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Mechanics of torque generation during quadrupedal arboreal locomotion

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Abstract

Quadrupedal animals moving on arboreal substrates face unique challenges to maintain stability. The torque generated by the limbs around the long axis of a branch during locomotion may clarify how the animals remain stable on arboreal supports. We sought to determine what strategy gray short-tailed opossums (*Monodelphis domestica*) use to exert torque and avoid toppling. The opossums moved across a branch trackway about half the diameter of their bodies. Part of the trackway was instrumented to measure substrate reaction forces and torque around the long axis of the branch. Kinematic analysis was used to estimate the center of pressure of the manus and pes; from center of pressure and vertical and mediolateral forces, the torque generated by substrate reaction forces versus muscular effort could be determined. Forelimbs generated significantly greater torque than hindlimbs, which is probably explained by the greater weight-bearing role of the forelimbs. Fore- and hindlimbs generated torque in opposite directions because contralateral fore- and hindlimbs typically contacted the branch. Torque generated by muscular effort, however, was often in the same direction in both fore- and hindlimbs. The muscle-generated torque is likely the result of mediolateral movement of the center of mass caused by mediolateral undulation of the torso. These results bear an important implication for the study of arboreal locomotion: center of mass dynamics are at least as important as static positions. *M. domestica* is a good representative for a primitive mammal, and comparisons with arboreal specialists will shed light on how proficient arboreal locomotion evolved.

Keywords: Center of mass; Dynamics; Force; Grip; Kinetics; *Monodelphis domestica*; Opossum

1. Introduction

Most small, quadrupedal mammals move with some proficiency on arboreal substrates (tree trunks, branches, twigs or foliage) (Jenkins, 1974). This ability is necessary because many small animals regularly negotiate fallen vegetation, shrubs, vines or trees. Some small mammals even use fallen logs and branches as arboreal runways, which enable more rapid locomotion through complex terrain because there are fewer obstacles (Ladine and Kissel, 1994; Montgomery, 1980). Moving on horizontal arboreal substrates narrower than an animal's body presents a challenge to maintain equilibrium because an animal can topple to one side (Cartmill, 1985). Many strategies exist to avoid toppling. Movement of the tail opposite the direction of a topple is common among some larger primates (Larson and Stern, 2006); some animals hang under a branch or move the center of mass (COM) closer to the substrate (Cartmill, 1985). Exerting a torque to oppose a topple is also common; a simple analogy is found among (human) gymnasts, who must exert torques to avoid toppling from a balance beam. However, few studies examine such torques in arboreal locomotion (Larson and Stern, 2006), and none directly measure torque.

Unless the animal's autopodia (manus and pes) and COM are perfectly balanced above the branch, there are two basic strategies that a quadruped should employ to grasp the branch and oppose toppling (Fig. 1). First, it can place its limb(s) on top of the branch while the COM moves mediolaterally. Here the animal must exert a torque around the long axis of the branch (craniocaudal torque, τ_{CC}) to counterbalance the torque in the opposite direction

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Nomenclature

BW	force expressed as a fraction of body weight.
BW cm	unit of torque; body weight unit multipled by moment arm length in centimeters.
COM	center of mass
F_{CC}	craniocaudal force
F_{ML}	mediolateral force
F_V	vertical force
R	radius of the branch trackway
τ_{CC}	torque around the long axis (craniocaudal axis) of the branch trackway
$\tau_{CC,SRF}$	torque around the long axis of the branch trackway resulting from the shear components of F_{ML} and F_V.
$\tau_{CC,musc}$	torque around the long axis of the branch trackway resulting from the movement and activity of the animal's muscles and body.
θ	angle between a horizontal axis passing through the center of the branch trackway and the location of the center of pressure of the hand or foot.

generated by the animal's movement and the distance of its COM from the craniocaudal axis of the branch (Cartmill, 1985; Preuschoft, 2002). As COM moves from the branch centerline, τ_{CC} must increase to prevent the animal from toppling, and the grip strength or adhesive force must also increase to allow the generation of τ_{CC} without the autopodium slipping (Cartmill, 1985). Because this strategy relies on the gripping strength of the manus and/or pes, we call this activity the *opposable digits strategy*. Because many animals that frequently move on arboreal substrates possess opposable digits and can presumably generate adequate grip, it is likely that they will employ the opposable digits strategy (in addition to or instead of tail movement, hanging under the branch, or bringing COM closer to the substrate). Because the animal's weight is applied more or less directly on top of the branch, the opposable digits strategy predicts that little or none of the τ_{CC} generated will be the result of substrate reaction forces being applied to the side of the branch ($\tau_{CC,SRF}$). All or nearly all of the τ_{CC} will be the result of muscular exertion ($\tau_{CC,musc}$) under this model.

