

Electromyographic studies of neck muscles in the intact cat

I. Patterns of recruitment underlying posture and movement during natural behaviors

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Summary. Natural head movements in alert, unrestrained cats were studied using video-filming, videofluoroscopy and electromyographic (EMG) recording methods. In each cat, up to sixteen neck muscles or neck-muscle compartments were implanted with recording electrodes. Patterns of muscle recruitment were examined during systematically-selected behavioral epochs in which the cat held a range of stationary postures, and when it performed volitional and exploratory behaviors such as flexion-extension or turning, grooming, eating, or head-shaking. Patterns of muscular activity were interpreted with reference to simultaneous video images of head and neck movements. In separate, videofluoroscopic analysis, flexion-extension movements were examined to gain insight into the underlying movements of the skull and cervical vertebrae. These and other movements were found commonly to depend upon changes in joint angles between lower as well as upper cervical joints. Stationary postures in which the neck was held vertically were consistently associated with tonic EMG activity in only two long dorsal muscles, biventer cervicis and occipitoscapularis. Less consistent activity was also present in dorsal intervertebral muscles crossing lower cervical joints. When the neck was held horizontally, the long dorsal muscles increased their EMG activity and moderate activity was also recorded in deeper intervertebral and suboccipital muscles. When flexion-extension occurred around upper cervical joints, greatest activity was recorded in rectus capitis posterior and complexus, but when it involved the lower cervical joints, large changes in EMG activity could also be detected in

biventer cervicis, occipitoscapularis, and the intervertebral muscles crossing lower cervical joints. During specialized, sagittal-plane movements such as grooming, well-defined patterns of synergy could be recognized that varied according to the degree of involvement of upper and lower cervical joint-sets. Movements in the horizontal plane were associated with EMG activity in a largely different subset of neck muscles including splenius, longissimus capitis and obliquus capitis inferior. The levels of EMG activity during flexion-extension or turning movements were much lower than those observed during other more vigorous behaviors, such as head shaking. Some neck muscles, such as clavotrapezius and sternomastoideus, could only be recruited during forceful or ballistic head movements. Results showed that the patterns of muscular activation were linked not only to the speed and trajectory of the movements of the skull, but also to the kinematics of the motion occurring across different parts of the cervical column.

Key words: Head movement – Electromyography – Muscle activity – Cervical vertebrae – Cat

Introduction

Head movement is a complex motor behavior. In the cat, eight joints with differing mobilities are interposed between the skull and the thoracic spinal column. These joints give the neck great flexibility and permit it to move in a variety of planes. Head movements are controlled by more than 20 pairs of muscles (Reighard and Jennings 1963; Crouch 1969; Richmond and Vidal 1988), whose functional roles and synergistic relationships are still quite poorly understood. Until recently, the individual actions of neck muscles have been predicted from anatomical information about their lines-of-pull (Reighard and Jennings 1963; Wickland et al. 1991). Using such an approach, many muscles have been considered to share

Muscle abbreviations. BC biventer cervicis; CM complexus; CT clavotrapezius; CTV centrotransversarius; LC longissimus capitis; LCe longissimus cervicis; LS levator scapulae; OCI obliquus capitis inferior; OCS obliquus capitis superior; OS occipitoscapularis; RCA rectus capitis anterior; RCP rectus capitis posterior; RH rhomboideus; SD spinalis dorsi; SM sternomastoideus; SP splenius; SSC semispinalis cervicis

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the same function. For example, the muscles occipitocapularis, biventer cervicis, complexus, and rectus capitis posterior major, medius and minor have all been classed as head "extensors", and at least five additional muscles have been postulated to have an extensor role under some conditions (c.f., Richmond and Vidal 1988). The presence of so many muscles with potentially similar roles has led some investigators to consider the neck as "functionally over-complete", i.e., as having more muscles than are necessary to control the degrees of freedom of the head (Pellionisz and Peterson 1988). Nevertheless, within each subset of functionally related neck muscles, substantial variations are present in other important features of muscle organization including their relative contents of fast and slow fibers, their fiber architecture, their sites of origin and insertion and the mechanics of their actions across the individual joints of the cervical column (c.f., Richmond and Vidal 1988). All of these variations suggest that each neck muscle may be adapted for a specialized motor role, but the nature of such a role can only be assessed if we have good information about their patterns of activation during normal head-neck postures and movements.

One of the most effective ways to study patterns of muscle activity is through the use of electromyographic (EMG) recording in alert, behaving animals. For more than two decades, chronic recordings of EMG activity from subsets of skeletal muscles have provided useful insight into recruitment patterns that underlie a number of reflexive behaviors or voluntary movements, particularly in muscles of the limb (Engberg and Lundberg 1969). In the head-movement system, the activities of a small number of muscles have been recorded while alert cats attempted to turn their heads in response to visual or optokinetic stimuli (e.g. Guitton et al. 1980; Vidal et al. 1982; Wilson et al. 1983; Denise et al. 1987; Akaike et al. 1989). More recently, such studies have been expanded in scope by implanting many neck muscles with EMG electrodes. By monitoring the concurrent activities of several different muscles, recruitment patterns could be compared and contrasted during a series of defined head movements. To date, studies using multiple EMG recordings have been carried out in trained cats and have focused on a restricted set of head movements produced either to shift the gaze onto a visual target (Roucoux et al. 1989) or follow a feeding tube (Peterson et al. 1989). However, little information is available concerning patterns of neck-muscle recruitment during a wider range of behaviors that involve head movements of varying speeds and complexity.

In the present studies, EMG recordings have been made simultaneously from up to sixteen neck muscles or muscle compartments in alert, freely-moving cats whose head movements were monitored with a combination of cinematographic methods and implanted length transducers. In the first paper, we describe the recruitment patterns of neck muscles during a range of normal motor behaviors. These behaviors include not only simple turning and lifting movements to explore auditory or visual stimuli of interest, but also stereotyped, rhythmic movements such as grooming and head shaking, which have

correlates with locomotion and paw-shaking behaviors that have been well-studied in the cat hindlimb. In the second paper, we extend these observations by examining the reflex effects of muscle-nerve stimulation during ongoing head movements in alert, freely-moving animals. Some of these results have previously been reported in abstract form (Richmond et al. 1985, 1990).

Methods

General procedures

Seven adult cats weighing 3.5–5.5 kg were implanted with arrays of chronically indwelling electrodes so that EMG activity could be recorded simultaneously from up to sixteen different neck muscles or neck-muscle compartments. Different combinations of muscles were implanted in each animal to obtain a broad comparative survey of activity (see Table 1). Surgery was performed under pentobarbital anesthesia (45 mg/kg intraperitoneally, supplemented intravenously) and aseptic conditions.

Layers of neck muscles, approached through dorsal or lateral incisions, were separated and then implanted with recording electrodes. In two cats, the C1 dorsal root ganglion was removed unilaterally in order to conduct studies of the neck-muscle reflexes, as described in the accompanying paper (Richmond and Loeb 1991). The mechanical integrity of each muscle layer was reestablished with sutures. Pre- and post-operative doses of cephalosporin antibiotic were administered prophylactically. By the third post-operative day, all animals appeared to be making normal head movements as they walked, ate and groomed. The animals showed no evidence of post-operative discomfort and appeared to enjoy palpation or scratching of their necks. No differences could be observed in the natural head movements of the two animals that were subjected to ganglionectomy. On postoperative days 4–6, simultaneous recordings were made of EMG patterns as head movements were captured on videotape. The animals were then re-anesthetized to confirm electrode placements and to permit acute physiological testing. The cats were killed with an overdose of sodium pentobarbital.

EMG recordings and signal processing

Where feasible anatomically, we used bipolar, epimysial "patch" electrodes (Loeb and Gans 1986) to record EMG from the surface of the various layers of muscles. Prior to surgery on each chronic animal, a custom set of electrode arrays was designed to fit the neck muscles in a pentobarbital-anesthetized cat of similar skeletal dimensions. Subsequently, this cat was killed prior to regaining consciousness with an overdose of barbiturate. Each set of recording electrodes consisted of a bipolar pair of Teflon-coated, multi-stranded stainless-steel wires affixed to Dacron-reinforced Silastic sheeting. The recording contacts were usually 3 mm long and spaced 3 mm apart along an axis parallel to the muscle fascicles. Often, 2–6 such pairs of recording contacts were positioned on a single Silastic sheet, to reduce the total number of implanted devices and to assure a fixed relationship between different recording sites (e.g., to record from adjacent compartments in a single muscle). The corners of the Silastic sheet were secured to the fascia of the underlying muscle in an appropriate orientation. The sheeting was effective in shielding potential cross-talk from adjacent muscles. It was extended between all fascial planes so that each recording site (except the most superficial and deep) was effectively sandwiched between two such sheets; in some cases, the sheeting was wrapped completely around a strap muscle to form an insulating cuff. The fixed orientation of the electrode contacts on the patches also tended to standardize the amplitude of the signal recorded from a muscle when maximally recruited (about 5–10 mV for the 2 ms integra-

Table 1. Distribution of implanted devices in the cats of this study. The side of the implanted stimulating and recording electrodes are designated L (left) or R (right). Electrodes marked + were configured as intramuscular hooks; the others were attached onto epimysial patches. Cats in which length transducers were implanted

Muscle		Compartment	Cat	1	2	3	4	5	6	7
<i>Recording electrodes</i>										
SP	splenius	1	L	L, R	—	—	R	—	L, R	L, R
		2	L	L, R	L, R	L, R	L, R	L, R	L, R	L, R
		3	L	—	L	—	R	—	—	—
BC	biventer cervicis	1	L+	—	—	L, R	R	—	—	—
	2 medial		R, L+	—	—	L, R	L, R	L, R	L, R	L, R
	2 lateral		—	—	—	—	—	L	—	—
	3 medial		L+	L, R	L, R	—	R	L	—	—
	3 lateral		L+	—	—	—	—	L	—	—
	4		L+	—	—	—	R	—	—	—
CM	complexus	1	L	R	—	L, R	L, R	L, R	L, R	L, R
		2	L+	—	L, R	—	R	—	—	—
OCI	obliquus capitis inferior			L	R	L, R	L, R	—	—	L
	superficial			—	—	—	L+, R+	L+, R+	—	L+, R+
	deep			—	—	—	—	—	—	—
RCP	rectus capitis posterior			L	R	L	L, R	R	L, R	L
SD	spinalis dorsi			—	—	L	L	R	L, R	—
SSC	semispinalis cervicis			L+	R+	—	—	L+, R+	—	L, R
RCA	rectus capitis anterior			—	—	—	—	—	L	L
CTV	centrotransversarius			—	—	—	—	—	L, R	—
CT	clavotrapezius			R, L	L, R	—	—	—	—	—
SM	sternomastoideus			—	—	L	L	—	L	—
OS	occipitoscapularis			L	R	L	—	—	—	—
LS	levator scapulae			—	—	L	—	—	—	—
RH	rhomboideus			—	—	L	—	—	—	—
LCE	longissimus cervicis			—	—	L	—	—	—	—
LC	longissimus capitis			—	—	—	—	—	—	L, R
OCS	obliquus capitis superior			—	—	—	—	—	—	L, R
<i>Stimulating electrodes</i>										
C1RC	C1 rectus capitis posterior			—	—	L	L, R*	—	L, R*	—
C2SP	C2 splenius			—	—	L, R	L	—	—	—
C3BC	C3 biventer cervicis			—	—	—	L	—	—	—
C2BC	C2 biventer cervicis+ greater auricular nerve			L+, R	—	—	—	—	—	—
<i>Length transducers</i>										
LLR	Rotation			—	—	—	—	—	—	—
LLE	Elevation			—	—	—	—	—	—	—

+ Hooks

* Ganglion removed

tion bins used here). With the exception of biventer cervicis in the first cat and certain intervertebral sites (e.g., deep portion of obliquus capitis inferior; see Table 1), muscles were implanted with patch electrodes. Intramuscular bipolar electrodes, formed by suturing together two wires with exposed tips (Loeb and Gans 1986), were used in muscle regions that were inaccessible for patch electrodes.

