Chapter 11
Head Posture and Visual Orientation in *Loris tardigradus* During Locomotion on Oblique Supports

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Abstract Primates moving through the trees must cope with a three-dimensional network of branches that differ in angular orientation. On oblique supports, an animal must not only avoid toppling or sliding off of a branch, it may also need to adjust its visual field orientation along the path of movement. Previous studies have found that primate quadrupeds walking on top of horizontal supports direct the orbital plane more inferiorly, whereas suspensory primates moving beneath branches direct the orbital plane more superiorly. If primates adjust the visual path to reflect substrate position, they should incline the orbital plane more on inclines than on declines. Alternatively, eye mobility within the orbits may permit collection of sufficient visual information without reorienting angular posture of the head. Lorisids are adept arboreal quadrupeds that routinely negotiate inclines and declines. We collected 150 strides of kinematic data on head postures for two adult slender lorises (*Loris tardigradus*) during locomotion on horizontal and oblique supports. In general, lorises adjusted head posture as predicted, directing orbits more superiorly on inclines and more inferiorly on declines. However, we observed higher angles on declines than predicted by substrate angle alone, suggesting that other locomotor and vestibular issues also influence head orientation.

Resume Lors des déplacements dans les arbres, les primates doivent se repérer au sein d'un réseau de branches dont les orientations diffèrent. Sur un support oblique, les animaux ne doivent pas seulement éviter de basculer ou de glisser, ils doivent

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aussi ajuster leur champ de vision à leur trajectoire. Des études antérieures ont montré que les primates quadrupèdes se déplaçant sur un support horizontal dirigent leur plan orbitaire vers le bas alors que les primates suspenseurs dont les déplacent se font sous les branches le dirigent vers le haut. Si les primates ajustaient l'orientation visuelle au support, ils devraient plus incliner leur plan orbitaire vers le haut pour des supports montants que descendants. Alternativement, la mobilité des yeux dans les orbites devrait permettre d'acquérir des informations suffisantes pour ne pas réorienter la position de la tête. Les lorisidés sont des quadrupèdes arboricoles qui évoluent fréquemment sur des supports montants et descendants. 150 enregistrements cinématiques se focalisant sur la position de la tête ont été collectés sur deux individus adultes de loris grêles (*Loris tardigradus*) lors de leur locomotion en supports obliques et horizontaux. En général, les loris ajustent la position de leur tête comme attendu, dirigeant les orbites vers le haut en montées et vers le bas en descentes. Cependant, l'angle de la tête en descente en bien plus fort que celui du support, suggérant que d'autres variables locomotrices et vestibulaires influencent la position de la tête.

Introduction

Most primates live and move about in three-dimensional, complex, arboreal habitats and traverse branches that vary unpredictably in their angular orientations (Grand 1972, 1984). Balancing and moving about on oblique supports requires postural and gait accommodations (Rollinson and Martin 1981; Stevens 2003, 2006; Nyakatura et al. 2008). Although head posture during locomotion may relate functionally to balance and visual orientation, the topic has received little experimental attention in arboreal nonhuman primates (e.g., Dabelow 1929; reviewed in Ross 1995). Stability of the head during locomotion is required to minimize disturbances to the visual and vestibular systems, both of which contribute to planning and execution of the travel path during the locomotor cycle (Spoor and Zonneveld 1998; Goldberg 2000; Goldberg and Hudspeth 2000; Patla et al. 2002; Hollands et al. 2004; Vallis and Patla 2004; Bagesteiro et al. 2006).

