RESEARCH ARTICLE

K. D. Statler · E. A. Keshner

Effects of inertial load and cervical-spine orientation on a head-tracking task in the alert cat

Abstract Simultaneous video-fluoroscopic and neck muscle EMG data were recorded from one cat performing ±15° sinusoidal (0.25 Hz) head-tracking movements in the sagittal plane in a standing body posture with two initial neck orientations and four inertial loads. Radio-opaque markers were inserted into the anterior/posterior and lateral aspects of the occipital ridge and C_1-C_7 to measure vertebral displacement. Kinematic data were analyzed, and a computer model was applied to the data to characterize the limits of movement in the cervical spine and to estimate the moment arms of the neck muscles at different orientations of head-neck movement. For each initial neck orientation, the cat utilized a distinct set of vertebral alignments, relative joint movements, and muscle-activation patterns to achieve the same movement outcome. As inertial load increased, vertebral alignments and relative joint movements were constant with a vertically oriented neck but differed when the neck was more horizontally oriented. Different muscle-activation patterns were used to maintain the same kinematic pattern with increased inertial loads. Some muscle EMG response gains (rectus capitis major and splenius capitis) increased with increasing mass, while others (biventer cervicis and occipitoscapularis) demonstrated an initial increase and then a plateau. EMG phases were not affected by changing the mass of the system but were affected by changing neck orientation. The model predicted that muscle moment arms would vary little for the different vertebral alignments, suggesting a robust biomechanical system minimally compensates for small changes in task geometry.

Keywords Neck muscles · Electromyography · Cinefluoroscopy · Posture · Biomechanical model

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Introduction

The effect of posture on muscle patterning and efficiency has been described for both bipeds and quadrupeds (Dunbar et al. 1986; Henry et al. 2001; Macpherson et al. 1989). Runciman and Richmond (1997) cited body posture as a determining factor for variability in the moment arm and pulling direction of certain neck muscles. Thomson et al. (1994) found that during rotation of the head with different orientations of the cervical spine, some neck muscles varied their patterns of activity, while others maintained a consistent pattern of activation. Keshner (1994) observed different patterns of neck-muscle activation in cats that were standing or prone.

It is not clear whether these postural effects are due to CNS selection of preferred muscle-activation patterns as a result of some internal geometric configuration (Lestienne et al. 2000). Muscle-activation patterns may be governed strictly by the demands of the mechanical task, including the mass of the system and the constraints imposed by the position of the thorax relative to the head (Richmond et al. 1992).

A tensorial model using the Moore-Penrose generalized inverse (Pellionisz and Peterson 1988) incorporated knowledge of vestibular pathways and simple joint geometry to predict experimental data from cat neck muscles. But although this model was accurate when predicting a well-defined input-output relationship, such as observed with the vestibulocollic reflex, it was not robust enough to explain how the voluntary tracking system operated. More complex models obviously are

required to account for the neural programming observed in more complex systems, such as the voluntary head-tracking system (Peterson et al. 1989). Statler and colleagues (1994, unpublished dissertation, 2001, Graf et al. 1997) developed a biomechanical model of the cat's neck to make predictions about muscle activation and selection while considering the complexity of the head-neck system. We applied this model in a previous study (Keshner et al. 1997) in an attempt to correlate neck muscle-activation patterns during a head-tracking task with mechanical parameters, such as cervical joint motion, force-length properties, and the moment arm of the muscles. But neck position was poorly controlled, and there were no consistent associations across all of the recorded muscles.

In the current study, we have more carefully controlled the orientation of the cervical spine during a constrained head-tracking task, as well as altered the passive mechanics of the system by applying an incremental load to the head. We employed simultaneous fluoroscopic and EMG measures to determine whether different vertebral orientations and muscle activations were used to make the same head-neck movement with different inertial loads. Data were analyzed with the biomechanical model to quantify muscle-mechanical parameters and to clarify whether different muscle-activation patterns were the result of shifts in the internal muscle properties associated with specific orientation or mass of the head and neck.

Methods

Behavioral training

A female adult cat, 2.5 kg, was the subject in these experiments. The cat was trained, using positive reinforcement, to perform sinusoidal (0.25 Hz) head-tracking movements as it followed a motor-driven water spout (drinker) with an excursion of $\pm15°$ in the vertical (pitch) plane (see Keshner et al. 1992, Fig. 1). The drinker was positioned directly in front of the animal. The cat was required to stand quietly and to drink without interruption for 10–20 trials lasting 20 s each. The cat was tested while suspended in a soft harness that permitted comfortable standing.

We investigated the effect of altering head mass and cervical-spine orientation on muscle activation. The animal was required to perform the tracking task while standing with two initial neck orientations. The task was performed with a more vertically oriented neck, where the neck was oriented 90° from horizontal. The task was also performed with a more horizontally oriented neck, where the neck was oriented 45° from horizontal. The task was performed with no additional weight or with 100 g, 200 g, and 500 g weights secured to the head. The mass of the head was estimated at 200 g (Hoy and Zernicke 1985).

