Stabilization and mobility of the head and trunk in vervet monkeys (*Cercopithecus aethiops*) during treadmill walks and gallops

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Summary

The brain requires internal or external reference frames to determine body orientation in space. These frames may change, however, to meet changing conditions. During quadrupedal overground locomotion by monkeys, the head rotates on a stabilized trunk during walking, but the trunk rotates on a stabilized head during galloping. Do the same movement patterns occur during in-place locomotion? Head and trunk pitch rotations were measured, and yaw and roll rotations estimated from cine films of three adult vervet monkeys (*Cercopithecus aethiops* L. 1758) walking and galloping quadrupedally on a treadmill. Head and trunk rotational patterns during treadmill walks were comparable to the patterns found during overground walks. The rotational velocities of these segments during both treadmill walks and gallops were also comparable to the velocities found during natural locomotion. By contrast, whereas head and trunk rotational patterns during treadmill gallops did occur that were comparable to the patterns practiced during overground gallops, a significantly different pattern involving large and simultaneous head and trunk rotations was more commonly observed. Simultaneous head and trunk rotations may be possible during treadmill gallops because the fixed visual surround is providing an adequate spatial reference frame. Alternatively, or in addition to this visual information, a re-weighting in other sensory modalities may be occurring. Specifically, the vestibular inputs used during overground locomotion to reference gravity or a gravity-derived vector may become less important than proprioceptive inputs that are using the treadmill belt surface as a reference. Regardless, the spatial reference frame being used, blinks that occur at specific times during the largest head yaw rotations may be necessary to avoid the initiation of unwanted and potentially destabilizing lateral sway brought on by sudden increases in optic flow velocity.

Key words: spatial reference frames, pitch, yaw, roll, gaze, visual input, optic flow, blinks, vestibular input, proprioception, sensory re-weighting, quadrupedal locomotion.

Introduction

Successful locomotion depends not only on the appropriate patterns of segmental movements, but also on the input and reliable processing of sensory (visual, vestibular and somatosensory) information to coordinate these movements. Treadmill locomotion provides the foundation for much of what we do know about sensorimotor coordination of locomotion. Treadmills constrain whole–body displacements, simplifying the recording of physical and neurophysiological signals, and the control and manipulation of physiological and environmental variables. Visual, vestibular and proprioceptive inputs during treadmill and overground locomotion, however, are not identical. Thus, the degree to which sensory processing and motor strategies for balance and spatial orientation in unnatural treadmill locomotion are similar to natural overground locomotion is unknown. Nevertheless, this information is critical for determining how treadmill data can be used to infer locomotor control strategies that have evolved in the nervous system. This study addresses the issue by focusing on one aspect of locomotion: head and trunk movement patterns during quadrupedal walks and gallops.

Previous studies of natural locomotion on the ground and flat surfaces by monkeys (*Macaca radiata* and *Semnopithecus entellus*) in the wild (Dunbar and Badam, 1998; Dunbar et al., 2004) and under semi-natural conditions (*Macaca mulatta*) (Dunbar and Badam, 1998) reveal that movement patterns of the head and trunk differ between gaits. During quadrupedal walks, which are characterized by a symmetrical footfall pattern, the trunk rotates through 10° or less in the pitch or sagittal plane. The head, however, is free to rotate in the pitch (>20°) and yaw or transverse (up to 180°) planes during quadrupedal walks without any apparent disturbance to balance or spatial orientation. By contrast, the relative degree of segmental mobility reverses during quadrupedal gallops, a gait that incorporates an asymmetrical footfall pattern and an airborne phase. The trunk experiences large pitch rotations of up to 50°. The head, however, experiences only small rotations

(<20°) in the pitch plane and minimal rotations in any other plane. Thus, using 20° as a threshold angle (for rationale, see Dunbar et al., 2004), the head rotates on a stabilized trunk during walks, but the trunk effectively rotates on a stabilized head during gallops.

The above findings were interpreted to indicate that the nervous system requires either the head or the trunk to be rotationally stabilized to provide a reference frame for determining body orientation relative to space (e.g. gravity vertical or gravito–inertial acceleration vector). During gallops, a stabilized head in a face-forward, downwardly pitched orientation that aligns the horizontal semicircular canals near earth-horizontal allows the eyes and vestibular apparatus to provide the brain with redundant reference frames for gaze (Berthoz and Pozzo, 1988; Clément et al., 1988; Grossman et al., 1988; Owen and Lee, 1986; Pozzo et al., 1990), and spatial orientation and heading (Gdowski and McCrea, 1999; Mayne, 1974; Pozzo et al., 1990). Evidence continues to accumulate that the vestibular apparatus functions as an inertial navigational system (Berthoz and Pozzo, 1994; Dunbar et al., 2004; Mayne, 1974; Pozzo et al., 1990) within the stable platform of the head (Pozzo et al., 1990), and is sensitive to the gravito–inertial acceleration vector (Imai et al., 2001). Together, these visual and vestibular cues can also determine locomotor velocity (speed of approach) and acceleration (Bertin et al., 2000; Prokop et al., 1997; Telford et al., 1995; Varraine et al., 2002). During walks, by contrast, a stabilized trunk can provide information about spatial orientation by combining signals from the vestibular apparatus and neck proprioceptors (Mergner et al., 1983, 1991, 1992), and from proprioceptors (Jacobs et al., 1985; Mittelstaedt, 1988; Taylor and McCloskey, 1990) and nonproprioceptive receptors (Mittelstaedt, 1995, 1996, 1997; Vaitl et al., 1997) in the trunk itself.

Visual, vestibular and somatosensory inputs are also important for eliciting body sway when necessary to correct posture (Allum, 1983; Berthoz et al., 1979; Bronstein, 1986; Day et al., 1997; Jeka et al., 1997; Kavounoudias et al., 1999; Lackner and DiZio, 1993; Lee and Lishman, 1975; Lestienne et al., 1977; Nashner and Wolfson, 1974), and to initiate neuromuscular activity during free-fall or at the appropriate time before touchdown to prepare the limb for absorbing the force of impact and supporting the body against the effects of gravity (Dietz and Noth, 1978; Dufek and Bates, 1990; Engberg and Lundberg, 1969; Greenwood and Hopkins, 1976; Lacour and Xerri, 1980; Liebermann and Goodman, 1991; McKinley and Pedotti, 1992; McKinley and Smith, 1983; Melvill Jones and Watt, 1971a,b; Santello and McDonagh, 1998; Santello et al., 2001; Vidal et al., 1979; Watt, 1976). The relative contributions of the different sensory inputs can change or become 're-weighted', however, depending upon the environmental conditions. In a posture control study, Peterka (2002) found that proprioceptive inputs concerning the support surface dominate when subjects correct for small perturbations without vision. As the size of the postural disturbance increases, however, the gain for gravity-related (vestibular) feedback increases while the gain for surface-related (proprioceptive) feedback decreases.

