Head Movements Produced During Whole Body Rotations and Their Sensitivity to Changes in Head Inertia in Squirrel Monkeys

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Submitted 21 March 2007; accepted in final form 23 February 2008

Reynolds JS, Gdowski GT. Head movements produced during whole body rotations and their sensitivity to changes in head inertia in squirrel monkeys. J Neurophysiol 99: 2369–2382, 2008. First published February 27, 2008; doi:10.1152/jn.00320.2007. The head’s inertia produces forces on the neck when the body moves. One collective function of the vestibulocollic and cervicocollic reflexes (VCR and CCR) is thought to be to stabilize the head with respect to the trunk during whole body movements. Little is known as to whether their head-movement kinematics produced by squirrel monkeys during whole body rotations are similar to those of cats and humans. Prior experiments with cats and human subjects have shown that yaw head-movement kinematics are unaffected by changes in the head’s inertia when the whole body is rotated. These observations have led to the hypothesis that the combined actions of the VCR and CCR accommodate for changes in the head’s inertia. To test this hypothesis in squirrel monkeys, it was imperative to first characterize the behavior of head movements produced during whole body rotation and then investigate their sensitivity to changes in the head’s inertia. Our behavioral studies show that squirrel monkeys produce only small head movements with respect to the trunk during whole body rotations over a wide range of stimulus frequencies and velocities (0.5–4.0 Hz; 0–100°/s). Similar head movements were produced when only small additional changes in the head’s inertia occurred. Electromyographic recordings from the splenius muscle revealed that an active process was utilized such that increases in muscle activation occurred when the inertia of the head was increased. These results are consistent with prior cat and human studies, suggesting that squirrel monkeys have a similar horizontal VCR and CCR.

INTRODUCTION

Motor control involves not only movement of the body but also maintaining a stable posture in the face of gravitational and other inertial forces that act on the body’s orientation. Despite the significance of inertial forces, limited evidence exists to support the hypothesis that the CNS incorporates inertial forces into calculations that are used to regulate movement. One example supporting this hypothesis comes from the investigation of human subjects who were positioned at the periphery of a rotating room and instructed to repeatedly point to the room’s center (Lackner and DiZio 1997, 1998). The subjects generated movement errors while initially attempting to point due to the inertial forces acting on the arm. Accurate pointing movements were produced only after subjects completed several repetitions in which they generated combinations of errors and corrections. This suggests that the CNS is able to quickly modify muscle activation patterns to counteract forces due to the body’s inertia so that voluntary movements can be produced accurately.

Such observations have motivated us to question if reflexes that function to stabilize posture are also calibrated with respect to the forces produced by the body’s inertia. For example, the head’s inertia exerts forces and torques on the neck when the body is accelerated. The head’s inertial torque acts against the viscoelastic properties of the neck and, in the absence of additional active muscle force, would be expected to produce a rotation of the head on the neck. At least two mechanisms could be used to control how the head’s inertial forces influence movement with respect to the trunk. First, neck muscles could be voluntarily contracted to change the neck’s stiffness. Second, reflexes could be used to dynamically activate neck muscles with respect to inertial forces produced during body motion. Conceptually, the second mechanism might explain our lack of conscious awareness of inertial forces. Reflexes could be calibrated precisely so that they produce forces that counteract inertial forces that are produced during body movements without requiring voluntary mechanisms for correction.

The vestibulocollic (VCR) and cervicocollic (CCR) reflexes are thought to work cooperatively to produce torque that counteracts the torque produced by the head’s inertia during whole body rotation (Goldberg and Peterson 1986; Keshner et al. 1995, 1999; Keshner and Peterson 1995; Lacour et al. 1987; Peng et al. 1996, 1999). When the whole body is rotated, the VCR activates the majority of the contralateral neck muscles and inhibits most, but not all, ipsilateral neck muscles (Shinoda et al. 1993, 1994, 1997). This pattern of activation causes the head to counter-rotate with respect to the stimulus (Ezure and Sasaki 1978; Ezure et al. 1978; Goldberg and Peterson 1986). When the head counter-rotates, the ipsilateral neck muscles are stretched, activating the CCR, which produces torque in the opposite direction of the torque produced by the VCR. This pattern of muscle activation has led to the hypothesis that the two reflexes could be used to stabilize the inertia of the head with respect to the trunk during whole body rotation.

A direct test of the interaction of the VCR and CCR with head inertia was performed in cats by adding inertia to the head and determining if the additional inertia effected the head movements that were produced during whole body rotation (Goldberg and Peterson 1986). Changing the head’s inertia had minimal consequences on the kinematics of head movements evoked during low-frequency whole body rotation (Goldberg...
and Peterson 1986). However, at higher stimulus frequencies, the head movements produced with respect to the body were significantly larger compared with the no-load condition. Later studies in human subjects also showed that when the head’s inertia was increased (Gauthier et al. 1986; Keshner et al. 1999; Smith et al. 1985), large compensatory head movements were produced at high stimulus frequencies that were not present when the head’s inertia was not increased. In contrast, small head movements were always produced during low stimulus frequencies, even when the head’s inertia was increased. Based on these observations, it has been hypothesized that the neural substrates of the VCR and CCR increase their output to produce sufficient compensatory torque to overcome the torque produced by added inertia. Despite the importance of such a function, there is currently no direct evidence to support this hypothesis.

We sought to test this hypothesis by conducting experiments in squirrel monkeys. The squirrel monkey is an ideal species for studying this system because many elements of their vestibular pathways have been extensively investigated, including: vestibular afferents (Fernandez and Goldberg 1971, 1976; Goldberg and Fernandez 1971a,b), neurons in the vestibular nuclei (Cullen et al. 1991, 1993; Highstein et al. 1987; McCrea et al. 1987a,b), projections of the vestibulospinal pathways from the vestibular nuclei to the neck cervical motor nuclei (Boyle 1993; Boyle et al. 1992, 1996), and the electromyographic activity of dorsal neck muscles (Killian and Baker 2005). Most importantly, we have already recorded from secondary vestibular neurons in head-free squirrel monkeys while they generated compensatory head movements during whole body rotations (Gdowski and McCrea 1999a,b, 2000). These studies suggest that the collic reflexes are active and functioning in squirrel monkeys when head movements are produced during whole body rotations. However, the kinematics of head movements in these monkeys were not systematically examined as has been done in the cat and human. One of the goals of the present study was to complete these comparisons and to determine if any nonlinearities were present in their head-movement kinematics that were consistent with nonlinearities that are present within the pathways thought to mediate the VCR. A second goal of the present study was to examine and quantify the effect of changing the head’s inertia on head movements produced during whole body rotations.

