

Musculoskeletal Kinematics During Voluntary Head Tracking Movements in Primate

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In this study we examined connections between vertebral motion and patterns of muscle activation during voluntary head tracking movements. A Rhesus (*Macaca mulatta*) monkey was trained to produce sinusoidal tracking movements of the head in the sagittal plane while seated. Radio-opaque markers were placed in the cervical vertebrae, and intramuscular patch electrodes were implanted to record from eight neck muscles. Videofluoroscopic images of cervical vertebral motion, and EMG (electromyographic) responses were simultaneously recorded. Experimental results demonstrated that head and vertebrae moved synchronously and that motion occurred primarily at skull-C₁, C₆-C₇ and C₇-T₁. Our findings illustrate that although the biomechanical constraints of each species may limit the number of solutions available, it is the task requirements that appear to govern CNS (central nervous system) selection of movement behaviors.

Key Words : Neck Muscles, Vertebral Alignment, Electromyography, Videofluoroscopy, Head Tracking

Nomenclature

C₁ : the 1st cervical vertebra
C₂ : the 2nd cervical vertebra
C₃ : the 3rd cervical vertebra
C₄ : the 4th cervical vertebra
C₅ : the 5th cervical vertebra
C₆ : the 6th cervical vertebra
C₇ : the 7th cervical vertebra
T₁ : the 1st thoracic vertebra

1. Introduction

Musculoskeletal mechanics indicate that each

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muscle exerts a specific directional force upon its vertebral attachments (Vasavada, Li, & Delp, 1998), which suggests that any variation in muscle activation contributing to motion of the head and neck would produce alterations in the motion of the bony vertebrae. But studies of cervical motion and neck muscle activation during voluntary head tracking in cats (Keshner, 1994; Keshner et al., 1992; Keshner, Statler, & Delp, 1997) have revealed that patterns of muscle activation can vary quite widely during apparently identical movements of the head and cervical spine.

Many neck muscles in cats have multiple functions or change their function depending on the initial position of each vertebral joint and the degree to which the joints are free to move in each of the planes of motion (Richmond, Thomson, & Loeb, 1992; Wickland, Baker, & Peterson, 1991). Runciman and Richmond (1997) cited the posi-

tion of the scapular as a determining factor for variability in the moment arm and pulling direction of certain neck muscles. Thomson, Loeb, and Richmond (1994) found that during rotation of the head with different orientations of the cervical spine, some neck muscles varied their activity levels while others maintained a consistent pattern of activation. The two groups of muscles consisted of those that were more superficial and attached to the lambdoidal crest (invariant) versus those that were lateral and caudal and attached intervertebrally or to the scapular (variable).

Keshner et al. (1997) hypothesized that increased variability in spatial patterns of muscle activity was due to cervical joint mobility that could produce alterations in the moment arms and force-generating capacity of the muscles. But they found that in only some cases could these factors account for the differences in observed muscle activation patterns. In other cases, differences in muscle activation patterns were observed without concomitant changes in muscle moment arms or force-generating potential. Muscle activation patterns were also found to differ depending on whether the animal was producing a reflex or voluntary head movement (Keshner et al., 1992).

Neural and mechanical redundancies in the head-neck complex potentially provide great flexibility for producing head and neck movements. Longer neck muscles cross many cervical vertebrae and can generate moments about both lower and upper cervical joints. Overall, the number of independently controlled muscle elements (including subdivisions of compartmentalized muscles) exceeds the number of degrees of freedom of neck motion. Our prior procedure of inducing voluntary head movements by having cats follow a moving water tube (Keshner et al., 1992, 1997) introduced a number of constraints. The cat's head position in space was dictated by the need to bring the tongue into position to lick from the tube. Head movements associated with licking further complicated the motions produced. It is also possible that the quadrupedal posture of the cat enforced a specific interaction between the neck muscles and the cervical alignment, and that

a species capable of sustaining a bipedal posture would exhibit a less complex relation between muscle activation patterns and cervical motion.

Cats have been used to understand the relationship between head movement, neck muscle activation, and cervical vertebral movements. But, use of cats has been less than ideal since the structure and function of the cat neck differ significantly from those in humans and since it is difficult to train cats to perform tasks analogous to those we humans employ. On the other hand rhesus monkey has the most similar musculoskeletal head-neck system as human's.