Even under natural conditions, all sources of sensory information are not constantly available. Visual input in particular is normally interrupted, albeit briefly, by blinks. These rapid and stereotyped eyelid movements serve to protect the cornea (Porter et al., 1993). Whether blinks occur only intermittently in response to corneal irritation or also at specific times during eye or head movements is unclear. The latter case would suggest that blinks serve an additional role in filtering visual input.

The nervous system's ability to interpret correctly sensory information on spatial orientation, balance, locomotor velocity, correct limb placement and antigravitational support has evolved in the context of the animal moving relative to its environment (e.g. overground). The issue then arises as to whether a stabilized segment is necessary for interpreting this information when the body remains stationary relative to its surroundings (i.e. in-place). One major difference between these two conditions concerns visual and vestibular input, especially the presence or absence of optic flow and otolith stimulation, respectively. This present study, therefore, addresses the following two questions: (1) are head and trunk movements during treadmill locomotion the same as, or different from, those movements occurring during overground locomotion? (2) During head movements, do blinks occur at particular times and, if so, when? The African vervet monkey (*Cercopithecus aethiops* L. 1758*)*, which has been studied previously in captivity during overground (Hurov, 1985; Larson and Stern, 1989), wooden beam (Strait and Ross, 1999), treadmill (Vilensky and Gankiewicz, 1990a,b; Vilensky et al., 1990), and jump-down (Dyhre-Poulsen and Laursen, 1984; Laursen et al., 1978) locomotion, will be the investigated species. I hypothesize that (1) head and trunk rotations during treadmill walks and gallops will be comparable to the rotations reported for overground locomotion (Dunbar et al., 2004), and (2) blinks that do occur will be associated with rapid head movements.

Materials and methods

Analysis was based on 16 mm cine films of three small (~2.5–3.0 kg) adult female vervet monkeys walking and galloping on a motorized treadmill (Commercial Engineering, Fort Wayne, IN, USA). The monkeys, which were trained and filmed by J. A. Vilensky (Indiana University, Fort Wayne, IN, USA), were initially introduced to the treadmill when it was not running. Beginning with a very slow setting, the treadmill speed was gradually increased over subsequent days. Training 7 days a week and using only food rewards, the entire process was completed in about 3 weeks.

The cine camera (Redlake, San Diego, CA, USA) was mounted on a tripod and recorded the treadmill gaits from lateral view at a 100 Hz (frames s^{-1}) filming rate. Both the cine camera and treadmill were leveled before filming, aligning the filmed image of the treadmill belt surface with earth horizontal.

A digital speedometer mounted on the treadmill and within the field-of-view of the camera lens indicated instantaneous belt speeds. A total of 10 walk cycles (3 cycles from monkey 1; 3 cycles from monkey 2; 4 cycles from monkey 3) and 10 gallop cycles (4 cycles from monkey 1, 3 cycles from monkey 2; 3 cycles from monkey 3) were extracted for quantitative analysis of pitch plane movements. For inclusion in this sample, head and trunk orientation and movements had to remain in approximately the same (pitch) plane and perpendicular to the camera lens. This perspective minimized parallax measurement error and allowed meaningful comparisons with overground gait cycles in the wild (Dunbar et al., 2004). In addition, a total of 60 (20 cycles/monkey) walk cycles and 60 (20 cycles/monkey) gallop cycles, which were separate from the cycles for quantitative analysis above, were analyzed for yaw and roll rotations and orientations of the head. Blinks (down-phase and up-phase of the eyelid combined) were also analyzed during these head yaw rotation cycles, as well as during 12 performances of one walking monkey turning around on the treadmill in response to reversals in belt direction (referred to in this study as 'turn-arounds'). The pale eyelids and dark eyes of this species made it possible to determine when blinks occurred.

Analysis followed previously described procedures (Dunbar et al., 2004). Briefly, a three-axis (pitch, yaw, roll) coordinate system defined rotations in the sagittal (pitch), transverse (yaw) and coronal (roll) planes, respectively. Each cycle was analyzed frame by frame with a digitizer (Numonics Corp., Montgomeryville, PA, USA) and computer. Head and trunk pitch-plane rotations were measured (SigmaScan, SPSS Inc., Chicago, IL, USA) quantitatively relative to earth-horizontal, using the treadmill belt surface as the reference. The head axis passed through the ear (external auditory meatus) and the tip of the mouth, with the ear serving as the apex for head angle (Fig. 1). The trunk axis passed through the hip and shoulder joints, with the hip serving as the apex for trunk angle. Head-to-trunk angles were then calculated from these head-in-space and trunk-in-space measurements. The head or trunk was considered to be rotationally stabilized when pitch displacements were 20° or less (for rationale, see Dunbar et al., 2004). The pitch displacement data were used to derive angular velocities. At each processing step, data were smoothed with engineering software (MATLAB, The Math Works, Inc., Natick, MA, USA), using a low-pass filter cut-off frequency of 10 Hz to minimize measurement error. The mean position or orientation of the head and trunk relative to earth horizontal were calculated from the maximum and minimum positional values measured throughout each cycle. A negative value indicated that the head axis (mouth down) or trunk axis (shoulders down) was tilted downward below earth horizontal (0°). The orientation of the horizontal semicircular canals relative to space, unknown in vervets, was estimated by adjusting the mean head positional angles by +40°, a corrective value that was derived from other monkey species (for rationale, see Dunbar et al., 2004).