**Methods**

**Surgical preparation**

All surgical and experimental procedures were approved by the University of Rochester Committee for Animal Resources. The animals were housed under conditions that comply with National Institutes of Health standards outlined in the Guide for the Care and Use of Laboratory Animals (2003) and the recommendations from the Institution of Laboratory Resources and the Association for Assessment and Accreditation of Laboratory Animal Care International. Five adult squirrel monkeys were surgically prepared for chronic recordings of head movements. All surgeries were conducted under sterile conditions using isoflurane anesthesia. An acrylic cap was attached to the cranium using small stainless steel bolts. A keyed bolt was stereotaxically embedded in the acrylic to orient the head so that yaw head movements maximally activated the horizontal semi-circular canals (Fernandez and Goldberg 1971; Goldberg and Fernandez 1971a,b). This was achieved by pitching the animal’s nose downward by 15° with respect to the keyed bolt. The bolt was centered on the sagittal suture on the most caudal aspect of the occipital bone.

One squirrel monkey was surgically prepared for chronic recordings of electromyography from neck muscles. A small incision was made on the lateral aspect of the dorsal surface of the neck. Neck muscles were bluntly dissected so that small bipolar steel silicone patch electrodes (Microprobe) could be sutured to each implanted muscle. Each pair of electrodes was composed of two stainless steel wires that were barbed at the end (2 mm) and spaced 2 mm apart. Electrodes were sutured perpendicular to muscle striations, and the electrode leads were run subcutaneously to the acrylic skull cap where they were soldered on to a permanent connector. Implanted muscles included: trapezius, rhomboids major, sternocleidomastoid, and splenius capitis.

**Experimental setup**

The experimental apparatus (Fig. 1) was similar to that used in our prior head-free studies using squirrel monkeys (Gdowski and McCrea 1997, 1999a, 2000; Gdowski et al. 1996; McCrea and Gdowski 2003; McCrea et al. 1999). Animals were seated on a chair. The chair was attached to a vestibular turntable (Fig. 1A). Each animal wore a jacket that was attached to the chair to maintain an upright posture and to prevent trunk movements with respect to the chair. The turntable rotated the animal’s whole body in the horizontal plane about the earth vertical axis. In some experiments, a multi-axis rotator was used (not shown). The animal was only permitted to rotate its head in yaw about the C1-C2 vertical axis with the head pitched 15° downward. The center of head rotation was aligned with the turntable’s center of rotation. The medio-lateral alignment was achieved based on the stereotaxic placement of the keyed bolt (see preceding text). The rostral-caudal alignment was achieved by curving the vertical rod so that its rotational axis was aligned with the interaural axis. Slight adjustments were made so that the animal could make fast, yaw head movements (±40°) with respect to the trunk. The system included an in-line torque sensor (iv, Lebow, 1701; inertia: 1 × 10⁻² kg·cm²) coupled to an in-line clutch (v, Placid Ind., 2CD; inertia: 6.4 × 10⁻⁴ kg·cm²) that was in turn coupled to a load. The torque sensor was used to restrain the head at the center of table rotation, allow the head to rotate in the horizontal plane, support the gravitational forces produced by the mass of the apparatus, and measure the torque (τₚ) imposed on the head by the passive inertial load during whole body rotation. The clutch limited the imposed torque and was used to position the load in the frontal plane.

**Relationship between Inertia and Torque.** In the first experiments, the horizontal rod and the masses (Fig. 1A) were removed to minimize the device’s inertia. The only inertia added to the head included the carbon-fiber vertical rod, torque sensor, and clutch. The inertia of the squirrel monkey head (Iₘ) was approximated as an ellipsoid with a total mass (mₘ) of ~115 g (100 g for the head, and 15 g for the surgical implant). The long (a) radii was measured roughly along the Frankfurt plane as half the distance from the maxillary central incisor to the occiput and ranged from 35 to 40 mm (37.5 ± 0.18 mm, n = 5). The short (b) radii, measured as the half the distance between the lateral margin of the bony orbits on the zygomatic bones, ranged from 20 to 25 mm (20.3 ± 0.25 mm, n = 5). The head’s moment of inertia was approximated as: Iₘ = mₘ[a² + b²]/5. The approximate head inertia, based on an estimated mass of ~115 g, ranged between 0.37 and 0.47 kg·cm² across the population (mean Iₘ = 0.42 ± 0.05 kg·cm²). These approximations were consistent with an inertia measurement that was carried out immediately postmortem in one squirrel monkey used in another study. In that case, the experimentally measured value for the head’s inertia (0.30 kg·cm²) was nearly equivalent to its approximation of 0.33 kg·cm² where: a = 3.5 cm, b = 2.0 cm, and mₘ = 0.1 kg. The inertia of the vertical rod and head restraint system (Iₑ) was measured experimentally and was 0.6 kg·cm². The total inertia of the head-free setup (Iₕf = Iₘ + Iₑ) was 1.02 kg·cm².
In the second set of experiments, inertia was added to the head by placing either one or two 1-oz (28.3 g) masses on each side of the horizontal rod equidistant from the center of rotation (\(m_t\) or \(m_m\); 15 g, length: L = 33 cm). The horizontal and vertical rods were constructed from carbon fiber to maximize strength and minimize their inertial contribution. The changes in inertia were reported with respect to the inertia of the unloaded head-free system such that: \(\Delta I = A \times I_{HF}\), where \(A = I/I_{HF}\). The magnitude of the additional inertia was varied by changing the location of the masses. The total inertia added to the head (\(I_t = I_t + I_m\)) included: the inertia of the horizontal rod used to hold the masses [\(I_t = (1/12) mL^2 = (1/12)(0.015)(33)^2 = 1.36\) kg cm\(^2\)], and the inertia of the two masses. In most cases, two 1-oz masses were placed on each side of the horizontal rod producing an inertia of \(0.113r^2\) kg cm\(^2\) \(I_m = 4mr^2 = 4(0.0283)(r)^2\). The smallest change in inertia that could be produced was when the horizontal rod was placed on the system \(I_t = I_t = 1.36\) kg cm\(^2\); yielding \(\Delta I = 1.36 \times I_{HF}\). The maximum additional inertia that could be produced with the 1-oz masses (\(r = 15.24\) cm) was \(I_t = 1.36\) kg cm\(^2\) + \(0.057(15.24)^2\) kg cm\(^2\) = \(14.5\) kg.cm\(^2\), which corresponded to: \(\Delta I = 14.3\) \(\times I_{HF}\). Doubling the masses yielded a maximum of \(\Delta I = 27.2\) \(\times I_{HF}\). In all cases, the torque sensor was used to quantify the actual total inertia added to the head (\(I_t\)) by rotating the table while the vertical rod was restrained to the table without the animal. The actual minimum and maximum inertial changes were \(\Delta I = 1.8\) \(\times I_{HF}\) and \(29.3\) \(\times I_{HF}\). This value is reported on all figures. The torque exerted on the head by the inertia (\(\alpha_{TS} = I_t \cdot \alpha_{HS}\)) depended on the head’s rotational acceleration in space (\(\alpha_{TS}\)). In some figures, the additional torque that had to be produced by the animal to maintain the same head-movement kinematics as when the head was unloaded was reported. This torque was the product of the total additional inertia (\(I_t\)) and the rotational acceleration of the turntable (\(\tau_{TS} = I_t \cdot \alpha_{TS}\)).

