

Effect of Neck Posture on the Activation of Feline Neck Muscles During Voluntary Head Turns

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SUMMARY AND CONCLUSIONS

1. To determine whether neck posture affects the usage of neck muscles during a specific motor task, we recorded the electromyographic (EMG) patterns of neck muscles in four cats, which made horizontal, head-turning movements to fixate eccentrically placed targets. In some trials, the cervical column was oriented vertically whereas in other trials, the cervical column was oriented more horizontally.

2. During horizontal head movements, five muscles (obliquus capitis inferior, splenius, levator scapulae, complexus, and biverter cervicis) displayed activation patterns that were consistent from cat to cat and did not change when the cats adopted a different neck posture. Most of these muscles are large, superficial muscles that attach to the skull and span many cervical joints.

3. Posturally dependent patterns of activation were observed in five other neck muscles (semispinalis cervicis, longissimus capitis, levator scapulae ventralis, scalenus anterior, and obliquus capitis superior). Most of these muscles lie deeper and more laterally within the neck musculature and generally span fewer cervical joints than the muscles that displayed invariant patterns of activation.

4. These results suggest that the set of invariantly activated muscles may compose part of a basic motor program that is triggered during head movements in the horizontal plane. This motor program appears to be modified by the selective activation of ancillary muscles, which are recruited in a manner related to the neck posture. The deep positioning of the ancillary muscles may permit them to regulate the mobility of the cervical column and to adjust the net muscular force applied across the neck to the skull. Organizing the motor output in this manner might simplify the task of computing the appropriate patterns of neck-muscle activation.

et al. 1985; Denise et al. 1987; Keshner et al. 1992; Roucoux et al. 1989; Vidal et al. 1982; Wilson et al. 1983). However, the relationship between the head and body is not the same as that between the eyes and head. The head is connected to the body, not by a single universal joint, but rather by a highly flexible, multiarticular neck. The joints at the upper and lower ends of the cervical column permit a wide range of motion in the sagittal plane (Selbie et al. 1993). Thus a cat can hold the orientation of its head and body relatively constant but still change substantially the posture of the intervening cervical column, from a horizontal to a vertical orientation.

In this study, we have taken advantage of the cats' ability to make horizontal gaze shifts from different, voluntarily assumed, initial postures: the head and body were held in similar, near-horizontal orientations, but the cervical column was held either vertically or horizontally (Fig. 1). Although the trajectory of the head is similar during turns from both of these postures, the kinematics of the underlying joint motion are quite different. When the cervical column is oriented vertically, small horizontal turns are accomplished principally by axial rotation of the specialized C1-C2 joint; larger turns involve increasing amounts of axial rotation at the lower cervical joints (Graf et al. 1992; Richmond and Vidal 1988), as has been described for human subjects (Kapandji 1974). However, when the cervical column is held horizontally, both small and large turns of the head are accomplished by lateral flexion distributed along the length of the cervical column (Richmond et al. 1992; W. S. Selbie, D. B. Thomson, and F. J. R. Richmond, unpublished observations).

The neck contains many muscles that pull in different directions at the various joints (Richmond and Vidal 1988), leading us to hypothesize that the patterns of recruitment in muscles responsible for head and neck movements would be quite different when head turns are made in the two different postures. To test this hypothesis, we have recorded electromyographic (EMG) signals from a wide range of muscles, including superficial, multiarticular muscles as well as deep muscles with more local actions. We observed consistent and large changes in the activity of many deep muscles. However, changes in cervical posture did not modify the recruitment patterns in another group that included some large muscles whose pulling directions would seem more appropriate for turns in only one of the two postures. These results seem to be inconsistent with the predictions of muscle activity based on previous biomechanical models (cf., Pellionisz and Peterson 1988), and they may suggest the presence of a neural computational strategy that simplifies the control of this complex system of

INTRODUCTION

When presented with a stimulus in their lateral visual field, cats and many other mammals make coordinated horizontal movements of the eyes and head to shift their gaze onto the new target. To describe the kinematics of the eye movements during such gaze shifts, it is necessary to define the orientation of the platform upon which the eyes rotate, namely the head. In fact, the head usually is held such that horizontal gaze movements are roughly aligned with the horizontal axis of the eye (Ezure and Graf 1984; Vidal et al. 1986; see also Pozzo et al. 1990); motion in this plane therefore can be controlled quite simply by a pair of antagonistic muscles, the medial and lateral recti. To describe the kinematics of head movements during lateral gaze shifts, the platform upon which the head rotates is generally considered to be the body. When experiments are performed on cats, care generally is taken to place the body in a consistent, usually recumbent, posture (Baker et al. 1985; Darlot

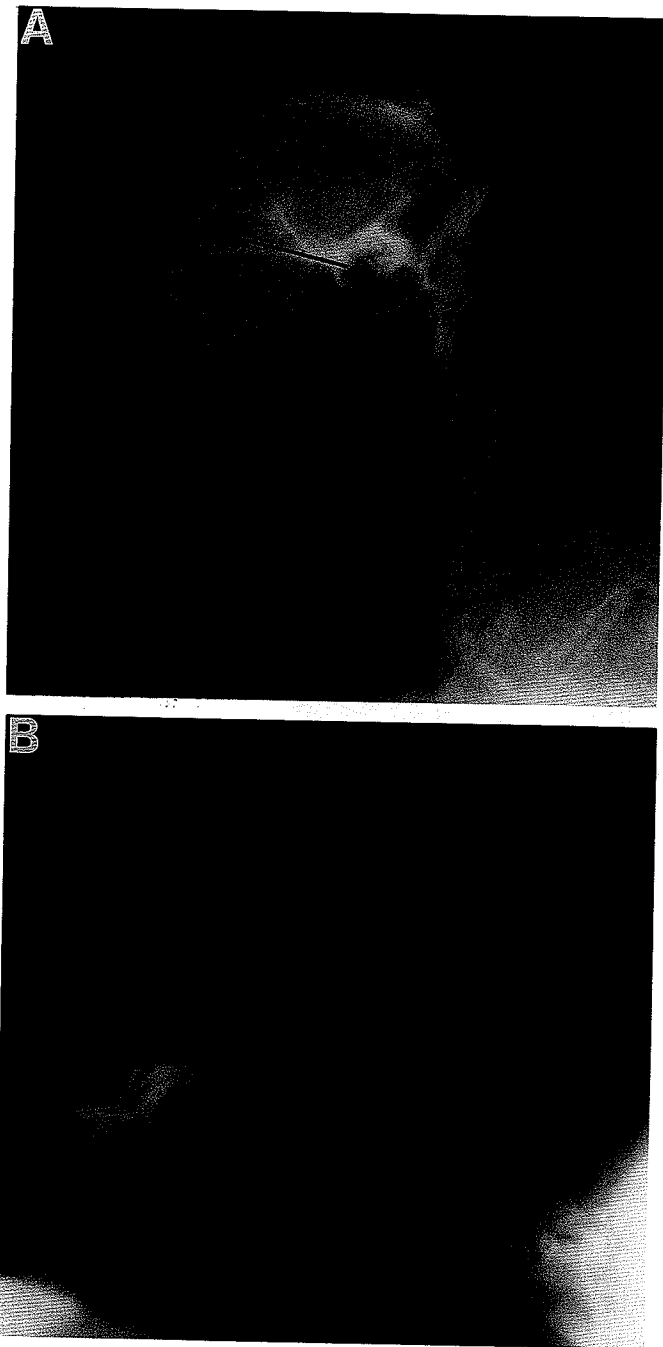


FIG. 1. X-ray images showing cat No. 4 in the vertical (A) and horizontal (B) neck postures. Black lines indicate the plane of the horizontal canals and the orientation of cervical vertebrae C3-C5.

muscles. Results of this study have been reported previously in abstract form (Thomson et al. 1993a,b).

