

Stabilization and mobility of the head and trunk in wild monkeys during terrestrial and flat-surface walks and gallops

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Summary

This study investigated the patterns of rotational mobility ($>20^\circ$) and stability ($\leq 20^\circ$) of the head and trunk in wild Indian monkeys during natural locomotion on the ground and on the flat-topped surfaces of walls. Adult hanuman langurs (*Semnopithecus entellus*) and bonnet macaques (*Macaca radiata*) of either gender were cine filmed in lateral view. Whole-body horizontal linear displacement, head and trunk pitch displacement relative to space (earth horizontal), and vertical head displacement were measured from the cine films. Head-to-trunk pitch angle was calculated from the head-to-space and trunk-to-space measurements. Locomotor velocities, cycle durations, angular segmental velocities, mean segmental positions and mean peak frequencies of vertical and angular head displacements were then calculated from the displacement data. Yaw rotations were observed qualitatively. During quadrupedal walks by both species, the head was free to rotate in the pitch and yaw planes on a stabilized trunk. By contrast, during quadrupedal gallops by both species, the trunk pitched on a stabilized head. During both gaits in both species, head and trunk pitch rotations were symmetrical about comparable mean positions in both gaits, with mean head position aligning the horizontal semicircular canals near earth horizontal. Head pitch direction countered head vertical displacement direction to varying degrees during walks and only intermittently during gallops, providing evidence that

correctional head pitch rotations are not essential for gaze stabilization. Head-to-space pitch velocities were below 350 deg. s^{-1} , the threshold above which, at least among humans, the vestibulo-ocular reflex (VOR) becomes saturated. Mean peak frequencies of vertical translations and pitch rotations of the head ranged from 1 Hz to 2 Hz, a lower frequency range than that in which inertia is predicted to be the major stabilizer of the head in these species. Some variables, which were common to both walks and gallops in both species, are likely to reflect constraints in sensorimotor control. Other variables, which differed between the two gaits in both species, are likely to reflect kinematic differences, whereas variables that differed between the two species are attributed primarily to morphological and behavioural differences. It is concluded that either the head or the trunk can provide the nervous system with a reference frame for spatial orientation and that the segment providing that reference can change, depending upon the kinematic characteristics of the chosen gait.

Key words: natural locomotion, kinematics, segmental stabilization, sensorimotor control, spatial orientation, reference frames, graviceptors, vestibular apparatus, vestibulo-ocular reflex, inertia, free-ranging monkeys, hanuman langur, bonnet macaque, *Semnopithecus entellus*, *Macaca radiata*.

Introduction

The vestibular system has been hypothesized to play a critical role in both gaze stabilization and the perception of spatial orientation. Morphological studies of the vestibular apparatus have included investigations of otolith organ and semicircular canal orientation, canal arc size and scaling to

body size, and/or how vestibular design relates to control of gaze, head and neck orientation, and balance during posture and locomotion (e.g. Blanks et al., 1985; Graf et al., 1997; Jones and Spells, 1963; Matano et al., 1985, 1986; Spoor and Zonneveld, 1998; Spoor et al., 1994). Physiological studies

have looked at the vestibular and visual systems and the interactions of these systems in balance control and eye-head coordination (Angelaki and Hess, 1994; Büttner and Henn, 1981; Dow, 1938; Fernandez et al., 1972; Fetter and Zee, 1988; Goldberg and Fernandez, 1981; Jäger and Henn, 1981; Lacour et al., 1981; Northington and Barrera, 1934; Peterson and Goldberg, 1981; Peterson et al., 1985; Raphan and Cohen, 1981). Psychophysical studies have investigated the perception of head and trunk movement by rotating one segment relative to the other (Jakobs et al., 1985; Mergner et al., 1983, 1991, 1992; Taylor and McCloskey, 1990).

Laboratory studies have produced a wealth of information on how the vestibular system works. The success of many of these studies, however, has required protocols that severely restrict the natural range of movement patterns practised by the animal and human subjects. Thus, much remains to be learned about vestibular function during natural or volitional movements, especially under real-world conditions. One major gap in this knowledge concerns the mechanical or environmental requirements of the vestibular system for perceiving and transmitting sensory information about the orientation of the body in space (i.e. relative to gravity vertical-earth horizontal). Specifically, are there restrictions on how the head-fixed vestibular apparatus can be positioned or reoriented *via* head movements without deteriorating the nervous system's perception of spatial orientation?

Behavioural studies of humans and birds that focus on head orientation and stabilization provide evidence that tolerable movements of the head-fixed vestibular apparatus are restricted. During resting postures and other activities, human head orientation pitches the horizontal semicircular canals upwards slightly at $\sim 16^\circ$ above earth horizontal (Graf et al., 1995). When humans perform a variety of locomotor tasks (walking, running, hopping), both with and without vision, the head rotates through no more than 20° in the pitch (sagittal) plane, and the horizontal semicircular canals remain closely aligned with earth horizontal (Pozzo et al., 1990). Furthermore, the head rotates through fewer degrees than the trunk when rotating in the roll (frontal) plane to maintain single limb stance on a narrow cylindrical beam or rocking platform, except when the trunk rotates through less than 3° (Pozzo et al., 1995). Birds stabilize the head during walking (Erichsen et al., 1989; Troje and Frost, 2000), perching, standing (Erichsen et al., 1989) and flying (Brown, 1948, 1951, 1952), even when trunk orientation changes. This stabilization, controlled in large part by vestibulocollic and optocollic reflexes (Gioanni, 1988a,b), appears critical to the physiological or optical requirements of the eyes (Dunlap and Mowrer, 1930; Fitzke et al., 1985; Friedman, 1975; Frost, 1978; Hodos and Erichsen, 1990; Troje and Frost, 2000). Head orientation in birds is also related to the control of posture, locomotion and gaze direction (Green, 1998a,b; Green et al., 1992). This orientation maintains the horizontal semicircular canals near earth horizontal, being tilted upward slightly by $\sim 10^\circ$ during the behaviours discussed above (Erichsen et al., 1989).

Under natural conditions, however, head movements are

frequently necessary, particularly for redirecting gaze through a greater number of degrees than is permitted of the eyes in the orbits alone. Slight pitch-plane rotations may correct for vertical translations in order to maintain gaze on a fixed target (Pozzo et al., 1990), anticipatory yaw-plane rotations occur when turning a corner while walking (Grasso et al., 1996, 1998) or driving a car (Land and Lee, 1994) and large rotations in multiple planes are commonly practised when walking to increase panoramic vision of the immediate surroundings. Thus, if the brain requires a stabilized head to correctly interpret information from the vestibular apparatus, how can large head movements occur without interfering with this interpretation?

The above studies of head stabilization are restricted to bird flight and to human subjects and birds performing upright bipedal or monopodal tasks. Does head stabilization also occur in quadrupeds? If so, when and to what degree? If not, what segmental movement patterns do occur? Quadrupedal mammals are similar to bipeds in that the cervical column is held relatively upright during resting postures and many voluntary activities but, during locomotion, at least some species (cats, guinea pigs) reorient the column more horizontally (Graf et al., 1995; Vidal et al., 1986). As in birds (Erichsen et al., 1989), the horizontal semicircular canals in many species are most commonly pitched up by $5\text{--}10^\circ$ during rest, but in some mammals, such as guinea pigs, this orientation is closer to 20° (Graf et al., 1995). Furthermore, a study of natural and volitional locomotion by jackrabbits reveals, in qualitative terms, that the head is commonly stabilized rotationally in space (Bramble, 1989).

Studies in the wild (Dunbar and Badam, 1998) and in captivity (Strait and Ross, 1999) reveal that the head in several primate species is commonly stabilized rotationally in space during natural and volitional quadrupedal locomotion. Preliminary evidence indicates, however, that the head frequently rotates through several degrees in the pitch and yaw planes during quadrupedal walks but rotates through less than 20° in the pitch plane and only minimally in any other plane during gallops (Dunbar and Badam, 1998). Thus, head movements are more restricted under some conditions than others.

In the present paper, we further pursue the issue of potential restrictions in orientation and movement of the vestibular apparatus in quadrupeds by investigating, in both qualitative and quantitative terms, the kinematics of head and trunk movements by wild, free-ranging monkeys practising volitional locomotor behaviours in natural habitats. Two species representing different primate subfamilies are investigated in an attempt to distinguish among those aspects of head and trunk movement patterns that are common across gaits or species or both. The specific question asked is how do the head and trunk segments rotate during quadrupedal walks and gallops on the ground and flat surfaces? Aspects of this study have been presented previously in abstract form (Dunbar, 1998; Dunbar and Badam, 1995; D. C. Dunbar, presented at satellite conference of *Neuronal Control of Movement Society*, Mexico, 1977 and the *13th Symposium of International Society for Postural and Gait Research*, Paris, 1997).