Table 1 summarizes the distribution of EMG recording electrodes and other devices implanted in all seven animals. In three cats, length gauges (Loeb and Gans 1986) were implanted to span

are also indicated. Numbers and lower-case letters associated with muscles SP, BC and CM designate compartments separated by tendinous inscriptions. Compartments were numbered sequentially from the cranial insertion; medial and lateral refer to different edges of the compartment that were implanted

from the lambdoidal crest to the spinous process of C2, and in one cat, a second gauge was implanted to span from the lateral process of C1 to the spinous process of C2. The outputs of these gauges were useful to assess the exact time of onset of a rapid flexion-extension or rotational movement, such as a head shake. Bipolar stimulating electrodes, also mounted on Silastic patches, were positioned over certain muscle nerves, as described in the companion paper (Richmond and Loeb 1991). The leads from all implanted devices were passed subcutaneously to the dorsal lumbar region where they were externalized through a small percutaneous incision and were sol-

dered onto a 40-pin saddle connector that was sutured to the lumbarosacral fascia (Hoffer et al. 1987). A flexible ribbon-cable that did not interfere with normal movements was used to link the connector to a distribution panel that fed the signal-processing electronics.

All EMG signals were amplified differentially with 50–5000 Hz bandwidth and recorded on an 18-track FM tape recorder (DC–10 kHz bandwidth) along with a voice track and IRIG-B time-code. Segments selected for analysis were rectified and integrated into 2 ms bins (Bak and Loeb 1979); up to 16 channels were digitized at synchronized 2 ms intervals by a PDP-11/73 computer. Calibration bars indicate the amplitude of a 1 kHz sinusoidal waveform (referred to amplifier input) processed in the same manner. Selected sequences of EMG data were smoothed by calculating running averages for each sample bin plus the ten bins (± 20 ms) before and after the sample.

Motion recording and analysis

During EMG recording sessions, all head movements were videotaped at 60 fields per second by two low persistence, high resolution plumbicon cameras using stroboscopic illumination. One camera was aligned to obtain a frontal view of the head and body; the other was placed at 90° to view the head and body in longitudinal profile. The split-screen views plus IRIG-B time-code and voice commentary were recorded on a Panasonic high-resolution video recorder. They were analyzed by playing selected 10 s segments through an Eigen video disk that permitted slow-motion forward and reverse and single-field stepping. Selected frames were hard-copied using a video printer (Mitsubishi) for convenient reference. Video fields could be correlated with the EMG recordings using the time-code.

In one cat (C3), a variety of normal behaviors (e.g., feeding, grooming, walking) were observed using videofluoroscopy to provide information about cervical postures and axes of motion. The head and neck were filmed from a lateral view and analysis of vertebral alignment focused primarily on postures and movements in a sagittal plane. Selected sequences of frames were analyzed through the Eigen video disc. To analyze the changes in angular rotation at upper and lower joint-sets associated with different postures, the orientation of the cervical column was assessed by drawing a line of best fit along the costal processes from caudal C2 to C5, and that of the thoracic column by drawing a line through the bases of the first four thoracic vertebrae. The orientation of the skull was assessed by drawing a second line from the base of the upper canine tooth through the X-ray-dense thickening of bone at the base of the zygomatic arch. This line is tilted downward from the plane of the horizontal semicircular canal by approximately 30° (determined with reference to Vidal et al. 1986) (Fig. 1). Fluoroscopic observations from cat C3 were compared to cinefluoroscopic and still x-ray records from 3 other alert cats, and these showed similar kinematics (Selbie et al. 1991). Because videofluoroscopic images are difficult to reproduce for publication and subsequent photoreproduction, the images in video frames of interest were reconstructed using cadaver bones (Fig. 1) by tracing the vertebral outlines onto transparencies affixed to the face of the video monitor, and then matching the orientations of the bones to the transparencies.

In most cats, spontaneous movements were generated without prior behavioral training. However, one cat (C7) was also trained to hold its head in a midline sitting posture, and then make head turns in the horizontal plane to foveate the source of an auditory stimulus presented 45°, 90° or 135° to the right or left. After holding the gaze in the turned posture for several seconds, the cat then made a concentric turn to return the head to its original posture in order to obtain a food reward. The degree of eccentricity of the auditory stimulus was randomized; a typical testing period involved 45 trials in each direction.

Analysis of EMG records

Records were searched systematically to identify sequences in which adjacent muscles were recruited at different times and thus could be compared to rule out cross-talk of their EMG signals. The sensitivity of most recording electrodes was found to be quite evenly matched. When a muscle was inactive, there was less than 50 µV of wideband noise and no spike-like events in the amplified signal; bin integrator noise was also less than 50 µV. For every muscle in every cat, activity levels characteristic of a variety of head movements were compared to those of forceful, ballistic movements, such as head shaking (i.e., Fig. 5), and forceful, resistive movements made by the cat to free its restrained head from the hand of the investigator. These forceful movements typically generated signals of 4–8 mV (bin integrator output). The descriptions that follow are based on (but not confined to) the systematic inspection of 70 behavioral sequences in which cats held their heads stationary in the mid-sagittal plane, 40 sequences of head extension, 120 sequences of head-turning movements, 260 sequences in which the head was held out of the mid-sagittal plane, 50 epochs of grooming behavior, and 30 sequences of head shakes. These observations were supplemented by examinations of many other diverse behaviors, some of which were conducted while the cat adopted side-lying or belly-up postures.

Results

Videofluoroscopic observations

The sitting, undistracted cat is known to hold its skull flexed forward at the top of a vertically oriented spinal column (the "resting" posture; Vidal et al. 1986). However, the head and neck can be flexed or extended from this posture by changing the angles of vertebral articulation at the two ends of the spinal column. In Fig. 1, cervical vertebrae from a cadaver have been used to illustrate the alignment of vertebrae observed fluoroscopically in a range of head and neck postures. Head movements between these postures were made by combining movements at two sets of joints, one between the skull and C2 and the other between C4–T1. Movements in these two regions occurred independently and even antiphatically. Flexion-extension movements between the skull and C1 altered the angle of inclination of the skull with respect to the cervical column through a range of motion of more than 90° (Fig. 1:2–4). Extension (dorsiflexion) or flexion (ventriflexion) at lower cervical joints elevated the skull with respect to the shoulder girdle (Fig. 1:4, 1:5) and rotated the cervical column through a range of motion of approximately 100° in the normal movements studied here. The cervical column between C1–C3 showed less bending than more rostral and caudal cervical vertebrae. However, some motion could be detected at joints between C1 and C4 when the cat was at postural extremes, such as when the head was tucked tightly to the chest (see also Fig. 3d in Vidal et al. 1986).

Stationary postures were also examined in which the cat's head was turned out of the sagittal plane. In these postures, the alignment of vertebral bones was more difficult to define because the X-ray-dense image of the skull obscured the features of the cervical vertebral column. In turns of less than 45°, the most marked changes in joint angle appeared to occur between C1 and C2.

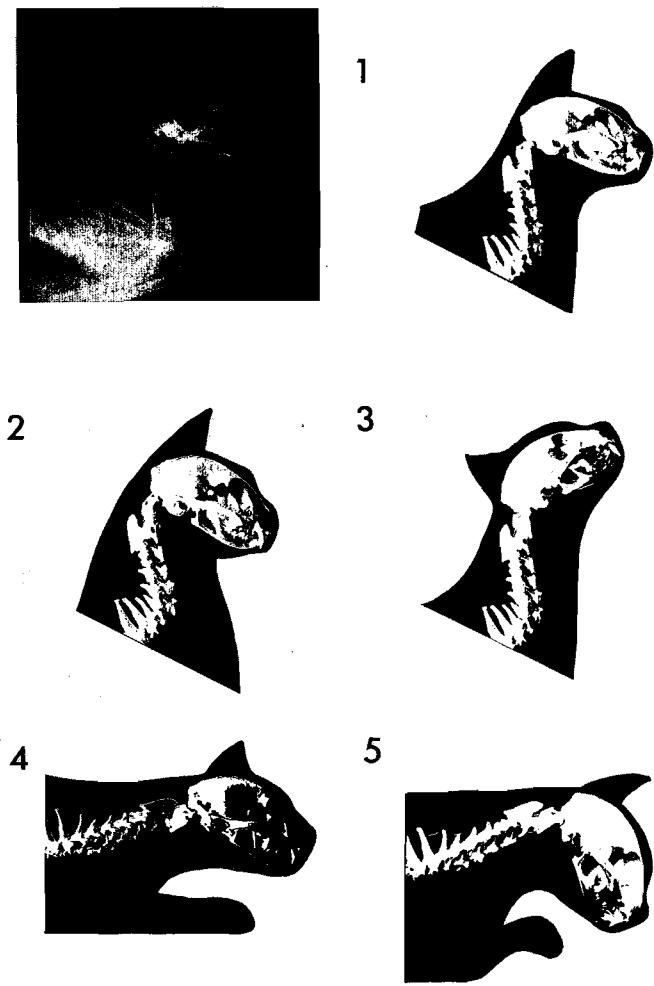


Fig. 1. Orientation of skull and cervical vertebrae in a range of postures observed by fluoroscopy. X-ray images (such as that in the upper left) were reconstructed using cadaver bones and then photographed for better reproduction. Silhouettes show the posture of the cat as reflected by external landmarks on the head and neck. 1: Resting posture. 2: Skull-C2 flexed to look downward. 3: Skull-C2 extended to look upward. 4: Skull-C2 as well as lower cervical joints extended. 5: Lower cervical joints extended, but skull-C2 flexed to inspect an object below the supporting surface

However, when the cat made larger head turns, the motion appeared to be distributed more widely, and involved lower cervical as well as upper cervical joints. More detailed analysis of vertebral alignment during turns and axial rotation was beyond the limitations of single-view fluoroscopic methods.