**Experimental paradigms**

Data acquisition and stimulus generation were controlled with a National Instruments system. The EMG activities of neck muscles were obtained using an eight-channel electromyography system (AMT-8; Octopus, Bortec Biomedical). Each neck muscle signal was amplified (\(\times 2,500–5,000\)), low-pass filtered (Bessel, 200-Hz cutoff), and recorded using A/D converters of the acquisition system (sampling rate: 500 Hz). The turntable’s velocity feedback signal was used as a measure of the trunk’s velocity in space (\(T_S\)). The animal’s head position was measured using a magnetic search coil technique (Remmel). A search coil attached to the vertical rod was used to measure head position with respect to the trunk because the field coils of the system were mounted on the turntable. Head position, head torque, position, and velocity were low-pass filtered (Bessel, 200-Hz cutoff) and recorded using A/D converters of the acquisition system (sampling rate: 500 Hz). Head velocity with respect to the trunk was computed off-line from the derivative of the recorded head-position signal. The head velocity in space (\(H_s\)) was computed as the sum of \(T_S\) and \(H_F\). All experiments were carried out in darkness while animals were continuously monitored using a three-camera infrared monitoring system.

**ISO-INERTIA FREQUENCY SERIES.** The whole body was sinusoidally rotated over a range of frequencies (0.5–4.0 Hz) while maintaining a constant moment of inertia (\(I_t = 8.6 \times I_h\)). One 1-oz mass (28.3 g) was placed on each side of the horizontal rod (Fig. 1B) at a radial distance of 10.7 cm. The stimulus acceleration was held constant to maintain a constant peak torque (\(\tau_{TS}\)). The paradigm was repeated for five peak torques (\(\tau_{TS} = 0.23, 0.35, 0.50, 0.70,\) and 1.0 N cm).

**SUM-OF-SINES (SSN) FREQUENCY SERIES.** A pseudorandom velocity stimulus was used that was composed of 10 sinusoids having frequencies that were harmonics (37, 49, 71, 101, 143, 211, 295, 419, 589, and 823) of a 0.05-Hz base frequency (see Keshner et al. 1999). Velocity was decreased with frequency to minimize the effects of higher accelerations at high frequencies as follows: 20°/s for 0.19–0.55 Hz; 19°/s for 0.51–1.06 Hz; 16°/s for 1.48–2.1 Hz, 15°/s for 2.95 Hz, and 13°/s for 4.12 Hz. One minute of data was collected for each trial. When inertia was added to the head, two 1-oz masses were placed on each side of the horizontal rod (Fig. 1B) at a radial distance of either 3 in (7.62 cm) or 6 in (15.24 cm), producing an inertial change of \(I_t = 8.2, 29.3 \times I_h\).
Data analysis

Analysis was carried out using custom software (Matlab and Igor). Neck EMG records were rectified and filtered to obtain the envelope of activation. Processed neck EMG signals were then treated like other rotational records (i.e., head position). Rotational records were analyzed by first identifying and removing voluntary head movements from raw data records. Voluntary head movements were identified using a threshold criterion equivalent to 30% above that of the input stimulus velocity ($T_S$). Typically 20–40 ms of data were removed before and after the point at which the head velocity crossed the threshold criterion (shaded area, Fig. 2A). Raw records of head-on-trunk velocity ($H_T$) and torque ($T_S$) were averaged cycle by cycle with respect to the table velocity ($T_S$). Typically, the responses to ≥20 stimulus cycles were obtained and a minimum of 10 cycles was required for averaging. Averaged head-movement records were fit with a sinusoidal function to quantify the DC-offset, peak amplitude, and phase. The torque signal ($T_S$) was processed identically. The gain and phase of the response was computed twice. The head-on-trunk gain and phase were computed as measures of the proprioceptive signals produced, and were defined as: $G_{HT} = H_T/T_S$ and $\phi_{HT} = \theta_{HT} - \theta_{TS}$. The head-in-space gain and phase were computed as measures of the vestibular signals produced and were defined as $G_{HS} = H_S/T_S$ and $\phi_{HS} = \theta_{HS} - \theta_{TS}$; where $H_S = T_S + H_T$. DC-offssets present on the $H_S$ signal were eliminated before the vector addition was carried out to compute $H_S$. SSN data were analyzed using a fast Fourier transform (see Keshner et al. 1999). The magnitude and phase at each stimulus frequency component were used to compute the gain and phase shift of the head movements with respect to the stimulus velocity.