METHODS

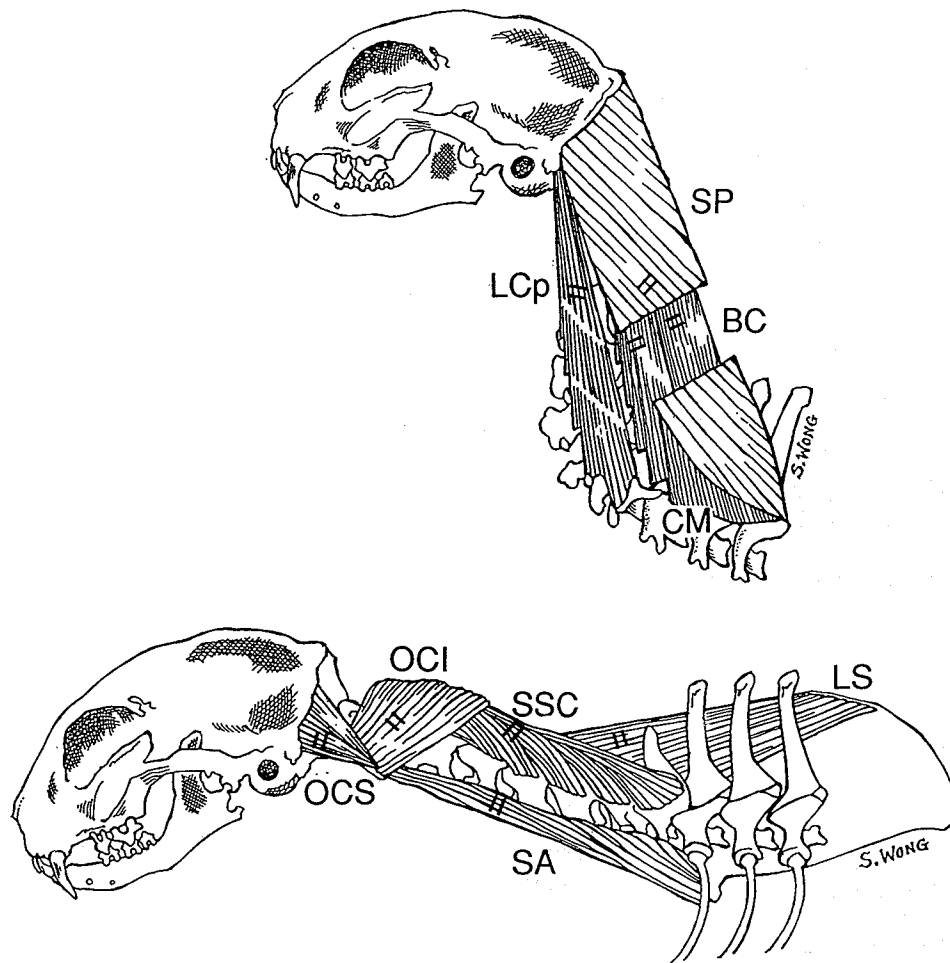
Initial training

Four cats (4.7–6.6 kg) were trained using positive reinforcement to lie prone in a restraining harness that was strapped around the chest. While in the harness, the body was held in a consistent, symmetric position and, from this recumbent posture, cats were trained further to make large-amplitude, horizontal turning move-

ments of the head. Such turns were evoked by the appearance of a target placed, at eye level, 70–90° from midline, which was at a more eccentric position than could be fixated by changing eye position only (Guitton et al. 1980). The movement of a feeding spoon cued the animal to orient toward the left or the right side and then rotate its head back toward midline to obtain a food reward (subsequently referred to as an "unilateral" turn). In some trials, the cat rotated its head toward a target on one side, then swept its head completely around toward a target on the opposite side before returning to midline (a "bilateral" turn). During head-turning movements, the height of a broad Plexiglas barrier above the cat's head was adjusted to one of two heights. In one set of trials, the barrier was held far above the cat so that the animal was free to orient its cervical column vertically. In another set of trials, the barrier was lowered close to the level of the shoulder blades, and the cat oriented its cervical column more horizontally so that its head did not rub against the barrier. To image the typical orientation of the skull and cervical column in these two different postures, X-rays were taken of one cat as it sat in the restraining harness (Fig. 1). The plane of the horizontal canals was superimposed on these images using the known relationship of the canals to bony landmarks of the skull (cf. Vidal et al. 1986). The orientation of the cervical column was determined by connecting the dorsal surfaces of the vertebral bodies of C3–C5 with a straight line.

Surgical procedures

Trained cats were anesthetized with sodium pentobarbital (35 mg/kg ip, supplemented intravenously to suppress withdrawal reflexes) and chronically indwelling EMG electrodes were implanted under aseptic conditions, using a similar approach to that described in Richmond et al. (1992). Muscle layers were separated from the dorsal midline raphe to gain access to the cleavage planes between the layered neck muscles and to expose implantation sites (Fig. 2). Either 18 or 19 muscles were implanted in each cat using both bipolar, epimysial patch electrodes and bipolar, intramuscular electrodes (Table 1). Muscles were chosen for implantation because they had shown modulated activity during horizontal turns in previous examinations (i.e., Akaike et al. 1989; Keshner et al. 1992; Roucoux et al. 1989; Vidal et al. 1982) or because they had anatomic relationships that seemed appropriate for participating in the head movements studied here (Fig. 2). Full details of the electrode design have been published (Loeb et al. 1987; Richmond et al. 1992). Briefly, patch electrodes consisted of one or more pairs of Teflon-coated, multistranded stainless steel wires, attached to Dacron-reinforced Silastic sheeting. The recording contacts were 3 mm long and were separated by 3 mm. Intramuscular electrodes consisted of pairs of Teflon-coated, multistranded stainless steel wires whose ends were bared of insulation. The ends of the wires were stitched into the muscle belly so that the electrode separation was about 3 mm. Some muscles that were implanted with intramuscular electrodes were shielded from the potential cross-talk of adjacent muscles by suturing nonreinforced Silastic sheeting to the overlying fascia. Muscle layers then were reestablished with sutures, and the leads from all implanted devices were passed subcutaneously to the dorsal lumbar region where they were externalized through a small incision. The leads were soldered onto a 40-pin connector that was sutured to the lumbosacral fascia (Hoffer et al. 1987). Prophylactic doses of penicillin G/streptomycin or trimethoprim/sulphadiazine antibiotics were administered pre- and postoperatively. Recording sessions usually began on the fifth post-operative day and continued for ≤ 10 days. After data collection, the animals were killed with an overdose of sodium pentobarbital and neck muscles were inspected carefully to determine the exact locations of the recording electrodes. If this postmortem examination indicated that a particular set of electrodes was poorly shielded or positioned improp-



