Mechanisms Controlling Human Head Stabilization. II. Head-Neck Characteristics During Random Rotations in the Vertical Plane

E. A. KESHNER, R. L. CROMWELL, AND B. W. PETERSON

Sensory Motor Performance Program, Rehabilitation Institute of Chicago; and Department of Physiology, Northwestern University Medical School, Chicago, Illinois 60611

SUMMARY AND CONCLUSIONS

1. In this study we have tested the hypothesis that the mechanisms controlling stabilization of the head-neck motor system can vary with both the frequency and spatial orientation of an externally applied perturbation. Angular velocity of the head with respect to the trunk (neck) and myoelectric activity of two neck muscles (semispinalis capitis and sternocleidomastoid) were recorded in eight seated subjects during pseudorandom rotations of the trunk in the vertical (pitch) plane. Subjects were externally perturbed with a random sum-of-sines stimulus at frequencies ranging from 0.35 to 3.05 Hz. Four instructional sets were presented. Voluntary mechanisms were examined by having the subjects actively stabilize the head in the presence of visual feedback as the body was rotated (VS). Visual feedback was then removed, and the subjects attempted to stabilize the head in the dark as the body was rotated (NV). Reflex mechanisms were examined when subjects performed a mental arithmetic task during body rotations in the dark (MA). Finally, subjects performed a voluntary head tracking task while the body was kept stationary (VT).

2. In VS and NV, gains and phases of head velocity indicated good compensation for the perturbation at frequencies up to 2 Hz. Between 2 and 3 Hz, gains dropped slowly and then steeply descended above 3 Hz as phases became scattered.

3. In MA, gains were lower and exhibited more scatter than in VS and NV at frequencies <1 Hz. Phases around −180° indicated that compensatory activity was occurring even with these low gains. Between 1 and 2 Hz, response gains steeply ascended, implying that reflex mechanisms were becoming the predominant mechanism for compensation in this frequency range. Above 2 Hz, gains dropped off to 0.5 and lower, but phases remained close to −180°, suggesting that the reflex mechanisms were not dominant in this frequency range, but that they were still contributing toward compensation for the trunk perturbation.

4. Neck muscle electromyographic (EMG) responses were similar in VS, NV, and MA, demonstrating decreasing gains between 0.35 and 1.5 Hz, and then increasing beyond the previous high level of activation. This U-shaped response pattern implies an enhanced participation of neural mechanisms, probably of reflex origin, in the higher frequency range.

5. Patterns observed during external perturbations of the trunk were not apparent in the response dynamics of voluntary head tracking. In VT, subjects successfully tracked the stimulus only at the lowest frequencies of head movement. A gradual and consistent decline was exhibited as frequency increased. EMG activation continued throughout the frequency range, however, suggesting a continued effort to track the target.

6. A comparison of response dynamics revealed that the greatest distinction between responses to pseudorandom rotations in the horizontal and vertical planes existed at very low (<0.5 Hz) frequencies and at frequencies >2 Hz. Low-frequency differences reflected improved gains in the vertical plane. High-frequency differences reflected the presence of resonant oscillations in the horizontal but not in the vertical plane. Response dynamics at these frequencies might have been the result of a stiffer head-neck system in the vertical plane due to the combination of smaller rotational amplitudes and greater muscle moment arms than in the horizontal plane.

7. The results of this study suggest that head stabilizing mechanisms are related to both the frequency and orientation of an external perturbation. Neck reflexes exhibit a greater operational bandwidth in the vertical than in the horizontal plane and may function to damp mechanical resonance and free the voluntary mechanisms for producing an efficient time-matched response to a continually changing environment.

INTRODUCTION

Our previous study (Keshner and Peterson 1995) demonstrated that more than one mechanism may contribute to the control of head stabilization, and that dominance by either the neural or biomechanical parameters of the system depended on the frequency content of a random external perturbation. Data from random rotations in the horizontal plane resembled those in a study of alert and anesthetized cats (Goldberg and Peterson 1986), where a biomechanical model indicated that system mechanics dominated the response at frequencies >3 Hz and reflexes appeared to support stabilization at frequencies up to at least 3 Hz. The model derived from these results may only be applicable to rotations in the horizontal plane, however. Dutia and Hunter (1985) have found vestibulococulic reflex characteristics in decerebrate cats sinusoidally rotated in the sagittal plane similar to those found in the horizontal plane (Bilotto et al. 1982; Peterson et al. 1985). But muscle activation patterns differ greatly between horizontal and vertical rotations (Keshner et al. 1992a), and the intact reflex and biomechanics of the response have not yet been investigated in the pitch (sagittal) plane.

Vertical plane movements have been considered more functionally important for investigations of postural stabilization and locomotion because of the gravitational demands in this plane of motion (Allum and Pfaltz 1985; Keshner et al. 1987; Nashner 1977; Pozzo et al. 1990; Winter 1991). Most of these studies have targeted a functional frequency range close to that found in our measures of head stabilization in the horizontal plane. Frequencies of head and neck angular velocity during natural locomotor activities have been recorded in the range of 1–2 Hz during slow and
fast locomotion (Keshner et al. 1992b). During horizontal rotations, 1–2 Hz was found to be the frequency at which the vestibulocolliecolic (VCR) and cervicocollic (CCR) reflexes seemed to dominate the response (Keshner and Peterson 1988, 1995). On a posture platform that rotated the ankle in the sagittal plane, head angular accelerations revealed oscillations at 3 Hz (Keshner et al. 1987), the same frequency at which resonance was observed during horizontal plane rotations (Keshner and Peterson 1988, 1995). Viviani and Berthoz (1975) have also demonstrated two resonant frequencies at the head and neck at 3 and 5 Hz after a perturbation applied directly to the head in the vertical plane.

