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RESEARCH ARTICLE

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Effect of neck posture on patterns of activation of feline neck muscles during horizontal rotation

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Abstract The electromyographic (EMG) patterns of neck muscles were recorded during whole-body horizontal rotation in head-free, alert cats and head-restrained, decerebrate cats. In some trials the cervical column of the animal was oriented vertically, whereas in others it was oriented more horizontally. In alert cats making head movements that compensated for the motion of the platform, neck muscles with modulated patterns of activity could be divided into a subset whose individual EMG patterns changed significantly when the neck posture was altered (including longissimus capitis, obliquus capitis superior and scalenus anterior) and a subset whose individual EMG patterns were invariant regardless of neck posture (including obliquus capitis inferior, levator scapulae and complexus). In head-restrained, decerebrate cats, electromyograms from all implanted muscles were modulated similarly in phase with the platform position. Changing the orientation of the neck had little effect upon these EMG patterns evoked by the horizontal vestibulocollic reflex. One decerebrate cat with strong extensor tone was tested further under head-free conditions. There was very little compensatory head movement, but individual neck muscles displayed patterns of activity that were more similar to those observed in alert, head-free animals.

Key words Head movement · Electromyography · Motor control · Vestibulocollic reflex

Introduction

Cats and other mammals move their heads by changing the alignment of the vertebrae in their flexible, multiarticulated necks. These movements are controlled by the activities of more than two dozen pairs of neck muscles, each with unique architectural, histochemical and biomechanical specializations (Richmond and Vidal 1988). Perhaps the simplest and certainly the most studied movements in which these muscles participate are head turns in the horizontal plane. A number of electromyographic (EMG) studies have been carried out in cats to identify the patterns of neck-muscle activation that underlie horizontal turning behaviors (e.g., Guitton et al. 1980; Vidal et al. 1982; Wilson et al. 1983; Baker et al. 1985; Denise et al. 1987; Roucoux et al. 1989; Keshner et al. 1992). Most of these experiments employed relatively simple paradigms and attempted to relate EMG patterns to just a single kinematic variable, the movement of the skull. Such an approach assumed that cats would exhibit a single, stereotyped "head movement synergy" (e.g., Shinoda et al. 1992) that would be determined solely by the speed and trajectory of the head movement. However, recent biomechanical studies of the neck have suggested that other factors, such as the initial posture of the neck, must also be taken into account when trying to understand patterns of neck-muscle usage underlying even simple head movements (Wickland et al. 1991; Selbie et al. 1993).

We have recently examined the EMG patterns of neck muscles during voluntary, horizontal head-turning movements, executed from two different initial postures in which the head and body were held in similar attitudes but the neck was oriented vertically or horizontally (Thomson et al. 1994). When the cervical vertebrae are oriented vertically, horizontal head movements appear to result largely from axial rotation about the long axis of the column, mostly at the C1–C2 joint (Vidal et al. 1988). When the column is oriented horizontally, movements of the head in the horizontal plane are made instead by lateral flexion along the entire length of the cervical column (Graf et al. 1992). Our results showed that neck-muscle activity changed in a consistent way when turns were made in different neck orientations, but the patterning of these changes was unexpected. In one group of laterally placed, phasically active muscles, ma-

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jor changes were found in the timing and amplitude of EMG activity when the neck posture was altered. However, in another group of large, more dorsally placed muscles, no significant changes in phasic EMG patterns could be detected, even though some of these muscles had pulling directions that seemed more appropriate for turns in only one of the two postures. These findings demonstrated that some neck muscles (called the "core" group) are activated in a posturally invariant manner during voluntary turns whereas others (called the "ancillary" group) display posturally dependent EMG patterns.

In the present study we have asked whether this strategy of "core plus ancillary" muscle recruitment underlies horizontal head movements made under different conditions or in response to other stimuli. First, we examined the neck-muscle EMG patterns of intact, chronically instrumented cats that maintained their gaze on a stationary, midline target during externally applied, horizontal rotations of the body. The use of whole-body rotation has been a popular method of evoking reproducible head movements whose direction and speed are quantified readily, and which may be driven by vestibular as well as visual input (e.g., Ezure and Sasaki 1978; Baker et al. 1985; Peterson et al. 1985). We compared the results obtained during these head-free compensatory head movements with those obtained in a previous study, in which the same alert cats turned their heads to look at laterally placed targets while their bodies were stationary (Thomson et al. 1994). Muscle-activity patterns and their postural dependence were generally similar. We next examined head movements evoked reflexly by the vestibular system, by studying the postural dependence of neck-muscle EMG patterns in head-fixed, conventionally decerebrated cats during the horizontal vestibulocollic reflex (VCR). No postural dependence was found, but the head fixation required in decerebrate cats changed the EMG patterns profoundly from those observed in head-free cats in either posture.

