RESEARCH ARTICLE

Anita N. Vasavada · Barry W. Peterson · Scott L. Delp Three-dimensional spatial tuning of neck muscle activation in humans

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Abstract The complex structure of the neck musculoskeletal system poses challenges to understanding central nervous system (CNS) control strategies. Examining muscle activation patterns in relation to musculoskeletal geometry and three-dimensional mechanics may reveal organizing principles. We analyzed the spatial tuning of neck muscle electromyographic (EMG) activity while subjects generated moments in three dimensions. EMG tuning curves were characterized by their orientation (mean direction) and focus (spread of activity). For the four muscles that were studied (sternocleidomastoid, splenius capitis, semispinalis capitis and trapezius), EMG tuning curves exhibited directional preference, with consistent orientation and focus among 12 subjects. However, the directional preference (orientation) of three of the four neck muscles did not correspond to the muscle's moment arm, indicating that maximizing a muscle's mechanical advantage is not the only factor in determining muscle activation. The focus of muscle tuning did not change with moment magnitude, demonstrating that co-contraction did not increase with load. Axial rotation was found to have a strong influence on neck muscle spatial tuning. The uniform results among subjects indicate that the CNS has consistent strategies for selecting neck muscle activations to generate moments in specific directions; however, these strategies depend on three-dimensional mechanics in a complex manner.

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Introduction

The neck musculoskeletal system is characterized by complex anatomy and apparent muscle redundancy. It is not known how the central nervous system (CNS) selects appropriate muscles to achieve a particular motor goal in the face of this complexity. If the system of muscles is redundant (more neck muscles than degrees of freedom), it is possible that individuals could exhibit large variation in neck muscle activation strategies for the same task. If, however, muscle activation strategies are consistent among subjects, examining these strategies in relation to the mechanical environment may reveal principles used by the CNS to select muscle activation patterns. Electromyographic (EMG) tuning curves, which depict muscle activity over a range of force or moment directions, have been used to study activation strategies of arm and neck muscles (Buchanan et al. 1989; Keshner et al. 1989; Flanders and Soechting 1990; Lee et al. 1990; Theeuwen et al. 1994; Dewald et al. 1995; van Bolhuis and Gielen 1997). When tuning curves are consistent among subjects, analyzing the orientation and focus (mean direction and spread of EMG activity, respectively; defined below) of EMG tuning curves in relation to musculoskeletal mechanics has provided insight into CNS control.

However, consistent neck muscle activation patterns among human subjects have not been reported. Of two previous studies of neck muscle tuning, one study reported results of only one subject (Lee et al. 1990), and the other study included 15 subjects but found large variation in tuning patterns for some muscles (Keshner et al. 1989). In both of these studies, loads were applied over pulleys; thus, subjects had to stabilize the head, and the position of the head was not monitored. The experimental setup allowed limited control of mechanical conditions, which may have led to variable EMG patterns. This has limited our understanding of neck muscle coordination

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and the relation between tuning curve parameters (orientation and focus) and musculoskeletal mechanics.

The *orientation* of a muscle tuning curve indicates the task direction in which its EMG activity is maximum. Examining the orientation of muscle tuning in relation to a muscle's moment arm can indicate whether maximizing a muscle's mechanical advantage might be a strategy used by the CNS. In human upper limb muscles under isometric conditions, the peak direction of EMG tuning curves in two dimensions often corresponds to moment arm direction (Buchanan et al. 1986, 1989, 1993). However, Flanders and Soechting (1990) found that the maximum EMG direction of two-joint upper limb muscles is sometimes a compromise between the direction of their moment arms at the shoulder and elbow. The constraints of three-dimensional equilibrium may require that muscles are activated in directions that do not correspond to their moment arm, especially when other muscles are active. At the elbow, the triceps is activated when subjects generate pronation or supination loads (for which it has no moment arm) in order to balance flexion moments generated by the pronator teres or biceps muscles (van Zuylen et al. 1988; Buchanan et al. 1989). In the neck, Lee et al. (1990) found that the sternocleidomastoid was not maximally activated according to its mechanical advantage, likely because it has the potential to generate moments in three directions (flexion, lateral bending, and axial rotation). The relation of muscle activation to biomechanics is even more complex under dynamic conditions. Arm muscle activity to initiate movements often does not correspond to either the joint movement direction or the endpoint force or acceleration necessary to reach to a target (Hasan and Karst 1989; Karst and Hasan 1991). These results indicate that each muscle's activation needs to be evaluated in the context of both activation of other muscles and three-dimensional mechanics.

The focus of a muscle tuning curve indicates the angular range over which the muscle is active and whether there is co-contraction (defined here as activation in directions in which the muscle moment arm is opposite to the net moment). Muscle strategies which change with load may affect the focus of EMG tuning curves. Buchanan et al. (1986, 1989) found that elbow muscles are generally active over an angular range of less than 180° around the moment arm direction, demonstrating little co-contraction; the shapes of their tuning curves do not change with load. However, Flanders and Soechting (1990) found that some upper limb muscles increased cocontraction or even changed their peak activation direction with increased load. In the neck, Lee et al. (1990) found that patterns of neck muscle activity did not change much with an increase in moment magnitude at low load levels (1.4 - 3.2 Nm). At higher load levels, Keshner et al. (1989) observed co-contraction in some neck muscles in particular directions. A shift to a co-contraction strategy would imply a broader (less focused) tuning curve at higher loads.