Visually directed animals may maximize the amount of the visual field perceived both above and below the horizontal in order to extract information on heading and locomotor velocity, as well as to perceive "time to intercept" for objects and obstacles within the travel path (Lee 1980; Gibson 1986; Schubert et al. 2003). This suggests that animals require stability of gaze direction, and to some degree, the head to align the visual field with the travel path. Studies on humans demonstrate that translations of the head due to locomotor velocity are minimized by compensatory head pitch (e.g., Hirasaki et al. 1999; Kao and Ringenbach 2004). Hildebrand (1959, 1961) noted cheetahs (*Acinonyx jubatus*) maintaining stable head and orbit posture during high speed running on a flat substrate. Dunbar et al. (2004) observed greater stabilization of head posture during galloping than walking in Old World monkeys negotiating horizontal terrestrial substrates. Arboreal primates face still more challenges related to balance and movement in a more structurally complex habitat, and
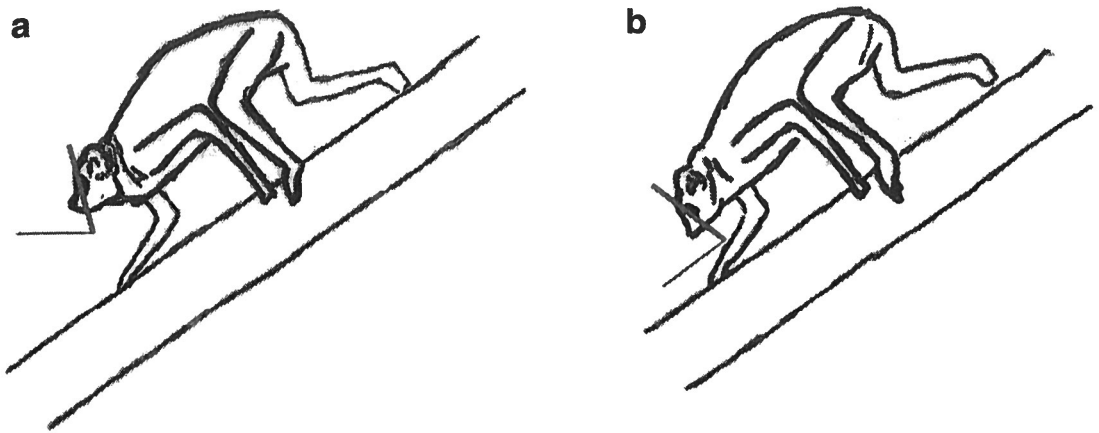
Fig. 11.1 Angles calculated in this study (**a**) orbit–ground angle, the angle between the orbital plane in lateral view and the *x*-axis and (**b**) orbit–substrate angle, the angle between the substrate and the orbital plane in lateral view

head posture may be influenced by the demands of both the visual and vestibular systems. Indeed, when walking on top of horizontal supports, arboreal primate quadrupeds direct the orbital plane more inferiorly, whereas suspensory primates moving beneath branches direct the orbital plane more superiorly (Strait and Ross 1999). Little is known about how head posture responds during arboreal quadrupedalism on the vast array of obliquely oriented supports that prosimian primates regularly utilize. We hypothesize that primates alter head posture when walking atop supports of differing angular orientations. Alternatively, the mobility of the eyes within the orbits may be sufficient to permit the collection of visual information without reorienting the angular posture of the head.

If arboreal primates orient gaze (and orbit) direction along the locomotor substrate like terrestrial taxa, one would predict that head posture varies according to substrate inclination, with absolute orbit inclinations measuring 30° higher on 30° inclines, 30° lower on 30° declines, and so forth. We expect the orbit–substrate angle to remain constant, or minimally, to exhibit a range of values that keep the substrate within the working visual field (Fig. 11.1). In this study, we quantify orbit and head orientation during locomotion on angular substrates in slender lorises (*Loris tardigradus*), adept arboreal, quadrupedal prosimians that regularly traverse variably oriented substrates in the wild (Nekaris and Stevens 2007).