Materials and methods

Experiments on alert cats

Cats were trained to recline in a prone position in a restraining harness that was attached to a motorized, moveable platform. They were required to make compensatory head movements in order to hold their gaze fixed on a midline, eye-level target while the platform rotated the body of the animal in the horizontal plane. The platform oscillated sinusoidally through a range of ±45° from midline at approximately 0.2 Hz. At this frequency, compensatory head movements were comparable in duration to bilateral head turns studied previously in these cats (see table 2 in Thomson et al. 1994). During the rotation, cats were required to hold their head and body in similar attitudes but to change the inclination of their neck according to the position of a Plexiglas barrier above their head. Two different neck postures were studied here and for convenience will be referred to as "vertical" and "horizontal". In the vertical posture, the orientation of the cervical column was aligned closely with earth-vertical. In the horizontal posture, the column was inclined upward from earth-horizontal by approximately 30° (see fig. 1 in Thomson et al. 1994). When an animal adopted the vertical posture on the platform, the axis of rotation was approximately collinear with the long axis of the cervical column, including the C1–C2 joint. When the animal was repositioned in the horizontal posture, the axis of rotation passed through only the most caudal part of the cervical column, near the C7–T1 joint. To determine whether the location of the axis of rotation had any effect on EMG patterns, the harness was adjusted in some trials to place the axis of rotation close to the C1–C2 joint. Little effect was observed; therefore, we have described only those patterns of muscle activation observed when the axis of rotation was positioned caudally.

EMG signals from implanted muscles – splenius (SP), complexus (CM), biventer cervicis (BC), obliquus capitis inferior (OCI), obliquus capitis superior (OCS), levator scapulae (LS), semispinalis cervicis (SSC), scalenus anterior (SA), longissimus capitis (LCp) and levator scapulae ventralis (LSv) – and video recordings of head and neck movements were collected using methods described elsewhere (Thomson et al. 1994). The EMG signals elicited by head turning were compared with signals accompanying more forceful and generalized movements such as head shaking, to ensure that an absence of activity in turning trials did not reflect a problem with the recording electrodes. The position signal of the platform was recorded simultaneously with the EMG recordings. Videotapes of the compensatory head movements were examined off line and the timecodes corresponding to sequences of interest were identified. Sequences of head movements were digitized if the cat did not deviate its head from midline for at least one cycle; deviation was determined by monitoring the overhead view of the cat to detect movement of reflective markers on the cat's head with respect to markers on the Plexiglas barrier over its head. The unprocessed platform-position signal was digitized by a Macintosh computer (300 samples/s) along with the corresponding rectified, bin-integrated (3.3 ms bins) EMG signals. Because the bin integrators were calibrated with a 1 kHz square wave and 1 ms bins, each digitized value was normalized by the sample interval (3.3 ms) to obtain the mean microvolt value for that bin. All electromyograms had normalized amplitudes greater than 100 μV in either the head-turning or head-shaking sequences except those from LSv in two cats (2 and 3; 30–50 μV peak), and SP left in cat 2 (66 μV peak). Typically, EMG records during head shakes had amplitudes between 100 and 500 μV. EMG values during compensatory turns in alert cats were usually 10–40% of values elicited by head shaking. Generally, the peak-to-peak (p-p) amplitude of the unprocessed EMG signals is about 10 times larger than integrated and normalized signals; therefore, a trace presented here with a 50 μV peak amplitude would correspond to about 500 μVp-p (referred to amplifier input).

From all four cats, sequences of compensatory head movements were digitized that contained a total of 153 cycles of platform rotation. Data from each cat were analyzed separately. Initially, the temporal patterns of muscle activation were assessed in the individual sequences. Once it had been determined that patterns of activation were consistent between cycles, a single averaged sequence was computed for each type of trial (i.e., vertical posture; horizontal posture with caudal axis of rotation); data from each day of data collection (5–13 individual cycles) were averaged separately. Subsequent analysis then focused on the averaged EMG patterns.

