Predicting control mechanisms for human head stabilization by altering the passive mechanics

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The purpose of this study was to clarify the mechanisms controlling head and neck stabilization in the horizontal (yaw) and vertical (pitch) planes by changing the passive mechanics of the head-neck motor system. Angular velocities of the head and trunk in space were recorded in seated subjects during external perturbations of the trunk with pseudorandom sum-of-sines (SSN) stimuli. Four subjects in yaw and nine subjects in pitch actively stabilized their heads in the dark, and performed a mental distraction task in the dark both with and without a weight atop the head. In yaw, the behavior of the head was found to change relatively little with added inertia. As adding inertia to a passive mechanical system should cause substantial changes in dynamics, we inferred that neural mechanisms were invoked to maintain the constant response dynamics. A mathematical model of head-neck control [11] was applied to predict the relative influence of the vestibulocollic and cervicocollic reflexes, and of inertia, stiffness, and viscosity. Using optimization methods to fit the model to experimental data, we identified stiffness and vestibulocollic reflex gain as the primary contributors to the control of head stabilization in space. In pitch, increasing inertia accentuated phase shifts at higher frequencies. Because our pitch model was insufficiently constrained, we only simulated responses due to passive mechanics. Model simulation predicted unstable head motion at all test frequencies. Subjects were able to compensate for trunk motion at most frequencies, however, suggesting that neural components were modulated to exert compensatory responses both with and without additional weight.

Keywords: Mathematical model, stiffness, inertia, neck reflexes

1. Introduction

Previous studies of voluntary and reflex head stability in the horizontal (yaw) and vertical (pitch) planes of motion [1, 2] revealed that participation of the mechanisms controlling stability of the head was related to frequency of the perturbation. Voluntary stabilization of the head occurred at lower frequencies of rotation (i.e., < 1 Hz) in either plane of motion. In the horizontal plane, frequencies above 3 Hz elicited poor compensation of the head for motion of the trunk. The head moved more rapidly than the trunk, as if it were mechanically resonating, thus suggesting that system mechanics were the dominant control mechanism. One would expect from biomechanical considerations that the head would eventually become stable in space and compensatory to the trunk due to inertial dominance at higher frequencies, but this was not tested. The details of the transition, from a compensatory response to resonance of the head, were interpreted as a modulation of system dynamics.

Participation of the vestibulocollic (VCR) and cervicocollic (CCR) reflexes in the head stabilizing response of intact humans is still somewhat unclear. Several studies that explored the mechanisms subserving human head stabilization in both the vertical and horizontal planes have suggested that these reflexes participate weakly if at all, and that stabilization is primarily

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due to voluntary mechanisms or viscoelastic properties of the system [3]. During sinusoidal rotations of seated subjects in the dark, investigators were unable to identify any reflex compensation for head angular acceleration across the frequency range of 0.5 to 20 Hz in either the horizontal or vertical planes [4,5]. When actively stabilizing the head [6] or the whole body [7] in response to transient external perturbations in the vertical plane, resonant frequencies of the head and neck emerged at 3 and 5 Hz, suggesting mechanical dominance at these frequencies. Following studies of head tracking in the horizontal plane, Bizzi et al. [8] concluded that the neck muscle stretch reflexes (including the CCR) were responsible for less than 10–30% of compensatory torques to an unexpected disturbance of the head. Mechanical properties of the neck muscles (inertial, viscous, and elastic) were considered to be responsible for the greater portion of force compensation. This would fit with the data of Richmond and Loeb [9] who found an absence of monosynaptic stretch reflexes in the neck muscles of the alert cat.

Most of these studies examined behaviors at frequencies below 1 Hz or with transient perturbations and did not fully control for the effects of attention, thus permitting subjects to voluntarily suppress reflex responses [10]. At higher frequencies and with subjects distracted, neck reflexes appeared to dominate the frequency range between 1.5–2.5 Hz in the horizontal plane with the overall effect of making the phase response smoother [1]. Reflex contributions emerged across a wider frequency range in the vertical plane [2]. In this plane, reflexes (possibly of otolith origin) were observed to participate in the response at frequencies below 1 Hz, and to maintain compensatory head stabilization up through 3 Hz.

