Reweighting Sensory Signals to Maintain Head Stability: Adaptive Properties of the Cervicocollic Reflex

J. S. Reynolds, D. Blum, and G. T. Gdowski

Departments of Biomedical Engineering and Neurobiology and Anatomy, University of Rochester, Rochester, New York

Submitted 13 July 2007; accepted in final form 23 April 2008

Reynolds JS, Blum D, Gdowski GT. Reweighting sensory signals to maintain head stability: adaptive properties of the cervicocollic reflex. J Neurophysiol 100: 3123–3135, 2008. First published April 24, 2008; doi:10.1152/jn.00793.2007. A major goal of this study was to characterize the cervicocollic reflexes (CCRs) in awake squirrel monkeys and compare it to observations in cat. This was carried out by stabilizing the head in space while rotating the lower body. The magnitude and phase of the torque produced between the head and the restraint system was used as an indicator of the CCR. Many properties of the squirrel monkey’s CCR were found to be similar to those of the cat. The torque decreased as a function of frequency and amplitude. In addition, the static level of torque increased with head eccentricity. One difference was that the torque was 90% smaller in squirrel monkeys. Biomechanical differences, such as differences in head inertia, could account for these differences. The second goal was to determine if the CCR was sensitive to increases in the head’s inertia. To test this, we increased the head’s inertia by a factor of 36 and allowed the reflexes to adapt by rotating the whole body while the head was free to move. The CCR was rapidly assessed by periodically stabilizing the head in space during whole-body rotations. The magnitude of the torque increased by nearly 60%, suggesting that the CCR may adapt when changes in the head’s inertia are imposed. Changes in the torque were also consistent with changes in head-movement kinematics during whole-body rotation. This suggests that the collic reflexes may dynamically adapt to maintain the performance and kinematics of reflexive head movement.

INTRODUCTION

Based on Newton’s second law of motion, the inertia of the head produces torque that is exerted on the neck when the body is angularly accelerated. This torque reacts against the viscoelastic properties of the neck and if unopposed can result in undesirable, and potentially dangerous, changes in the orientation of the head with respect to the trunk. Although the inertial torque can be counteracted by voluntary changes in the neck’s stiffness, they may also be opposed by reflex mechanisms that evolved so that ongoing voluntary movement could occur without attending to the ever-changing direction and magnitude of inertial changes. Two collic reflexes are thought to work synergistically toward maintaining the head’s stability by activating the neck’s musculature including: the vestibulocollic reflex (VCR), which utilizes vestibular sensory information, and the cervicocollic reflex (CCR), which utilizes proprioceptive sensory information (Ezure and Sasaki 1978; Ezure et al. 1976, 1978). One might expect the reflexes to be sensitive to changes in the head’s inertia because the head’s mass can change throughout the aging process and can change transiently when protective head gear is used. The goal of the present work was to determine if proprioceptive sensory reflexes adapt to compensate for changes in the head’s inertia to maintain the head’s stability.

The combined function of the VCR and CCR has been inferred from simulations that have modeled their interaction as a linear combination of their individual functions. The VCR has been studied by fixing the head’s position with respect to the trunk so that the consequence of vestibular stimulation during whole-body rotation could be evaluated in the absence of proprioceptive feedback. In this condition, the VCR’s function was thought to produce compensatory head movements when the whole body was rotated based on the reciprocal activation patterns of the neck musculature that were observed (i.e., by activating contralateral neck muscles while simultaneously inhibiting ipsilateral neck muscles) in combination with the torque that was produced on the restraint device. The VCR, however, is rarely evoked in isolation of proprioceptive signals when the head is free to move. When the head is moved in the contralateral direction, it is accompanied with a proprioceptive signal that occurs when the ipsilateral neck muscles are stretched. This proprioceptive signal presumably activates a stretch reflex (CCR) that prevents the ipsilateral muscles from being stretched further. Consequently, the functions and the mechanisms of action of the VCR and CCR are dynamically opposed. The resulting head movement depends on the relative gains and strengths of each of the reflexes. Modeling studies of the interactions between the VCR and CCR have considerably improved our understanding of their combined functions with respect to the head movements they produce. For example, if the gain of the CCR was attenuated or turned off and the gain of the VCR was increased, the result would be the production of head movements that were compensatory with respect to the direction of whole-body rotation. Similarly if the gains of both the VCR and CCR were increased, the combined function would be to increase the stiffness of the neck to reduce head-on-trunk movement during whole-body rotation. Consequently the combined function of the VCR and CCR are likely context dependent and are dynamically regulated by the CNS to obtain a desired outcome: either to stabilize the head in space or with respect to the trunk. This might explain why the two reflexes appear to function to stabilize the head with respect to the trunk during passive whole-body rotations in the dark (Keshner et al. 1995, 1999; Peterson et al. 1981, 1988), while activities like walking or
running appear to elicit the function of stabilizing gaze (Imai et al. 2001a,b; Raphan et al. 2001).

The head’s inertia complicates the control of the head movement regardless of the overall functions of the two reflexes. The torque produced by the head’s inertia is proportional with whole-body angular acceleration and if unopposed would result in head-on-trunk movements that were also in phase with whole-body acceleration. Adding inertia to the head only exacerbates the problem in addition to modifying the passive biomechanics of the head/neck plant (Cross and Serenelli 2003; Hamalainen 1993; Smith et al. 1985). We hypothesize that an active process exists; the goal of which is to maintain the kinematics of reflexive head movements with respect to the trunk. Such a process would have to be sensitive to changes in any parameter (e.g., head inertia and/or neck viscosity), which if uncompensated would cause changes in kinematics. This hypothesis is supported by previous studies in cats and humans that have revealed that when the head’s inertia is increased, only small changes are observed in the head-movement kinematics produced when the whole body was rotated (Goldberg and Peterson 1986; Keshner et al. 1999). It has been hypothesized that the VCR, CCR, or both reflexes adapt to increase the activation of neck muscles to produce more torque to compensate for the torque produced by the mass added to the head. However, there currently is no evidence that the gains of the VCR or CCR can be dynamically altered. A fundamental goal of the present study was to determine if the gain of the CCR changes to compensate for changes in the head’s inertia.