Methods

Subjects

We followed the principles of ethical treatment of nonhuman primates, using non-invasive kinematic data collection protocols approved by the Institutional Animal Care and Use Committees (IACUC) at Stony Brook University, Duke University,

Table 11.1 Orbit orientations at forelimb lift-off on declined, horizontal, and inclined supports

Substrate	N	Orbit–ground angle		Orbit–substrate angle	
		Mean	SD	Mean	SD
60° decline	30	14.33	7.14	74.33	7.14
30° decline	30	32.78	9.12	62.78	9.12
Horizontal	30	59.47	7.92	59.47	7.92
30° incline	30	82.01	7.90	52.01	7.90
60° incline	30	113.94	7.07	53.94	7.07

See Fig. 11.1 for orbit–ground angle and orbit–substrate angle calculation

and Ohio University. Study subjects included two adult *Loris tardigradus* individuals housed at the Duke University Lemur Center (DLC). Laboratory animals had regular access to naturalistic supports in their large enclosures, enabling them to move in a way reflective of their wild counterparts. Animals moved upon simulated branches constructed from 2.44 m sections of polyvinyl chloride (PVC) pipes, 2.5 cm in diameter, coated with a nonslip surface and oriented horizontally and at 30° and 60° angles from the horizontal. Animals had access to these substrates in their naturalistic enclosures prior to data collection, minimizing the impact of the experimental setting on their performance. Stevens (2003) provides a more comprehensive description of the experimental setup. Using standard 2D kinematic techniques, we positioned cameras to capture lateral views of the study subjects, placing Panasonic AG-195 VHS video cameras 4 m from the path of movement of the subjects, a sufficient distance to reduce parallax (Spencer and Spencer 1995). We optimized frame rates to catch rapid movements by splitting interlaced video fields to achieve 60 Hz, setting shutter speeds at 1/1,000 s to reduce motion blur.

Using Peak Motus (version 9.1) to import video clips, we collected 15 symmetrical strides per individual per substrate, selecting strides with no visible changes in speed, the total number of individual ($n=2$) and support ($n=5$) combinations yielding 150 strides (Table 11.1). The orbital plane refers to the plane made by connecting three anatomical points along the orbit: orbitale superioris, orbitale inferioris, and orbitale anterioris (Cartmill 1970). Lorises have more convergent (similarly facing) but less frontated (vertically oriented) orbits than most primates (Cartmill 1970, 1972; Ross 1995), and the orbital inclination can be approximated in lateral view by a line connecting the upper and lower borders of the orbit. The orbital plane is virtually perpendicular to the sagittal plane in lorises (Cartmill 1970, 1972; Ross 1995). We digitized the orbit at forelimb and hind limb touch down (the first frame in which the limb contacted the support), midstance, and lift-off (the last frame in which the limb contacts the support) to measure head orientation relative to the substrate and gravity vector. We measured orbital angular data relative to the ground (orbit–ground angle, Fig. 11.1a) and adjusted to the support (orbit–substrate angle, Fig. 11.1b) by adding or subtracting 30° or 60°. In addition, we calculated speed using markers placed at 5 cm intervals along the support.

As kinematic data cannot be expected to follow a normal distribution, we employed the Kolmogorov–Smirnov test to assess normality of the data. We rank

transformed nonnormally distributed data and then used an ANCOVA to take into account kinematic differences related to velocity (Conover and Iman 1981; Sokal and Rohlf 1981).

Results

Lorises showed regular head posture patterns during locomotion. For any given support orientation, we found fairly consistent mean orbital inclinations throughout the stride cycle. Despite variation in head angle in different subjects and in individual strides, each individual typically carried its head at a constant angular orientation from forelimb touchdown through hind limb toe off (Fig. 11.2).

Consistent differences in head posture emerged among supports of different angular orientations, with significantly lower orbit–ground angles observed on declined supports and significantly higher angles observed on inclined supports (Fig. 11.3a). This indicates that, as predicted, lorises exhibited more superiorly directed orbits on inclines and more inferiorly directed orbits on declines ($p < 0.001$ for all comparisons).