Materials and methods

Animals and environment

Wild, free-ranging groups of hanuman langurs (*Semnopithecus entellus* Dufresne 1797) and bonnet macaques (*Macaca radiata* E. Geoffroy 1812) were investigated in India. For brevity, hanuman langurs (subfamily Colobinae) and bonnet macaques (subfamily Cercopithecinae) will be referred to as 'hanumans' and 'bonnets', respectively, throughout the remainder of the text. Hanumans are large monkeys, having head-trunk lengths (not including tail) in the range of 51–108 cm and body masses in the range of 9–21 kg for males and 8–18 kg for females. By contrast, bonnets are medium-sized monkeys, having head-trunk lengths in the range of 35–60 cm and body masses in the range of 6–12 kg for males and 3–6 kg for females. Both species have tail lengths that exceed head-trunk length (Roonwal and Mohnot, 1977). Hanumans practise a much broader spectrum of terrestrial and arboreal behaviours than do bonnets (Dunbar and Badam, 1998).

The hanuman group lived in a large city whereas the bonnet group lived in an agricultural village. Both groups followed particular pathways through their geographic home range or territory, making it possible to predict when and where the monkeys could be found. The present study focused on walks and gallops by adults of either sex on flat and continuous surfaces along which the monkeys followed a rectilinear course; the hanumans practised these gaits on the flat top of a straight stonewall. The bonnets, by contrast, walked on the ground, following the edge of a straight irrigation ditch. Hanuman wall locomotion was compared with available ground locomotor cycles in this species in order to determine if the two substrate designs had notably different impacts on movement patterns. No clear influence on locomotor kinematics could be identified. Thus, comparisons between bonnet ground locomotion and hanuman wall locomotion were considered valid.

Data collection, definitions and variables

Cine recordings of the monkeys were made at a frequency of 100 Hz with a tripod-mounted and levelled super-8 movie camera (Mekel Engineering, Inc., Covina, CA, USA) equipped with an 11–70 mm video zoom lens (Canon, USA Inc., Lake Success, NY, USA). The camera lens was oriented perpendicular to the linear pathway to provide a lateral view and was not panned or tilted. Ten walk and 10 gallop cycles per species were retained for further analysis. Film sequences were chosen in which segmental and whole-body movements remained in the same perpendicular plane, minimizing subsequent parallax measurement error. The walk samples were collected from three hanuman (two males, one female) and four bonnet (two males, two females) subjects, and the gallop samples were collected from four hanuman (two males, two females) and six bonnet (two males, four females) subjects.

Head and trunk rotations were considered in terms of a three-axis coordinate system: pitch, yaw and roll. Rotations about the pitch axis were in the sagittal (pitch) plane, rotations

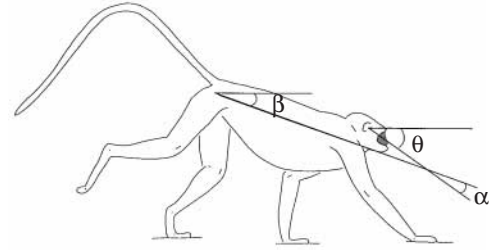


Fig. 1. Measured axes and angles in the pitch plane. Head axis was a line passing through the external auditory meatus and the apex of the prognathous mouth. Trunk axis was a line passing through the hip and shoulder joints. Head angle relative to space (θ) and trunk angle relative to space (β) were measured in reference to earth horizontal. Head-to-trunk angle (α) was calculated from the head-to-space and trunk-to-space angles.

about the yaw axis were in the transverse (yaw) plane, and rotations about the roll axis were in the coronal (roll) plane. Filming in lateral view only allowed quantitative measurements of rotations about the pitch axis. Yaw-axis rotations were analyzed in qualitative terms using locomotor cycles that were separate from the cycles used for quantitative analysis of pitch-axis rotations. Roll-axis rotations were not included in the study because accurate analysis was unreliable.

Owing to the complexity of segmental movements and associated forces during locomotion, no segment will be completely stabilized (0° rotation). How much rotation can occur, however, before a segment is no longer considered stabilized? To answer this question requires the selection of a threshold value. Rather than make an arbitrary decision, we adopted the 20° of pitch-plane rotation already known for human subjects (Pozzo et al., 1990) as the threshold value. We feel justified in extrapolating this value to monkeys because they are closely related phylogenetically to humans and preliminary evidence indicates that pitch-plane rotations in these species are often less than 20° (Dunbar and Badam, 1998). Furthermore, the neural mechanisms controlling locomotion and posture, at least in terms of limb movements, appear to be conservative among tetrapods in general (Dunbar et al., 1986; Jenkins and Goslow, 1983; Jenkins and Weijs, 1979; Peters and Goslow, 1983; Vilensky and Gehlsen, 1984).

The following body landmarks were digitized (Numonics Corp., Montgomeryville, PA, USA) frame by frame (10 ms sampling rate): tip of mouth, ear (external auditory meatus), shoulder joint and hip joint. These landmarks were used to create head (mouth apex–ear) and trunk (shoulder joint–hip joint) axes in order to measure (SigmaScan SPSS Inc., Chicago, IL, USA) head and trunk rotations in the pitch plane relative to earth horizontal throughout the locomotor sequence (Fig. 1). Head axis-to-trunk axis angles (α) were calculated from these head-to-space (θ) and trunk-to-space (β) angles. The base of the tail was also digitized for subsequent calculation of locomotor velocity. The raw data were then smoothed with a 10 Hz cut-off frequency to minimize measurement error.

The variables of interest included pitch axis displacements and velocities of the head and trunk relative to space and of the head relative to the trunk, mean head and trunk positions (mean angle) relative to space, estimated mean position of the horizontal semicircular canals relative to space, vertical linear displacement and velocity of the head, and peak frequencies of linear and angular head displacements. Preferred locomotor velocities and cycle durations were also collected to lend context to the head and trunk variables. The 100 Hz sampling rate and objects of known size along the locomotor pathways provided time and scaling variables, respectively, for velocity calculations.

The mean position in space of the horizontal semicircular canals during gait cycles was estimated from the mean head position values as follows. Measurements on rhesus monkey (Blanks et al., 1985) – *Macaca mulatta* is closely related to bonnets – and hanuman (Spoor and Zonneveld, 1998) skulls reveal that the horizontal semicircular canals are pitched upward anteriorly at 22°, on average, to the Frankfort plane or line. This imaginary line passes through the external auditory meatus and the inferior orbital margin. Our measurements on rhesus and hanuman skulls further revealed that the measured head axis in both species is approximately 20° below the Frankfort horizontal plane. Combining the above information, we estimated that the horizontal semicircular canals in both species were pitched up by 42° from the measured head axis.

Finally, Fourier frequency analyses were conducted on both the smoothed angular and linear displacement data for the head in order to determine peak frequencies for each species during walks and gallops. Owing to constraints of the research protocol, individual locomotor performances of long enough duration for meaningful frequency analyses could not be recorded. Average frequency profiles, however, were derived for each gait type and species by performing a frequency analysis of each individual cycle and then averaging the frequency spectra across these cycles. This technique produced clear average peak frequencies. Harmonics, however, were not clearly produced and, thus, were not included in the analysis.

Statistics

Variables were compared across gaits (quadrupedal walks vs gallops) and across species (hanumans vs bonnets) using two-way analysis of variance. The following statistical procedure determined what mean percentage variance in head-to-trunk angle was explained by head position and by trunk position. Pearson's product moment correlation coefficients were obtained for head-to-space and trunk-to-space angle against head-to-trunk angle for each gait cycle. The mean percentage of the variance explained was calculated from the mean of the z -transformed correlations. The correlation coefficients for each cycle were compared using a test of homogeneity (Sokal and Rohlf, 1981) in order to ascertain whether head or trunk positions were significantly different determinants of head-to-trunk angle. The joint probabilities for these individual comparisons were then calculated to determine the significance of the difference in the mean percentage of the head-to-trunk

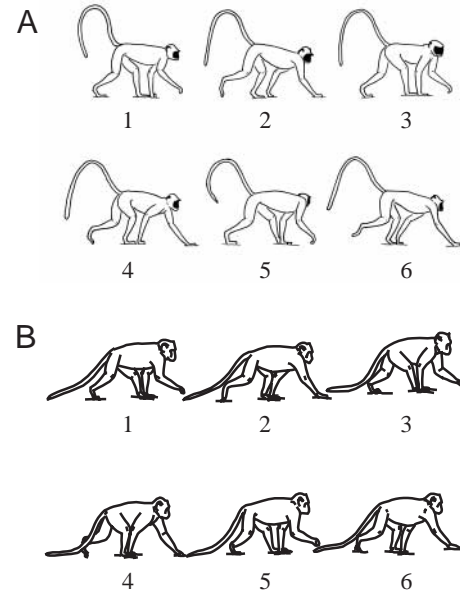


Fig. 2. Cine film tracing of diagonal-sequence walks by (A) a hanuman langur and (B) a bonnet macaque. Note the large yaw rotations of the head as the hanuman looks to its right (A_3) and left (A_5).

variance explained by head and trunk positions. In addition, Spearman's coefficients of rank correlation were calculated to determine how angular and vertical linear displacement of the head co-varied. Coefficients were obtained for each trial and then z -transformed to determine the average correlations and standard deviation by gait type and species. P -values less than or equal to 0.05 were considered significant for all statistical tests.