In the present experiments, we identified the frequency-related characteristics of three mechanisms that potentially control head-stabilizing responses in the vertical (pitch) plane. Our results indicate that reflex stabilization of the head plays a significant role in the frequency bandwidth identified for natural locomotion activities, and also that neck reflexes participate in a wider frequency range of head stabilization in the vertical than in the horizontal (yaw) plane. Comparison of responses to random rotations in the two planes reveals how the head stabilization response is altered by the combined control of semicircular canals and otoliths, and the addition of a second axis of rotation (Vidal et al. 1986). Preliminary results have been reported previously (Keshner et al. 1992b,c).

METHODS

Eight healthy subjects, 20–40 yr old, gave informed consent to participate in this study. Subjects were seated in a rigid, molded chair that provided support to the whole body, so that the feet were placed flat at the bottom of the chair, and the knees were raised. The chair was coupled to the same high torque (500 ft lb), servo-controlled rotatory turntable (Contraves) used in the study of horizontal rotations (Keshner and Peterson 1995). In the current experiment, the rotatory turntable was placed so that the earth-horizontal axis was aligned with the interaural axis of the subject. The entire apparatus was enclosed in a light-tight room. Soft cushions, shoulder and lap belts, and a chest-level metal gate were used to secure the subject firmly and minimized relative movement between the torso and the rotating chair; measures of trunk angular velocity in some subjects revealed that the trunk exactly matched chair angular velocity at all frequencies. Because of these findings, we treated all measures of chair velocity and position as equivalent to trunk velocity and position. The head was free to rotate in any plane, but measures of angular velocity in the horizontal and roll planes proved to be insignificant.

Subjects wore a molded helmet assembly with a triaxial angular rate sensor (Watson Industries, WI) positioned at the temporal lobe. A head-referenced visual target, a portable laser pointer, was positioned on the opposite side so that the apparatus was balanced. The weight of this apparatus did not exceed 950 g. The helmet was well secured to the head, and the sensors demonstrated no slip even at high frequencies of voluntary head shaking. A servo-controlled projector provided a fixed target for visual reference during body rotations and a moving spot that served as a target during visual tracking runs. Distance from the screen to the eye was 1.6 m.

Procedure

Subjects began each trial sitting in a stationary, vertically upright orientation. Each subject underwent five trials in each of four instructional sets in one experimental session. Subjects were exposed to a minimum of one complete cycle of stimulation before data collection began in each trial, so that each trial lasted 40 s. Data from the five trials of each instructional set were averaged for each subject, but data for different subjects were not pooled. Experimental order was as follows. During mental arithmetic (MA), a mental calculation task was provided so that the subject’s attention was removed from the task of stabilization while rotation in the dark was ongoing. Voluntary stabilization (VS) required that the subject keep the head-referenced light signal coincident with a stationary target spot while the chair was rotated. The no vision condition (NV) was performed in the dark while the subject was given the task of stabilizing the head by imagining both the stationary target spot and the head-referenced light signal. System dynamics during voluntary movement as opposed to head stabilization was also assessed via a visual tracking task (VT). In this case the target spot was moved, the body remained stationary, and subjects were instructed to follow the moving target with the head-referenced light signal.

Stimulus

We chose not to use the same waveform for vertical rotations as used in horizontal rotations for two reasons. First, the mechanical apparatus could not tolerate frequencies >3 Hz in the vertical plane, and second, we hoped to better characterize responses to the individual input frequencies. Thus instead of a velocity command, we provided a position command to the chair as a sum of 5 sinusoids (SSN) 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 the following harmonics: 7, 15, 29, 43, and 61. By using a fundamental frequency of 0.05 Hz, we were able to characterize the response for frequencies spanning the range of 0.35–3.05 Hz. Peak excursion from vertical was ±12°. Chair velocities changed as frequency increased as follows: 10°/s at 0.35 Hz; 12°/s at 0.75 Hz; 10°/s at 1.45 Hz; 4°/s at 2.15 Hz; 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. For the VT condition, the light spot was driven with the same SSN provided to the chair, but with a reduced amplitude. Peak velocity of the laser stimulus was 12°/s and the peak excursion was ±3°.

Responses to a predictable 0.1-Hz sinusoid were also recorded from four of the subjects in order to examine directional properties of the muscle electromyographic (EMG) responses. Peak excursion of this stimulus was ±19°, and peak velocity was 11°/s.

