Modulating active stiffness affects head stabilizing strategies in young and elderly adults during trunk rotations in the vertical plane

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Abstract

Healthy young and elderly adults were asked to actively modulate neck muscle stiffness during random rotations of the trunk in the vertical plane. Angular velocity of head with respect to trunk and myoelectric activity of semispinalis capitis and sternocleidomastoid muscles were recorded. A MANOVA was performed on group, condition, and frequency variables. A gain and phase drop at 2.15 Hz in young adults indicated neural (i.e. reflex) damping of system mechanics. In the elderly, a steady rise in gain and drop in phase ($P < 0.0002$) was indicative of a second order underdamped system. Even when instructed to not intervene elderly subjects exhibited cocontraction. Ineffective reflex mechanisms may underlie the emergence of this strategy.

Keywords: Head control; Cocontraction; Stiffness; Aging; Neck reflexes

1. Introduction

In young adults, voluntary and reflex head stabilization in the horizontal and vertical planes of motion was related to the frequency of the perturbation [1,2]. Voluntary mechanisms successfully controlled head stabilization at frequencies of rotation below 1 Hz in either plane of motion. During this compensation, response phases of the neck muscles (semispinalis capitis, sternocleidomastoid, and splenius capitis) had a well-defined reciprocal activation pattern with a $180^\circ$ phase shift between flexor and extensor muscles. Compensation by the vestibulocollic reflex (VCR) and cervicocollic reflex (CCR) in the neck occurred between 1.5–2.5 Hz. In the horizontal plane, frequencies above 3 Hz elicited a mechanical resonance so that the head moved more than the trunk. In the vertical plane, however, compensatory head stabilization was maintained up through 3 Hz; mechanical resonance of the head was not observed in the vertical plane in young adults. Elderly subjects, however, produced responses with lower gains and poorer compensation when trying to stabilize the head during trunk rotations, and only approximated a stable head in the vertical plane when visual feedback was available [3]. Lower response amplitudes below 1 Hz and the appearance of mechanical resonance at higher frequencies of rotation ($> 2$ Hz) implied an insufficient control of head stabilization.

Smaller response amplitudes in the elderly are suggestive of changes in both the reception of the signal and in the ability to produce adequate force. Elderly subjects may not have perceived the same stimulus intensity because of diminished receptor capacity [4–8], or they may have been unable to produce the velocities necessary to compensate for the stimulus intensity because of weakened effectors [9,10]. A common strategy used to compensate for weakness at a joint is cocontraction of the antagonist muscles [9–12]. Stiffening of the joint by cocontraction is reportedly a strategy used when maintaining a limb posture against a load [13,14] even though lower levels of muscle activation have actually been observed during cocontraction against a static load in wrist [15], neck [16], and lower limb muscles [17]. In clinical populations, muscle cocontraction is a common strategy [17–20] believed to result
primarily from weakness at the joint. Elderly adults have been reported to rely upon stiffening of body segments through muscular cocontraction [9,21,22], possibly because of the generalized weakness found in this population [10,12]. Evidence for a stiffening strategy on the posture platform or during whole body rotations is not consistently supported with findings of cocontraction of muscles in the trunk and lower limbs [23,24], however.

In order to determine if elderly subjects were relying on cocontraction during a head stabilizing task, subjects were asked to actively modulate their neck muscle stiffness during random rotations of the trunk. Subjects were either distracted from the task, asked to resist the perturbation, or asked to not intervene. One way to distinguish between the limitations of the input or output signal is through the directional pattern exhibited by the muscle. Several studies have demonstrated that muscles have well defined areas of primary activation during motion in a single plane [16,25], and that each head motion is executed by a specific muscular pattern [16,26,27]. When forces are increased, however, muscles begin to activate in their non-preferred directions and demonstrate a cocontraction pattern [25]. Thus, stiffening through a cocontraction strategy should appear as a poorly defined phase response indicating that the muscle is responding in multiple directions of motion rather than in its primary direction of activation. Diminished compensatory motion but with maintenance of a well defined directional response would describe a reciprocal activation pattern but a diminished reception of the sensory signal.