Other researchers have also demonstrated the importance of reflex control mechanisms to head stabilization. Specifically, Allum and Pfaltz [11] and Shupert and Horak [12] recorded from human subjects who were labyrinthine deficient and found that loss of the VCR produced disordered responses of the head during vertical plane perturbations on a posture platform or following direct perturbations to the head. They suggested that the VCR was necessary to produce a normal postural stabilizing reaction of the head and trunk. It would be intuitive to suggest that these reflexes were optimally tuned to respond to the frequency most often encountered in its plane of motion. This is not true in yaw, however, where predominant frequencies of angular head motion during locomotion fall below 1.5 Hz [13,14]. In pitch, predominant frequencies of angular head motion are between 1–2 Hz [13–15] which is within the frequency range identified for reflex control [2].

In order to clarify the relative role of system mechanisms and neural mechanisms in stabilization of the head and neck, we increased the inertia of the system by adding a weight to the subject’s head. Adding inertia to a simple mechanical system causes substantial changes in its dynamics; thus, we could hypothesize that an absence of change would confirm that a simple mechanical system was not dominant and, furthermore, that neural mechanisms were invoked to maintain constant response dynamics. We have also applied a mathematical model of head-neck control [16] to help identify the mechanisms responsible for stabilizing responses in both the yaw and pitch planes. Previous application of the model to impulse responses at the head and neck has suggested that mechanical properties dominate the control of horizontal head stabilization with a minor role for the VCR and even less of a role for the CCR [16,17]. To improve our estimates of the stiffness, viscosity, VCR gain and CCR gain parameters, we now applied optimization methods to obtain a better fit of our model to the experimental data. Our results demonstrated no change in response dynamics with the change in inertia, from which we conclude that subjects used neural mechanisms to maintain constant head dynamics despite large changes in head mechanics.

2. Methods

2.1. Subjects and procedures

Thirteen healthy subjects (9 in pitch and 4 in yaw), aged 20–40 years, gave informed consent to participate in this study. Subjects sat with their legs extended perpendicular to the torso and the knees raised in a rigid, molded chair that provided support to the whole body. In pitch, the chair was coupled to a high torque (500 ft-lb) servo-controlled rotary turntable (Neurokinetics, PA) with the interaural axis of the subject aligned with the earth-horizontal axis. In yaw, the turntable and chair were configured such that the earth vertical axis passed through the occipito-caudal axis of the head. Cushions, shoulder and lap belts, and a chest level metal gate were used to secure the subject firmly, and to minimize relative movement between the torso and the rotating chair. The head was free to rotate in any plane, but measures of angular velocity in any but the planes of interest proved to be insignificant. All measures of
chair velocity and position were treated as equivalent to trunk velocity and position [1]. The entire apparatus was enclosed in a light-tight room.

Subjects wore a soft helmet assembly with a triaxial angular rate sensor (Watson Industries, WI) positioned at the temple for pitch and at the vertex of the head for yaw. A head-referenced visual target, a portable laser pointer, was positioned on the side. The weight of this apparatus was 950 gm. A floor mounted laser projector provided a fixed target for visual reference during body rotations. Distance from the screen to the eye was 1.6 m.