Results

Quadrupedal walks

Quadrupedal walks are a type of symmetrical gait (i.e. equal timing between footfalls and handfalls) in which each limb is touching the support surface for more than 50% of the cycle time (Alexander, 1982; Hildebrand, 1966). The monkeys most commonly walked with a diagonal sequence footfall pattern that, following Hildebrand's definition (Hildebrand, 1966), is characterized by a hind limb touchdown being followed by that of the opposite (contralateral) forelimb (Fig. 2).

Qualitatively, the trunk in both species remained in an essentially fixed horizontal position during walks. Only minimal pitch, yaw and roll rotations occurred in response to the sequential limb movements. Vertical linear displacements of the head were also minimal. Head rotations, however, were variable. At times, the head would be held in a relatively static position, as when the monkeys focused gaze on the upcoming support surface and on a specific or distant target. At other times, by contrast, the head commonly rotated through several degrees about the pitch and yaw axes, as the monkeys visually scanned their physical surroundings.

Table 1. Summary of mean measurements and analysis of variance^a

	Walk	Gallop	<i>P</i> -value ^b
Locomotor velocity (m s ⁻¹) (± S.D.)			
Hanuman	0.77 (±0.08)	3.42 (±0.40)	<0.001
Bonnet	1.02 (±0.16)	2.13 (±0.28)	<0.001
<i>P</i> -value ^c	<0.001	<0.001	
Gait cycle duration (ms) (± S.D.)			
Hanuman	1030 (±55)	536 (±51)	<0.001
Bonnet	718 (±44)	433 (±40)	<0.001
<i>P</i> -value ^c	<0.001	<0.001	
Head-to-space pitch displacement (deg.) (± S.D.)			
Hanuman	17 (±5)	15 (±2)	>0.05
Bonnet	13 (±4)	13 (±3)	>0.05
<i>P</i> -value ^c	<0.05	<0.05	
Trunk-to-space pitch displacement (deg.) (± S.D.)			
Hanuman	10 (±3)	42 (±4)	<0.001
Bonnet	6 (±1)	30 (±8)	<0.001
<i>P</i> -value ^c	<0.001	<0.001	
Head-to-trunk pitch displacement (deg.) (± S.D.)			
Hanuman	21 (±1)	35 (±4)	<0.001
Bonnet	14 (±4)	22 (±4)	<0.001
<i>P</i> -value ^c	<0.001	<0.001	
Head-to-space mean pitch velocity (deg. s ⁻¹) (± S.E.M.)			
Hanuman	63 (±4)	68 (±5)	>0.05
Bonnet	58 (±5)	58 (±5)	>0.05
<i>P</i> -value ^c	>0.05	>0.05	
Trunk-to-space mean pitch velocity (deg. s ⁻¹) (± S.E.M.)			
Hanuman	38 (±2)	155 (±5)	<0.001
Bonnet	24 (±2)	130 (±8)	<0.001
<i>P</i> -value ^c	<0.001	<0.001	
Head-to-trunk mean pitch velocity (deg. s ⁻¹) (± S.E.M.)			
Hanuman	72 (±5)	138 (±5)	<0.001
Bonnet	59 (±5)	112 (±7)	<0.001
<i>P</i> -value ^c	<0.001	<0.001	
Head-to-space maximum pitch velocity (deg. s ⁻¹) (± S.E.M.)			
Hanuman	241 (±27)	216 (±17)	>0.05
Bonnet	181 (±15)	183 (±13)	>0.05
<i>P</i> -value ^c	<0.05	<0.05	
Trunk-to-space maximum pitch velocity (deg. s ⁻¹) (± S.E.M.)			
Hanuman	129 (±11)	356 (±30)	<0.001
Bonnet	83 (±7)	353 (±33)	<0.001
<i>P</i> -value ^c	<0.01	>0.05	
Head-to-trunk maximum pitch velocity (deg. s ⁻¹) (± S.E.M.)			
Hanuman	284 (±27)	341 (±22)	>0.05
Bonnet	178 (±15)	350 (±30)	<0.001
<i>P</i> -value ^c	<0.01	>0.05	
Head-to-space vertical displacement (cm) (± S.D.)			
Hanuman	6.67 (±2.10)	19.22 (±3.52)	<0.001
Bonnet	6.53 (±2.40)	11.22 (±5.01)	<0.01
<i>P</i> -value ^c	>0.05	<0.001	
Head-to-space mean vertical velocity (cm s ⁻¹) (± S.E.M.)			
Hanuman	19.87 (±1.45)	68.89 (±4.41)	<0.001
Bonnet	15.66 (±0.74)	38.99 (±3.03)	<0.001
<i>P</i> -value ^c	<0.001	<0.001	

	Walk	Gallop	<i>P</i> -value ^b
Head-to-space maximum vertical velocity (cm s ⁻¹) (± S.E.M.)			
Hanuman	55.35 (±6.99)	147.69 (±8.76)	<0.001
Bonnet	37.75 (±1.02)	85.21 (±7.50)	<0.001
<i>P</i> -value ^c	<0.001	<0.001	
Head pitch displacement peak frequency (Hz) (± S.D.)			
Hanuman	0.98 (±1.82)	1.56 (±0.71)	>0.05
Bonnet	1.17 (±1.52)	1.37 (±1.01)	>0.05
<i>P</i> -value ^c	>0.05	>0.05	
Head vertical displacement peak frequency (Hz) (± S.D.)			
Hanuman	1.95 (±0.32)	2.15 (±0.22)	>0.05
Bonnet	0.78 (±1.09)	1.17 (±0.70)	>0.05
<i>P</i> -value ^c	>0.05	>0.05	
Head-to-earth horizontal mean position (deg.) (± S.E.M.)			
Hanuman	-35 (±1)	-33 (±1)	>0.05
Bonnet	-38 (±2)	-40 (±1)	>0.05
<i>P</i> -value ^c	<0.001	<0.001	
Trunk-to-earth horizontal mean position (deg.) (± S.E.M.)			
Hanuman	-11 (±1)	-13 (±1)	>0.05
Bonnet	-5 (±1)	-5 (±1)	>0.05
<i>P</i> -value ^c	<0.001	<0.001	
Head-to-trunk mean position (deg.) (± S.E.M.)			
Hanuman	-24 (±1)	-21 (±1)	>0.05
Bonnet	-34 (±2)	-34 (±2)	>0.05
<i>P</i> -value ^c	<0.001	<0.001	

^a*N*=10 locomotor cycles per gait per species.

^bWalk vs Gallop.

^cHanuman vs Bonnet.

When subjected to quantitative analysis, both similarities and differences between hanuman and bonnet walks emerged, as revealed in Table 1. Compared with bonnets, hanumans walked slower, but with longer cycle durations, and experienced larger head and trunk rotational displacements about the pitch axis. Nevertheless, the basic kinematic pattern was comparable in both species, in that head rotations were greater than trunk rotations (Fig. 3), and the mean pitch-plane rotational ranges of both segments were less than 20°. Note, however, that whereas these rotations were always less than 20° for the trunk in both species, head rotations often approached 25° in bonnets and 30° in hanumans (Fig. 3). Furthermore, yaw-plane head rotations, while not measured directly, often approached 180° as the hanumans and bonnets looked to the right and left (Fig. 2A).

Vertical head translations were not significantly different between the two species during walks, although both the mean and maximal instantaneous velocities of these translations were higher in hanumans than in bonnets. Vertical head movements were not strongly correlated with rotations about the pitch axis (hanuman $r^2=-0.16$, S.D.=0.35; bonnet $r^2=-0.15$, S.D.=0.42). Whereas the direction of rotation at times paralleled vertical displacements (i.e. head rise with upward rotation, head drop with downward rotation), this relatively in-phase pattern was interrupted with periods during which

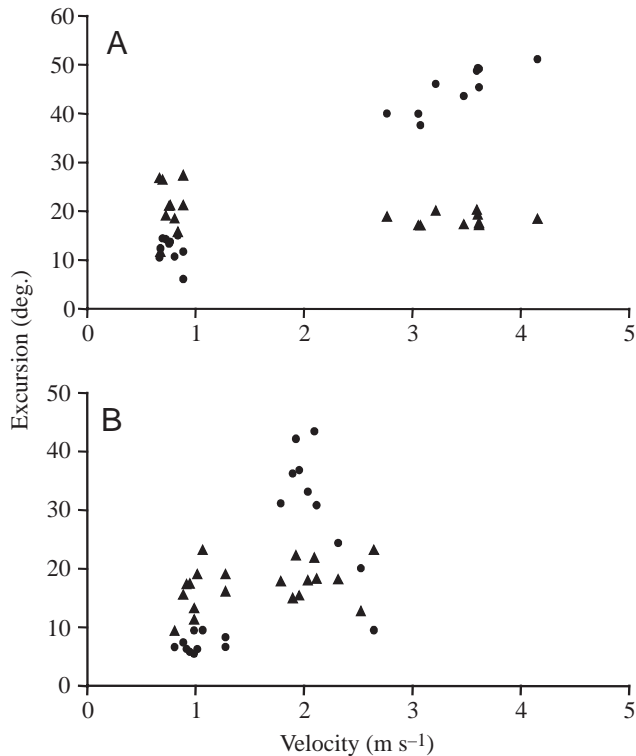


Fig. 3. Range of head (triangles) and trunk (circles) excursions in the pitch plane during walks and gallops ($N=10$ cycles/gait/species). For both (A) hanumans and (B) bonnets, the clusters of symbols to the left (lower velocities) are for walks, whereas the clusters to the right (higher velocities) are for gallops. Note that the head usually pitches through more degrees than the trunk during walks. By contrast, the trunk usually pitches through more degrees than the head during gallops. These basic patterns are seen in both species but are more extreme in hanumans.

vertical translation and rotation were nearly 180° out of phase (Fig. 4A,B). Out-of-phase periods occurred primarily near touchdown of a hand when the forelimbs were also nearly 180° out of phase and one hind limb was near midsupport. The resultant whole-body deceleration, combined with decreased cranial trunk height, caused the head to pitch and drop downward. The head compensated for the downward pitch and drop, however, by rotating upward. This upward rotation, often anticipatory, peaked at or near maximal vertical descent. Occasionally, a downward compensatory head rotation also occurred near peaks in vertical ascent (Figs 2, 4). Any particular association between vertical and angular head displacements could apparently be largely overridden voluntarily, however; as when the monkeys visually inspected their surroundings (Fig. 4A).

