# Cutting corners: the dynamics of turning behaviors in two primate species

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## Summary

In an attempt to characterize more fully the variation in substrate reaction forces in the locomotor repertoire of primates, we recorded the forces involved in directional changes for two species. These are the first records of turning forces for vertebrate quadrupeds, much less primates. Three ring-tailed lemurs and two patas monkeys performed turns of approximately 30° as they crossed a force platform. The ring-tailed lemurs also turned on a horizontal branch-like support with a segment attached to the force transducer. Mediolateral forces of up to 40% body weight were recorded. These are considerably higher than during linear locomotion. Pivot limbs in ground turns and turns on the branch differed in the lemurs, suggesting that substrate influences turning strategies. Limbs encountered both medial and lateral reaction forces, and as a result, they may be exposed to variable bending regimes in the frontal plane. The stereotypy in bending regimes suggested by *in vivo* bone strain studies, therefore, may characterize linear locomotion only. The lemurs showed hindlimb dominance in turns, both in terms of frequency used as well as force magnitude (hindlimb steering). Hindlimb dominance in weight support characterizes both species (and primates in general), but it is more pronounced in the lemurs. In the patas monkeys, forces were more evenly distributed among the two pairs of limbs. The mediolateral turning forces therefore seem to track the amount of weight to be shifted sideways. Overall variance in mediolateral forces was greater in the arboreal and versatile lemurs than in the terrestrial and cursorial patas monkeys.

Key words: substrate reaction force, turning behavior, ring-tailed lemur, *Lemur catta*, patas monkey, *Erythrocebus patas*.

## Introduction

Much has been learned from experimental studies of primate locomotion (for recent reviews, see Larson, 1998; Schmitt, 2003b). However, in a laboratory setting, the focus is often on steady state, linear progression. In their natural habitats, animals accelerate and decelerate, move up and down, use a variety of substrates, and change direction. Great variability certainly characterizes primate locomotor repertoires, some more than others. Being an arboreal radiation, all primates spend at least some time in trees. Here they are faced with discontinuous substrates that require constant balance and postural adjustments and frequent changes in the direction of travel. Gait mechanics in the 'real world', therefore, almost certainly different from that typically studied in a gait laboratory.

We explore one particular aspect of natural variation in locomotor repertoires: the dynamics of directional changes. We recorded substrate reaction forces (SRFs) experienced during turning on both flat surfaces and branch-like, horizontal supports. Two species of primates were studied in this project: ring-tailed lemurs and patas monkeys. The ring-tailed lemur *Lemur catta* is a strepsirrhine species with a locomotor repertoire that includes arboreal as well as terrestrial quadrupedalism, and interspersed bouts of climbing and jumping (Sussman, 1974; Petter et al., 1977). *Erythrocebus patas* is one of the most highly terrestrial of all primate species. Patas monkeys live in open grasslands where they move by quadrupedal walking and running, though they are known to utilize trees for sleeping (Kingdon, 1971; Isbell et al., 1998). They are very fast runners, capable of traveling long distances, and converge on nonprimate cursors in many aspects of their musculoskeletal anatomy (Gebo and Sargis, 1994). Comparing these two animals creates a contrast between species representing highly variable locomotion on a variety of substrates *vs* predominantly terrestrial and less variable progression. In addition, these species differ in limb use as well as limb proportions. Whereas the lemur carries a significantly greater share of its body weight on the hindlimbs (Franz et al., 2005), and also has considerably longer hindlimbs (intermembral index=70: Fleagle, 1999), weight distribution among fore- and hindlimbs is more even in the patas monkey (Polk, 2001; Schmitt and Hanna, 2004), and the two pairs of limbs are more similar in length (intermembral index=92: Fleagle, 1999).

Side-to-side forces are primarily responsible for turning behaviors. These are usually low in linear locomotion of mammals and often ignored (but see Schmitt, 2003a; Carlson et al., 2005). The vertical and fore/aft components of the SRF vector are well documented during linear locomotion on both flat substrate and horizontal poles for both species; including the same animals that we use in the present study of turning forces (Schmitt, 1996; Polk, 2001; Schmitt and Hanna, 2004; Franz et al., 2005). Both species, like mammals in general, propel themselves from the rear, but unlike nonprimate mammals, they also carry more weight on the hindlimbs. However, the difference in vertical forces between forelimbs and hindlimbs in the patas monkey is more subtle during overground locomotion than in the ring-tailed lemur (Schmitt and Hanna, 2004; Franz et al., 2005). It is generally unclear whether primates or mammals exhibit limb dominance in steering; in other words, whether animals use front-limb steering or back-limb steering. Kimura et al. (1979) assumed that '*the forelimb in quadrupedal walking of all mammals plays the role of steering and orienting the body*' (p. 305). Schmitt (1999) also assumed an important role of the primate forelimb in steering, based on the lower peak forces that this limb bears. Li et al. (2004), on the other hand, argued, on the basis of more variable braking and propulsive forces generated by the hindlimbs of chimpanzees, that hindlimb steering is the prevalent condition in chimpanzees. The choice of two species that vary in vertical force distribution between the two pairs of limbs will allow us also to explore whether limb dominance in weight support and propulsion is tied to limb preference in steering.

The only comparative data on forces involved in directional changes are for humans (Andrews et al., 1977; Patla et al., 1991; McClay et al., 1994; Hase and Stein, 1999; Jindrich et al., 2004), cockroaches (Jindrich and Full, 1999) and crayfish (Domenici et al., 1999); i.e. bipeds, hexapods and octopods. The first goal of our study, therefore, was to address the general mechanics of turning behavior in quadrupeds. In so doing, the following specific questions were addressed. (1) What is the magnitude and range of mediolateral forces and, by inference, limb loading in the frontal plane? (2) Is there preferential limb use during steering? (3) In particular, is there a functional differentiation between forelimbs and hindlimbs? (4) Does substrate influence the mechanics of turning? This question will be addressed with data on *L. catta* because of its extensive use of arboreal substrates. (5) Does a more behaviorally versatile species (lemur) differ from a more behaviorally stereotypic species (patas monkey) in turning dynamics?