In the head-weighted protocol, a soft cylindrical molded 4.376 kg weight of 10 cm diameter was laid on the head, centered on the axis of rotation. The inertia of the weight was approximated using the formula for the inertia of a cylinder [18]:

\[ I_w = \frac{mr^2}{2} \]

where \( I_w \) was inertia of the weight; \( m \) was mass of the head; and \( r \) was the radius of the weight. From this formula, the weighted head had a moment of inertia about the yaw axis of 0.0271 Kg-m\(^2\), nearly double the unweighted head inertia of 0.0148 Kg-m\(^2\) [16]. In the pitch plane, inertia was computed by treating the weight as a point mass using the formula:

\[ I_w = md^2 \]

where \( d \) was the distance between the center of rotation of the head and the center of mass of the weight. Although the mass of the head and weight was the same as in yaw, inertia was larger because the weight was placed eccentric to the axis of rotation (C\(_1\)) of the head. The weighted head inertia about the pitch axis was 0.2222 Kg-m\(^2\), nearly five times greater than the unweighted head inertia of 0.0453 Kg-m\(^2\) [16].

**Instructional Sets.** Subjects were tested in three tasks: Voluntary stabilization (VS) required that the subject keep the head-referenced light spot coincident with a stationary target spot while the chair was rotated. NV (no vision) required voluntary head stabilization in the dark. MA (mental activity) required attention to a cognitive task in the dark so that subjects were distracted from the stabilization task. Only the data from NV and MA will be presented because the only differences observed between VS and NV were lower head with respect to trunk velocities [1,2]. All subjects were tested on a single day with the order of presentation being unweighted MA, VS, and NV followed by weighted MA, VS, and NV.

### 2.2. Stimulus

In yaw, the position command provided to the chair was a sum of 10 sinusoids (SSN) that consisted of relatively prime (i.e., having no common divisors) harmonics of a common base frequency. The pseudorandom SSN waveform used for all subjects in this study was composed of frequencies from 0.185 Hz to 4.115 Hz. Chair velocities decreased as frequency increased as follows: 20°/s from 0.185–0.355 Hz; 19°/s from 0.505–1.056 Hz; 16°/s from 1.476–2.096 Hz; 15°/s at 2.947 Hz and 13°/s at 4.115 Hz. In each trial, data were collected over a single period of the fundamental frequency equal to 200 sec.

In pitch, a position command was provided to the chair as a sum of 5 sinusoids that consisted of relatively prime (i.e., having no common divisors) harmonics of a common base frequency. The SSN waveform used for all subjects in this study was composed of frequencies with relatively prime harmonics of a common fundamental frequency spanning the range of 0.35 to 3.05 Hz. Chair velocity decreased as frequency increased from 10°/s at 0.35 to 1.45 Hz, 4°/s at 2.15 Hz, and 2°/s at 3.05 Hz. In each trial, data were collected over a single period of the fundamental so that the stimulus pattern did not repeat during data collection. Subjects received three 20 sec trials in each condition. Data from the three trials of each condition were averaged for each subject. Subjects were exposed to a minimum of one complete cycle of stimulation before data collection began in each trial.

### 2.3. Data collection and reduction

Measures of neck muscle EMGs, chair velocity in space, head velocity in space, and chair position were recorded. To prevent aliasing, all signals were filtered with an 8 pole lowpass Bessel filter with a corner frequency of 20 Hz (Frequency Devices, MA) prior to digitization. The filtered signals were sampled digitally at 50 Hz, viewed on a monitor during testing and stored in digital form for later reduction and analysis.

Surface EMG recordings were taken bilaterally from the splenius capitis (SPL) and sternocleidomastoid (SCM) muscles in yaw and the semispinalis capitis (SEMI) and SCM muscles in pitch (see [19] for placement). EMG potentials of the neck muscles were amplified, bandpass filtered (10–200 Hz), full-wave rectified, and integrated (20 ms time constant) before anti-alias filtering and digital sampling. No normalization of the EMG data was performed. Accordingly, EMG
response gain values were only compared within subjects across conditions. EMG transfer function gain and phase patterns, however, were compared across subjects. All of the data within a subject were collected on the same day. Because we have previously presented similar results for the unweighted yaw and pitch paradigms [1,2], we will concentrate here on data from trials with the head weighted.

