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Kinematics of the freely moving head and neck in the alert cat

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Abstract In this study we examined connections between the moment-generating capacity of the neck muscles and their patterns of activation during voluntary head-tracking movements. Three cats lying prone were trained to produce sinusoidal (0.25 Hz) tracking movements of the head in the sagittal plane, and 22.5° and 45° away from the sagittal plane. Radio-opaque markers were placed in the cervical vertebrae, and intramuscular patch electrodes were implanted in five neck muscles, including biventer cervicis, complexus, splenius capitis, occipitoscapularis, and rectus capitis posterior major. Videofluoroscopic images of cervical vertebral motion and muscle electromyographic responses were simultaneously recorded. A three-dimensional biomechanical model was developed to estimate how muscle moment arms and force-generating capacities change during the head-tracking movement. Experimental results demonstrated that the head and vertebrae moved synchronously, but neither the muscle activation patterns nor vertebral movements were constant across trials. Analysis of the biomechanical model revealed that, in some cases, modification of muscle activation patterns was consistent with changes in muscle moment arms or force-generating potential. In other cases, however, changes in muscle activation patterns were observed without changes in muscle moment arms or force-generating potential. This suggests that the moment-generating potential of muscles is just one of the variables that influences which muscles the central nervous system will select to participate in a movement.

Key words Neck muscles · Videofluoroscopy · Head tracking · Moment arms · Biomechanical model · Cat

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Introduction

Although anatomical studies provide evidence that a resting cat will hold its neck in a vertical orientation (Graf et al. 1995; Vidal et al. 1986; de Waele et al. 1989), neural and mechanical redundancies in the head-neck complex suggest greater flexibility for producing head and neck movements. Long neck muscles such as biventer cervicis (BIV), complexus (CPX), and splenius capitis (SPL), cross many cervical vertebrae and can generate moments about both the lower and upper cervical joints. Some investigators (Richmond et al. 1985, 1992; Wickland et al. 1991) have found that, because of their multiple insertions, many of the neck muscles 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.

The extent of functional variability in the neck muscles appears to depend upon the task being studied. Studies of the spatial patterns of neck muscle activation during the vestibulocollic reflex (VCR) were found to be consistent in both head-fixed and head partially free paradigms (Banovetz et al. 1995). During rotation of the head with the cervical column oriented perpendicular or parallel to gravity (Thomson et al. 1994), some neck muscles varied their activity levels when the neck was horizontally or vertically positioned, while others maintained a consistent pattern of activation regardless of vertebral alignment. The two groups of muscles were separated into those that were more superficial and attached to the lambdoidal crest (invariant) and those that were lateral and caudal and attached intervertebrally or on to the scapular (variable). In a study of free head movements in 24 different planes of motion, Keshner et al. (1992) have reported that superficial neck muscles exhibit consistent strategies within a cat, but that these spatial patterns are different from those exhibited during the VCR in that cat, and they also differ from patterns exhibited by other cats during a voluntary head-tracking task.

Increased variability in spatial patterns of muscle activity may be due to greater cervical joint mobility during the tracking task, which could produce alterations in the moment arms and force-generating capacity of the muscles. Increased cervical mobility also presents more control variables to the central nervous system (CNS) and greater variety in the motion-dependent feedback. In this study we examined both motion of the cervical joints and the associated changes in the moment arms and force-generating properties of the neck muscles to determine how they influence the patterns of activation exhibited during voluntary head-tracking movements in three alert cats.

Material and methods

Behavioral training

Three adult cats, one female and two males (2.5–4.5 kg), were subjects in these experiments. The total number of data collection periods varied for each cat, but a minimum of 5 days of complete data were collected. The cats were trained, using positive reinforcement, to perform sinusoidal (0.25 Hz) head-tracking movements as they followed a motor-driven water spout (drinker) with an excursion of $\pm 15^\circ$ in the vertical (pitch) plane (see Keshner et al. 1992, their Fig. 1). The drinker was positioned directly in front of the animal, with the axis of rotation of the drinker always placed as close as possible to the tip of the spinous process of T2. The cats were wrapped in a body bag, placed in a wooden crib, and tested while lying prone in an earth-horizontal position. They were required to lie quietly and to drink without interruption for 10–20 trials lasting 20 s each. The cats were also tested in two additional planes of motion, 22.5° and 45° away from the sagittal plane (see Keshner et al. 1992, their Fig. 1). In these planes, the drinker moved along a right-ear-up and left-ear-down diagonal.

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. On completion of behavioral training, surgical procedures were performed with the animals under halothane (1%) and nitrous oxide (80% N₂O, 20% O₂) anesthesia to prepare them for chronic recording. Radio-opaque markers (stainless steel screws 1/16 inch) were anchored in the spinous or transverse processes of the cervical and first thoracic vertebrae and the occipital protuberance (head; Fig. 1). Intramuscular electromyographic (EMG) electrodes, consisting of stainless steel wires lying along a silastic sheath (Microprobe), 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. Muscles receiving implants included BIV, CPX, SPL, occipitoscapularis (OCC), and rectus capitis posterior major (REC; see Richmond and Vidal 1988 for a detailed explanation of muscle anatomy). Different approaches used in each cat to anchor the screws in the vertebrae necessitated muscles on different sides of the body being given implants. In one male cat, all muscles except BIV were implanted on the right side. In the other male cat, all muscles except OCC were implanted on the left side. CPX, SPL, and REC were implanted on the left and BIV and OCC on the right in the female cat. When all recording was completed, the animals were killed with an overdose of pentobarbital sodium and decapitated. Postmortem examination of the neck was carried out to

check the location of the radio-opaque markers and EMG patch electrodes.