During these head movements, the firing levels of many neck muscles appeared to be modulated sinusoidally by the sinusoidally oscillating platform. A least-squares procedure was used to fit averaged EMG signals with a sine wave at the fundamental frequency of the platform plus a constant DC offset. Most EMG signals were fitted with this sinusoidal model ($P<0.05$), including signals that displayed modulation during only part of a cycle and were silent the rest of the time. Although such signals might be better modeled as clipped sinusoids with the appropriate *negative* DC offset, this additional modeling step was not necessary for our purposes because the most relevant model parameter was the phase shift of the EMG signal, which would not be affected by fitting a clipped sinusoid to the signal. The other model parameters – gain of the sine wave and the offset – are not reported here; instead, the amplitudes of muscle activity are described qualitatively rather than quantitatively. Phase shifts were expressed with respect to the position of the platform; each average cycle began from midline with rotation counterclockwise (as viewed from above) by 45° followed by clockwise rotation of 90° and then by counterclockwise rotation of 45° back to midline (see lower panel in Fig. 1). Thus, a right muscle whose modulated activity peaks at the same time as the platform reaches its maximum excursion during the initial counterclockwise rotation would have a phase shift of 0°, and its response would be described as "position-related". A right muscle whose modulated activity peaks at the same time as the platform crosses midline during the clockwise rotation would have a phase shift of 90° and its response would be described as "velocity-related". For ease of comparison, all EMG recordings and phases are presented below as though they were obtained from muscles on the right side of the neck. Some EMG signals were fitted with a sine wave whose amplitude was <20% of the DC offset (i.e., BC; Figs. 2 and 3). In such cases we have described these EMG patterns only as "non-modulated" and not in terms of a fitted sinusoidal model.

Experiments on decerebrate cats

Four cats (3.1–5.4 kg) were anesthetized intravenously with alphaxalone-alphadolone acetate (Saffan, Glaxovet). In each cat, a tracheotomy was performed and anesthesia was maintained with halothane (Fluorane, Ayerst) vaporized in oxygen. The external carotid arteries were ligated, a midcollicular decerebration was performed and anesthesia was subsequently discontinued. Blood pressure was monitored from a femoral artery. Bipolar epimysial "patch" electrodes and bipolar intramuscular electrodes were implanted as described elsewhere (Thomson et al. 1994) to record EMG signals bilaterally from six pairs of muscles: SP, CM, OCI, OCS, SA and LCp. In one cat (5), both LCp electrodes were implanted incorrectly and were subsequently eliminated from the analysis, and in another cat (6) SA was implanted on only one side. The surgical incision was reapproximated with sutures and the cat was placed prone in a restraining harness on the same turntable used in the previous experimental series. The head of the cat was secured in a head-holder attached around the nose and upper jaw. The head-holder was bolted onto the turntable so that the head rotated together with the body. The height and inclination of the head were adjusted to approximate the usual "resting" posture of alert cats (Vidal et al. 1986), in which the cervical column is oriented vertically and the line of gaze is directed parallel to earth.

EMG and video recordings were made as described above while each cat was rotated sinusoidally on the platform (as with alert cats, ±45° amplitude at approximately 0.2 Hz) for a continuous sampling period of up to 5 min. The neck was then realigned near earth-horizontal, with the line-of-gaze still directed parallel to earth. In this posture, EMG and video recordings were again recorded for a 5 min period while the cat was rotated on the platform. To confirm that the decerebrate animals were placed in vertical and horizontal postures similar to those adopted by alert cats, radiographs were taken of the head and cervical column of one decerebrate animal in both positions. In one animal (5), extensor tone was sufficiently high to allow testing to be carried out with the head unrestrained and in a near-vertical posture when the head was released from the restraining device. The EMG data from all decerebrate cats, along with the position signal of the platform, were digitized at 150 samples/s. Averaged cycles were computed from 25–35 individual cycles and were then analyzed in a manner similar to that described above for experiments on alert cats.

Results

Responses in alert cats

When unrestrained cats turned their heads to compensate actively for the imposed rotation, the observed EMG patterns were similar to those recorded previously during horizontal, gaze-shifting head movements (Thomson et al. 1994), although neck-muscle activity was generally lower in amplitude during the present, compensatory head movements. As in the previous study, one group of muscles – composed of OCI, LS and CM – displayed invariant patterns of activation regardless of the neck posture, whereas a second group of muscles – composed of LCp, SA, OCS and SSC – displayed posturally-dependent patterns of activation.