In yaw, incoming data were binned so as to produce a 64 point cycle average at each of the ten component frequencies of the SSN wave. The resulting 64 point data records were fit with sinusoids at the component frequency (first harmonic) and at twice that frequency (second harmonic) plus a constant offset (DC) term using a least squares procedure. The angular velocity vector of the neck was derived from the vectorial difference between head and chair angular velocity vectors at each stimulus frequency. Transfer functions between the trunk velocity input and neck velocity or EMG output (TFn) were calculated to identify experimental input-output response characteristics. Gains were described by the output/input amplitude ratio at each frequency; phases were equal to the difference between response and stimulus phase angles, with positive phase indicating a relative lead and negative phase indicating a lag.

In pitch, amplitude and phase of chair and head velocity and EMG responses were calculated with a Fast Fourier Transform. Components corresponding to the five frequencies in the input wave indicated the first harmonic response of the system at each input frequency. Real and imaginary components of the signal at a given frequency provided the amplitude and phase of the response. Amplitude was derived from the square root of the sum of squares of the real and imaginary components. Phase was calculated as the arc tangent of the imaginary divided by the real components. Neck velocity (head with respect to the trunk) was calculated by the vectorial difference between the response vectors of head and chair velocity. Input-output transfer functions were calculated as described above in the yaw plane.

Operationally, a gain of one and phase of ±180° represented perfect compensation of the head for motion of the trunk (no movement of the head relative to space). Phases of 0° or 360° indicated that the head was not compensating for motion of the trunk, and was moving in phase with the trunk.

2.4. Model development

In our past work, our group has developed mathematical models of the head and neck incorporating head mechanics and reflex control. Head mechanics were modeled as a second order system having inertia, stiffness, and viscosity parameters. The stiffness and viscosity terms represented the combined active (non-reflex) and passive contributions of the musculoskeletal structure of the joint. We will hereafter use the terms ‘stiffness’ and ‘viscosity’ in this context. Reflex controllers included the VCR and the CCR modeled as feedback loops. The VCR was modeled as a second order transfer function with a gain, two poles and two zeros. The CCR was modeled as a second order transfer function with a gain and two zeros. Figure 1 shows the general features of the yaw and pitch models – details of the models are available elsewhere [16, 17], and values assigned to the model parameters are listed in Table 1. The models were implemented using the Matlab mathematical software package with the Simulink toolbox (Mathworks, Nantick, MA). Model simulations generated input-output transfer functions (TFm), using trunk in space input and head in space output. TFm of a system controlled only by its mechanical properties were generated by setting the VCR and CCR gain parameters to zero.

In the horizontal plane, the model has previously been documented to fit experimental MA yaw data well [16]. For the fits to the current experimental MA yaw data we used optimization methods (Matlab optimization toolbox) to iteratively adjust viscosity, stiffness, VCR gain and CCR gain in order to minimize an error function based on the vector differences between TFe and TFm. The model was fit to head in space rather than head on trunk TFe because the transducers directly measured head in space making it a more exact measure of the response. Voluntary control is not represented in the model, therefore we did not attempt to fit the model to TFe from the voluntary conditions, NV and VS.

In the vertical plane [17], an additional torque due to gravity was incorporated into the model. Rotation was assumed to be about the C1 vertebra. A similar model, with suitable adjustments of free parameters had also been shown to provide a good fit to MA pitch data [17]. Because less is known about the physiology of reflexes that control the head in the vertical plane, the pitch model was less constrained and therefore more conjectural than the yaw model. We therefore, did not attempt to optimize the model to fit experimental data.

3. Results

3.1. Unweighted responses in the yaw plane

Although data from other subjects in the unweighted protocol have previously been published [1], for pur-
poses of comparison, the unweighted data from these four subjects are shown in Fig. 2 in which each symbol represents the response of a single subject.