	Origin	Insertion	Number of Joints Crossed	Primary Action on Skull	
				Vertical	Horizontal
BC	C5-T2	skull	8	P	P
SP	midline raphe	skull	7	R(Y/P)	Y(R)?
CM	C3-C6	skull	5	R(P)	Y
LS	dorsal scapula	C2-C7	5	Y(P)?	R(P)?
OCI	C2	C1	1	Y(R)	R(Y)?
SSC	C4-T1	C3-C6	4	P(R)	Y
LCp	C3-C7	skull	6	R	Y
OCS	C1	skull	1	R	Y

FIG. 2. *Top*: head and neck in 2 postures showing muscles studied in this experiment and the locations of the recording electrodes. One line drawing (*top*) illustrates the more superficial muscles whereas the other (*bottom*) shows the muscles with closer relationships to the cervical vertebrae. Levator scapulae ventralis (LSv) is not illustrated. *Bottom*: table to show anatomic relationships and presumed pulling directions of muscles. Anatomic information was taken from Richmond and Vidal (1992) and Reighard and Jennings (1963). Primary actions (Y, yaw; R, roll; P, pitch) are suggested in bold; actions in brackets denote components ≥ 0.5 times that in the primary direction. Muscle actions upon the skull in the vertical posture were taken from Wickland et al. (1991). The actions of levator scapulae (LS), semispinalis cervicis (SSC), and longissimus capitis (LCp) were not tabulated by Wickland et al (1991); instead, they were inferred from anatomic relationships. Muscle actions upon the skull in the horizontal posture were postulated according to the altered pulling directions of the muscles (see also Reighard and Jennings 1963). BC, biventer cervicis; SP, splenius; CM, complexus; OCI, obliquus capitis inferior; OCS, obliquus capitis superior; SA, scalenus anterior.

TABLE 1. Recorded muscles and abbreviations

Muscle	Cat			
	1	2	3	4
Biventer cervicis (BC)	X	X R	R	L R
Complexus (CM)	L R	L R	X R	l r
Levator scapulae (LS)	R	X R	L R	l r
Levator scapulae ventralis (LSv)	L R	L R	L R	
Longissimus capitis (LCp)	L X	l r	l r	x r
Obliquus capitis inferior (OCI)	l r	l r	X R	l r
Obliquus capitis superior (OCS)	L X	X X	X R	l r
Scalenus anterior (SA)	l r	X R	l r	x x
Semispinalis cervicis (SSC)	X R	L	L R	L R
Splenius (SP)	L R	L R	X R	L R

Muscles that were implanted with patch electrodes are designated by L (left) or R (right) to indicate the side of the implanted device. Intramuscular electrodes are designated by a lowercase letter. X indicates a channel that was excluded from analysis because of cross-talk, breakage, or inappropriate placement as determined at the postmortem examination.

erly, then the signal from that muscle was excluded from further analysis (Table 1).

Data collection and analysis

EMG signals were amplified differentially (50- to 5,000-Hz bandwidth) and recorded on an 18-track FM tape recorder (DC-10 kHz bandwidth). During a single recording session, signals from 15 muscles were recorded simultaneously. In some cases, the 15 muscles were chosen by eliminating channels whose signals were unreliable; in other cases, a subset of 15 muscles was varied from one recording session to another to sample from the full range of implanted muscles. Other FM recording channels were used for a timecode (Society of Motion Picture and Television Engineers) and a voice track. Head movements were videotaped (60 fields/s) using two shuttered cameras that were placed at right angles above and to one side of the cat. To better visualize certain external landmarks of the skull, reflective markers were placed on head during recording sessions. A split-screen view of the two camera images, the voice track, and the timecode were recorded on a video recorder. In addition to the head-turning movements described above, recording sessions also included untrained head movements such as head shaking elicited by placing a drop of water in the pinna.

Videotapes were examined off-line and timecodes were identified that corresponded to sequences of interest; these timecodes were used to locate the appropriate sequences of EMG data on the FM tape. Sequences of head-turning movements were digitized if they met certain criteria: the eccentric endpoint(s) of the movement had to reach 45° from midline, the cat's head must have moved without interruption throughout the entire sequence, and the duration of the turn had to fall within one SD of the mean duration of all analogous turns (Table 2). This latter step was

taken to produce a data set of comparable voluntary head turns, free of unusually fast or slow movements. All EMG signals were rectified and integrated into 3.3-ms bins and were digitized at synchronized 3.3-ms intervals by a Macintosh computer. Because the bin integrators were calibrated with a 1-kHz square wave and 1-ms bins, each digitized value was divided by the sample interval (3.3 ms) to obtain the mean microvolt value for that bin. Generally, EMG signals processed in this manner are ~10 times smaller than the peak-to-peak (p-p) amplitude of the unprocessed signals; therefore, a trace presented here with a 50-μV peak amplitude would correspond to ~500 μV_{p-p} (referred to amplifier input). In total, 244 voluntary head turns were digitized (Table 2). This set of data from all four cats was examined for cross-talk of EMG signals. Cross-talk was suspected if sequences could not be identified in which adjacent muscles were recruited at different times and, on this basis, some channels were excluded from analysis (Table 1). The background noise level from all channels was ~5 μV. The descriptions of EMG patterns that follow are based on inspection of many individual sequences of rectified, bin-integrated signals, some of which are depicted in Figs. 4-7 (top). Within a set of similar head-turning movements obtained from a single animal (i.e., all unilateral turns to left side, vertical posture), the patterns of EMG activity were found to be quite consistent across trials and any observed differences did not appear to be related to the relatively small differences in duration of the sequences. However, when such a set of turning sequences was compared across animals, some differences were noted in the usage of individual muscles, particularly in their firing levels. To assess and to illustrate the intertrial and interanimal variability in the EMG patterns, averaged sequences (i.e., Figs. 3-8, bottom) were computed from 5 to 13 individual sequences of comparable movements from each animal. Initially, individual sequences were subdivided into epochs in which the head moved smoothly in a single direction. Unilateral turns (i.e., Figs. 3, 4, and 8) were divided into two epochs (an eccentric rotation away from midline and a concentric rotation back to midline) whereas bilateral turns (i.e., Figs. 5, 6, and 7) were divided into three epochs (eccentric rotation from midline, a sweeping movement from the ipsilateral to the contralateral side and concentric rotation back to midline). These divisions between epochs were determined by inspection of the video record to find the single field (half a video frame; equivalent to 16.7 ms) during which the head began to rotate in a different direction. The length of each epoch was normalized (20 points/epoch), and, for each corresponding point, the data were averaged and a SD was computed. Data from left and right muscles were not pooled during the averaging step.