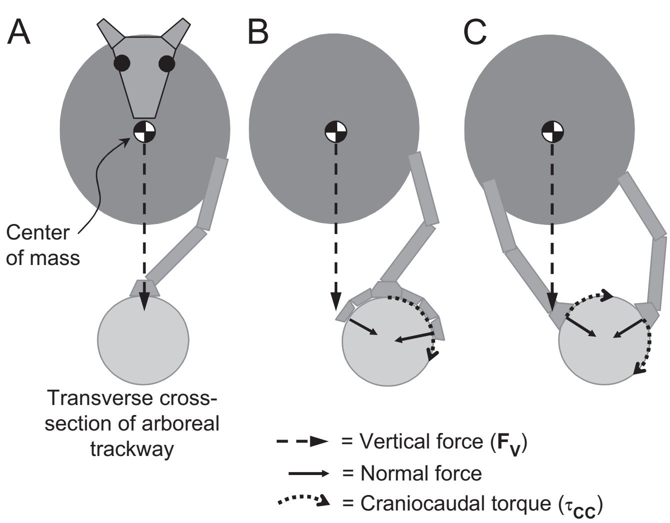

Fig. 1. (A) Limb (or limbs) contacts the branch at the top, requiring no torque around the long axis of the branch. (B) At least one limb with opposable digits contacting the branch at the top. The COM is not centered above the branch, and the limb in contact with the branch must exert a torque to counter the tendency to topple. If digital grip strength is sufficient, then balance in the transverse plane can be maintained with one limb. (C) Contralateral limb grip; most mammals trot, including *M. domestica*, therefore it is likely that the opposing limbs are a forelimb and a contralateral hindlimb. No opposable digits are required, but if only one limb is in contact with the branch, the animal may lose its balance in the transverse plane. Note that in (B) and (C), normal forces are generated, which allow friction force to develop. The indicated direction for craniocaudal torque is the substrate reaction torque.

In the second torque-generating strategy, an animal can place opposing autopodia (at least one right and one left limb) on opposite sides of the branch (although not necessarily 180° apart from each other). Thus, we call this the *opposable limbs strategy* (in contrast to the opposable *digits* strategy). Regardless of COM location, some τ_{CC} will be generated by the application of body weight into the substrate. This strategy should require less morphological specialization of the autopodia than the first strategy; if the musculature can generate adequate normal force, then the animal can remain stable. The opposable limbs strategy predicts that a substantial proportion of the τ_{CC} generated will be $\tau_{CC,SRF}$, but that at least some of the τ_{CC} will be $\tau_{CC,musc}$.

We examined limb contact position and τ_{CC} in the manus and pes of *Monodelphis domestica*, the gray short-tailed opossum, during locomotion on an arboreal trackway approximately half the diameter of the animals' torso. Their steps appear to be compliant; the shoulder and hip height are closer to the substrate in the middle of the step as compared with the beginning and end of the step (Lammers, 2004). Fore- and hindlimbs are similar in length, but hindlimbs are slightly longer (Lammers and German, 2002). Protraction and retraction angles of both limb pairs are largely similar (Lammers, 2004). They have a thick, fairly muscular tail that might act as a balancing appendage.

The central question of this study is: which strategy does the opossum use, or does it use a combination of strategies? This is evaluated by comparing $\tau_{CC,SRF}$ and $\tau_{CC,musc}$. These opossums nearly always use trotting gaits (Lammers and Biknevicius, 2004; Lammers, 2007) in which opposing, contralateral limbs simultaneously contact the narrow branch trackway. Thus, it seems likely that the opossums