Surgery

All experiments followed the principles of laboratory animal care set forth by the National Institutes of Health in the guide for care and use of laboratory animals and were approved by the Institutional Animal Care and Use Committees at Northwestern University and the Veterans Administration. Surgical procedures were performed under halothane (1%) and nitrous oxide (80% N2O, 20% O2) anesthesia to prepare the animals for chronic recording. On completion of behavioral training, radio-opaque markers (stainless-steel screws – 1.5 mm) were anchored in the spinous or transverse processes of the first, second, fourth, sixth, and seventh cervical and first thoracic vertebrae, and the occipital protuberance (head). Intramuscular EMG electrodes, consisting of stainless-steel wires lying along a silastic sheath (Microprobe, Inc.), were stitched with 3–0 mersilene suture to the connective tissues around the muscles through a dorsal midline incision. Electrode wires were then threaded into a connector cemented on the skull of each cat. Implanted muscles included biventer cervicis (BIV), complexus (CPX), splenius capitis (SPL), occipitoscapularis (OCC), and rectus capitis major (REC) (see Richmond and Vidal 1988 for a detailed explanation of muscle anatomy). All muscles were implanted on the right side except BIV, which was implanted on the left side. When all recording was completed, the animal was sacrificed with an overdose of pentobarbital sodium and decapitated. Post mortem examination of the neck was done to check the position of the radio-opaque markers and EMG patch electrodes.

Video motion and EMG analysis

Cinefluoroscopic data were collected (sampling rate 60 Hz) directly on to a VHS videotape (Mitsubishi, Inc.) and included a sagittal view of the cat from occiput to thoracic vertebrae, the arm of the drinker, and a videocounter signal (Thalner Electronics, Inc.). During recording, the behavior of the animals was monitored on a standard television monitor. A position signal for the drinker was recorded both on-line and on the videotape to temporally correlate movement of the head and neck and EMG data.

A computer-based video-motion analysis system (Automatix, Inc.) was employed to derive the x-y coordinates of each anatomical marker and the drinker position signal every 300 ms. EMG signals (sampling rate 100 Hz) were differentially amplified, full-wave rectified, and filtered (time constant 3–10 ms). Signals were stored in digital form on a computer for later reduction and analysis.

An FFT performed on the position signal, muscle EMG responses, and vertebral-position data provided real and imaginary values at 0.25 Hz from which response orientations (i.e., phase=arctan imaginary/real) and response amplitudes (square root of the squared real and imaginary values) could be calculated. Differences in the EMG-response magnitudes were examined across inertial load and starting neck orientation. Vertebral-position data could not be compared between trials because the camera focal length changed as the camera was repositioned on most trials. All EMG and vertebral-response phases were calculated relative to the position of the drinker, such that peak up position was 0° and peak down position was $\pm180°$. A phase of 90° lagged peak up position and corresponded to peak downward velocity. A phase of $-90°$ was phase leading of peak up position and corresponded to peak upward velocity. Inertial mass of the head was increased by securing 100 g, 200 g, and 500 g brass weights to the connector on the skull.

Biomechanical analysis

A computer graphics-based model that focused on accurate characterization of isometric moment-generating characteristics of the head-neck musculoskeletal system was constructed (Software for Interactive Musculoskeletal Modeling, Delp and Loan 1995). This static model consists of four components: bone geometry, muscle anatomy, muscle force-generating parameters, and joint kinematics. The surfaces of the skull, C_1-C_7, and T_1 were digitized from a single cat cadaver, with the head in the physiological rest position (Graf et al. 1995; Vidal et al. 1986) and displayed on a computer-graphics workstation. Muscle paths of rectus capitis, complexus, biventer cervicis, occipitoscapularis, and splenius capitis neck muscles were defined using bony landmarks as references. The origin and insertion of each muscle were defined in five cats, as well as any intermediate wrapping points necessary to accurately represent the muscle paths as a series of line segments. A

generic musculotendon model (Zajac 1989) was scaled by a muscle's maximum isometric force based on physiologic cross-sectional area, optimal muscle-fiber length, pennation angle, and tendon slack length to determine the force-length relation of that specific muscle. The muscle's maximum isometric force was based on its physiological cross-sectional area (Wickland et al. 1991). Optimal muscle-fiber length was measured in three cats. The cats were allowed to go into rigor, while the head and neck were held in stereotaxic posture (Graf et al. 1995; Vidal et al. 1986), to fix fiber and sarcomere length. Sarcomere lengths were measured from biopsies of small bundles of rigored fibers, as described by Selbie et al. (1993). These measurements were used to normalize the fiber lengths measured in stereotaxic posture to a sarcomere length of 2.5μm (optimal length in Herzog et al. 1992). Pennation angle and tendon-slack length was measured in five cats. Motion of the neck in the sagittal plane was defined by revolute joints allowing rotation at Skull-C_1 and between each of the cervical vertebrae. The axis of rotation was calculated for each joint using rigid body techniques (Spiegelman and Woo 1987) applied to vertebral position data from four cats in a range of voluntarily assumed head-neck postures. The tracking movement for each of the postures was modeled by matching the position of the model to positions of the cat's cervical vertebrae observed in the cinefluoroscopic recordings. The coordinates of markers in T_1, C_7, C_4, C_2, C_1, and the Skull were matched for five positions distributed from peak head up to peak head down during the tracking movement. In each case, the model was placed, with any required rotations or translations so that the position of T_1 in the model corresponded to the digitized marker positions of T_1 from the experimental cinefluoroscopic recordings. The T_1-C_7 joint was then varied in the model until the position of C_7 in the model matched the digitized position of C_7 from the experimental data. The procedure was repeated for markers in C_4, C_2, C_1, and the Skull. At this point, the position of the model was the same as the position of the cat digitized from the cinefluoroscopic recording. The model was then used to determine the relative motion of each vertebral joint for the motion from peak head up to peak head down. The musculotendon length, muscle-fiber length, moment arm, force, and moment that each muscle can develop for any body position observed during the tracking movement could be estimated by combining the musculotendon models with the musculoskeletal geometric data and the skeletal kinematic model.

Results

Effects of system mechanics on muscle-activation patterns

Both neck orientation and increased inertial mass of the head had an effect on muscle activation (Fig. 1). EMG response gains for REC, SPL, and BIV were about 2–3 times larger with a horizontally oriented neck than with a vertical neck orientation. Response gains for CPX, however, were about 1.5 times larger with a vertical neck orientation than for the horizontally oriented neck. OCC gains were similar in both neck orientations.