Video motion and EMG analysis

Videofluoroscopic data was collected (sampling rate 60 Hz) directly on to a VHS videotape (Mitsubishi) and, as seen in Fig. 1, included a sagittal view of the cat from occiput to thoracic vertebrae, the arm of the drinker, and a videocounter signal (Thalner Electronics). 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 with the EMG data. During trials in which the drinker moved out of the sagittal plane, the fluoroscope was aligned with the angle of the drinker to minimize parallax. A computer-based video-motion analysis system (Automatix) 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 low-pass filtered (time constant 3 ms). Signals were stored in digital form on computer for later reduction and analysis.

A fast Fourier transform (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., $\text{phase} = \arctan(\text{imaginary}/\text{real})$] and response amplitudes (square root of the squared real and imaginary values) could be calculated. Comparisons between EMG response amplitudes in the sagittal and two off-axis planes were tested for significance with a Kruskal-Wallis nonparametric ANOVA and posthoc analyses were performed using Dunn's multiple comparison test. Comparisons between the vertebral amplitudes could not be made because they changed with the focal distance of the camera, which 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° , peak down was 180° , $+90^\circ$ was in phase with peak downward velocity of the drinker (lagging peak up position), and -90° was in phase with peak upward velocity of the drinker (leading peak up position).

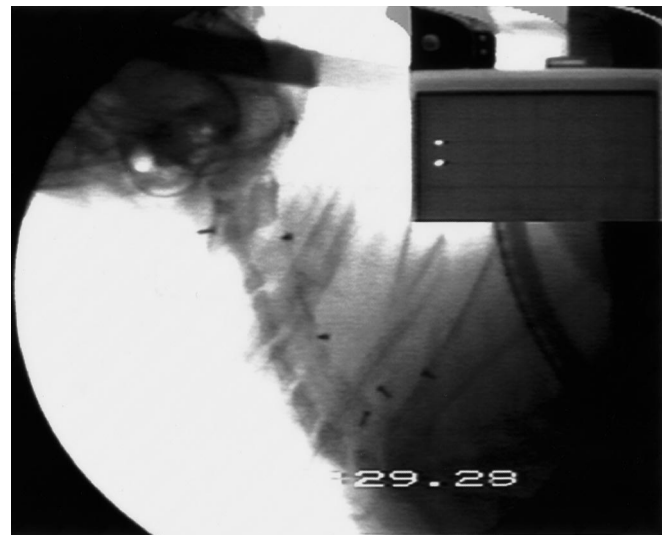


Fig. 1 Digitized fluoroscopic image presenting a sagittal view of the head and neck with radio-opaque markers positioned in the occiput, C1, C2, C4, C6, C7, and T1. The horizontal bar crossing the skull is the arm of the drinker in its upward position. The video-counter signal is at the bottom. The split-screen image permitted a constant view of the oscilloscope trace representing drinker position

Biomechanical analysis

A model was constructed to represent the moment-generating characteristics of the neck muscles (Statler et al. 1994). This model was implemented using musculoskeletal modeling software (Delp and Loan 1995) and consisted of four components: bone geometry, muscle geometry, muscle force-generating parameters, and joint kinematics. The surfaces of the skull, C1–7, and T1 were digitized from a single cat cadaver with the head in the physiological rest position (Vidal et al. 1986), and displayed on a computer-graphics workstation. Muscle paths of the REC, CPX, BIV, OCC, and SPL neck muscles were defined using bony landmarks as references. The origin and insertion of each muscle were defined, as well as any intermediate points necessary to accurately represent the muscle paths over a range of head-neck positions.

A generic musculotendon model (Zajac 1989) was scaled by each muscle's maximum isometric force, optimal muscle fiber length, pennation angle, and tendon slack length to determine the force-length relation of that specific muscle. Each muscle's maximum isometric force was computed by multiplying measured physiological cross-sectional area by a specific tension of 22.5 N/cm² (Wickland et al. 1991). Optimal muscle fiber lengths were measured in three cats. The cats were allowed to go into rigor to fix fiber and sarcomere lengths while the head and neck were held in physiological rest position with a stereotaxic frame. Sarcomere lengths were measured from biopsies of small bundles of rigor fibers as described by Selbie et al. (1993). Fascicle lengths were also measured. These measurements were used to determine the sarcomere length corresponding to the vertical resting posture (L_0) and to determine the optimal muscle fiber lengths. Optimal fiber lengths were calculated by multiplying fascicle lengths by $L_0/2.5$, where 2.5 μm is the optimal sarcomere length reported by Herzog et al. (1992).

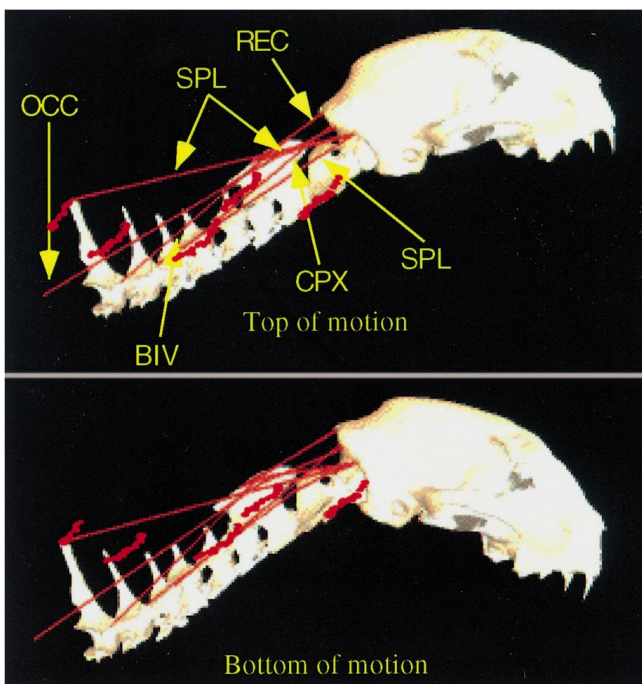


Fig. 2 Orientation of the head and cervical vertebrae at peak down and peak up positions of the drinker during the tracking task. Views produced by manipulating joints of the biomechanical model to match the locations of the stainless steel screws (**bold red lines**) in the five vertebrae from a captured video frame superimposed over the model. *Arrows* identify the five muscles recorded with intramuscular electrodes (*BIV* biventer cervicis, *CPX* complexus, *OCC* occipitoscapularis, *REC* rectus capitis posterior major, *SPL* splenius capitis)