A change in the *orientation* or *focus* of tuning curves with increased degrees of freedom may also provide insight into CNS control strategies. No studies have documented the influence of axial rotation on neck muscle tuning curves. The fact that most neck muscles are oriented obliquely (i.e., able to contribute to axial rotation) and the importance of axial rotation for horizontal gaze stabilization suggest that axial rotation may have a potent influence on CNS control.

The goal of this study was to examine EMG tuning curves of neck muscles while subjects generated threedimensional isometric moments. We hypothesized that: (1) consistent patterns of neck muscle tuning would emerge in a study with well-defined mechanical conditions and adequate control of head position; (2) the orientation of neck muscle tuning curves would not necessarily correspond to moment arm, because of the constraints of musculoskeletal geometry and three-dimensional equilibrium; (3) the focus of neck muscle tuning curves would decrease with load magnitude because of increased co-contraction; (4) both focus and orientation of neck muscle tuning curves would be strongly influenced by axial rotation moment, because of musculoskeletal geometry and the importance of axial rotation for gaze. To test these hypotheses, we developed an experimental apparatus that controls head position and provides subjects feedback of isometrically generated moments in three dimensions (Vasavada et al. 2001), allowing constrained mechanical conditions for analyzing neck muscle tuning. In addition, we used rigorous statistical methods (Batschelet 1981; Fisher et al. 1987) to analyze the orientation and focus of neck muscle tuning curves.

Materials and methods

Twelve healthy adults (seven males and five females) with no history of neck disorders participated in this experiment. The protocol was approved by the Institutional Review Board of Northwestern University, and informed consent was obtained from all subjects. The age of the subjects ranged from 24 to 43, with a mean age 32 for males and 30 for females (Table 1).

Electromyography and target-matching protocol

Surface electrodes (Conmed, Utica, N.Y.) were placed bilaterally on the sternocleidomastoid, splenius capitis and semispinalis capitis, and unilaterally on the trapezius (Fig. 1), with electrode placement verified by palpation as described in Keshner et al. (1989). In seven subjects, intramuscular electrodes were used to record from the splenius capitis and semispinalis capitis. The electrodes, made of bifilar 50-µm-fine wire, were inserted through a cannulated needle near the location of the surface electrode. Intramuscular electrode placement in the splenius capitis mad semispinalis capitis was verified by registration with existing MRI images for one subject. The data from the splenius capitis intramuscular electrode were discarded from one subject, and the data from splenius capitis surface electrode and semispinalis capitis intramuscular electrode were discarded in another subject due to motion or electrical artifacts.



Fig. 1A–C Muscle anatomy and placement of EMG electrodes (*black oval marks*). The approximate location of the axes about which moments were resolved is also indicated (*x* lateral bending, *y* flexion-extension, *z* axial rotation) **A** Lateral view of sternocleido-

mastoid. **B** Posterior view of trapezius and splenius capitis. **C** Posterior view of semispinalis capitis. Adapted from Gray's Anatomy (Gray 1977)

Table 1 Anthropometric and postural data of subjects in muscle tuning experiment. Mean (standard deviation) of data

	Age (years)	Weight (kg)	Height (cm)	Neck circumference (cm)	Head circumference (cm)	Frankfort plane (degrees) ^a	Neck angle (degrees)
All subjects	31 (5)	74 (13)	173 (11)	38 (3)	57 (2)	8 (7)	52 (3)
Males (<i>n</i> =7)	32 (5)	80 (12)	180 (7)	40 (2)	58 (1)	8 (8) ^b	52 (3) ^b
Females (<i>n</i> =5)	30 (6)	65 (10)	164 (9)	36 (2)	56 (3)	8 (6)	51 (3)

^a Frankfort plane is positive if the inferior border of the orbit is higher than the tragus of ear

^b Posture data were not available for two male subjects

Subjects were seated with their heads in the neutral posture and shoulders and torso firmly restrained (Fig. 2A). The head was rigidly coupled to a six-degrees-of-freedom load cell (ATI, Garner, N.C.) by a device with eight pads that were tightened around the head. Subjects pushed against the pads in different directions to produce the desired moments. Anatomical landmarks were digitized to record subject posture and to calculate the points about which moments were resolved. Posture was quantified by the angles of two lines relative to horizontal (Table 1): Frankfort plane [the line between the tragus of the ear and the inferior border of the orbit (Bjerin 1957)] and neck angle [the line between the C7 spinous process and tragus of the ear (Braun and Amundson 1989)].

The axes about which moments were resolved were identified based on digitized anatomical landmarks. Flexion-extension and lateral bending moments were resolved about horizontal axes through the midpoint of the line between the spinous process of C7 and the sternal notch. Although axes of rotation for flexionextension and lateral bending vary with the kinematics of movement performed, the axes defined here provide a consistent reference in the upper part of the T1 vertebral body (Harms-Ringdahl et al. 1986). Axial rotation moments were resolved about a vertical axis in the mid-sagittal plane, through the midpoint of the tragi of the ears. This is a more physiological location to resolve axial rotation moments because it is aligned in the anteriorposterior direction with the dens of C2, about which approximately 50% of axial rotation motion occurs (White and Panjabi 1990). Thus, the three axes (for flexion-extension, lateral bending, and axial rotation) are orthogonal, but only the axes for flexionextension and lateral bending intersect at a common point; the axis for axial rotation lies anterior to this point. These axes were chosen to best represent the kinematics based on a consistent set of external markers and have been used in several previous biomechanical studies (Harms-Ringdahl et al. 1986; Mayoux-Benhamou and Revel 1993; Queisser et al. 1994; Siegmund et al. 1997; Vasavada et al. 2001). The muscles from which EMG data were obtained all cross the defined axes (Fig. 1).