Data collection and reduction

Surface EMG recordings were taken bilaterally from the semispinalis (SEMI) and sternocleidomastoid (SCM) muscles (see Keshner and Peterson 1995, for placement). During recording, EMG potentials of the two neck muscles were amplified, band-pass filtered (10–200 Hz), full-wave rectified, and integrated (20-ms time constant). Measures of angular chair velocity in space, angular head velocity in space, and chair position were also recorded. To prevent aliasing, all signals were filtered with an 8-pole low-pass Bessel filter with a corner frequency of 20 Hz (Frequency Devices, MA) before digitization at 50 Hz. Signals were viewed on a monitor during testing and stored in digital form on a PDP 11/23 computer for later reduction and analysis.

Amplitude (vector length) and phase (vector orientation) of chair and head velocity and EMG responses were calculated with a fast Fourier transform (FFT). The first component of the FFT was the DC signal, and the next component was the first harmonic of the SSN wave. Components corresponding to the five frequen-
cies in the input wave indicated the first harmonic response of the system at each input frequency. Responses at harmonics corresponding to twice the frequency of each input wave provided a measure of harmonic distortion for that frequency. Summation of all other harmonics, those neither primary nor two times that of the five input frequencies, yielded a signal-to-noise ratio of each response that was computed as the amplitude of the first harmonic response at that frequency divided by the square root of the sum of squares of real and imaginary components at frequencies not corresponding to one of the five input frequencies or twice those frequencies.

Harmonic distortion measures appear inflated and signal/noise measures diminished as compared with responses in the horizontal plane (Keshner and Peterson 1995), because the short collection epochs used in this paradigm allow random noise to enter the data (see Fig. 1). Harmonic distortion values do not exceed 50% at any frequency and are noticeably lower in the two visually guided conditions. Signal-to-noise ratios are most robust in the two visually guided conditions (VS and VT) with values >10. Weaker signal-to-noise ratios emerge in NV and MA, and are <0.5 at frequencies >1 Hz. We believe that our gain and phase responses can be considered robust because of the very small intrasubject variability demonstrated across multiple trials. To verify this assumption, we have calculated the coherence of head velocity to chair velocity at each stimulus frequency. Sixty-three percent of the values have a coherence >0.9, and 83% of the values fall between 0.7 and 1.0, suggesting that most of the variance of the response signal at each frequency can be accounted for by the base frequency of the stimulus. Given these results, we are confident that our use of linear analysis methods is appropriate for the data.

For the data in Fig. 2, where the stimulus was a single 0.1-Hz sinusoid, data records were fit with sinusoids at the component frequency (1st harmonic) and at twice that frequency (2nd harmonic) plus a constant offset (DC term) using a least-squares procedure as described in the first paper of this series (Keshner and Peterson 1995). In some instances, multiple data records were concatenated to allow enhanced frequency resolution in the data analysis. Results did not differ from those obtained from the analysis of single records.

Data analysis

As in our previous paper (Keshner and Peterson 1995), head and chair angular velocity data from all pseudorandom rotation paradigms (VS, NV, and MA) are presented as a response ratio vector representing angular velocity of the neck with respect to (wrt) the trunk. Angular velocity of the neck was derived from the vectorial difference between head and chair angular velocities at each stimulus frequency. Gain of the response ratio vector is described by its length and is equal to the response/stimulus amplitude ratio; phase is equal to the difference between response and stimulus phase angles. Vector averages for the population of subjects were derived by averaging the real and imaginary components of each subject’s gain and phase responses and then calculating the gain and phase of the average response ratio vector.

In VS, NV, and MA, phase is expressed relative to chair velocity. As illustrated in Fig. 2, neck velocity in the VS condition has a phase close to −180° when the neck is producing a peak extension velocity that fully compensates for the peak flexion chair velocity so that the head is held still. Phases of 0° indicate that the neck is not compensating and the head is moving in phase with the chair. Lead of the neck with respect to the trunk is defined as neck phases between 0 and −180°. Lag of the neck with respect to the trunk is defined as phases between −180 and −360°. A gain of one and phase of −180° represents perfect compensation of the head (or no movement of the head relative to space).

In the head tracking task (VT), movement of the head reflected movement at the neck because the trunk was stationary. Thus the data will be presented as a response ratio vector indicating head velocity with respect to target velocity. In this condition the ideal response is represented as a gain of one and phase of 0° to indicate that the head is moving in phase with the target.

EMG responses were analyzed in a more descriptive fashion. Gains of the muscle EMG responses were collected in arbitrary units and are compared only within a muscle and across instructional sets. Interpretation of phase results in each case will depend on the known actions of the muscles; thus phase responses of each muscle are presented with respect to peak chair position or velocity. As illustrated in Fig. 2, response phases around +90° indicate that SCM responses lag peak extensor velocity and are in phase with peak extensor position of the chair. Phases between −45 and −90° in the SEMI muscle indicate responses between peak flexor velocity and peak flexor position of the chair. These results are appropriate to the functional activation of these muscles because SEMI muscles produce extension of the head, and SCM produces flexion of the head (Keshner et al. 1989). A muscle response phase of 0° indicates that the muscle is responding in phase with peak flexor velocity of the chair; a −180° phase indicates a response related to peak extensor velocity of the chair.