2. Methods

2.1. Subjects and procedures

The equipment and methods used here are identical to a previous experiment [3]. Six healthy young adult subjects, aged 20–40 years, and six female and four male elderly subjects, ages ranging from 65 to 88 years, gave informed consent to participate in this study. All subjects had no current medical complaints and no history of neurological disorder, falling, or postural instability. Active range of motion was within normal limits. All of the elderly subjects were active on a daily basis, performing their activities of daily living (e.g. shopping, gardening, housecleaning) without assistance. Three of the subjects (67, 87, and 88 years old) participated in exercise classes for at least 30 min 3 days per week. One subject (87 years old) was legally blind in one eye. (i.e. a visual acuity of 20/200 or less in the better or stronger eye with best correction).

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. 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. The entire apparatus was enclosed in a light-tight room. 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. Pilot studies comparing trunk and chair angular velocity during chair rotation confirmed that movement of the trunk relative to the chair was insignificant at all test frequencies. Thus, all measures of chair velocity and position were considered to be equivalent to trunk velocity and position [1].

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. Subjects wore a soft helmet assembly with a triaxial angular rate sensor (Watson Industries, WI) positioned at the temple. A head-referenced visual target, a portable laser pointer, was positioned on the side. The weight of this apparatus was 950 g. The mass of the helmet was evenly distributed around the circumference of the head, and the center of mass of the helmet was positioned close to the center of mass of the head, thus, with the helmet, the center of mass of the head remained constant.

2.2. Instructional sets

In the relax condition (RLX), subjects were advised to relax and to not think about anything, thus minimizing active stiffness which should enhance passive properties and lower the resonant frequency of the head–neck system. Mental arithmetic (MA) required attention to a cognitive task in the dark so that the subject’s attention was removed while rotation in the dark was ongoing in order to lessen voluntary intervention in the process of head stabilization. In the cocontract (CC) condition, subjects were asked to stiffen their necks and keep their head locked to their trunk. Increasing stiffness through active cocontraction should enhance voluntary stabilization and raise the resonant frequency of the system.

All subjects were tested on a single day with the same order of presentation: RLX, MA, CC. Subjects received five 40 s trials in each condition. Data from the five trials of each condition were averaged for each subject, but data for different subjects were not pooled. Subjects did not report any discomfort, fatigue or loss of effort in following instructions during the experiment.

2.3. Stimulus

A position command was provided to the chair in the vertical plane as a sum of five sinusoids (SSN) that consisted of relatively prime (i.e. having no common
divisors) harmonics of a common base frequency. The pseudorandom SSN waveform was composed of frequencies spanning the range of 0.35–3.05 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. Peak excursion from the vertical was ±12° and mean excursion was 0°. 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 were exposed to a minimum of one complete cycle of stimulation before data collection began in each trial.

2.4. Data collection and reduction

Bilateral electromyographic (EMG) activity from semispinalis capitis (SEMI) and sternocleidomastoid (SCM) was detected by Ag–AgCl electrodes, 4 mm in diameter, spaced 1 cm apart. SEMI was palpated while subjects performed pitch extension with rotation of the head; electrodes were placed on the muscle belly approximately 2 cm below the occipital bone at C1–C2 and 2 cm lateral to the midline. SCM was palpated during contralateral rotations of the head against resistance placed at the chin. Placements of electrodes on the muscle belly were approximately one third of its length rostral to its sternal attachment. EMG electrode locations have been verified anatomically and physiologically by a previous study of isometric head stabilization [16]. In our elderly subjects, the skin of the neck tended to fold loosely over the neck muscles, thus presenting greater difficulty in obtaining robust EMG signals. Data were excluded if signal loss was observed in the EMG signals. Although bilateral muscle EMG signals were collected, only responses of the right-sided muscle will be presented here.

Surface EMG recordings of the two neck muscles were amplified, bandpass filtered (10–200 Hz), full-wave rectified, and integrated (20 ms time constant) before anti-alias filtering (Frequency Devices, MA) 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. Measures of angular trunk velocity in space, angular head velocity in space, and chair (trunk) position were also recorded. Signals were viewed on a monitor during testing and stored in digital form for later reduction and analysis.

Amplitude and phase of trunk and head angular 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.