In this study, we have examined activity of both superficial and deeper muscles in the neck of a seated rhesus monkey in a voluntary head tracking task, and tried to understand the relationship between neck muscle activation patterns and movements of head and cervical vertebrae.

2. Methods

2.1 Behavioral training

One adult male (7.7 kg) Rhesus monkey, *Macaca mulatta*, was trained, using positive reinforcement, to perform sinusoidal (0.25 Hz) head tracking movements with an excursion of $\pm 20^\circ$ in the vertical (pitch) plane as he followed a green cross projected by a laser mirror-galvanometer system. The monkey was seated in an upright posture within a Plexiglas box that enclosed his whole body below the neck. The monkey's head and neck projected through a small opening at the top of the box, thus permitting full and free motion of the head and cervical spine. The

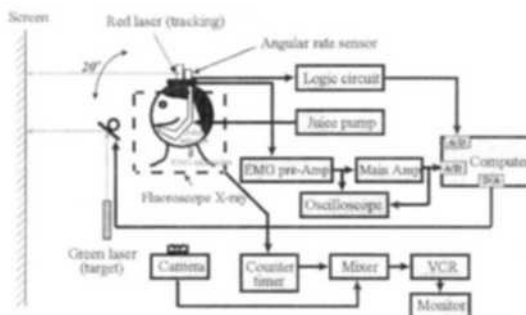


Fig. 1 Schematic diagram of the experiment

monkey was required to sit quietly and to follow the green cross for 30 sec without interruption with a red spot projected by a laser attached to a connector atop his head. A second laser attached to the same connector projected a red line that allowed us to record a video image of roll orientation of the head. Schematic diagram of the experiment is shown in Fig. 1.

2.2 Surgery

All surgical procedures were performed under halothane (1%) and nitrous oxide (80% N₂O, 20% O₂) anesthesia. Initially, a metal collar to hold the lasers and head velocity sensor was attached to the head with screws and dental acrylic. On completion of behavioral training, a second surgery was done to implant intramuscular wire electrodes in twelve muscles of the neck and to attach radio-opaque markers (tantalum washers) to spinous processes of the C₁, C₂, C₅, and C₇ vertebrae. Muscles from which we observed reliable modulation during pitch head motions included left biventer cervicis (BC), complexus (COM), sternocleidomastoid (SCM), rectus capitis posterior major (RCmaj), semispinalis cervicis (SSC), obliquus capitis inferior (OCI), and splenius capitis (SPL), and right rectus capitis posterior minor (RCmin). Electrode wires were threaded into the connector cemented on the apex of the skull.

2.3 Video motion and EMG analysis

Videofluoroscopic data were recorded (sampling rate 30 Hz) directly on an S-VHS videotape (Panasonic model AG 7750, Hi-Fi Professional/Industrial Video System). Data included a sagittal view of the monkey from occiput to the T₁ vertebrae, a video image of the green target cross, and red laser spot and line, and a videocounter signal (Thalner Electronics, Inc). During recording, the behavior of the animal was also monitored on a standard television monitor. A triaxial angular rate sensor (Watson Industries, WI) was attached to the connector on the head and sampled at 200 Hz. During each trial, eight channels of full-wave rectified, low-pass filtered (time constant 5 ms) EMG data, the target position

signal, and angular rate signals of the head were collected at 200 Hz on a Macintosh computer which also generated the sinusoidal output controlling the laser galvanometer. Signals were stored in digital form for later reduction and analysis.

A computer based video-motion analysis system (NIH Image) was employed to derive the x-y coordinates of vertebral reference points every 333 ms. Anatomical markers (i.e., tantalum washers) inserted during surgery were used to help localize the vertebrae. At least three complete data sets were collected to accompany EMG signals recorded from each muscle.