The following quasi-quantitative observational system classified head yaw rotations: head facing forward = 0°, head facing laterally into or directly away from camera lens = 90°,
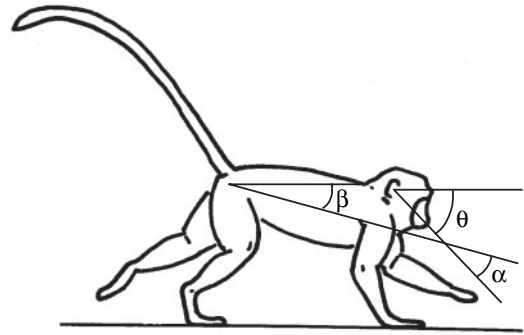

Fig. 1. Measured axes and angles in the pitch plane. Head axis was a line passing through the external auditory meatus and the apex of the mouth. Trunk axis was a line passing through the hip and shoulder joints. Head angle relative to space (θ) and trunk angle relative to space (β) were measured in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

head facing backwards over shoulder = approaching 180°, head facing halfway between forward and laterally = 45°, and head facing halfway between laterally and backwards over shoulder = 135°. Measurements of blink duration were based on the number of elapsed cine film frames.

Quantitative variables were compared between gaits with Student's *t*-test. To determine what mean percentage of head-to-trunk angular displacements were contributed by changes in head-to-space angle versus trunk-to-space angle, the following procedure was used (Dunbar et al., 2004). Pearson's product moment correlation coefficients were obtained for head-to-space and trunk-to-space angles against head-to-trunk angles for each cycle, and the mean percentage of variance was calculated from the means of the z-transformed correlations. For each cycle, a test of homogeneity (Sokal and Rohlf, 1981) was used to compare the correlation coefficients, and to reveal if head and trunk positions were significantly different determinants of head-to trunk angle. Finally, joint probabilities for each comparison were calculated to determine the significance of the differences in the mean percentage of head-to-trunk angle that were explained by head-to-space angle versus trunk-to-space angle. For all statistical tests, *P*-values less than or equal to 0.05 were considered significant.

Results

Head rotations in the yaw plane characterized the majority of quadrupedal walks and gallops on the treadmill. Nevertheless, 10 walk and 10 gallop cycles were found in which head movements were confined to the pitch plane. Table 1 summarizes the mean measurement for each variable and the results of *t*-tests comparing these latter walk and gallop cycles.

Treadmill walks

The vervet monkeys usually walked with a diagonal sequence pattern (i.e. hind limb followed by opposite forelimb)

Table 1. *Summary of mean measurements and* t-*tests*[a]

	Walk	Gallop	*P*-value
Treadmill speed (m s^{-1}) (±S.D.)	1.54 (±0.40)	2.76 (±0.26)	<0.001
Gait cycle duration (ms) (±S.D.)	446 (±44)	365 (±47)	<0.05
Head-to-space pitch displacement (deg.) (±S.D.)	15 (±7)	14 (±7)	>0.05
Trunk-to-space pitch displacement (deg.) (±S.D.)	6 (±2)	25 (±7)	<0.001
Head-to-trunk pitch displacement (deg.) (±S.D.)	14 (±6)	22 (±6)	<0.01
Head-to-space mean pitch velocity (deg. s^{-1}) (±S.E.M.)	66 (±10)	80 (±12)	>0.05
Trunk-to-space mean pitch velocity (deg. s^{-1}) (±S.E.M.)	38 (±4)	126 (±8)	<0.001
Head-to-trunk mean pitch velocity (deg. s^{-1}) (±S.E.M.)	74 (±9)	123 (±12)	<0.01
Head-to-space maximum pitch velocity (deg. s^{-1}) (±S.E.M.)	194 (±25)	202 (±29)	>0.05
Trunk-to-space maximum pitch velocity (deg. s^{-1}) (±S.E.M.)	87 (±9)	271 (±27)	<0.001
Head-to-trunk maximum pitch velocity (deg. s^{-1}) (±S.E.M.)	197 (±20)	311 (±33)	<0.01
Head-to-earth horizontal mean position (deg.) (±S.E.M.)	−31 (±2)	−34 (±3)	>0.05
Trunk-to-earth horizontal mean position (deg.) (±S.E.M.)	−10 (±7)	−15 (±1)	<0.001
Head-to-trunk mean position (deg.) (±S.E.M.)	21 (±2)	20 (±3)	>0.05

[a]*N*=10 locomotor cycles per gait.
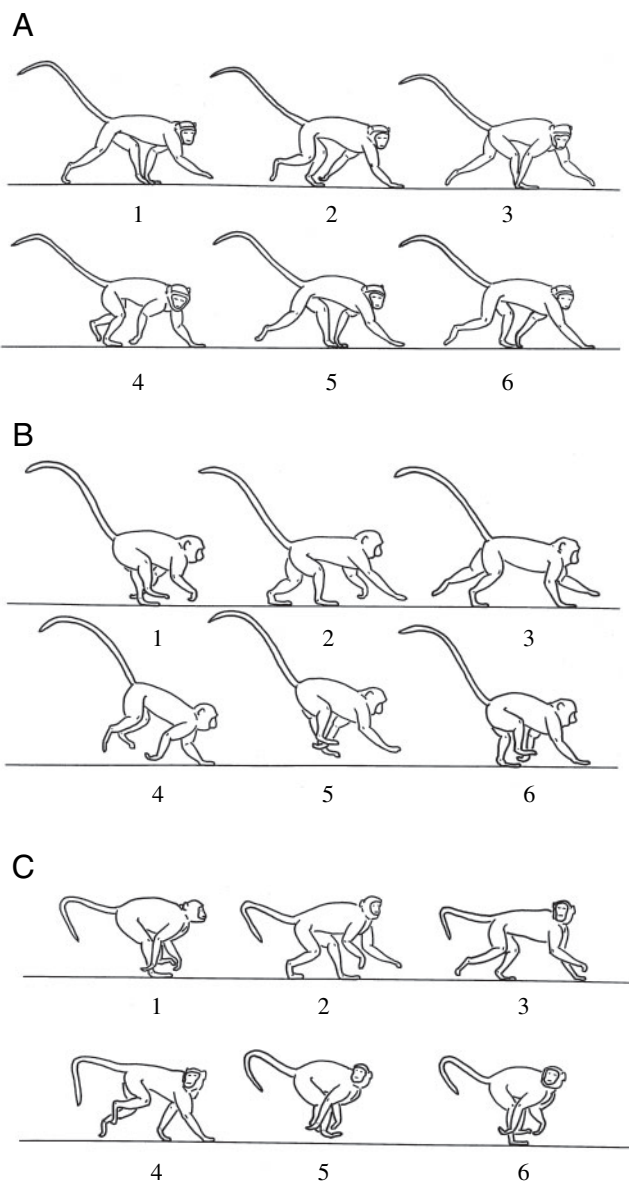
(Fig. 2A), although lateral sequence patterns (i.e. hind limb followed by ipsilateral forelimb) also occurred. Head angular motions occurred in the yaw and pitch planes. Yaw-plane rotations were usually 45° and 90° as the monkeys looked toward or directly into the camera lens, but in 13 episodes lasting 1 to 3 cycles these rotations approached 180° as they looked over the shoulder at the trainer standing behind the treadmill. The latter head rotations included a noticeable roll component as the monkeys looked backward and upward.