2.5. Data analysis

2.5.1. Head–neck kinematics

The complex geometry of the neck was simplified by treating it as a hinge joint, and neck velocity (head with respect to the trunk) was calculated by the vectorial difference between the response vectors of head and trunk velocity. Data for all rotation conditions will be presented as responses at the neck with respect to the trunk (neck velocity divided by trunk velocity for gain and neck velocity minus trunk velocity for phase), and called the neck re trunk vector. Response phase was expressed as the number of degrees by which the response led (+ phase) or lagged (− phase) the stimulus (cf. Fig. 2 in Ref 2). Phase of the trunk was expressed relative to velocity, with peak forward flexion velocity at 0°. A phase difference of ±180° was defined as perfect phase compensation between the head and the trunk. Phase leading was defined as a phase between 0 and −180°; phase lags fell between −180° and −360°. 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.

Composite gains and phases (Table 1) can be used to describe the kinematic response strategies. Operationally, a gain of one and phase of ±180° represented perfect compensation of the head for motion of the trunk (or no movement of the head relative to space). Smaller gains indicated that the head was moving at smaller velocities than the trunk (i.e. overcompensating for the stimulus) as would occur with increased stiffness. Gains greater than one indicated that the head was moving at higher velocities than the trunk (i.e. resonating). When paired with phases sharply dropping towards −180°, these responses suggested control by system mechanics rather than neural processes.

<table>
<thead>
<tr>
<th>Response strategy/control mechanism</th>
<th>Head–neck</th>
<th>Muscles</th>
</tr>
</thead>
<tbody>
<tr>
<td>Good compensation/ reciprocal activation</td>
<td>Gain = 1</td>
<td>Standard gain</td>
</tr>
<tr>
<td></td>
<td>Phase = ±180°</td>
<td>Well defined phase</td>
</tr>
<tr>
<td>No active compensation/ system mechanics</td>
<td>Gain &gt; 1 Phase</td>
<td>Decreased gain</td>
</tr>
<tr>
<td></td>
<td>90–180°</td>
<td>Well defined phase</td>
</tr>
<tr>
<td>Stiffening of the joint/co-contraction</td>
<td>Gain = 0</td>
<td>Increased gain</td>
</tr>
<tr>
<td></td>
<td>Phase = 0</td>
<td>Variable phase</td>
</tr>
</tbody>
</table>
2.5.2. EMG Responses

In a previous study [2] the linearity of the response was tested at similar frequencies and with increasing amplitudes. Even with a fourfold increase in amplitude (from \( \pm 5 \) to \( \pm 20^\circ \)), response gains and phases did not change significantly with stimulus amplitude. Since this amplitude difference was much greater than the differences existing between the two experimental conditions, we believe that we have been working within a linear range of head–neck responses in this study. Coherence between neck velocity and trunk velocity was also calculated at each stimulus frequency [3]. Trials that had coherence values below 0.6 at three or more frequencies were removed from the analysis. Given these results, we are confident of a linear dynamic relation between the stimulus and the measured response.

Although coherence of the EMG response to trunk velocity was more variable than the head velocity measures, the gains and phases of the EMG responses can be considered reliable because of the consistent patterns demonstrated across subjects. Interpretation of phase responses depended on the known actions of the muscles with respect to head movement [16], and was presented with respect to peak trunk position or velocity [1]. Thus, response phases around \( \pm 90^\circ \) corresponded to peak backward position of the trunk. Phases of \(-90^\circ\) corresponded to peak forward trunk position. A muscle response phase of 0° indicated that the muscle was responding in phase with peak forward (trunk flexion) velocity; a \(-180^\circ\) phase indicated a response related to peak backward (trunk extension) velocity.

Unique combinations of EMG response gains and phases were predicted for characterization of the expected response strategies (Table 1). When compensating for the rotations the response gains were considered to be the standard for each subject. Phases would be well defined and reciprocally activated with muscles exhibiting a peak output in their preferred response direction [16]. If the subject was cocontracting, response gains would increase and the directional response of the muscle would become less precise as the muscle responded in more than its primary direction of action. If system mechanics were predominant, a decrease in EMG response gains would occur although the directional activation of the muscle would remain well defined.

Repeated measures multivariate analyses of variance (MANOVA) were performed to test for group condition, and frequency differences on the neck gain and phase data and the EMG response gain and phase data (Myers, 1979). A Bonferroni adjustment was used for multiple comparisons with a corrected \( P \)-value of \(< 0.0002\) required for statistical significance.