Motion of the neck in the sagittal plane was defined by revolute joints allowing rotation at skull-C1, 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 digitized at five points over the entire range of vertebral movement observed in the three cats during voluntary head-tracking movements. Head tracking was characterized by aligning the computer model to the cats' vertebral alignment observed in the videofluoroscopic recordings during the tracking movement. The model was aligned to the mean vertebral coordinates from five trials for each cat, selected from trials in which the cat's head moved in synchrony with drinker position. Coordinates of the T1, C7, C4, C2, C1, and skull markers for the five positions selected during the tracking movement from peak head up to peak head down were matched. In each case, the model was placed so that the position of T1 corresponded to the digitized marker positions of T1 from the experimental videofluoroscopic recordings. The angle of the T1–C7 joint was then varied until the position of C7 in the model matched the digitized position of C7 from the experimental data. This procedure was repeated for each joint and vertebra until the model matched the overall position of the cat. By comparing the differences in each joint angle between peak head up and peak head down, the relative motion of each vertebral joint over the whole excursion of the head could be determined. Figure 2 illustrates the cervical alignment and muscle attachments and the path of the radio-opaque markers during excursions of the head from peak up to peak down.

By combining the musculoskeletal geometric data, musculotendon models, and the skeletal kinematics, we were able to estimate the musculotendon lengths, muscle fiber length, muscle fiber velocity, moment arm, and force-generating capacity for the range of head and cervical vertebral alignments observed during the tracking movement.

Results

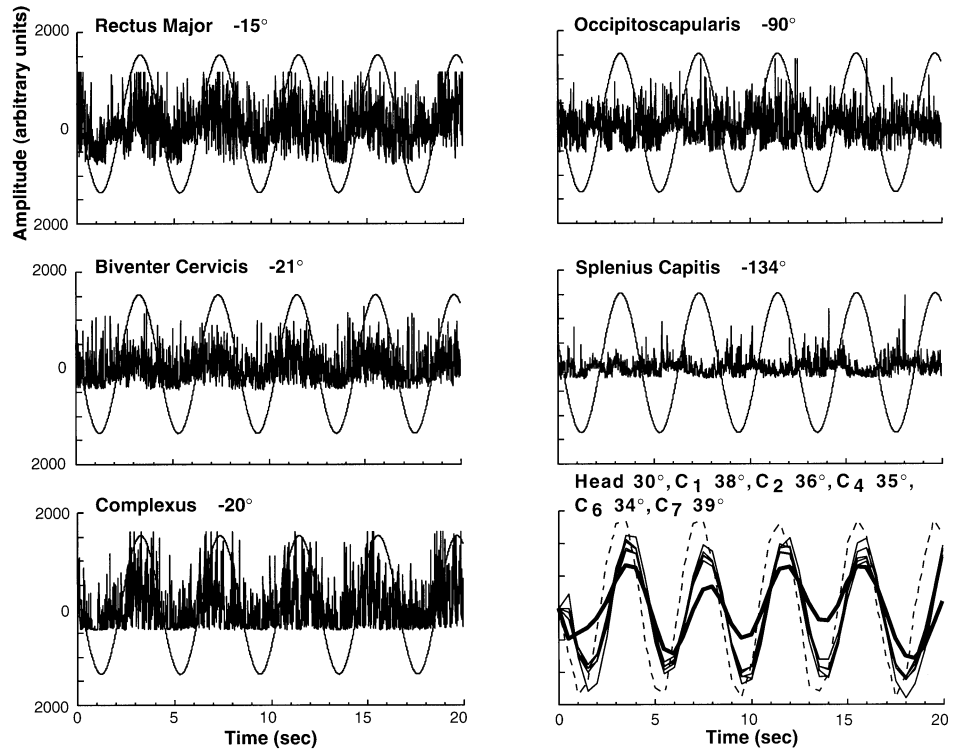
Patterns of muscle and vertebral activation in the sagittal plane

A typical pattern of activation for each of the recorded muscles in one cat, as well as motions of the vertebrae and the drinker, is shown in Fig. 3, where the head and vertebrae exhibited a sinusoidal pattern that closely resembled the sinusoidal shape of the drinker motion. In this trial, the cervical spine and head lagged the peak up position of the drinker.

Relative joint motion was observed between skull-C1, C3–4, C4–5, C5–6, C6–7, and C1–T1. The relative intervertebral motions used to accomplish the tracking task were different for the female and male cats, possibly as a result of the smaller size of the female as compared to the two male cats (Fig. 4). The female was the smallest of the cats (2.8 kg as compared to 4.6 kg), fit comfortably into the crib, and had room to weight shift during the trials. The smaller size of the female cat required that she make greater excursions of the upper cervical joints to accomplish the tracking task. Thus, the female cat used rotations of 35° at skull-C1, 7° at C2–3, 7° at C3–4, 5° at C4–5, and 2° at C6–7. The male cats used rotations of 20° at skull-C1, 6° at C2–3, 2° at C3–4, 2° at C4–5, 3° at C5–6, 2° at C6–7, and 4° at C7–T1.