Head posture was not completely explained by support orientation alone. We had predicted similar orbit–substrate angles on all support types. Although head postures generally tracked substrate angle on horizontal and inclined supports, we observed departures from the predicted pattern on 30° and 60° declines. Figure 11.3b demonstrates orbit–substrate angles at forelimb lift-off. On steep declines, orbits were significantly more superiorly directed than would be predicted if the visual tracking of the substrate constituted the sole determinant of head posture ($p < 0.001$).
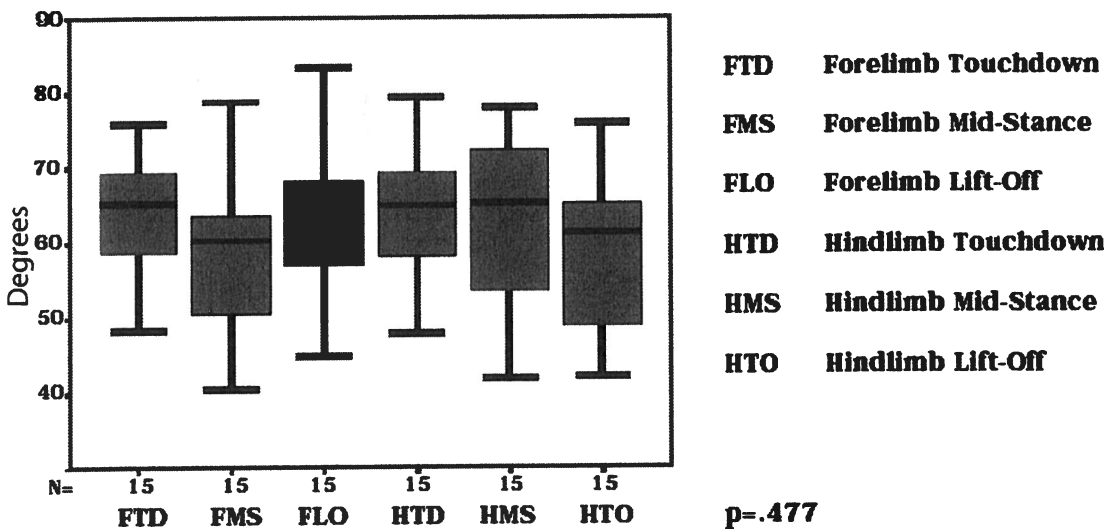

FTD	**Forelimb Touchdown**
FMS	**Forelimb Mid-Stance**
FLO	**Forelimb Lift-Off**
HTD	**Hindlimb Touchdown**
HMS	**Hindlimb Mid-Stance**
HTO	**Hindlimb Lift-Off**