Pitch-plane rotations of the head relative to the trunk during walks were larger in hanumans than in bonnets (Fig. 5). In both species, however, head-to-trunk angles were more highly correlated with head-to-space angles ($r^2=0.74$ for hanuman and 0.85 for bonnets) than with trunk-to-space angles ($r^2=0.33$ for hanuman and 0.10 for bonnets), verifying that the head was

rotating on the trunk rather than the trunk on the head. All combined probabilities (Sokal and Rohlf, 1981) were significantly different at the 0.001 level.

Mean instantaneous rotational velocities of the head about the pitch axis relative to space did not differ significantly between the species during walks. The maximal instantaneous velocities, however, were significantly higher in hanumans than in bonnets. In both species, mean instantaneous rotational velocities of the trunk relative to space were much lower than those of the head. These mean velocities were greater in hanumans than in bonnets, however, as were maximal instantaneous trunk pitch velocities. Both mean and maximal instantaneous rotational velocities of the head relative to the trunk were also greater in hanumans than in bonnets (Fig. 5), as were both mean and maximal instantaneous velocities of head vertical translations.

Mean peak (fundamental) frequencies of pitch-plane rotations and vertical displacements of the head during walks were 0.98 ± 1.82 Hz (mean \pm s.d.) and 1.95 ± 0.32 Hz in hanumans and 1.17 ± 1.52 Hz and 0.78 ± 1.09 Hz in bonnets, respectively. These frequencies did not differ significantly between rotational and vertical displacements or between species.

Mean angular head position in the pitch plane relative to space during walks differed slightly between species (Fig. 6A,C). When the measured values were adjusted by $+42^\circ$ (see Materials and methods), the estimated mean position of the horizontal semicircular canals was pitched upward rostrally above earth horizontal by $+7^\circ$ in hanumans and by $+4^\circ$ in bonnets. Mean angular trunk position in the pitch plane relative to space revealed that the shoulder joints were lower than the hip joints (indicated by negative values in Table 1) in both species. This mean angular position was greater in hanumans, however, than in bonnets (Fig. 6B,D). By contrast, mean head-to-trunk angular position formed a significantly smaller angle in hanumans than in bonnets.

Gallops

Gallops differ from quadrupedal walks in that limb movements are asymmetrical (i.e. unequal timing between footfalls and handfalls), each limb is in contact with the support surface for less than 50% of the gait cycle time, and the cycle includes an airborne phase (Alexander, 1982; Hildebrand, 1977). The hanumans used two different types of gallops, as defined by Hildebrand (1977). In transverse gallops, touchdown of the leading hind limb – the second hind limb to contact the support surface – was followed by touchdown of the contralateral forelimb. In rotary or rotatory gallops, touchdown of the leading hind limb was followed by touchdown of the ipsilateral forelimb (Fig. 7A). The bonnets were observed using only the transverse gallop (Fig. 7B).

Qualitatively, the pattern of head and trunk movements during gallops was in marked contrast to the pattern during walks. Neither the head nor the trunk ever appeared to rotate about the roll or yaw axes (Fig. 7). The trunk, however, made large rotations about the pitch axis that were necessary for the

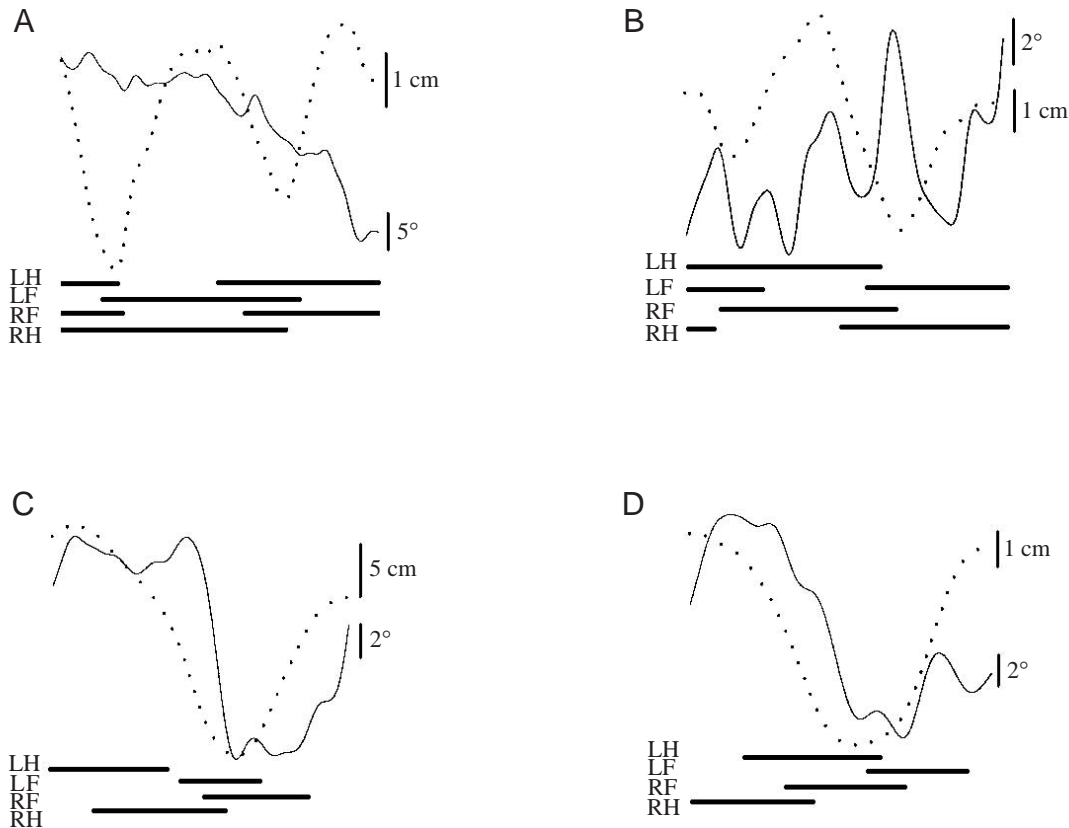


Fig. 4. Graphs of vertical translations (dotted lines) and pitch rotations (solid lines) of the head during single representative cycles of (A,B) walks and (C,D) gallops by (A,C) hanumans and (B,D) bonnets. Horizontal lines below each graph depict the support phases of the left hind limb (LH), left forelimb (LF), right forelimb (RF) and right hind limb (RH). Note that the phase relationship between head translation and head rotation is variable during the walk cycle, ranging from nearly 180° out of phase to more closely in phase. By contrast, head translation and rotation are nearly in phase over most of the gallop cycle, with small counter rotations occurring primarily when the head reaches maximal heights and depths of translation. Also note that in the depicted hanuman walk cycle (A), the head pitched downward ($>20^\circ$) throughout the cycle as the monkey looked down at the support surface. In the remaining three cycles depicted (B–D), by contrast, the monkeys rotationally stabilized ($<20^\circ$) their heads.

mechanics of gallops. Specifically, in the initial portion of the gait cycle, the cranial end of the trunk raised upward to lift the forelimbs and allow the feet to completely support body weight. Subsequently, the caudal end of the trunk rose upward to lift the hind limbs, while the cranial end dropped downward to lower the forelimbs, enabling the hands to completely support body weight. Finally, near the end of the cycle, the hands lifted off the support surface to allow a brief airborne phase as the caudal end of the trunk lowered once again to bring the feet into contact with the support at the beginning of the next cycle. The head, in contrast to the trunk, rotated minimally about the pitch axis, but those rotations that did occur were usually in the same direction as the trunk. The head, however, did experience large vertical translations due to the rise and fall of the cranial end of the trunk. Near peak ascent or descent of the trunk, the head appeared to rotate downward or upward, respectively, suggesting an adjustment in head orientation.

Quantitatively, gallops differed from walks and hanuman gallops differed from bonnet gallops in several aspects (Table 1). In both species, mean gallop (diagonal and rotary

combined) velocities were faster and mean cycle durations were shorter than in walks. Hanumans, however, galloped faster and with longer cycle durations than bonnets.