The experimental procedure consisted of two parts: measurement of the maximum moments along three principal axes, and three-dimensional target moment matching. First, subjects generated maximum extension, flexion, lateral bending (right and left), and axial rotation (right and left) moments. Subjects attempted three trials lasting 3 s each in all six directions; the order of directions was randomized among subjects. Maximum moment was calculated by finding a 200-ms window during each trial in which the averaged moment was greatest. The largest value of the three trials was considered to be the subject's maximum, which was used to calculate the magnitude of target moments in the subsequent part of the experiment.

In the target-matching phase of the experiment, subjects were presented with targets on the computer screen representing combinations of moments in the three principal directions (Fig. 2B). The horizontal and vertical position of the target on the screen indicated the magnitude of the lateral bending moment and extension-flexion moment, respectively, that the subjects were to generate. Within each circular target, the vertical offset of an angular wedge indicated the axial rotation moment that the subjects were to generate. The magnitudes of the moments generated by the subject in lateral bending, extension-flexion, and axial rotation were indicated by the horizontal and vertical positions of a cursor and rotation of a dial within the cursor. Subjects were instructed to generate moments to move the cursor into the target (within 10%) tolerance). They maintained the moments for 300 ms and were provided with auditory and visual feedback when the task was completed.

Target moment directions can be described by their direction cosines, the cosines between the target direction and each of the three principal axes (lateral bending, extension-flexion, and axial rotation). Because the axes for lateral bending and extension-



Fig. 2 A Experimental apparatus for neck strength measurement. Head holder with pads was attached to a load cell located behind the subject's head, and thick straps restrained the shoulders and torso. **B** Representation of computer screen for real-time feedback of three moments. The position of the target (*bold circle*) indicates the lateral bending and extension-flexion moments that the subjects were to generate. The angular wedge indicates the axial rotation moment that the subjects were to generate. (The target moment shown is a combination of extension, right lateral bending, and right axial rotation). The cursor (*light circle*) indicates the moment generated by subjects. The task was to generate the appropriate moments to move the cursor into the target and the dial into the angular wedge

flexion are located in the transverse (or horizontal) anatomical plane, those moments will be termed "transverse plane moments" for simplicity. The *x*-axis was defined as positive for right lateral bending moment, the *y*-axis positive for extension, and the *z*-axis (orthogonal to the transverse plane) positive for right axial rotation moment. The absolute magnitude of moment was constant in all directions; thus, the set of target moments can be visualized on a sphere in "moment space" (Fig. 3).

Target directions in moment space were chosen to answer specific questions about neck muscle directional tuning. To investigate two-dimensional muscle tuning, targets were distributed circularly in the transverse plane (extension, flexion, and lateral bending moments only). At low and medium load levels (defined below), targets were distributed at 45° intervals (Fig. 3A); at the high load level they were distributed at 22.5° intervals. To examine three-dimensional spatial tuning, a spherical distribution in moment space (Fig. 3B) included the pure moments in each direction, equal combinations of any two moments, and equal combinations of the three moments (26 directions total).

Three load levels were examined. At each load level, the absolute value of target magnitude was a fixed percentage of the subject's maximum axial rotation moment. For the two lower load levels (low and medium), the target magnitude was 40% or 80% of the subject's maximum axial rotation moment. Low load magnitudes averaged 2.3 Nm in female subjects and 4.7 Nm in male subjects (11% of maximum extension moment and 15–17% of maximum flexion or lateral bending moment). The high load level was twice the medium level. Because this value was greater than the subjects' maximum axial rotation moments, the high load level consisted of moments in the transverse plane only (magnitudes ranged from 40–60% of the subjects' maximum moments in extension, flexion, and lateral bending). Load levels were presented in random order to subjects, and at each load level target directions were presented randomly. Three trials were collected for each direction. Three subjects completed only two of the three load levels, and one subject completed only one load level.

Three trials of baseline EMG data were collected at the beginning of the session and in between each load level. Maximum moment data were collected for one trial in each direction at the end of the session to test for fatigue.

Data analysis

EMG data were pre-amplified and low-pass filtered at 500 Hz before A/D collection at 1,000 Hz. EMG gains ranged from 8,000 to 40,000 and were set to maximize the signal from each muscle. EMG records were band-pass filtered between 30 and 400 Hz, detrended, rectified and low-pass filtered at 7 Hz. For the target matching trials, the EMG values were averaged over the center 200 ms of the 300 ms of data that were collected. During maximum trials, a 200-ms window was found in which the EMG of each muscle reached its maximum. EMG levels during all trials were normalized with respect to their maximum value using the following formula (Dewald et al. 1995):

$$EMG_{norm} = \frac{(EMG_{trial} - EMG_{base})}{(EMG_{max} - EMG_{base})},\tag{1}$$

where EMG_{max} was the maximum value throughout the experiment, and

$$EMG_{base} = MEAN - \frac{2 * S.D.}{\sqrt{n}}$$
(2)

was calculated using the mean (MEAN) and standard deviation (S.D.) of all baseline trials, and n the total number of baseline trials.