To control for the fact that peak amplitudes and velocities differed somewhat between the waveforms presented for the horizontal and vertical rotations, in a separate study we examined the effect of stimulus amplitude and frequency on head movement gains and phases in both planes of rotation. Two tests were performed: one where stimulus amplitude was held constant across a frequency range of 0.35–2.65 Hz, and another where frequency was held constant (0.5 Hz) and amplitudes were varied from 5 to 20°. In both planes of motion, the gain and phase response to any one frequency was the same regardless of the frequency composition of the stimulus. In yaw, there was no significant effect of amplitude on the response gains and phases. In pitch, amplitude only affected the gains and phases when it was increased to ≥20°, twice that of the peak excursion in these experiments. These results suggest that the system is sufficiently linear to permit comparison between the stimuli used in these two studies. Thus we selected five frequencies in the horizontal plane SSN that were closest to those in the vertical plane SSN to compare the responses between the vertical and horizontal planes. Significant differences between the neck angular velocity responses at each stimulus frequency and instructional set were examined through a 5 × 4 repeated measures
analysis of variance performed on the vectorial difference between the subjects’ response ratio vectors.

RESULTS

Response characteristics during head stabilization

To characterize the muscle EMG responses, some subjects were tested with a predictable 0.1-Hz sinusoid. Data from one subject are portrayed in Fig. 2. In all three instructional sets, the vertical component of neck rotation was compensatory for chair rotation (note the near −180° phase difference between the peaks of neck and chair velocities). In VS, NV, and even MA (unlike the horizontal plane as seen in Fig. 2, Keshner and Peterson 1995), amplitude of the head velocity in space was near zero, and the head was kept stationary by the compensatory neck angular velocities. Phases of the two muscles reflect the reciprocal action of the neck flexor (SCM) and extensor (SEMI) muscles in all three instructional sets. As in horizontal rotations, the flexor SCM muscle was in phase with chair position, acting to pull the head toward flexion when the trunk was in peak extension. The extensor muscle, SEMI, reached peak activation levels as the chair moved toward peak forward flexion position, reaching its peak activity between peak flexor velocity and position. At this low frequency, therefore, the muscles are acting eccentrically (i.e., lengthening) to stabilize the head against external perturbations of the trunk.

Neck wrt trunk velocity responses of the eight subjects are presented as a Bode diagram in Fig. 3. Gains and phases from the 0.1-Hz sinusoidal data shown in Fig. 2 are replotted here on the vertical axis demonstrating a consistent pattern of response to both complex and simple stimuli. The solid line in each plot represents the vector average for the group, and the shaded area is ±1 SE of the average. Standard errors of this three-dimensional data were derived by first calculating standard errors of the real and imaginary components, and plotting these as x and y error bars at each gain point on the vector average. A rectangle was drawn around the error bars, and a diagonal drawn through the rectangle. The length of the diagonal was taken as a conservative estimate of error gain. The angle subtended between the average gain, and the error gain was calculated as a conservative estimate of phase error. There were no apparent effects of repetition on the gains and phases of repeated trials for each subject (i.e., within subject variability was small), and subjects did not complain of fatigue at any time during the test. According to our conventions, a neck velocity gain of 1 and phase of −180° represents perfect compensation for the applied trunk perturbation. Phases of 0° indicate that the head is moving with the chair rather than compensating.

In VS and NV, compensation was best at lower frequencies as demonstrated by phases of −180° and gains around 0.7 for both conditions. Increased intersubject scatter in NV as compared with VS implies that some subjects were more dependent on visual inputs to produce voluntary head stabilization. Below 2.15 Hz, gains dropped gradually as a function of frequency. Above 2.15 Hz, gains dropped more steeply, and the compensatory phases observed below 1.45 Hz were lost. Thus subjects were able to maintain reasonable head stabilization up until 1.45−2.15 Hz. Anticompensatory phases or low gains seen above 2.15 Hz imply poor stabilization of the head at this high-frequency end.

Gains in MA fell below 0.5 and exhibited more intersubject variability at frequencies <1 Hz than in VS and NV.
MA gains in Fig. 3 also differed greatly from the good compensatory gain and phase elicited during the predictable 0.1-Hz sinusoid illustrated in Fig. 2. Because MA responses to the predictable sinusoid are the same as in the NV condition, it is probable that, for the predictable paradigm, subjects were able to rely on voluntary mechanisms even when attention was diverted from the task. During pseudorandom rotations, gains and phases varied widely at 0.35 Hz, yielding an average response with gain around 0.2. But the presence of phases around $-180^\circ$ for all but two of the subjects indicated the presence of compensatory activity even in the low-frequency range. Just as in the horizontal rotation paradigm, response gains during MA increased, and phases clustered more closely about $-180^\circ$ as frequency increased up to 2 Hz, implying improved head stabilization. Above 2 Hz, gains were maintained, but phases became scattered. Phases in most subjects remained close to a compensatory $-180^\circ$, however, in contrast to the lags that appeared at 2.15 Hz when subjects attempted to voluntarily stabilize the head in the VS and NV conditions.

We were concerned that the subjects with response vectors furthest from the vectorial average might exhibit a different frequency response pattern. But individual records suggest that only one subject (Fig. 3, ▼) replicated the pattern seen in MA during horizontal rotations (a drop-off and rise of gain associated with phase errors at high frequencies). This tendency was observed in VS and NV but was not large enough to exclude this subject from the average. Another subject (●) had large gains and phases that nearly lagged chair velocity at low frequencies in MA, but, at higher frequencies and in the other paradigms, this subject looked more like the group.