EMG patterns in neck muscles

Postures and movements in the sagittal plane

The "resting" posture. Of the long neck muscles, only biventer cervicis (BC) and occipitoscapularis (OS) were active tonically when cats sat or reclined quietly in a "resting" posture (cervical column erect, long axis of skull in the sagittal plane) (Fig. 1:1). Little or no EMG

activity could be detected in the other long muscles, including splenius (SP), clavotrapezius (CT), sternomastoides (SM) and complexus (CM) (Figs. 2, 3). Amongst the shorter muscles close to the cervical column, EMG activity was modest if present at all and was observed most commonly in the muscles crossing lower cervical joints. Records from semispinalis cervicis (SSC) showed intermittent or low-level tonic activity in at least 50% of sequences in all cats during quiet sitting. Its immediate neighbour, spinalis dorsi (SD), showed consistent levels of tonic activity in only two of the four cats in which this muscle was studied (compare Fig. 2 with Fig. 3). Little or no spike activity was recorded from the superficial layers of rectus capitis posterior major (RCP) (Figs. 2, 4) or the superficial or deep layers of obliquus capitis inferior (OCI) (Fig. 3). The ventral muscle rectus capitis anterior major (RCA) showed a low but consistent level of EMG activity when the cat was sitting or reclining quietly (Fig. 2).

Flexion-extension of suboccipital joints. In other postures, the head and neck were held in the mid-sagittal plane but the inclination of the skull was changed by flexing or extending at suboccipital joints (Fig. 1). When the neck was held vertically, extension at suboccipital joints was associated primarily with EMG activity in the previously silent suboccipital muscles, RCP and CM (Fig. 2). When a new posture was reached, EMG firing in these muscles stabilized at a level of tonic firing related to the degree of upward inclination of the skull. BC also showed a modest increase in its activity during extension across suboccipital joints; this increased activity showed little diminution during the subsequent stationary phase. Activity in the ventral muscle, RCA, showed an antagonistic pattern to that of dorsal muscles. Activity in RCA diminished progressively when the suboccipital joints were extended and could no longer be detected when the nose was directed upward by more than 10–20% from the resting position (Fig. 2). Muscles showing little or no detectable change in their firing patterns during these movements included rhomboideus (RH), SD, SSC, CT, SM, SP, OCI and OS.

When the cat made a very large extension movement to direct its gaze skyward, suboccipital joints were extended close to their limit and lower cervical joints often underwent extension as well. In these postures, EMG activity increased most markedly in RCP and CM (Figs. 2, 4) and to a lesser extent, in BC, OS, SSC and SD. Levels of activity characteristically seen during maximum extension were large (400–800 µV/bin in smoothed records) compared to those in the resting posture (<200 µV/bin) but they were very much lower than activities during vigorous movements such as head shakes (>4 mV during active phases) (Fig. 5). Further, levels during maximum extension were lower than those observed when the cat attempted to lift its head against the restraining hands of the investigator.

Flexion-extension across the lower cervical joints. In the "resting" posture (Fig. 1:1), the lower cervical joints are held close to maximum extension. Thus, the largest sagit-

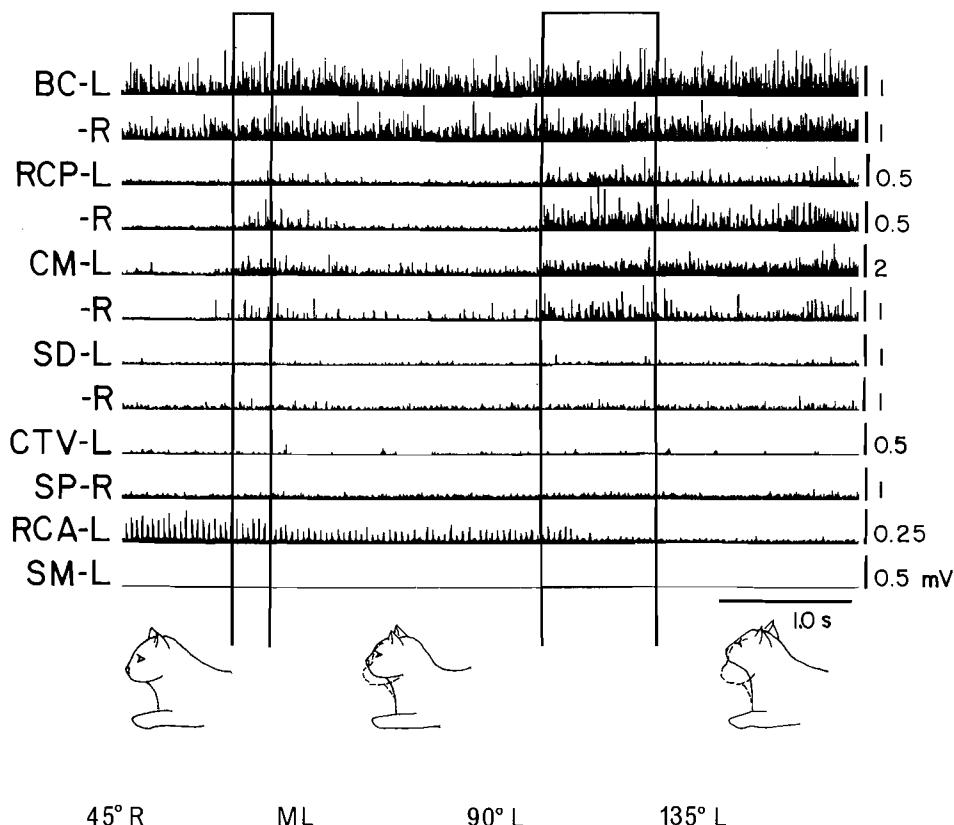


Fig. 2. EMG patterns in neck muscles during dynamic and stationary phases of two small extensions that incline the nose upward. Boxed regions indicate the dynamic phase of the movement. During the intervening epochs, the head was held stationary in the position shown by solid lines in the drawings below (reproduced from photographs of single video frames). The original position is shown by the dashed profile. Note the increased activity in RCP, CM, and to lesser extent, BC. RCA initially shows a rhythmic discharge whose characteristics have been described elsewhere (Loeb et al. 1988); it becomes silent as the head extends. Muscle abbreviations are defined in Table 1; records from cat C6

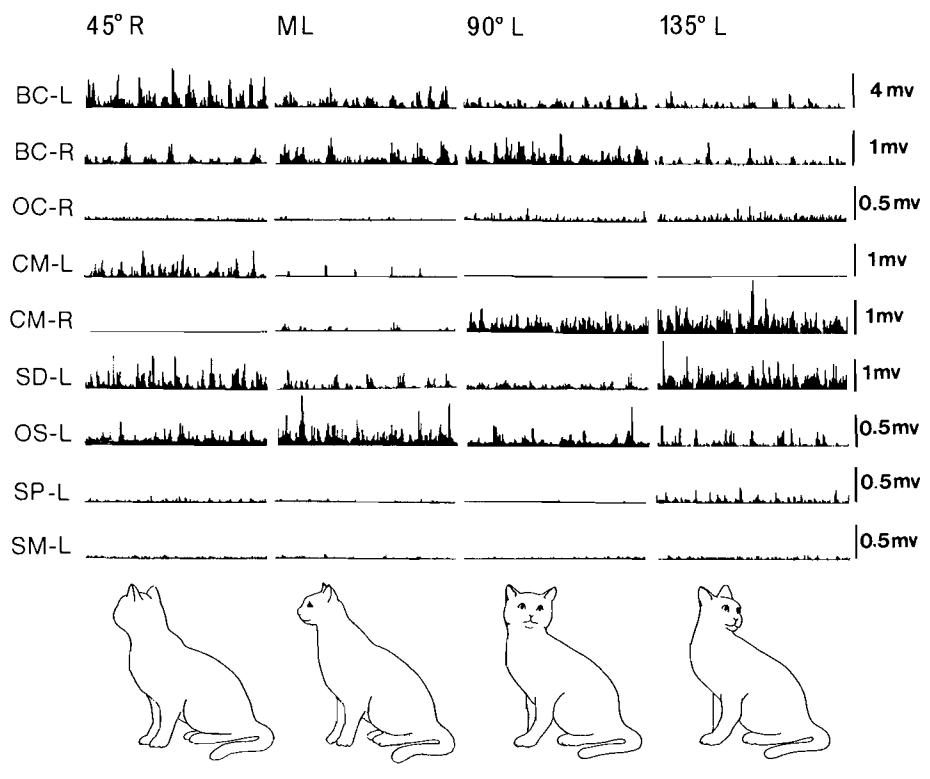


Fig. 3. Tonic levels of EMG activity when cat C3 held stationary postures with its head turned in the horizontal plane. Traces above the line drawings show records that were digitized into 2 ms bins. Traces below the drawings are the same records from the extensor muscles which have been smoothed (see methods) to facilitate a comparison of EMG amplitudes in different postures (same scales as in tracings above). The second vertically-oriented panel shows the EMG levels characteristic of a resting (ML) posture. Changes from this pattern were modest within a range of 90°. Note however the clear alterations in CM and more subtle changes in BC and SD on the two sides of the cat. Strongly turned postures ($> 90^\circ$) caused a marked diminution in BC activity but a strong augmentation of discharge in CM and SD. SP and OCI (designated OC) showed little tonic activity even in the most strongly turned postures