Circular and spherical statistics provide quantitative measurements to analyze the orientation and focus of distributions in space (Batschelet 1981; Fisher et al. 1987). In this case, the spatial tuning of normalized EMG amplitude as a function of moment direction was analyzed. Directions in three-dimensional space can be described by three direction cosines, $[x_i, y_i, z_i]$, or by two angles

Fig. 3A, B Distributions of targets in "moment space." A Circular distributions of moments. Pure flexion-extension and lateral bending moments (also called transverse plane moments) are visualized as a circle in the plane z=0. B Spherical distribution with moments distributed uniformly in each octant of the sphere. Direction cosines of select moment directions are noted



Table 2 Directions of moment arm vectors. Mean vector direction and range. Azimuth angle is defined such that 0° =right lateral bending, 90° =extension, 180° =left lateral bending and -90° =flex-

ion. Elevation angle is defined such that 90° =right axial rotation and -90° =left axial rotation

	Right sternocleido- mastoid	Right splenius capitis and cervicis	Right semispinalis capitis and cervicis	Right trapezius
Azimuth angle (range)	-8° (-18°, 2°)	54° (37°, 78°)	74° (62°, 82°)	15° (5°, 24°)
Elevation angle (range)	-16° (-19°, -12°)	19° (9°, 28°)	-9° (-26°, -3°)	-37 (-45°, -24°)

in spherical coordinates (azimuth and elevation). For neck muscle tuning data, the azimuth angle,

$$\phi = \arctan\left(\frac{y_i}{x_i}\right),\tag{3}$$

represents the angle in the transverse plane, where 0° is right lateral bending, 90° is extension, 180° is left lateral bending and 270° (-90°) is flexion. The elevation angle,

$$\theta = \arcsin(z_i),\tag{4}$$

represents the amount of axial rotation. An elevation angle of 90° is pure right axial rotation, and -90° is pure left axial rotation. (In the two-dimensional case, $\theta = 0$ and the only relevant angle is the azimuth angle, ϕ).

The *orientation* and *focus* of directional data are quantified by two parameters: *mean vector direction* and *dispersion about the mean* (Batschelet 1981; Fisher et al. 1987). The mean vector direction is the direction of the resultant vector. In the case of muscle EMG tuning data, the resultant vector, R, is the vector sum of normalized EMG magnitudes over all target moment directions:

$$R = \sum_{i=1}^{n} EMG_i \begin{bmatrix} x_i \\ y_i \\ z_i \end{bmatrix}$$
(5)

where x_i , y_i , and z_i are the direction cosines of the moment vector direction.

The dispersion of data about the mean direction is defined by the normalized magnitude of the resultant vector. For EMG tuning data, this is equivalent to the resultant vector magnitude divided by the sum of the magnitudes in all directions:

$$r = \frac{|R|}{\sum_{i=1}^{n} EMG_i} \tag{6}$$

The parameter r is identical to the "index of spatial focus" defined by Dewald et al. (1995) to examine spatial tuning in forearm muscles; we will also refer to this quantity as *spatial focus*. The index ranges from 0 to 1; it is close to 0 if the muscle is relatively uniformly active in all directions and approaches 1 if a muscle is primarily active in a specific direction. The dispersion is analogous to the variance in linear statistics, and angular variance (S^2) or angular deviation (S) can be defined (in radians) using the transformation

$$S^2 = 2(1-r) \tag{7}$$

for circular data (Batschelet 1981), or

$$S^2 = 1 - r \tag{8}$$

for spherical data (Mardia 1972). Because the definition of angular variance is different for two- and three-dimensions, we have chosen to report spatial focus (r) in tables, from which the angular variance or deviation can be readily calculated; however, for illustrative purposes we have depicted angular deviation in Figs. 5 and 8.

The orientation and shape of neck muscle tuning curves were characterized in several ways. First, EMG tuning curves were tested for directionality using the Rayleigh test. The null hypothesis is that the data are uniformly distributed around the circle or sphere. It can be rejected if r is greater than a critical value (for details, see

Batschelet 1981 and Fisher et al. 1987). If the distribution is not uniform and also unimodal, the resultant vector direction is termed the *preferred direction*. The existence of a preferred direction is necessary for meaningful statistical comparison of mean vector directions.

EMG tuning curve distributions were tested for differences among load levels, subjects, and muscles using a χ^2 test (Batschelet 1981). The χ^2 test can distinguish inhomogeneity of distributions, but not specific differences in resultant vector or spatial focus. However, because of the discrete (non-continuous) nature of the EMG distributions, the χ^2 test was the only statistical method available to examine differences in EMG tuning curves.

Secondary analyses were also performed on the resultant vectors and spatial focus of all the subject data. By treating the group of resultant vectors as a distribution, the mean vector direction and dispersion of resultant vectors were calculated for the group of subjects. Resultant vectors were tested for a common mean direction among loads (Batschelet 1981; Fisher et al. 1987). Changes in spatial focus were tested using ANOVA. In all of the statistical tests, the significance level of p < 0.05 was chosen.