Nomenclature

Positive values corresponded to rightward movements. Both head-in-space and head-on-trunk movement gains were reported. The first corresponds to the vestibular signal ($H_S/T_S$), and the second corresponds to the proprioceptive signal ($H_T/T_S$). Both gain and phase responses were calculated with respect to stimulus velocity. No voluntary tasks were used in this study. From an operational standpoint, we defined stability in terms of the magnitude of the head movement that was produced with respect to either the stimulus or the vestibular sensory signal. If the head was stabilized with respect to space, it would correspond to gain values of $H_S/T_S = 0$ and $H_T/T_S = 1$, with $\phi_{HT} = 180°$ (see Fig. 1C). Similarly, if the head was stabilized with respect to the trunk, it would correspond to gain values of $H_S/T_S = 1$ and $H_T/T_S = 0$, with $\phi_{HT} = 0°$ (see Fig. 1D). The phase response was computed as the difference between the phase of the head velocity signal and the phase of the trunk-in-space velocity signal. A phase lag of $-180°$ were head movements that were compensatory with respect to the stimulus velocity.

RESULTS

Normal head movements produced during whole body rotation

In all experiments, the animal’s whole body was rotated (stimulus) while its head was free to move in the yaw plane. The response was the head-on-trunk movement that was produced and correlated with the stimulus. Experiments were conducted using five squirrel monkeys. Two squirrel monkeys were removed from the study early because of problems associated with their implants. An example of the head-on-trunk movements produced during sinusoidal whole body rotation (2.0 Hz, 50°/s) is shown in Fig. 2A. Voluntary head movements produced during the stimulus were eliminated from the data records, and the remaining data were averaged (Fig. 2B). The head-movement kinematics (gain and phase) were obtained by fitting the averaged head-on-trunk ($H_T$) and head-in-space ($H_S$) velocity signal with a sinusoidal function. Perfect head stability with respect to its trunk was operationally defined as the condition when no head-on-trunk movements would have been produced during the stimulus. Perfect head stability with respect to the trunk rarely, if ever, occurred. Small head-on-trunk movements were always observed in the opposite direction with respect to the stimulus. The gain of the head-on-trunk movements was typically small with respect to the stimulus ($G_{HT} = 0.30$), resulting in a vestibular sensory signal (head velocity-in-space) that was close in magnitude to that of the stimulus ($G_{HS} = H_S/T_S = 0.75$). These observations were consistent with that of the entire population, which had similar head-on-trunk gains ($G_{HT} = 0.24 \pm 0.13$) and head-in-space gains ($G_{HS} = 0.79 \pm 0.11$) for a 2.0-Hz, 50°/s stimulus. The response phase was also quantified from the averaged head-movement records (Fig. 2B). The head-movement response phase was always in the opposite direction of the table velocity signal ($\phi_{HT} = \theta_{HT} - \theta_{TS} = -147°$), and the head velocity-in-space signal was in the direction of whole body rotation ($\phi_{HS} = \theta_{HS} - \theta_{TS} = -10°$). This was also consistent with the response phase of the population ($\phi_{HT} = -153 \pm 5°$) and ($\phi_{HS} = -7 \pm 5.4°$) for the 2.0-Hz, 50°/s stimulus.

The EMG activity of the left splenius capitis muscle was also recorded in one squirrel monkey to determine if the kinematics that were observed arose as a consequence of only the physical forces of the head’s inertia reacting with the mechanical viscoelastic properties of the head and neck. When small head-on-trunk...
movements were produced during whole body rotation, the left splenius muscle was also activated during rightward rotations (Fig. 2). These results are consistent with splenius muscles being activated by vestibular sensory signals arising from the contralateral semi-circular canals. These results also show that a component of the head-movement kinematics likely arises as a consequence of vestibular sensory processing in addition to those related to the biomechanical properties of the head and neck.

Head movement as a function of stimulus frequency

In cats, small head-on-trunk movements were produced over a wide range of stimulus frequencies (0.2–5 Hz) when the whole body was rotated either sinusoidally or using a sum-of-sines stimulus (Goldberg and Peterson 1986). We observed similar head-on-trunk movements in squirrel monkeys over the same frequency range. The head-on-trunk movements were characterized as a function of frequency by recording the response to sinusoidal whole body rotation over a stimulus frequency range spanning 0.5–4.0 Hz at 25°/s. The head-on-trunk gains and phases ($G_{HT}$ and $\phi_{HT}$) are shown as a function of frequency for five animals in Fig. 3A. The gain of the head-on-trunk movement with respect to the stimulus velocity was usually small ($G_{HT} = 0.24 \pm 0.03$), and the corresponding head velocity-in-space gain was near one (Fig. 3B, $G_{HS} = 0.80 \pm 0.03$). One animal ($315$, Fig. 3A) had a slightly higher head-on-trunk gain ($G_{HT}$) compared with other animals. However, as a population, squirrel monkeys produced small head-movement responses that were in the opposite direction with respect to the table velocity (Fig. 3C).

The frequency response was also obtained from head movements produced during a SSN stimulus. Most time periods
throughout the SSN trials resulted in small head-on-trunk movements with respect to the stimulus velocity. Although some variance was observed between animals, the average of the population for head-on-trunk gain ($G_{HT} = 0.48 \pm 0.12$) and phase ($\phi_{HT} = -160 \pm 32^\circ$) remained remarkably consistent across all stimulus frequency components (Fig. 3D, ●). When compared with the single sinusoid trials (Fig. 3D, ■), the head-on-trunk gain increased on average from 0.24 to 0.48 (100% increase) during the unpredictable SSN stimulus, while the phase responses were nearly identical. Overall the gain and phase response to the SSN was more variable when compared with the responses during the single sinusoid trials. This suggests that smaller gains during the sinusoidal stimulus could occur as a consequence of the stimulus being more predictable by the animal.