### *Dynamics of directional changes*

As animals change directions, their velocity vector has to be redirected onto the new path, which requires a force impulse acting perpendicular to the initial direction (Fig. 1A). This can be accomplished by medially directed reaction impulses on the outside limbs or laterally directed reaction impulses on the inside limbs. In addition, a (yaw) rotation around the center of
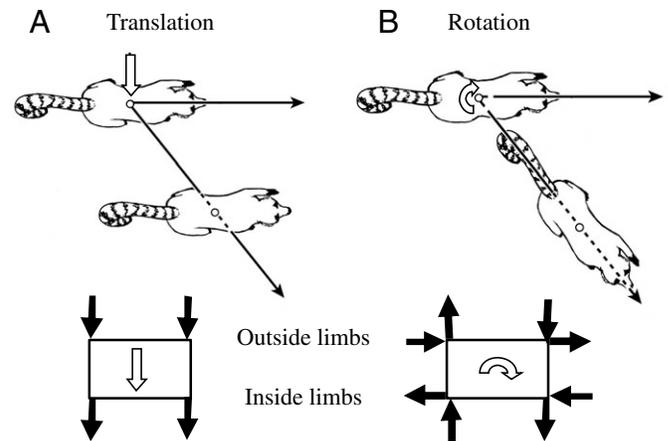


Fig. 1. Dynamics of turning. A turn requires a sideward translation (A) and a rotation that aligns the animal with the new direction of movement (B). The cartoons at the bottom depict the forces that are capable of accomplishing these positional changes. They are mediolateral forces for the translation, and mediolateral and/or fore/aft forces for the rotation.

mass is required that aligns the animal's body axis with the new direction of movement. This calls for a torque that can be generated by transverse reaction impulses, or also by fore/aft impulses when the limbs are not placed under the midline of the body (Fig. 1B). Transverse reaction impulses must be directed towards the outside of the turn at the hindlimbs, or towards the inside of the turn at the forelimbs. Braking impulses at the inside limbs, or propulsive impulses at the outside limbs, can also contribute to the requisite torque (Fig. 1B). Because of a restricted track width during branch locomotion, this latter strategy would be logical only for overground locomotion, where the fore/aft forces act with a lever arm on the center of mass.

Humans adopt two strategies for turning: direction can be opposite to the planting foot, or in the direction of the planting foot (Andrews et al., 1977; Patla et al., 1991; Hase and Stein, 1999). If the contralateral foot (the foot on the outside of the turn) is in contact with the ground at turn initiation, this foot is used to generate the transverse impulse. This strategy is termed sidestep or step turn. If the ispilateral foot (the foot on the inside of the turn) is in contact with the ground, the body spins around this foot (a yaw rotation) and the contralateral foot crosses over for the next contact. This strategy is termed crossover or spin turn. The sidestep turn is considered safer because the projected base of support (a virtual support for the swinging leg that is projected to the ground) is wide (Patla et al., 1991). During a crossover turn, the swing leg is in line with the planted foot as it crosses over, thus creating a narrower projected support. Humans prefer sidestep turns to crossover turns (Patla et al., 1991). It is not immediately obvious whether one strategy offers advantages over the other for four-legged animals that can sidestep or crossover within a pair of limbs. Monkeys perform both crossover or sidestep movements with their forelimbs when initiating turns (Larson and Stern, 2006),

but it is not clear whether they exhibit a preference for either as humans do.

## Materials and methods

Our study included one male and two female *Lemur catta* L. and one male and one female *Erythrocebus patas* Trouessart 1897. The average mass of the nondimorphic ring-tailed lemurs was 3.1 kg (range=3.0–3.3 kg), whereas the male patas monkey weighed 13.7 kg and the female 7.6 kg. All animals were adults. Procedures were approved by the Institutional Animal Care and Use Committee of Stony Brook University.

Forces were recorded using a Kistler 9281B force plate (Kistler Instruments Corp., Amherst, NY, USA). For overground locomotion, animals moved on a plywood runway, with a 0.6 m×0.2 m hardwood cover plate attached to the top of the force plate, making it flush with the runway. Animals traveled through a Lexan tunnel 10.5 m long × 0.7 m wide, with the force plate located in the center. For overground turns, obstacles were placed in the tunnel that forced the animals to turn predictably on the force plate (Fig. 2A). Distance between obstacles was varied to solicit similar turning angles of around 30° for the small female and large male patas monkey, and turning angles of 45° and 20° for *L. catta*. For simulated arboreal locomotion, the ring-tailed lemurs walked on PVC poles with a diameter of 3.2 cm. (The patas monkeys were not used in this part of the study.) A short pole segment was attached to the force platform in line with one of the long segments, but separated by a small longitudinal gap, while the other long segment was offset by a 20 cm longitudinal and 30 cm transverse gap (Fig. 2B). This experimental design required the animals to cross the gap with a turning angle of approximately 30°. The Kistler 5217 summing amplifier algorithms allow correct determination of force components (but not coordinates of the force application point) with an attachment that potentially transmits tensile forces in the vertical direction. This was confirmed by calibrations with known weights applied to the pole attachment.

As the animals navigated around the obstacles or crossed the gap in the branch setup, they made two consecutive turns in opposite directions. Only limb contacts that initiated one of these turns were taken into consideration; e.g. in Fig. 2 a forelimb contact in a right turn or a hindlimb contact in a left turn. For contacts to be considered, the animal's trunk had to be aligned with the runway direction at initial forelimb contact or at hindlimb toe-off, respectively. Limb contacts in the center of the plate were not scored because they were associated with the diagonal passage between the two turns. The single force plate setup allowed us to evaluate contact forces generated by a single limb, rather than all limb contacts in a complete stride. Because a large number of limb contacts and forces were collected, we are confident that average forces are representative of any particular limb. All animals were familiar with the Lexan tunnel from previous experiments and readily moved back and forth for food rewards offered at the ends of the tunnel.
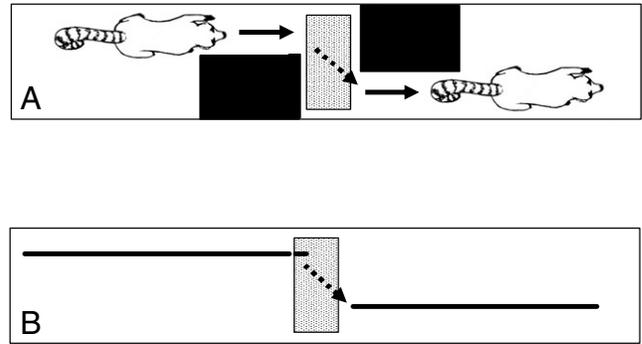


Fig. 2. Experimental setup to record turning forces. Animals either walked on a wooden runway and were forced by two obstacles to turn (A), or they walked on PVC pipes with a gap that forced them to turn (B). The force platform is the rectangle in the center of the runway.