Blink activity varied depending upon the degree and direction of head yaw rotation. Blinks did not occur when the head turned up to 90° backwards (from anterior to posterior) or forwards (from posterior to anterior). Blinks also did not occur when the head rotated backwards to nearly 180°. By contrast, in 4 out of 7 behavioral episodes when the head rotated forwards rapidly and without delay back into the pitch plane, a blink of approximately 50 ms in duration occurred beginning at 90° and ending at 45°. Furthermore, in 6 out of 12 sequences during which one of the monkeys performed a turn-around, a 50 ms blink also occurred at comparable angles during forward head turns. In 7 of the 9 remaining episodes (head rotation only + turn-arounds) in which the eyes did not blink on the forward return, the head stopped momentarily at 90° before completing its forward rotation.

The mean ranges of pitch rotations from the quantitative sample (Table 1) reveal that, although both the head and trunk were usually stabilized (<20°) during walks, the head rotated significantly more than trunk (Figs 3A, 4A). Head-to-trunk angles were more highly correlated with head-to-space angles (r^2=81.92%) than with trunk-to space angles (r^2=14.05%), verifying this head-on-trunk rotational pattern. All combined probabilities (Sokal and Rohlf, 1981) were significantly

Fig. 2. Cine film tracing of (A) a diagonal-sequence walk with the head oriented between 45° and 90° to the trunk while rotating downwards and upwards, (B) a rotary gallop with no head rotation in the yaw plane, and (C) a rotary gallop with a large head rotation to the right of more than 90° in the yaw plane.

different at the 0.01 level. The head, however, was commonly observed to pitch through a much larger range – 32° in one cycle – as the monkeys looked overhead or down at the treadmill belt. By contrast, the trunk remained rotationally stabilized in all planes. Paralleling the displacement values above, mean and maximal pitch velocities were much larger for the head than the trunk during walks, and head-to-trunk pitch velocities were closer to those of the head than the trunk (Fig. 4C,E,G).

Whereas mean trunk position was closer to earth horizontal (Fig. 3D), mean head position was pitched downward (–31°) (Fig. 3C). When this value is adjusted by +40° (see Materials and methods), the predicted orientation of the horizontal semicircular canals would be 9° above earth horizontal (upward tilt rostrally). The monkeys, however, commonly fixed gaze on objects immediately above the treadmill or on the treadmill belt immediately before them, requiring the head be held in positions of upward (e.g. ~30°) or downward (e.g. ~–90°) pitch, respectively. These head positions moved the horizontal semicircular canals into more vertical orientations relative to space. The head was also commonly rotated and held in a position of yaw (~90°) to fix gaze on the cine camera located to one side (Fig. 2A), and in a combined position of yaw (approaching 180°) and roll in order to fix gaze on the trainer standing behind the treadmill.

Treadmill gallops

The vervet monkeys galloped with either a transverse (i.e. leading hind limb followed by contralateral forelimb) or rotary (i.e. leading hind limb followed by ipsilateral forelimb) pattern (Fig. 2B,C). As during walks, head rotations were most commonly at 45° and 90°, but in 7 episodes, which also lasted 1–3 cycles, these rotations approached 180° to look over the shoulder (Fig. 2C). Blink activity also corresponded to that during walks and turn-arounds, but was even more consistent. In 6 out of 7 cycles in which one of the monkeys looked backwards over its shoulder, no blink occurred when the head turned from forwards to backwards, but a 50 ms blink occurred beginning at 90° and ending at 45° when it turned from backwards to forwards. During the one cycle in which the blink did not occur, the head stopped turning momentarily at 90° to
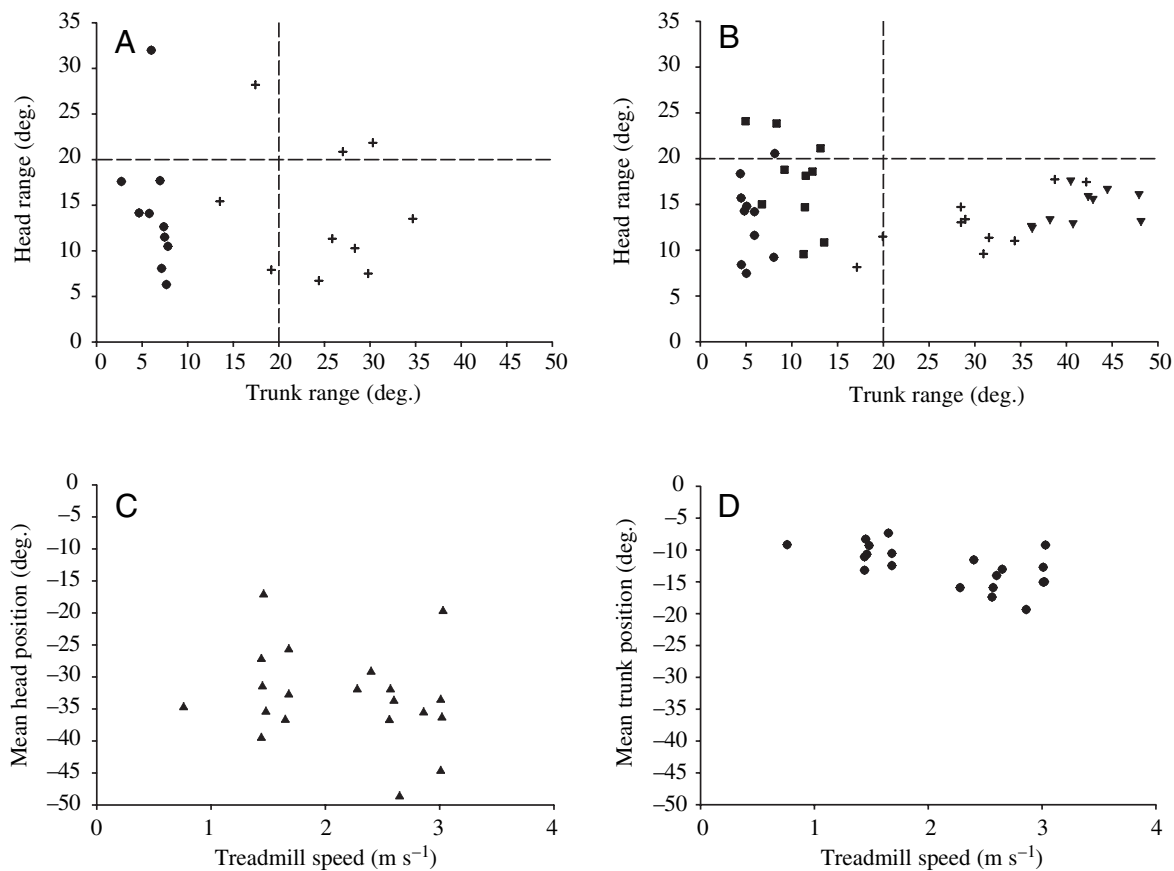