Potential crosstalk between adjacent muscles was examined by plotting the activation patterns of SPL and COM, the muscle lying directly beneath. Based on the random patterns emerging from this plot we concluded that there was no significant crosstalk. Relative intervertebral angles were obtained by calculating slope of a line between two points on each vertebral body and calculating the angle formed by the intersection of the lines of two adjacent vertebrae. A Fast Fourier Transform (FFT) was performed on the target position signal, muscle EMG responses, and vertebral position data to obtain the real and imaginary values at each frequency of head tracking. Response timing (i.e., phase = arctan [imaginary/real]) and response amplitudes (square root of the squared real and imaginary values) were then calculated. All EMG and vertebral response phases were calculated relative to position of the target. According to our phase conventions peak up position was 0°, peak down was 180°, -90° was in phase with peak downward velocity (lagging peak up position), and +90° was in phase with peak upward velocity (leading peak up position). To derive EMG response gains, all muscle amplitudes were normalized to the average muscle EMG amplitude from three trials in which the animal was encouraged to produce a vigorous head shaking threat response in the frontal plane, thereby eliciting large voluntary EMG activity. When phase responses of a muscle varied by more than 45°, EMG response gains were compared using a Welch alternate

t-test.

3. Results

3.1 Vertebral alignment

A typical pattern of motion for the skull and each vertebra demonstrates that the head and vertebrae exhibited a sinusoidal pattern closely resembling the sinusoidal shape of the target motion (Fig. 2). In most trials, the cervical spine and head exhibited small phase lags relative to peak up position of the target (Table 1). In some trials, the skull and vertebrae would lead the target, but these phases were less than 10°. Similar phases in the vertebral motions shown in Table 1 indicate that all joints are contributing to the overall motion of the head. Intervertebral ranges described in the table and in previous studies (Graf, De Waele, & Vidal, 1995; Keshner et al., 1997; Vidal, Graf, & Berthoz, 1986) suggest that the greatest proportion of the motion was made

at skull-C₁, C₆-C₇, and C₇-T₁ with smaller contributions from C₁, C₂, C₃ and C₄.

3.2 Muscle EMG patterns

Phase of the mean head pitch angular velocity signal led the target position signal by 87° and its

Table 1 Mean (±S.D.) angular excursion of each head-neck segment with respect to (wrt) the adjacent vertebra and mean phase relative to position of the visual target

	Mean Range(±S.D.)	Mean Phase (±S.D.)
Skull wrt C ₁	14°±6°	-8°±11°
C ₁ wrt C ₂	5°±2°	-7°±10°
C ₂ wrt C ₃	3°±1°	-9°±12°
C ₃ wrt C ₄	6°±2°	-10°±13°
C ₄ wrt C ₅	7°±3°	-13°±15°
C ₅ wrt C ₆	7°±2°	-11°±14°
C ₆ wrt C ₇	11°±4°	-14°±19°
C ₇ wrt T ₁	9°±3°	*

• Intervening tissue made it difficult to obtain sufficiently clear images of T₁ to accurately measure the phase of this angle.

Table 2 Mean (±S.D.) of EMG and head angular velocity response gains, phase, and coherence with respect to position of the visual target for 0.25 Hz target motion

	Gain ^a	Phase	Coherence
BC	3.9±1.5	123°±19°	0.90
COM	6.3±2.4	109°±14°	0.90
SCM	1.8±1.8	8°±39°	0.80
RCmaj	2.0±1.2	101°±45°	0.80
RCmin	1.5±0.8	78°±38°	0.68
SSC	7.2±5.4	116°±41°	0.92
OCI	1.9±0.4	99°±16°	0.95
SPL	0.7±0.3	104°±8°	0.92
Head Pitch	1.04±0.1	87°±10°	0.97
Head Roll	0.26±0.1	-33°±76°	0.66
Head Yaw	0.24±0.2	72°±64°	0.58
Target Pitch	1.57	90°	1.00

^aMuscle gains are expressed as % maximum activation/degree of target motion. Head and target gains are expressed as movement velocity/target position. Hence the "ideal" gain is 2πf or π/2 for this 0.25 Hz motion. (BC=biventer cervicis; COM=complexus; SCM=sternocleidomastoid; RCmaj=rectus capitis posterior major; RCmin=rectus capitis posterior minor; SSC=semispinalis capitis; OCI=obliquus capitis inferior; SPL=splenius capitis.)