Relation of muscle tuning to musculoskeletal geometry

A biomechanical model of the neck musculature (modified from Vasavada et al. 1998) was utilized to interpret the EMG results. This model represented skeletal geometry, muscle anatomy, and joint kinematics to calculate muscle moment arms in three dimensions. In the original model, the sternocleidomastoid, splenius (capitis and cervicis portions), semispinalis (capitis and cervicis portions) and trapezius were modeled with two or three muscle segments each. To examine the variation of muscle moment arm directions throughout the muscle, they were modeled with 6-20 lines of action representing a more anatomical distribution of muscle fibers. Both the capitis and cervicis portions of the splenius and semispinalis were included in the moment arm calculations even though EMG data came from only the capitis portion; it was assumed that the capitis and cervicis portions were activated together. The mean and range of moment arm directions throughout each muscle is noted in Table 2. To compare the orientation of neck muscle EMG activity to the muscle moment arm, the angular difference between the EMG resultant vector and the range of muscle moment arm vectors was calculated.

Results

Muscle tuning curves in the transverse plane

The resultant vector, or orientation, of a tuning curve is considered to be a preferred direction if the distribution is unimodal and significantly different from a uniform distribution. More than 80% of tuning curves had preferred directions in the transverse plane (e.g., Fig. 4). That is, 200 of 244 EMG distributions (over all subjects, muscles, and three load levels) were unimodal (by visual inspection) and had a spatial focus greater than the critical



Fig. 4A–D Tuning curves in the transverse plane for one subject at three load levels (4, 8 and 16 Nm). Shaded area indicates range of three trials. Numbers in upper right hand corner indicate the peak muscle activation as a percent of maximum. All data are from surface electrodes. A Right sternocleidomastoid. B Right splenius capitis. C Right semispinalis capitis. D Right trapezius. Azimuth angles are 0°=right lateral bending (RLB), 90°=extension (EXT), 180°=left lateral bending (*LLB*) and 270°= -90° =flexion (*FLX*)

value for a non-uniform distribution. The muscles for which a uniform distribution most often could not be rejected were the trapezius and surface electrode data of the semispinalis. These two muscles were more broadly tuned than the sternocleidomastoid or splenius, but for all muscles the average spatial focus over all subjects was always greater than the critical value for a non-uniform distribution.

Further, each muscle's preferred direction was unique and consistent among subjects (Table 3). For most load levels and muscles, a χ^2 test did not find significant differences in EMG tuning curves among subjects. The dispersion of resultant vector directions among subjects ranged from 0.99 to 0.8 (corresponding to angular deviations of $8-35^{\circ}$), except for the trapezius at the low load level, which had larger inter-subject variation. The sternocleidomastoid was tuned toward activation in flexion, without a strong directional preference toward either right or left lateral bending. The splenius capitis was tuned primarily toward lateral bending. The semispinalis capitis was tuned more towards extension than lateral bending. The trapezius was tuned toward lateral bending, but it had the lowest activation levels and greatest variability among subjects.

The resultant vector direction did not always correspond to the moment arm direction. The resultant vector of the sternocleidomastoid was almost orthogonal to its moment arm direction, which had its largest component in lateral bending (Fig. 5A, B). The range of moment arm is defined such that 0°=right lateral bending, 90°=extension, 180°=left lateral bending, and -90°=flexion. Elevation angle is defined such that 90°=right axial rotation and -90°=left axial rotation. (SCM Sternocleidomastoid. SPL solenius capitis. SEMI Sternocleidomastoid,

angle

Resultant vectors of all subjects. Mean direction (and dispersion) of all subjects'

Table 3

resultant vectors : subjects correspo deviation can be o dimensional data, all subjects' spatia	at all load levels. I nds to the angula calculated from dis respectively). Disj I focus values (wh	Note that the disper ur deviation (gray spersion according t persion in this table ich are shown in ba	rsion of the results <i>arcs</i>) in Figs. 5 : to Eqs. 7 and 8 fou e is not the same a r graphs in Figs. 6	int vectors of all and 8. (Angular r two- and three- is the average of and 7). Azimuth	bending, and −90°= and −90°=left axia semispinalis capitis electrode data	flexion. Elevation I rotation. (SCM :, TRAP trapezius	angle is defined s Sternocleidomastc , <i>surf</i> surface el	uch that 90°=right id, <i>SPL</i> splenius ectrode data, <i>i-m</i>	t axial rotation capitis, <i>SEMI</i> intramuscular
	Right SCM	Left SCM	Right SPL (surf)	RightSPL (i-m)	Left SPL	Right SEMI (surf)	Right SEMI (i-m)	Left SEMI	Right TRAP
2D resultant vector	or: azimuth								
Low	-84 (0.98)	-102 (0.94)	4 (0.89)	24 (0.99)	174 (0.80)	66 (0.93)	(66.0) 89	105 (0.81)	10 (0.63)
Medium	-87 (0.96)	-104(0.98)	-1(0.95)	18(0.998)	179(0.86)	64 (0.92)	(0.98)	120 (0.92)	(0.89)
High	-84(0.98)	(90, 0)	-13(0.95)	24 (0.99)	-171 (0.92)	35(0.89)	57 (0.98)	128 (0.90)	-7 (0.96)
All levels	-85 (0.98)	-102(0.97)	-4 (0.92)	21 (0.99)	-179 (0.85)	57 (0.89)	64 (0.98)	118 (0.87)	4 (0.81)
3D resultant vector	or: azimuth								
Low	-82 (0.95)	-107 (0.97)	3 (0.90)	24 (0.99)	178 (0.83)	(69)	(96) (0) (0) (0) (0) (0) (0) (0) (0) (0) (0	129 (0.65)	17 (0.56)
Medium	-86(0.85)	-103(0.97)	(0.96)	18(0.83)	-180(0.89)	(0.90)	63(0.81)	125 (0.74)	9 (0.73)
Both levels	-84 (0.90)	-105(0.97)	1(0.93)	22 (0.91)	179 (0.86)	67 (0.89)	66 (0.89)	127 (0.70)	13 (0.63)
3D resultant vector	or: elevation								
Low	-63 (0.95)	(0.02) (0.97)	64 (0.90)	71 (0.99)	-63 (0.83)	59 (0.89)	43 (0.96)	-59(0.65)	-20(0.56)
Medium	-55 (0.85)	64 (0.97)	60(0.96)	71 (0.83)	-65 (0.89)	63 (0.90)	43(0.81)	-59 (0.74)	-43 (0.73)
Both levels	-59 (0.90)	67 (0.97)	62 (0.93)	71 (0.91)	-64 (0.86)	(0.89)	43 (0.89)	-59 (0.70)	-33 (0.63)