Vertical ($v$), fore/aft (braking/propulsive), and side-to-side (mediolateral; $m$–$l$) components of the substrate reaction force (SRF) were recorded digitally using a SCXI-1000 A-D converter (National Instruments, Austin, TX, USA) whose signals were acquired at a sampling rate of 2700 Hz by LabView version 5.0.1 software (National Instruments) installed on a computer. A virtual instrument written in the LabView software displayed the force traces on a computer monitor that simulated a storage oscilloscope with a 4 s sweep and stored each sweep of data in a computer file. The complete monitor image was D–A converted to a standard video signal and superimposed onto a video image of the subject crossing the force plate, using a special effects generator WJ 45P (Panasonic, Secaucus, NJ, USA). The image overlay of the three force traces and the animal was recorded subsequently onto videotape. This provided us with a tape record that could be used to identify sequences and associated files with limb contacts on the force plate (or pole segment attached to the plate). Force data were taken relative to the coordinate system of the plate with fore/aft forces in the direction of linear progression on the runway. The obstacles or pole arrangements forced the animals to approach the force transducer or come off it moving strictly parallel to the runway's long axis. With the foot or hand planted on the transducer, the force components relative to these distal segments do not change throughout the turn; i.e. measured $m$–$l$ substrate reaction forces are true $m$–$l$ forces acting on these segments. As the trunk gradually changes direction during the turn, rotatory movement at some limb joint(s) must take place.

A side view camera was directed at a 1.5 m long center section of the runway and used to evaluate limb contacts with the force transducer. An overhead camera was used to monitor the movement path and the turning angle, and to ensure that appropriate limb contacts were associated with the initiation of a turn.

Files containing complete and separate or partially separate limb contacts were imported into the software package Igor (WaveMetrics, Lake Oswego, OR, USA) (Note that in the diagonal footfall sequences used by the two primate species,

forelimb and hindlimb contacts often overlap, at small overlap, peak forces may still be extracted.) Subsequently, forces were smoothed using a binomial curve fit algorithm with a window of 400. At a sampling rate of 2700 Hz, this corresponds to a binomially averaged mean that is taken over 0.15 s (400/2700) and replaces each data point. In effect, this eliminated high frequency noise, similar to low-pass filtering. Raw voltage data were transformed into force units using calibration factors derived from the amplifier settings. Forces were transformed into body weight units to facilitate comparisons across animals of varying body mass. Body weight is the force associated with body mass under the influence of the earth's gravitational field. The following variables were quantified and statistically evaluated. (1) Magnitude of peak mediolateral, fore/aft and vertical forces. These were used to evaluate differentiation between force directions in the frontal plane, inside and outside limbs, and fore- and hindlimbs. (2) Frequencies of limbs used to initiate turns. (3) Variances in mediolateral forces to evaluate interspecific differences in force variability.

Limbs in contact with the force transducer were identified on the side view videotape and sorted into limbs on the inside of a turn *vs* the outside of a turn. They were then further differentiated into limbs that push medially (lateral SRF) and limbs that push laterally (medial SRF), using the sign of the force signal in combination with the direction of movement.

Standard descriptive statistics for all variables were calculated using SPSS 11 (SPSS Inc., Chicago, IL, USA).

Statistical comparisons between forelimbs and hindlimbs, inside and outside limbs, and the two force directions (medial and lateral) were conducted for the mediolateral forces. Speed is a potentially confounding factor in gait studies. We tested for correlations with speed using Pearson correlations. Only one *m–l* variable was found to be significantly correlated with speed (the peak mediolateral SRF of the outer forelimb in *E. patas*). We therefore ignored speed when analyzing *m–l* forces and proceeded with the use of analysis of variance (ANOVA) for testing the significance of differences in mediolateral forces. Fore/aft and vertical forces were compared between forelimbs and hindlimbs only. Although they vary with speed, ANOVAs were justified for interlimb comparisons since speeds are highly correlated for the two pairs of limbs. Frequencies of limb use were tested against random distributions using $\chi^2$ tests of independence for 2×2 tables, or row-by-column tests if more than two limb categories were involved (Sokal and Rohlf, 1981). The Levene test statistic was calculated to evaluate heterogeneity in variances of mediolateral forces between species.

## Results

### *Turning forces and limbs used to initiate turns*

Descriptive statistics and magnitude and frequency comparisons for mediolateral peak forces are presented in Table 1. (Impulse data show similar patterns and are not presented here.) Data for the three *L. catta* individuals are