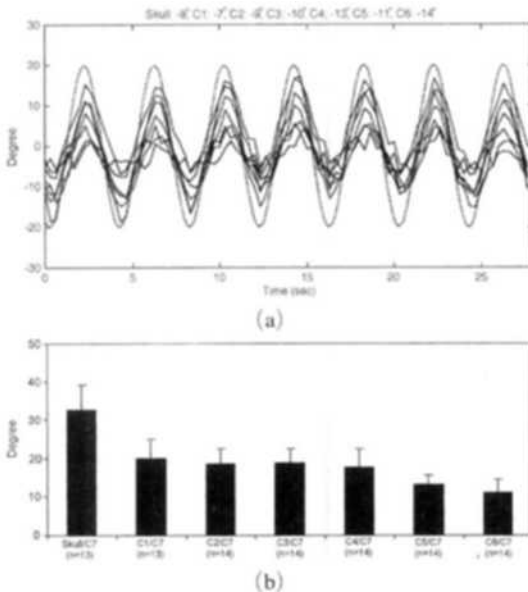


Fig. 2 Ranges of motion of the visual target (broken line), skull and each vertebra (solid lines) in a single trial plotted relative to time. The positive direction represents upward motion of the visual target. Mean phase of each segment with respect to the visual target is printed above the figure

gain of 1.04 was close to the ideal gain of 1.57 (Table 2) indicating that the monkey was accurately matching the velocity of the target in the sagittal plane. Although the head was free to move in any plane, we believe the animal tracked primarily in the sagittal plane because of the poor coherence and head angular velocity gains that were < 0.3 in roll and yaw (Fig. 3a). On most trials the muscles supported this strategy by exhibiting peak activation that slightly led upward velocity of the target. Considerable variation was present, however, and this variability even occurred across trials collected on a single day as demonstrated in the responses of SCM, a neck flexor and rotator (Fig. 3a). This muscle

was most frequently in phase with peak up position of the head, but 20% of the time responded more in phase with downward velocity. BC, a long extensor muscle, had a mean phase that led upward velocity of the head by 33° , but in four trials this lead approached 60° , while in one it was only 2° . RCmaj is primarily an extensor muscle with a short moment arm, but there were about 20% of the trials in which it responded when the head was in its flexed position (180°) rather than when moving toward extension. Overall, phases for this muscle ranged from 55° to 180° . SSC and RCmin, long and short extensor muscles, respectively, also exhibited variability (Fig. 3b). SSC responded more closely to the