Fig. 3. Ranges and mean positions of the head and trunk during treadmill walks and gallops (*N*=10 cycles/gait). Vervet head range is plotted against trunk range (A). The circles depict walks and the crosses depict gallops. A comparable head range-trunk range plot (B) based on overground locomotor data for two other species (*Macaca radiata* or bonnet macaque, *Semnopithecus entellus* or hanuman langur) is provided for comparison (Dunbar et al., 2004). The circles depict walks and the crosses depict gallops by bonnet macaques, whereas the squares depict walks and the inverted triangles depict gallops by hanuman langurs. In A and B, the horizontal and vertical dashed lines indicate the 20° threshold for stabilization of the head and trunk, respectively. Mean head (C) and trunk (D) positions are plotted against locomotor velocity. In A and C, the clusters of symbols to the left (lower velocities) are for walks, whereas the clusters to the right (higher velocities) are for gallops.

fix gaze on the camera lens before completing the forward rotation, as was observed during walks and turn-arounds.

In the quantitative sample in which the head remained in the pitch plane (Table 1), pitch rotations of the trunk relative to space during gallops were much larger than during walks, but mean head pitch rotations relative to space were equivalent (Figs 3A, 4B). Head-to-trunk pitch rotations were closer to those of the trunk relative to space than to the head relative to space, and significantly larger than during walks. Head-to-trunk angles were more highly correlated with trunk-to-space angles (r^2=78.39%) than with head-to space angles (r^2=20.99%). Thus, in contrast to walks, when the head was restricted to the pitch plane, the trunk effectively rotated on the head. All combined probabilities (Sokal and Rohlf, 1981) were significantly different at the 0.01 level. The relative magnitudes of the segmental velocities, once again, paralleled those of the
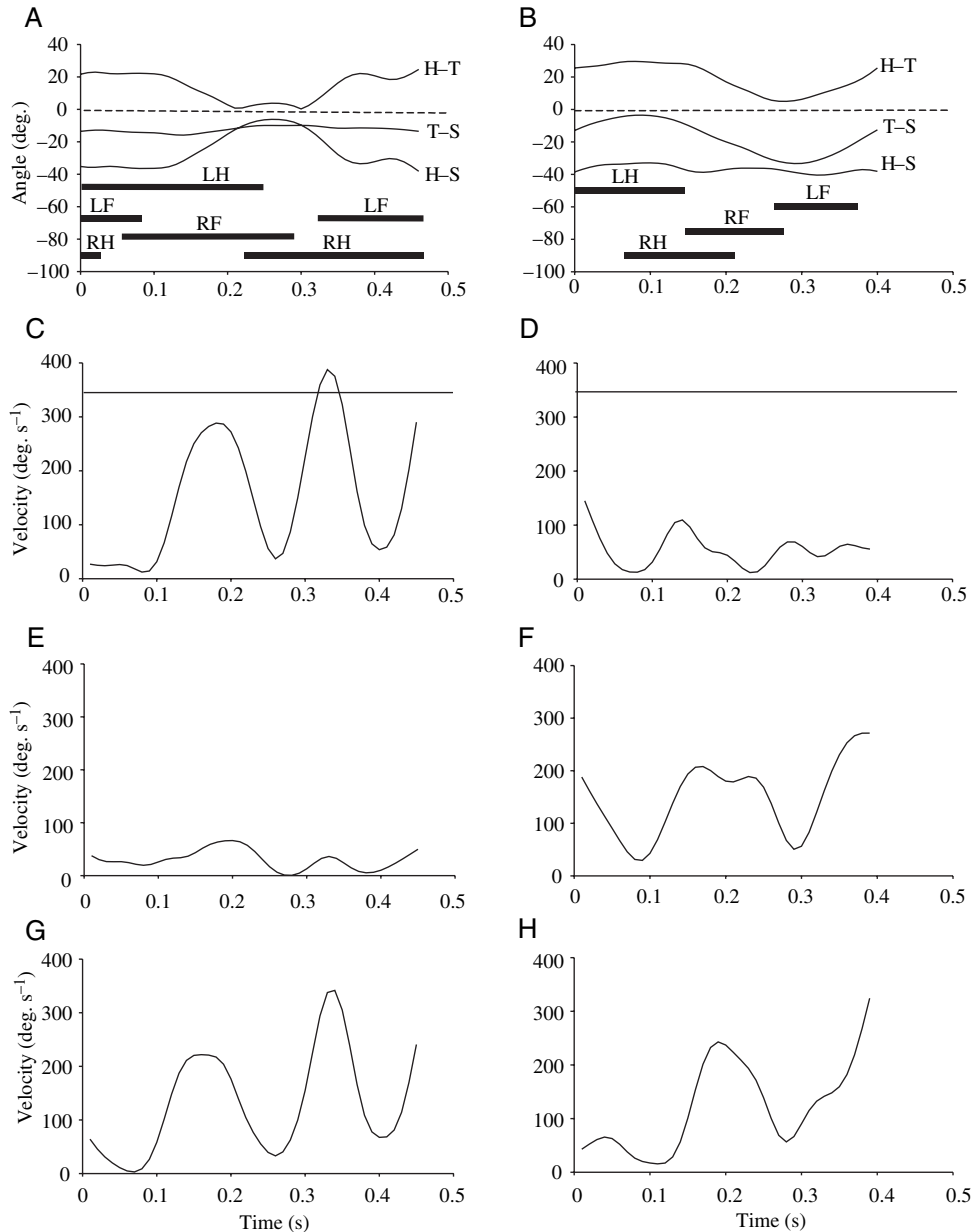