Although in most trials both the vertebral column and the head tended to be in phase with the drinker, there were some trials in which response phases of the head or

Fig. 3 A single trial of raw EMG data from each muscle. The oscilloscope trace representing movement of the drinker (*thin line*) overlies the data. Positive directions of the trace represent upward motion of the drinker. Phases of the muscles relative to peak up position of the drinker are printed above each plot. The *lower right plot* contains the digitized traces of the cervical vertebrae, the head (*bold line*), and the drinker (*dashed line*). Phases of the head and each vertebra relative to the drinker are printed above the plot



Relative Joint Movement

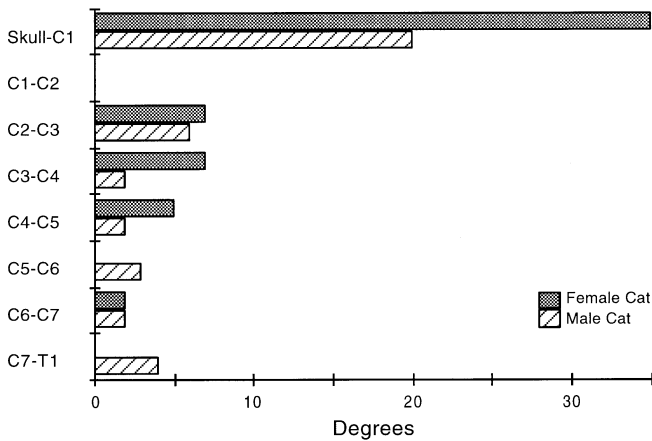


Fig. 4 Relative intervertebral movements exhibited by one female (*shaded bars*) and two male (*hatched bars*) cats at each joint of the cervical spine

vertebrae did not match the position of the drinker. Two of the cats had at least one trial where the animal appeared to be tracking the drinker and successfully completing the task, but response phases were greater than 90° out of phase with the drinker. Observation of the videotapes revealed that, in these trials, movement of the head or vertebrae continued in the original direction of motion after the drinker had reached peak up or down position and began to move in the reverse direction. In other trials, the motion of the lower cervical vertebrae differed greatly from the head and upper cervical vertebrae. In this case, the animal began moving the head and upper spine first, followed by motion in the lower verte-

brae after the head and drinker had already reversed their direction of movement. In the majority of responses, however, phases tended to lead or lag within 30° of peak up position and differences between the vertebrae were small, varying by no more than 20° (Fig. 5). In some trials the intervertebral phases differed more noticeably. Particularly in the female cat presented in the bottom plot in Fig. 5, intervertebral variability was markedly increased with some trials differing as much as 130° between the vertebrae.

Comparisons of the muscle EMG responses across cats revealed discernible patterns of muscle activation. Normalized amplitudes and phases of the EMG responses are plotted on polar plots in Fig. 6. BIV was activated close to peak up position of the drinker for all three cats. CPX responded primarily in phase with peak up position of the drinker. But in some trials, CPX responses were in phase with peak down position or peak upward velocity (-90°) of the drinker. Response phases for OCC were broadly scattered between peak position down and peak position up of the drinker, revealing a muscle poorly matched to any parameter in the sagittal plane. SPL EMG responses demonstrated the most dichotomy with respect to individual strategy; the preponderance of responses were related to peak position up, but in one cat these responses were closer to peak position down. For all cats, REC EMG responses were mostly in phase with, or phase-leading, peak position up of the drinker.

Musculoskeletal patterns during off-axis head tracking

We also tested neck muscle EMG responses with the drinker positioned 22.5° and 45° away from the sagittal

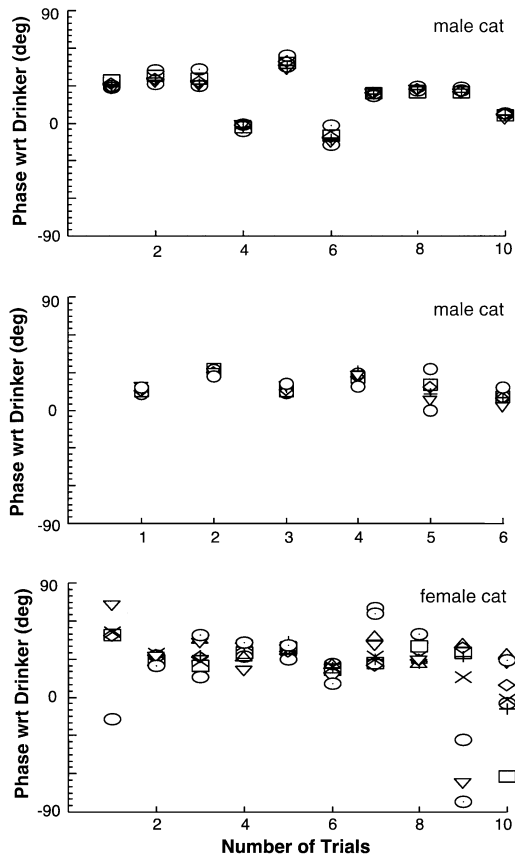
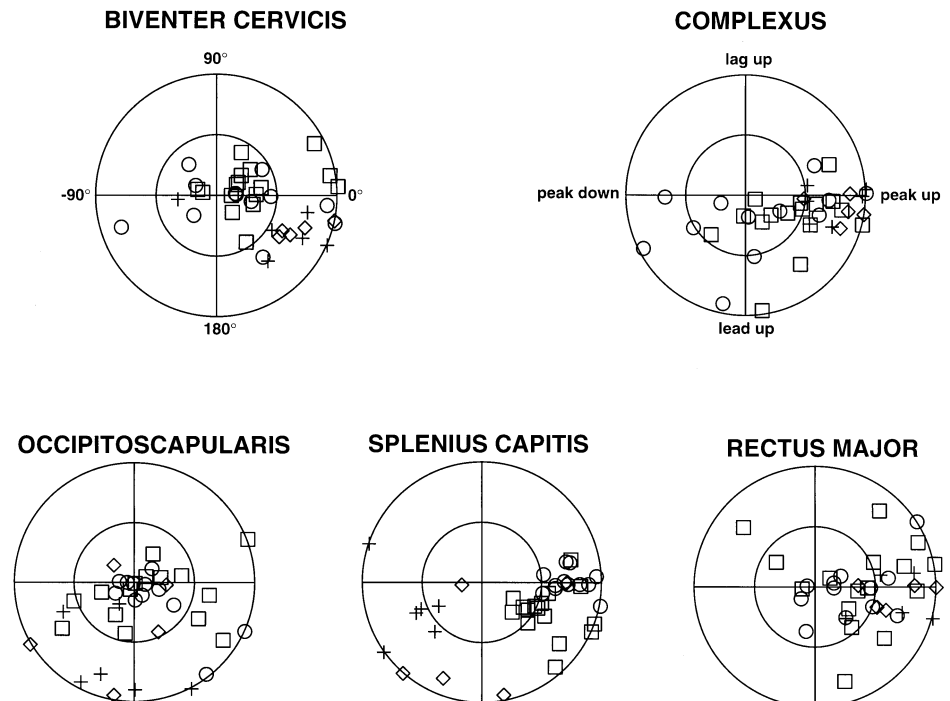