There are three frequency regions in Fig. 2 that bear comment. At frequencies below 1 Hz in NV, three of the four subjects exhibited gains above 0.5 and phases near −180° demonstrating a reasonable ability to stabilize the head in the absence of vision. This response...
Fig. 2. Neck relative to trunk velocity gain and phase responses from four subjects in NV (top two plots) and MA (bottom two plots) with an unweighted (left plots) and weighted (right plots) head in yaw. Each plot symbol represents a different subject. Neck velocity gain and phase values, elicited during SSN stimulus in the horizontal plane, are computed relative to trunk velocity. Responses with phases at $\pm 180^\circ$ perfectly compensate for the direction of the external perturbation; phases from $0^\circ$ to $-180^\circ$ lead the stimulus; phases between $-180^\circ$ and $-360^\circ$ lag the stimulus; a phase at $0^\circ$ indicates head motion in the same direction as the trunk.

has been observed previously in both NV and VS and suggests that voluntary mechanisms are capable of producing head stabilization in this lower frequency range. Between 1–2.5 Hz, gains began to drop and phases to rise indicating poorer compensation for trunk motion as a result of the lessened capacity of voluntary mechanisms to compensate for trunk related torques in this frequency range. Finally, above 3 Hz the subjects exhibited gains that increased above unity with decreasing phases suggesting mechanical resonance. The eventual return to phases of $-180^\circ$ suggests inertial stabilization of the head at the higher frequencies. The one subject that did not follow the group tended to exhibit a response pattern similar to that observed in MA. In MA, response gains remained low (around 0.2) up to about 0.5 Hz, and then gradually increased with a slope close to 40 dB/dec at frequencies above 0.8 Hz, thus resembling a passive, 2nd order mechanical system. Phase behavior at low frequencies, however, did not resemble a 2nd order system, and we previously postulated that
mechanisms were active, albeit in varying degrees. Viscosity and CCR gain were best fit by 0, thereby providing additional evidence that the CCR and viscosity played an insignificant role in yaw head stabilization.

3.2. Responses in the pitch plane

Responses of the nine subjects tested here (Fig. 4) agree with data from the unweighted protocol in pitch that were previously published with different subjects [2]. In NV, stability was maintained until about 1.5 Hz with response gains close to one and phases near \(-180^\circ\). A drop-off of gains and phases occurred between 1.5–2 Hz. Then response gains were maintained or began to rise as phases steeply descended between 2 and 3 Hz. Pitch response gains at frequencies below 1 Hz in MA were higher than in yaw, but exhibited greater inter-subject variability; response phases were greatly scattered. Response gains during MA ascended, and phases clustered more closely to \(-180^\circ\) as frequency increased up to 2 Hz, suggesting a compensatory action of the head. At 2 Hz, response gains and phases actually demonstrated a pattern similar to NV rather than continuing to rise to a resonant peak as in yaw.

Simulation of a response due only to head mechanics (Fig. 4) predicted a resonant peak and phase drop around 1 Hz for the unweighted protocol. Gains above 1 prior to the resonant peak, and a more gradual phase drop than seen in the yaw plane (Fig. 3), illustrated the effects of gravity on this second-order system. When the modeled head inertia and mass were increased, the resonant peak was smoothed, although response gains above 1 appeared throughout the frequency range (Fig. 4).

Because the actual data differed greatly from the simulation, we inferred that active control was critical for head stability in pitch. In fact, experimental data
for pitch deviated to a much greater extent from the predicted response mechanics than did the yaw data, implying a correspondingly greater influence of reflex or voluntary mechanisms. This was not surprising, as it was clear that active controllers were needed to prevent the intrinsically unstable head from "falling over". The mechanics represented interplay between the effects of gravity, stiffness, and inertia. Gravity is destabilizing and causes the response gains to be greater than one. Stiffness reduces gain and pushes phase towards 0°. Inertia is stabilizing and pushes gain towards 1 and phase towards 180°. Quite different simulations of mechanics could be obtained by postulating different degrees of stiffness that could "lock the head" to the trunk. The large number of "free" and unconstrained variables in our present models of the head in pitch, such as the range of multi-segmental motion in the neck, precluded any attempt at optimal fits of the simulation.
to experimental data as the results were unlikely to be of any significance.