Fig. 4. Segmental angular displacements and instantaneous angular velocities during single representative cycles of a diagonal sequence walk (left column) and a rotary gallop (right column) at treadmill speeds of 1.68 m s^{-1} and 2.56 m s^{-1}, respectively. Note that in this gallop cycle (B), the head is pitching through less than 20° and is not rotating in any other plane. The (A,B) 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° (dashed 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 (C,D) the head relative to space, (E,F) the trunk relative to space and (G,H) the head relative to the trunk. In (C,D) the head-to-space velocity graphs, the solid horizontal lines indicate 350° s^{-1} that, at least in humans, is the saturation velocity for the vestibulo–ocular (VOR) reflex (Pulaski et al., 1981).

displacement data above (Fig. 4D,F,H). Both mean and maximal pitch velocities of the trunk relative to space were greater than those of the head, and greater than during walks. These velocities for the head relative to the trunk were closer to those of the trunk relative to space and also greater than during walks. The mean and maximal pitch velocities for the head, however, were comparable to those during walks.

There were notable exceptions to the mean pitch rotational pattern of treadmill gallops described above. Head rotations of more than 20° occurred in the pitch plane, even though trunk rotations were also more than 20° (Figs 3A, 5A). These pitch excursions, however, were of a much smaller magnitude than those in the yaw plane, falling near the stabilization threshold defined in this study. Specifically, with increases in head pitch rotation of more than just a few degrees beyond 20°, trunk pitch rotations diminished. For example, cycles with head pitch

rotations of 21° and 22° had trunk pitch ranges of 30° and 27°, respectively (Fig. 5A). By contrast, a cycle with a head pitch rotation of 28° had a trunk pitch rotation of only 17° (Fig. 5B). The latter gallop cycle is distinctive in that it presented a walk-like rotational pattern consisting of a head rotating on a stabilized trunk and this walk-like pattern extended to the velocity profiles (Fig. 5D,F,H).

Mean trunk position during treadmill gallops was at a slightly, but significantly, steeper pitch angle to earth horizontal than during walks (Fig. 3D). Mean head position relative to space, however, was comparable to the position during walks (Fig. 3C). In this position, the horizontal semicircular canals would be tilted upward rostrally at approximately 6° above earth horizontal. As described above for walks, however, the head was frequently held in positions requiring large rotations in the pitch, yaw and roll planes.
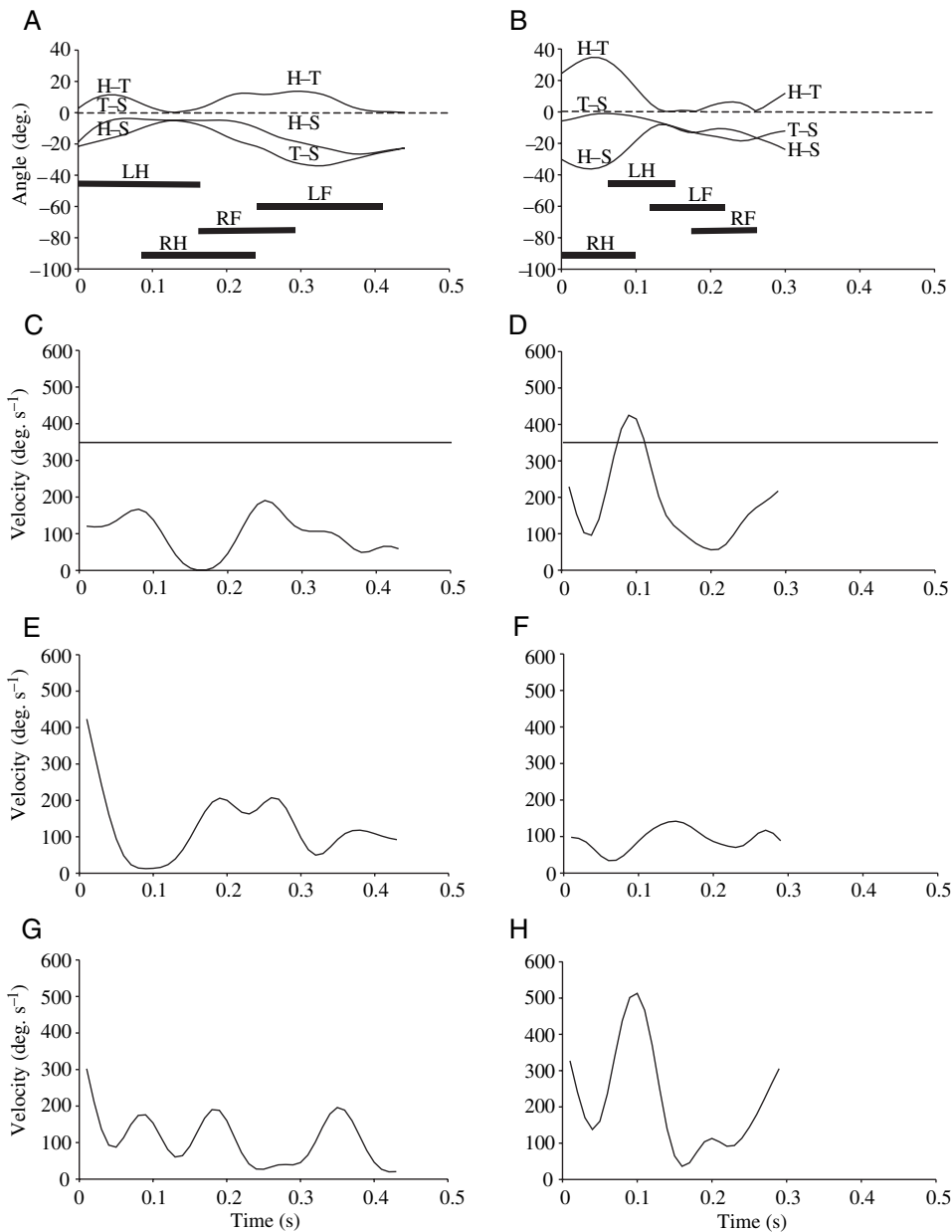

Fig. 5. Segmental angular displacements and instantaneous velocities during single representative cycles of rotary gallops at treadmill speeds of 2.57 m s^{-1} (left column) and 3.03 m s^{-1} (right column). Note that in left gallop cycle (A), both the head and trunk are rotating through more than 20° in the pitch plane, but that the head has just surpassed this threshold. Note also that in the right gallop cycle (B), head rotation in the pitch plane exceeds 20° by several degrees, but that trunk rotations have dropped to below 20°. In both cycles, however, head rotations do not occur in any other plane. The (A,B) 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° (dashed 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 (C,D) the head relative to space, (E,F) the trunk relative to space, and (G,H) the head relative to the trunk. In (C,D) the head-to-space velocity graphs, the solid horizontal lines indicate 350° s^{-1} that, at least in humans, is the saturation velocity for the vestibulo–ocular (VOR) reflex (Pulaski et al., 1981).