The firing levels of individual muscles are reported below as the peak amplitudes (μV) observed during averaged head-turning sequences. These values are compared only with those observed in the same muscle during averaged turns under different postural conditions. We initially intended to relate all EMG values to the average peak signal observed during head shaking; this would reflect the EMG firing associated with a particularly vigorous form of head movement (Richmond et al. 1992). Although the strong

TABLE 2. Voluntary turning sequences

Cat	Unilateral Turns				Bilateral Turns			
	Vertical posture	n	Horizontal posture	n	Vertical posture	n	Horizontal posture	n
1	2.4 ± 0.6	20	2.8 ± 1.0	25	3.3 ± 0.5	16	3.3 ± 1.0	5
2	2.7 ± 0.7	13	2.6 ± 0.4	11	4.8 ± 1.2	7	4.7 ± 0.7	9
3	2.9 ± 0.4	13	2.6 ± 0.4	17	4.2 ± 0.5	19	4.5 ± 0.5	17
4	2.7 ± 0.7	22	2.5 ± 0.5	18	4.5 ± 0.7	13	4.4 ± 0.7	19

Values expressed as means ± SD (in seconds) of voluntary turning sequences in 4 cats.

firing observed during head shaking may still be less than the maximal, voluntary output of a given muscle, it was hoped that we could derive a relative measure of the strength of discharge associated with head turning. However, the firing levels of several neck muscles were found to be greater during head turns than during head shakes, probably indicating that the recruitment level of some neck muscles is rather low during the latter behavior. Thus we can only describe the pattern of discharge observed in a particular muscle during certain head turns and how the change in neck posture affected the average amplitude of firing.

RESULTS

When a cat was fastened into the harness, it adopted a neck posture that was dictated by the height of the barrier above the supporting surface. Judging from the consistent relationship of external landmarks on the skull to reference marks on the supporting surface and Plexiglas barrier, each cat was seen to adopt the same posture in multiple trials, as long as the height of the barrier was consistent. If the barrier was high above the head, the cat held its neck vertically; if the barrier was lowered to just above the height of the shoulder blades, the cat oriented its neck more horizontally. For convenience, the terms vertical and horizontal are used throughout this paper to refer to these two postures; however, this usage is not meant to imply that the orientation of the cervical column in these postures corresponded exactly to earth-vertical or earth-horizontal. It was not possible to use radiographic methods to evaluate the precise configuration of the skull and cervical column in every trial; however, X-rays were taken of one cat while it adopted each of the two postures. When this animal adopted the vertical posture, the cervical column (vertebrae C3-C5) was aligned within 1° of earth-vertical and the horizontal semicircular canals were pitched upward from earth-horizontal (Fig. 1A). This configuration of the head and neck is consistent with the resting posture described by Vidal et al. (1986), in which the cervical column tended to be inclined backwards and the horizontal canals were tipped upwards. In the horizontal posture, the cervical column was oriented 27° above earth-horizontal and the horizontal canals were pitched downward (Fig. 1B). Each of the cervical joints from C2-C3 to C7-T1 appeared to have undergone some degree of flexion whereas the skull-C1 joint appeared to extend. The C1-C2 joint did not appear to have undergone any sagittal-plane motion.

Some muscles displayed similar patterns of activation in both postures

During head-turning movements, five of the muscles displayed patterns of activation that were consistent from cat to cat and did not change when the cats adopted different neck postures. Within this group, muscles were activated in characteristic ways.

OBLIQUUS CAPITIS INFERIOR, SPLENIUS, AND LEVATOR SCAPULAE. Three muscles—obliquus capitis inferior (OCI), splenius (SP) and levator scapulae (LS)—displayed similar patterns of activation during head-turning movements (Fig. 3). These muscles consistently discharged most intensely during rotation of the head to the ipsilateral side, regardless of whether the cat adopted the vertical posture or the horizontal posture. Typically, firing levels in-

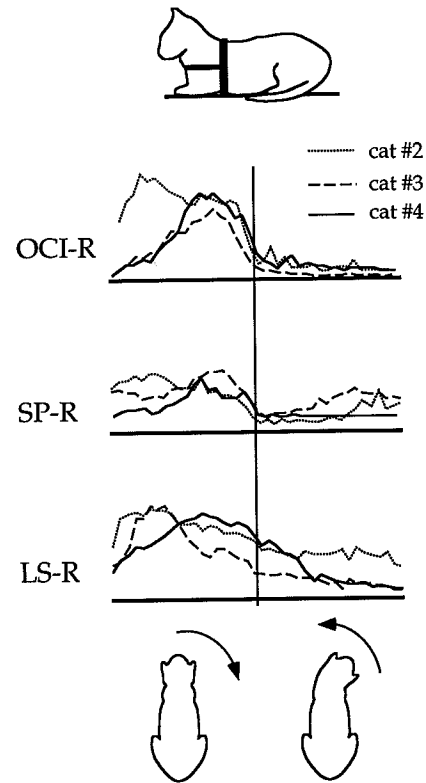


FIG. 3. Electromyographic (EMG) patterns of 3 muscles whose activity appeared to be unaffected by neck posture. The thin vertical bisecting line in this and subsequent figures divides the turn into epochs; here a unilateral turn is divided into an eccentric rotation away from midline and a concentric rotation back to midline. Averaged sequences depicting unilateral head turns to the right in the vertical posture. For cat No. 2, $n = 7$; for cat No. 3, $n = 7$; for cat No. 4, $n = 11$. The thick vertical bar indicates the gain of EMG signals. For OCI-R, the bar is equivalent to $90 \mu\text{V}$ (cat No. 2), $40 \mu\text{V}$ (cat No. 3), or $80 \mu\text{V}$ (cat No. 4). For SP-R, $90 \mu\text{V}$ (cat No. 2) or $20 \mu\text{V}$ (cats No. 3 and No. 4). For LS-R, $30 \mu\text{V}$ (cat No. 2), $20 \mu\text{V}$ (cat No. 3), or $40 \mu\text{V}$ (cat No. 4).

creased at the onset of head rotation toward the ipsilateral side (Figs. 4A and 5A). These muscles remained active until the head was rotated to its most eccentric position; movement of the head in the opposite direction was paralleled by decreased activity in the ipsilateral muscles and by increased activity in their contralateral counterparts. In averaged sequences, the signal from ipsilateral OCI peaked at amplitudes of $100\text{--}200 \mu\text{V}$, depending on the cat. These peak levels were not affected by the change in posture. The peak firing levels of ipsilateral SP and LS were lower, usually in the range of $50\text{--}65 \mu\text{V}$ (SP) and $80\text{--}100 \mu\text{V}$ (LS). Although the different neck postures did not affect the overall EMG patterns of OCI, SP, and LS, there did appear to be less intertrial variability during averaged head-turning sequences in the horizontal posture (Figs. 4B and 5B; note SD of averaged sequences).

COMPLEXUS. Complexus (CM) displayed a different pattern of activity than did OCI, SP, and LS. In all sequences, whether the neck was oriented vertically or horizontally, CM was active on the side opposite to the direction of rotation of the head (Fig. 5). Thus left CM discharged moderately and right CM was inactive as the head rotated from midline toward the right side. In most sequences, activity