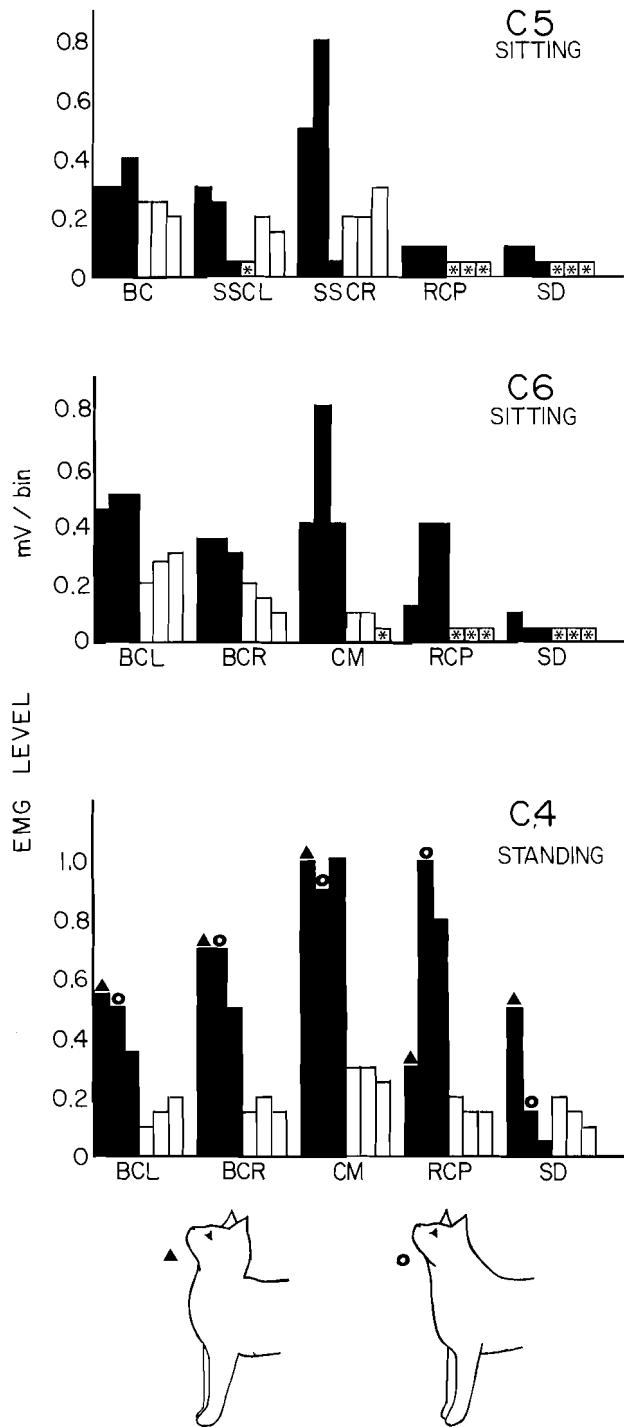


Fig. 4. Changes in tonic EMG activity characteristically seen during extensions across upper cervical joints while the neck was oriented vertically in 3 cats. For each cat, the three different shaded bars show mean EMG level (expressed as mV/2 ms bin) for 3 separate sequences of posture in which gaze was directed upward. Open bars are three sequences in which the gaze was held roughly parallel to earth. Bars with activity less than 0.05 mV/bin represent tracings with little or no detectable EMG activity (marked with asterisks in open bars). Note that the largest consistent shifts in mean activity occurred in CM and RCP; BC showed a more modest increase in firing. Examples shown for cat 4 include a sequence (marked by a triangle) in which there was a larger component of extension across lower cervical joints, as shown in the line drawings below. In this instance, the relative levels of activity increased in the intervertebral muscles SD and SSC (not shown) but decreased in RCP

tal-plane movements across these joints are made when the cat flexes the lower cervical column so that the neck is cantilevered in front of the shoulders (Fig. 1:4). To move the neck from a vertical to a horizontal orientation, the long extensor muscles of the neck change their activity in a complex way. The dynamic phase of the flexion was generally associated with a reduction but not a loss of EMG activity in BC and OS. The residual activity presumably permits the cat to slow the flexion to avoid a precipitous drop of the head. When the cantilevered posture was obtained, BC and OS reestablished a level of tonic firing at least equal to and often greater than that in the upright posture. BC and OS were active most strongly when the head was held level with the shoulders, especially when the suboccipital joints were also extended so that the line of gaze was held parallel to earth (Fig. 6). The intervertebral muscles SD and SSC also showed stronger levels of tonic activity when the neck was held horizontally rather than vertically. During flexion-extension movements across lower cervical joints, modest increases were observed in the activity in RCP even when suboccipital joints showed little extension. The increased activity may reflect an increased need for extensor torque around both the upper and lower cervical joints to oppose gravitational forces on the skull (which act via longer moment arms when the neck adopts a horizontal posture). When the neck was flexed even further until it was held close to the ground, extensor muscles showed activity patterns that depended upon the extent to which the neck was kept rigid and stretched out in front of the body. For example, BC, OS, SD and SSC showed substantial activity when the head and neck were extended to reach a food dish during eating ($> 100 \mu\text{V}/\text{bin}$) but were much less active when the head was allowed to hang in a more pendular fashion close to the paws. Behaviors to lower the neck and head close to the forepaws (for example, to eat from the floor) were commonly accomplished using a strategy in which the forelimbs were flexed to lower the shoulders at the same time as flexion occurred across lower cervical joints. This action decreased the required amount of nuchal flexion and presumably occurred because flexion across the lower cervical column is limited by the anatomical constraints of vertebral ligaments, joint structures and discs (Slipjer, 1946).

During extension across lower cervical joints (to bring the neck from a horizontal to a vertical orientation), increased levels of EMG activity were always recorded in many dorsal neck muscles including BC, CM, RCP, SD, SSC and OS. After the vertical posture was achieved, EMG activity abruptly decreased and tonic levels described earlier for the “resting” posture were reestablished.

Coordination of flexion-extension at suboccipital and lower cervical joints. In some instances, flexion-extension movements appeared to be confined to only a few cervical joints, but in others they occurred across the whole of the cervical column. The flexion-extension movements at upper and lower cervical joints were not always complementary. Antiphasic movements were seen, for exam-

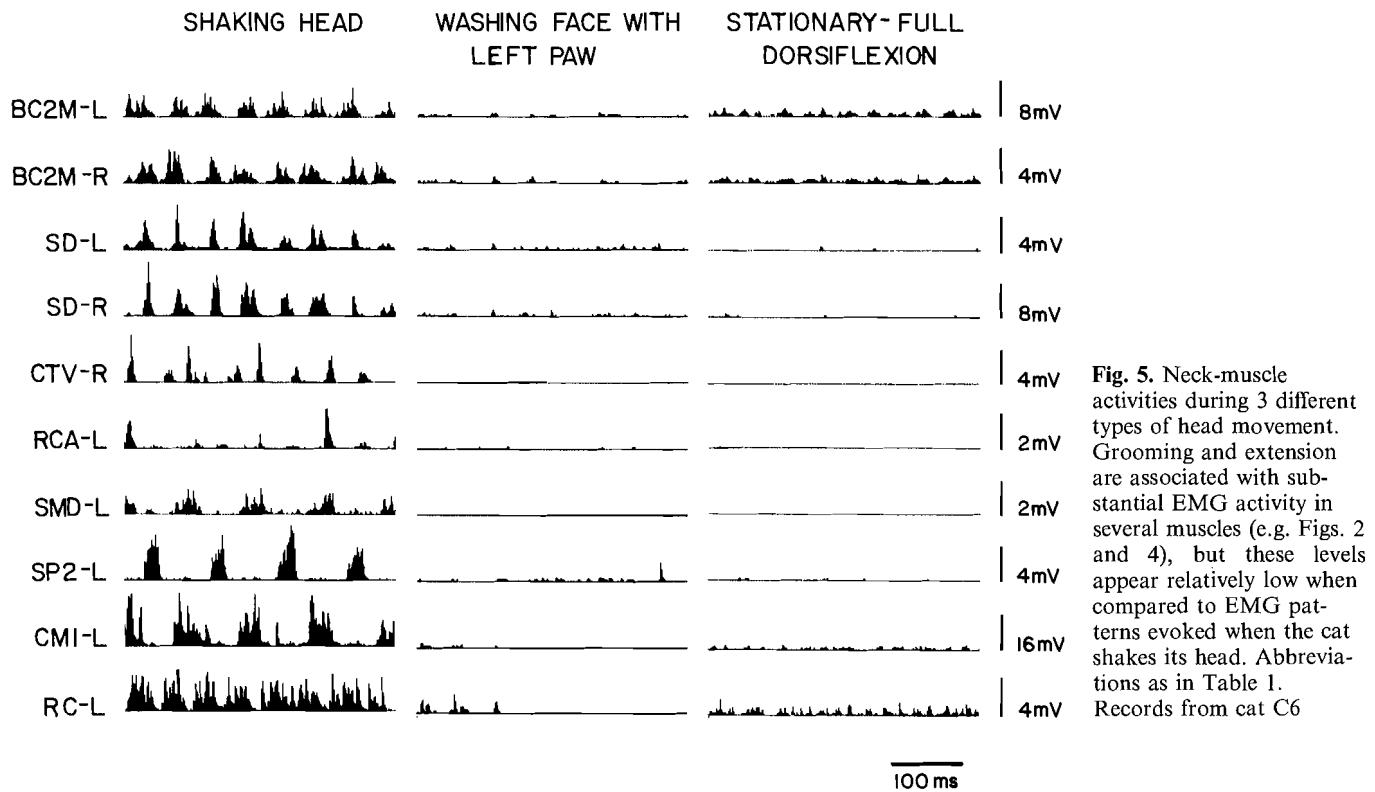


Fig. 5. Neck-muscle activities during 3 different types of head movement. Grooming and extension are associated with substantial EMG activity in several muscles (e.g. Figs. 2 and 4), but these levels appear relatively low when compared to EMG patterns evoked when the cat shakes its head. Abbreviations as in Table 1. Records from cat C6

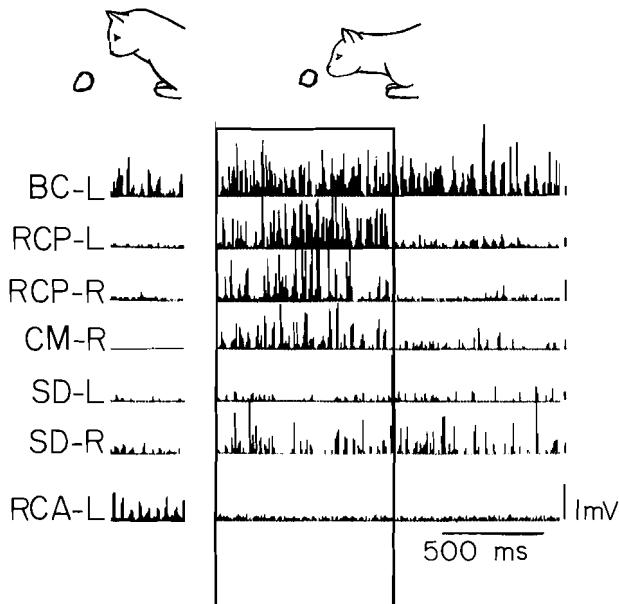


Fig. 6. Changes in EMG activity during and after the head and neck were lowered by moving lower cervical joints. In the right panel, the cat is crouching with its neck held vertically. After a period in which this posture was held, the cat made a combined movement of lower cervical flexion and upper cervical extension. The dynamic phase is marked by the box; a stationary period follows in which activity in all of the extensor muscles (top 6 traces) is increased with respect to the initial posture. Note that the ventral muscle, RCA, becomes silent. Records from cat C6

ple, when the cat lowered its head by flexing the lower cervical column, but kept its line of gaze parallel to the earth by extending simultaneously across the suboccipital joints (Fig. 6). In such behaviors, EMG activity was found in the suboccipital extensors, in CM, and in the long dorsal muscles, BC and OS.