Modulated muscles with invariant patterns of activity in both postures

Obliquus capitis inferior and levator scapulae. In alert head-free cats rotating on the platform, OCI and LS were active in a manner that appeared appropriate to move the head in a direction opposite to the motion of the platform (Fig. 1). For example, whenever the platform rotated counterclockwise (as viewed from above), activity increased in the right OCI and LS. Therefore, the muscles were active on the same side as the direction to which the cat turned its head in order to compensate for the motion of the platform. Both muscles displayed responses that peaked just before the platform reached its maximum excursion, with phase leads generally less than 45° (Table 1). This pattern of response was also observed when the cats adopted a horizontal posture (Fig. 1); amplitudes of discharge were essentially unchanged.

Complexus. CM also exhibited a modulated pattern of activity, but this pattern had a different phase relationship with respect to platform position. The muscle discharged out of phase with ipsilateral OCI and LS and was active phasically on the side *contralateral* to the direction of head rotation (Fig. 1). Thus, peak discharge of right CM occurred as the platform reached its maximum excursion on the right side. According to our convention

Table 1 Phase relationships of modulated muscles in alert cats. Phase shifts are presented as a range of values (deg) from cats that displayed similar patterns of activation. Position-, velocity- and acceleration-related phases would have values of 0°, 90° and 180°, respectively (*OCI* obliquus capitis inferior, *LS* levator scapulae, *CM* complexus, *LCp* longissimus capitis, *SA* scalenus anterior, *OCS* obliquus capitis superior, *SSC* semispinalis cervicis)

Muscle	Cat no.	Vertical posture	Horizontal posture
OCI	1–4	14–46	14–52
LS	1–4	18–49	12–38
CM	1–4	175–199	158–194
LCp	1, 3	Not active	43–68
	2, 4	20–42	19–24
SA	1	29	Not modulated
	2	197	Not modulated
	3	Not active	Not active
OCS	1, 3, 4	65–85	56–85
SSC	1, 4	Not modulated	Not modulated
	2	−18	Not modulated
	3	164	Not modulated

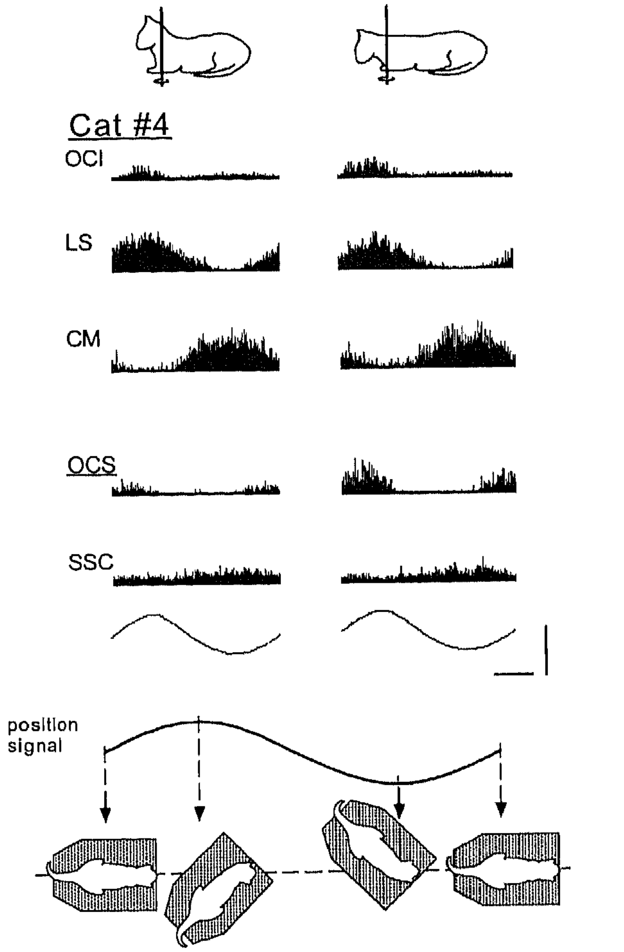

Fig. 1 Electromyographic (EMG) patterns of five muscles (*OCI* obliquus capitis inferior, *LS* levator scapulae, *CM* complexus, *OCS* obliquus capitis superior, *SSC* semispinalis cervicis) during compensatory head movements including one (*OCS*) that displayed posturally dependent activity. These averaged sequences depict the vertical posture (*left*) and the horizontal posture (*right*). The *lower panel* illustrates the relationship between the movement of the platform and the position signal. For OCI and SSC, the *vertical bar* represents 45 μV; for LS and CM, 90 μV; for OCS, 25 μV. The *horizontal bar* represents 1 s

for describing phase shifts, such a response should be termed "acceleration-related" (Table 1); with these slow movements, however, it is probably more accurate to state that this is a position-related signal that has been referred to the opposite side. In all cases, this seemingly paradoxical activity of CM was essentially unchanged when the compensatory head movement was made in the horizontal posture (Fig. 1).