Table 1. *Mediolateral peak substrate reaction forces (in body weight units)*

|  | Inner | | Outer | | | |
|  | Lateral | Medial | Lateral | Medial | ANOVA | $\chi^2$ |
|---|---|---|---|---|---|---|
| **Forelimb** | | | | | | |
| *L. catta* | | | | | | |
| Ground | 0.075±0.025 (4) | –0.088±0.004 (2) | – | –0.278±0.013 (27) | *P<0.05* | *P<0.001* |
| Branch | 0.111±0.017 (2) | – | – | –0.104±0.054 (13) | ns | *P<0.001* |
| *E. patas*, ground | | | | | | |
| Combined sexes | 0.077±0.034 (13) | –0.008 (1) | – | –0.120±0.057 (18) | ns | *P<0.001* |
| Female | 0.056±0.039 (5) | – | – | –0.137±0.055 (13) | ns | *P<0.001* |
| Male | 0.065±0.026 (8) | –0.008 (1) | – | –0.077±0.041 (5) | ns | *P<0.001* |
| **Hindlimb** | | | | | | |
| *L. catta* | | | | | | |
| Ground | 0.151±0.103 (8) | –0.236±0.097 (7) | 0.222 (1) | –0.410±0.184 (46) | *P<0.01* | *P<0.001* |
| Branch | – | –0.252±0.043 (25) | – | – | | *P<0.001* |
| *E. patas*, ground | | | | | | |
| Combined sexes | 0.113±0.025 (17) | –0.108±0.058 (13) | 0.071±0.015 (10) | –0.155±0.064 (9) | ns | ns |
| Female | 0.109±0.033 (6) | –0.166±0.070 (4) | – | –0.221±0.130 (2) | ns | ns |
| Male | 0.114±0.021 (12) | –0.083±0.030 (9) | 0.071±0.015 (10) | –0.136±0.027 (7) | *P<0.01* | ns |

The outer contacts are sidestep turns, the inner contacts crossover turns.

– indicates a limb use never observed.

Values are means ± s.d. (*N*).

ANOVA, *P*-values for comparison of mean peak reaction forces on forelimbs or hindlimbs; $\chi^2$, *P*-values for row-by-column tests of frequency distributions against random distributions; ns, not significant.

combined because we found no significant differences between them in analyses of variances (statistics not presented). Data for the two turning angles in overground locomotion of the lemurs also are combined, making the average angle of 32.5° similar to the 30° angle for the patas monkeys' overground turns. On the ground, the limbs generating the highest forces are the limbs on the outside of the turn, and they exert a laterally directed force; i.e. the medial reaction force translates the animal in the direction of the turn. Turns on the branch by *L. catta* differ from this pattern in that the inner hindlimb is the pivot limb. The medial reaction force on this limb is opposite to the direction of translation, but generates a torque that rotates the animal to face the new direction. The patas monkeys show a more even distribution of forces across limbs, with only the hindlimb force magnitudes of the male significantly different.

Most of the mediolateral forces are in the 'right' direction to provide the requisite impulse for redirecting the velocity vector and/or re-aligning the animals' longitudinal axis with the new direction of movement. However, transverse forces that do not promote translation or rotation in the correct direction were observed on occasion. Forces that had an opposite effect on both rotation and translation were exceptionally rare (i.e. the four instances of low medial reaction forces recorded for the inner forelimb; Table 1). Lateral forces on the outer forelimb that would have a similar effect of opposing both rotation and translation were never observed.

In the large sample of single limb contacts collected here, an approximately even number of fore- and hindlimb contacts and inner and outer limb contacts would be expected if limb placement were random. $\chi^2$ values for row-by-column tests of frequency distributions indicate that limb use frequencies in the lemurs deviate significantly from random distributions (Table 1). Limbs that are used more frequently to initiate a turn are also the ones that generate high turning forces. For the patas monkeys, only forelimb frequencies deviate significantly from random distributions.

The vast majority of ground turns (73 out of 95) in the lemurs are sidestep turns (*sensu* Andrews et al., 1977), with the outside limb being the pivot limb and pushing laterally (medial reaction forces on outside limbs in Table 1). Crossover turns, with the pivot being an inside limb, were rarely observed for the forelimbs, but all 25 hindlimb contacts on the branch were inside limbs in crossover mode. The patas monkeys used sidestep and crossover turns at more similar frequencies during ground turns (female 15 *vs* 15, male 22 *vs* 30: Table 1).

As outlined above, braking and propulsive forces can contribute to the rotation of the body to align it with the new direction. Braking and propulsive forces that rotate the animals opposite to the direction of the turn occur frequently; these are the propulsive forces on the inner limbs and the braking forces on the outer limbs (bold numbers in Table 2). Forelimbs invariably deliver a higher braking than propulsive force and hindlimbs (with one exception) a higher propulsive than

Table 2. *Braking and propulsive peak forces (in body weight units)*

| | Forelimb | | Hindlimb | |
|---|---|---|---|---|
| | Inner | Outer | Inner | Outer |
| *L. catta* | | | | |
| Ground | | | | |
| Braking | –0.325±0.091 (8) | **–0.188±0.088 (19)** | –0.131±0.105 (9) | **–0.218±0.280 (7)** |
| Propulsive | **0.069±0.14 (5)** | 0.062±0.053 (11) | **0.123±0.051 (15)** | 0.472±0.234 (43) |
| *L. catta* | | | | |
| Branch | | | | |
| Braking | –0.077±0.022 (2) | **–0.116±0.063 (12)** | –0.142±0.067 (8) | – |
| Propulsive | – | 0.043±0.036 (6) | **0.160±0.042 (14)** | – |
| *E. patas*, combined sexes | | | | |
| Ground | | | | |
| Braking | –0.207±0.052 (12) | **–0.196±0.114 (18)** | –0.090±0.041 (28) | **–0.082±0.036 (14)** |
| Propulsive | **0.043±0.035 (9)** | 0.081±0.075 (8) | **0.146±0.084 (30)** | 0.108±0.046 (19) |
| *E. patas*, female | | | | |
| Ground | | | | |
| Braking | –0.202±0.077 (3) | **–0.203±0.133 (13)** | –0.087±0.032 (9) | **–0.001 (1)** |
| Propulsive | **0.034±0.030 (3)** | 0.081±0.075 (8) | **0.153±0.121 (9)** | 0.149±0.094 (2) |
| *E. patas*, male | | | | |
| Ground | | | | |
| Braking | –0.208±0.047 (9) | **–0.178±0.041 (5)** | –0.092±0.046 (19) | **–0.088±0.029 (13)** |
| Propulsive | **0.048±0.040 (6)** | – | **0.144±0.067 (21)** | 0.103±0.040 (17) |