We expected that increasing the mass of the cat's head would produce increased EMG response gains, but this result was not consistent across muscles. REC exhibited constant response gains regardless of the mass added to the head when the neck was more vertically oriented. With a horizontal neck orientation, an initial peak rise from 0.4 to 0.8 occurred with the addition of 100 g to the head, but response gains dropped to 0.6 when 200 g were placed on the head and stayed there even with additional mass. With a more vertically oriented neck, response gains of CPX decreased as the added mass was increased from 0 g to 100 g and then remained fairly constant as the
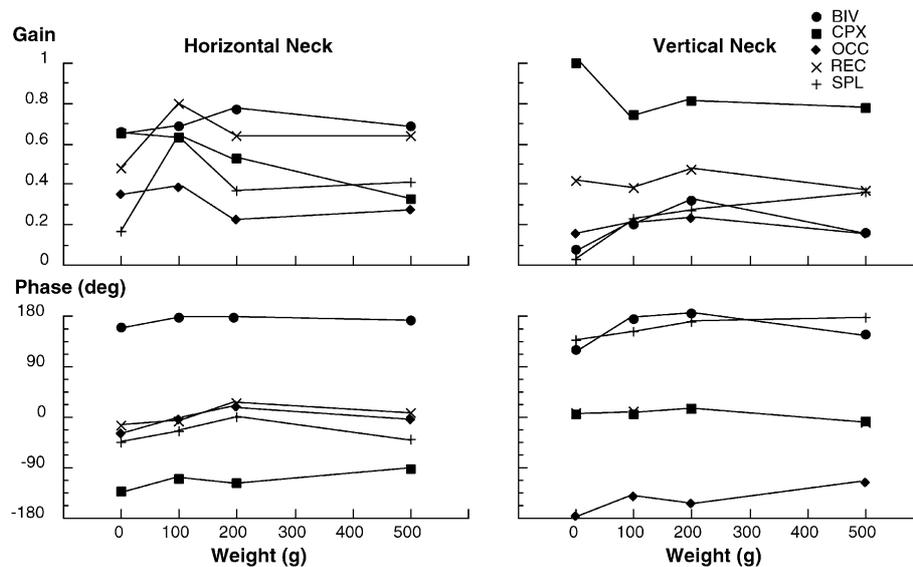

Fig. 1 Bode plots of EMG gain and phase responses for each muscle with respect to the drinker in the two cervical-spine orientations with incrementing weights. Four weights were added to the head when the neck was horizontally (*left plots*) and vertically (*right plots*) oriented. Gains of the EMG responses may be compared across all trials of each muscle. The mass of the head was estimated to be 200 g (Hoy and Zernicke 1985). Increased EMG gains without phase changes were expected with increased inertial load (Lestienne 1979). With a horizontal neck orientation, muscle gains increased as weight was initially added then remained constant or decreased with additional weight increases. Muscle phase was largely unaffected by weight increases. With a vertical neck orientation, muscle gains increased only slightly, remained constant, or decreased with weight increases. Muscle phase was largely unaffected by weight increases. BIV= biventer cervicis; CPX= complexus; OCC= occipitoscapularis; REC= rectus capitis major; SPL= splenius capitis
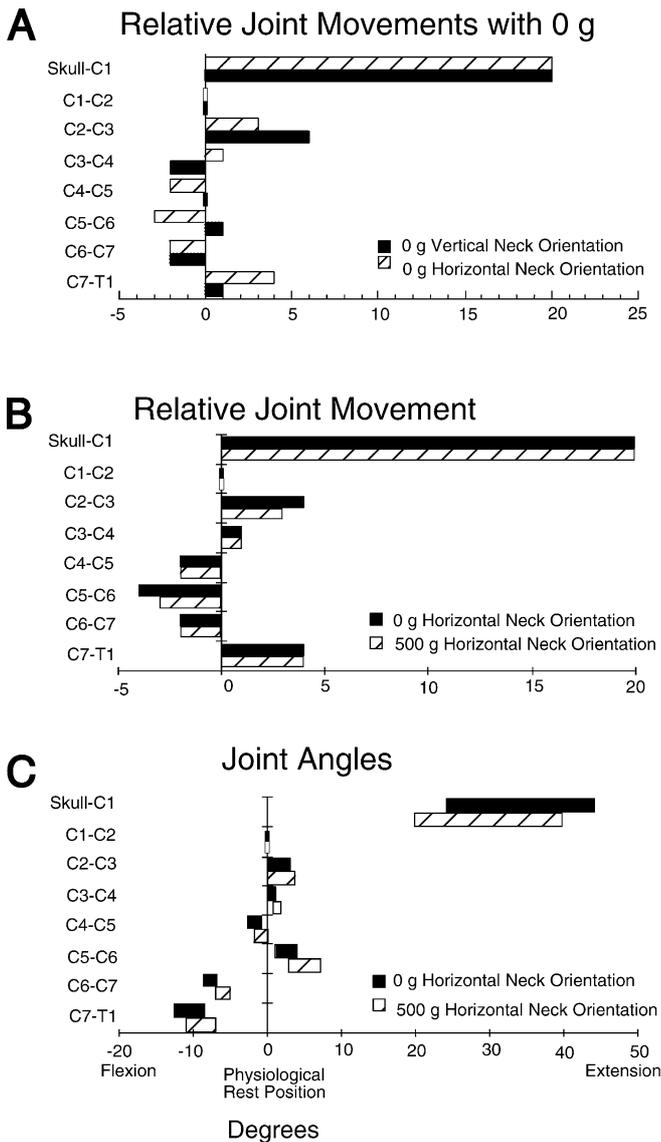
A Relative Joint Movements with 0 g