Modulated muscles with posturally dependent patterns of activity

Changing the posture of the neck produced striking changes in the EMG patterns of LCp and SA. More subtle changes were observed in the activity of OCS and SSC.

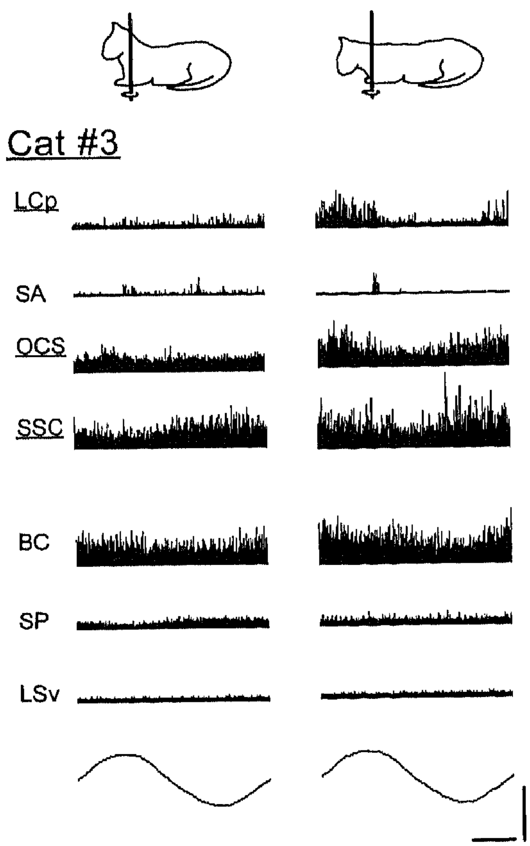

Fig. 2 EMG patterns of seven muscles (*LCp* longissimus capitis, *SA* scalenus anterior, *OCS* obliquus capitis superior, *SSC* semispinalis cervicis, *BC* biventer cervicis, *SP* splenius, *LSv* levator scapulae ventralis) during compensatory head movements including three (*LCp*, *OCS* and *SSC*) that displayed posturally dependent activity. For LCp, SSC and SP, the *vertical bar* represents 45 μV; for SA and BC, 90 μV; for OCS and LSv, 25 μV. The *horizontal bar* represents 1 s

Longissimus capitis. In the vertical posture, the activation of LCp was observed to vary between cats. In two cats (1 and 3), LCp appeared to be inactive (Fig. 2). In two other cats (2 and 4), LCp exhibited a low-amplitude, position-related response (Table 1), similar to that observed in ipsilateral OCI and LS (Fig. 3).

In all cats, LCp showed a change in activity when the neck was oriented horizontally rather than vertically. In the two cats in which no activity was detected in the vertical posture, LCp became active (Fig. 2) with somewhat advanced phases (Table 1). In the two cats that previously showed some phasic activity, the modulation became more pronounced (Fig. 3); however, the muscle phases continued to be position-related (Table 1).

Scalenus anterior. The most complex and variable patterns of activation were observed in SA. In each cat, SA displayed a different pattern of activity when compensatory head movements were made in the vertical posture. In two cats, the firing levels were modulated (Fig. 3). The discharge of SA in cat 2 was modulated in a pattern like that recorded in CM (Table 1). In contrast, the aver-