At no time in any of the three instructional sets were patterns characteristic of resonance (as indicated by response gains $>$1 and steeply descending phases) observed in the average group bode plots. In fact, comparison of these plots with the Bode plots in the horizontal paradigm (Fig. 3, Keshner and Peterson 1995) suggests that the dynamic characteristics have been shifted toward a higher frequency. Gain drops and phase shifts observed between 1 and 2 Hz in the horizontal plane do not begin until 2–3 Hz in the vertical plane, and the resonant gain peak seen with horizontal rotations does not fall within the frequency range tested here.

Muscle EMG response gains wrt chair velocity exhibited modulated activity across the frequency range (Fig. 4) and were remarkable for the similarity of performance in all three conditions of external perturbation. Phases of the flexor and extensor muscles were $180^\circ$ apart, indicating reciprocal activation of the two muscles. Gains gradually decreased until 1.5 Hz, the frequency at which the head started its steep decline and phases in MA moved closer to compensation. Then, at frequencies $>1.5$ Hz, EMG response gains rose beyond the activation observed at low frequencies. SEMI EMG activity was slightly lower in MA than in the other conditions at frequencies $<1$ Hz, but above 2 Hz no differences were observed. Both muscles’ EMG responses began with phases close to trunk angular position. By 1.5 Hz both muscles advanced to a phase related to velocity. This phase advance with increasing frequency resembles that seen in the VCR of decerebrate (Baker et al. 1985; Bilotto et al. 1982) and alert (Goldberg and Peterson 1986; Keshner et al. 1992a) cats. Larger EMG response gains and advancing phases at higher frequencies suggest continued neuromuscular participation in the compensatory action of the head and neck.

Response characteristics of head tracking

Gain and phase responses for VT indicate that voluntary mechanisms fail to track the stimulus as frequency increases (Fig. 5). At the lowest frequency, the head was moving in phase with the target as indicated by phases near 0°. Gains around 0.5 and below indicate, however, that subjects did not fully match the target velocity and thus were not accurately
tracking the target in space. As frequency increased, response gains continued to decrease and intersubject variability to increase. Phase lags between the projected spot and head velocity increased with frequency so that the response was 180° out of phase at 1 Hz. Despite the decrements in gain and increasing phase lags above 1 Hz, continued efforts to track the stimulus can be inferred at the highest frequencies because the EMG response gains exhibited continued modulation of the muscles.

EMG response phases presented a muscle activation pattern unique to the VT condition. As seen in the response of the subject presented in Fig. 5, at 1.5 Hz, SCM produced an almost 180° phase advance similar to that seen in Fig. 4. SEMI, however, failed to phase advance at high frequencies, producing activation of the extensor muscle in phase with the flexor muscle. Some subjects demonstrated this tactic of phase shifting only one muscle, whereas others kept both muscles in phase with each other across the frequency range. Concurrent activation of the flexor and extensor muscles is indicative of a change in strategy for the tracking task from

![Bode plots of one subject's (△) right sternocleidomastoid (SCM) and right semispinalis (SEMI) muscle EMG responses.](image1)

![Bode plots of one subject's (△) right sternocleidomastoid (SCM) and right semispinalis (SEMI) muscle EMG responses.](image2)

![Bode plots of one subject's (△) right sternocleidomastoid (SCM) and right semispinalis (SEMI) muscle EMG responses.](image3)

**FIG. 4.** Bode plots of one subject's (△) right sternocleidomastoid (SCM) and right semispinalis (SEMI) muscle EMG responses. Gain and phase responses are plotted with respect to trunk velocity for each instructional set. Gains are in arbitrary units corresponding to rectified EMG amplitude per deg/s trunk velocity. Neck wrt trunk velocity response gains and phases for this subject in each of the three instructional sets are inset on the graphs. Phases corresponding to peak flexor and extensor position and velocity of chair rotation are identified. Phase values from the neck with respect to trunk responses in Fig. 2 (0.1 Hz) are also plotted on the y-axis of each graph (symbols as per legend). Gain values are not included because data in this figure and Fig. 2 are from different subjects.

![Plots on the left represent head velocity responses of all subjects in the visual tracking condition.](image4)

![Plots on the left represent head velocity responses of all subjects in the visual tracking condition.](image5)

**FIG. 5.** Plots on the left represent head velocity responses of all subjects in the visual tracking condition. Gain and phase responses of head velocity are plotted with respect to the target light velocity. Solid line is the vector average of the group; shaded area is ±1 SE of the average. On the right, EMG responses of the SCM and SEMI muscles from the subject portrayed in earlier figures (△) are plotted for the VT condition with respect to the target light velocity. Ordinate axes of the 2 plots are the same as in Figs. 3 and 4, respectively, so that perfect head tracking has a gain of 1 and a phase of 0°.
one of reciprocal activation to one of coactivation. A change in control strategy could represent a centrally generated phase lag in SEMI output that would act to partially offset the lagging behavior of the head at frequencies >1 Hz. Coactivation would change the mechanical properties of the head-neck system by increasing the stiffness and resonant frequency, thereby explaining the greatly diminished head velocities observed through the decreased gains.