Values are means ± s.d. (*N*).
Bold values indicate forces that deliver a rotating impulse opposite to the turn direction.
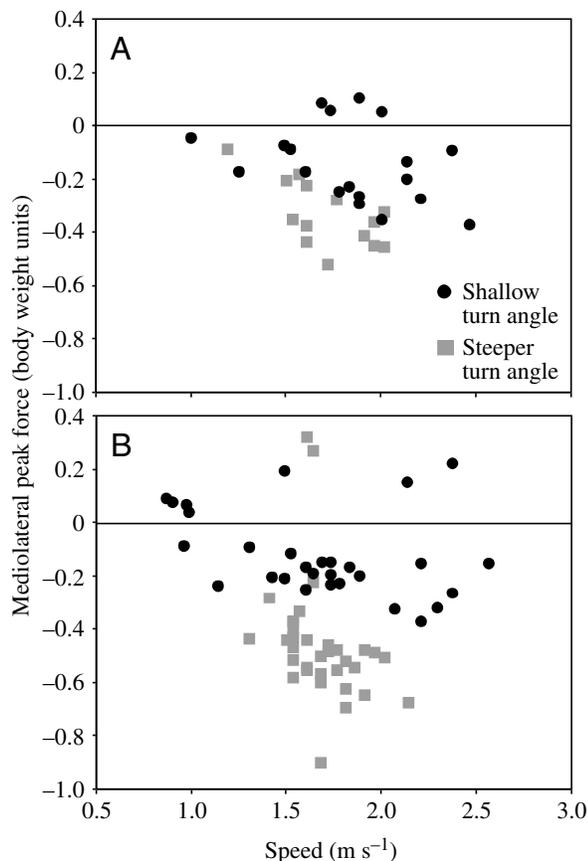
Fig. 3. Mediolateral peak reaction forces (as body weight units) on the forelimbs (A) and hindlimbs (B) of the ring-tailed lemurs performing turns of 20° and 45°. Medially directed reaction forces are negative, laterally directed reaction forces are positive in A and B.

braking force, independent of their placement on the inside or outside of the turn.

For the lemurs using overground locomotion only, data were

collected for two turning angles. The mediolateral forces for shallow (20°) and steeper (45°) turns show the expected pattern of higher forces associated with the greater deflection angle (Fig. 3). The other components of the force vector do not show much differentiation between turns, with the exception of the propulsive force on the outer hindlimb that was higher in the steeper turns (not shown).

### Medially vs laterally directed forces

Table 3 presents the results of statistical comparisons between medially and laterally directed reaction forces. Forces on inside and outside limbs are combined for these comparisons. When differences in force directions are present in the lemurs, the medially directed reaction forces are either significantly higher than laterally directed forces, or the latter were not or rarely observed. For the lemurs, there is a significant preference for pushing laterally in turns (medial reaction forces; Fig. 4). The patas monkeys are more diverse in limb use, with medially directed and laterally directed forces occurring at similar frequencies and similar magnitudes (no significant differences in $\chi^2$ and ANOVA tests; Table 3).

### Inside vs outside limbs

Comparisons of force magnitudes on the inside and outside limbs are shown in Table 4. Absolute values for medial and lateral forces are combined for these comparisons (signs disregarded). Vertical forces are also presented to evaluate whether animals shift weight between limbs as they turn. In the mediolateral forces, outside limbs are more dominant in overground turns of the lemurs. Comparisons for branch turns are limited because of the lemurs' selective limb use. The patas monkeys again show less of a limb use differentiation, while mediolateral forces on inside limbs are often less than on outside limbs, but not significantly so. Vertical forces are not statistically different (i.e. not indicative of a weight shift towards the outside limb, Table 4), but they are more indicative of a forelimb/hindlimb differentiation (see below).

Table 3. *Comparison of medial and lateral peak turn reaction forces*

| | m–l peak force | N (lat/med) | F | P | ANOVA | $\chi^2$ |
|---|---|---|---|---|---|---|
| | | | | | Significance | |
| *L. catta* | | | | | | |
| Ground | FL | 4/29 | 8.2 | 0.007 | med>lat | P<0.001 |
| | HL | 9/53 | 12.9 | 0.001 | med>lat | P<0.001 |
| Branch | FL | 2/13 | 0.0 | 0.879 | ns | P<0.05 |
| | HL | –/25 | – | – | | P<0.001 |
| *E. patas* | | | | | | |
| Female | FL | 5/13 | 2.3 | 0.149 | ns | ns |
| | HL | 6/6 | 4.1 | 0.071 | ns | ns |
| Male | FL | 6/8 | 0.1 | 0.982 | ns | ns |
| | HL | 21/16 | 1.3 | 0.267 | ns | ns |

Inner and outer limb forces were combined for these comparisons. Sample sizes (N) are therefore larger than those in Table 1.
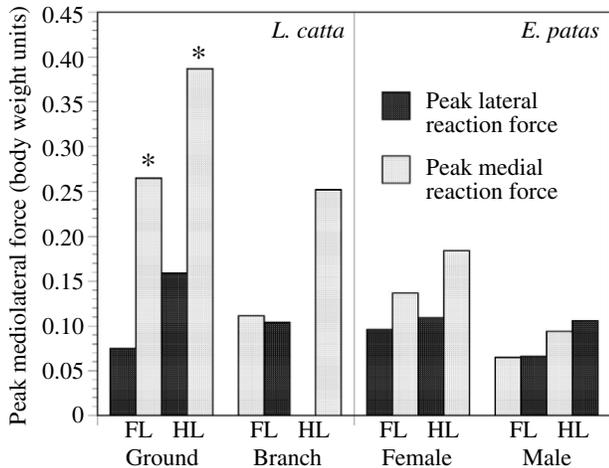*m–l*, mediolateral; FL, forelimb; HL, hindlimb; med, medial; lat, lateral.

Fig. 4. Magnitude of peak average peak medial and lateral reaction forces for *L. catta* (left) and *E. patas* (right). The asterisks indicate significantly higher medial reaction forces for any particular limb. A laterally directed reaction force was never registered for hindlimb contacts of the female patas monkey. FL, forelimb; HL, hindlimb.