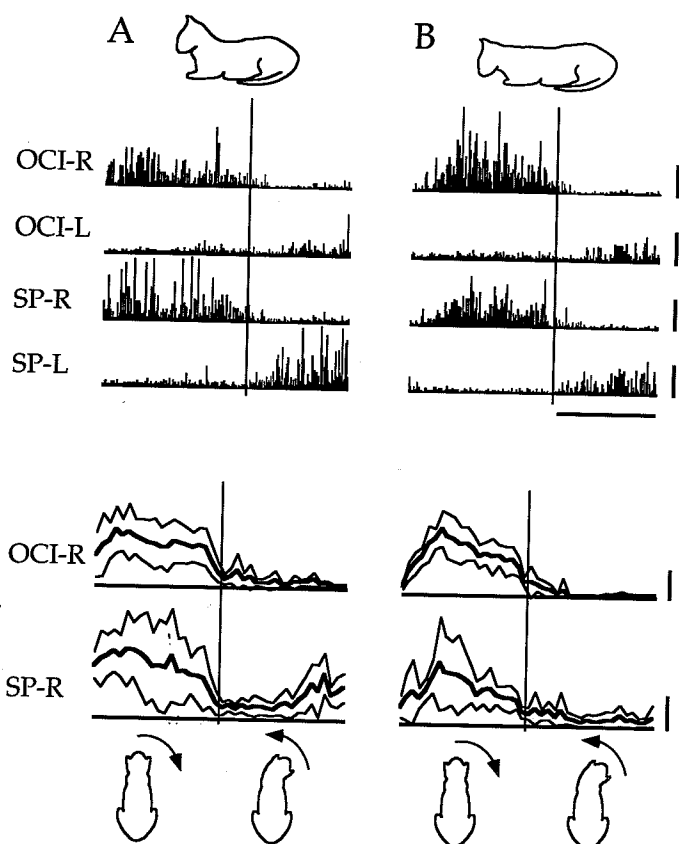


FIG. 4. Consistent EMG patterns of OCI and SP during unilateral head turns to the right (*cat No. 2*). Individual head-turning sequences (*top*) and averaged head-turning sequences (*bottom*) are depicted (thick traces, averaged signals; thin traces, ISD). *A*: vertical posture; *n* = 7. *B*: horizontal posture; *n* = 6. Vertical bars: 60 μ V (OCI) or 15 μ V (SP). Horizontal bar: 1 s.

peaked just before the head reached the point of maximum eccentricity on the contralateral side. At the onset of head rotation back from the right side toward midline, discharge in the contralateral (i.e., left) CM decreased, whereas the ipsilateral (i.e., right) CM became more active. During averaged turning sequences, the peak firing levels of CM were generally in the range of 80–100 μ V. As with OCI, SP, and LS, changing posture had the effect of decreasing inter-trial variability in the activity of CM, but otherwise did not affect the discharge intensity or the overall pattern of muscle activation.

BIVENTER CERVICIS. Biventer cervicis (BC) stood apart from the other muscles in this group because it was active tonically rather than phasically (Fig. 5) and its firing level did not change markedly during the head-turning movement (100–150 μ V in averaged sequences). During some sequences in the vertical posture, activity was lower in the BC muscle contralateral to the movement; this difference was difficult to detect when turns were made in the horizontal posture.

Other muscles displayed posturally dependent patterns of activation

SEMISPINALIS CERVICIS, LONGISSIMUS CAPITIS, AND LEVATOR SCAPULAE VENTRALIS. In the vertical posture, longissimus capitis (LCp) and semispinalis cervicis (SSC) were often

barely active (peak firing levels: <60 μ V in averaged sequences). In sequences in which a low level of discharge was detected, the EMG signals of these muscles showed little modulation as the cat rotated its head (Fig. 6*A*). The third muscle, levator scapulae ventralis (LSv), was usually inactive during turns in the vertical posture. At most times, the EMG signal from this muscle rarely exceeded the level of background noise (Fig. 6*A*).

Dramatically different patterns of discharge in LCp, SSC, and LSv were observed when the cats adopted the horizontal posture. In this posture, sustained bursts of activity occurred in all three muscles on the side ipsilateral to the movement (Fig. 6*B*). Activity ceased in these muscles when the head reached the point of maximum eccentricity; at this point, the contralateral LCp, SSC, and LSv muscles became active. In all cats, these muscles discharged more

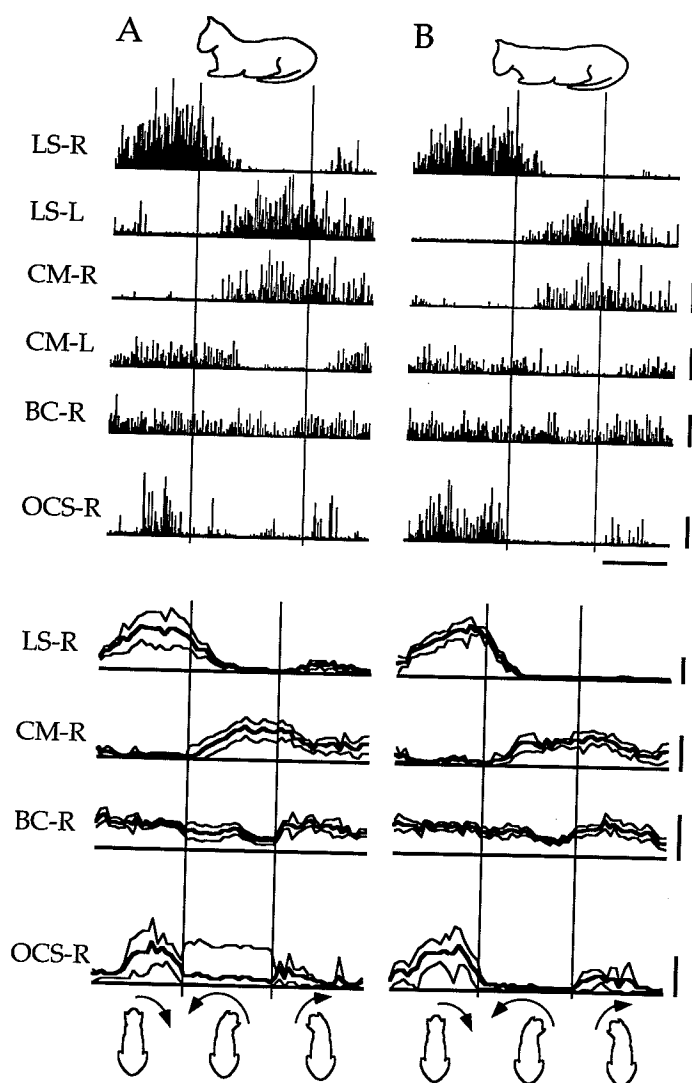


FIG. 5. Consistent EMG patterns of LS, CM, BC, and OCS during bilateral head turns to the right, followed by a full rotation around to the left, and concluding with a small rotation back to midline (*cat No. 4*). As in previous figures, thin vertical lines divide the sequence into these 3 epochs. Individual head-turning sequences (*top*) and averaged head-turning sequences (*bottom*) are depicted; traces are as in Fig. 4. *A*: vertical posture; *n* = 8. *B*: horizontal posture; *n* = 7. Vertical bars: 30 μ V (LS), 60 μ V (CM), 120 μ V (BC-R), or 15 μ V (OCS-R). Horizontal bar: 1 s.

vigorously than was normally observed in the vertical posture, reaching peak levels of 90–200 μV (LCp) or 200–300 μV (SSC). In averaged sequences of head turns in the horizontal posture, the discharge of LSv reached 50 μV . These increases in firing levels were accompanied by increases in the intertrial variability of averaged turning sequences (Fig. 6).