Grooming: an example of coordinated flexion-extension. The complex recruitment patterns that can occur during movements in the sagittal plane are well-illustrated by examining neck-muscle activity during the stereotyped, cyclical movements of grooming. Grooming movements were divided for descriptive purposes into two categories: 1) those in which the face or paw is washed by coordinating movements of the head, forelimb and paw (e.g., Figs. 7, 8), and 2) those in which the cat cleans the fur of the lower body or tail by moving the head together with the shoulders and trunk (e.g., Fig. 8). To wash the paw, the paw is first brought to the mouth as the head is tucked, and the paw is then licked as the head extends. The alternating flexion-extension movements appear to occur primarily across upper cervical joints at a frequency of 1–2 Hz. To wash the face, paw-licking alternates with a second movement, in which the moistened paw is lifted toward the lowering head, and then wiped briskly against the ipsilateral whiskers, ear or eye. Figure 7 shows the typical EMG activity in a number of neck muscles during three different grooming movements in the same cat. In all examples, BC, RCP, and CM were recruited synergistically during extension. During flexion, a different set of muscles was recruited, but the identities of the recruited muscles and their level of re-

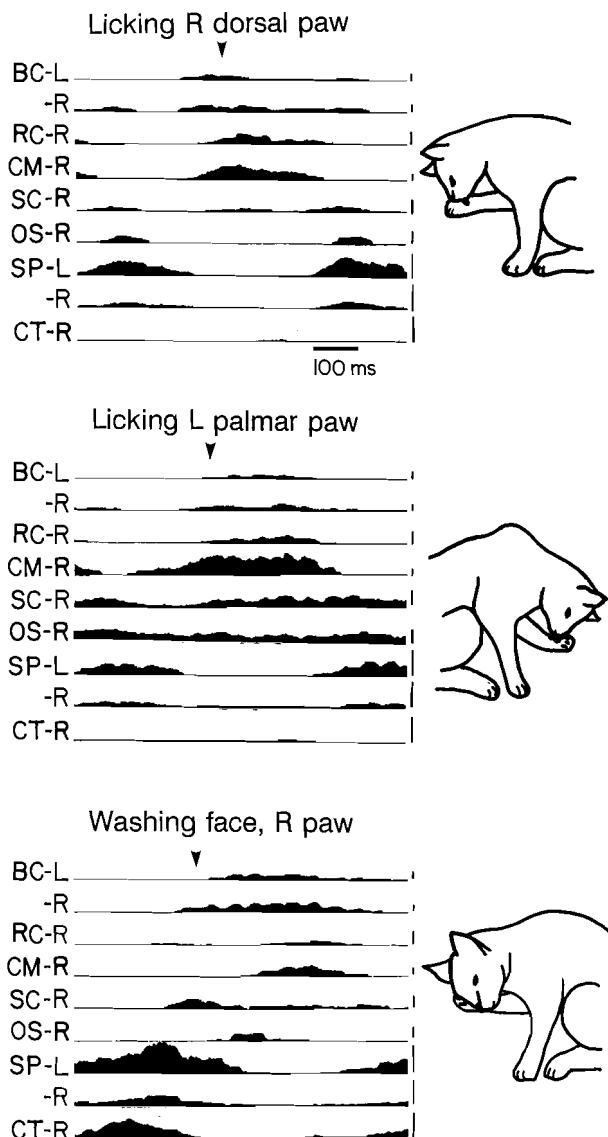


Fig. 7. Patterns of EMG activity in several neck muscles during different grooming behaviors. Records have been smoothed to permit comparison. The onset of head extension is marked by an arrow in each panel. Stronger activity in the muscles CM, SSC, and OS was typically seen when the neck was flexed more strongly and when movements were more vigorous (compare top with middle panel). In the lowermost panel, CT is recruited as part of the face-washing behavior. SP is recruited bilaterally during the flexion phase of these movements. The relatively small amplitude of SP-R compared to SP-L reflects the kind of variations in gain typically seen between different sets of patch electrodes. Bars = 1 mV/bin; RC = RCP; SC = SSC; other muscles abbreviated as in Table 1; records from cat C2

cruitment varied with the specific kinematics of the movement. Presumably gravitational forces promote head flexion even in the absence of muscular participation when the head is held erect. However, SP was commonly recruited in the flexion phase as shown in Fig. 7. Its activity appeared strongest when the neck was cantilevered forward so that the neck was held quite horizontally; less SP activity was observed when the neck was held vertically. SP was commonly active bilaterally

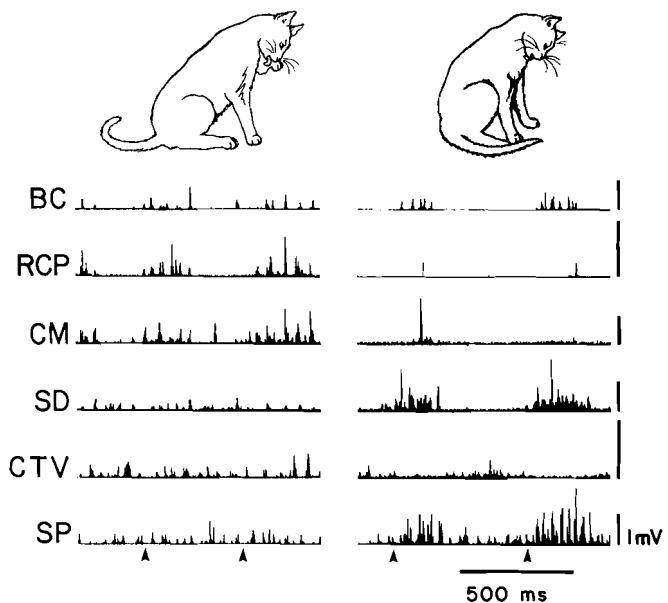


Fig. 8. Differences in EMG patterns during two types of grooming. In the left panel, cyclical modulation is observed primarily in CM and RCP during paw-licking. In the right panel, chest-licking is associated with modulated activity in a different set of muscles, including more caudal intervertebral muscles, SD and CTV (active antagonistically), and the long multiarticular muscles, BC and SP. The arrows in both panels mark the time at which the head is beginning to extend. Records from cat C6

when movements were made in the mid-sagittal plane, but activity could be weighted to SP on one side when washing movements involved a rolling or turning component. Increased activity during flexion could also be observed in the deeply-placed ventral muscles RCA and CTV and in the long, laterally-placed muscle longissimus cervicis (LCe) in the single cat from which records were obtained. Activity was detected in SM or CT only during vigorous paw-licking or face-washing sequences that required large movements of the paw and forelimb.

Although face-washing and paw-licking involved a similar cyclical alteration in the recruitment of flexors and extensors, subtle differences were present in the amount and timing of activity in individual muscles. In part, these differences appeared related to the initial posture of the neck and limb, and in part they reflected variations in the kinematics of the movements. Even within a grouping of synergistically active muscles, differences in patterning of activity could be recognized from one muscle to another that presumably reflected different kinematics at upper and lower cervical joints. For example, during the extension phases shown in Fig. 7, activity in SSC did not follow the pattern of the suboccipital extensor RCP, and activity in BC was synergistic with, but not exactly matched to the temporal patterning of EMG in CM.

Recordings were also made when the cat licked the fur of its upper limb or body. To reach these body parts, the cat first made a large movement of the trunk and neck to bring its mouth close to the site to be washed. The subsequent flexion-extension movements of the head and neck generally were accomplished with a larger degree of

neck movement and a greater involvement of muscles crossing lower cervical joints. This is apparent in Fig. 8, which compares the recruitment patterns in suboccipital muscles and more caudal intervertebral muscles during paw-licking versus chest-licking. When the chest was licked, the intervertebral muscles around lower cervical joints showed strong cyclical changes in activity that were not seen during paw licking, whereas the cyclical activities in suboccipital extensors were relatively weak. Epochs of movement were also recorded in which the cat attempted to reach the least accessible parts of its body, such as its belly or tail. During such grooming behaviors, patterns of recruitment became quite specialized and previously inactive muscles, including LCE, SM, and OCI were recruited together with the more commonly used muscles, such as BC, CM, SP and RCP.

Two muscles, SP and OS, had particularly variable patterns of recruitment during grooming. SP was usually active phasically during flexion, but sometimes it was active tonically throughout the whole grooming sequence. When the cat licked its body rather than its paw, SP changed its pattern and became active phasically in synergy with CM and BC during the phase of head extension rather than flexion. OS was also active during grooming, but its pattern of recruitment was variable. In some grooming sequences, it fired tonically with little modulation, whereas in others its activity was modulated in a pattern that did not seem to match the patterns in other recruited muscles (Fig. 7). OS attaches to the scapula and its action may be related to the nature of

combined movements involving the forelimb and shoulder girdle as well as the head.

Postures and movements in the horizontal plane

In freely-moving, untrained cats, head turns of nearly 180° degrees could be observed. In some instances even large turns were carried out in a single, sweeping movement to investigate the source of an unexpected sound, as previously described by Guitton and others (Guitton et al. 1984). However, more commonly, a large movement was made in shorter, discontinuous steps separated by pauses in head movement (Fig. 9). In sequences in which the cat was trained to make head movements in response to an auditory cue, head movements were made in a single large step. No obvious differences were observed in the patterns of EMG activity or in the execution of this trained behavior when compared to large, uninterrupted turns made by untrained cats. The description presented below is based on the inspection of turns made while the cat sat with its neck oriented vertically, and its gaze directed horizontally.

Stationary postures. Cats commonly adopted stationary postures in which their heads were held turned (Fig. 3). In these postures, the extensor muscles, BC, CM and OS, each had their own unique patterns of tonic firing related to the degree of eccentricity of the head. Differences in EMG activity (compared to that in the resting posture) were modest when the head was turned less than 45° from