### Forelimbs vs hindlimbs

The results of forelimb and hindlimb comparisons are shown in Table 5. For comparative purposes, this table includes all force components. Although vertical and fore/aft forces change with speed, ANOVAs were performed for limb comparisons as speed ranges for forelimb and hindlimb data are similar. The absolute force values for the mediolateral forces are combined, no matter whether they are medially or laterally directed, or associated with inside or outside limbs. Vertical, propulsive and mediolateral forces are significantly higher for the hindlimb in the lemurs, doing turns executed on the ground and on the branch (Fig. 5, Table 5). The braking forces are not significantly different for the two pairs of limbs. In *E. patas*, on the other hand, only the male has significantly higher *m–l* and vertical peak forces on the hindlimb. With the exception of branch turns for the lemurs, propulsive forces are higher for the hindlimb, and braking forces higher for the forelimb.

### Variability in mediolateral forces in patas monkeys vs ring-tailed lemurs

Fig. 6 visualizes variation of the reaction force vectors in the frontal plane. Force vectors in the lemurs predominantly lean medially (negative angles), whereas in the patas monkeys they cluster on both sides of vertical. The ranges in angles are greater in the lemurs. Levene statistics on the homogeneity of variances in the mediolateral force components confirm that the variances are significantly greater at $P<0.001$ in the lemurs (forelimb variance $P=0.026$, hindlimb variance $P=0.049$) than in the patas monkeys (forelimb variance $P=0.012$, hindlimb variance $P=0.015$).

Table 4. *Mediolateral and vertical peak turn reaction forces on inside and outside limbs (in body weight units)*

| | Peak force | | Inside | Outside | Significance ($P<0.05$) |
|---|---|---|---|---|---|
| *L. catta* | | | | | |
| Ground | *m–l* | FL | 0.079±0.020 (6) | 0.278±0.126 (27) | out>in |
| | | HL | 0.191±0.106 (15) | 0.406±0.184 (47) | out>in |
| | *v* | FL | 0.856±0.213 (9) | 0.892±0.148 (27) | ns |
| | | HL | 1.095±0.163 (16) | 1.241±0.201 (48) | out>in |
| Branch | *m–l* | FL | 0.110±0.017 (2) | 0.104±0.054 (13) | ns |
| | | HL | 0.252±0.043 (25) | – | |
| | *v* | FL | 0.517±0.021 (2) | 0.461±0.130 (15) | ns |
| | | HL | 0.921±0.185 (25) | – | |
| *E. patas* | | | | | |
| Female | *m–l* | FL | 0.096±0.039 (5) | 0.137±0.055 (13) | ns |
| | | HL | 0.132±0.056 (10) | 0.221±0.130 (2) | ns |
| | *v* | FL | 0.784±0.456 (5) | 1.234±0.505 (13) | ns |
| | | HL | 1.025±0.324 (10) | 1.531±0.964 (2) | ns |
| Male | *m–l* | FL | 0.059±0.031 (9) | 0.077±0.041 (5) | ns |
| | | HL | 0.099±0.029 (21) | 0.098±0.038 (17) | ns |
| | *v* | FL | 0.574±0.086 (9) | 0.612±0.150 (5) | ns |
| | | HL | 0.856±0.208 (21) | 0.883±0.177 (17) | ns |

Values are means ± s.d. (*N*).
Significant differences reported in the last column are based on ANOVAs; ns, not significant.
Medial and lateral forces were combined for these comparisons. Sample sizes for *m–l* forces are therefore larger than those in Table 1.
*m–l*, mediolateral; *v*, vertical; FL, forelimb; HL, hindlimb.

Table 5. *Comparison of forelimb and hindlimb forces associated with limbs in a turn (in body weight units)*

| | Peak force | Forelimb | Hindlimb | Significance (P<0.05) |
|---|---|---|---|---|
| *L. catta* | | | | |
| Ground | Vertical | 0.883±0.164 (36) | 1.204±0.021 (64) | HL>FL |
| | Braking | −0.228±0.108 (27) | −0.169±0.198 (16) | ns |
| | Propulsive | 0.065±0.084 (16) | 0.381±0.254 (58) | HL>FL |
| | *m–l* | 0.242±0.138 (33) | 0.354±0.192 (62) | HL>FL |
| Branch | Vertical | 0.467±0.124 (17) | 0.921±0.185 (25) | HL>FL |
| | Braking | −0.107±0.059 (14) | −0.142±0.067 (8) | ns |
| | Propulsive | 0.043±0.036 (6) | 0.160±0.042 (14) | HL>FL |
| | *m–l* | 0.105±0.050 (15) | 0.252±0.043 (25) | HL>FL |
| *E. patas*, ground | | | | |
| Female | Vertical | 1.109±0.522 (18) | 1.110±0.458 (12) | ns |
| | Braking | −0.203±0.123 (16) | −0.078±0.041 (10) | FL>HL |
| | Propulsive | 0.068±0.068 (11) | 0.152±0.113 (11) | HL>FL |
| | *m–l* | 0.125±0.053 (18) | 0.147±0.073 (12) | ns |
| Male | Vertical | 0.587±0.109 (14) | 0.868±0.193 (38) | HL>FL |
| | Braking | −0.198±0.046 (14) | −0.090±0.039 (32) | FL>HL |
| | Propulsive | 0.047±0.040 (6) | 0.126±0.059 (38) | HL>FL |
| | *m–l* | 0.065±0.034 (14) | 0.098±0.033 (38) | HL>FL |

Values are means ± s.d. (*N*).
Significant differences reported in the last column are based on ANOVAs; ns, not significant.
Medial and lateral peak forces were combined for these comparisons. Sample sizes are therefore larger than those in Tables 1 and 2.
*m–l*, mediolateral; FL, forelimb; HL, hindlimb.

## Discussion

Our data provide the following answers to questions asked in the introduction.

### *What is the magnitude and range of mediolateral forces and, by inference, limb loading in the frontal plane?*

Turning behaviors in *L. catta* and *E. patas* are associated with relatively high mediolateral forces and impulses. These are appreciably higher than mediolateral forces in linear locomotion for the same animals (Schmitt, 2003a; Carlson et al., 2005). Whereas in linear locomotion average *m–l* peak forces rarely exceed 10% body weight (Table 6), they are routinely above 10% and frequently surpass 20% body weight in turns (Table 1). Limbs experience both medially and laterally directed forces and, consequently, a reaction resultant that is inclined medially or laterally during turns (Fig. 6). Although limb postures have not been quantified in our study, it is likely that this extended range of mediolateral forces is associated with more variable bending moments in the frontal plane relative to linear locomotion.