3. Results

3.1. Head–neck kinematics during mental distraction

Previous papers from this laboratory [1–3] reported that when vision was available or when subjects attempted to stabilize their heads voluntarily, head stabilization in space was best at low frequencies (< 1 Hz). Subjects were able to maintain reasonable head stabilization up until 2 Hz. Distinct differences in the response to MA suggested that subjects were not voluntarily intervening when presented with a task to divert attention from the disturbance at the head, therefore, any compensation would be due to reflex activation. Below 1 Hz, young adult subjects exhibited response gains below 0.5. Phases between 0 and 180° suggested phase leading of the response, but the low gains made the functionality of this response doubtful. We have previously suggested that a phase lead at frequencies below 1 Hz could be indicative of otolith compensation in this rotation plane [2].

In this study, response gains during MA ascended steadily, and the majority of phase responses moved closer to 180° at frequencies between 1.45 and 2.15 Hz, indicating improved compensation of the head for trunk rotations (Fig. 1). At 2.15 Hz, gains exhibited the sharp drop observed in previous studies [1–3] and ascribed to 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. While some subjects maintained a compensatory 180°, others began to exhibit phase leading at this frequency. Differences between the phase response at 2.15 Hz and lower frequencies were significant (Table 2). At 3.05 Hz gains began to rise above one and were significantly greater than at the lower frequencies suggesting the beginning of mechanical resonance. Phase responses, however, tended to rise rather than drop off as would be expected if the response reflected the strictly passive mechanical 2nd order system predicted from the homeomorphic model of head control proposed by Peng et al. [29]. The rising phase response implies that neural elements (i.e. neck reflexes) continued to exert control over this behavior.

The predicted response of a linear, 2nd order underdamped system [28] is embedded in the gain responses of the elderly in MA (Fig. 2). They demonstrate the expected gradual rise in gains and decrease in phases expected of a passive mechanical system [29] across the frequency spectrum (data from the 88 year old subject was lost due to a faulty transducer). This response pattern was similar to that observed in a deeply anesthetized animal [30], and would suggest that neural influences were absent in the responses of this population. At 0.35–0.75 Hz, the elderly had gain and phase responses more closely matching those of the young.
adults. A significant difference between the two groups appeared in the phase responses at 2.15 Hz where the young adults more steeply descended toward phase leading and the elderly subjects continued to lag the stimulus. Except in the 69, 70, and 73 year old subjects whose gains plateaued and phases fell closer to 180° throughout the frequency range, the response could be described by steeply ascending gains and descending phases. In fact, gains at 3.05 Hz were significantly greater than gain responses at all other frequencies ($P < 0.0002$). The significant drop in phase above 2.15 Hz (Table 2) associated with a rise in gain characterized a resonant response of the head.

### Table 2
Significant within and between group comparisons ($P<0.0002$)

<table>
<thead>
<tr>
<th>Group</th>
<th>Significant Differences</th>
</tr>
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<tbody>
<tr>
<td><strong>Young adults</strong></td>
<td></td>
</tr>
<tr>
<td>Neck gain</td>
<td>3.05 Hz &gt; 0.35 Hz and 0.75 Hz</td>
</tr>
<tr>
<td>Neck phase</td>
<td>2.15 Hz &lt; 0.35 Hz, 0.75 Hz, 1.45 Hz</td>
</tr>
<tr>
<td>SEMI Gain</td>
<td>3.05 Hz in CC &gt; all other CC frequencies</td>
</tr>
<tr>
<td></td>
<td>3.05 Hz in MA &gt; 0.35 Hz in MA</td>
</tr>
<tr>
<td></td>
<td>MA &lt; CC</td>
</tr>
<tr>
<td></td>
<td>RLX &lt; CC</td>
</tr>
<tr>
<td>SCM Gain</td>
<td>3.05 Hz in CC &gt; 1.45 Hz in CC</td>
</tr>
<tr>
<td></td>
<td>3.05 Hz in MA &gt; 0.75, 1.45 Hz in MA</td>
</tr>
<tr>
<td></td>
<td>3.05 Hz in RLX &gt; all other RLX frequencies</td>
</tr>
<tr>
<td><strong>Elderly adults</strong></td>
<td></td>
</tr>
<tr>
<td>Neck gain</td>
<td>3.05 Hz &gt; all other frequencies</td>
</tr>
<tr>
<td>Neck phase</td>
<td>2.15 Hz &lt; 0.35 Hz, 0.75 Hz</td>
</tr>
<tr>
<td></td>
<td>3.05 Hz &lt; 0.35 Hz, 0.75, 1.45 Hz</td>
</tr>
<tr>
<td><strong>Young versus elderly</strong></td>
<td></td>
</tr>
<tr>
<td>Neck phase</td>
<td>2.15 Hz</td>
</tr>
<tr>
<td>SEMI phase</td>
<td>CC</td>
</tr>
<tr>
<td>SCM phase</td>
<td>CC, MA, RLX</td>
</tr>
</tbody>
</table>