The first series of studies we conducted were to characterize the CCR of squirrel monkeys so that it could be compared with previous cat studies. In these studies, the neck was stretched by stabilizing the head in space while the whole body was rotated. The torque exerted on the device used to stabilize the head was used as a quantitative measure of the CCR’s strength. Experiments were also conducted to determine if the CCR changed as a consequence of adding inertia to the head. A method of rapidly assessing the CCR was used to quantify changes that occurred as a result of increasing the head’s inertia. Large increases in the gain of the CCR were observed immediately following the increased inertial load. These results are the first evidence of direct modifications in the gain of the CCR as a consequence of changing the head’s inertia. These results suggest that the CCR has a larger contribution to the stabilization of the head than was previously thought.

Methods

Surgical preparation

All surgical and experimental procedures were approved by the University Committee for Animal Resources at the University of Rochester and have been described previously (Reynolds and Gdowski 2008). The animals were housed under conditions that comply with National Institutes of Health standards as stated in the Guide for the Care and Use of Laboratory Animals (2003) and the Association for Assessment and Accreditation of Laboratory Animal Care International.

Six adult squirrel monkeys were surgically prepared for chronic recording of head movements. All surgeries were conducted under sterile conditions using isoflurane anesthesia. A cap made from dental acrylic was attached to the cranium using small stainless steel bolts. A key bolt was embedded in the acrylic which was used to attach the animal’s head to the experimental apparatus in the ~15° nose down position. This head orientation optimally activates the horizontal semicircular canals during yaw head movements in squirrel monkeys.

Experimental setup

The squirrel monkeys were seated in a chair on top of a motor that rotated about the earth-vertical axis. Animals wore custom mesh vests that were used to secure the upper torso and shoulders to the chair (Fig. 1). The key bolt on the skull was connected to a carbon-fiber rod (Fig. 1, v) that was collinear with the chair’s rotational axis. The rod was attached to a rotational inline torque sensor (LeBow, 1701; Fig. 1, iv) that allowed the animal to produce yaw head movements while restricting movements in other planes. The other end of the rotational torque sensor was attached to a clutch (Placid Industries, C2D; Fig. 1, iii). The axle of the clutch could be quickly restrained with a pin (Fig. 1, ii), which engaged a ceiling-mounted superstructure (Fig. 1, i). This configuration held the animal’s head stationary in space. The neck was stretched by rotating the motor and the animal’s upper trunk and torso about the C1–C2 vertebral axis. The head’s rotation with respect to the trunk was limited to ±45°, and the motor was disengaged if it was exceeded. The torque that was exerted on the neck never exceeded 4 N·cm. A search-coil system (Remmel) was used to measure horizontal and vertical head positions with respect to the table by placing a search coil on the rod connected to the animal’s headbolt. Head velocity was computed as the derivative of the position signals. Table position signals were recorded from the motor control system, which was calibrated using a velocity sensor (Watson Industries). Head velocity in space was computed as the vector addition of the head velocity with respect to the table and table velocity ($H_s = H_t + T_s$).

**FIG. 1.** A: schematic illustration of experimental components including: ceiling attachment (i), stabilization pin (ii), clutch (iii), rotational torque sensor (iv), vertical rod (v), head bolt (vi), search coil (vii), field coils (ix), and servo-motor (x). The expanded portion of this figure shows the conversion of the system so that the inertia of the head could be modified. A horizontal rod (green) was placed on the stabilization pin so that a mass (m) could be added to the rotational axis. The change in inertia and in torque produced by the additional mass depended on its distance from the axis of rotation (r, see text). B: top-down graphic illustration of the head-stationary in space paradigm. The animal’s head was always centered with respect to the trunk prior to rotating the body. C: top-down graphic illustration of the head-stationary in space paradigm as a function of head eccentricity. The animal’s head was positioned with respect to the trunk with a specific head eccentricity prior to rotating the body. ←, rotation of servomotor.
The data-acquisition system (NI) consisted of a computer that communicated with a real-time data collection processor. The system included analog inputs and outputs (16-bit), digital I/O lines, and event clocks (100 μs). The system acquired signals, controlled the rotational motor, and monitored the paradigms. Each signal was filtered (200 Hz) and sampled at 500 Hz. In all figures, positive torques and rotations corresponded to clockwise rotations of the monkey’s head. Measures of torque are reported in N·cm.

**SUM-OF-SINUSOIDS STIMULUS.** A sum-of-sinusoids stimulus (SSN) was used to minimize stimulus predictability. A velocity command (bandwidth: 0.19–4.12 Hz) was generated that consisted of 10 sinusoids having frequencies that were a prime harmonics (37, 49, 71, 101, 143, 211, 295, 419, 589, and 823) of a common base frequency (0.05 Hz). The velocity of each component was: 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 at 2.95 Hz, and 13°/s at 4.12 Hz. The angular acceleration and displacement were limited to 628°/s² and ±45°.