(bar chart — vertical axis joints Skull-C1, C1-C2, C2-C3, C3-C4, C4-C5, C5-C6, C6-C7, C7-T1; horizontal axis -5 to 25)

■ 0 g Vertical Neck Orientation
▨ 0 g Horizontal Neck Orientation

B Relative Joint Movement

(bar chart — vertical axis joints Skull-C1, C1-C2, C2-C3, C3-C4, C4-C5, C5-C6, C6-C7, C7-T1; horizontal axis -5 to 20)

■ 0 g Horizontal Neck Orientation
▨ 500 g Horizontal Neck Orientation

C Joint Angles

(bar chart — vertical axis joints Skull-C1, C1-C2, C2-C3, C3-C4, C4-C5, C5-C6, C6-C7, C7-T1; horizontal axis -20 Flexion, 0 Physiological Rest Position, 50 Extension)

■ 0 g Horizontal Neck Orientation
□ 500 g Horizontal Neck Orientation

Degrees

Fig. 2A–C Relative joint movements and range of joint angles during the tracking motion. **A** Relative joint movements in both initial neck orientations with no additional inertial load. The movement at each joint was determined by applying the model to the experimental data. 0° is the physiological rest position. Extension is represented as a positive value. Flexion is represented as a negative value. Joint movements are shown for tracking movement from head down to head up. In the horizontal neck orientation (*hatched bars*), the tracking motion was accomplished with a large extension movement at Skull-C$_1$, extension movements of similar magnitude at the upper and lower cervical joints, and flexion movements at the middle cervical joints. In the vertical neck orientation (*solid bars*), the tracking motion was accomplished with a large extension movement at Skull-C$_1$, extension movements that were larger in the upper cervical spine than in the lower cervical spine, and flexion movements in the middle cervical spine. Adding inertial load did not have any effect on the kinematics of the vertically oriented neck; thus subsequent graphs will only demonstrate changes in the horizontally oriented neck. **B** Relative joint movements in a horizontally oriented neck with 0 g (*solid bars*) and 500 g (*hatched bars*) additional inertial load. The cat used smaller magnitude flexion movements at C$_2$-C$_3$ and smaller magnitude extension movements at C$_5$-C$_6$ to complete the task with added inertial load. **C** Joint angles in a horizontally oriented

added mass was increased to 500 g. Gains also decreased from 0 g to 500 g in CPX with a horizontally oriented neck.

Response gains of BIV increased as weight was increased from 0 g to 200 g and then declined slightly as the added mass was increased to 500 g (to about the same gain value as for 100 g) for both vertical and horizontal neck orientations. In OCC, response gains increased as the added mass was increased from 0 g to 200 g and then remained fairly constant as the additional mass was increased to 500 g with a more vertically oriented neck. When the neck was more horizontally oriented, response gains did not shift until the added mass was increased to 200 g. Gains then decreased and remained constant with additional increases in mass. SPL increased its gain as the added mass was increased from 0 g to 500 g for both neck orientations.

EMG response phases for each muscle were not affected by increasing the inertial mass of the system, but except in REC, a short suboccipital muscle that always responded near peak upward position of the head (0°), response phases were affected by changing the orientation of the cervical spine (Fig. 1). Phase responses of BIV were strongly related to peak head down position (180°) with a horizontal neck but demonstrated small phase shifts toward downward head velocity with a vertical neck. CPX exhibited a phase shift from peak up position (0°) with a vertical neck to peak upward velocity (-135°) with a horizontal neck.

With a vertical neck, SPL responded in phase with near peak downward velocity (135°) but shifted its response to peak upward velocity (–45°) when the neck was more horizontally oriented. OCC phase shifted from a response matched to peak downward position (–180°) with a vertically oriented neck to a response nearing peak upward position (22.5°) when the neck was horizontally oriented.

Effects of system mechanics on joint kinematics

Altering the inertial mass of the head did not change the kinematics of the movement when the neck was initially vertically oriented. Altering the inertial mass of the head did change the kinematics of the movement when the neck was initially horizontally oriented. Thus, the range of joint angles in a task requiring more force output

neck with 0 g (*solid bars*) and 500 g (*striped bars*) additional inertial load. While the magnitude of the joint movement at each joint is quite similar, the range of values that each joint moves through differs. Less flexion at the lower cervical vertebral joints occurred with additional inertial load so that the spine was in a more vertical orientation through the tracking movement. With the more vertical spine orientation, amount of head (Skull-C$_1$) extension required to complete the task was reduced, although the magnitude of the Skull-C$_1$ movement was the same

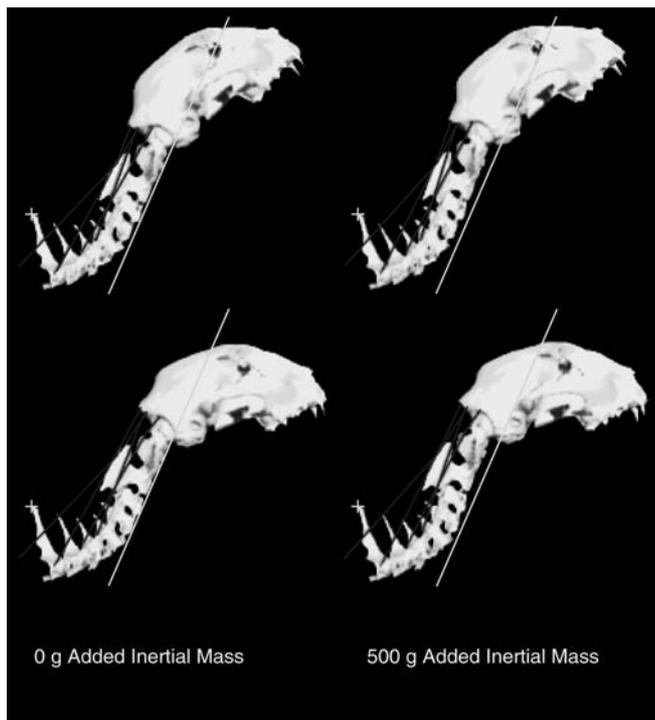0 g Added Inertial Mass   500 g Added Inertial Mass