### 3.2. Actively altering system mechanics

In order to alter the active mechanics of the neck, subjects were asked either to not intervene and relax (RLX) or to resist the motion (stiffen) so that their head was locked to their trunk (CC). No significant differences emerged in the response kinematics between instructional sets (Table 2), but the pattern of the response provided some indication of how subjects were adapting to the change in motor command. Response gains were more scattered in young adults during RLX than MA at low frequencies, which might simply reflect to what extent each subject was able to follow the instructions. But at 2.15 Hz, the frequency at which reflexes presumably are operative [1,2], the response was less variable across subjects and a steep drop in
Fig. 2. Neck angular velocity relative to trunk angular velocity from ten elderly subjects in MA, RLX, and CC. Each plot symbol represents a different subject and subject ages are identified in the lower right graph. The bold solid line in each graph is the group average. The bold dashed line is the response of a passive 2nd order underdamped system [29]. See Fig. 1 for explanation of phase relations with respect to trunk velocity.

Gain combined with a drop in phase was indicative of a loss of voluntary control. This was followed by a definite rise in both gain and phase at 3.05 Hz as would occur if system mechanics became predominant. Elderly subjects also exhibited a response pattern in RLX that was very similar to MA (Fig. 2).

In the young adults during the CC condition (Fig. 1), gains of the neck with respect to the trunk fell below 0.3 at frequencies below 1 Hz in all subjects. This indicated that no change was occurring at the neck, thus the head was indeed moving with the trunk. The ability to synchronize the head with the trunk appeared only at frequencies below 1 Hz. Between 1–3 Hz, gains steadily increased but did not rise above unity in the majority of subjects. Both the gain and phase drop observed at 2.15 Hz in MA and RLX did not begin until 3.05 Hz in CC. It would appear that the intent to voluntarily stiffen the system shifted system dynamics so that control by the reflexes and the subsequent shift to system mechanics was delayed.

Below 1 Hz, gains from the elderly in CC were lower than in the MA condition (below 0.2) indicating that subjects were successful in voluntarily minimizing head motion at low frequencies of rotation. Gradually rising gains and sustained phase leads in some elderly (Fig. 2) indicated that they were still exerting voluntary control over their responses at frequencies up to 3 Hz. At 3.05 Hz, however, gains above 1 paired with a sudden phase descent were evidence for loss of voluntary control and subsequent reliance on system mechanics.

Significant phase differences between the young and elderly subjects at 2.15 Hz reveals differences in the control processes operating for these two groups. Young adults have a greater drop in gain and phase at that frequency whereas the elderly exhibited a steady rise in gains with phases holding around 180°. These behaviors suggest that elderly subjects continued to rely upon voluntary control at frequencies above 1 Hz, although unsuccessfully. When the voluntary mechanisms became inadequate for accomplishing the task, a resonant response of the head emerged. Young adults, however, had an alternate neural control mechanism (i.e. neck reflexes) available to damp down the resonant mechanics.