In both species, rotations of the trunk about the pitch axis relative to space were larger than head rotations during gallops and larger than trunk rotations during walks. Trunk rotations were larger in hanumans, however, than in bonnets (Fig. 3). The ranges of head rotation relative to space were less than 20° but slightly larger in hanumans than in bonnets. These head rotations were comparable within each species, however, to the average rotations found during walks (Fig. 3). Head rotations about the pitch axis relative to the trunk were also larger than during walks in both species and were larger in hanumans than in bonnets.

Mean vertical head translations and both mean and maximal vertical head velocities during gallops were larger than during walks in both species and were larger in hanumans than in bonnets. Vertical head movements were positively correlated with pitch-plane rotations of this segment in both species, but more strongly in bonnets

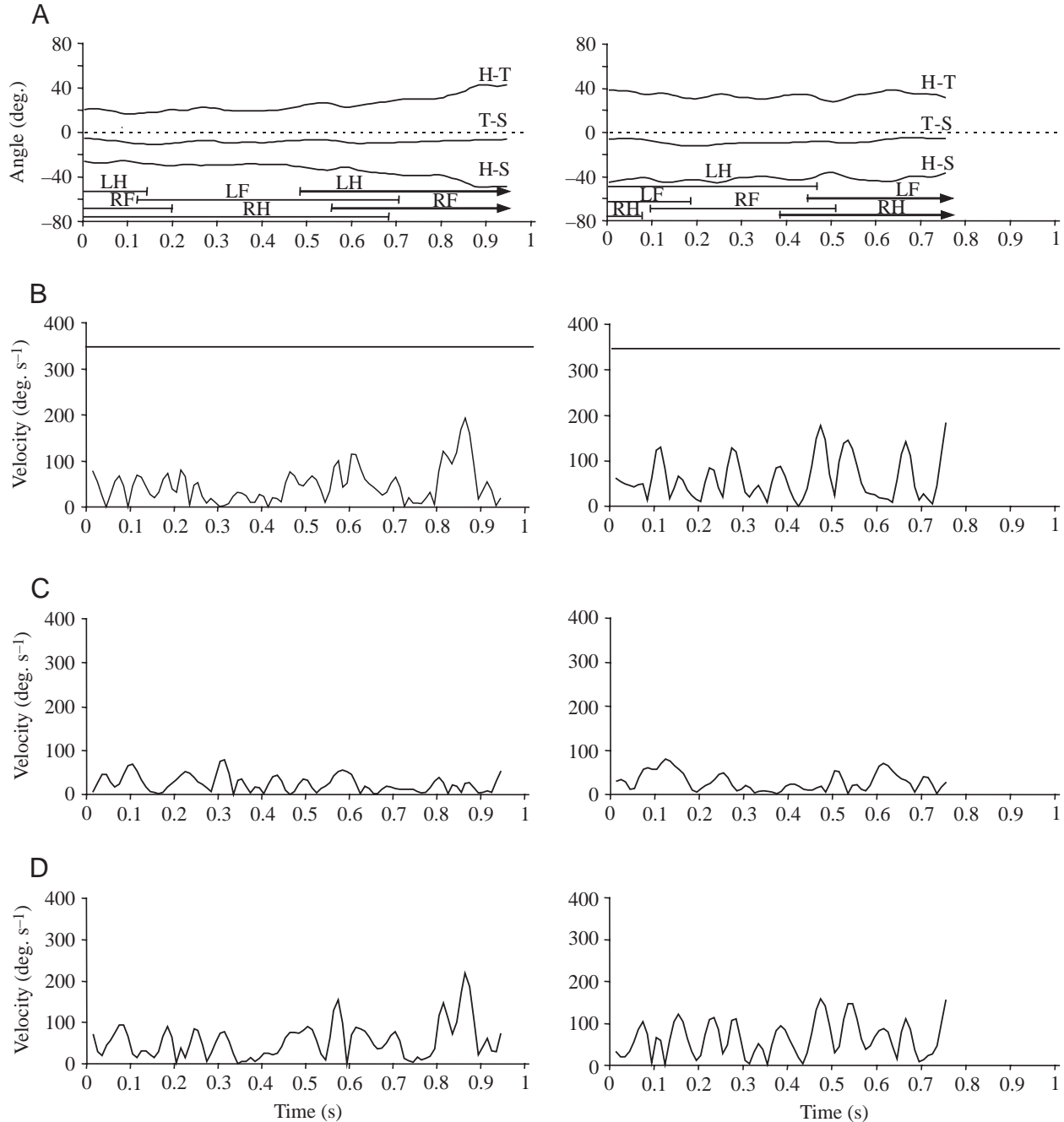


Fig. 5. Segmental angular displacements and instantaneous angular velocities during single representative cycles by a hanuman walking at 0.9 m s^{-1} (left column) and a bonnet walking at 1.0 m s^{-1} (right column). (A) The segmental displacement graphs depict changes in head-to-space (H-S), trunk-to-space (T-S) and head-to-trunk (H-T) angles. Earth horizontal is indicated by 0° (broken horizontal line), and negative values indicate a nose-down angle of the head axis and a shoulders-down angle of the trunk axis. The horizontal lines depict the support phases of the left hind limb (LH), left forelimb (LF), right forelimb (RF) and right hind limb (RH). The remaining graphs depict instantaneous angular velocity changes of (B) the head relative to space, (C) the trunk relative to space and (D) the head relative to the trunk. In B, the head-to-space velocity graphs, the solid horizontal lines indicate 350 deg. s^{-1} , which, at least in humans, is the saturation velocity for the vestibulo-ocular (VOR) reflex (Pulaski et al., 1981). Note that the pitch velocities of the head-to-space angular displacements are greater than those of the trunk-to-space angular displacements and that head angular velocities remain below 350 deg. s^{-1} throughout the cycle duration.

($r^2=0.73$, $s.d.=0.37$) than in hanumans ($r^2=0.37$, $s.d.=0.31$). This finding indicated that the direction of head rotation and vertical displacement were in phase to a greater degree in gallops than in walks (Fig. 4). Nevertheless, the direction of

head rotation was at times out of phase with vertical translations. Unlike during walks, head rotations during gallops were most affected by the large pitch-plane rotations of the trunk, characteristic of this gait, and by hind limb

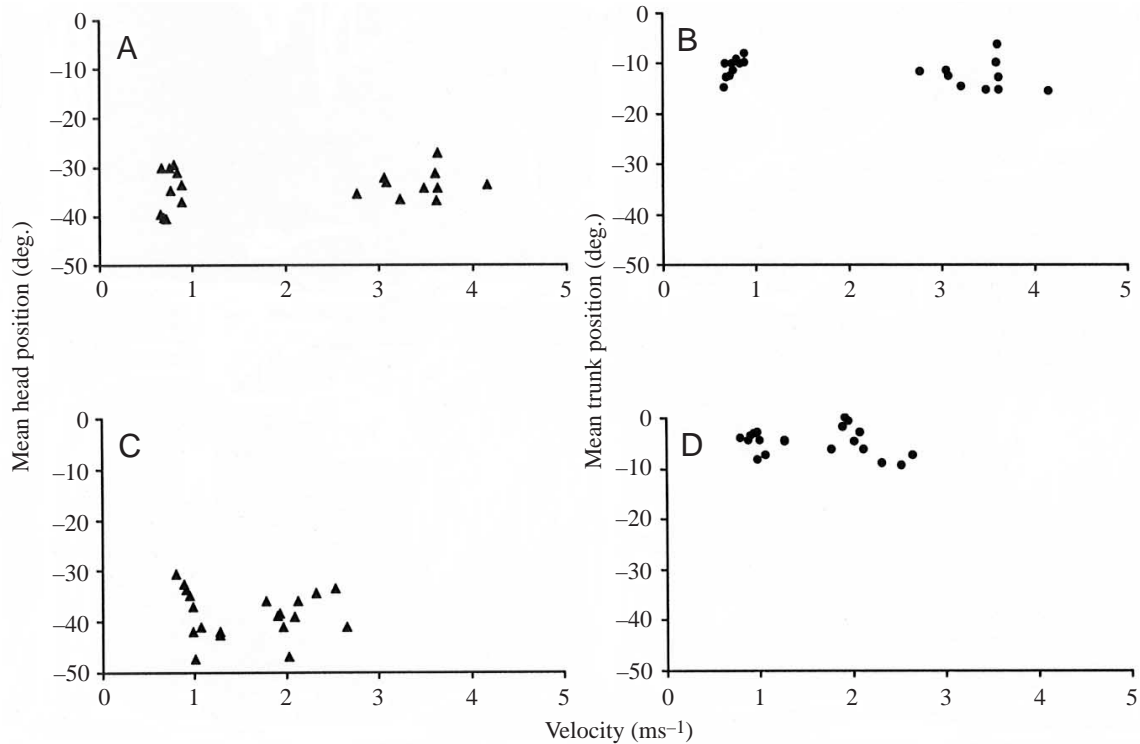


Fig. 6. Mean angular positions of the (A,C) head (triangles) and (B,D) trunk (circles) segments in the pitch plane during walks and gallops by (A,B) hanumans and (C,D) bonnets ($N=10$ cycles/gait/species). Within each graph, the clusters of symbols to the left (lower velocities) are for walks, whereas the clusters to the right (higher velocities) are for gallops. Note that in both species, the range of mean positions for each segment is very similar during both walks and gallops.

touchdowns (Figs 4, 7). Specifically, during ascent or descent of the cranial trunk, the head made intermittent, adjusting pitch rotations in the downward or upward direction, respectively. In addition, following touchdown of the leading

hind limb and prior to touchdown of the trailing forelimb, the head pitched upward with the extending trunk, as the latter segment countered the downward pitch of the body and increased stride length (Fig. 7A₂,A₇,B₂).