3.3. Effects of increasing inertial mass of the head

As shown by the simulations of system mechanics with no contributions from the VCR and CCR (Figs 3 and 4), the mechanical system in both yaw and pitch would be expected to exhibit a lower resonant frequency and greater resonance when weighted. However, when the subjects' heads were weighted for both the NV and MA tasks in yaw, gain and phase plots of the neck exhibited only a minor shift in the resonant frequency (Fig. 2) although inertia of the head was approximately doubled. In order to identify the mechanisms responsible for this inertial compensation, two model simulations were performed to predict responses of the weighted head with respect to space (Fig. 3). First, using the unweighted parameters (Table 2) while correcting for increased inertia – assuming that stiffness, viscosity, VCR gain, and CCR gain remained constant. Second, using the optimized parameters from the fit to the weighted head TF_e and increased model inertia. The model simulations using unweighted parameters and increased inertia demonstrated a good fit at frequencies below 1 Hz, then diverged from the weighted head TF_e at higher frequencies. When we allowed the model to vary stiffness, viscosity, VCR gain and CCR gain, the fit at high frequencies was improved. As seen in Table 2, optimal fits to the weighted head TF_e accounted for 94–98% of the experimental response variances. Stiffness more than doubled in two of the subjects, and VCR gains increased by a factor of 1.5 or more when compared to the unweighted model; viscosity and the CCR gains were best fit by 0. Thus, the subjects primarily adjusted stiffness and VCR gain to maintain constant head-neck dynamics despite large changes in head inertia.

In pitch, the frequency of the gain peak and most aspects of the response remained constant across both the weighted and unweighted protocols (Fig. 4). Response gains and phases in NV exhibited a small shift so that a gain drop at 2 Hz became more apparent and was associated with a greater scatter of response gains and phases at the higher frequencies. In MA, a gain drop at 2 Hz followed by a trend towards an increased gain and scattered phases at high frequencies suggested a similarity to responses in NV. The similarity between the weighted and unweighted data and the two instructional sets suggests that subjects were modulating stiffness, viscosity, and reflex action to maintain consistent behavioral results.

EMG responses were also analyzed when the head was weighted. EMG responses when the head was unweighted were the same in these subjects as in those that were previously presented [1,2]. The principal effect of increasing inertial mass occurred in the phase responses of both planes where a steeper descent at high frequencies was observed (Fig. 5). Opposing neck muscles continued to be reciprocally activated, however, as seen by the presence of a 180° phase difference between the two muscles across frequencies even with an increased inertial mass. An increased response gain was also observed in the pitch plane when the head was weighted, but not in the yaw plane.

4. Discussion

In this study we examined how increasing the inertia of the head altered the control mechanisms for head stabilization. If one assumes that the head is primarily controlled with fixed reflexes and fixed mechanical properties (stiffness and viscosity), then doubling the inertia of the head should produce an enlarged resonant peak combined with a shifting of the resonance to lower frequencies. Instead, only a small difference was seen in head dynamics when the head was weighted or unweighted in yaw. Accordingly, one can infer that active readjustment of muscle activation that changes joint stiffness and viscosity and active readjustment of reflex action must have occurred.

Stiffness is operationally defined here as the relationship between joint torque and angular position after the effects of reflexes have been subtracted. Our methodology thus allows us to lump the combination of position dependent passive muscle properties and force from muscle activation into one parameter. Similarly, we operationally infer viscosity from the relationship between joint torque and angular velocity after the effects of reflexes have been subtracted – presumably produced by a combination of passive muscle properties and muscle activation.