**Experimental paradigms**

The majority of the experiments were conducted with six squirrel monkeys. Some experiments were conducted using a subgroup of this population. The torque associated with the CCR was quantified by monkeys. Some experiments were conducted using a subgroup of this population. The frequency response was assessed by using anesthesia to eliminate torque components that arise as a consequence of the neural components influencing the CCR. All paradigms were conducted in complete darkness. Animals were monitored using an infrared camera system, and paradigms were discontinued when the animal was not alert.

**FREQUENCY RESPONSE PARADIGM.** The frequency response was obtained by recording the torque while the trunk was rotated and the head was restrained to the ceiling (Fig. 1B). The peak velocity was 30°/s for sinusoidal motions. The stimulus frequency was randomly selected and was varied from 0.5 to 4 Hz in increments of 0.5 Hz. The response to a SSN stimulus was obtained for comparison.

**CCR GAIN LINEARITY PARADIGM.** The linearity of the gain was characterized by recording the torque produced during sinusoidal table rotations while the head was restrained to the ceiling (Fig. 1B). Three frequencies were tested (0.5, 1.0, and 4.0 Hz). Several trials were collected for each frequency covering a wide range of stimulus amplitudes (peak change in position: 1.5–16°). The order of stimulus amplitudes was randomly selected.

**HEAD-ON-TRUNK ECCENTRICITY PARADIGM.** The effect of head-on-trunk position was studied by changing the initial head-on-trunk position before a 1.0-Hz, 10°/s stimulus was applied. Multiple trials were acquired as the head-on-trunk offset was randomly varied between ±30° in 5° increments (see Fig. 1C). A 1.0-Hz stimulus at 10°/s was chosen because its excursion (±1.6°) was less than half of the 5° increment in head-on-trunk offset. This stimulus allowed the paradigm to be tested over a larger range of head-on-trunk positional offsets without exceeding the maximum head-on-trunk excursion (±45°).

**PARADIGM FOR ASSESSING VISCOELASTIC PROPERTIES.** The contributions of the viscoelastic properties of the neck musculature were assessed by using anesthesia to eliminate torque components that arise as a consequence of the neural components influencing the CCR. Monkeys were anesthetized with ketamine (20 mg/kg) and diazepam (1.0 mg/kg). The torque measured while the animal was anesthetized was attributed to the neck’s viscoelastic properties. The frequency response properties of the CCR were obtained both before and during anesthesia.

**ADAPTATION PARADIGM.** A sequence of paradigms was repeated three times (without, with, and without additional mass) to determine if proprioceptive signals were modified by changing the head’s mass. As a reference, the moment of inertia of the squirrel monkey’s head was approximated as an ellipsoid with a mass of ~115 g. The short and long radii of the population ranged between 45–55 and 60–80 mm, respectively. The head’s moment of inertia was calculated as $I_h = m^2(a^2 + b^2)/5$. 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 $I_h = 0.42 ± 0.05$ kg·cm²), yielding $I_h = 0.4–0.55$ kg·cm². The inertia of the vertical rod and head restraint system ($I_v$) was measured experimentally and was 0.6 kg·cm². The total inertia of the head free setup ($I_{HF}$) was 1.02 kg·cm². 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 $A = I/I_{HF}$.

Adaptation was initiated by adding inertia to the head and allowing a period over which voluntary head movements and reflexive head movements evoked by rotating the body were produced. The inertial load was added by placing three 1-oz masses on each side of the rod that rotated with the head (6-in from the center of rotation, Fig. 1A). The produce of the peak change in inertial of $I = 36.4 \times I_{HF}$. The head was then allowed to move while the following was repeated for 15 min: the turntable was rotated using the SSN stimulus for 1 min and then was halted for 1 min so that voluntary movements could be produced. When the adaptive period was completed, the torque was quantified by stabilizing the head in space when the table rotated to its maximum excursion and its velocity was zero. Head stabilization was maintained for several cycles and then released. This was repeated until 10–20 cycles of head stabilization were obtained. The inertial load was removed and the paradigm was repeated after the animals had re-acclimated for 30 min.

**Data analysis**

The data were analyzed using customized software algorithms (Matlab and Igor). Small head movements in space were occasionally produced during the head-restrained paradigms. These were excluded from the analysis. All signals were averaged with respect to the stimulus frequency. A multivariate regression was used to fit the averaged signals with a fixed frequency sinusoid function to quantify their amplitude, offset and phase. Gain measures of the recorded torque were computed with respect to head-on-trunk position (N·m/m²) or acceleration (N·m/s²) and are reported in decibels $[20 \times \log_{10}(gain); \text{db}]$. Responses to the SSN stimulus were analyzed using a Fourier transform (FFT) to calculate the magnitude and phase plots. The nearest points in the magnitude and phase plots to each of the frequency components of the SSN stimulus were used to compute the relative gain and phase shift for each stimulus component.

The data for assessing the plasticity of the CCR were analyzed by first identifying the cycles during whole-body rotation in which the head was stabilized in space. The first cycle when the head was stabilized was discarded to ensure head stability in space. The subsequent cycles were selected for use and the process was repeated until all potential cycles were selected for analysis (typically: >10). The selected cycles were then processed as described in the preceding text.