Comparison between horizontal and vertical plane responses

In Fig. 6, each subject's NV and MA gain and phase responses for vertical and horizontal (Keshner and Peterson 1995) rotations are plotted on polar plots. Included are the most overlapping frequencies from the two rotational paradigms (i.e., 0.35, 0.75, 1.45, 2.15, and 3.05 Hz from the vertical plane and 0.35, 0.72, 1.48, 2.10, and 2.95 Hz from the horizontal plane). Descriptive statistics are inadequate for quantitative comparison of responses described by two interactive characteristics like gain and phase. Thus, to test whether head stabilizing responses to yaw and pitch rotations differed significantly, we calculated the scalar distance of each subject's neck vectors with the use of the law of cosines (Munem and Yizzi 1970). Scalar distances were then entered into a factorial analysis of variance to determine whether, at each frequency cited above, group differences between the two rotational paradigms were greater than intersubject variability. In other words, were differences between responses to each rotation direction too large to be accounted for by the inherent variability between subjects?

A summary post hoc analysis using a Scheffe F-test was performed on these data revealing that the effect of stimulus orientation was strongest at the lowest frequency (0.35 Hz), producing significant or near significant (NV was at the $P < 0.06$ level) differences in all conditions of external perturbation. Significant differences also appeared at 2.0 Hz and above for VS, NV, and MA. Significance at the lowest frequency of rotation was probably due to the higher gains and thus improved stabilization, observed during vertical rotations. Significant differences above 2.0 Hz were reflective of the rising gains and decreasing phases associated with the resonant response exhibited only during horizontal rotations. VT differed between the two rotational paradigms at the two lowest frequencies of rotation (0.35 and 0.75 Hz). Significant differences at low frequencies in VT were the result of the wider scatter and lower gains appearing during vertical as opposed to horizontal rotations. Results from this analysis suggest that stabilizing response characteristics have an inherent variability that is not completely overridden by the plane of rotation. Stimulus orientation was significant, however, at the frequency eliciting the greatest voluntary control, and at the frequency in which a marked shift in control from neural to mechanical characteristics was observed in the horizontal rotation paradigm.

Discussion

Schor et al. (1988) identified several sources of input to the head control system including central commands to the motoneuron pool, movements of the body in space, movements of the visual environment with respect to the head, and external torques applied to the head. In these studies we have attempted to examine the effects of the first three factors.
Central commands for movement

Our data provide information about the interaction between the reflex and voluntary mechanisms that contribute to the command to stabilize the head. The two reflexes that we refer to are the VCR and CCR, although previous studies suggest that vestibular inputs are more crucial to the organization of the head stabilizing reflex response than the cervical proprioceptive inputs. Banovetz et al. (1987) showed that there was no cervicocollic response in alert animals when the body was rotated about a fixed head in multiple rotational planes. Bizzi et al. (1978) found that vestibulocorticated and rhizotomized monkeys were not able to compensate fully for unexpected loads during orienting head movements in the horizontal plane as would be expected if a high gain cervicocollic reflex were responsible for that compensation. The picture that emerges from our analysis, however, is that both reflexes participate in the observed movement of the head.

In the horizontal plane, head movement is dominated by voluntary mechanisms at low frequencies and head-neck mechanics at high frequencies. Reflexes serve to damp mechanical resonance at high frequencies and to smooth the transition from voluntary to mechanical control. At low frequencies in VS and NV, the CCR reflex opposes horizontal head stabilization (see Keshner and Peterson 1995). In the vertical plane at low frequencies, responses in the MA condition had similar phases and only moderately lower gains than those in VS and NV, indicating that reflexes (presumably dominated by a VCR activated by combined otolith and canal input) were contributing significantly to vertical head stabilization. At higher frequencies, the rising gain and advancing phase of EMG output, which almost certainly arises from reflex dynamics like those observed in decerebrate cats (Bilotto et al. 1982; Peterson et al. 1985), appears to allow neural mechanisms to maintain control of the head. The large dip in gain and shift in phase that occurs in horizontal plane rotations during the transition from voluntary signals that have a compensatory phase, to mechanical signals whose phase is still in the anticomparative direction (Keshner and Peterson 1995), is thereby avoided. Data in Fig. 3 suggest that such a shift might be occurring at frequencies beyond the range tested, but mechanical considerations suggest it should be more modest because the phase of head-neck mechanical signals should be closer to compensatory in this higher range. Thus it appears reflexes make a significant contribution to vertical head stabilization over the entire frequency range, and these enhanced reflex contributions significantly damp the performance of the head stabilizing system.