Fig. 3 Model representation of the top (nose up) and bottom (nose down) of the head-tracking movement for 0 g (*left figures*) and 500 g (*right figures*) additional inertial loads in the horizontal neck orientation. The *cross* (+) located above the T_1 spinous process, and the *solid white line drawn* through the skull are for ease of comparison. The *grey lines* illustrate the origins and insertions of the Occipitoscapularis, Biventer Cervicis, Complexus, and Rectus Capitis Major muscles. The tracking movement was successfully completed with two different sets of relative joint movements. With the addition of inertial load, the amount of extension at the lower cervical joints was increased so that the amount of Skull-C_1 extension required was reduced

depended more upon initial postural orientation than upon the inertial loading.

The changes in relative vertebral movements with increased inertial mass were dependent upon the initial starting neck orientation. The relative vertebral movements used to accomplish the tracking task for vertical or horizontal neck orientations with no additional inertial load (0 g) were estimated from the model (Fig. 2A). When the neck was *vertical*, the cat used 20° of extension at Skull-C_1, 6° at C_2-C_3, 1° at C_5-C_6 and 1° at C_7-T_1, and 2° of flexion at C_3-C_4 and C_6-C_7 to move from peak head down to peak head up. When the neck was *horizontal*, the cat used 20° of extension at Skull-C_1, 2° at C_2-C_3, 1° at C_3-C_4 and 4° at C_6-C_7, and 2° of flexion at C_4-C_5, 3° at C_5-C_6 and 2° at C_6-C_7 to move from peak head down to peak head up.

When the inertial load was increased with a *vertical* neck orientation, minimal increases (<1°) in flexion at C_7-T_1 and increases in extension at C_6-C_7 were observed. The changes in kinematics when the neck was horizontal and the inertial load was increased from 0 g to 500 g were more significant. When the inertial load was increased

(Fig. 2B), smaller flexion movements occurred at C_2-C_3, and smaller extension movements occurred at C_5-C_6 so that less individual joint movement was required to complete the tracking task.

Both the position of the joints (Fig. 2C), as well as the amount of rotation at each joint is necessary to describe the movement during the tracking task. The position of the joints during the tracking movement differed with increased inertial load. These changes in joint position enabled the cat to accomplish the tracking task with a less extended neck and a more vertical cervical alignment when the inertial load was increased. The neck orientation can be described by examining the range of angles at each joint during the tracking movement (Fig. 2C). Rotation of the T_1 vertebrae in the model was required to match the initial T_1 marker position when the inertial load was increased. This corresponds to movement of vertebral joints caudal to T_1 and was modeled by placing the T_1-T_2 joint in a position 4° more extended for the 500 g inertial load than for the 0 g inertial load. Less flexed joint positions at C_7-T_1, C_6-C_7 and C_4-C_5 and more extended joint positions at C_5-C_6, C_3-C_4 and C_2-C_3 were used to accomplish the same tracking movement with increased inertial loads (Fig. 2C). This resulted in a more vertical spine orientation with increased inertial load.

The model can be used to easily visualize the different neck alignments used to accomplish the tracking task with added inertial load. Model representations of the top (nose up) and bottom (nose down) of the head-tracking movement for 0 g (left figures) and 500 g (right figures) additional inertial loads in the horizontal neck orientation are shown in Fig. 3. The cross above the T_1 spinous process and the solid white line drawn through the skull are for ease of comparison. The tracking movement was successfully completed with two different sets of relative joint movements. For an added inertial load, the cervical spine was realigned closer to vertical. By altering the set of joint angles used to complete the task, the neck was maintained in a more vertical orientation throughout the tracking motion. A corresponding set of vertebral rotations was chosen to complete the movement with the set of joint angles that used as vertical a spinal orientation as possible within the constraints of the task. The moment required to support the head and added load was reduced by 12% because of the more vertical neck orientation.