**Head movements as a function of stimulus velocity**

Many response nonlinearities exist throughout the vestibulocollie pathways as previously discussed. The head-on-trunk movements produced during whole body rotation were characterized as a function of stimulus velocity to determine if nonlinearities related to stimulus amplitude affected the head-movement kinematics produced during high stimulus velocities. Figure 4 shows the head-on-trunk (A) and head-in-space (B) gains and phases ($G_{HT}$, $\phi_{HT}$, $G_{HS}$, and $\phi_{HS}$) as a function of velocity for a 2-Hz stimulus for three animals. The corresponding population response is plotted in Fig. 4C. No significant changes in response gains or phases were observed from 10 to 50°/s. Head movements produced in response to other stimulus frequencies (0.5–4 Hz) were also recorded, and similar responses were observed (data not shown). At low stimulus frequencies (<1 Hz), no significant changes in the head-on-trunk gain were observed over an even wider range of stimulus velocities (25–100°/s) for all animals tested. Higher stimulus frequencies were only evaluated over a smaller velocity range due to limitations of the rotator. No changes in head movements were observed at high stimulus peak velocities and frequencies in all but one animal that was tested. In one animal (312), there were slight increases in the head-on-trunk gain at the highest peak velocities and frequencies. In summary, even though vestibular neurons located within the VCR pathways can exhibit either excitatory or inhibitory saturated responses at high stimulus velocities, such nonlinear neural response properties appear to not result in nonlinear changes in head-movement velocity produced by the animal.

**Influence of inertia on head-movement kinematics**

In prior cat and human studies, the gain and phase of the head-movement kinematics exhibited distinct properties as a function of the stimulus frequency when inertia was added to the head. Here we report that the head-movement kinematics (gain and phase) exhibited similar behaviors in squirrel monkeys when inertia was added to the head during whole body rotations.

**Gain response of the head-movement kinematics.** Figure 5 (A–C) shows the averaged head-movement response for whole body rotations at three stimulus frequencies (1.5, 2.5, and 4 Hz) having a peak acceleration of 628°/s². In each case, inertia was added to the head by placing one 1-oz mass on each side of the horizontal rod at a radial distance of 10.7 cm from the center of rotation, which provided an inertial load of 8.8 kg·cm² (or 8.6×$I_{HP}$). When the 1.5-Hz stimuli were used (Fig. 5A), the size of the head-on-trunk movements were small and the head-on-trunk gain ($G_{HT}$) was similar to when no inertia was added to the head. As the stimulus frequency was increased, there was a rapid increase in the size of the head-on-trunk movements. This change in response has been characterized as a transition frequency ($f_t$), which is the frequency at which the response becomes dominated by the inertial torque. Each set of graphs in Fig. 5, D–F, shows the gain and phase response of the head-on-trunk movement kinematics ($G_{HT}$ and $\phi_{HT}$) for all three animals during whole body rotation (WBR) for several stimulus accelerations (157, 235, 314, 471, and 628°/s²). Each trace in Fig. 5, D–F, is the response to stimuli having the same acceleration (see legend). The transition frequency varied from animal to animal and varied slightly as a function of stimulus acceleration. In two of the animals (311 and 313, top and bottom in Fig. 5), the transition frequency was between 2.0 and 2.5 Hz, and in the third animal, it was slightly lower, ~1.5 Hz. Despite these slight differences, the general trend exhibited by $G_{HT}$ due to the increase in head inertia remained remarkably consistent. Each animal had a different transitional frequency as would be expected based on having different initial head inertias. However, the change in the gain and phase of the head-on-trunk movement produced during stimuli having frequencies below, slightly above, and at much higher frequencies relative to the transitional frequency were the same.

**Fig. 4.** Head-movement kinematics as a function of velocity during sinusoidal whole body rotations (2 Hz) for 3 animals indicated in legend key. A and B: $H_T/T_S$ and $H_S/T_S$ gain and phase plotted as a function of stimulus velocity. C: The population average as a function of stimulus velocity (error bars are ± SE). The SEs for the highest and smallest velocities were too small to visualize for the scale of the graph.
The head-on-trunk gain responses of four animals are shown in Fig. 6 (A and B) for each level of additional inertia with the population average shown in C. The animals were able to stabilize their heads with respect to their trunk for the lower frequency components of the SSN stimulus. A transitional frequency was also observed in the response to the SSN stimulus, and it was found to decrease for increasing levels of inertia. The transitional frequency of the population average was 1.5 Hz for the $8.2 \times I_{HF}$ inertial load and 0.3 Hz for the $29.3 \times I_{HF}$ inertial load. The head movements produced in response to frequency components above the transitional frequency were large and functioned to stabilize the head in space.

**PHASE RESPONSE OF HEAD-MOVEMENT KINEMATICS.** In cats and humans (Goldberg and Peterson 1986; Keshner and Peterson 1995), the transition frequency was accompanied with a rapid increase in phase ($\phi_{HT}$) from $-180$ to $-90^\circ$, which was followed by a rapid decrease in phase from $-90^\circ$ back to $-180^\circ$ as a function of frequency. The frequency at which the responses phase was close to $-90^\circ$ was referred to as the phase transition frequency ($f_{\text{max}}$). This phase response was occasionally apparent but was not consistent in the responses of squirrel monkeys during sinusoidal WBR. In two cases, the phase response ($\phi_{HT}$) remained around $-90^\circ$ for most frequencies tested when the head was loaded (Fig. 5, B and C). In the third animal, the response remained around $-135^\circ$ (Fig. 5D). The phase transition frequency was more apparent in the average population responses during the SSN stimulus. The individual phase responses for each condition (Fig. 6, A and B) were significantly noisier in comparison to the single sinusoid data (Fig. 5). Previous studies have reported that the phase plot exhibits trends such that the phase transitions from $-180$ to $-90$ to $-180^\circ$ (Goldberg and Peterson 1986). This was only apparent in our averaged phase plots despite the large variability across individuals.