Fig. 5 Average tuning curves in two dimensions, normalized to maximum value recorded in the transverse plane. The means and standard deviations (gray shaded area) of all subjects and load levels are shown. The bold line is the mean resultant vector of all subjects and the gray arc is the angular deviation of the subjects' resultant vectors. The arrow indicates the mean and range of moment arm directions calculated from a musculoskeletal model (Vasavada et al. 1998). Axis directions are noted on first plot only (EXT extension, FLX flexion, RLB right lateral bending, LLB left lateral bending)

1.0

0.8

0.6

0.4

0.2

0.0

Right

40

Spatial Focus (r)



Fig. 6 Two dimensional spatial focus of muscles in the transverse plane (no axial rotation moments) at three load levels. Note that spatial focus does not change with load

Fig. 7 Spatial focus of muscles (mean and standard deviation of all subjects and load levels) for two- and three-dimensional target moment distributions. *White bars* indicate two-dimensional circular distribution, and *black bars* indicate three-dimensional spherical distribution of moments

Fig. 8A-F Muscle tuning curves in three orthogonal planes, normalized to the maximum value for each subject. Each muscle is shown in one row. A Right sternocleidomastoid. **B** Right trapezius [note that the resultant vectors and moment arms are indistinguishable in columns (i) and (iii)]. C Right splenius capitis (surface electrodes). D Right splenius capitis (intramuscular electrodes). E Right semispinalis capitis (surface electrodes). F Right semispinalis capitis (intramuscular electrodes). Data shown are mean and standard deviation (gray shaded area) of all subjects and load levels. The *bold line* is the mean and the gray arc is the angular deviation of all subjects' resultant vectors. The arrow indicates the projection of the three-dimensional moment arm directions in each two-dimensional plane (however, the relative magnitude of the moment arm projection would be different in each of the three planes). Axis directions are noted in first row only. Columns: *i* Transverse plane [flexion (FLX), extension (EXT) and lateral bending (RLB/LLB)]. ii Plane of axial rotation (RAR/LAR) and lateral bending (RLB/LLB). iii Plane of axial rotation (RAR/LAR), flexion (FLX) and extension (EXT)



directions of splenius were $40-80^{\circ}$ away from the mean resultant vector calculated from surface electrodes (Fig. 5D, E) and $15-55^{\circ}$ from that of intramuscular electrodes (Fig. 5F). Although the resultant vector direction for intramuscular data of the splenius capitis was closer to moment arm direction than surface electrode data, both were significantly different from the range of muscle moment arm directions. For the semispinalis and trapezius, the moment arm and resultant vector directions were within $10-15^{\circ}$ of each other, and the angular deviation of the resultant vectors among subjects overlapped with the range of moment arm directions (Fig. 5C, G–I).

Tuning in the transverse plane was consistent over the three load levels, although the magnitude of EMG increased with load (Fig. 4). When magnitude was normalized, for each subject individually there were no differences in tuning curves with load (χ^2 test). With subject data pooled, there were also no significant differences among load level for resultant vector direction (Table 3) or spatial focus (Fig. 6).

Muscle tuning curves in three dimensions

In three dimensions, 87% of the tuning curves had a preferred direction (151 of 174 tuning curves over all subjects, muscles, and two load levels). Similar to the transverse plane, the distributions for trapezius and semispinalis (surface electrode data only) had the lowest spatial focus and were more likely to be indistinguishable from the uniform distribution. However, for all muscles,

the average spatial focus over all subjects always exceeded the critical value for a non-uniform distribution.

Each muscle had a unique preferred direction in three dimensions, which was consistent among subjects and which often included a strong axial rotation component indicated by a large elevation angle. At most load levels and muscles, a χ^2 test did not find differences in EMG tuning curves among subjects, and the dispersion of resultant vectors ranged from 0.97 to 0.86 (Table 3) for most muscles (corresponding to angular deviations of 10–22°), except for the trapezius and left semispinalis, which showed more dispersion among subjects. In three dimensions, the azimuth angles of resultant vectors were not significantly different from the two-dimensional resultant vector.

Three-dimensional resultant vectors had less correspondence with moment arm than two-dimensional resultant vectors (compare Tables 2 and 3). Except for the trapezius, all muscle resultant vector directions were greater than 45° from the muscle moment arm directions. The difference between the mean resultant vector (all subjects and both load levels) and the range of moment arms for the sternocleidomastoid varied from 60 to 70° . For the splenius capitis, the difference was $45-65^{\circ}$ for both surface and intramuscular data. For the semispinalis capitis, the difference was $70-80^{\circ}$ for surface electrodes and $50-60^{\circ}$ for intramuscular electrodes. The mean resultant vector for the trapezius, however, was only 5- 15° from the range of its moment arms.