Fig. 11.2 Orbit–ground angles for female loris on horizontal branches. Angles were not significantly different at forelimb and hind limb touchdown, midsupport, and lift-off events, indicating head posture stability throughout the stride cycle. Male loris exhibited similar pattern
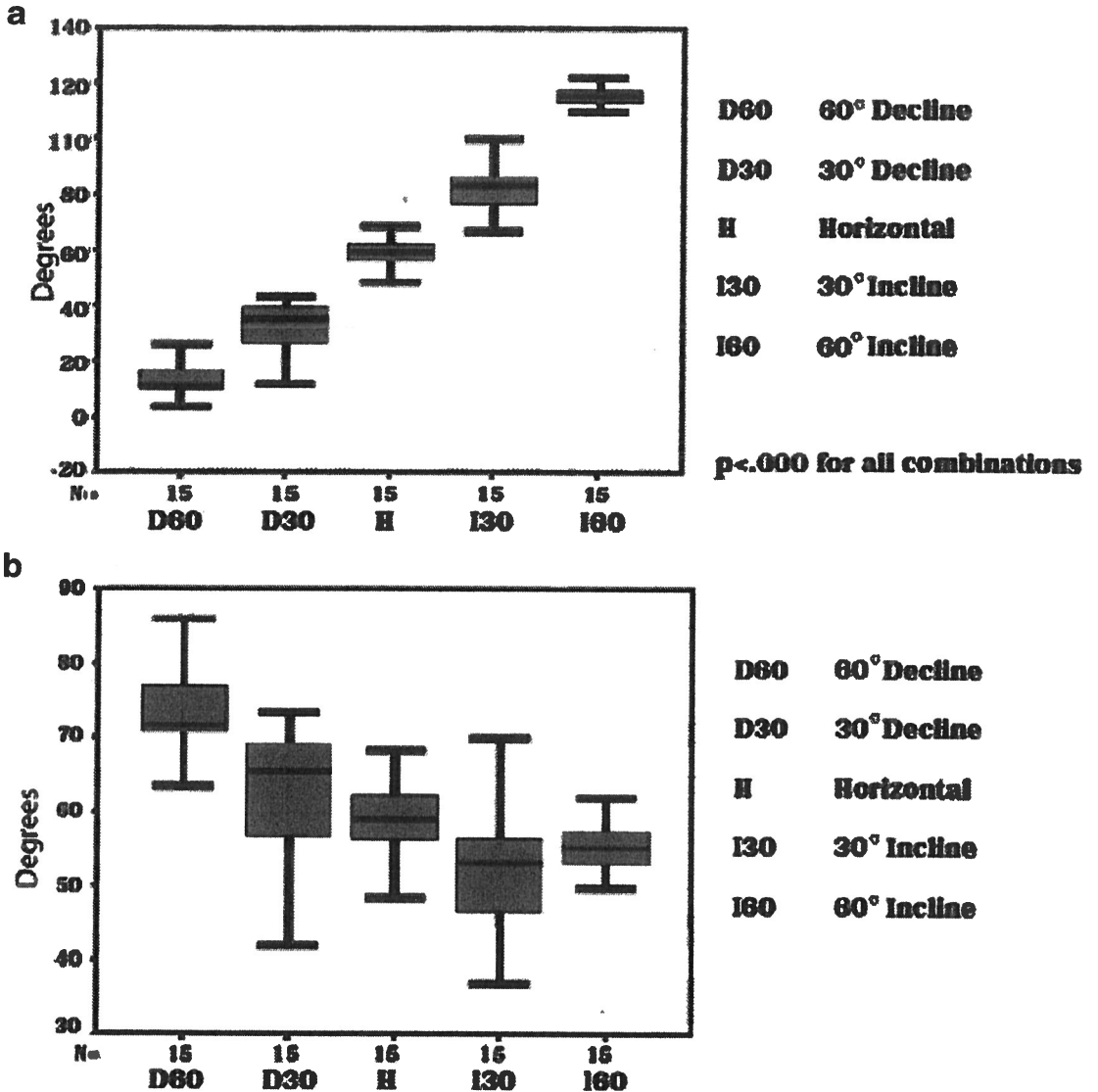
Fig. 11.3 Head posture for female loris at forelimb lift-off as a function of support orientation. (a) Orbit–ground angles were significantly different among all support types ($p < 0.001$ for all contrasts). (b) Orbit–substrate angle was higher than expected on declines, significantly so on 60° declines. The male loris exhibited a similar pattern

Discussion and Conclusions

The data presented here for *Loris tardigradus* suggest that head stability is important during arboreal locomotion, as mean head posture remains relatively constant throughout a stride cycle. These results are generally similar to those collected for terrestrial primates (Hirasaki et al. 1999). The alignment of the visual field also appears to play an influential role in head posture during travel, as lorises make clear accommodations on oblique supports, directing their orbits significantly more superiorly on inclines and more inferiorly on declines. These data expand upon

previous studies of terrestrial primates traversing horizontal substrates (Strait and Ross 1999), and both studies indicate that primates generally align their visual fields with the locomotor substrate. However, the relatively higher orbit–substrate angles observed on steep declines indicate that substrate orientation alone is not sufficient to predict head posture. On steep declines lorises exhibit less declined head postures than expected, possibly reflecting a tendency to look further ahead to compensate for potentially greater acceleration during forward locomotion due to gravity.

Balance during arboreal locomotion requires vestibular system stability and proprioception. The maintenance of head stability within a stride cycle reported here, along with the alteration of head posture on steep declines, may together reflect ways of accommodating and reducing perturbations to the vestibular system. The combined imperatives of balance and stability in the arboreal setting are particularly compelling given the discovery of high velocity locomotion in wild slender lorises negotiating supports of differing angular orientations (Nekaris and Stevens 2007). Future studies are needed to address the relative contributions of visual orientation and vestibular integrity during prosimian arboreal locomotion on oblique substrates.

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