Discussion

Comparison of vervet treadmill locomotion with overground locomotion by other species

Comparing treadmill locomotion by vervet monkeys with overground locomotion by bonnet macaques and hanuman langurs runs the potential risk that observed differences are attributed more to behavioral, morphological or physiological differences between the species than to environmental conditions. This possibility, however, appears unlikely. Bonnet macaques and hanuman langurs, members of two separate phylogenetic subfamilies (Cercopithecinae and Colobinae, respectively) and who differ in body size and proportions, nevertheless practice comparable head and trunk movement patterns during walks and gallops (Dunbar et al., 2004). This finding is consistent with the combined experimental evidence from other studies that the neural mechanisms underlying dynamic posture (Dunbar et al., 1986), locomotion (e.g., Peters and Goslow, 1983; Vilensky and Gehlsen, 1984) and gaze (Vidal et al., 1986) are conservative in organization among tetrapods. *Cercopithecus aethiops* is not a phylogenetically distant species differing so dramatically in morphology and lifestyle that differences in sensorimotor capabilities would be expected. Rather, vervet monkeys are comparable to bonnet macaques in that they are also members of the Cercopithecinae and are similar in habitats, diet, social structure, body size and proportions (e.g. Melnick and Pearl, 1987; Napier and Napier, 1967).

Regarding proportions, relative differences in forelimb to hind limb lengths between vervets and the other two species could be considered a potential source of variation in head and trunk displacements during treadmill versus overground locomotion. To determine the feasibility of this possibility, measurements of limb segment lengths from the cine films of representative vervet, bonnet and hanuman individuals were used to approximate the osteometric intermembral index (humerus + radius length / femur + tibia length $\times$ 100).   The resultant indices were 86 for the vervet, 91 for the bonnet macaque and 83 for the hanuman langur, which fall within the respective generic index ranges for *Cercopithecus* (79–91), *Macaca* (83–95) and *Presbytis* (73–84), the former generic classification of hanuman langurs (Napier and Napier, 1967). The values indicate that vervets, like hanuman langurs, have longer hind limbs than forelimbs, suggesting that these proportions may underlie differences between vervet and bonnet macaque head and trunk displacements. The proportional differences among all three species are relatively small compared to those of several other primate species (Napier and Napier, 1967), however and the functional significance of an index that does not consider foot and hand length, segmental orientation, or soft tissues is doubtful. Much more likely influences on head and trunk displacements are segmental orientation, range and coordination of joint rotations, associated musculotendinous forces and duration of limb contact with the support surface. Thus, while the reader should be aware that the comparisons between treadmill and overground locomotion involve different species, the combined evidence presented above supports a strong likelihood that the fundamental head and trunk movement patterns of vervet monkeys would be similar to the patterns found in bonnet macaques and hanuman langurs. The finding that vervet monkeys *can* walk and gallop on a treadmill with head and trunk movements that are comparable to those used by bonnet macaques and hanuman langurs during overground locomotion (Dunbar et al., 2004), only strengthens this likelihood.

Comparison of head and trunk rotations during treadmill versus overground locomotion

Hypothesis 1, which stated that head and trunk rotations during treadmill walks and gallops will be comparable to the rotations reported for overground locomotion (Dunbar et al., 2004), is supported only in part. Treadmill and overground walks are comparable in that the head commonly rotates in the pitch and yaw planes on a stabilized trunk. By contrast, treadmill gallops are not always comparable to overground gallops, in that the head can rotate through several degrees in the pitch and yaw planes as the trunk rotates simultaneously through several degrees in the pitch plane. Thus, unlike during overground gallops (Dunbar et al., 2004), the head is not required to be rotationally stabilized. Furthermore, treadmill and overground locomotion differ in that maximal instantaneous head pitch velocities occasionally exceed $350°\ s^{-1}$ during treadmill walks (Fig. 4C) and gallops (Fig. 5D), the threshold velocity above which, at least in humans (Pulaski et al., 1981), the vestibulo-ocular reflex (VOR) saturates and visual input is disrupted. The duration of these high velocities is brief, however, falling within the period of blinks observed in this study and reported for other monkey (*Macaca*) species (Baker et al., 2002; Porter et al., 1993). Other studies comparing treadmill and overground locomotion in humans and quadrupeds also reveal differences, though less dramatic, in angular and linear displacements (Alton et al., 1998; Barrey et al., 1993; Nigg et al., 1995; Stolz et al., 1997; Vogt et al., 2002), as well as in temporal characteristics (e.g., Alton et al., 1998; Barrey et al., 1993; Buchner et al., 1994; Nelson et al., 1972; Stolze et al., 1997; Wetzel and Stuart, 1976; Wetzel et al., 1975) and generated forces (White et al., 1998).

Simultaneous pitch–plane rotations of the head and trunk in excess of 20°, however, only occur when the rotation of head is slightly greater than 20° (Fig. 5A). When head pitch rotations become larger, the range of trunk pitch rotation drops below 20° (Fig. 5B). This inverse relationship between magnitude of head and trunk pitch excursions most likely indicates osteoligamentous constraints on motion between the head, neck and trunk in this plane (Dunbar et al., 2004; Graf et al., 1995). Alternatively, trunk rotations may drop below 20° in order for it to provide a stable reference frame, as hypothesized for overground locomotion (Dunbar et al., 2004). This latter possibility seems unlikely, however, because head rotations in the yaw plane commonly far exceed 20° at even

the largest trunk excursions and the head is often held in that rotated position. If truly detrimental to overground gallops (Dunbar et al., 2004), how can the head and trunk rotate simultaneously during treadmill gallops without disrupting balance and orientation?