The importance of the orientation of the substrate reaction resultant in the frontal plane for the loading regime of long bones recently has been demonstrated for *in vivo* bone strain studies. The predominant bending regime in the macaque ulna as well as the goat radius is in the frontal plane (Demes et al., 1998; Main and Biewener, 2004). These studies involved linear locomotion only. The higher mediolateral force components in turning behaviors probably invoke frontal bending moments that are higher than those in linear locomotion.

### *Is there limb dominance in steering?*

The animals in our study tend to adjust their footfalls prior to turning so that they are able to initiate direction changes with preferred limbs. This is particularly obvious in the lemurs that
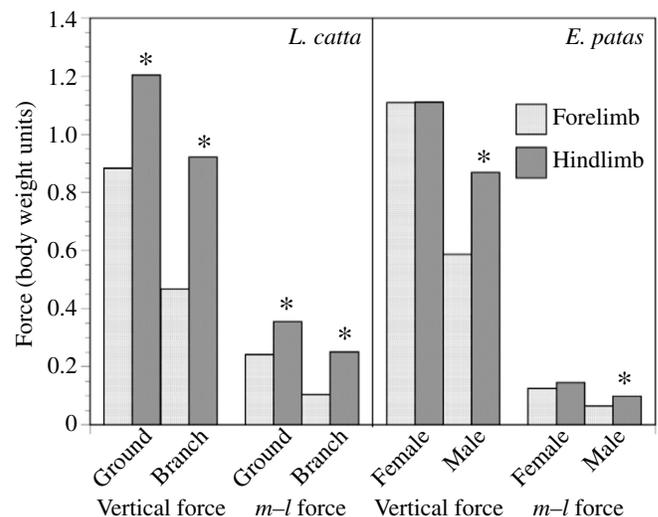


Fig. 5. Vertical and mediolateral (*m–l*) average peak reaction forces for the fore- and hindlimbs of *L. catta* (left) and *E. patas* (right). The asterisks indicate significantly higher hindlimb than forelimb forces.
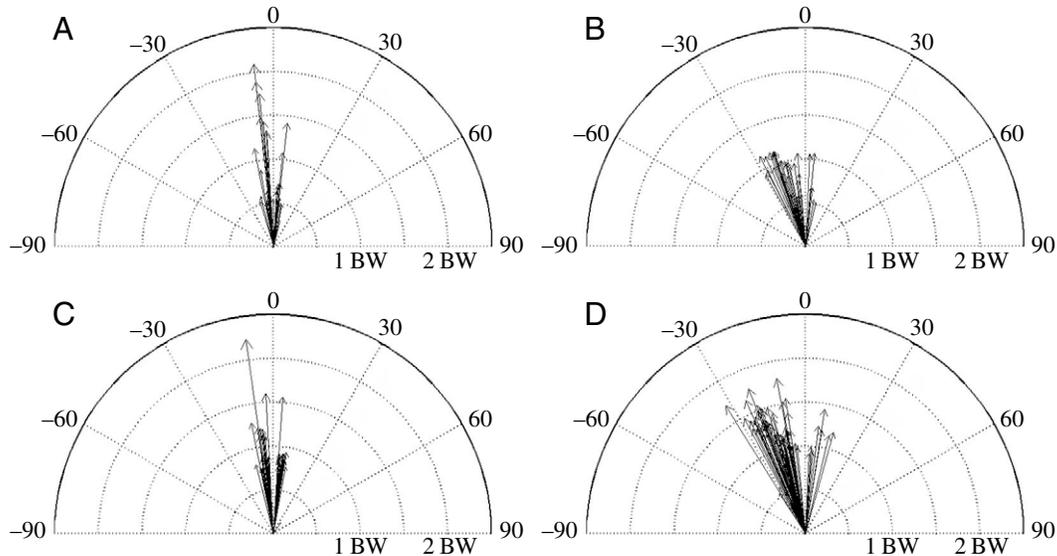
Fig. 6. Polar plots of substrate reaction force vectors in the frontal plane. Each arrow represents an individual reaction force with the arrow length representing its magnitude in body weight (BW) units, and arrow orientation its deviation from vertical. SRF vectors leaning medially have negative angles, those leaning laterally have positive angles. *E. patas* forelimb (A), *L. catta* forelimb (B), *E. patas* hindlimb (C), *L. catta* hindlimb (D).

favored hindlimbs over forelimbs, and the outer hindlimb in ground turns and inner hindlimb in branch turns. Medial reaction forces were observed more frequently and they are higher than lateral reaction forces (Fig. 4, Table 3). This may indicate a preference for pushing out, rather than pushing in, which in turn could be correlated with a preference for sidestep turns and use of outer limbs, rather than crossover turns and use of inner limbs. The patas monkeys, on the other hand, do not exhibit a similar preference in limb use during turns.

No uniform pattern was observed in the forces of limbs on the inside of the turn *vs* the outside of the turn, with significantly greater outside limb mediolateral forces only for ground turns of the lemurs. Vertical forces also do not differ significantly between inside and outside limbs. When running along a curved path, the transverse (centripetal) acceleration shifts weight onto the outside limbs. The centripetal acceleration and associated weight shift is proportional to running speed and inversely proportional to the radius of curvature (Hamill and Knutzen, 1995). It is likely that the

rather slow turns and rather shallow turning angles in our experimental set up were not sufficient to lead to a consistent difference in weight force between inside and outside limbs. We also did not observe notable leaning into the curve that animals and people adopt to avoid rolling over (Alexander, 2002), but these qualitative observations require quantification.