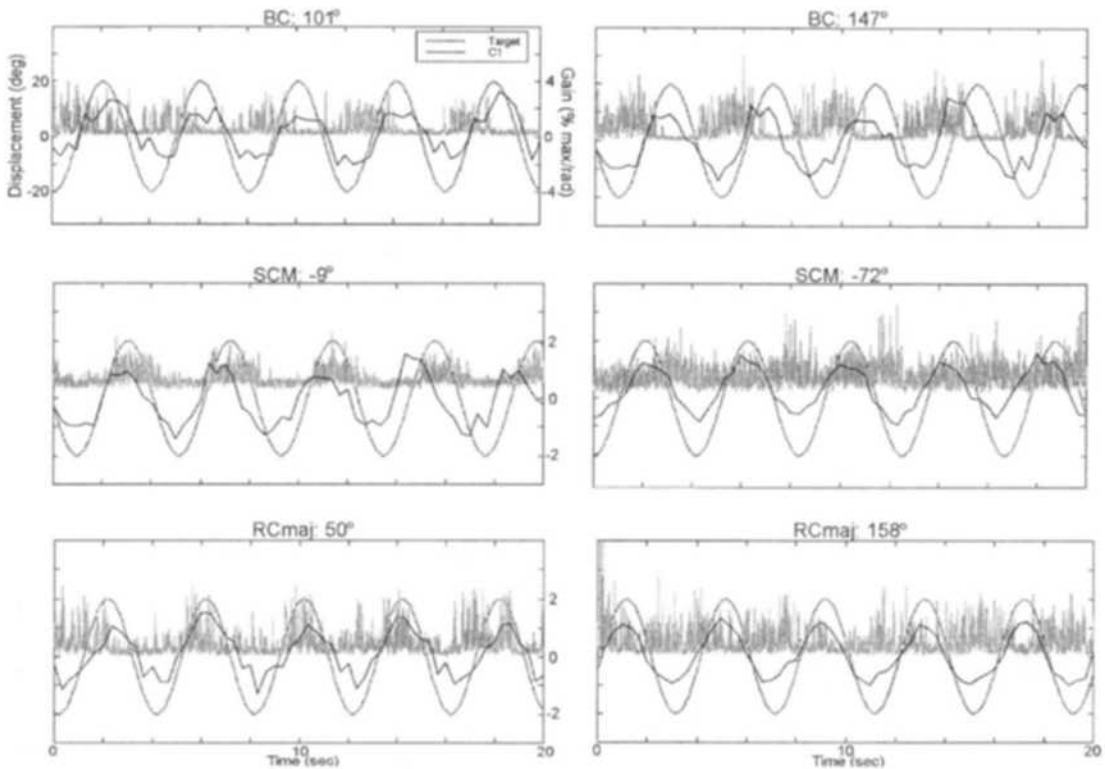


Fig. 3(a) Two trials of raw EMG data from three muscles (BC=biventer cervicis; SCM=sternocleidomastoid; RCmaj=rectus capitis posterior major) are plotted side by side to illustrate phase differences that emerged for each muscle. Responses of SCM are from two trials collected on the same day. Motion of the visual target (dotted line) and C_1 (solid line) has been overlaid for each trial. Muscle response phase with respect to peak up position of the visual target is printed above each plot. The left side y-axis represents the excursion of the target ($\pm 20^\circ$) and C_1 . The right side y-axis is the gain of the rectified EMG signal defined as the percent of the greatest EMG activation occurring during the head shaking response divided by the excursion of the target in radians ($40^\circ=0.349$ rad)

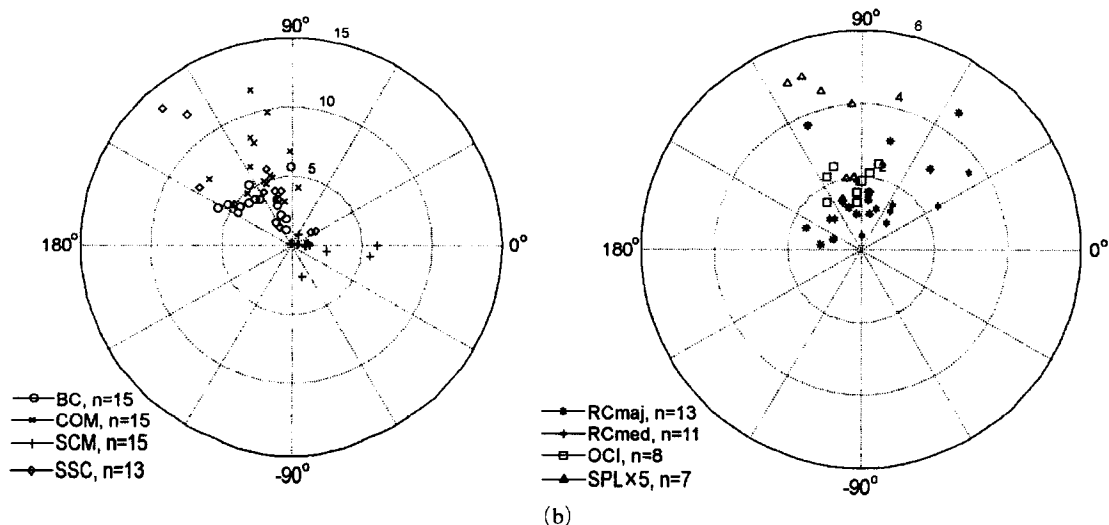


Fig. 3(b) Polar plots illustrating muscle EMG response gains with respect to the head shaking response and response phases with respect to target position. The muscle's response is plotted according to its amplitude, incrementing outward from the origin in multiples of five on the left and multiples of two on the right (SPL responses are also multiplied by five) and phase (polar angle representing the phase shift between muscle and target). Phase conventions are relative to the peak up position of the target (0°); +90° leads peak up position and -90° lags peak up position. Muscle name abbreviations are as reported in the text; n =the number of trials shown for each muscle.