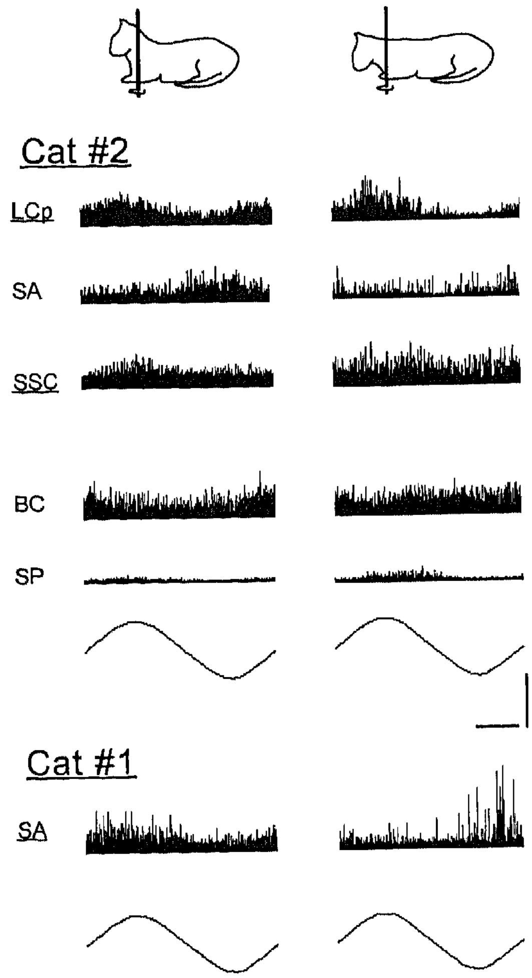

Fig. 3 EMG patterns of six muscles (abbreviations as in Fig. 2) during compensatory head movements including four (*LCp*, *SSC* and, in both cats, *SA*) that displayed posturally dependent activity. For LCp, SA and SP, the *vertical bar* represents 45 μV; for SSC and BC, 90 μV. The *horizontal bar* represents 1 s

aged EMG signal recorded from SA in cat 1 had a phase relationship similar to that of OCI (Table 1). These discharge patterns changed when the cats adopted the horizontal posture (Fig. 3). In both cases, the response of SA no longer appeared to be modulated by the oscillation of the platform (Table 1).

In a third cat (3), SA was virtually inactive during compensatory head movements. In this cat, SA was also inactive during trials in the horizontal posture, except for occasional bursts of activity that did not appear to be related to the rotation of the platform (Fig. 2).

Obliquus capitis superior. In the vertical posture, the peak firing levels of OCS were usually close to the level of background noise, especially in cat 3 (Fig. 2). In cats 1 and 4, however, there was often a small burst of activity as the platform rotated from the maximum excursion on the side ipsilateral to the recorded muscles toward the maximum excursion on the contralateral side (Fig. 1). This velocity-related response was more apparent during compensatory head movements in the horizontal posture (Table 1), which were always associated with a marked increase in firing levels (Figs. 1, 2).

Semispinalis cervicis. In all cats, the EMG patterns of SSC contained a prominent tonic component. In two cats (1 and 4), it was difficult to detect any modulation of the continuous low-amplitude discharge of this muscle (Fig. 1). In two other cats, the modulation was somewhat more apparent, but the phase relationships were 180° out of phase from one animal to another (Figs. 2, 3). The response observed in one of these latter cats (2) displayed a position-related phase *lag;* the other cat (3) displayed a phase lead that approached acceleration (Table 1). When the cats adopted the horizontal posture, modulation became difficult to detect (Figs. 2, 3).

Non-modulated muscles

Biventer cervicis. BC was active continuously in both the vertical and the horizontal postures (Figs. 2, 3). Although its firing levels fluctuated as the platform rotated, the resulting average EMG pattern did not show clear modulation.

Splenius. SP is normally considered to have a role in horizontal head movement (Reighard and Jennings 1963), and in these same cats SP was observed to discharge in a modulated manner during gaze-shifting head movements (Thomson et al. 1994). However, SP was seldom active during the compensatory head movements reported here (Fig. 2). During some trials, the weak signal of SP was observed to display a pattern of modulation similar to that of OCI and LS (i.e., Fig. 3). But in most trials, the signal from SP remained near the level of background noise.

Levator scapulae ventralis. LSv appeared to be inactive during compensatory head movements. Occasional, low-amplitude bursts of activity were recorded, but these seemed unrelated to the movement of the platform and the averaging procedure tended to obscure them (Fig. 2).

Responses in decerebrate cats

The EMG responses of all decerebrate cats were tested initially by rotating the platform under the cat while supporting the neck in the vertical and then the horizontal posture using a head-holder mounted on the platform. Under these head-restrained conditions, a different and simpler pattern of neck-muscle recruitment was observed consistently: all implanted muscles, including SP, were active and all discharged on the side toward which the head would have rotated in order to compensate for the perturbation (i.e., contralateral to the side of platform rotation) (Fig. 4). Thus, the activities of CM and SA were not modulated as would have been expected from the