### *Is there a functional differentiation between forelimbs and hindlimbs?*

Hindlimb dominance characterizes turning behavior in the lemurs. The mediolateral hindlimb forces are significantly higher than the forelimb forces, and in this respect they resemble the vertical forces associated with turns that also show hindlimb dominance in the lemurs (Table 5). The hindlimbs are also involved more frequently in initiating the turns, which suggests that the animals adjust their gait to be able to use a hindlimb in turning. Lemurs also show hindlimb dominance with higher vertical forces in linear locomotion (Franz et al., 2005), and they appear to use the hindlimbs for

Table 6. *Mediolateral reaction forces in linear locomotion (in body weight units)*

| | Forelimb | | Hindlimb | |
|---|---|---|---|---|
| | Lateral | Medial | Lateral | Medial |
| *L. catta* | | | | |
| Ground, linear | – | −0.152±0.061 (37) | 0.159±0.032 (4) | −0.206±0.078 (44) |
| Branch, linear | 0.046±0.027 (22) | −0.032±0.016 (3) | 0.096±0.07 (11) | −0.054±0.015 (10) |
| *E. patas* | | | | |
| Ground, linear | – | −0.087±0.018 (10) | | |

Values are means ± s.d. (*N*).
Lemur data from Carlson et al. (2005); patas monkey data from Schmitt (2003a).

balancing on branches in linear locomotion more than they use the forelimbs (Carlson et al., 2005). In the patas monkeys, mediolateral forces are more similar for the two pairs of limbs, which coincides with more similar vertical peak forces, both in turns (Table 5) as well as in linear locomotion (Schmitt, 1996; Polk, 2001; Schmitt and Hanna, 2004). The force distribution between fore- and hindlimbs of these two species suggests that the mediolateral forces during turns are tuned to the amount of weight to be moved into the new direction.

Previously, researchers have speculated on the role of the limbs in turning quadrupeds. Kimura et al. (1979) characterized nonprimate quadrupeds as 'front steering–front driving', and primates as 'front steering–rear driving'. Li et al. (2004) suggested on the basis of magnitudes of the accelerative and decelerative forces in linear locomotion that chimpanzees steer with their hindlimbs, while in dogs the two pairs of limbs play a more similar role. Our data suggest that *L. catta* steers predominantly with its hindlimbs, whereas *E. patas* does not have a clear preference for one or the other pair of limbs.

For both species, braking and propulsive forces during turns are not dictated by the need to rotate the body into the new direction of movement, but rather follow the pattern of fore/aft force distribution in linear locomotion: forelimbs brake and hindlimbs propel (Demes et al., 1994; Franz et al., 2005).

### Does substrate influence the mechanics of turning?

For the lemurs, the outside hindlimb is frequently the pivot limb in ground turns, whereas the inside hindlimb is the pivot limb in branch turns. A major propulsive force on the outside hindlimb characterizes ground turns only (Table·2). It may not be effective to generate a rotatory (yaw) impulse on the branch because of the restricted track width and consequent smaller torque lever

### Do versatile lemurs differ from patas monkeys in their turning dynamics?

The major difference between the two species is the force distribution between forelimbs and hindlimbs that was discussed earlier. In addition, the limb use pattern by lemurs is more selective during turning than that by the patas monkeys. Whereas the three lemurs are similar to each other in limb preferences, the two patas monkeys differ from one another in some aspects of their turning strategies. The male patas monkey frequently used the outer hindlimb to realign its body's longitudinal axis with the new direction of movement, whereas the female patas monkey never did. Although they exhibit comparatively more selective limb use than the patas monkeys, the range and variability in mediolateral force magnitudes is higher in the lemurs. The locomotor repertoire of the ring-tailed lemur is highly versatile, whereas that of the patas monkey is considerably more restricted and arguably the most stereotypic among primate species. Versatile and particularly arboreal locomotion has been related to highly variable loading regimes of long bones, and ultimately to circular bone diaphyses, whereas stereotypic, and particularly terrestrial locomotion, has been related to more uniform loading regimes and uniplanar expansion of bone diaphyses (Lovejoy et al., 1976; Jungers and Minns, 1979; Schaffler et al., 1985; Burr et al., 1989; Carlson, 2005). Even though the variation in turning forces is greater in the versatile species, supporting these assumptions, it is worth noting that the limbs of the presumed stereotypic patas monkey are exposed to substrate forces with lateral as well as medial directions during turns. Thus, it may be the case that even presumably stereotypic animals exhibit variation in limb loading orientations when a broader range of naturalistic locomotor activities is considered.

### Comparison with other animals

These are the first vertebrate quadruped force data on steering. Turning forces have been collected for cockroaches (Jindrich and Full, 1999), crayfish (Domenici et al., 1999), and humans (Jindrich et al., 2004). There are commonalities between these insect hexapods, arthropod octopods or primate bipeds and the primate quadrupeds. In crayfish, the caudal outer limb generates the greatest yaw torque, and the caudal limbs also produce the highest forces in linear locomotion. In cockroaches, the outside limbs contribute the majority of force and torque impulse for the turn. Forces against the turn direction also can be found in cockroaches, particularly on the inside limbs. In a study of human running turns, Jindrich et al. (2004) documented braking forces with a rotatory effect opposite to the turn direction. They interpreted them as compensatory for the over-rotating effect of the transverse impulse. Like humans (Patla et al., 1991), the lemurs used mostly sidestep turns, whereas the patas monkeys used sidestep and crossover turns at similar frequencies.

### Conclusions

High mediolateral reaction forces that clearly exceed those in linear locomotion characterize the turning behavior of ring-tailed lemurs and patas monkeys. Whereas the hindlimb dominates steering in the lemurs, patas monkeys seem to steer with either pair of limbs. These preferences correspond to the weight force distribution between limbs, with the lemurs carrying a greater share of weight on their hindlimbs, and patas monkeys carrying body weight more evenly distributed between fore- and hindlimbs. Limb use during turning is less variable in the lemurs than in the patas monkeys, although distinct limb usage and force patterns characterized turns on the ground *vs* turns on a simulated branch. Limbs in both species experience medially and laterally directed reaction forces, though lemurs experience more variable force magnitudes and orientations. The inclination of the reaction force vector in the frontal plane is more variable in the versatile lemurs. It is likely, however, that limbs are exposed to frontal bending moments of variable directions in both taxa to some degree. Stereotypy in locomotion that is characteristic of the patas monkeys may thus not translate into limb loads that are as stereotyped.

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