**CCR model**

A CCR model based on cat studies was used for comparison to the squirrel monkey behavioral data (Peng et al. 1996, 1999). The model is based on the observation that when the left neck muscles were stretched by head rotation toward the right shoulder, it resulted in an increase in the left neck muscle’s electromyographic (EMG) activity that was in phase with head-on-trunk position (Dutia and Hunter 1985; Peterson et al. 1981, 1985). The relationship between the EMG activity and head-on-trunk position was described using the following equation

$$\text{EMG}_{\text{CCR}}(s) = K_{\text{CCR}}[\tau_{\text{MS1}}s + 1](\tau_{\text{MS2}}s + 1)H_T(s)$$

(1)
The magnitude of the EMG signal produced as a consequence of the head-on-trunk rotation was controlled by the gain parameter \( K_{\text{CCR}} \), and the system dynamics were defined by the two time constants \( \tau_{\text{MS1}} \) and \( \tau_{\text{MS2}} \). The conversion of the EMG signal into torque was based on previous human studies that have shown that the primary difference is a phase shift (Gottlieb and Agarwal 1971). Equation 2 was used to transform Eq. 1 into a relationship between torque and head-on-trunk position where: \( K_{\text{TC}} \) is the gain and \( \tau_{\text{TC}} \) is the time constant of conversion
\[
\text{TRQ}_{\text{CCR}}(s) = \frac{K_{\text{TC}}}{(\tau_{\text{TC}} + 1)} \text{EMG}_{\text{CCR}}(s)
\]
\[
= \frac{K_{\text{TC}}K_{\text{CCR}}(\tau_{\text{MS1}}s + 1)(\tau_{\text{MS2}}s + 1)}{(\tau_{\text{TC}}s + 1)} H_T(s)
\]  
(2)

Equation 2 was expressed as a function of head-on-trunk acceleration using a Laplacian operator \((s^2)\)
\[
\frac{\text{TRQ}_{\text{CCR}}(s)}{H_T(s)} = K_{\text{TC}}K_{\text{CCR}}(\tau_{\text{MS1}}s + 1)(\tau_{\text{MS2}}s + 1)}{s^2(\tau_{\text{TC}}s + 1)}
\]
(3)

Prior CCR models have used the following parameter values:

\[
K_{\text{CCR}} = -0.1, \tau_{\text{MS1}} = 0.1s, K_{\text{TC}} = 1, \text{and} \tau_{\text{TC}} = 0.1s.
\]

A negative \( K_{\text{CCR}} \) gain value was used to account for the direction of activation where rightward head-on-trunk rotations activate left neck muscles and vice versa.

RESULTS

The first goal of this study was to determine if the CCR evoked in squirrel monkeys was similar to that reported in the cat. The majority of the experiments were conducted with six squirrel monkeys; however, some experiments were conducted using a subgroup of this population.

Frequency response characteristics

A frequency response of the CCR was obtained so that several variables \( \tau_{\text{MS1}}, \tau_{\text{MS2}}, \text{and} K_{\text{CCR}} \); see Eqs. 1 and 2) could be quantified to produce a model appropriate for squirrel monkeys. Figure 2 \((A1-C1)\) shows the responses during 0.5-, 2.0-, and 3.5-Hz stimuli (all 10°/s). Records of the head movement with respect to the trunk \((H_T)\) and the torque \((\tau)\) that were produced are shown. In these experiments, the head was fixed and stationary in space, and the head-on-trunk movement corresponds to movement of the trunk in the direction opposite of table movement. The raw records were averaged with respect to the stimulus cycle \((Fig. 2, A2-C2)\). At the lower frequency \((0.5 \text{ Hz})\), the peak torque was 1.2 N-cm. As the frequency was increased by two octaves, the magnitude decreased to \(1.06 \times 10^{-1} \text{ N-cm} \) at 2 Hz and then dropped considerably to \(3.04 \times 10^{-2} \text{ N-cm} \) at 3.5 Hz. In all three cases, the torque phase response was nearly \(-90^\circ\) with respect to peak head-on-trunk velocity \((-76, -89, \text{and} -85^\circ; \text{respectively})\), which was consistent with signals originating from muscle spindle afferents.

The gain and phase of the torque response is shown as a function of stimulus frequency in Fig. 3 for all six animals. All stimuli had a peak velocity of 30°/s. The gain and phase response was computed with respect to stimulus acceleration to be consistent with conventions that have been used in other vestibular studies. The maximum torque gain varied from animal to animal, but the change in gain \((\text{slope; dB/decade})\) as a function of frequency was similar. These properties were quantified by regressively fitting a line to each animal’s torque gain versus frequency plot. Each animal’s linear regression was then normalized with respect to the average y intercept of the entire population. A summary of linear regressions fit to the torque gain and a normalization value for each animal is given in Table 1. At low frequencies, the phase response of the torque was in phase with table position, suggesting that the animals were producing torques to maintain their head centered on their trunk. With increases in frequency, the phase responses in squirrel monkeys varied from animal to animal. In some animals, the phase response changed minimally throughout the frequency range tested, staying in phase with table position, while in others it continued to lag. In Fig. 3B, a population average of the normalized gain and phase obtained using a pure sinusoidal stimulus \(\bullet\) is compared with the response obtained using a nonpredictable pseudorandom SSN stimulus in three animals \(\bigcirc\). The torque gains were similar but were slightly higher for the pure sinusoidal stimulus. The phase response of the SSN paradigm was more variable at lower frequencies but was more consistent at higher frequencies, producing torques in phase with table position, similar to the pure sinusoidal response.