3.3. Neck muscle EMG responses

Significant differences ($P < 0.0002$) appeared in the EMG response gains of young adult subjects as a result of instructional set and frequency (Table 2). Specifically, response gains of both muscles at 3.05 Hz were significantly greater than at some of the lower frequencies, and SEMI response gains were greater in CC than in MA and RLX. Plots of the neck muscle gain re-
sponses with respect to trunk velocity (Fig. 3) demonstrated a previously described U-shaped pattern of response [1,2], with gradually decreasing gains between 0.35 and 2.15 Hz, and then a steep increase that exceeded the previous level of activation. The $180^\circ$ phase reversal indicative of reciprocal activation of the two neck muscles was maintained in the young adults in the MA and RLX conditions (Figs. 3 and 4). SEMI initially responded in phase with forward position of the trunk and then exhibited a $90^\circ$ phase shift to forward velocity with increasing frequency. SCM was initially matched to backward position of the trunk and then phase shifted $90^\circ$ to backward velocity at higher frequencies. A $90^\circ$ phase advance from position to velocity as frequency increases is characteristic of control by the VCR in decerebrate [31,32] and alert [27,30] cats. In CC, the high frequency response of SCM shifted $135^\circ \text{ to } 180^\circ$ so that it was phase matched to forward velocity or position. Thus the SCM muscle was responding in phase with SEMI at higher frequencies, which is characteristic of cocontraction of the two muscles.

Changing the instructional set had no significant effect on muscle EMG response gains in any of the elderly subjects. As seen in Fig. 3, the U-shaped pattern was present in the response gains. But significant differences did emerge between the two populations in the phase of the EMG response as a result of instructional set (Table 2). Response phases of both SEMI and SCM were significantly different between the two populations in CC, and SCM phases differed significantly in MA and RLX as well.

A more diffuse directional pattern of neck muscle activation emerged in the elderly subjects than in the young adults (Fig. 4) suggesting a reliance on cocontraction of the two muscles in all of the instructional sets. In MA and RLX, SEMI was matched to forward or backward position of the trunk at low frequencies, and then phase shifted to forward velocity or position at higher frequencies. SCM response phases were matched to backward position of the trunk at low frequencies and advanced toward backward velocity or forward position as frequency increased. In CC, both SEMI and SCM initially responded in phase with forward position or velocity and then phase shifted to backward velocity or position at higher frequencies. For both populations, activation of the two muscles in the same direction of trunk rotation was not associated with an increase in EMG response gain.

**Fig. 3.** Bode plots of the EMG responses in (A) one young adult and (B) one elderly adult subject's right sternocleidomastoid and right semispinalis muscle in MA, RLX, and CC. Gain and phase responses are plotted with respect to trunk velocity. Gains correspond to the uncalibrated envelope of the rectified EMG amplitude per °/s trunk velocity. As indicated on the figure, phases correspond to peak forward position ($-90^\circ$), forward velocity (0 or $-360^\circ$), backward position ($+90^\circ$ or $-270^\circ$), and backward velocity ($\pm 180^\circ$) with respect to trunk rotation.
4. Discussion

This study explored the selection of strategies for head stabilization in both young adult and elderly subjects by having subjects change the active parameters of the head–neck system through actively relaxing or stiffening their neck muscles. Previous findings [3] have revealed that elderly subjects produce responses with lower gains and poorer compensation when trying to stabilize the head during trunk rotations. One possibility was that elderly subjects were relying on an alternate strategy for compensation because muscle weakness prevented them from producing the velocities necessary to compensate for the stimulus intensity [10,12]. Another possibility was that elderly subjects did not perceive the same intensity of the stimulus signal because of a diminished receptor capacity [4–8].

Comparison of the young adults’ response dynamics in MA in this study with those of previous data (Ref. [2,3] and Chen KJ. Unpublished Masters Thesis, 1997) indicates a distinct difference at 3.05 Hz. In the previous data there was no rise in gains above 1 and phases did not descend toward 360°. The singular difference between this study and those performed previously is the order of presentation of the instructional set. In the prior studies on young adults, MA followed two series of trials requiring voluntary stabilization; in this study, MA followed a series of trials requiring relaxation. The presence of a rise toward resonance and steep drop-off in phases in MA in this study suggests that the intent to decrease system stiffness had a definitive effect on system dynamics that carried over into subsequent trials.