Biomechanical modeling of a head-tracking task

We modeled how the moment-generating ability of the muscles changed between more vertical and more horizontal starting neck orientations in the standing posture and also how the moment-generating ability changed with the anatomical adjustments the cat made when the inertial load of the head was increased (Fig. 4). We found that the muscle moment arms for any of the muscles varied little for the two starting neck orientations. The moment arms varied between starting neck orientations by 2–20%. These changes were less than 0.2 cm and were always less
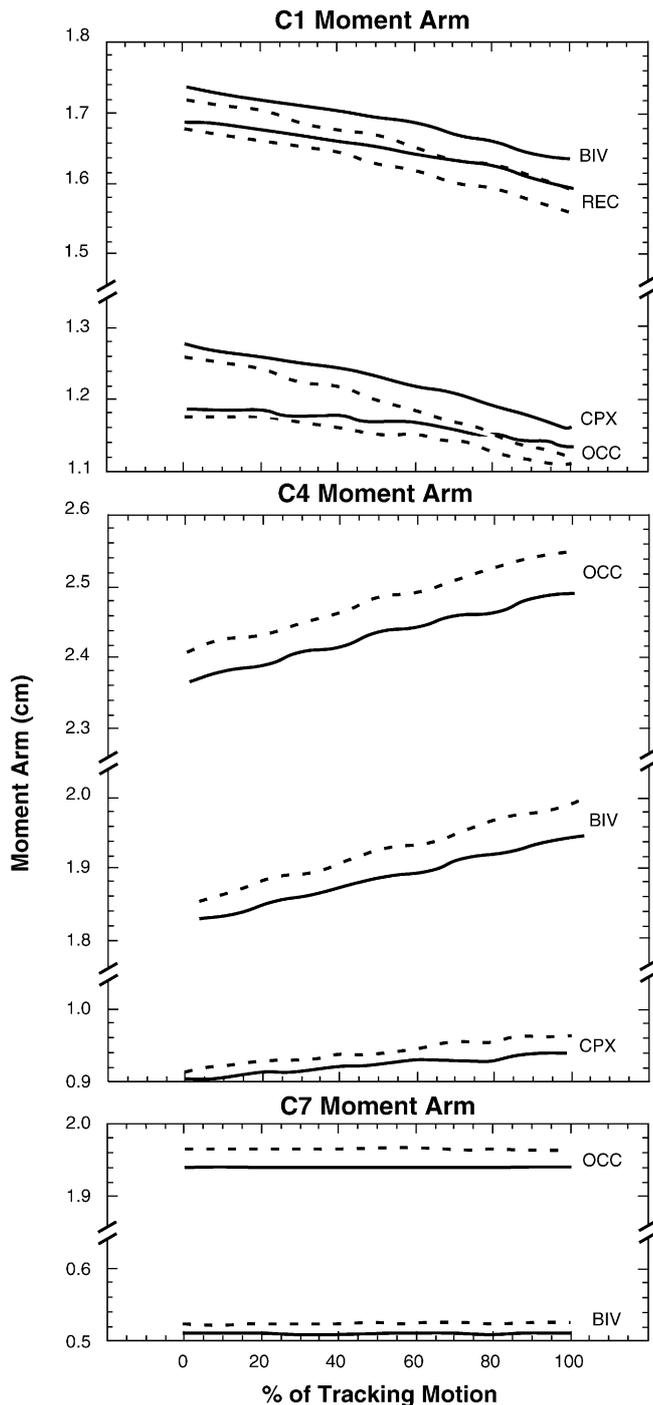
C1 Moment Arm

C4 Moment Arm

C7 Moment Arm

Moment Arm (cm)

% of Tracking Motion

Fig. 4 Three panels show the moment arms for three muscles for the upper (Skull-C_1), middle (C_3-C_4), and lower (C_6-C_7) cervical joints in a horizontally oriented neck with 0 g (*solid lines*) and 500 g (*dashed lines*) added inertial mass. All moment arms (muscles identified on *right* of graph) at the upper cervical joint decrease slightly with additional inertial load. The moment arms of occipitoscapularis (OCC), biventer cervicis (BIV), and complexus (CPX) increase at the middle cervical joint with increased inertial load. The moment arms of OCC and BIV increase at the lower cervical joint with increasing inertial load. The force-generating potential of the muscles changed little with added inertial load since the muscle lengths and operating ranges on the force-length curve were very similar for the two cases. The differing alignment of the cervical spine during the tracking task with increasing inertial load increased the moment-generating potential of the muscles while maintaining the animal's ability to successfully track the drinker. REC=rectus capitis major

than the amount a given moment arm changed during the course of a cycle from peak head up to peak head down. These moment arm differences are too small to account for differing muscle activations between the two starting neck orientations. When the movement was made from a more vertical starting orientation, the muscle moment arms did not differ as the inertial load of the system increased. We infer that because the movement was made with the same relative joint movements with increased inertial load, the geometry of the head neck system, and the muscle moment arms remained the same as inertial load increased. These inferences were confirmed by the model. When the neck was more horizontally oriented, different relative joint movements were used to complete the tracking task as inertial load increased (Fig. 3).

These differing alignments of the cervical spine resulted in small changes in muscle moment arms with increasing inertial load (Fig. 4). As inertial load increased, muscle moment arms at the uppermost cervical joints decreased by up to 1.5%. Moment arms for BIV, CPX, OCC, and REC about the Skull-C_1 joint (Fig. 4, top panel) all decreased. The moment arms about the middle cervical joints increased by 1–3%. The moment arms for BIV, CPX, and OCC about the C_3-C_4 joint (Fig. 4, middle panel) all increased. The moment arms for BIV and OCC about the C_6-C_7 joint (Fig. 4, bottom panel) both increased. The changes in the moment arms of the muscles will decrease the moment-generating potential about the upper cervical joint while increasing the moment-generating potential of the muscles about the middle and lower cervical joints. The overall effect is to increase the net moment-generating potential of the muscle with added inertial load.

In addition to looking at muscle moment arms, we examined the capability of each muscle to produce force by determining the operating ranges of the muscle on the isometric force-length curve for the vertical and horizontal initial neck orientations. By looking at the similarity of the operating ranges, we can determine how altering the orientation of the neck affects the ability of the muscle to produce force. Muscles operating primarily in the plateau region of the force-length curve will be able to produce similar forces for postures throughout the tracking movement. Muscles operating on the ascending region of the curve will not be capable of generating as large a force at the shorter muscle lengths occurring for postures near peak position up as they will for the longer muscle lengths occurring for postures near peak position down in the tracking movement. If a muscle operates over a similar region of the force-length curve for the different experimental cases, it will be capable of producing similar forces for each of the cases. The muscle-operating ranges did not vary with inertial load for a more vertically starting neck orientation. When the movement was made from a more horizontal neck orientation, the muscles operated over a similar range of lengths, but these lengths slightly increased as inertial load increased (0.1 cm).