As with the two-dimensional data, there were no differences in tuning curves with increases in load when the magnitudes were normalized (χ^2 test). A test for a common mean (Fisher et al. 1987) showed that the resultant vector directions were not significantly different at the two load levels (Table 3). There was also no significant difference in spatial focus among load levels. However, the spatial focus for three-dimensional distributions was lower than for two-dimensional distributions (Fig. 7); this difference was significant for all muscles except the trapezius and splenius capitis.

The influence of axial rotation is evident when tuning curves are displayed in the planes orthogonal to the transverse plane (Fig. 8). Elevation angles (the component of the resultant vector aligned with axial rotation) were greater than 45° for sternocleidomastoid and splenius, close to 45° for semispinalis and generally less than 45° for trapezius (Table 3).

In summary, neck muscle tuning was consistent among subjects, and the four neck muscles exhibited unique preferred directions. Neither the resultant vector direction nor the spatial focus changed significantly with load level. Preferred direction and moment arm did not always correspond; this was particularly evident when threedimensional moments were examined because of the strong influence of axial rotation.

Discussion

The objective of this study was to evaluate neck muscle activation strategies using EMG tuning curves, which have proven to be a valuable tool to study control strategies in the upper limb (e.g., Buchanan et al. 1989; Flanders and Soechting 1990; Theeuwen et al. 1994; Dewald et al. 1995; van Bolhuis and Gielen 1997). Prior to evaluating the hypotheses outlined in the Introduction, several aspects of the experiment and analysis in relation to neck musculoskeletal biomechanics need to be discussed.

First, the two-dimensional results are clearly a subset of the three-dimensional results. Flexion-extension and lateral bending have commonalities in terms of joint kinematics, muscle moment arms, and moment magnitude that are different from axial rotation. Examining results in two dimensions also aids in the visualization of threedimensional results. Thus, it is instructive to analyze neck muscle tuning in two dimensions. However, it is acknowledged that the two-dimensional results provide a limited perspective of the three-dimensional mechanical function of the muscles.

Second, because of the complex multi-joint kinematics of the neck musculoskeletal system, axes of rotation cannot be defined as fixed with respect to anatomical landmarks, as can often be done in the limbs. Therefore, we resolved moments about axes that were consistent with anatomy and biomechanics and which also corresponded with other studies (Harms-Ringdahl et al. 1986; Mayoux-Benhamou and Revel 1993; Queisser et al. 1994; Siegmund et al. 1997; Vasavada et al. 2001). In a previous study, we found that flexion, extension, and lateral bending moments decreased as the axes about which the moments were resolved were more superior (Vasavada et al. 2001). This implies that if more superior axes of rotation were chosen for flexion, extension, and lateral bending, the ratios of the those maximum moments with respect to maximum axial rotation moment would change. This would likely affect the elevation angle of threedimensional muscle tuning; however, further studies are necessary to understand the effects of different axes of rotation on muscle activation patterns.

Third, some differences were found between results for surface and intramuscular electrodes for the muscles splenius capitis and semispinalis capitis. In the case of the splenius capitis, the resultant vector directions obtained from surface and intramuscular electrodes were different, and there was more variation among subjects in surface electrode data. There is a small "window" between the sternocleidomastoid and trapezius where the splenius capitis can be palpated (Keshner et al. 1989), and it is possible that splenius surface electrodes can pick up cross-talk from the sternocleidomastoid (Mayoux-Benhamou et al. 1995), particularly in subjects with a small neck circumference. In the case of the semispinalis capitis, the resultant vector directions for surface and intramuscular electrode data were not different. For both muscles, the spatial focus of intramuscular data was higher than for surface electrode data. This may be a result of intramuscular electrodes sampling from a more limited population of motor units. Although other investigators have found differences in directional tuning characteristics of motor units from the same muscle (van Zuylen et al. 1988; Herrmann and Flanders 1998), Mayoux-Benhamou et al. (1997) examined intramuscular EMG data simultaneously at four different sites of the semispinalis capitis and found they were almost identically activated. In this study, we found intramuscular electrode data to be consistent among subjects.

Our first hypothesis was that consistent patterns of neck muscle tuning would be evident under controlled mechanical conditions. This was the first study to use statistical methods to determine that human neck muscles have unique preferred directions and to quantify the distribution. Furthermore, we confirmed that the orientation and focus of spatial tuning were consistent among subjects.

The consistent activation patterns of neck muscles are in agreement with studies at other joints that have demonstrated subject-independent patterns of muscle activation with controlled loads (e.g., Valero-Cuevas et al. 1998). This is in contrast, however, to the study of Keshner et al. (1989), in which neck muscle tuning differed among subjects, especially for the splenius capitis. In the present study, we found more consistent tuning patterns for the splenius capitis using intramuscular electrodes than surface electrodes, but this was not the case for the data of Keshner et al. (1989). The authors of that study suggested that differences in muscle tuning among subjects could result from inter-individual differences in musculoskeletal geometry or past motor learning experiences. However, the variation in muscle tuning may also be related to the experimental design. Specifically, since head position was not fixed and three-dimensional moments were not monitored simultaneously in the study of Keshner et al. (1989), the mechanical tasks may have been different. In this study, we found that controlling head position while subjects had feedback of the threedimensional moments generated resulted in consistent patterns of neck muscle activation.