**Inertia versus torque—relationship to system dynamics**

Past VCR and CCR studies have suggested that the transition frequency represents when the system’s response becomes dominated by the head’s inertia (Goldberg and Peterson 1986). Alternatively, the transition frequency could represent limitations in the output or overall magnitude of the torque that can be produced by the two reflexes. Experiments were carried out to determine if the changes in the head-movement kinematics observed when inertia was added to the head were better correlated with the additional inertia itself or the additional torque needed to counteract the torque produced by the additional inertia. The additional torque needed was calculated as the additional inertia multiplied by the stimulus acceleration $\tau_{TS}$.

The head-movement kinematics produced during 0.5-, 1.0-, and 2.0-Hz whole body rotation (50°/s) were recorded as the inertia added to the head was increased by increasing the radial distance of the two masses on each side of the horizontal rod (Fig. 1). Figure 7 shows the head movements that were recorded during 2-Hz WBR (50°/s) when the inertia of the head-free system ($I_{HF}$) was increased by a factor of $1.8 \times$, $6.1 \times$, and $29.3 \times$ (A–C, respectively). A progressive change in both the gain and phase of the head-movement kinematics were observed as a function of the amount of inertia added to the head (Fig. 7). The gain and phase of the head-movement kinematics were individually plotted as a function of the inertia.
added to the head in Fig. 8A for each of the three animals (animal 312 in A, 1 and 2; 313 in B, 1 and 2; 315 in C, 1 and 2). No direct relationship was observed between the inertia that was added to the head with either the gain or the phase of the head-movement kinematics that were recorded. When the stimulus frequency was 0.5 Hz, all three animals had smaller head-on-trunk gains \(G_{HT}\) for considerably large changes in the head’s inertia compared with responses for higher stimulus frequencies. The same data were replotted as a function of the additional torque needed during each stimulus condition (Fig. 8B). Distinct relationships were observed between both the gain and the phase of the head-movement kinematics and the magnitude of the additional torque needed \(\tau_{TS}\) during each stimulus condition. It appeared as if each animal had a maximum torque \(\tau_{max}\) that could be produced. If \(\tau_{TS} < \tau_{max}\), then the head-movement gains were small \(G_{HT} \approx 0.5\) regardless of the stimulus condition. As might be expected, \(\tau_{max}\) varied from animal to animal (0.7, 0.6, and 0.25 N·cm). Similarly, whenever \(\tau_{TS} > \tau_{max}\), the head moved more with respect to the trunk and the magnitude of the head-on-trunk movement was larger for larger differences between \(\tau_{TS}\) and \(\tau_{max}\). The amount of head movement produced in this circumstance was frequency dependent such that it was higher for higher stimulus frequencies. Relationships also existed between the phase response of the head-movement kinematics and \(\tau_{TS}\). When \(\tau_{TS}\) was small, the phase response was in the opposite direction of turntable motion \(\phi_{HT} \approx -180^\circ\). As \(\tau_{TS}\) approached \(\tau_{max}\), the phase response of the head-movement kinematics rapidly increased \(\phi_{HT} \approx -90^\circ\). Finally, when \(\tau_{TS}\) exceeded \(\tau_{max}\), the phase response of the head-movement kinematics decreased gradually back toward \(\phi_{HT} \approx -180^\circ\). These results suggest that the transition frequency \(f_t\) or the phase transition frequency \(f_{max}\) or both represent the stimulus conditions at which the torque needed to overcome the torque produced by the inertia added to the head exceeded the maximum torque \(\tau_{max}\) that could be produced.

Is an active process used when inertia is added to the head?

In Fig. 2, the EMG activity of the left splenius muscle was shown to be modulated during whole body rotations when the head was free to move and no inertia was added to the head. Here we address whether the EMG modulation was modified when inertia was added to the head. Figure 9 shows the EMG activity of the left splenius muscle during sinusoidal whole body rotations for the unweighted condition and when different magnitudes of inertia were added to the head. Only small changes in head-on-trunk movements were observed when small amounts of inertia were added to the head during 2.0-Hz whole body rotation (Fig. 9B; \(\Delta I = 1.8 \times I_{HF}\); C; \(\Delta I = 6.1 \times I_{HF}\)). These small head movements were accompanied with larger splenius EMG signals in comparison to the condition when no inertia was added to the head. Large head-on-trunk head movements were produced when the magnitude of inertia added to the head was increased to \(\Delta I = 29.3 \times I_{HF}\) (Fig. 9D). The head-on-trunk movements caused the head velocity in space to be phase shifted with respect to the stimulus (table velocity in space). The corresponding EMG signal was smaller in this condition and phase shifted so that the modulation was still in phase with the head velocity-in-space signal. A large DC shift was also apparent in the splenius EMG recordings during this condition, suggesting that the animal also produced a constant volun-
Does the VCR function as a closed-loop reflex when inertia is added to the head?

The VCR has been referred to as a closed-loop reflex because the head movement it produces is in the opposite direction of the vestibular sensory signal driving the reflex. Consequently, the head movement produced tends to decrease the head’s movement in space. However, the head movement that was produced when inertia was added to the head usually functioned to increase rather than decrease the head’s movement in space.

Figure 7 (A2, B2, and C2), —, highlights the head velocity in space during 2.0-Hz whole body rotation (50°/s) for increasing levels of inertia added to the head. The head-on-trunk movement was in the opposite direction with respect to the head’s acceleration in space as opposed to the head’s velocity in space when inertia was added to the head. The consequence of this head-on-trunk movement was to increase the vestibular sensory signal (head movement in space) so that it was even larger than the turntable velocity (stimulus). Figure 10 was derived from the same data illustrated in Fig. 7, where the gain and phase of the vestibular sensory signal was computed with respect to the table velocity in space (\(G_{HS}/T_S\)). Figure 10A shows the gain and phase of the vestibular sensory signal for each animal (\(G_{HS}, \varphi_{HS} = \theta_{HS} - \theta_{TS}\)). Figure 10A shows the average gain and phase for the entire population. Larger amounts of inertia resulted in larger head-on-trunk movements which increased the head velocity in space by as much as 50%. In Fig. 10B, the population response shows that the head-on-trunk gain increased (\(H_S/T_S\)) while the vestibular sensory signal remained the same or increased. At the highest levels of inertia, the head moved in the opposite direction of head velocity in space. However, at that point, the head movement was so large that it reduced the magnitude of the sensory signal (\(H_S/T_S\)) to nearly zero.