Head-to-trunk angles were more highly correlated with trunk-to-space angles ($r^2=0.91$ for hanumans and 0.81 for bonnets) than with head-to-space angles ($r^2=0.18$ for hanumans and 0.28 for bonnets), verifying that the trunk was effectively rotating on the head rather than the head on the trunk (Fig. 8). All combined probabilities (Sokal and Rohlf, 1981) were significantly different at the 0.001 level.

Mean instantaneous rotational velocities of the head about the pitch axis relative to space during gallops did not differ between species or from mean head rotational velocities during walks. Whereas the maximal head-to-space velocities also did not differ from the velocities that occurred during walks in either species, these maximal velocities were higher in

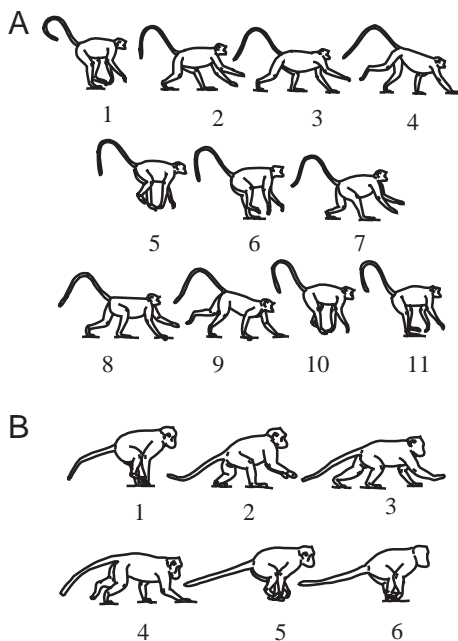


Fig. 7. Cine film tracing of (A) a rotary gallop by a hanuman langur and (B) a transverse gallop by a bonnet macaque. Note the minimal rotations of the head in any plane by both species. Airborne or flight phases occur at the end of the cycles by both (A₅,A₁₀) hanumans and (B₅) bonnets. Note also that two rotary gallop cycles are depicted for the hanuman: a clockwise touchdown sequence (A₁–A₅) followed by a counterclockwise sequence (A₆–A₁₀).

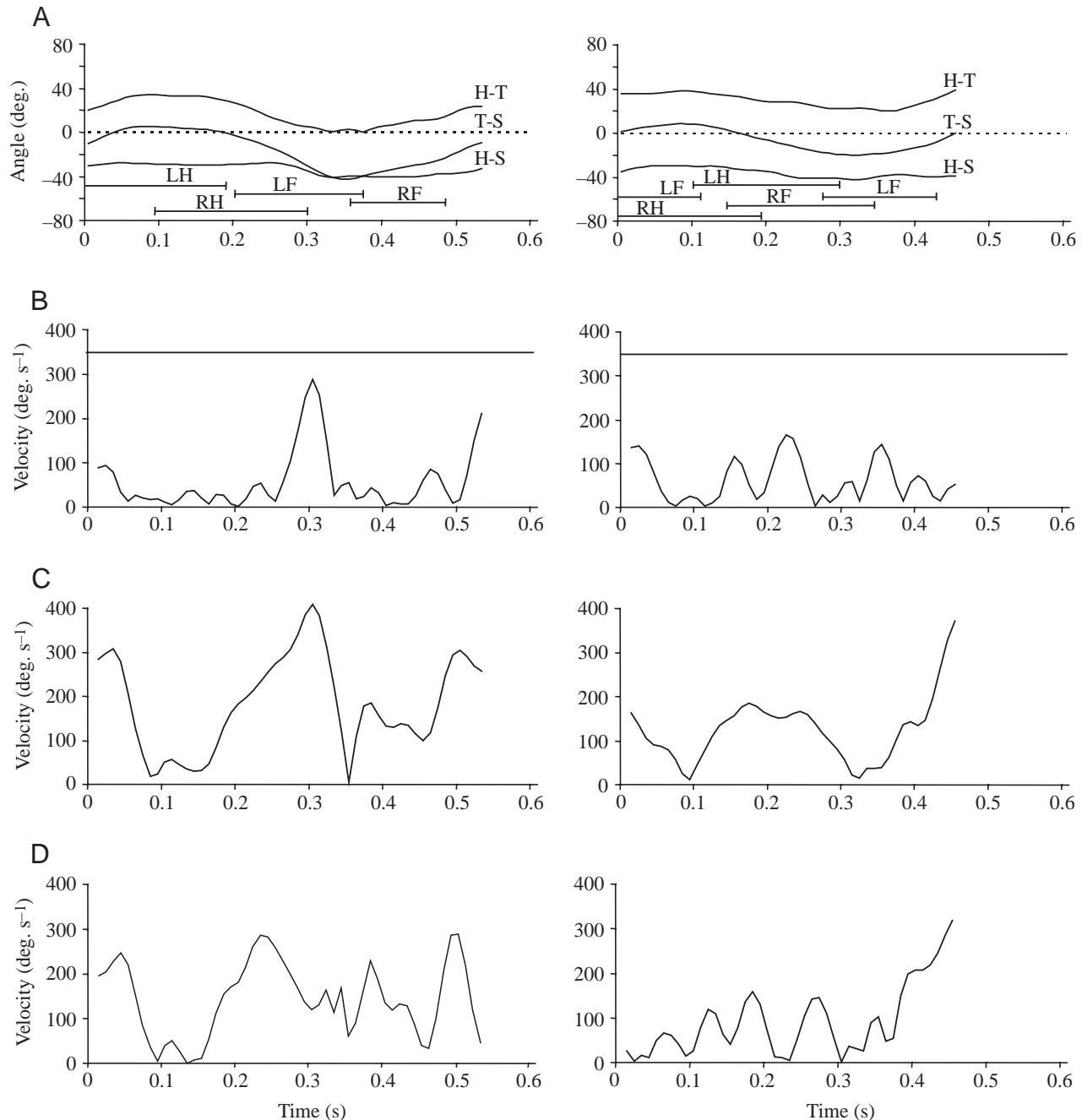


Fig. 8. Segmental angular displacements and instantaneous velocities during single representative cycles by a hanuman galloping at 3.2 m s^{-1} (left column) and a bonnet galloping at 2.1 m s^{-1} (right column). (A) The segmental displacement graphs depict changes in head-to-space (H-S), trunk-to-space (T-S) and head-to-trunk (H-T) angles. Earth horizontal is indicated by 0° (broken horizontal line), and negative values indicate a nose-down angle of the head axis and a shoulders-down angle of the trunk axis. Positive values, seen in T-S, indicate a shoulders-up angle. The horizontal lines depict the support phases of the left hind limb (LH), left forelimb (LF), right forelimb (RF) and right hind limb (RH). The remaining graphs depict instantaneous angular velocity changes of (B) the head relative to space, (C) the trunk relative to space and (D) the head relative to the trunk. In B, the head-to-space velocity graphs, the solid horizontal lines indicate 350 deg. s^{-1} , which, at least in humans, is the saturation velocity for the vestibulo-ocular (VOR) reflex (Pulaski et al., 1981). Note that head angular velocities remain below 350 deg. s^{-1} throughout the cycle duration and that the pitch velocities of the head-to-space angular displacements are similar to those during walking. The pitch velocities of the trunk, however, increase to or surpass the levels of the head.

hanumans than in bonnets. Mean rotational velocities of the trunk relative to space were higher in gallops than in walks for both species and were higher in hanumans than in bonnets

(Fig. 8). Maximal trunk-to-space rotational velocities were also higher in gallops than in walks but did not differ significantly between species. Mean head-to-trunk rotational

velocities were higher in gallops than in walks in both species, and were higher in hanumans than in bonnets. By contrast, maximal head-to-trunk rotational velocities did not differ significantly between species. In addition, whereas maximal head-to-trunk rotational velocities were greater during gallops than during walks in bonnets, these velocities did not differ significantly between gallops and walks in hanumans.

Mean peak frequencies of pitch-plane rotations and vertical displacements of the head during gallops were 1.56 ± 0.71 Hz and 2.15 ± 0.22 Hz for hanumans and 1.37 ± 1.01 Hz and 1.17 ± 0.70 Hz for bonnets, respectively. These mean peak frequencies did not differ significantly between rotational and vertical displacements, from walks or between species.