SCALENUS ANTERIOR AND OBLIQUUS CAPITIS SUPERIOR. During turns in the vertical posture, scalenus anterior (SA) was observed to discharge briefly on the side *contralateral* to the movement (Figs. 7A and 8A). This burst of EMG activity in SA ended before the head reached its most eccentric position. Its peak amplitude of firing was fairly low (30–60 μV in averaged sequences). When the cats adopted the horizontal posture, a different pattern of activation was observed. EMG activity was somewhat more vigorous, reaching peak firing levels of 50–70 μV , and it was always observed on the side *ipsilateral* to the movement (Figs. 7B and 8B). Further, bursts of activity in SA were more sustained in the horizontal posture than in the vertical posture

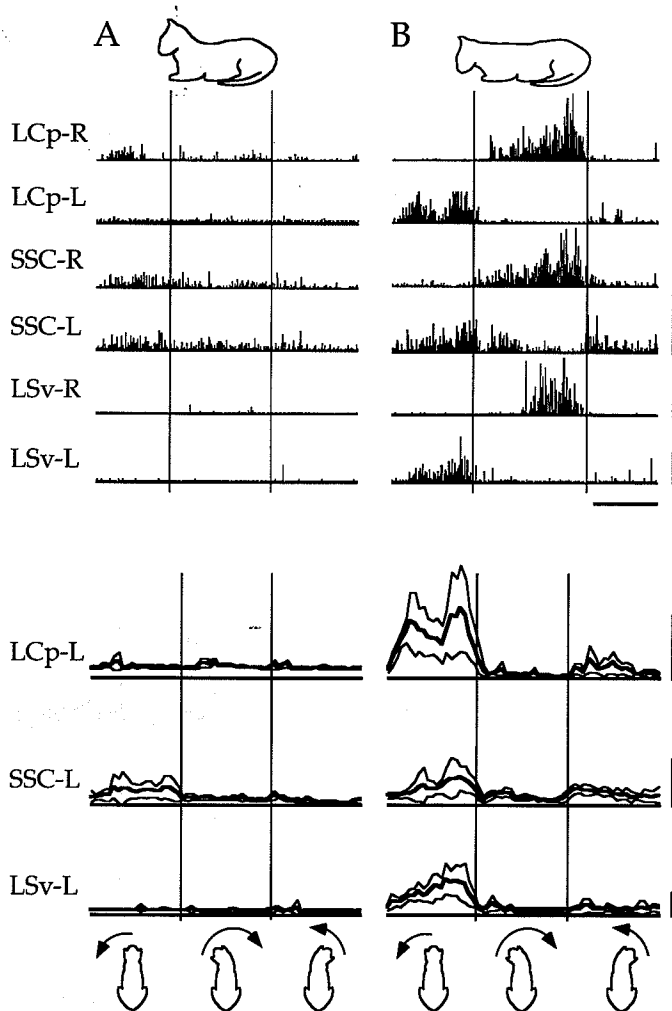


FIG. 6. Changes in the EMG patterns of LCp, SSC, and LSv during bilateral head turns to the left and then the right (cat No. 3). Individual head-turning sequences (top) and averaged head-turning sequences (bottom) are depicted; traces are as in Fig. 4. A: vertical posture; $n = 6$. B: horizontal posture; $n = 9$. Vertical bars: 60 μV (LCp and SSC) or 15 μV (LSv). Horizontal bar: 1 s.

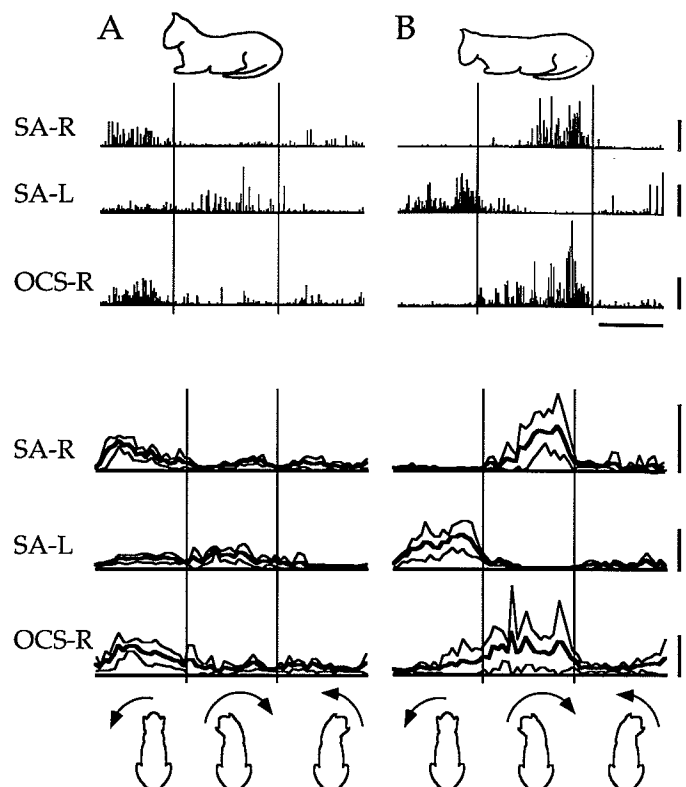


FIG. 7. Changes in the EMG patterns of SA and OCS during bilateral head turns to the left and then the right (cat No. 3). Individual head-turning sequences (top) and averaged head-turning sequences (bottom) are depicted; traces are as in Fig. 4. A: vertical posture; $n = 6$. B: horizontal posture; $n = 9$. Vertical bars, 60 μV ; horizontal bar, 1 s.

and there was a greater degree of intertrial variability in the lowered posture.

Obliquus capitis superior (OCS) displayed EMG patterns and levels of discharge that were similar to those observed in SA, especially in the horizontal posture (Figs. 7B and 8B). In this posture, OCS also discharged with sustained bursts of activity on the side ipsilateral to the head movement. In the vertical posture, however, OCS was used by different cats in different ways. In two cats (No. 1 and No. 3), OCS was active phasically on the contralateral side during gaze-shifting movements (Fig. 7A), whereas when cat No. 4 adopted the vertical posture, OCS continued to be active on the ipsilateral side (Fig. 5A). In all cats, OCS discharged less vigorously (peak firing levels: 30–60 μV in turning averaged sequences) and bursts of activity were less sustained in the vertical posture than in the horizontal posture. Some variability in the muscle activity may be because of differences in the implantation site. Indeed, this small, relatively inaccessible muscle proved to be difficult to implant successfully. We excluded half the OCS muscles from which we recorded, because we could not be confident that the electrodes were positioned correctly and that the signal was free of cross-talk from neighboring muscles (Table 1).