Fig. 5 Head and vertebral phase responses relative to the drinker. Each plot illustrates responses across trials for one animal; responses of the female cat are in the *bottom plot*. Phase conventions are relative to (*wrt*) the peak up position of the drinker (0°), where $+90^\circ$ lags peak up position and -90° leads peak up position (*empty ellipse* head, *rectangle* C1, *empty diamond* C2, *diagonal cross* C3, *upright cross* C4, *filled diamond* C5, *upright triangle* C6, *inverted triangle* C7, *ellipse with dot* T1)

Fig. 6 Polar plots of each muscle illustrate the amplitude and phase responses of that muscle with respect to the drinker for each trial collected in the sagittal plane. Polar angles are identified on the *top left plot*, and each of these values relative to drinker position are labeled on the *top right plot*. Muscle EMG responses in each cat are normalized to the largest response of that muscle across all trials. The muscle's response is plotted according to the amplitude (incrementing outward from the origin, with the outer circumference = 1) and phase (polar angle representing the phase shift between muscle and drinker) of the response (*squares* male cat, *circles* male cat, *diamonds* and *upright crosses* female cat positioned close to or farther from the drinker, respectively)



plane so that the head moved along a right-ear-up to left-ear-down diagonal (Fig. 7). We anticipated that directional properties might emerge from the right compared with left-sided muscles when moving out of the sagittal plane, but there was no indication of this in the phase data.

Movement in the diagonal plane had two principal effects. First, in the two pure extensor muscles BIV and REC, phase responses became more scattered as the animals moved further away from the sagittal plane, so that the muscles responded primarily to velocity rather than position of the head. The second effect was that the OCC responses became more focused so that most were in phase with peak head down position. A Kruskal-Wallis nonparametric ANOVA revealed that the BIV and REC EMG response amplitudes for all three cats dropped significantly ($P < 0.05$) as the stimulus moved 22.5° away from the sagittal plane.

Biomechanical analysis of the head-tracking task

We used the biomechanical model to examine the muscle moment arms and force-generating potential during the tracking movement. Dorsal neck muscles have a moment arm and exert a moment about each joint that is spanned by that muscle. We found little change in the muscle moment arms of any of the muscles in the three cats. Moment arms about skull-C1, C3-4, and C7-T1 are shown in Table 1 for each of the muscles when the head was close to the physiological rest position.

The capability of each muscle to produce force was determined using the model to calculate the operating ranges of the muscle on the force-length curve (Fig. 8). Muscles that operate on the plateau region of the force-length curve

Fig. 7 Polar plots of each muscle in the three cats illustrate the amplitudes and phase responses of the muscle with respect to the drinker for each trial collected in planes 22.5° and 45° away from the sagittal plane. Polar angles are the same as in Fig. 5, and their values relative to drinker position are labeled on the *top right plot*. EMG response amplitudes are normalized to the largest response of that muscle in each plane (*squares* male cat, *circles* male cat, *diamonds* female cat)