Figure 3B compares the population statistics of the torques recorded in squirrel monkeys to the EMG activity \((\times)\) and torques \((+\) reported previously for alert cat (Peterson et al. 1985) and the torques predicted by a neuromechanical model \((\cdots\) for humans (Peng et al. 1996). In general, the slope of line fit to the torque gain from 0.5 to \(4.0 \text{ Hz} \) recorded in squirrel monkey \((-9.3 \pm 1.7 \text{ dB/dec})\) was similar to that of the torque \((-7.3 \text{ dB/dec})\) predicted by the neuromechanical model. These results suggest that the time constants used to approximate transfer functions of the peripheral and central processes in the CCR model (Peng et al. 1996, 1999) are similar for the two species \(\tau_{\text{MS1}}, \tau_{\text{MS2}} \text{ and} \tau_{\text{TC}}\). However, the overall gain of the transfer function obtained in squirrel monkeys was significantly different in comparison to cats. This difference corresponds to a smaller gain constant, \(K_{\text{CCR}}\), in the CCR model (Peng et al. 1996, 1999). The gain constant \(\left(K_{\text{CCR}}\right)\), was approximated by regressively fitting the torque transfer function, yielding a gain constant of \(K_{\text{CCR}} = 6.6 \times 10^{-3}\) as an approximation for the population of squirrel monkeys. The estimated torque gain using the modified \(K_{\text{CCR}}\) is plotted as a solid trace in Fig. 3B. A smaller CCR gain in squirrel monkeys is not surprising because the inertia of the cat’s head is nearly 20 times larger than the estimated inertia of the squirrel monkey’s head. In sum, the results of both the sinusoidal and SSN stimuli suggest that the CCR in squirrel monkeys acts like a second-order system similar to that reported for cat and humans.

CCR gain linearity

Prior cat studies have shown that the CCR gain has higher gains for smaller stimulus amplitudes (Peterson et al. 1985). From a functional point of view, a nonlinear gain could be significant when the head is free to move during whole-body rotation because the head-on-trunk movement amplitude and its corresponding proprioceptive sensory signal are small compared with the vestibular sensory signal. Experiments were conducted in four squirrel monkeys to determine if similar
nonlinearities in torque gains occurred at low stimulus amplitudes. The torque gains and phases for 0.5-Hz stimuli are plotted as a function of stimulus amplitude in Fig. 4A. Nonlinear gains were observed in four of six squirrel monkeys tested. As previously reported in cats, the highest gains computed with respect to stimulus position were observed at the lower amplitudes (≤ 5°, Fig. 4A). At 0.5 Hz, higher gains were observed at lower stimulus amplitudes in five of six animals tested. A quantitative measure of the gain nonlinearity was obtained by computing the ratio of the average of the three smallest amplitudes and the average of the three largest amplitudes tested. On average, the gain for small amplitude stimuli was 35.4 ± 17% larger than the gain observed at large amplitudes. Similar trends were observed in the data obtained using a 1.0-Hz stimulus. All six animals also had higher gains at lower stimulus amplitudes and, on average, exhibited nonlinearity ratios of 34.4 ± 17%. In both cases, the nonlinearities observed in Fig. 4A were less apparent when the torque gains were recomputed with respect to stimulus acceleration (Fig. 4B). At all frequencies tested, the torque gain and phase remained constant with respect to stimulus acceleration across the entire population. In general, the torque gain nonlinearity decreased with frequency with the phase consistently in phase with table position. Therefore even though torque gain nonlinearity existed, it may be of less importance in stabilizing the inertia of the head because the torque produced on the neck due to the head’s inertia depends on head acceleration rather than small changes in head position.

Effect of head-on-trunk eccentricity

The sensitivity of the muscle spindle afferent responses can depend on the muscles initial length (Matthews and Stein 1969). We hypothesized that a similar effect might be observed in stretch reflexes of the neck. This hypothesis was tested by repeating the paradigm at a frequency of 1 Hz and peak velocity of 10°/s while the initial head-on-trunk orientation was manipulated sequentially over ±30° in 5° increments (see Fig. 1C).

The effect of head-on-trunk eccentricity on torque gain was evaluated in four animals. Figure 5, A and B, shows the gain...
and phase of the dynamic torque response with respect to the
stimulus acceleration plotted as a function of initial head-on-
trunk position for all animals. Higher gains at the higher
head-on-trunk eccentricities were not observed over the range
of head eccentricities tested (±30°). Slight variations in torque
gain and phase were observed, but none that were correlated
with eccentric head-on-trunk position. Figure 5C shows the
constant value of static torque recorded during the trunk
rotation plotted as a function of the initial head-on-trunk
position. All four animals produced a small, constant static
torque that was related to the initial head-on-trunk position. In
general, when the animal’s head was turned left with respect to
the body, there was a positive static torque pushing the head
toward the right (clockwise) to center the head on the trunk.
When the animal’s head was turned to the right with respect to
the body, there was a negative static torque pushing the head
leftward. A linear regression was used to characterize the
relationship between static torque and initial head-on-trunk
position and the average slope of the regressions was −0.02 ±
0.01 (N·cm/°).

Contribution of viscoelastic properties

One question we tried to assess was how much the viscoelas-
tic properties of the neck muscle contributed to the torque
measurements that were recorded. To address this question,
recordings of the torque were obtained while the animals were
anesthetized to assess the torque produced in the absence of the
CCR. Figure 6A compares the torque produced by the CCR
while the animal (−) was alert and while the animal was
anesthetized (−−−) for sinusoidal body rotations (0.5, 1.0, and
1.5 Hz; 20°/s). Shaded regions in Fig. 6 highlight the differences in torque between the alert and anesthetized conditions. In all three animals, the torque responses during the alert conditions were larger than those during the anesthetized conditions. This was true for nearly all stimuli tested. Several possibilities could explain this result. One possibility is that this difference could arise as a change in active processes related to the CCR. However, it is also interesting to note that the change in torque was frequency dependent such that most reductions were observed during low-frequency stimuli and almost no difference at the highest frequencies. This could suggest that higher order processes producing voluntary changes in stiffness might contribute to the torques observed at low frequencies in the awake state. Another possibility could be that the viscoelastic properties of the neck could be affected by the presence of anesthesia producing changes in the observed torque. One conclusion that can be drawn from this data are that the CCR is likely to be more active in the awake state because the torque produced in the awake state was almost always larger than that observed during the anesthetized condition.