Throughout the experiment BIV, OCC, REC, and SPL operated primarily around their plateau region. CPX

operated primarily along the ascending limb of the curve, near the plateau region. The ability of these muscles to produce force varied little across postures of the head and neck during the tracking movement, and their force-producing capability was similar in both starting neck orientations. Only the ability of CPX to produce force declined during the tracking motion with a 25% decrease in force-producing potential for postures near peak position up as compared to peak position down. Although changes in the moment-producing potential of the muscles are in the right direction, muscle moment-generating potentials between the two conditions are too small to account for the different muscle-activation patterns.

Discussion

Previous descriptions in the literature identify changes in muscle selection and patterning that appear to be associated with overall body posture (Dunbar et al. 1986; Keshner 1994; Macpherson et al. 1989), the goal of the neural task (Keshner et al. 1992), or specific segmental alignments (Runciman and Richmond 1997; Thomson et al. 1994). In this study, we examined whether these patterns were the result of biomechanical changes that altered the functional capacity of specific muscles. We found that orientation of the cervical spine was a significant variable in determining both the range of cervical joint motion and the amplitude (gain) and timing (phase) of the neck-muscle responses.

Contribution of intrinsic muscle mechanics

Changing the orientation of the neck did not lead to a large change in the moment arms of any of the five muscles we examined. As observed in our earlier study (Keshner et al. 1997), differences in muscle moment arms that did occur were too small to account for the different muscle-activation patterns. The muscles also operated over similar ranges of the force-length curve for both neck orientations. It would appear that the functional capacity of the muscles studied here was not compromised by the small changes in head-neck geometry required in this task, from which we must infer that the mechanical properties of the muscles were not the relevant parameters generating the switch between muscle-activation patterns.

Contribution of passive mechanics

When tracking began from a more vertical neck orientation, increased inertial load on the head did not affect the muscle moment generated. In the vertical orientation, the task was accomplished with similar vertebral alignments and intervertebral joint movements whether or not inertia was increased. Thus, there was no need for muscle moment arms and moment-generating potentials to vary

as inertial load was increased. When the tracking movement initiated with a more horizontal neck orientation, however, the cat used different vertebral alignments and relative joint movements as the inertial load was increased. These adjustments to the vertebral alignments and changes in the intervertebral joint movements resulted in changes in the muscle moment arms as well as slightly longer (1–2%) working musculotendon lengths as inertial load was increased. The changes in muscle moment arm and force-generating potential led to increased moment production with increased inertial load.

Disparity between the two orientations can be explained by the system mechanics. With a vertical neck orientation, the neck was oriented close to the earth vertical, and the moment arm between gravity and the head and neck was small. The moment required to counteract the pull of gravity on the head, therefore, was also relatively small. The weight of the head, even with additional inertia, could largely be supported by the bony structure of the spine when vertically oriented, or with a relatively small muscle moment to counteract the torque applied to the head by gravity. The neck remained mostly vertical throughout the tracking motion, so the force demands on the muscles were not greatly increased at any point in the tracking path. Consistent force demands would mean that changes to the vertebral orientation were largely unnecessary.

When the tracking task was performed with a horizontal neck orientation, the moment arm between gravity and the head and neck was larger so the moment required to counteract the pull of gravity on the head needed to be larger. Additional inertia in this orientation would further increase the moment required to support the head. One option for compensating for the increased moments demanded in this orientation would be to use a more vertical orientation of the cervical spine thereby reducing the gravitational moment arm. Indeed, the corrective relative joint movements and cervical joint angles reduced the moment due to gravity that must be overcome to hold up the head. The adjustments in relative joint movements and cervical joint angles that were observed with increased inertial load in the horizontal orientation resulted in small increases in the muscle moment arms without decreasing the force-generating capacity of the muscles, thus the moment-generating capacity of the muscles was increased.

Although tracking the drinker with a horizontal neck was more mechanically demanding than tracking with a vertical neck, both tasks were relatively easy for the musculoskeletal system to accomplish. The moment arms and force producing capability of the muscles were similar for the four experimental conditions (i.e., vertical- and horizontal-oriented neck with and without additional inertia); therefore, comparable joint moments could be produced regardless of the orientation of the neck. Consequently, we saw no change in joint kinematics or muscle-moment generating capacity with added inertial weight for a vertical neck orientation, and only small changes with a horizontal neck orientation.

Muscle-activation patterns

With changes in cervical orientation, both timing and amplitude of the muscle responses were changed. With increased inertial loading, muscle response timing was unchanged, but response gains were observed to both increase and decrease. This observation of a stepwise change in EMG activation, even for one muscle in the negative direction, are similar to results observed in humans during isometric (Keshner et al. 1987; Mayoux-Benhamou and Revel 1993) and active head stabilization (Keshner 2000), particularly when additional inertia had been added to the head. Muscle moment arm differences and force-generating potentials between the two orientations were too small to account for the different muscle activations in this study. Adjustments to the muscle-activation patterns with initial orientation could be explained, however, by a shift in the gravitational-force vectors on the mechanical system requiring additional energy from the muscles to maintain a common output.

In humans attempting to stabilize a weighted head during whole-body rotations (Keshner et al. 1999), a mathematical model of head-neck control (Peng et al. 1996) identified stiffness and vestibulocollic reflex gain as the primary contributors to the control of head stabilization in space. Both stiffness and reflex gain parameters are under neural control and could be readjusted to maintain a consistent frequency response pattern of head movement whether the head was weighted or unweighted. This implies that the changes in muscle-activation patterns observed in this study were the result of central processing of both the head-neck geometry, as defined by the initial orientation of the cervical spine, and the force demands, defined here as the mass of the system, with the goal of maintaining a consistent behavioral output.