DISCUSSION

Two main observations emerged from the present experiments. First, a diverse range of neck muscles, including muscles in the shoulder region, were found to be active

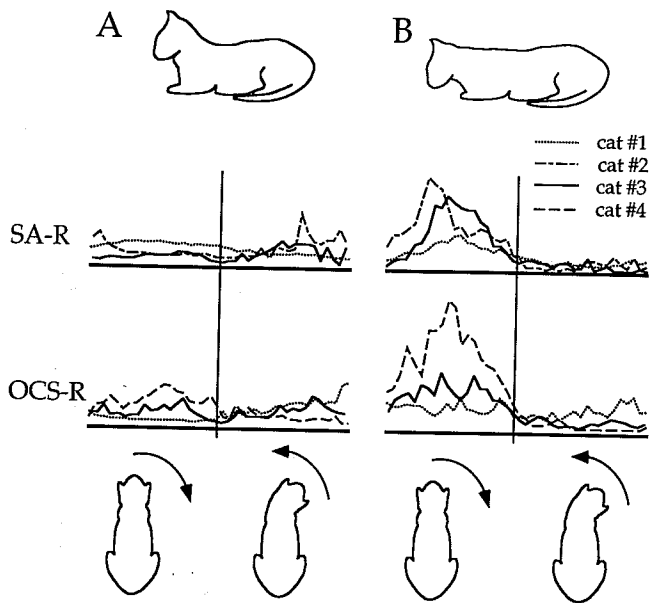


FIG. 8. EMG patterns of 2 muscles whose activity changed with neck posture. Averaged sequences depicting unilateral head turns to the right in 2 postures. A: vertical posture; cat No. 1, $n = 12$; cat No. 2, $n = 7$; cat No. 3, $n = 7$; cat No. 4, $n = 11$. B: horizontal posture; cat No. 1, $n = 12$; cat No. 2, $n = 6$; cat No. 3, $n = 6$; cat No. 4, $n = 7$. Vertical bar indicates gains of EMG signals. For SA-R, the bar is equivalent to $60 \mu\text{V}$ (cat No. 1) or $30 \mu\text{V}$ (cats No. 2 and No. 3). For OCS-R, $25 \mu\text{V}$ (cat No. 1), $50 \mu\text{V}$ (cat No. 3), or $12 \mu\text{V}$ (cat No. 4).

during horizontal turns. Second, the patterns of muscle activity in all cats were found to be quite stereotyped. Muscles appeared to belong to one of two subsets. One subset of deep muscles that ran along the lateral margin of the cervical column (SSC, LCp, LSv, SA, and OCS) displayed EMG patterns that were posturally dependent and changed markedly when turns were made in a horizontal rather than a vertical posture. In a given posture, the primary pulling direction of each of these muscles generally laid in one of the standard planes of head movement (yaw, pitch, or roll; Fig. 2). In a second subset of neck muscles (OCI, SP, LS, CM, and BC), the observed EMG patterns did not vary when the orientation of the cervical column was altered. Except for one muscle (OCI), this latter subset was composed entirely of larger, more dorsally and superficially placed muscles. Further, the pulling directions of these muscles generally had components in more than one plane (Fig. 2).

Head turns involve muscles with a range of skeletal relationships

In most previous studies of horizontal head movements, muscle activity has been recorded primarily from muscles in the upper cervical region that lie close to the dorsal midline (i.e., SP, BC, CM, and OCI). From what was generally assumed to be a vertically oriented neck posture, two muscles, SP and OCI, have been reported to discharge phasically during turns to the ipsilateral side (Akaike et al. 1989; Keshner et al. 1992; Richmond et al. 1992; Roucoux et al. 1989; Vidal et al. 1982) whereas, CM was found to be active phasically on the contralateral side (Akaike et al. 1989; Richmond et al. 1992; Roucoux et al. 1989). These pat-

terns of phasic activity suggested that the three muscles have an important role to play in head turning, especially turns greater than 45° from midline (i.e., Akaike et al. 1989; Richmond et al. 1992; Roucoux et al. 1989; Vidal et al. 1982). In contrast, BC was found to display a tonic, relatively unmodulated pattern of activity (Keshner et al. 1992; Richmond et al. 1992; Roucoux et al. 1989), which was consistent with a role in head elevation as postulated previously on the basis of its anatomic attachments (Reighard and Jennings 1963).

All of these reported patterns were confirmed in the present study. However, the present study also showed that at least six other muscles (LS, SSC, LCp, LSv, SA, and OCS) display phasic EMG discharge during head turns. Of these muscles, only the two most rostrally located muscles, LCp and OCS, have been implicated as head-turning muscles in previous reports (Denise et al. 1987; Roucoux et al. 1989; Vidal et al. 1982). The lack of previous study of the remaining muscles may reflect the fact that they do not span the suboccipital joints and therefore might seem to contribute little to movements of the head (Reighard and Jennings 1963). However, it is clear from biomechanical considerations that head movements can be produced by motion in the lower cervical joints as well as the upper cervical joints (Selbie et al. 1993) in the same way that the orientation of the hand can be changed by motion at the elbow as well as the wrist. Movement of the lower cervical joints may, in fact, be essential to extend the potential range of head turning movements beyond the 50° limit permitted in the horizontal plane at the C1-C2 joint when the neck is oriented vertically (Graf et al. 1992) and the much smaller limit permitted at suboccipital joints when the neck is oriented horizontally. From the present results, it is clear that muscles crossing lower cervical joints also participate in head movement. This involvement would necessarily imply that motor programs underlying head turns are directed not only at muscles that cross upper cervical joints, that have their motoneurons rostral to C4, but also to more caudal muscles crossing lower cervical joints, that have motoneurons caudal to C4 (Linnaamaa and Richmond 1993). Neural projections to these populations of motoneurons have received little attention in the past.

Reorientation of the cervical column changes some recruitment patterns

In the present study, the patterns of activity of many muscles were found to change when the orientation of the cervical column was altered. Many of the resulting differences in activity appear to be consistent with the changed kinematics of the turning movement in the two different postures. When the cervical column is oriented vertically, head turns result from axial rotation about the long axis of the column. The C1-C2 joint is specialized for axial rotation and appears to be the primary site of rotation during head turns in the vertical posture (Vidal et al. 1988). However, when the cervical column is oriented horizontally, horizontal turning of the head can no longer be made by axial rotation; such a movement would roll the ear downward without turning the nose to the side. Instead, the cervical column must bend laterally. Because no single joint ap-

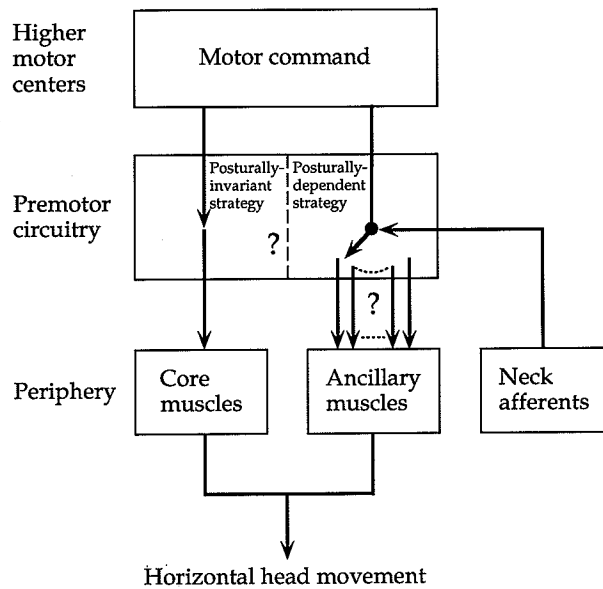


FIG. 9. Block diagram to illustrate how neuronal activity may be organized to generate horizontal head movements. Question marks indicate uncertainty with regard to the potential neuroanatomic structures involved in the recruitment of core muscles versus ancillary muscles and the number of ways in which ancillary muscles may be activated singly or in combination to adjust the trajectory of the head.

pears to have a large freedom to move in lateral bending, horizontal head turns in this posture must be accomplished by lateral bending of the whole cervical column, including the lower cervical joints (Graf et al. 1992). Thus it is perhaps not surprising that head turns made in the horizontal posture are associated with strong activity in a number of muscles that lie along the lateral aspects of the cervical column (i.e., LCp, SSC, SA, and LSv).