From our model fits in yaw, a feasible way for the head dynamics to remain constant in spite of a two-fold increase in inertia was via idiosyncratic combinations of an increase in the VCR gain and stiffness. While online changes in the VCR gain have not been previously reported, there is evidence that cervico-ocular [24], otolith-ocular [25], and VOR [26,27] responses can be modified by mental set. Also, it is well known that
the VOR gain in the dark can be almost entirely suppressed or enhanced to a gain of 0.95 depending on the instructions given to subjects [28]. Similarly, under more controlled conditions of VCR testing [29,30], it has been difficult to reliably record a VCR response in intact subjects, implying that the individual performer has the ability to suppress or modulate the appearance of this reflex as well. Given the ability to adjust the gains of other reflex mechanisms that are generated by vestibular and cervical inputs, and that the head and eyes appear to have shared neural mechanisms for control of gaze [31,32], it is plausible to suggest that the VCR can be modified by mental set.

For the pitch stimulus, our experimental protocol caused head inertia to increase by a factor of five and substantial changes in the head response were predicted from the model. The experimental result, however, documented behavior strikingly similar to the unweighted condition. Resonant oscillations of the head, predicted by the mechanics-only model and indicated by response gains greater than one and steeply descending phases, were rarely observed in the range of frequencies tested. The simulation of system mechanics in pitch MA suggests that the head counter-rotates for motion of the trunk, but with twice as much amplitude. Thus, the purpose of the neural controllers would be to dampen system mechanics and shift resonance outside of the stimulus bandwidth so that the motion of the head was minimized even if not exactly stable in space [1]. At the higher frequencies there was a disproportionately large phase lag as compared to the relatively flat gain response. Flat gain accompanied by increasing phase lag suggests the presence of a delay. This might be due to voluntary corrective head movements needed to compensate for the large gravitational torques associated with weighting the head. Another possibility is that use of otolith signals to stabilize the head contributes additional delay as vertical plane rotations, unlike yaw plane rotations, also stimulate the otoliths.

Comparisons of responses in pitch NV to those in yaw suggest that the dynamic characteristics were shifted toward a higher frequency. The gain drop and phase shift observed between 1–2 Hz in yaw did not appear in pitch unless the head was weighted, and then not until almost 3 Hz. This may indicate that stiffness modulation, which has the effect of shifting resonance toward higher frequencies, played a more significant role in the vertical than in the horizontal plane under normal inertial conditions. Such an effect would not be surprising because of the greater influence of gravity on motions in the vertical plane that stimulates muscle receptors, thereby altering muscle preactivation levels and initial muscle stiffness. Other differences between
the two planes may reflect the functional requirements of the musculoskeletal system. Kinematics of the cervical spine permits potential rotation about several axes in pitch whereas, in yaw, the head is constrained to rotate about one primary axis [33]. Furthermore, in the pitch plane, neck muscles must counteract gravitational torque on the head while in yaw there is little gravitational demand on muscle activation.

With increased stiffness we might have expected muscle cocontraction and larger magnitudes of muscle activation. There was some evidence of increasing EMG gains in the pitch plane with increased inertia, but not in the yaw plane. It is possible that the deeper muscles of the neck are more responsible for stabilization of the cervical spine in the horizontal plane [34]. A kinematic model [35] that incorporated detailed neck muscle morphometric data into a model of cervical musculoskeletal anatomy and intervertebral kinematics has shown that the muscles recorded here were activated during the stabilizing response in the vertical plane. An increased phase lag was observed in both planes at higher frequencies with added inertia, indicating a shift to velocity dependant activation at lower frequencies than in the unweighted condition that would reflect more of a contribution from the neck reflexes [36,37].

Our model of pitch head movement was insufficiently constrained to perform an optimal fit. It seems likely, nevertheless, that stiffness and the VCR were under central control and that one or all of these were readjusted to maintain a consistent frequency response pattern of head movement when the head was weighted or unweighted. One reason why previous studies implicated mechanics as the dominant control mechanism may be that they used simple generic models which lump reflex torques with joint torques from active and passive muscle properties or used nonparametric models to interpret their results. When more detailed models which reflect actual physiology were used [36], results implicated more reflex control. In this series of experiments, we have used a model having physiologic correlates and were, therefore, able to identify the importance of neural control contributions to head stabilization.

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