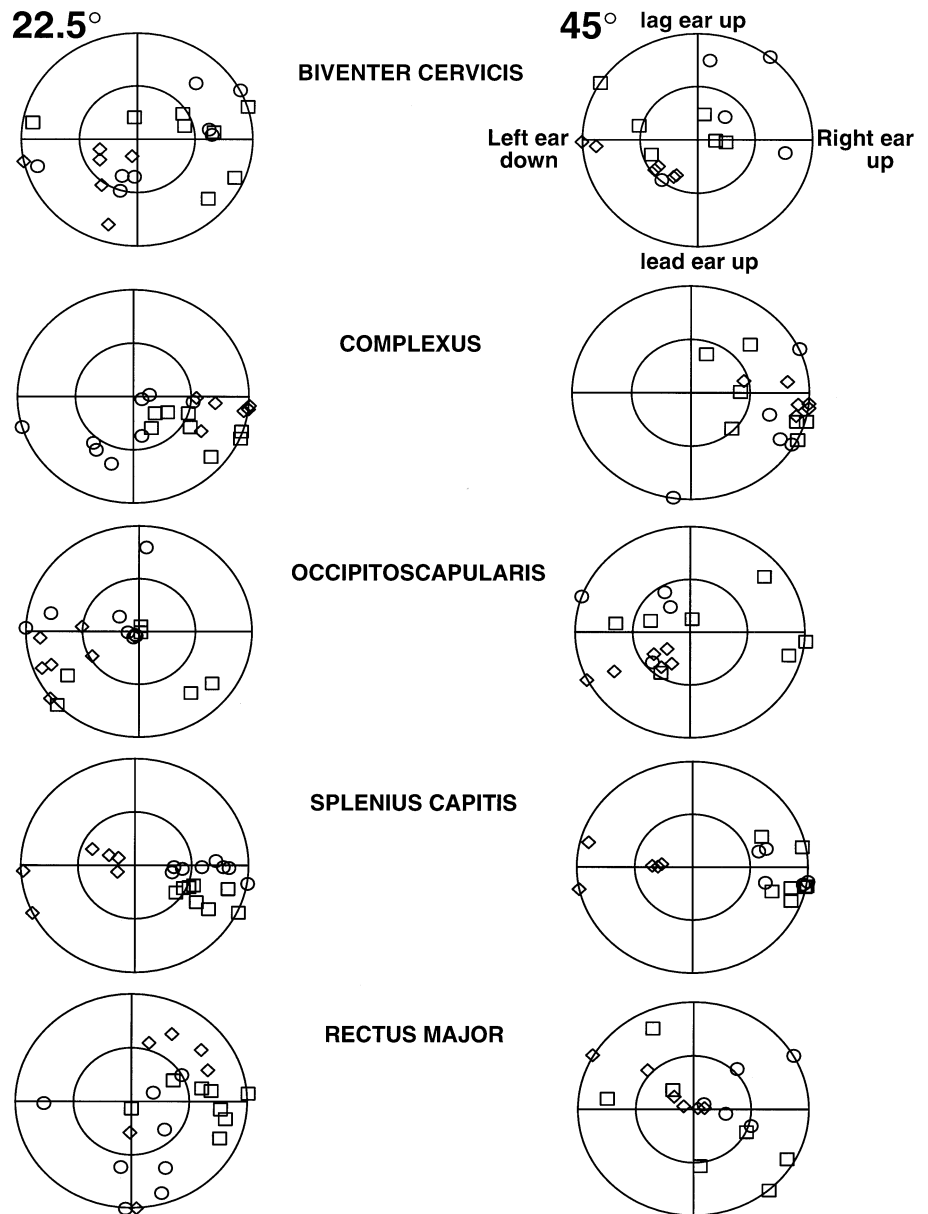


Table 1 Moment arms for a prone cat at peak up position

Muscle	Moment arm (cm)		
	Skull-C1	C3-4	C7-T1
Biventer cervicis	1.68	1.83	0.55
Complexus	1.19	0.91	— ^a
Occipitoscapularis	1.14	2.46	2.04
Splenius capitis	0.62	2.03	— ^a
Rectus capitis posterior major	1.63	— ^a	— ^a

^a Muscle does not cross this joint

are capable of generating similar forces throughout the tracking movement. In contrast, for muscles operating on the ascending region of the curve, the force-generating capacity would decline substantially as the muscle shortens at vertebral alignments near peak up position.

We found that BIV, OCC, and SPL operated primarily on the plateau region of their force-length curves. Thus, the isometric force-generating capacity of these muscles varied little during the tracking movement. In contrast, CPX operated along the ascending limb of the force-length curve. As the muscle shortened for vertebral alignments near peak up position in the tracking movement, the ability of CPX to produce force declined. This decline was particularly evident in the female cat, where the force-generating capacity decreased from 10.2 to 4.9 N when the head moved from peak down to peak up during the tracking movement. REC operated along the ascending limb of the curve for the female cat and along the plateau region of the curve for the other cats. In the female cat, REC could produce 2.5 N for vertebral alignments near peak up as opposed to 5.1 N near peak down. In the other cats, the force-generating capacity of REC

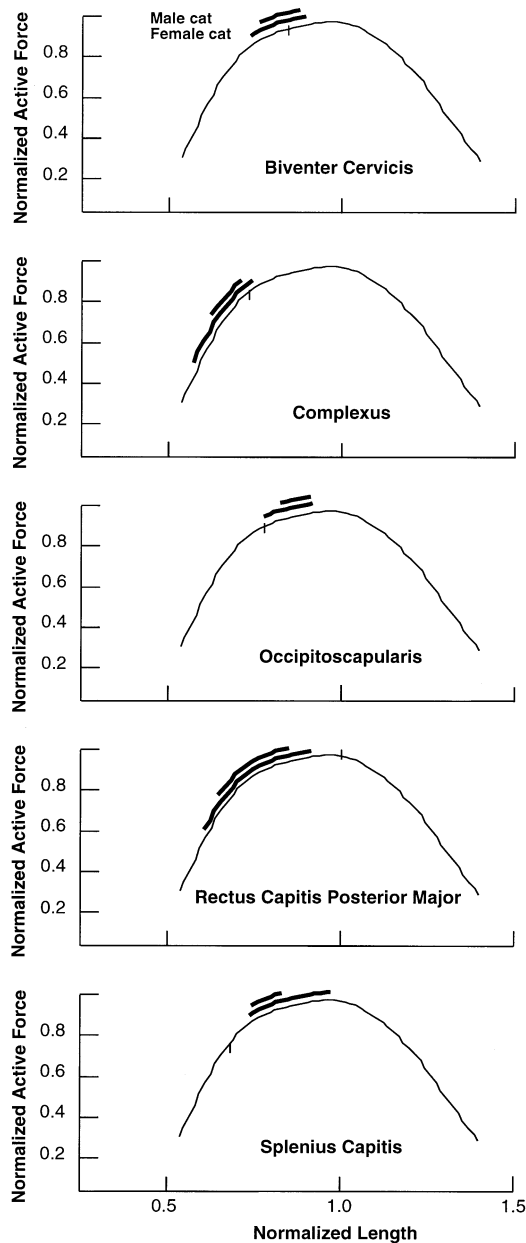


Fig. 8 Operating ranges of the five neck muscles on the isometric force-length curve estimated by the biomechanical model. The *thin curved line* represents the entire force-length relation of the muscle. *Crosses* indicate the point on the force-length curve corresponding to physiological resting posture. Model results (*bold lines*) are drawn for one male and one female cat. Biventer cervicis, occipitoscapularis, and splenius operated primarily around the plateau region. Complexus operated primarily along the ascending limb. Rectus capitis posterior major operated along the ascending limb and plateau region

varied from 4.3 to 5.1 N. These differences occurred because the smaller female cat had greater joint angular excursions than did the larger male cats (Fig. 4), thus, REC and CPX had to operate over a greater range of lengths in the female cat.