Kinematic data previously collected from alert cats indicate that an altogether different response network exists for reflex and voluntary mechanisms. Entirely different patterns of muscle activation were recorded when cats performed a voluntary head movement or when a VCR response was elicited during a head movement in the same direction (Keshner et al. 1992a). In the present study, large phase errors observed in the VS and NV data at the two highest frequencies when responses in MA remained close to compensatory would support the presence of two pathways. It is interesting that voluntary efforts to stabilize the head are actually counterproductive at higher frequencies. We might expect the most economic strategy for the CNS would be to engage in switching or gating between the voluntary and reflex pathways at high frequencies, but this was not supported by our data. Instead, reflex pathways appeared to operate in conjunction with voluntary pathways (Forssberg et al. 1975). During natural movements (i.e., a study of walking at different speeds), we have observed that frequencies of the head fall within the 1.5- to 2.5-Hz range identified for reflex control of head stabilization (Cromwell and Keshner 1992; Keshner et al. 1992b). Thus in more complex tasks, such as locomotion, the system may rely more heavily on reflex stabilization as an optimal behavioral strategy. Voluntary mechanisms could then be freed to participate interactively with a dynamically changing environment.

Even when the task presents a continuous demand on the voluntary system, as in our voluntary tracking task (VT), frequency-related changes in response dynamics have been observed. As seen in Fig. 5, our subjects demonstrated greatly diminished gains of head velocity above 1 Hz in spite of steady EMG activation in the neck muscles. Muscle response phases shifted from a reciprocal activation to a coactivation strategy at high frequencies, which could explain the diminished head velocity gains. The shift from reciprocal activation to coactivation is consistent with previous reports that motor system response strategies alter with changes in frequency (Viviani and Berthoz 1975). Increased stiffening, resulting from the coactivation and gravitational effects, would produce decreased amplitude of head displacement as frequency increases (Kearney and Hunter 1982). Thus the product of this shift in strategy would be reduced efficiency of the tracking response.

In all but the visual tracking condition, it is unlikely that the visual environment (either through visual input or eye position) contributed a great deal to the head stabilizing response. Only one of our other conditions (VS) supplied any visual information, and that was a stationary light source requiring that eye position in the head should remain relatively stationary. In both the current and in a prior study (Guitton et al. 1986), the primary difference in the response during visual stabilization versus voluntary stabilization without visual feedback was somewhat higher neck response gains, indicating improved compensation when visual feedback was present. There have been some studies suggesting that neck muscle activity was directly related to eye position in the alert cat (Roucoux et al. 1989; Vidal et al. 1982). In this laboratory, Banovetz et al. (1987) correlated neck torques with eye position in alert cats in both the presence and absence of visual stimulation. When visual inputs were present, the eye and neck were coactivated to produce proper orientation of the head. In the absence of visual stimulation, however, neck muscle activity was more strongly related to vestibular stimulation than to eye position.

Orientation-related dynamics of the vestibular reflexes

By testing responses to both vertical and horizontal rotations, we have been able to explore whether the dynamics of head stabilization are related to stimulus orientation. Overall,
gains in the vertical plane were higher than those in the horizontal plane, suggesting a more robust neural response to vertical plane rotations. As was true for horizontal rotations, the best compensation for vertical rotations was exhibited in the response gains and phases of VS and NV at frequencies <1 Hz, and during MA between 1 and 2 Hz. At 2 Hz, where gains began dropping off in the horizontal paradigm, response gains became more variable among the subjects in the vertical plane. A resonant response of the head was observed around 3 Hz in the horizontal plane, suggesting a transition from voluntary and reflex control to that of system mechanics. Resonance never appeared in the frequency range presented in the vertical plane, suggesting superior head stabilization over a wider bandwidth in pitch than in yaw.

Physiological correlates of orientation-dependent neck muscle responses can be found in the literature. For example, planes of maximum sensitivity or preferred rotation axes have been found in studies of vestibular receptors (Blanks et al. 1975; Fernandez and Goldberg 1976; Loe et al. 1973). Dynamics of secondary vestibular neurons in alert cats, and of the VCR in decerebrate cats, have been shown to depend on both orientation and frequency of the rotation stimulus. Response dynamics of the VCR in the biventer cervicis muscle of decerebrate cats have been recorded in pitch and roll (Baker et al. 1985). Contraction of this muscle produces extension of the head and is analogous to the action of semispinalis capitis in humans. Unlike our subjects, decerebrate reflex gains in the pitch plane demonstrated a continual increase with frequency, but phase responses were consistent with the observations of this study, i.e., muscle EMG modulation was position related at the lowest frequency (0.07 Hz) and gradually phase advanced toward a velocity phase as frequencies increased to 1.6 Hz. In roll, muscle EMG gains exhibited a sharp increase at the same time as a phase shift toward velocity occurred. In our subjects, gains of splenius capitis (a lateral rotator and extensor muscle) began to increase in MA during horizontal rotations as a phase shift toward velocity occurred at 1.0 Hz.

The explanation put forward by Baker et al. (1984, 1985), that changes in response dynamics with direction reflected converging semicircular canal and otolith inputs having different dynamics and spatial orientations (or preferred axes of rotation), could be applied to our results as well. Significant differences in the responses to the two rotational paradigms emerged at the lowest (<0.5 Hz) and highest (>2 Hz) frequencies. At the lowest frequency, this change was apparently due to higher gains during vertical rotations, particularly in the conditions without vision (NV and MA), where vestibular information became more important. One explanation for the observed difference is that the otolith receptors were activated by the vertical but not by horizontal rotations at the lower frequencies, which fall within the sensitivity bandwidth of the otolith organs (Schor and Miller 1982). Participation of the otoliths in head stabilization could also explain why the resonant response was observed only in the horizontal plane at high frequencies. If static otolith inputs were responsible for increasing muscle stiffness, then the resonant frequency in the vertical plane would be raised.