peak head down position (or peak up acceleration) in some trials and to upward velocity in others. RCmin responded in phase with either peak upward velocity or peak upward position. Significant ($p < 0.05$) changes in EMG gain that were related to these shifts in phase relations were present in BC, RCmaj, and SSC (Fig. 3b). Less distinct modulation of the muscles when their phases were shifted (Fig. 3a) suggests that these muscles were not responding in their primary direction of activation (Keshner et al., 1992).

4. Discussion

Recent fluoroscopy studies of the head and neck have affirmed a correspondence in the basic arrangements of bones and muscles in humans and most quadrupeds (Graf et al., 1995; Vidal et al., 1986). Differences might exist in the range of motion of specific joints of the cervical column from one mammalian species to another, but in all of these species the skull is commonly held at the top of a vertically oriented cervical column.

This current study has clarified the selection of primary axes of cervical motion during voluntary head tracking in the rhesus monkey. Keshner et al. (1997) reported that during a head tracking task in the sagittal plane, cats moved primarily at skull-C₁ with additional motion at all cervical intervertebral joints. We have now observed primary motion to occur at the skull-C₁, C₆-C₇, and C₇-T₁ joints during this same task in rhesus. Like prior studies of active head tracking in the cat (Keshner, 1994; Keshner et al., 1997), variability in muscle response patterns did not appear to affect the vertebral motion, which, by comparison, was very consistent. Thus, motion of the cervical spine resulting from the muscular forces again emerged as an invariant parameter in this task whereas the selection of synergic muscle patterns varied.

Actions of the neck muscles are not dissimilar in cat, rhesus, and human, although there are variations in their geometry (Howell & Straus, 1933; Lockhart, Hamilton, & Fyfe, 1972; Richmond & Vidal, 1988). Semispinalis capitis is a

single muscle in the human but divides into biventer cervicis (medially) and complexus (laterally) in both cat and rhesus. Sternocleidomastoid, a single muscle in humans, is comprised of two muscles, sternomastoideus and cleidomastoideus, in cat and rhesus. In both rhesus and human, splenius capitis and splenius cervicis are one muscle stretching from the ligamentum nuchae to the upper five thoracic vertebrae (Lockhart et al., 1972; Howell & Straus, 1933). The cat has a separate splenius cervicis muscle located caudolaterally and linking thoracic vertebrae T₃-T₆ with the upper cervical vertebrae. Rectus capitis posterior is divided into three parts (major, medius, and minor) in the cat (Selbie, Thomson, & Richmond, 1993), but only two divisions (major and minor) have been identified in humans and rhesus (Lockhart et al., 1972; Howell and Straus, 1933). Obliquus capitis inferior appears to be similar across the species, as is semispinalis cervicis, an intervertebral muscle that runs between the vertebral spines. But although the musculoskeletal system varies across species, remarkable similarities have emerged in the organization of postural responses that are determined by stance configuration rather than being species specific (Dunbar et al., 1986; Macpherson et al., 1989).

Variability in muscle selection during the head tracking task has been a consistent finding. In the cat, each animal was observed to exhibit its own unique strategy for voluntary muscle selection (Keshner et al., 1992). In this study, the head was not fully constrained in the sagittal plane and the rhesus did have the opportunity to incorporate roll and yaw components into the pitch head extension movements. However, this did not appear to be the explanation for the variable muscle patterns because these persisted even when we compared trials with essentially identical head postures. It is interesting to speculate that animals may be able to use different behavioral strategies to track highly predictable target motions. In addition to visual following, non-visual predictive generation of head movements would likely suffice to follow the target with sufficient accuracy to obtain a reward. If visual and non-visual

predictive tracking were mediated by neural circuits that connected with neck muscles through different synergic patterns to generate head movements, then switching between control strategies would produce the variations in muscle patterns we observed. Variability in muscle responses did not seem to affect vertebral motion even though the muscles are the primary actuators of the joint movement.

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