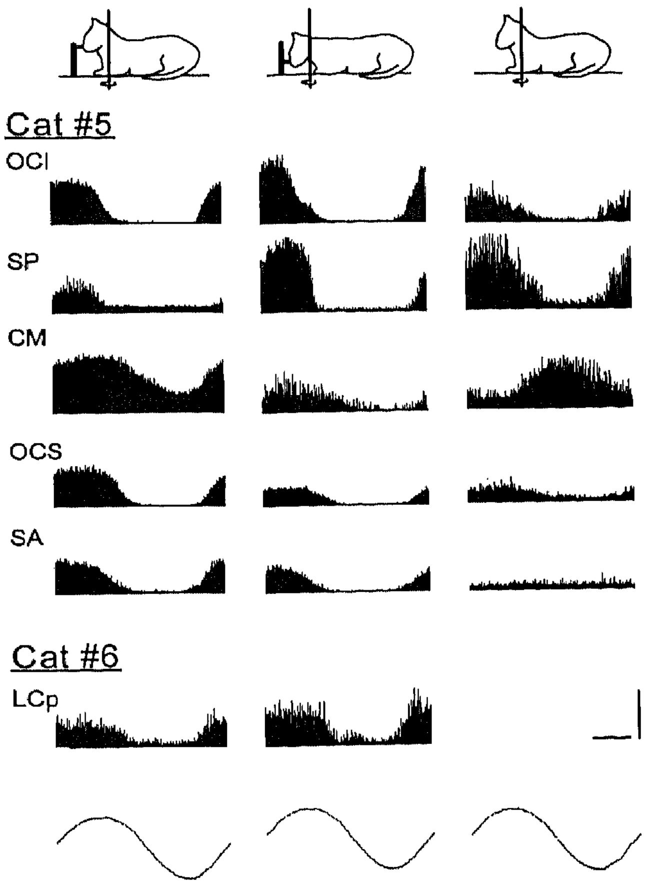

Fig. 4 Averaged EMG patterns of six muscles (abbreviations as in Figs. 1 and 2) during head-fixed rotation in decerebrate cats. *Left* vertical posture, head-restrained; *center* horizontal posture, head-restrained; *right* near-vertical posture, head-free. For OCI and SA, the *vertical bar* represents 45 μV; for SP, CM and LCp, 25 μV; for OCS, 90 μV. The *horizontal bar* represents 1 s

Table 2 Phase relationships (deg) of EMG recordings in decerebrate cats. Values for head-free condition from one cat only (5). Muscle abbreviations as in Table 1

Muscle	Vertical posture	Horizontal posture	Head-free
OCI	45–64	58–62	57
SP	31–40	38–43	40
CM	13–18	18–34	233
LCp	53–65	55–63	
OCS	27–50	35–57	26
SA	45–62	44–61	Not modulated

previously recorded responses in alert cats; instead of being active contralaterally, they were activated ipsilaterally in a pattern similar to that of the other modulated muscles.

The phase relationships of muscle responses observed in decerebrate cats did not change substantially when the neck posture was altered (Table 2). Nevertheless, changes in neck orientation did affect the amplitude of the EMG responses in ways that varied from animal to animal. For instance, in the vertical posture SP exhibited a relatively short, low-amplitude burst of firing as the platform approached its point of maximum eccentricity. In the horizontal posture, activity in SP became stronger in two cats (nos. 5 and 7), but changed little in cats 6 and 8. In cat 5, activity diminished in CM, OCS and SA when the neck was placed in a horizontal posture (Fig. 4), whereas in one or more of the other cats, similar or increased levels of EMG activity were recorded in CM, OCS, SA and LCp (not illustrated). In general, however, all the implanted muscles showed very modest levels of activity.

Cat 5 was tested further while its head was unsupported by the head-holder. This cat could hold its neck in a near-vertical posture, provided that we occasionally stroked the skin on the ventral neck. Under head-free conditions, the patterns of neck-muscle recruitment changed markedly to resemble more closely the patterns observed in alert, head-free cats (Fig. 4). OCI, SP and OCS continued to fire on the side ipsilateral to the direction of the compensatory head movement and displayed generally similar phase relationships with platform position, but CM reversed its pattern and became active phasically on the contralateral side (Table 2). The amplitude of EMG activity increased in OCI, SP and CM, but diminished in OCS and SA. In addition, the discharge of SA was no longer modulated. LCp was not available for testing in this animal. It should be noted that this activity of the neck muscles produced no detectable horizontal deviations in head position as evidenced by inspection of the video records (sensitivity estimated at 3°).

Discussion

Compensatory movements in alert cats

The results presented here demonstrate that alert, head-free cats and decerebrate, head-fixed cats have quite different patterns of neck-muscle activities when they are rotated on a turntable in the horizontal plane. In alert, head-free cats the compensatory movements made to stabilize the gaze on a midline target were associated with neck-muscle activities similar to those recorded previously in head-free cats making eccentric, horizontal turns to track or capture a visual target (Richmond et al. 1992; Thomson et al. 1994). During both the eccentric, gaze-shifting movements studied previously (Thomson et al. 1994) and the gaze-stabilizing movements examined here, neck muscles could be divided for descriptive purposes into two subsets: one group demonstrated the same patterns of muscle activity regardless of neck posture (OCI, CM and LS) whereas the others showed changes in activity when neck posture was altered (LCp, SA, OCS and SSC).