But the definitive clustering and dropping of gains between 1.5–2.5 Hz that was associated with response phases moving toward compensation characterizes the shift from control by passive mechanics to active control mechanisms-most likely the VCR and CCR [1,2]. In contrast, the absence of a gain drop in the elderly subjects in both the distraction and relaxation conditions leading to a continuous rise toward resonance and a steady phase drop is indicative of continuous control by second order system mechanics in this frequency range [30,33]. Less effective reflex compensation in elderly individuals was not unexpected because age-re-
lated deterioration in the vestibular system [4–8] would produce higher thresholds and delayed processing of the generative signal.

For both populations studied here, differences between a distracting condition (MA) and one in which subjects intentionally relaxed (RLX) were minimal. Variability between subjects in each population may reflect fluctuations in their ability to satisfy the requirements of non-intervention or to be suitably distracted from the task. It is also possible that differences in the structure of each individual musculoskeletal system could alter the response dynamics. Small differences in musculoskeletal mechanics can produce large differences in moment arms and force generation [34]. But these differences are not explained simply by differences in passive mechanics. A recent study in this laboratory [33] examined head–neck response dynamics to vertical plane rotations when inertial mass was increased five-fold. Response characteristics were found to remain constant. Using a mathematical model [28], we demonstrated that neural components were modulated to maintain compensatory responses both with and without additional weight.

If the changes across frequency when instructed to stiffen the head and neck were simply a reflection of inertial stabilization, we would expect to see a constant rise in gains and steep drops in phase until the resonant peak was achieved. The opposite of this picture was demonstrated in the young adults where the rise in gain reached compensation and then exhibited a drop off at a higher frequency than in the other two conditions. Resonance did not appear within the frequency spectrum tested here. Subjects tended to stay within 90° of phase compensation and phases tended to rise or plateau rather than drop. Thus, in this condition, young adults were able to maintain some control by neural mechanisms over a greater bandwidth than they did when distracted or relaxed. The implication here is that VCR and CCR can be modified by mental set. There is evidence that cervico-ocular [35], otolith-ocular [36], and VOR [37,38] 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 [39]. Similarly, under more controlled conditions of VCR testing [40,41], 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 [42,43], it is plausible to suggest that the VCR and CCR can also be modified by mental set.

Elderly subjects exhibited a pattern of gain and phase responses in the cocontraction condition that were very similar to those they exhibited when distracted or relaxed. This finding paired with the presence of a cocontraction strategy in all three instructional sets suggests that, even when instructed to not intervene, elderly subjects exerted voluntary control across the bandwidth of responses. When that control mechanism failed, the only option available to these subjects were the responses generated by system mechanics.

The role of cocontraction in postural stabilization is unclear. Although it has been suggested that cocontraction may help stabilize the spinal column by increasing general stiffness [44], others suggest that a dynamic bursting pattern in the postural muscles is necessary for postural maintenance whereas cocontraction would introduce oscillations into the system [45]. In fact, these oscillations would explain the mechanical resonance observed in our elderly subjects. The clinical literature continues to focus upon coactivation of opposing musculature as a deleterious factor in joint motion [17–20]. Persistence of voluntary control over behaviors that ordinarily are automatic and reactive [46] may, in fact, be one explanation for the postural instability regularly observed in elderly populations.

It is evident from these results that cocontraction is the strategy of choice in the elderly subjects. Although muscle weakness is often cited as the reason the system selects this method of control, several recent studies have suggested that cocontraction actually produces a weaker response. Studies of wrist stabilization [15] indicate that maximum stiffness achieved by cocontraction was less than 50% of the maximum value predicted during reciprocal activation of flexor and extensor muscles. Reduced stiffness was due to lower levels of activation during cocontraction than during reciprocal activation. Measures of moments produced during isometric lower limb contractions in children with cerebral palsy revealed lower maximum moments and increased cocontraction thus implicating antagonist cocontraction in the extension weakness observed in this group [17].

Ineffective reflex mechanisms that would normally contribute to a damping of system mechanics may underlie the emergence of the cocontraction strategy in the elderly subjects [47]. Loss of reflex compensation in correspondence with decreased response amplitudes implies an impaired reception of the peripheral stimulus. In the absence of a stimulus adequate to evoke directionally specific responses, the CNS may well choose to generate activity in multiple muscles in order to make the system rigid. Thus, cocontraction may not be the most effective strategy for stabilization but may be the only neural option available when reciprocal mechanisms fail.
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