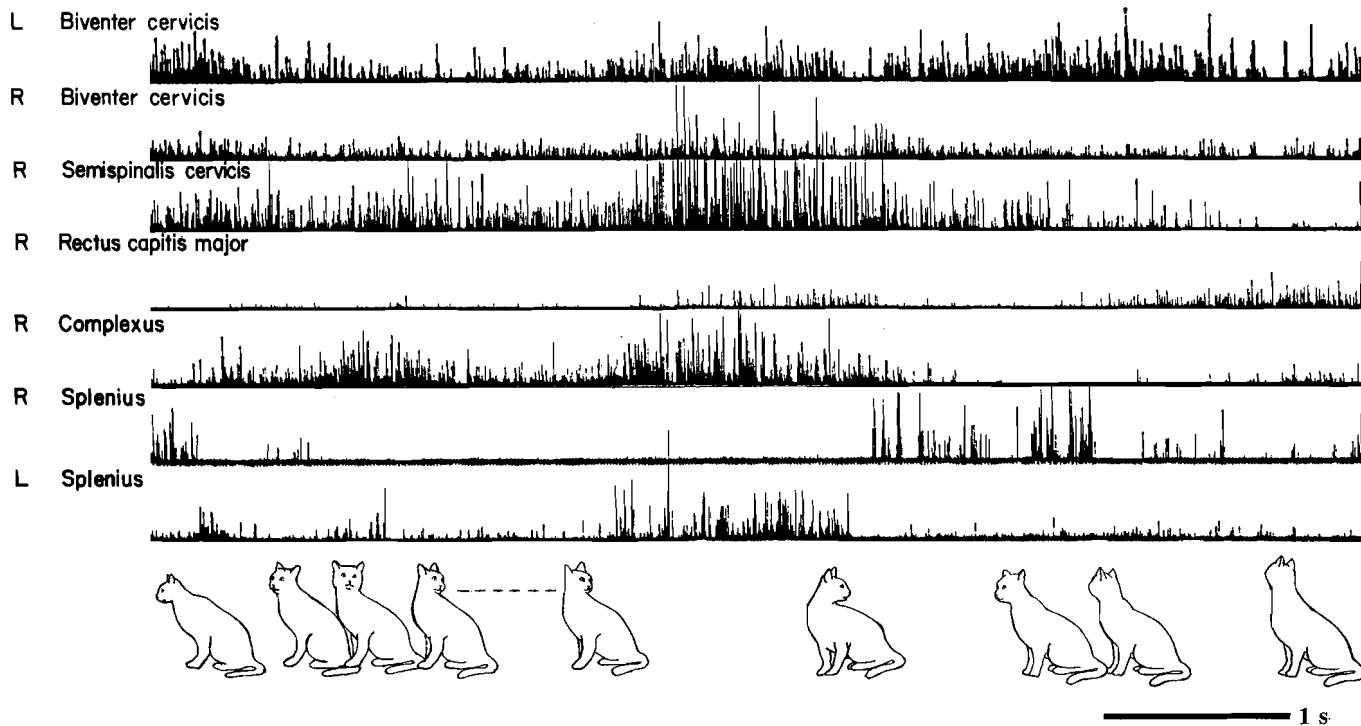


Fig. 9. Typical patterns of EMG activity during head turns. The initial left turn occurs in two steps separated by a pause in motion (marked by interrupted line between line drawings). Note the stronger EMG activity in SP and SSC during the second, most eccentric step. Activity in contralateral CM parallels that in ipsilateral SP.

The subsequent right turn is also made in two steps, the first with the head directed horizontally, the second with an upward as well as rightward component. In these steps, low levels of activity in RCP are associated with concurrent extension across suboccipital joints. Vertical bars = 0.5 mV/bin. Records from cat C2

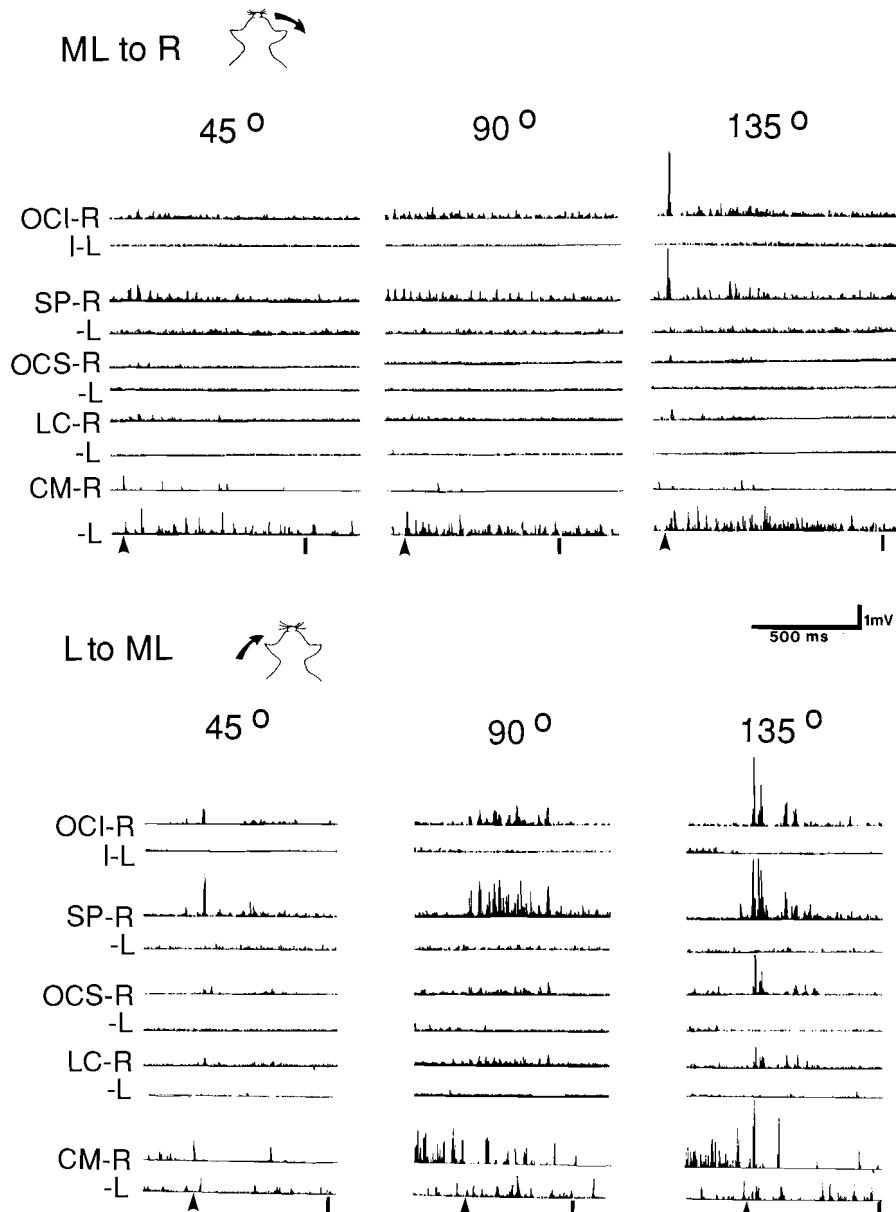


Fig. 10. Comparison of EMG activities in four sets of muscles during eccentric (top) and concentric (bottom) turns of different magnitudes. Concentric turns were associated with stronger EMG activity than eccentric turns. Arrowheads indicate point of approximate point of movement onset; vertical bar shows end of movement. Records from cat C7

midline and became more apparent when the head was turned by 90° or more (Fig. 3). In CM, activity on the contralateral side increased progressively with the increasing degree of eccentricity. Ipsilateral CM generally remained silent during turns of all magnitudes (Fig. 3), unless the skull was simultaneously inclined upwards (e.g., right turn in Fig. 9). Activity in BC increased contralaterally and decreased ipsilaterally in register with increasing degrees of eccentricity up to 90°. However, activities in BC diminished bilaterally in the most strongly turned (135° or more) postures. Activity in OS diminished bilaterally as the degree of eccentricity was increased.

When the head was turned by 45–90°, little or no tonic activity was generally recorded in ipsilateral SP, OCI, obliquus capitis superior (OCS), or longissimus capitis (LC). However, SP and OCI on the ipsilateral side fired tonically when the head was held turned by more than

90°. As well, particularly high levels of discharge were recorded in the lower intervertebral muscles, SD and SSC (Figs. 3, 9).

Eccentrically-directed turns. During the dynamic phase of a turn, increased EMG activity was observed consistently in a grouping of ipsilateral muscles including OCI, SP, OCS and LC. The magnitude of EMG firing in all of these muscles was modest (< 500 µV/bin, peak firing) unless the angle of eccentricity exceeded 90°. Figure 10 compares the recruitment of different muscles during typical turns of varying amplitudes and shows that OCI and SP are recruited quite consistently. For turns of small magnitude (< 45°), EMG activity took the form of a small initial burst of firing close to the onset of the movement, sometimes followed by a very low level of firing for the duration of the dynamic phase. For turns of larger magnitude (particularly those exceeding 90°),

this initial burst of firing was much stronger ($> 1 \text{ mV/bin}$, peak firing) (Fig. 9, 10). Sometimes, activity subsequent to this large burst took the form of a smooth, sustained increase of EMG activity, but more commonly the burst was followed by one or more small additional bursts spaced about 30 ms apart. Despite this segmented pattern of EMG activity, the turn was executed in a single, smooth movement.

The increased activity in ipsilateral OCI and SP during a single, large turn was generally paralleled by an absence of EMG activity in OCI and SP on the contralateral side (e.g., Figs. 9, 10). In contrast to previous findings of Roucoux and others (1989), no "braking pulse" of activity in contralateral muscles was observed close to the end of the movement. However, a slightly different pattern was observed during cyclical movements in which the head was turned alternately from one side to another in an uninterrupted series of sweeps in order to track an object that was waved slowly back and forth in front of the face. During these behaviors contralateral OCI often had a low level of EMG firing during the eccentric phase of the movement coincident with the much stronger activation of ipsilateral OCI. Activity was not seen in contralateral SP during the eccentric phase of these same movements.

In addition to activity in ipsilateral muscles, two contralateral muscles were consistently recruited during turns. Contralateral CM always showed increased activity during eccentric turns of all magnitudes (Fig. 9) whereas ipsilateral CM was generally silent (Figs. 9, 10). Contralateral SSC also showed increased activity during a turn, with strongest firing when the head approached maximum eccentricity during very large turns (Fig. 9).

Concentrically-directed turns. Concentrically-directed turns were studied in less detail than eccentrically-directed turns. Descriptions reported here are based on inspection of 40 sequences from two different cats in which concentric turns of 45° , 90° and 135° were made from a sitting posture with the neck held vertically. In Fig. 10, typical records from concentric turns directed to the left are compared to those of rightwardly-directed eccentric turns; these two types of turns engage a similar grouping of muscles, including right SP, OCI, LC, and OCS, and left CM and SSC. During turns of small magnitude (45° or less), bursts of EMG activity in OCI and SP were always smaller ($< 1.2 \text{ mV/bin}$, peak firing) than those during turns of larger amplitude (90° or more) ($> 2 \text{ mV/bin}$, peak firing) (Fig. 9, 10). Activities in OCS and LC, recorded in only one cat, were altered in a similar pattern to that of OCI and SP. Interestingly, the EMG bursts during concentric turns of a specific magnitude were larger than those observed during eccentric turns of the same magnitude (Fig. 10). Further, EMG activities were commonly recorded in both contralateral and ipsilateral CM during concentrically-directed but not eccentrically-directed turns.

Effect of inclination of the skull. EMG patterns during head turns were influenced by the degree of flexion-extension between the skull and the upper cervical joints.

Activity of the suboccipital muscles, RCP and OCI, decreased when turns were made while the skull was inclined downward, but increased when the skull was inclined upward. Activity in ipsilateral CM could be elicited and that in contralateral CM could be increased when turns were made with the skull inclined upward, whereas contralateral CM was silent and ipsilateral CM showed a lower level of activity when the skull was inclined downward. Some epochs of turning behavior were also recorded while the standing cat held its neck horizontally and turns were made to track items of interest on the floor. During these turns, EMG activity appeared stronger in SP and reduced in OCI compared to turns made with the neck held vertically.