Environmental factors, reference frames, sensorimotor tasks and sensory re-weighting

The environmental differences between treadmill and overground locomotion have a profound impact on visual and vestibular inputs, with the number of potential reference frames increasing and sensorimotor tasks decreasing under treadmill conditions. In contrast to overground locomotion, the treadmill monkeys are stationary relative to their surroundings. Thus, the fixed physical surroundings under these artificial conditions provide an external (extracorporal) spatial reference frame (Clément et al., 1988; Owen and Lee, 1986) that allows the head (and vestibular apparatus) to rotate through several degrees during gallops without inducing disorientation. Other potential reference frames on the treadmill include belt orientation, which largely determines heading, and sounds and mechanical vibrations during operation, which provide auditory (Goldring et al., 1996; Goossens and Van Opstal, 1999; see Blauert, 1996 for review) and proprioceptive (Lackner, 1988) information, respectively. The treadmill, however, is not unique in possessing these latter two sensory cues. While less regular and directionally specific than on the treadmill, notable auditory and vibrational cues are nevertheless also a component of natural environments. The comparative data on overground locomotion (Dunbar et al., 2004) was collected in village (bonnet macaque) and urban (hanuman langur) habitats in which heavy road traffic and industrial machinery produced ongoing cacophonous sounds near, and vibrations within, many of the locomotor pathways. Furthermore, vibrations can provide an unreliable reference frame. Tonic vibration reflexes in skeletal muscles that result from abnormally high muscle spindle stimulation will induce an illusory sense of motion in a stabilized (e.g. support phase) limb that resists the reflex contraction (Goodwin et al., 1972; Lackner, 1984, 1988). Thus, if vervet monkeys require a reference frame not available during overground locomotion to rotate the head during treadmill gallops, the most likely candidate is the fixed visual surround.

The number of sensorimotor tasks that must be accomplished for successful locomotion is reduced on the treadmill. Whereas balance must be maintained during both overground and treadmill locomotion, the tasks of integrating visual information with vestibular and proprioceptive inputs to propel the body and maintain a desired trajectory (Bertin and Berthoz, 2004; Dietz, 1992; Grillner, 1981; Schubert et al., 2003) are minimized. The need to inspect the surface for obstacles and proper hand and foot placement, which are primarily visual tasks (Patla and Vickers, 1997; Patla et al., 1991; Sherk and Fowler, 2001), is reduced because the unnatural smoothness and regularity of the treadmill belt surface exceeds that of flat surfaces available for overground

locomotion, such as the ground and wall-tops used by the bonnet macaques and hanuman langurs (Dunbar et al., 2004). The trunk can also rotate through fewer degrees while still enabling the hands and feet to clear the belt surface safely. For example, although galloping at higher speeds on the treadmill, vervet mean trunk displacements were less than those of the bonnet macaque on the ground (Dunbar et al., 2004) and the fastest vervet treadmill gallop cycle sampled (3.03 m s^{-1}) had the smallest measured trunk-to-space rotation (17°). In addition, the need is reduced to constantly monitor visual, vestibular and proprioceptive inputs to properly adjust the timing of anticipatory extensor muscle activity in the limbs to accommodate changes in ground elevation, adequately absorb ground reaction forces at contact (braking) and prevent unwanted joint flexion due to gravitational force (Dietz and Noth, 1978; Dufek and Bates, 1990; Greenwood and Hopkins, 1976; Liebermann and Goodman, 1991; McKinley and Smith, 1983; Melvill Jones and Watt, 1971a,b; Santello et al., 2001; Watt, 1976). Because the belt surface is so dependably flat and the sensorimotor tasks of accommodating surface changes are so reduced, overall limb movements during treadmill locomotion could be largely determined by efference copy (von Holst, 1954; von Holst and Mittelstaedt, 1950; see Desmurget and Grafton, 2000; Wolpert, 1997; Wolpert and Ghahramani, 2000 for reviews).

Treadmill locomotion nevertheless creates an incongruity between the different sensory inputs. Visual and vestibular information indicate that the body is stationary, but proprioceptive information from the limbs cycling on the belt indicates that the body is moving forward. This informational conflict is most likely overcome through a re-weighting (change in relative importance) of visual and vestibular information on the one hand and the proprioceptive information on the other, as is known to occur during dynamic posture control (Peterka, 2002). Specifically, the brain can depend upon proprioceptive inputs and use the consistently smooth and regular treadmill belt surface as the spatial reference frame. Thus, the head can rotate in the pitch and yaw planes without disturbing balance and spatial orientation because the visual or vestibular inputs are not providing the critical reference frames. If this sensory re-weighting develops gradually during the period when the monkeys learn to gallop on the treadmill, it could be considered a training effect.

Blinks and optic flow

Hypothesis 2, which stated that those blinks that do occur during treadmill locomotion would be associated with rapid head movements, was supported by the results. The monkeys blink during head yaw rotations in both treadmill walks and gallops. Blinks temporarily eliminate optic flow input, the presence of which in humans is known to have an impact on postural maintenance (Bronstein and Buckwell, 1997; Dietz et al., 1994; Gielen and van Asten, 1990; Stoffregen, 1985; Wolsley et al., 1996) and locomotor heading (Bardy et al., 1996; Pailhous et al., 1990; Patla and Vickers, 2003; Prokop et al., 1997; Schubert et al., 2003; Warren and Kay, 1997;

Warren et al., 2001). Changes in optic flow rate induced by head and eye rotations elicit lateral body sway, especially when optic flow is artificially increased by 2–4 times the normally experienced flow rate to create an incongruity with somatosensory inputs (Schubert et al., 2003). The 50 ms monkey blinks found in this study occur between 90° and 45° of forward head rotation, the range through which optic flow would be most rapid and laminar. Removing optic flow input during this brief time period would therefore avoid the greatest potential for inducing detrimental lateral body sway. The blinks, which are rapid for monkeys (Baker et al., 2002; Porter et al., 1993), are most likely reflexes that are triggered by head or eye movements or some other stimulus and that have evolved to accommodate large, forwardly-directed gaze shifts during overground locomotion when the increase in optic flow rate is of significant magnitude. If and when these blinks occur during overground locomotion, however, is unknown.

The results of this study reveal that head and trunk kinematics during treadmill and overground locomotion can differ profoundly and that these differences are associated primarily with the presence or absence, respectively, of large head movements during gallops. This comparison not only provides insights into the contributions of vision and other sensory inputs to locomotion, but also demonstrates the value of combining information from the field and laboratory to increase our understanding of biological phenomena.

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