Differences in system mechanics and the influence of gravity could also underlie the high-frequency dynamic differences in the two planes. By placing the axis of rotation at the ear in seated pitch rotations, the axis of rotation was approximated through the center of mass of the head, and otolith input was restricted to gravity-related stimulation. Amplitudes of rotation in this study were small, so we could assume that the free neck rotated primarily about the C1-skull joint, which is approximately level with the interaural axis in the human. The moment of inertia in this situation will approach its smallest value because mass of the head is equally distributed about this axis. In the case of yaw rotations, the whole body was rotated about the stimulus axis, and the axis approximated the spinal column. Hence the distribution of the head mass was located at a distance from the stimulus axis. This would cause a larger moment of inertia in the yaw plane. An increased moment of inertia in a second-order underdamped system such as the head and neck (Goldberg and Peterson 1986; Schor et al. 1988) should reduce the resonant frequency. Thus the larger moment of inertia, possibly coupled with smaller muscle stiffness in yaw, would likely cause resonance to occur at lower frequencies in yaw than in pitch.

The apparent shift of resonance to higher than expected frequencies with a higher moment of inertia in pitch could also be indicative of a higher stiffness in that plane. There are two possible mechanisms behind increasing stiffness. First, different levels of tonic force may be required to keep the head “centered” in the two planes. Neck extensor muscles may have to apply a continuous force against gravity in pitch that is not required in yaw. These experiments did not produce the data necessary to support an assumption of higher tonic activation in pitch than in yaw. Current studies in this laboratory in which a 10-lb weight is placed on the head during vertical plane rotations suggest that increasing the mass, moment of inertia, and gravitational load on the head does increase tonic activity in the neck muscles and elicits the appearance of a resonant response around 3 Hz during pitch rotations (Keshner et al. 1992b).

A second explanation for increased stiffness in pitch would be that rotations of smaller amplitude were used in the vertical plane. Stiffness and viscosity decrease with increasing amplitudes (Kearney and Hunter 1982), and the peak excursion in the horizontal plane was almost twice that in the vertical plane in these experiments. A test of the linearity of the response with increasing amplitudes was performed in the two rotational planes, and we found that even with a fourfold increase in amplitude (from ±5 to ±20°), response gains and phases did not change significantly with stimulus amplitude. Because this amplitude difference is much greater than the differences existing between the two experimental paradigms, we believe that we have been working within a linear range of head-neck responses in these two papers.

Neck muscles may just exert greater torques in the vertical than in the horizontal plane and be better able to compensate for high-frequency perturbations of the head. In a study of isometric head stabilization, we found that, when resisting horizontal rotations of the head, EMG activation of the SEMI, splenius capitis, and SCM muscles was, on average, twice as large as when each muscle generated the same
torque in the vertical plane (Keshner et al. 1989). We inferred from these findings that the muscle had to work harder against an equivalent force to maintain stabilization in the horizontal plane. Studies attempting to model muscle activity during stabilization of the cervical spine have concluded that the large, multiarticular superficial muscles with larger moment arms are actually more effective stabilizers than are the deep, paraspinal muscles (Crisco and Panjabi 1990; Winters and Peles 1990). Inspection of the prime movers identified for each plane of rotation revealed that fewer muscles participate in the horizontal than in the vertical plane (Rasch and Burke 1963; White and Panjabi 1978), and these tend to be the deeper paraspinal muscles. Actual muscle torques in the two rotational planes have not been calculated, but preliminary calculations from a detailed kinematic model of the human head-neck system by Dr. S. Li in our group suggests that muscles typically have larger moment arms in pitch than in yaw. This would imply greater spring stiffness and hence higher resonant frequencies in pitch.

Through analyses of complex motor systems, such as the head and neck, during natural movements, we can explore how the CNS operates when multiple mechanisms are available to control a single motor task. The overlapping frequency and kinematic characteristics of each of these mechanisms suggest that command parameters during normal activity are not preprogrammed, but depend on task constraints (e.g., the frequency and informational content of the stimulus). The contribution of each mechanism might be determined automatically by the frequency content of the stimulus, but the CNS would be responsible for tuning the frequency characteristics of each mechanism, and for selecting sensory inputs for feedback in any given task. A system whose control mechanisms were frequency as well as context dependent would have greater flexibility to compensate to a variety of natural stimulation frequencies, whether they arose from self-generated or externally imposed movements.

We thank Dr. Fred Prior for advice on data analysis methods and critical reading of this paper, and G. Rovai and S. Pope for technical assistance. This study was supported by National Institutes of Health Grants NS-22490 and DC-01125.

Present address of R. L. Cromwell: Dept. of Physical Therapy, Temple University, Philadelphia, PA 19140.

Address for reprint requests: E. Keshner, Sensory Motor Performance Program, Rm 1406 (MC E809), Rehabilitation Institute of Chicago, 345 East Superior St., Chicago, IL 60611.

Received 26 October 1992; accepted in final form 1 February 1995.

REFERENCES


SCHOR, R. H., KESNER, R. E., AND DIERINGER, N. Reflex stabilization of