Head shaking

Head shaking is a stereotyped, cyclical behavior that could be elicited by blowing or placing a drop of water in or near the pinna. The resultant shake usually consisted of 1–5 rapid cycles of oscillation, in which the head was rolled first to one side and then to the other. These fast alternating movements have temporal features similar to paw shaking responses (Smith et al. 1985). A full cycle was generally completed in 100–150 ms and a vigorous head-shake containing several oscillations could be executed in less than a second. In one half-cycle of the movement, the head was seen to accelerate in a rolling motion, brake abruptly and then return toward midline. In some sequences, the trajectory of the head followed a symmetrical path on either side of the midline, but in others, a single ear was favoured and the degree of motion was larger when the head was directed toward the favoured side.

Strong EMG firing (usually ranging from 2–8 mV/bin) was recorded in every neck muscle during vigorous head shakes. Muscles could be grouped into three sets according to the phase of the cyclical behavior during which they were recruited. One set, comprising BC, RCP, SD, SSC, and OS, was active bilaterally and had two bursts of activity during the full cycle of a shake (Fig. 11). The bursts occurred at regular intervals, with each burst beginning when the head began to approach the midline, and continuing until the head approached its most deviated position on either side. Burst discharges in RCP were often longer than in other muscles and seemed to merge into an almost tonic pattern of discharge. The second set, including CM, CT and SM, had alternating actions from one side of the neck to the other. Each muscle exhibited a single large burst of activity which began as the head returned toward midline from its ipsilateral extreme position and continued until the head approached a contralateral extreme. In some records, a second, much smaller burst could be observed as the head approached its most extreme point of ipsilateral deviation. The discharge in CT and SM ended abruptly as the head completed each cycle but the burst of EMG in CM often had a longer duration, so that it continued for several ms as the head began to accelerate in the reverse direction. The third set of muscles, including SP and OCI, had an inverse pattern, with a single large burst

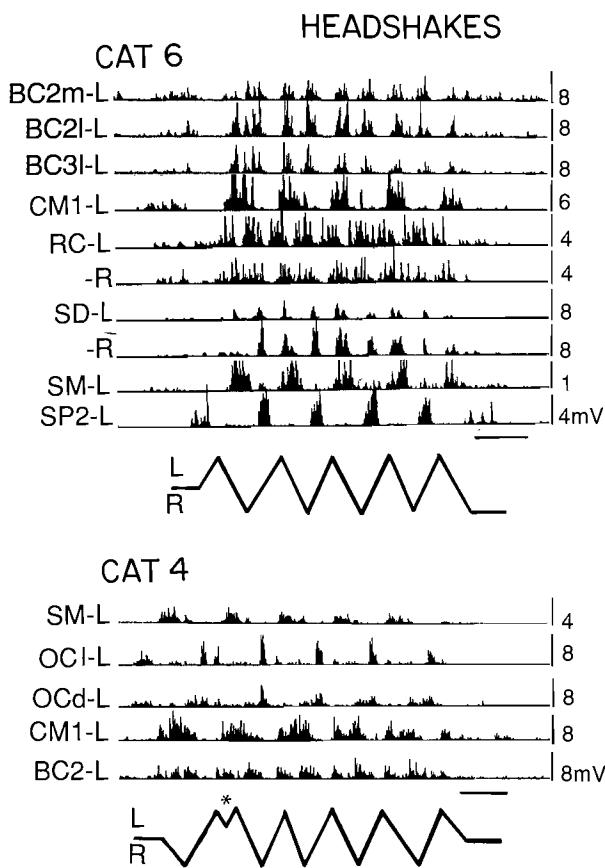


Fig. 11. Patterns of neck muscle activity during head shakes in two different cats. The line below each panel of EMG illustrates the points at which the ear reached its maximum displacement to the left (L) and right (R); no attempt was made to define the temporal characteristics of the motion between these extremes. In cat 4, the wide cyclical movement was interrupted by a short pause marked by the asterisk. OCI and OCd are records from superficial and deep regions of OCI respectively. A more phasic firing pattern is apparent in superficial layers and a sharper double burst is associated with the unusual pause. In cat 6, the recorded shake (lower panel) has a slightly longer cycle, so that the time base was adjusted to show the similar patterning between cats. In both panels, the horizontal bar = 100 ms

of discharge occurring when the head rotated toward the ipsilateral rather than the contralateral side. Records from the deep layers of OCI showed the broadest and least sculpted pattern of firing that commenced as the head began to return from its most deviated contralateral position. Bursts in superficial layers of OCI and SP were sharper and occurred several ms later as the head approached the midline in the course of its ipsilaterally directed trajectory. Notably, most muscles had bursts of EMG activity at times when they were lengthening (as is also typical for paw-shaking responses; Smith et al. 1985).

Relevance of whole body posture

In the behavioral sequences outlined above, cats always sat, stood or reclined with their thoracolumbar column

oriented in a straight line and their paws placed symmetrically on the supporting surface. However, behavioral sequences from such postures were only one part of a broader range of head and neck movements. Systematic analysis of these additional behavioral sequences was beyond the scope of this study. However, it was clear from inspection of a sampling of these behaviors that muscle activities were influenced strongly by the initial posture of the cat. In cats that adopted different postures, major changes of muscular recruitment were observed, presumably to cope with the altered gravitational relationships and changes in relative locations of bony structures. For example, cats commonly chose to recline in side-lying or ventral-up postures which were associated with decreased tonic firing in the neck extensors, BC and OS, and increased firing in ventral muscles, such as RCA and SM.

Discussion

Head movement or head-neck movement?

The role played by neck muscles can only be properly understood in the context of cervical kinematics. Head movement in the cat is often conceptualized quite simply by assuming that all motion occurs at a single universal joint located between the skull and C2 (Pellionisz and Peterson 1988; Wickland et al. 1991). Thus, little attention has been paid to the potential actions of lower cervical vertebrae which, until the last five years, were generally assumed to lie in a horizontal orientation collinear with the thoracic and lumbosacral column. In 1986, however, Vidal and coworkers demonstrated using fluoroscopy that the skull of the sitting cat was borne on top of a vertically-oriented cervical column. More recently, they have suggested that head movements in cats, like head movements in humans, depend upon motion at lower cervical as well as upper cervical joints (de Waele et al. 1987). These results were confirmed and extended by the fluoroscopic observations described in this work. The cervical column acted as if it were divided into two functionally-independent joint-sets (one between skull-C2, the other between C3-T1). These had different capabilities to produce head movement in the cat as in man (e.g. Penning 1968; Kapandji 1974; Winters and Peles 1990). Movements of the suboccipital joints were found to change the angle of inclination of the skull without greatly affecting the orientation of the lower cervical joints. However, the much larger flexion-extension movements of cervicothoracic joints not only rotated the neck with respect to the shoulder but caused a significant translation and reorientation of the skull and the suboccipital region. This effect necessarily changes the operating conditions of suboccipital muscles as well as muscles crossing lower cervical joints. For example, flexion of lower cervical joints cantilevers the skull in front of the cervical column, so that the column no longer bears the weight of the skull and increased muscular activity is required to oppose gravitational forces on the head (Vidal et al. 1986). This greater requirement for muscular

force appeared to be reflected by the increased activity in extensor muscles crossing both the upper and lower cervical joints when the cervical column was oriented horizontally rather than vertically.

Flexion across lower cervical joints also reorients the long axis of the skull, so that the skull must counterrotate around the suboccipital joints to maintain a stable line of gaze or to keep the horizontal semicircular canals parallel to earth. To execute this counterrotatory movement, increased activity will be needed in suboccipital muscles such as RCP and CM despite the fact that the larger concurrent flexion across the lower cervical joints will have a dominant action to lower rather than lift the head. Therefore, any control schema developed by the nervous system to ensure a particular orientation of the skull (and thus the eyes and ears) must be organized to produce compensatory forces and counterrotatory movements across the suboccipital joints whenever the lower cervical joints are flexing or extending the neck. The common use of antiphasic movements at the two joint-sets presents an interesting problem for the control of long neck muscles that cross both joint-sets. It is not yet clear whether the actions of individual multi-articular muscles are tied primarily to movements across only one of the joint-sets or whether the muscles have two different "controllers" engaged in developing movements across the upper and lower joint sets respectively. These controllers would have to interact when the long muscles were active during antiphasic movements across the two joint sets.

The specialized movements responsible for sagittal-plane motion may be organized quite differently than movements such as head turning, that involve movement in other planes. The kinematics of turning have never been analyzed quantitatively in cats, so that it is not yet clear whether upper and lower cervical joints always move dependently, as seems to be suggested by the literature on man. When humans turn their heads, the movement appears to be distributed asymmetrically along the cervical column. The upper cervical joints are considered to be the site at which the first 40° of motion takes place; lower cervical joints contribute the additional motion required for turns of larger magnitude (White and Panjabi 1978). If motion is distributed asymmetrically across the feline cervical column as well, this may explain why muscles that cross lower cervical joints (e.g., SP, SSC) were found to be activated so strongly during turning movements greater than 90°.

Because head-neck movements are complex, they are difficult to describe using a succinct, unambiguous terminology. In the past, vestibular physiologists have described movements of the skull according to their effect on the labyrinth, with movements in pitch, roll, and yaw serving as synonyms for flexion-extension, lateral bending and axial rotation respectively (e.g. Baker et al. 1985; Suzuki et al. 1985). However, the use of vestibular terms is insufficient to give a total picture of head-neck movement because kinematically different head movements can have a similar action on the vestibular system, depending upon the orientation of the neck. For example, a movement "in yaw" would depend upon axial rotation

around upper cervical joints when the neck is oriented vertically, but lateral bending of the cervical column when the neck is held horizontally. Thus, a more complete specification is needed. At the least, one might hope for information on the orientation and direction of movement of the cervical column in addition to the skull. Some who study human cervical kinematics have suggested that the x, y and z coordinates for every vertebra be specified with respect to the adjacent vertebra (Panjabi et al. 1974). Such detailed quantitative information cannot be provided by current laboratory methods for monitoring head movements, such as search-coil techniques (e.g. Guittot et al. 1984; Roucoux et al. 1989). More ambitious analyses will have to rely on fluoroscopic methods, which are only beginning to be used to study feline head movements.

Patterns of muscular activation

Previous studies of EMG activity during head movement have focused largely on the operation of a subset of neck muscles whose activities were monitored during a single behavioral paradigm (e.g. Roucoux et al. 1989; Peterson et al. 1989). In the present study, we have attempted to provide a broader framework for understanding neck-muscle usage, first by extending the range of studied behaviors and second by recording from a wider range of muscles. The challenge is to extract general principles from these large quantities of observational data. The present discussion will focus on only a few of the more striking observations that may have general implications for the way in which we study and describe the motor control of neck muscles.