**DISCUSSION**

This study quantified the head-movement kinematics produced during whole body rotations in squirrel monkeys to compare them to head movements reported in previous studies carried out in cats and humans. Furthermore, inertia was added to the head to critically evaluate its effect on head movements produced during whole body rotations.

All of the experiments were designed to minimize volitional movements from confounding the observations. The animals were rotated in the dark in each of the studies conducted. The animals were not trained, nor were they expected to carry out any particular task. Nonetheless given this environment, the animal could have chosen to stabilize its head with respect to space (thus minimizing the torques exerted on the neck by the additional load), stabilize its head with respect to its trunk (resulting in the additional load producing considerable torque on the neck), or, finally, do nothing (thus allowing inertia to cause movement of the head with respect to the trunk). While it is not possible to know precisely which choice the animal made, or if the choice varied throughout a trial, it is possible to speculate on this decision based on the physics, head-movement kinematics, and EMG records that were observed. The third choice, to do nothing, seems unlikely because in many cases, the EMG records showed that an active process was present. More importantly, based on the laws of physics, one would have expected increases in the inertia of the additional load to produce linear increases in head movement. This rarely occurred except when large loads were attached to the head. This point is important even in the case of the first choice, which was to stabilize the head with respect to space. This choice is attractive because stabilization of the head in space physically minimizes the torque exerted on the neck by the
load. Despite the appealing nature of this mechanical condition, it was rarely the choice of the animal unless the loads were very high. The second choice, to stabilize the head with respect to the trunk, is perhaps the least appealing because some mechanism would have to be utilized to prevent the torque produced by the additional load from moving the head with respect to the trunk. It was particularly surprising that the data suggested that this was the predominant choice of the animal. In many cases, the kinematics of the head movements were unaffected by small additional loads, suggesting the presence of a compensatory mechanism. These observations were also supported by EMG recordings that showed an increase in the level of activation when loads were attached to the head. We acknowledge that any one of the three choices

FIG. 8. Response gain and phase and their relationship to inertia and torque. A1–C1: head-movement kinematics (gain and phase) recorded during WBR (0.5, 1.0, and 2.0 Hz at 50%) as a function of the change in inertia applied to the head for 3 animals. A2–C2: head-movement kinematics (gain and phase) replotted as a function of the torque needed to counteract the torque produced by the additional inertia. The torque needed was calculated by multiplying the inertia by the stimulus acceleration. Head-movement kinematics changed when \( \tau_{TS} > \tau_{max} \).
Mechanisms that might have been used to help stabilize the head with respect to the trunk.

Mechanisms that regulate head movement during whole body rotation

In the following, we consider the behavior of the head movements produced during whole body rotations with respect to the VCR and CCR. Although it is plausible that the head-movement kinematics we quantified occurred solely as a consequence of inertia and the passive viscoelastic properties of the neck, it is highly likely that the VCR and CCR contributed to the kinematics observed in these studies. The head movements that we reported exhibited comparable properties to those reported in similar cat and human studies in which neck muscle EMG recordings were used to confirm active processes related to the VCR and CCR (Goldberg and Peterson 1986; Keshner et al. 1999). Vestibular afferents in squirrel monkeys (Fernandez and Goldberg 1971, 1976; Goldberg and Fernandez 1971a,b), and their targets within the vestibular nuclei (Cullen et al. 1991, 1993; Highstein et al. 1987; McCrea et al. 1987a,b), are known to be active during all the stimuli that were used. The dorsal neck muscles in squirrel monkeys are also active in these contexts based on our EMG recordings from splenius muscles and the neck EMG recordings from that of other labs (Killian and Baker 2005). Finally, our prior recordings from secondary vestibular neurons in head-free squirrel monkeys have shown these pathways to be active during the same head movements evoked during whole body rotation (Gdowski and McCrea 1997, 1999a, 2000; Gdowski et al. 1996). Based on our observations in the vestibular nuclei, if one considers the metabolic energy in conveying such signals from the vestibular labyrinth to the spinal cord it seems highly unlikely that the two reflexes would be inactive and have no role in controlling the head movements reported in this study.

Other contributing factors could include voluntary changes in neck stiffness, which are known to affect head movements produced during whole body rotations (Keshner 2000). In our experiments, it was not usually possible to identify voluntary changes in neck stiffness with the one exception when EMG records were obtained. We tried to minimize this contribution.
by designing the apparatus so that the gravitational forces imposed by the additional inertia were exerted on the supra-structure as opposed to the head or neck. Consequently, the only force due to the additional inertia that was experienced by the animal was a rotational torque that occurred only during whole body rotation. The occurrence of voluntary changes in stiffness could not be ruled out and might account for some variability in the results across the population. Indeed in cases where EMG records were obtained, there was some evidence of voluntary changes in muscle activity.