The biomechanical model also allowed us to examine the portion of the force-velocity curve over which the

muscles operated during the experimental tracking movements. The 30° movement was performed at 0.25 Hz, so we expected force-velocity effects to be small. Indeed, muscle velocities were always very small, so force-velocity effects were minimal. The muscle-tendon velocity of BIV, CPX, OCC, and SPL varied from 0.02 to 0.07 fiber lengths per second. The muscle-tendon velocity of REC varied from 0.07 to 0.12 fiber lengths per second. These fiber velocities are much lower than 10 fiber lengths per second, the maximum contraction velocity for mixed muscle (Zajac 1989); such small velocities would produce less than a 10% change from isometric force.

Discussion

With 30 muscles, seven joints, and input from at least four systems (vestibular, neck afferent, voluntary, and visual), the head and neck should be able to accomplish a voluntary motor task through a variety of kinematic and muscle actions. This study attempted to determine whether length-tension characteristics or moment arms of the neck muscles could completely explain the patterns of muscle activation and joint displacement exhibited during voluntary head tracking movements.

Muscle activation patterns during voluntary head tracking

Considerable heterogeneity can be seen among the neck muscles through differing lengths, cross-sectional areas, tendon arrangements, and fiber-type compositions (Richmond and Abrahams 1975). Long neck muscles (e.g. BIV, CPX, SPL) cross many cervical vertebrae and can generate torques around both the lower and upper cervical joints. BIV and CPX motoneurons receive similar inputs from segmental and descending systems (Anderson et al. 1977; Wilson and Maeda 1974), although they act very differently in the alert animal (Keshner et al. 1992). Richmond et al. (1991) have divided the intervertebral and suboccipital muscles into two groups: those that act between the skull and C2, and those that link the vertebrae of C2 through T1. These investigators suggested that the superficial suboccipital muscles (e.g., REC and obliquus capitis inferior) have a large proportion of fast fibers that would make them well suited for fast head movements. The deeper layer suboccipital muscles have slower fibers. Thus the suboccipital system may serve to both quickly orient and then hold a new head position. The lower intervertebral muscles are not as well understood, but appear to act in heterogeneous groupings of fiber bundles. For example, the spinalis dorsi and semispinalis cervicis have nonuniform distributions of slow and fast fibers and are tonically active during quiet sitting to maintain vertical orientation of the cervical column. The dissociation between the suboccipital and intervertebral muscles (Richmond et al. 1992) and between the suboc-

capital REC and long neck muscles suggests that these muscles might be targeted by different central mechanisms for selective recruitment during functional activities.

Each of the muscles in this study exhibited distinctive spatial-temporal relations with the stimulus. Spatial activation patterns and temporal relations between each muscle and the vertebrae was affected by the plane of motion. Because the actions of each muscle had a distinctive character, they are presented below in individual summaries.

Complexus

CPX is a long muscle with moment arms that allow it to raise and to roll the head. EMG studies have demonstrated that CPX is active mostly in the roll (right-left-ear-down rotation) plane with a smaller response component in pitch (flexion-extension), and that it is activated opposite to its expected pulling direction (Keshner et al. 1992; Richmond et al. 1992). In this study, CPX exhibited qualities of a roll muscle performing in the pitch plane. Some of the most consistent EMG responses across animals were observed in CPX, because it remained mostly in phase with peak up position of the stimulus regardless of the plane of motion. Although moment arms of CPX about the upper (skull-C1), middle (C3-4), and lower vertebral joints (C7-T1) did not vary substantially over the range of motion, the muscle's ability to produce force diminished as the head neared peak position up. Thus, the activity of this muscle may have been increased to compensate for its decreased force-generating potential in the peak up position.

Biventer cervicis

In this study, EMG response magnitudes for BIV increased when the motion occurred in planes other than pure vertical (pitch), supporting previous observations that BIV was maximally activated for movements consisting primarily of pitch combined with roll and yaw (right-left lateral rotation; Keshner et al. 1992; Wickland et al. 1991). This is consistent with our biomechanical model, which estimates that BIV has moment arms that contribute to motions in both pitch and yaw when the head moves out of the sagittal plane. Moment arms for pitch were estimated by the model to be 1.76 cm about skull-C1, 1.71 cm about C3-4, and 0.61 cm about C7-T1 when the head was at peak up and the movement was in the sagittal plane. Pitch moment arms were similar for movements in and out of the sagittal plane. Yaw moment arms with motion in the sagittal plane at peak head up were estimated to be 0.01-0.08 cm. For motion in a plane oriented 45° out of the sagittal plane, yaw moment arms were estimated to be 0.28 cm at skull-C1, 0.24 cm at C3-4, and 0.16 cm at C7-T1. Thus, for movements in the sagittal plane, BIV had large pitch mo-

ment arms and small yaw moment arms. The force-generating capacity of BIV changed very little through the range of motion used in this task. Changes in force output were most probably modulated by changes in the central commands for this muscle's activation.