Adaptive properties of the CCR: effect of increased head inertia on the CCR

The raw data shown in Fig. 7 illustrate the gain of the CCR during each of the three conditions including: before (A), during (B), and after (C) the masses were added to the head causing the inertia of the entire system to change by a factor of 36 (\(\Delta I = 36.4 \times I_{HG}\)). The vertical dashed line denotes the time point at which the head was rapidly restrained to quantify the CCR. In each of the three conditions, the point at which the head was restrained varied slightly with respect to the table velocity signal. The first cycle occurring after the point of restraint was typically discarded to ensure that the head was stable in space. This was done to minimize the potential contribution of the VCR to the torque response that was observed. Figure 7D shows the averaged data for each of the three conditions in A–C shown in the preceding text. The horizontal lines in Fig. 7D are

<table>
<thead>
<tr>
<th>Animal</th>
<th>Slope</th>
<th>DC</th>
<th>P</th>
<th>Slope</th>
<th>DC</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>312</td>
<td>-11.817</td>
<td>-68.50</td>
<td>0.974</td>
<td>-12.243</td>
<td>-64.76</td>
<td>0.907</td>
</tr>
<tr>
<td>313</td>
<td>-8.6689</td>
<td>-69.14</td>
<td>0.985</td>
<td>-10.321</td>
<td>-69.52</td>
<td>0.881</td>
</tr>
<tr>
<td>315</td>
<td>-8.5062</td>
<td>-70.24</td>
<td>0.952</td>
<td>-9.76</td>
<td>-69.52</td>
<td>0.881</td>
</tr>
<tr>
<td>608</td>
<td>-7.5376</td>
<td>-78.63</td>
<td>0.906</td>
<td>-9.76</td>
<td>-69.52</td>
<td>0.881</td>
</tr>
<tr>
<td>609</td>
<td>-11.01</td>
<td>-28.55</td>
<td>0.859</td>
<td>-10.481</td>
<td>-64.66</td>
<td>0.885</td>
</tr>
<tr>
<td>610</td>
<td>-8.3604</td>
<td>-76.95</td>
<td>0.924</td>
<td>-11.015</td>
<td>-66.31</td>
<td>0.991</td>
</tr>
<tr>
<td>Mean ± SD</td>
<td>-9.31 ± 1.69</td>
<td>-65.33 ± 16.90</td>
<td>0.933 ± 0.047</td>
<td>-11.015 ± 1.066</td>
<td>-66.31 ± 2.27</td>
<td>0.891 ± 0.014</td>
</tr>
</tbody>
</table>

Data for all six animals are given. Values are means ± SD.
aligned with the peak torque during condition A to facilitate comparisons of the gains observed in the two subsequent conditions. The torque exerted by the neck increased during the loaded condition and then dropped to its original magnitude once the added inertia was removed. The shaded region represents the change in neck torque produced during the loaded condition compared with the unloaded condition. The phase response is consistently in phase with table position, continuing to stabilize the head with respect to the trunk. Similar observations were recorded in two of three animals tested (data not shown). In one animal, there were small, if any, changes in gain after inertia had been added to the head. In most cases, the gain and phase response of the torque returned to its original state once the added inertia was removed and the animal was allowed to acclimate to the original condition (without added mass on the head).

Are the changes in CCR gain sufficient?

The ability to compensate for the torque imposed on the neck by adding mass to the head ($\tau_{\text{mass}}$) can be accomplished by increasing the gain of the VCR, CCR, or both. An important question is whether or not the CCR was primarily responsible for this compensation. To address this question, the change in peak neck torque produced after the mass was added to the head (shaded region; Fig. 7D) was plotted as a function of stimulus frequency for all three animals in Fig. 8. The magnitude of the torque imposed on the neck as a consequence of the increased mass added to the head ($\tau_{\text{mass}}$) is also shown in Fig. 8 (—). In one animal, only small changes in gain after inertia had been added to the head. In most cases, the gain and phase response of the torque returned to its original state once the added inertia was removed and the animal was allowed to acclimate to the original condition (without added mass on the head).

Do other mechanisms contribute to head stabilization when mass is added to the head?

The ability of the CCR gain to adapt varied both as a function of frequency and between animals. One plausible explanation for the variability in CCR gain adaptation could be that compensation was incomplete at higher frequencies and torque loads. In this case, head stabilization, as observed in the unloaded condition, would not be possible and would be reflected in the head-movement kinematics when the head was free to move in the horizontal plane. Alternatively, other mechanisms (e.g., the angular and linear VCRs) could contribute toward the maintenance of head stability. If this hypothesis was true, the kinematics of head-on-trunk movements would be expected to be similar in the loaded and unloaded conditions even if the CCR did not produce sufficient compensatory torque. To address this question, we quantified the head movement kinematics immediately prior to the point of restraint when the CCR gain was quantified (Fig. 8). The changes in the gain of the head movement kinematics (e.g., peak head-on-trunk velocity/table velocity) were then compared at different levels of change in CCR gain ($\Delta \tau/\tau_{\text{mass}}$).