The mean head angular position in the pitch plane relative to space during gallops differed between species (Fig. 6A,C). When adjusted by $+42^\circ$, the estimated mean position of the horizontal semicircular canals was pitched slightly upward rostrally above earth horizontal by $+9^\circ$ in hanumans and by $+2^\circ$ in bonnets. Mean trunk angular position relative to space was more steeply pitched (shoulders down) in hanumans than in bonnets (Fig. 6B,D). Furthermore, as during walks, the mean head-to-trunk angular position during gallops formed a smaller angle in hanumans than in bonnets. Nevertheless, during gallops, the mean angular positions of the head and the trunk relative to space, and the head relative to the trunk, were not significantly different from the mean positions during walks within each species.

Discussion

During natural quadrupedal locomotion by free-ranging hanuman langurs and bonnet macaques, either the head or the trunk remains stabilized rotationally relative to space (earth horizontal–gravity vertical), as defined in this study. During quadrupedal walks, the trunk is stabilized. Whereas the head can be stabilized, it frequently rotates through more than 20° about the pitch axis and up to 90° to the left or right (180° combined) about the yaw axis as the monkeys visually inspect their surroundings. During gallops, by contrast, the head is always stabilized in all planes whereas the trunk rotates through several degrees ($>20^\circ$) about the pitch axis. Thus, during walks, the head rotates on a stabilized trunk, but during gallops, the trunk effectively rotates on a stabilized head. Mean head position in the pitch plane during both gaits closely aligns the horizontal semicircular canals with earth horizontal, and pitch rotations are symmetrical about that position.

Comparisons between gaits and species

Those measured variables that differ significantly between gaits ($P \leq 0.05$; Table 1) can be attributed primarily to differences in the mechanics of walks and gallops. These variables include locomotor velocity, cycle duration and the characteristics of trunk pitch rotation required to achieve these velocities and durations. By contrast, those measured variables that are comparable between gaits ($P > 0.05$) are more likely to reflect morphological or physiological constraints or both.

These variables are associated with the head, including mean pitch displacement, velocities and peak frequencies. Note, however, that although the head pitch-plane rotations are comparable *on average* between gaits of the measured sample, rotations greater than 20° are commonly practised by both species during walks but not during gallops. Furthermore, although not measured directly, head yaw-plane rotations are also known to be frequently large during walks but minimal or absent during gallops.

Interspecific differences in the measured variables are likely to be attributed, in large part, to morphological and behavioural differences between hanumans and bonnets. Hanumans are greater in size and mass than bonnets (Roonwal and Mohnot, 1977). Furthermore, as in comparisons between langurs and macaques in general (e.g. Napier and Napier, 1967; Schultz, 1930; Washburn, 1942), the ratio of hind limb to forelimb length is greater in hanumans than in bonnets, as reflected in the mean trunk position values (Table 1). Behaviourally, the two species move differently through human habitats (Roonwal and Mohnot, 1977; D. C. Dunbar, personal observation). Hanumans appear confident, but aloof, and interact minimally with people as they move through human communities. By contrast, bonnets appear less confident but interact with and react to human activity around them. The slower average preferred walk velocity of hanumans reflects these differences (Table 1). Gallop behaviours also differ. Bonnets will gallop only when necessary (e.g. to avoid danger), preferring to walk whenever possible. By contrast, hanumans often prefer to gallop, using a slow lope at the running walk velocities of bonnets. Furthermore, hanuman segmental movements during gallops appear fluid and graceful, whereas bonnet movements appear rigid and tense. Thus, differences in morphology and psychology appear to contribute to species differences in locomotor kinematics. Some of the measured kinematic differences, however, may become reduced at more closely matched locomotor velocities. Nevertheless, regardless of differences due to morphology, behaviour or locomotor velocity, head position and displacement remain comparable across gaits in both species.

Mechanisms of segmental stabilization

Stabilization of the head or trunk or both can be attributed to the intrinsic mechanics of the musculoskeletal system (stiffness, viscoelasticity, joint design, segmental inertia) and the sensorimotor nervous system (reflexive and voluntary control). Studies attempting to flesh out the relative contributions of these variables have focused primarily on head stabilization (Bizzi et al., 1978; Goldberg and Peterson, 1986; Keshner and Peterson, 1995; Keshner et al., 1992, 1995, 1999). Kinematic and electromyographic studies of human head stabilization reveal that the relative contribution of mechanical *versus* neural mechanisms varies with the plane and frequency of head movement (Keshner and Peterson, 1995; Keshner et al., 1992, 1995, 1999). For rotations in the yaw plane, voluntary control mechanisms dominate head stabilization at lower frequencies, whereas mechanical mechanisms dominate

at higher frequencies. Reflexes (vestibulocollic, cervicocollic) smooth the transition from voluntary to mechanical control and damp the mechanical resonance that occurs at higher frequencies. For rotations in the pitch plane, by contrast, reflexes are significant at both low and high frequencies. This extended reflex role may allow voluntary control mechanisms to focus on compensating for perturbations or stimuli from the surrounding environment (Keshner et al., 1995).

The protocol of the current study allows us to consider the role of inertia in hanuman and bonnet head stabilization during locomotion. As its resonant or natural frequency is approached, the head's inertial properties will cause it, for example, to rotate in the pitch plane approximately 180° out of phase to the direction of vertical displacement under passive (e.g. minimal neuromuscular activity) conditions. Thus, inertia effectively stabilizes the head through compensatory rotations. Among humans, inertia is likely to play a dominant role in head stabilization during runs and hops but much less so during walks (Pozzo et al., 1990, 1991). Is inertia the primary stabilizer of the head during hanuman and bonnet locomotion or does it play a less important role than other mechanisms?

Inertia is predicted to become a significant factor influencing head stabilization in cats at ~5 Hz (Peterson and Goldberg, 1981). Using the cat frequency as a reference point, Guitton et al. (1986) calculate a 2–4 Hz frequency range within which inertia becomes a major factor for human head stabilization. This range was obtained by applying the following mathematical equation, based on dimensional similarity between species (Jones and Spells, 1963):

$$t \propto M^n$$

where M is mass, t is the time taken to accomplish a movement, $1/12 < n < 1/3$, and frequency $\alpha = 1/t$. Following the same procedure, we find that the theoretical ranges within which the head is at or approaching resonance are 4–5 Hz for bonnets, which have twice the mass of cats, and 3–4 Hz for hanumans, which have four times the mass. Thus, with mean peak frequencies for angular and vertical displacements ranging from 0.78 Hz to 2.15 Hz for both species and both gaits, the head's inertia is not in itself likely to be the primary stabilizer of the hanuman or bonnet head during walks and gallops. Rather, based on the frequency ranges revealed in experimental studies of humans (Keshner and Peterson, 1995; Keshner et al., 1992, 1995) and cats (Goldberg and Peterson, 1986), hanuman and bonnet heads are more likely to be stabilized by vestibulocollic and cervicocollic reflexes or voluntary neural control. The dominant role of neural mechanisms gains further support from the finding that increasing the human head's inertia by adding weights does not change its response dynamics (Keshner et al., 1999). Furthermore, normal head and trunk stabilization during posture is disrupted in vestibular patients who have lost their vestibulocollic reflex (Allum and Pfaltz, 1985; Shupert and Horak, 1996).

Segmental stabilization and mobility

Several muscles that traverse the head and neck, neck and

trunk or both the head and trunk can stabilize one segment in order to allow the other segment to move effectively (Gowitzke and Milner, 1988). Owing to differences in mass between the segments, the activity pattern of the same group of muscles will probably change, depending upon whether the head moves on the trunk (walks) or the trunk moves on the head (gallops). In support of this hypothesis, Horak et al. (1994) found for bipedal humans that, depending upon which segment moves and which is stabilized (body on head *versus* head on body), the electromyographic activity pattern for the same muscle group changes.

Segmental stabilization and spatial reference frames

Laboratory studies provide evidence that the body depends upon different segments (head, trunk, feet) to function as reference frames for supplying sensory information about spatial orientation (Berthoz, 1991; Mayne, 1974; Mergner et al., 1983, 1991; Nashner, 1985; Pozzo et al., 1990, 1991; Wilson and Melvill Jones, 1979). However, which segment provides the spatial coordinate system during a wide range of natural postural and locomotor activities with differing segmental trajectories and velocities is unclear. The *choice* of reference frame apparently depends upon the segment being spatially oriented and the task requiring this orientation. The hind limbs (and forelimbs when quadrupedal), through tactile and proprioceptive inputs, can supply information about earth horizontal during quiet stance and small postural disturbances when physical contact with the support surface is continuous (Berthoz, 1991; Nashner, 1985). During locomotion, by contrast, limb contact with the support surface is intermittent and often brief. Thus, the head and trunk segments are more likely to provide spatial reference frames during most locomotor activities.

