their morphological constraints on the foot by spreading their first and second digits. As a result the area of foot contact increases during pole locomotion. Thirdly, the stable limb position allows the hindlimbs to generate similar m-l impulses to the forelimbs. Furthermore, we observed a more digitigrade touch-down position of both forelimbs and hindlimbs on the small pole (Fig. 6). It might be that this is due to less space being available on the smaller substrate compared to the large pole.

Placing the limb underneath the body results in an adducted limb position that means that the shoulder joint and hip joint come to lie laterally to the distal joints, which have contact with the substrate (Figs 5, 7). In order to minimize the torques that tend to topple the animal over the poles, rats adopt a crouched posture and lower the CoM relative to the locomotor surface (Fig. 9). This is typical for animals moving on substrates with a diameter equal to or smaller than the animal's body width (Schmitt, 1994; Schmitt and Lemelin, 2002; Schmitt, 2003a; Schmitt, 2003c; Stevens, 2003; Lammers and Biknevicius, 2004; Schmitt and Hanna, 2004; Carlson et al., 2005; Franz et al., 2005; Stevens, 2008; Demes and Carlson, 2009).

Because the highly adducted limb position adopted on arboreal substrates increases instability during pole locomotion, rats utilize complex lateral spine movements to counteract this (Figs 4, 5). During locomotion on the large and small poles an inward rotation of the forelimb takes place shortly before touch-down until midstance, allowing the shoulder joint and the CoM to follow the line of travel (Fig. 5). Just before midstance and at the beginning of the stance phase of the contralateral forelimb, forelimb adduction reaches its maximum. This was observed in the hindlimbs during locomotion on the small pole only, possibly as a result of differences in hindlimb placement caused by the BOS. The significance of these limb excursions reflects the need to reduce side-to-side fluctuations. High degrees of limb adduction also reduce the propulsive function of the limb because the more that adduction of the whole extremity increases, the more joint stabilization is required (Witte et al., 2002; Schmitt, 2003b; Fischer et al., 2009). This is reflected in the calculated discrepancy angles. The latter decrease the more the substrate diameter decreases. Impulse angles are thus vertically orientated during the stance phase, despite highly adducted limbs. Consequently, the necessity of joint stabilization in the transverse plane increased during the locomotion on the poles. Furthermore, the results indicate that lateral flexion of the spine permits foot placement in a relatively stable limb position (Fig. 5). Without this lateral flexion it would be impossible to place the hind foot underneath the body and thus underneath the center of mass due, presumably, to the anatomical constraints (e.g. degrees of freedom) of the elbow and knee joints as well as limb proportions in relation to body size. The lateral flexion of the vertebral column is thus induced by substrate size and limb proportions (see Shapiro et al., 2001), and as a consequence is not restricted to primates with prehensile feet. Complex lateral spine movements during pole locomotion have also been suggested as a possible way of increasing limb stride length (Pridmore, 1992; Ritter, 1992; Shapiro et al., 2001; Schmidt, 2005).

The influence of different substrates on limb protraction in mammals has never been tested. Our results show that rats place their lower arm in a much more horizontal position during pole locomotion than on terrestrial supports (Fig. 9). The average protraction angle is 28 deg when walking on flat surfaces, which ties in with previous data (Schmidt, 2008) (33 deg). During locomotion on the small pole, limb protraction increased by about 30% relative to terrestrial locomotion (Fig. 8). It is probable that the large intervertebral movements of the lumbar spine, which result in lateral rotations of the thoracic cage and the pelvis, contribute to the greater protraction angles in rats. This is supported by the fact that greater limb protraction enables the rats to retain stride length during pole locomotion with simultaneous much more flexed limbs (Fig. 9). By contrast, lower protraction angles during terrestrial locomotion are related to higher positions of the proximal pivots of the limbs (Fig. 9). In primates, the greater degree of forelimb excursion during arboreal locomotion is proposed as a way of preventing limb interference (Larney and Larson, 2004; Schmidt, 2008; Wallace and Demes, 2008). Unfortunately, the effects of small branches on fore- and hindlimb protraction in primates are unknown because protraction angles have only been investigated in the upper arm (Schmitt, 2003c). The lower arms of primates are relatively much longer than those of other mammals (Schmidt, 2008), and assuming that these are placed more horizontally during small branch locomotion than on the ground, it seems likely that forelimb protraction also increases on small substrates in primates. However, greater forelimb protraction in primates could also be an 'artefact' of the complex spine movement observed on narrow branches. Greater protraction angles in the forelimbs than observed in the present study increase the risk of instability (Franz et al., 2005; Fischer and Blickhan, 2006; Hackert et al., 2006) because forelimb protraction positions the forelimb away from the CoM at touch-down. This risk is especially acute in rats that do not have the ability to grasp when moving on thin perches. Moreover, greater forelimb protraction angles would also lead to a lateral shift of the thoracic cage and inevitably to a disadvantageous position of the CoM (Fig. 5). However, large hindlimb protraction angles (as observed) position the limb closer to the center of mass. The CoM is held above the poles to avoid lateral oscillation. This theory is supported by our observations of rats moving on branches smaller than 20 mm in diameter. The animals become increasingly unstable, are unable to walk at a constant speed and actuate against gravitational forces to avoid falling down.

In summary, the comparison of the locomotion of rats on the ground and on branchlike, horizontal supports reveals that on narrow substrates, strategies are used which increase stability. These include a lateral sequence gait, similar travel speed of the animals and similar contact times, mediolateral impulses, and higher or similar peak vertical forces in the forelimbs and the hindlimbs. Our findings tie in with the results of previous studies on clawed mammals. We conclude that a reduction of vertical oscillations and side-to-side fluctuations, a crouched posture and an increase in lateral flexion of the vertebral column are behavioral adaptations caused by comparable biomechanical constraints during small branch locomotion, regardless of the way they make contact with the substrate.

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