Occipitoscapularis

OCC, a superficial muscle that extends beyond the cervical spine to attach to the scapula, has been identified primarily as a horizontal plane actuator during voluntary head tracking (Keshner et al. 1992). During pure sagittal plane motion, OCC exhibited variable responses across animals, although the force-generating capacity changed very little, and the pitch moment arms were similar in magnitude throughout the range of motion. OCC exhibited more consistent response phases across cats when the head movement was out of the sagittal plane so that the movement contained some horizontal plane components. While OCC has large moment arms in pitch (1.17-2.26 cm), it also has substantial moment arms in yaw (0.53-0.90 cm). OCC moment arms in pitch were changed little by movement away from the sagittal plane, but moment arms in yaw increased as the head was moved away from the sagittal plane. Thus, OCC was used more consistently in movements out of the sagittal plane as the yaw moment arms increased.

Splenius capitis

SPL exhibited some of the most consistent responses within each animal, yet exhibited more variability between experimental animals. During voluntary head tracking, the direction of maximal activation of this three-compartment muscle was identified as roll with pitch (Keshner et al. 1992), although the strength of activation in either of these two planes varied between animals. In fact, previous studies have distinguished SPL as a complex muscle that can reverse its direction of maximal activation across both animals (Keshner et al. 1992) and humans (Keshner et al. 1989). During this series of experiments, SPL was observed to respond in phase with pitch upward and downward motion. The force-producing capabilities and moment arms of this muscle are very similar over the entire range of motion used in the tracking task, so these parameters would not be expected to account for the large variation in the EMG responses. There was no evidence of EMG response phase or amplitude differences in the different planes of motion, and the calculated moment arms in yaw were comparable in magnitude with those in pitch. We might infer from these results that SPL response variability results from each individual nervous system selecting a unique contribution of this muscle to the tracking movement.

Rectus capitis posterior major

REC is a short, suboccipital muscle that performs solely in the pitch plane for head extension (Richmond et al. 1991). Functionally, it appears that this muscle was continually acting to move the head about the upper cervical joint, as would be expected of a muscle with a consistently large moment arm about the skull-C1 joint. REC exhibited its largest EMG response amplitudes in the sagittal plane. When performing in planes other than sagittal, however, REC responses were poorly defined. This is reasonable considering the small moment arm of REC in the other planes of motion. The moment arm of REC about skull-C1 is 0.35 cm in the horizontal plane and 0.32 cm in roll when the head is at the top of the tracking motion, whereas pitch moment arms are 1.7 cm for peak head up. Thus, REC was used primarily in the sagittal plane, where it had a consistently large moment arm.

In summary, BIV, REC, and OCC produced peak EMG activation at times when they had large moment arms and were operating on the plateau region of their force-length curves, which gave them a mechanical advantage to assist the movement. Conversely, CPX did not produce peak EMG activation when it had large moment arms, because it was operating on the ascending region of the force-length curve with a reduced capacity to produce force. SPL had highly variable EMG responses that were not easily characterized by its muscle moment arms or force-producing capacity. The ability of the muscles to produce force varied little as the head and neck moved through the tracking path, and their force-producing capability was mostly similar for the three cats. The effects of the force-velocity property were also minimal. Force generated by these muscles must, therefore, be modulated by their excitation patterns rather than by their intrinsic properties.

Mutability of musculoskeletal motion

Differences in the phase relations between the vertebral motion and the tracking device have been described previously (Keshner 1994). In this study, those differences were not as profound, possibly as a result of improved videoanalysis techniques. In the trials where large phase differences between the vertebrae and the tracking device did occur, the animal was observed to continue moving toward peak position up or down even when the device had begun to reverse its direction. In the trials where large phase lags between the head and vertebrae occurred, the animal was observed to use the upper and lower cervical spine successively rather than simultaneously. Variability in muscle responses did not appear to affect the vertebral motion, which, by comparison, was very consistent. Motion of the cervical spine resulting from the muscular forces was, therefore, an invariant parameter in this task.

Given the relative invariance in joint motion, it is surprising that the selection of the primary actuators and

their phase relationships were so variable. The orientation of the cervical spine has previously been targeted as the parameter controlling the selection of specific synergic muscle patterns. Thomson et al. (1994) recorded from deep and superficial muscles in the cat neck during head-turning movements and found that some muscles varied their activity levels when the neck was horizontally or vertically positioned. Other muscles exhibited the same activity in either position, leading these investigators to purport the presence of both a varying and an invariant synergy in the neck. The two groups of muscles seemed to be separated into those that were more superficial and attached to the lambdoidal crest (invariant) and those that were lateral and caudal and attached intervertebrally or on to the scapular (variable). The variable synergy was assumed to reflect the changing lever arms of the muscles with changes in body position.

In this study, we have recorded from three of the muscles identified as invariant (i.e., SPL, CPX, and BIV) and observed very different results. SPL in particular exhibited large differences between animals, as were observed in another study of intact cats during voluntary head tracking (Keshner et al. 1992). CPX and BIV were reasonably consistent across cats in the sagittal plane, but this consistency did not carry over to the other planes of motion. In some cases, the differences in muscle activation patterns were explained by changes in muscle moment arms or force-generating potential. In other cases, however, differences in muscle activation patterns were observed without changes in muscle moment arms or force-generating potential. We conclude that the moment-generating potential of a muscle is only one of the factors that influences the patterns of muscle activation. Selection of muscle strategies could depend on the movement dynamics, afferent feedback, or central control (Tax et al. 1990), where the muscle activation patterns reflect differing solutions to Bernstein's (1967) problem of redundancy. Certainly, all of the signals to which the CNS attends when switching between muscle actuators while still maintaining vertebral consistency are yet to be determined.

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