Remarkably, the head-movement kinematics observed when the head was free to move during whole-body rotation changed in a manner that was consistent with the changes and variability in the gain changes of the CCR. Figure 9A shows the cycle-averaged head-movement kinematics during whole-body rotation without and with added inertia for the data illustrated in Fig. 7. The gain of the CCR and the gain of the head-free head-movement kinematics were inversely related, such that when large changes in the CCR gain were observed, only small changes in head-free head-movement kinematics were produced. Similarly when smaller changes in the CCR gain were
observed, large changes in the head-free head movement kinematics were produced (Fig. 9, B and C). This was true in most cases for all three animals tested, including the animal (610) that tended to have a small CCR throughout the entire set of experiments. In a few cases, the change in gain of the CCR was small even though the kinematics of the head-on-trunk movements were similar in the loaded and unloaded conditions. This suggests that other mechanisms in addition to the CCR (e.g., VCR) could also be involved in adaptively stabilizing the head when mass is added.

**DISCUSSION**

The main contributions of this study can be summarized as follows: 1) the CCR in squirrel monkeys was characterized and quantified by measuring the overall torque exerted on the rod that was used to restrain the animal’s head in space while the trunk was rotated. 2) Most of the response properties of the CCR in squirrel monkeys were similar to those of cats. 3) A paradigm was developed for quickly assessing the CCR that was used to characterize the adaptive properties of the reflex when mass was added to the head. 4) The adaptation exhibited by the CCR was found to be inversely related to the gain of head-on-trunk movements produced during head-free whole-body rotation. These results not only provide the foundation for modeling the CCR in squirrel monkeys but also provide the first evidence that the gain of the reflex may be adaptive and serve to help maintain head stability when mass is added.

**Comparative physiology of the CCRs**

We expected to observe significant differences in the behavior and kinematics of the CCR compared with the previous
reports in cat (Bilotto et al. 1982; Dutia and Hunter 1985; Ezure et al. 1983; Goldberg and Peterson 1986). In non-human primates, neck proprioceptive-mediated reflexes have only been studied with respect to voluntary gaze shifts and, in that context, were reported to produce torques that were considerably smaller than those produced by the inertia of the head (Bizzi et al. 1978; Dichgans et al. 1973, 1974). There are also significant differences in the morphology and histochemistry of neck muscles in humans, cats, and non-human primates (Corneil et al. 2001; Kamibayashi and Richmond 1998; Richmond et al. 1999, 2001). The largest differences appear to be in the arrangement of shoulder muscles, such as the trapezius and sternocleidomastoid, which are considerably different in their structure (e.g., pennation angle) in the cat than in the primate. Based on these morphological differences alone, it was surprising that the reflexes were so similar in cats and squirrel monkeys.

The major difference observed in these studies was that the magnitude of the torque produced during neck rotation was significantly smaller than in previous measurements obtained from cats. Such differences are consistent with differences in the biomechanics of the head/neck plant of the two species. The inertia of the head is nearly 20 times larger for cats in comparison to squirrel monkeys. Consequently, the torque produced by the inertia of the head during whole-body rotation would be expected to be larger in cat. Indeed the largest torques that we measured (see Fig. 3A, leftward triangles; monkey 609) that were comparable to those observed in cat were obtained from the largest monkey in our colony. These results suggest that if the function of the CCR was to compensate for inertial torque produced by the mass of the head, its output might depend on the mass of the head of the individual species.

Higher-order processes that are presumably active in awake animals could also potentially alter the responses that were observed (Banovetz et al. 1995). Such processes could be most apparent when testing reflexes at low stimulus frequencies. In the paradigms utilized in these studies, the animals were

FIG. 7. Changes in the gain of the CCR evoked by modifying the inertia of the head. Shown are raw and averaged data records obtained before (A), during (B), and after (C) the inertia of the head was modified by adding mass to the head-free system producing a 36-fold change in inertia ($\Delta I = 36.4 \times I_{HF}$). In each condition, the head was initially free to move. The vertical line in the raw data records denotes the time at which the head was quickly restrained so that the head was stationary in space. The head was restrained for several cycles, released, and then repeated. The averaged data records on the right are the average response of the first few cycles after the head was restrained. The number of cycles in the averaged records is as follows: 11, 12, and 10, respectively. Note the large change in torque gain after the inertia of the head was increased (B) in comparison to the gain of the torque produced before the inertia was increased (A).
rotated in the dark and were not assigned any particular behavioral task. In the context of these studies, it seems rather unlikely that the animal would voluntarily increase the stiffness of its neck because that would require "more" conscious effort. It seems more likely that the animal would relax its neck to reduce strain. In any event, either of these scenarios is feasible. Such processes could underlie some of the variability in responses we observed at low stimulus frequencies. It is also possible that the CCR could have been underestimated in this study because the awake animal may be more likely to relax the neck during the paradigm in which the CCR is assayed. In addition, we did not record the EMG activity of neck muscles as was done in previous studies (Bilotto et al. 1982; Goldberg and Peterson 1986; Peterson et al. 1985), so it was not possible to attribute all of our observations directly with an active process. Prior studies, however, have shown a strong correlation between torque and EMG activity of neck muscles over a wide range of stimulus frequencies and intensities (Peterson et al. 1985). This suggests that the torques we observed in the squirrel monkey are a relatively good indicator of the CCR. The similarity of the torque recordings in both cat and squirrel monkey also suggests that the underlying processes are likely similar.