Head mobility and stabilization

The ranges of head pitch-plane displacement during gallops by these two monkey species correspond to the ranges found in human subjects performing a variety of locomotor tasks (Pozzo et al., 1990), suggesting that the head has a preferred range of movement in the pitch plane that is restricted to 20° or less. Whereas head rotation appears to be restricted in this or any other plane during gallops, the same restrictions do not apply during quadrupedal walks. Head rotations larger than 20° do occasionally occur in the pitch plane and frequently in the yaw plane, with no apparent effect on stability. Why head excursions are larger and more common in the yaw plane than in the pitch plane during walks is unclear. One possibility may be related to differing osteoligamentous constraints on motion at the atlanto-axial joint, which allows at least 180° of yaw-plane rotation, and at the atlanto-occipital joint, which restricts motion to ~13° of pitch-plane rotation in monkeys. To increase pitch-plane rotation requires flexion and extension of the entire head-neck complex at the cervicothoracic joints between the 6th cervical and 3rd thoracic vertebrae (Graf et al., 1995). A second possibility is that, unlike yaw-plane rotations, large pitch-plane rotations may stimulate unwanted sensory inputs

from the utricular maculae. Rapid changes in tilt may result in imprecise estimation of linear motion from the maculae (Pozzo et al., 1990), and perhaps even trigger sensations of disequilibria during walking. A third possibility is that in urban and rural India, dangers (e.g. dogs, cars) usually approach in the horizontal plane, whereas dangers from overhead (e.g. birds of prey, snakes) are infrequent and require less vigilance.

What would be the benefit of a rotationally stabilized head? The head–neck system contains sensory receptors (vestibular, visual, stretch) and neural pathways (vestibulocollic, vestibulo-ocular, vestibulospinal) that influence muscles controlling eye, head, neck, trunk and limb movements. Large head rotations combined with the large trunk rotations essential for gallops may create conditions under which the brain's interpretation of sensory information about body orientation in space would be exceedingly complex and overly vulnerable to error. A stabilized head with the horizontal semicircular canals closely aligned with earth horizontal, however, can function as a reference frame or inertial guidance system by simplifying the brain's interpretation of information provided by sensory receptors about balance, and segmental and whole-body orientation relative to space (Berthoz, 1991; Mayne, 1974; Pozzo et al., 1990, 1991).

Head movements, gaze stabilization and vision

The small head rotations that do occur about the pitch axis may serve to actively counter vertical body displacements in order to reduce the degree of eye rotation necessary for maintaining gaze on a fixed object or point in space (Fuchs, 1981; Peterson et al., 1985; Pozzo et al., 1990, 1991; Robinson, 1981). When human subjects focus gaze on a target while performing bipedal locomotor tasks, the head makes compensatory movements by rotating downward when it rises vertically, and rotating upward when it falls vertically (Pozzo et al., 1990, 1991). The phase relations of these rotational and translational movements are variable during walks but are nearly 180° out of phase during runs. What phase relations do hanumans and bonnets display during walks and gallops, and are these relations the same as in humans?

Similar to human bipedal walks, the phase relation between pitch-plane rotation and vertical translation of the head during quadrupedal walks varies from being nearly in phase to being 180° out of phase. For both human and monkey walks, head rotations probably do not need to correct for vertical translations during much of the cycle because the amount of vertical displacement is small enough for corrections to be achieved by eye rotation alone. Head pitch-plane rotations and vertical translations are most often nearly 180° out of phase, however, during the two periods when the forelimbs are also nearly 180° out of phase (Figs 2, 4). At these times, when the trunk pitches downwards and the head drops the greatest distance, a rotational adjustment of the head is probably required to assist the eyes in maintaining a stable gaze.

In contrast to that seen during quadrupedal walks and during human bipedal walks and runs, pitch-plane rotations and vertical displacements of the head are largely in phase during

quadrupedal gallops (Figs 4, 7). Specifically, when the head drops, it rotates downward, and *vice versa*. Those few correctional or adjusting counter-rotations that do occur are in response to the maximal rise and fall of the head or to specific kinematic features of quadrupedal gallops (e.g. horizontally oriented trunk experiencing large pitch rotations, asymmetrical four-limb footfall and handfall pattern, trailing hind limb touchdown, trunk extension).

The finding that head rotations are not typically 180° out of phase during either quadrupedal walks and gallops or bipedal walks leads us to question the importance of fine-tuned angular adjustments for gaze stabilization and maintenance in monkeys or even humans, as suggested by Pozzo et al. (1990). Based on the relatively stable orientation of the head that always occurs during gallops and is common during walks, the monkeys appear to focus gaze on so distant a target that the change in eye-to-target angle would probably be minimal, even when head rotation corresponds to trunk rotation. Furthermore, the human locomotor tasks in which head pitch is most out of phase with head translation (i.e. running and hopping) are also the two tasks in which inertial properties of the head are most likely to dominate head stabilization (Pozzo et al., 1990). Thus, we suggest that adjusting head rotations about the pitch axis are associated less with gaze stabilization and more with maintaining vestibular pitch orientation near earth horizontal and within the 20° threshold range.

Experiments with monkeys running in a circular path, however, reveal that correctional head rotations compensate for trunk movements about the yaw axis, indicating that gaze stabilization requires both eye and head nystagmus in the horizontal plane (Solomon and Cohen, 1992). Specifically, gaze velocity is able to compensate for body velocity, suggesting that compensatory head rotations about the yaw axis are required to maintain gaze.

Head velocities during locomotion become relevant here because, at least among human subjects, the vestibulo-ocular reflex (VOR) saturates at around 350 deg. s⁻¹ (Pulaski et al., 1981). The retinal slip that occurs above this threshold velocity results in interruptions in visual input. The VOR threshold for monkey head movements during natural locomotion is unknown but, considering phylogenetic closeness and experimental evidence supporting a common neuronal organization controlling gaze and its associated reflexes in quadrupeds and bipeds (Vidal et al., 1986), the thresholds may be similar. If so, then VOR saturation is not a problem for either hanumans or bonnets because both the mean and maximal velocities of head rotations and translations remain below 350 deg. s⁻¹ during both walks (Fig. 5) and gallops (Fig. 8). A more definitive statement cannot be made, however, until VOR saturation velocities are determined experimentally for monkeys.

Trunk stabilization

During quadrupedal walks, visual inspection of the physical surroundings is common, requiring large rotations of the head and frequent changes in gaze direction. The potential problem

for the brain to correctly interpret vestibular information on spatial orientation while the head rotates may be overcome by trunk stabilization, which is characteristic of this gait. Psychophysical studies on human subjects indicate that the trunk provides a spatial reference frame. In a series of studies investigating the *perception* of head and trunk rotations and object motion in the horizontal plane, Mergner et al. (1983, 1991, 1992) demonstrate that a stabilized trunk can provide information about body orientation relative to space by combining vestibular information with proprioceptive information from the neck. They also provide evidence that the central nervous system uses a hierarchy of coordinate systems for controlling segment-to-segment and whole-body orientation in space. Specifically, the trunk (combined vestibular and nuchal signals), not the head, provides the reference frame for orientation in external space, and the coordinate systems for the head (nuchal signals) and eyes (visuo-oculomotor signals) are dependent upon the trunk-in-space coordinate system. Proprioceptors within the human trunk are also critical to the perception of verticality (Jakobs et al., 1985; Mittelstaedt, 1988) and rotation of the trunk (Taylor and McCloskey, 1990). Furthermore, non-proprioceptive receptors located within the trunk can provide the brain with information about trunk posture relative to space (Mittelstaedt, 1995, 1996, 1997, 1998; Vaitl et al., 1997). Together, these latter studies have revealed that the mass of the kidneys, and possibly other organs, as well as shifts in blood mass within major vessels, function as somatic graviceptors for position sense and for the perception of angular velocity. The human trunk, however, experiences only small rotations during bipedal locomotion. If and how these graviceptors provide postural information about the trunk during quadrupedal locomotion, particularly during gallops when the trunk experiences large pitch rotations, is unknown.

Head and trunk mean position

Mean positions of the head and trunk relative to space (earth horizontal) and the head relative to the trunk are comparable between walks and gallops, indicating that the head and trunk are making symmetrical pitch rotations about these mean positions. In addition, the mean pitch position of the head closely aligns the horizontal semicircular canals with earth horizontal. The estimated mean position of the horizontal semicircular canals is pitched slightly above earth horizontal rostrally in both species. This mean horizontal canal alignment with absolute space corresponds closely to that reported for several vertebrate species at rest (Vidal et al., 1986) and during voluntary movements (Graf et al., 1995). Furthermore, when converted to the measurement system used in the present study, the mean head positional values of three macaque species (*M. mulatta*, *M. fuscata* and *M. fascicularis*) walking on wooden beams under zoo conditions (Strait and Ross, 1999) fall within the ranges of motion for hanumans and bonnets. That the values from this zoo study do not correspond to the *mean* positional values for hanumans and bonnets more likely reflects differences in methodology than species.

Neck

The shortness of the neck in monkeys, combined with the technical limitations of filming wild animals under natural conditions, makes accurate kinematic analysis of this segment fall beyond the scope of the current protocol. The neck, forming the physical link between the head and trunk and containing essential somatosensory receptors, is nevertheless a significant segment in the mechanics and neural control of head and trunk movements. Thus far, head and trunk movements have been studied primarily in short-necked primates (monkeys, humans). Details of contributions by the neck to head and trunk movements during natural locomotion may be best revealed, however, through investigations of long-necked species (e.g. horses, giraffes).

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