Our results suggest that the most relevant parameter controlling task-dependent muscle-activation patterns was the posture adopted by the animal prior to the movement (i.e., the angles of various linked segments with respect to gravity and to the desired target). Changes in the timing and amplitude of the muscle response and in the relative vertebral movements used to achieve the same behavioral outcome depended upon the inertial load and starting neck orientation. The neck musculoskeletal system is quite robust and able to generate the moments necessary to accomplish head and neck movement even with added inertial load for a variety of head and neck geometries. However, changes in neck muscle and cervical kinematics need to be explored during a more challenging head-tracking task to more fully understand the causative relations between mechanical and neural components of head and neck movement.

References

Delp SL, Loan JP (1995) A graphics-based software system to develop and analyze models of musculoskeletal structures. Comput Biol Med 25:21–34

Dunbar DC, Horak FB, Macpherson JM, Rushmer DS (1986) Neural control of quadrupedal and bipedal stance: implications for the evolution of erect posture. Am J Phys Anthropol 69:93–105

Graf W, De Waele C, Vidal PP (1995) Functional anatomy of the head-neck motor system of quadrupedal and bipedal mammals. J Anat 186:55–74

Graf W, Keshner E, Richmond FJ, Shinoda Y, Statler K, Uchino Y (1997) How to construct and move a cat's neck. J Vestib Res 7(2–3):219–37

Henry S, Fung J, Horak FB (2001) Effect of stance width on multidirectional postural responses. J Neurophysiol 85:559–70

Herzog W, Kamal S, Clarke HD (1992) Myofilament lengths of cat skeletal muscle: Theoretical considerations and functional implications. J Biomech 25:945–948

Hoy MG, Zernicke RF (1985) Modulation of limb dynamics in the swing phase of locomotion. J Biomech 18:49–60

Keshner EA (1994) Vertebral orientations and muscle activation patterns during controlled head movements in cats. Exp Brain Res 98:546–550

Keshner EA (2000) Modulating active stiffness affects head stabilizing strategies in young and elderly adults during trunk rotations in the vertical plane. Gait Posture 11:1–11

Keshner, EA, Allum JH, et al. (1987). Postural coactivation and adaptation in the sway stabilizing responses of normals and patients with bilateral vestibular deficit. Exp Brain Res 69(1):77–92

Keshner EA, Baker J, Banovetz J, Peterson BW (1992) Patterns of neck muscle activation in cats during reflex and voluntary head movements. Exp Brain Res 88:361–374

Keshner EA, Statler KD, Delp SL (1997) Kinematics of the freely moving head and neck in the alert cat. Exp Brain Res 115:257–266

Keshner EA, Hain TC, Chen KC (1999) Predicting control mechanisms for human head stabilization by altering the passive mechanics. J Vestib Res 9:423–434

Lestienne F (1979) Effects of inertial load and velocity on the braking process of voluntary limb movements. Exp Brain Res 35:407–418

Lestienne FG, Thullier F, Archambault P, Levin MF, Feldman AG (2000) Multi-muscle control of head movements in monkeys: the referent configuration hypothesis. Neurosci Lett 283:65–68

Macpherson JM, Horak FB, Dunbar DC, Dow RS (1989) Stance dependence of automatic postural adjustments in humans. Exp Brain Res 78:557–566

Mayoux-Benhamou MA, Revel M (1993) Influence of head position on dorsal neck muscle efficiency. Electromyogr Clin Neurophysiol 33:161–166

Pellionisz A, Peterson BW (1988) A tensorial model of neck motor activation. In: Peterson BW, Richmond FJR (eds), Control of Head Movement. Oxford Univ Press, New York, pp 178–186

Peng GC, Hain TC, Peterson BW (1996) A dynamical model for reflex activated head movements in the horizontal plane. Biol Cybern 75:309–319

Peterson BW, Pellionisz AJ, Baker JF, Keshner EA (1989) Functional morphology and neural control of neck muscles in mammals. Amer Zool 29:139–149

Richmond FJR, Thomson DB, Loeb GE (1992) Electromyographic studies of neck muscles in the intact cat. I. Patterns of recruitment underlying posture and movement during natural behaviors. Exp Brain Res 88:24–40

Richmond FJR, Vidal PP (1988) The motor system: Joints and muscles of the neck. In: Peterson BW, Richmond FJR (eds), Control of Head Movement. Oxford Univ Press, New York, pp 1–21

Runciman RJ, Richmond FJ (1997) Shoulder and forelimb orientations and loading in sitting cats: implications for head and shoulder movement. J Biomech 30:911–919

Selbie WS, Thomson DB, Richmond FJ (1993) Suboccipital muscles in the cat neck: morphometry and histochemistry of the rectus capitis muscle complex. J Morphol 16:47–63

Spiegelman JJ, Woo SL-Y (1987) A rigid-body method for finding centers of rotation and angular displacements of planar joint motion. J Biomech 20:715–721

Statler KD, Peterson BW, Delp SL, Keshner EA (1994) Control of free head movements in cats analyzed using a three-dimensional musculoskeletal model. IEEE Eng Med Biol, pp 327–328

Thomson DB, Loeb GE, Richmond FJR (1994) Effect of neck posture on the activation of feline neck muscles during voluntary head turns. J Neurophysiol 72:2004–2014

Vidal PP, Graf W, Berthoz A (1986) The orientation of the cervical vertebral column in unrestrained awake animals. Exp Brain Res 61:549–559

Wickland CR, Baker JF, Peterson BW (1991) Torque vectors of neck muscles in the cat. Exp Brain Res 84:649–659

Zajac FE (1989) Muscle and tendon: properties, models, scaling, and application to biomechanics and motor control. Crit Rev Biomed Eng 17:359–411