Our second hypothesis was that the orientation of neck muscle tuning (preferred direction) would not necessarily correspond to moment arm. In three dimensions, the trapezius is the only muscle whose resultant vector is within 15° of its moment arm. However, the magnitude of trapezius activation while subjects generated neck moments was small compared to its maximal activation during shoulder elevation. Thus, the correspondence of activation to moment arm for the trapezius has less importance than for other muscles which contribute more to neck moments. For all muscles, the elevation angles of resultant vectors were greater than the elevation angles of moment arm vectors (Tables 2 and 3), meaning that the differences between resultant vector and moment arm were even greater in three dimensions than in two dimensions. The lack of correspondence between preferred direction and moment arm indicates that maximizing mechanical advantage is not the main factor used by the CNS to determine neck muscle activation, even under isometric conditions.

Three-dimensional equilibrium constraints may influence the lack of correspondence between preferred direction and moment arm. For example, the sternocleidomastoid may be more strongly activated in flexion than in lateral bending because there are fewer muscles available to generate flexion moment. The lack of directional preference for lateral bending may also be explained because the sternocleidomastoid muscles on both sides must be activated to compensate for the extension moment generated by the splenius capitis during lateral bending. Based on a model incorporating muscle architecture (Kamibayashi and Richmond 1998) and moment arms of the major neck muscles (excluding the deep intervertebral muscles such as the multifidus), the four muscles examined in this study have the potential to generate 70-80% of the maximum moment generated by the major neck muscles (Vasavada et al. 1998). However, it is difficult to determine conclusively the role of equilibrium constraints because the activation patterns of deeper muscles potentially involved in the tasks are not known.

Third, we hypothesized that the focus of neck muscle tuning curves would change with load, based on evidence of Keshner et al. (1989) of a shift to a co-contraction strategy. Specifically, we expected that spatial focus would decrease with increasing load. The load magnitudes used in this study (2.3–9.2 Nm for females and 4.7–18.8 Nm for males) were higher than those of previous studies of neck muscle tuning by Lee et al. (1.4–3.2 Nm) or Keshner et al. (1.4–2.3 kg; approximately 3–5 Nm). Even at these higher loads, we did not observe decrease in spatial focus of EMG tuning curves with load magnitude, indicating that subjects did not increase co-contraction as load increased.

The design of the experimental apparatus, which provided both measurement of loads and maintenance of head position, may have also influenced the finding that neck muscle tuning did not change with load magnitude. If co-contraction exists to increase system stability, this experimental design may have had less stringent stability constraints because subjects were voluntarily generating isometric moments with head position fixed rather than resisting loads (as in Keshner et al. 1989). Thus the shift in muscle activation patterns observed by Keshner et al. (1989) may have been related to a shift in motor strategy, which was not required in our paradigm. To test the importance of stability constraints more rigorously, it would be necessary to develop different methods of controlling both load and posture independently.

Fourth, we hypothesized that the orientation and focus of neck muscle tuning curves would be influenced strongly by axial rotation. This hypothesis is supported by the observation that, in most muscles, the largest component of the three-dimensional resultant EMG vector was in the direction of axial rotation. Spatial focus for three-dimensional tuning curves was also less than for two-dimensional tuning curves. These results indicate the important influence of axial rotation loads on neck muscle activation.

The dominance of axial rotation may be related to musculoskeletal geometry and mechanical constraints. The constraints of this task (equal magnitude of moments in all directions) could explain why muscles would be maximally activated in the direction of axial rotation, which is generally the smallest of the moment arms. For muscles with significant moment arms in more than one principal direction, muscles could be most strongly activated in inverse proportion to the moment arm. In other words, if the muscle's moment arm vector is

$$MA = a\hat{x} + b\hat{y} + c\hat{z},\tag{9}$$

then instead of the resultant vector being aligned with moment arm (MA), the resultant vector may be aligned with the inverse vector (INV), where

$$INV = \frac{1}{a}\hat{x} + \frac{1}{b}\hat{y} + \frac{1}{c}\hat{z}.$$
 (10)

Comparison of this "inverse" moment arm vector to the three-dimensional resultant vectors shows a better correspondence for the sternocleidomastoid and splenius capitis. The mean resultant vector for the sternocleidomastoid was found to be between $35-45^{\circ}$ of the inverse moment arm vector, while the resultant vector for the splenius capitis (both surface and intramuscular) was within 20° of the *INV* vector. Correspondence between resultant vector and *INV* vector was worse for the semispinalis capitis because the axial rotation component of its resultant vector was opposite to its moment arm. In the case of the trapezius, its resultant vector was already closely aligned to its moment arm.

Although maximizing a muscle's mechanical advantage may not be a strategy used by the CNS to control neck muscles, that does not imply that musculoskeletal geometry is irrelevant to the CNS. It has been suggested that central representation may include the effects of all muscles' mechanical actions, mediated by force- and length-dependent pathways between muscles (Nichols 1994). There is evidence in the pathways of the vestibulocollic reflex of projections of vestibular neurons to groups of neck motoneurons that constitute directionally relevant synergies for head movement generation (Fukushima et al. 1979; Shinoda et al. 1994, 1997). Experiments required to detect similar synergies in spinal or cortical circuits have not yet been performed. Examining the inhibitory and excitatory pathways among neck muscles, in the context of musculoskeletal geometry, may provide more insight into CNS control strategies for this complex system.

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