Dynamic range of neck muscles. A remarkable feature of neck-muscle recruitment was the wide-ranging amplitude of EMG signals recorded during different behaviors. During ballistic movements such as head shaking, levels of EMG activity were many times higher than those during slower, less forceful movements, such as turning or lifting the head for the purposes of saccade or visual pursuit. Indeed, from the results presented here, it would appear that turning and flexion-extension of the head are amongst the least taxing tasks that the neck muscles are called upon to accomplish. If we can assume that motor units in neck muscles as in limb muscles are recruited in an orderly fashion according to type (Henneman and Mendell 1981), we might speculate that simple, unloaded movements such as elevation and turning might be carried out primarily, if not exclusively, by the slow motor units which constitute 25–50% of fibers in most neck muscles (Richmond and Vidal 1988).

High levels of EMG activity were also recorded when cats attempted to move their heads against resistance imposed by the hands of the investigator. These results corroborate the findings of Roucoux and coworkers (1989) that neck-muscle EMG activities were much higher in head-restrained cats than cats whose heads were free to move during gaze-shifting behaviors. Observations during head shaking and head restraint suggest that neck

muscles have a greater force-developing capacity than is generally required to execute simple movements such as those elicited by most current experimental paradigms. The free-ranging cat uses its head to oppose or carry a load in many situations that are critical to its survival. These behaviors, including prey-catching and killing, fighting, mating and carrying kittens and other objects in its mouth, must also be recognized when attempting to understand the significance of the size and organization of the neck musculature.

The level of EMG activity recorded in a muscle has often been regarded as an index by which its force production can be gauged. However, the force-developing capabilities of neck muscles, like other skeletal muscles, will also be shaped by length-tension and force-velocity relationships (cf. Zajac 1989), and these will vary with head-neck posture and movement dynamics, respectively. Many neck muscles were found to be active over a wide range of postures for which their lengths might be expected to change considerably. For example, EMG activity was observed in BC when the head and neck were both extended (Fig. 2) and flexed (Fig. 5). Previous morphometric studies of BC would suggest that the muscle may be stretched to as much as 130% of its shortest length over such a physiological range (Fig. 7, in Richmond and Armstrong 1988). Force-velocity relationships must also be considered, for example, during some forceful movements such as head shakes, when many muscles were recruited as they lengthened. This pattern of recruitment is appropriate to decelerate the inertial mass of the head but it also serves to enhance the force-developing capabilities of the muscle by ensuring that the muscle operates on the lengthening part of its force-velocity relationship.

Actions of long neck muscles. The long dorsal muscles BC, CM, and SP have been subjected to intensive study (e.g., Brink 1988; Richmond and Vidal 1988; Rose and Keirstead 1988), yet their roles remain difficult to understand. All three muscles cross many of the cervical vertebrae and thus can generate torques around both lower as well as upper cervical joint-sets. However, the extent to which these torques will cause movement at these joint-sets will depend on a complex combination of factors: the relative sizes of the torques (dictated by the relative moment arms across the two joint-sets in any particular posture); the available ranges of motion at the two joint sets; and the relative stiffnesses of the two joint-sets (dictated in part by the synergistic or antagonistic actions of deep, short neck muscles) (Richmond et al. 1991). It is therefore difficult to assess the contributions of these functionally "biarticular" muscles until a fairly complete analysis of the biomechanics of this system can be carried out.

Nevertheless, it is clear from the EMG records that each dorsal neck muscle is controlled by the nervous system in a different and specific way that presumably relates to its biomechanical organization. The marked differences in recruitment between SP and BC were anticipated from previous EMG studies of these two muscles in alert cats; SP is known to be recruited during head

turning (Vidal et al. 1982; Roucoux et al. 1989) whereas BC is most active during extension (Roucoux et al. 1989; Baker and Wickland 1988). However, the substantial differences in recruitment between BC and CM were not expected. Previous electrophysiological studies of BC and CM motoneurons have shown that they receive similar inputs from those parts of the segmental and descending systems studied to date. For example, a close relationship has been described between the Ia inputs from one muscle onto the motoneurons of the other (Wilson and Maeda 1974; Anderson 1977), and between the Renshaw effects elicited from antidromic stimulation of one set of motoneurons onto the other (Brink and Suzuki 1987). The temptation to view these muscles as a single functional unit has been reinforced by their closely-related peripheral organization: the two muscles lie side-by-side in the same fascial plane; they are innervated by nerve branches that travel together in shared nerve bundles; their motoneurons have similar structural features and are located in the same part of the cervical ventral horn (Richmond et al. 1978; Rose 1981). However, the results presented here suggest that BC and CM cannot be regarded as obligatory synergists. For example, BC and CM had different patterns of recruitment during head turning and head shaking. The behavior of CM in both of these movements appeared to be linked more strongly to the activity of the contralateral turning muscles, SP and OCI. The increased activity in contralateral, but not ipsilateral CM, has also been noted during turning movements in alert cats elicited by electrically stimulating the caudate nucleus (Akaike et al. 1989). However, the significance of this synergy remains difficult to explain. Unlike BC, which runs parallel to the vertebral column, CM angles obliquely and has been suggested to have force-vector components that serve to pull the head in pitch (extension) and roll (axial rotation) but not in yaw (lateral turning) (Wickland et al. 1991). Further, it is a shorter muscle that does not extend caudal to C5, where most lower cervical motion appears to take place. We might speculate that its contralateral recruitment during head turns may serve to balance components generated by flexor muscles that would tend to roll the ipsilateral ear downward (Kapandji 1974). The specialized recruitment in CM underscores the need for great caution in predicting the actions of a single neck muscle from its anatomical characteristics without considering the synergistic or antagonistic roles of other concurrently active muscles.

Only two muscles, BC and OS, exhibited consistent extensor activity during quiet sitting. Their tonic activity appears to be associated with fatigue-resistance as reflected by their predominant content of slow, oxidative fibers (Richmond and Abrahams 1975). However, BC and OS were not always matched in their patterns of recruitment during other behaviors, such as grooming. Occipitoscapularis (which originates from the scapula) was found to have a particularly variable pattern of activity, presumably because the shoulder girdle participated in movements of the forelimb, as well as those of the head and neck. Comparisons of BC and OS illustrated a general rule governing all of the neck extensors: epochs

of behavior could be found in which different "extensor" muscles (including BC, CM, RCP, OS, SD and SSC) were all used in synchrony, but no two muscles were found to have consistently similar patterns of activation across the whole range of behaviors in which they participated. Further, under some postural conditions, synergistic extensor actions could be contributed by muscles that operated antagonistically at other times (e.g., SP vs. BC in Figs. 6, 7).

In addition to the relatively well-studied dorsal neck muscles, EMG recordings were also obtained from several lateral and ventral muscles that have previously been assigned a role in head movement largely on the basis of anatomical considerations (LC, LCe, CT, SM, RCA; Reighard and Jennings 1963). Two muscles of particular interest were CT and SM, which are unique anatomically in several respects. Both are innervated by the spinal accessory nerve; both span between the skull and the shoulder girdle; and both contain a higher proportion of fast, glycolytic fibers than most other muscles in the body (Richmond and Vidal 1988). In the present study, neither CT nor SM was found to be active during most unloaded head movements such as those associated with orienting, feeding or visual pursuit. These observations confirm the report by Wickland and her coworkers (1991), who observed that EMG activity in feline CT was not linked to head movements under unspecified behavioral conditions. However, the failure to observe activity in CT during movements of modest amplitude and speed may not be sufficient to rule out its participation in head movements of any other type. In the present study, both CT and SM were recruited strongly during forceful head movements such as head shaking. It may be that the roles played by CT and SM can only be understood by investigating vigorous behaviors that depend on strong, fast muscles with little fatigue-resistance. These observations underline another general principle that must be considered when assigning functions to neck muscles – that the recruitment of an individual muscle may depend not only on its biomechanical relationships but also on metabolic considerations such as its fiber-type composition.

Intervertebral and suboccipital muscles. It was not the intention of this study to provide a systematic description of activity in the many small, deep muscles investing the cervical column. It is technically challenging to record from these muscles because they are difficult to implant with electrodes and to shield from the cross-talk of neighbours. Yet it became apparent from the limited observations in the present study that patterns of activity in suboccipital and intervertebral muscles often provided critical clues about movements at different joint-sets. Because suboccipital and intervertebral muscles have strategic locations across the vertebral joints, they are well-situated to influence the mobility of particular parts of the cervical column, as has been discussed in greater detail elsewhere (Richmond et al. 1991). One significant observation was the frequent dissociation between activities in suboccipital as compared to lower intervertebral muscles (e.g. Figs. 7, 8). Such differentiation in the pat-

terns of recruitment must have a neural substrate. In the future it will be important to explore the central mechanisms responsible for the selective recruitment of these different muscle groupings. We might speculate, for example, that suboccipital muscles will be the logical targets for the descending pathways of vestibulocollic reflexes to produce small but rapid compensatory movements of the head in coordination with compensatory eye movements. In contrast, systems that coordinate larger shifts of posture might be expected to have more extensive projections into the caudal as well as rostral cervical segments in order to coordinate the long dorsal muscles, intervertebral muscles and shoulder muscles that were often observed to be active synergistically during many natural behaviors.

Is the musculature of the neck over-complete?

Movements of the head and neck result from the combined work of many neck muscles. If we are to formulate hypotheses about the coordination of this system, it is desirable to identify relatively simple "rules" that adequately summarize the more complex phenomenology. One useful tool for identifying the minimal complexity necessary for such rules is the enumeration of the degrees of freedom of the system. In the case of the cervical spine and its planar articulating facets it seems likely that each of the eight joints from skull to T1 has at least two degrees of freedom, resulting in a sixteen-dimensional control problem. Because muscles can act in only one of two directions at a joint (i.e., they pull but cannot push), a minimally complete set of muscles would number thirty-two, not far from what is actually observed (Richmond and Vidal 1988). It has been suggested that some of these degrees of freedom can be excluded on the grounds that the joints are operating at or near mechanical limits of their range of motion (Graf et al. 1991). Although it is true that the angular excursion of some cervical joints is smaller than is generally the case in limb joints, it is also true that measurable movements occur in all of the intervertebral joints (Selbie et al. 1991), and that the distribution of these movements depends on behavioral context. Thus, these degrees of freedom cannot be ignored; they exist and must be controlled actively by muscular contraction.

The results of this study suggest that the coordination of muscles during head movement may pose a more sophisticated problem of motor control than has generally been acknowledged. In previous work, the complexity of the motor-control problem has necessarily been constrained by considering only a small subset of behaviors in which the degrees of freedom are reduced (e.g., low-amplitude turning movements confined primarily to upper cervical joints). If the set of muscles is minimally complete for the control of unrestricted motion in the cervical spine, then it must necessarily appear to be "overcomplete" for such restricted subsets of motion. This raises two interrelated questions:

- 1) What possible processes might lead to stereotyped patterns of muscle activation during such restricted paradigms?

2) How should we design and select among such restricted paradigms to be certain that the observed patterns of activity will shed light on neurophysiological mechanisms?

No experimental study can answer these important conceptual questions. However, this and other systematic studies of normal and hence less restricted behaviors provide a critical context for the design and interpretation of more restrictive experimental paradigms.

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