Other EMG patterns are more difficult to relate directly to the inferred kinematics of the turning movement. For instance, three muscles (SA, CM, and, in one cat, OCS) were found to be active on the contralateral side when cats made turns in a vertical posture. In these cases, the contralateral muscles cannot shorten; they must remain at least isometric and may even be *lengthened* actively by the turning movement. Such contralaterally active muscles could play a number of possible roles. The force output of a lengthening muscle might be used to confine the trajectory of a movement by correcting off-axis motion or to slow a movement by providing a braking force. It might also restrict the motion at one or more cervical joints, which would alter the distribution of motion along the entire cervical column (cf., Zajac and Gordon 1989). It is difficult to determine exactly what roles are being played by ipsilaterally and contralaterally active muscles without more detailed information about cervical kinematics during these simple head movements. Unfortunately, our current understanding of the biomechanical properties of the cervical column is far from complete (cf., Selbie et al. 1993).

How does the nervous system recognize the need to alter the output of neck muscles in response to changes in inclination of the cervical vertebrae? Sensory input would seem to be needed so that neural circuits could identify the orientation of the neck (see Fig. 9). The vestibular apparatus seems to be an unlikely source because the inclination of

the skull may change independently of the cervical posture. It seems more likely that such information would come from the wealth of proprioceptors that have been previously identified in the neck musculature (Richmond et al. 1988).

Some recruitment patterns are unaffected by neck posture

A surprising observation in all cats was the absence of change in the activities of some muscles (OCI, SP, LS, and CM) whose pulling directions with respect to the trajectory of the head would be altered by changes in the orientation of neck vertebrae. For example, OCI spans between the dorsal process of C2 and the lateral process of C1 (Fig. 1). It is therefore well situated to have a primary action in horizontal head rotation when the neck is oriented vertically, but would act to roll the ear downward rather than turn the head laterally when the neck is oriented horizontally. The fact that recruitment patterns in this and the other muscles did not change despite major changes in the kinematics of the underlying movement could be interpreted in one of two ways. On the one hand, we might assume that the motor programs chosen by the nervous system reflect an "optimal" mechanical solution to the problem of turning the head horizontally in different postures. If this assumption is correct, we must then try to understand why current biomechanical models do not seem to predict the synergies observed in this study. For instance, tensorial methods introduced for the study of head movements by Pellionisz and Peterson (1988) fail to identify the patterns of activity seen in at least one of the muscles, CM, which is active contralaterally. Current tensorial models assume that neck muscles will be activated in proportion to the alignment between their pulling direction and the desired trajectory of the head. Reorienting the neck, from vertical to horizontal, should change this alignment for all neck muscles that act in axial rotation or lateral flexion. So, why would several such muscles show no changes in their patterns of activity from one condition to the other?

Is it possible that tensorial models could be improved to account for these data? In its present form, the model assumes that all motion in the neck occurs only at the suboccipital joints (Wickland et al. 1991). This simplified view of neck biomechanics will limit the ability of the model to predict patterns of muscle activity during multisegmental head and neck movements (see also Keshner et al. 1992). Conceivably, the EMG patterns observed in our study might have been predicted if the same optimality criterion of the tensorial model (minimize muscle recruitment) was applied to a biomechanically correct model of the neck. There is, however, no particular reason why the performance criterion to be minimized should be the total activation of neck muscles. Criteria such as total force or energy consumption might lead to different predictions because some muscles will be working concentrically (shortening) whereas others work eccentrically, thereby producing more force with less energy expenditure (Curtin and Davies 1975; Hill and Howarth 1959). Criteria related to overall accuracy also might be invoked; this probably would lead to very different predictions including, perhaps, the contralateral activation of CM reported here. Tensorial methods

could be used to predict recruitment patterns that are optimized for these and many other possible performance criteria, but this would require a much more complete description of the musculoskeletal system.

On the other hand, the muscle synergies identified here may not represent the most "efficient" or mechanically "optimized" way to make head turns. This particular motor task does not appear to be especially demanding energetically, and it is possible that more than one strategy of muscle usage may produce motor solutions that differ only marginally in their energetic cost. In such a situation, the nervous system may choose to calculate patterns of muscle activation in a manner that is "optimal" in terms of the underlying neural computations. A considerable problem facing the nervous system is that of orchestrating a large number of diverse neck muscles. Bernstein (1967) proposed that the nervous system might "master" this complex periphery by using only a subset of the possible combinations of muscles and reaction forces that would satisfy the mechanical requirements of the movement. He left open the question of the rules underlying the selection of this preferred subset, but there are at least two possibilities. Such combinations of muscles might be activated consistently during a specific motor task because some of the premotor connections are hardwired according to genetic instructions; alternatively, the premotor circuitry might converge during motor learning upon a set of connections whose resulting motor output is efficient for the given range of motor tasks with which the animal has been presented.

The present results may be evidence of such a neural strategy for the calculation of the appropriate pattern of muscle activation. Our data suggest that a consistent subgroup of neck muscles is recruited whenever the nervous system acts to rotate the head in the horizontal plane. Within this synergy, there appears to be a "core" group of at least four muscles (OCI, SP, LS, and CM; BC does not appear to participate in head turning) whose invariant patterns of activation presumably act to rotate the head to one side (Fig. 9). These muscles are generally long and multiarticular and have pulling directions that can contribute to head turns in either posture (Fig. 2), suggesting that this set of muscles may be part of a basic motor program for horizontal head movement whose underlying neural circuitry is relatively simple. This "default" program might, by itself, produce the horizontal head movements that are made from the normal resting posture (i.e., vertically oriented cervical column) (see Vidal et al. 1986). The ancillary muscles (such as OCS, SA, LCp, SSC, and LSv), whose activity depends on neck posture, would then reflect specialized strategies that are added to the invariant core program (Fig. 9). These deep muscles would be well positioned to regulate the mobility of the cervical column and thereby modify the joint movements that would otherwise result from the actions of the core group alone. If these refinements were learned rather than hard wired, then this process might account for the interanimal variability that was observed in the activities of some posturally dependent muscles (i.e., OCS). This strategy is somewhat counterintuitive because deep muscles are not usually thought to act in a variable manner during voluntary movement; rather, they are often regarded as postural muscles that act in a stabilizing man-

ner. However, as Crisco and Panjabi (1992) recently pointed out, long multiarticular muscles are much more efficient at stabilizing the spine than are the deep intervertebral muscles. The relatively stereotyped usage of the long muscles might therefore "free" the deep muscles from postural control and permit them to respond to the moment-to-moment biomechanics, thus ensuring that the head moves along the correct trajectory.

Organizing the motor output in this manner would help the nervous system both to cope with the redundancy of the head-neck system and to simplify the task of computing the appropriate patterns of neck-muscle activation. Grouping together several neck muscles would permit the nervous system to activate the entire group with a single command, effectively reducing the number of variables that need to be regulated for a given motor task (Bernstein 1967). Because this group of neck muscles would be constrained to act in a characteristic manner, there would be fewer ways in which the remaining muscles could be activated to produce a specific head movement. Thus the nervous system may not calculate patterns of muscle activation solely to produce an optimal mechanical solution, but also to optimize, or at least simplify, the neural computations required to arrive at that solution.

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