Role of the VCR and CCR in maintaining stability of the head with respect to the trunk

The relative weighting of the sensory signals could contribute to the head-movement kinematics that were observed during rotation. The proprioceptive signal that was produced when the head moved on the trunk had a corresponding gain equivalent to $G_{HT}$. Similarly, the gain of the vestibular sensory signal corresponded to the gain of the head movement in space ($G_{HS}$). Thus during normal unloaded conditions, the head movements produced during WBR had a vestibular signal ($G_{HS} = 0.76 \pm 0.03$) that was larger than the proprioceptive signal ($G_{HT} = 0.24 \pm 0.03$) for all stimuli tested. In these circumstances, the vestibular sensory signals were significantly larger than proprioceptive signals. This imbalance, favoring the VCR, might explain why the default head movement was in the opposite direction and nearly in phase with the stimulus velocity. Without the VCR, the inertia of the head would cause head movements in the opposite direction of the stimulus but in phase with stimulus acceleration, as was observed during high-frequency rotations when the inertia of the head was increased. In the case of the SSN stimulus, the two sensory signals were more equivalent ($G_{HS} = 0.52 \pm 0.12$ and $G_{HT} = 0.48 \pm 0.12$). Larger proprioceptive signals during this condition might explain why the phase response observed during the SSN stimulus was far more variable.

Adding inertia to the head would be expected to assist in keeping the head stationary in space, thereby resulting in larger head-on-trunk movements when the trunk was rotated. In all cases, larger head movements were not observed until the torque produced by the additional inertia exceeded a critical value. Once the critical torque value was exceeded, the magnitude of the head-on-trunk movements increased with further increases in inertia. The critical value of torque was found to be correlated with what has been described as the transitional frequency by prior studies. The transitional frequency represented the point in the frequency response at which higher stimulus frequencies resulted in a rapid increase in the magnitude of the head-on-trunk movement. Once the stimulus frequency was above the transition frequency, the head movements that were produced functioned to reduce the vestibular sensory signal to zero, essentially turning off the VCR. If the VCR contributed to controlling the head during WBR, it would most likely be within the spectral region of the frequency response where the vestibular sensory signal was the largest.

That spectral region corresponded to frequencies located below and slightly above the transition frequency. Further studies are needed to determine if the change in bandwidth arises as a consequence of the mechanics of the head/neck plant or as a consequence of a limitation in the output of the neural substrate underlying the VCR and CCR.

The CCR’s contribution toward controlling head movement during whole body rotations has been debated in studies using...
cats and humans. The CCR was found to be active during neck rotations in decerebrate cats based on EMG recordings of neck muscles (Goldberg and Peterson 1986; Peterson et al. 1981, 1988). However, later studies using similar methods found the CCR to be absent in the awake behaving cat (Banovetz et al. 1995). Modeling studies have also suggested that the CCR has a minimal role in yaw head stabilization when inertia is added to the head (Keshner and Peterson 1995; Keshner et al. 1999). Studies are currently being carried out to determine if the CCR has a role in controlling head movements in squirrel monkeys. The CCR could have a more prominent role for stimulus frequencies slightly below or above the transition frequency when inertia is added to the head. In this spectral region of the frequency response, large head movements are produced in phase with stimulus acceleration. Therefore proprioceptive signals produced during these stimuli could increase activation of the CCR and reduce oscillations that might occur in its absence.

**Plasticity of the collic reflexes**

In many cases, when inertia was added to the head, it had little or no impact on the gain of the head-on-trunk movement produced during WBR. This result implies that either more torque or stiffness must be produced to counteract the torque produced as a consequence of the additional inertia. Interestingly, our data suggest that as long as the additional torque needed to stabilize the head was lower than a critical torque ($T_{TS} < T_{max}$), then the head movements that were produced were unaffected in gain. Modeling of the two reflexes has suggested that this can be accomplished by changing the stiffness of the plant or by increasing the gain of the VCR (Keshner et al. 1999). The change in stiffness could arise as a voluntary change in stiffness. Alternatively it could arise by simultaneously increasing the gain of both the VCR and CCR. Our EMG recordings from the splenius muscles suggest that the gains of the two reflexes were dynamically changed to accommodate different loads. It was not possible to determine if both reflex gains changed or if an individual reflex gain changed in our experiments. From a behavioral perspective, it is well known that the collic reflexes rapidly adapt during different contexts. A subject’s awareness of the approaching or pending stimulus by providing auditory or visual precues can affect the kinematics or muscle activity produced by collic reflexes (Blouin et al. 2006a, b; Kumar et al. 2000, 2004). Activation of neck muscles can be modified if the subject initiates a whole body perturbation (Blouin et al. 2003b). Finally, reflexive activation of the neck muscles can habituate following repeated perturbations of the same stimulus (Blouin et al. 2003a; Keshner et al. 1987; Siegmund et al. 2003a, b). Further experiments are needed to tease out the mechanisms that might underlie the ability to maintain head stability when inertia is added to the head.

**Conclusion**

Our findings show that squirrel monkeys only produce small head movements with respect to their trunk during whole body rotation over a wide range of stimulus frequencies (0.5–4 Hz) and accelerations ($\approx 628/\text{s}^2$). This may simply be due to the relatively low moment of inertia of the squirrel monkey’s head compared with that of cat or human. However, some active processes also occur as indicative by active EMG responses from the neck splenius muscles. No resonant frequencies were observed for these stimuli. The ability to stabilize the head with respect to the trunk over these stimulus parameters is likely attributable to the fact that the inertia of the squirrel monkey’s head is lower than that of human or cat. In addition, our findings indicate that squirrel monkeys produce similar head movements before and after the addition of small amounts of inertia to their heads. Our findings also showed that the ability to compensate for changes in inertia extended over a wide range of stimulus accelerations. One consequence of adding inertia was to decrease transitional frequencies as observed in prior cat and human studies. This suggests that the ability to compensate for changes in inertia is frequency dependent such that higher changes in inertia can be preferentially accommodated at lower stimulus frequencies. Further investigation is required to determine if the gain of the collic reflexes (VCR and CCR) change when inertia is added to the head.

**Acknowledgments**

We thank J. Leblanc for help during surgical preparations and animal care. We also thank C. Kumar for assisting in the development of instrumentation that was essential to the project. We thank A. Green for her assistance in obtaining and analyzing the neck EMG data set. We also thank Dr. Martha Johnson Gdowski and the reviewers for helpful comments on this manuscript.

**Grants**

This work was supported by Whitaker Foundation Grant RG-01-0272 and National Institute on Deafness and Other Communication Disorders Grants R01DC-006498 and P30-DC-05409.

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