Prior studies have modeled the frequency-dependent behavior of the CCR as a second-order lead system (Peterson et al. 1985, 1988). To characterize the frequency-dependent nature of the reflex across the entire population, each individual’s frequency response was subjected to a linear regression with a second-order polynomial function and then normalized by the constant coefficient of the function (DC term). Each normalized curve was then offset by the mean constant coefficient of the population. The normalized curves were then averaged to generate the mean frequency-dependent behavior of the torque produced in squirrel monkeys. The shape of the mean population curve was nearly identical to that observed in the cat such that the reflex acted as a second order system with low-pass characteristics. This suggests that in both species the CCR likely functions similarly over the same stimulus frequency range and may primarily serve to help stabilize the head at lower frequencies (approximately equal to <1.5 Hz) where the CCR was larger. At higher frequencies, the reflex could still be active. However, its contribution diminishes significantly with

FIG. 8. Summary of changes in torque gain for three animals evoked by changing the head’s inertia as a function of stimulus frequency. Traces shown include the torque required to restabilize the head due to the change in inertia (—) and the relative change in torque produced by the CCR after the head inertia change was introduced as a function of stimulus frequency for 3 animals.

FIG. 9. Effects of head inertia on head movement kinematics during whole-body rotation. A: shown are the cycle-averaged head movement kinematics during whole-body rotation without and with added inertia for the data illustrated in Fig. 7. Number of cycles in each average: 12 and 11. B: head movement kinematics (313) during high-frequency whole-body rotation without and with added inertia. Number of cycles in each average: 10 and 13. C: head movement kinematics (610) during high-frequency whole-body rotation without and with added inertia. Number of cycles in each average: 10 and 11.
increasing frequency. It is also possible that the torque we measured at higher frequencies could be related to a tonic or static level of stiffness in the head/neck plant. Differentiating the difference between neck stiffness and reflex activation would necessitate recording the EMG activity from neck muscles.

Finally, we also observed nonlinearities in the sensitivity of the reflex in which higher sensitivities were observed for smaller angles of neck rotation (Peterson et al. 1985, 1988). These characteristics have been thought to be related to similar properties of muscle spindle receptors and primary Ia afferents (Hasan and Houk 1972, 1975; Matthews and Stein 1969). Although these properties are readily apparent in the cervico-collic reflexes, it remains unclear if the higher sensitivities serve any function when the head is free to move.

Adaptive properties of the CCRs

From a behavioral perspective, it is well known that the collic reflexes rapidly adapt during different contexts. For example, a subject’s awareness of the stimulus through either auditory or visual cues 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 self-initiates a whole-body perturbation (Blouin et al. 2003b). Reflexive activation of the neck muscles can also habituate following repeated perturbations of the same stimulus (Blouin et al. 2003a; Keshner et al. 1987; Siegmund et al. 2003a,b). One specific behavior in which the CCR could adapt is when head stability has been reduced by added mass (Keshner et al. 1999). In these studies, mass was directly attached to the head and could have increased compression of the cervical joints. This brought into question whether the changes observed occurred due to an increase in compression or because of an increase in proprioceptive stimulation. One advantage of our experimental setup was that the axial loading due to the additional inertia was supported by the apparatus not by the neck. In our previous study (Reynolds and Gdowski 2008), the reflexive head movements produced by squirrel monkeys during whole-body rotation were found to adapt to reestablish head stability after mass had been added to the head. These results can arise if the VCR, CCR, or both reflexes adapt to produce more torque to compensate for the torque due to the mass that has been added to the head.

In some cases, if the CCR gain did not adapt sufficiently to compensate for the mass added to the head, then the gain of head-on-trunk movements during head-free whole-body rotations were found to be larger. In other cases, the head-on-trunk movements were similar during head-free whole-body rotations even though only small changes in the gain of the CCR were observed. These results confirm that the CCR does adapt to help maintain head stability. However, other mechanisms, such as the VCR, may also contribute to this process when gain changes in the CCR are insufficient to stabilize the head. There is currently no evidence that the VCR pathways adapt during such contexts. However, many pathways could modify the output of neurons that are putatively involved in the production of the VCR in response to increasing head inertia. Such signals could arise from cerebellar (Andre et al. 1993, 1995, 1998; Boyle and Pompeiano 1981; Pompeiano et al. 1995; Wilson et al. 1996) or cortical pathways (Akbarian et al. 1993; Fukushima 1997; Guldin et al. 1992) to the vestibular nuclei.

Conclusion

A goal of this work was to characterize the horizontal CCR in squirrel monkeys over a wide range of stimulus parameters to compare the CCR in primate to prior measurements obtained in the cat. Our findings indicate that squirrel monkeys have a CCR that is similar to that of the cat and that the differences that were observed are likely to be resultant from differences in morphology between the two species. In addition, our findings indicate that squirrel monkeys have a CCR that can adapt to small increases in inertia that were produced by adding mass to the head. These results are consistent with prior human studies and suggest that the neural substrate adapts to produce additional compensatory torque to manage small changes in inertia of the head. Further investigation is required to determine what aspects of the CCR and vestibulocollic reflexes adapt. One possibility is that vestibular or proprioceptive sensory signals or both could change as the inertia of the head is modified. Current work is being directed at dissociating/isolating the contributions of vestibular and proprioceptive signals during conditions in which the inertia of the head is modified.

Acknowledgments

We thank J. Leblanc for help during surgical preparations and animal care. We thank C. Kumar for assisting in the development of instrumentation that was essential to the project and L. Honge for helping with some of the figures. M. Johnson Gdowski provided invaluable comments on the manuscript and data interpretation. Finally, we would like to thank the reviewers for thoughtful comments on the contents of the manuscript.

Grants

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

References

Morphometry of human neck muscles.