The similarities in recruitment patterns from one behavioral paradigm to another suggest that similar neural processes may be responsible for the activation of neck muscles in both these situations. Such a conclusion might not be surprising given that both the gaze-stabilizing and gaze-shifting movements involve vision and thus might be classed as visual tracking tasks. However, in the experiments presented here, vestibular input could also be used by the animal as a cue to execute appropriate compensatory head movements. If vestibular input indeed plays a role in this motor behavior, it does not appear to alter the synergies associated with horizontal turns stimulated by visual signals alone.

Evidence that a common motor strategy might underlie horizontal head turns regardless of the stimulus modality used to cue the movements has been suggested previously by experiments in which horizontal movements were evoked by auditory stimuli in alert, head-free cats (Richmond et al. 1992). In those experiments, EMG recordings revealed similar features of neck-muscle recruitment, including ipsilateral activation of OCI and SP and contralateral activation of CM; however, a systematic evaluation of neck-muscle responses in different head-neck postures was not carried out.

Effects of decerebration and head fixation

Compared with their alert, head-free counterparts, decerebrate, head-fixed cats were found to have several differences in their patterns of neck-muscle activity when they were rotated on a turntable moving at the same speed and amplitude. Two differences were particularly clear.

First, the usual division of activity between ipsilateral and contralateral muscles was no longer present during the rotations in decerebrate head-fixed cats. Instead, all muscles were active *ipsilaterally*. Even a muscle such as CM that normally is active *contralaterally* was observed to be activated ipsilaterally. Thus, the phase of the CM response became similar to those of OCI and the other modulated muscles. The ipsilateral, rather than contralateral, activation of CM in decerebrate, head-fixed cats has been reported previously when vestibulocollic reflexes were tested by others under similar experimental conditions (Peterson et al. 1985).

Second, the postural dependence exhibited by several muscles in the alert, head-free cat could no longer be detected when neck posture was changed in the decerebrated, head-fixed cats.

If we presume that the changing patterns of muscle activity seen in different neck postures are functionally important to ensure a head movement with correct trajectory and dynamics, then the disappearance of these modifications would seem to indicate a distortion or loss of normal capabilities. During vestibulocollic reflexes, for example, the nervous system must coordinate an *appropriate* compensatory head movement in response to a particular vestibular stimulus indicating the nature of the perturbation of the head. To do this it must transform a sensory stimulus, coded in vestibular coordinates, into motor patterns appropriate for making the corrective movement (Pellionisz and Peterson 1988). This transformation is complicated because the kinematic features of even a simple movement, such as a horizontal head turn, change markedly when the posture of the neck is altered from a vertical to a horizontal orientation (Vidal et al. 1988; Graf et al. 1992; discussed in Thomson et al. 1994). Changes in neck posture also alter the pulling directions of neck muscles, changing their potential usefulness in the head movement of interest (Wickland et al. 1991). Thus, even when the skull is held in the same orientation (so that the vestibular input codes the perturbation in an identical way), the muscular synergies needed to perform the compensatory movements would be expected to differ when the alignment of the cervical vertebrae is altered. Unless the motor output is tailored to the neck posture, a stereotyped vestibular stimulus could produce an inappropriate movement under some postural conditions. It was therefore surprising to observe that changes in neck orientation were not associated with any consistent changes in neck-muscle usage in decerebrate, head-fixed cats. However, we cannot dismiss the possibility that the same motor responses in both postures could produce acceptable compensatory head movements without a more quantitative biomechanical analysis. Methods for such an analysis are currently being developed (e.g., Statler et al. 1994) so that this possibility can be tested explicitly.

It is unclear whether the disappearance of posturally dependent patterns of activation in decerebrate, head-fixed animals should be attributed to the decerebration, the head fixation or both. Decerebration might seem to be the most likely factor to affect muscle recruitment. For instance, it is possible that the effects of posture in the normal cat are mediated by regions of the cerebral cortex that have been removed in the decerebrate preparation. However, there is no direct evidence in support of this assertion.

There are at least two reasons for suspecting that the key difference between the two preparations is not the decerebration.

First, Banovetz et al. (1995) recently found no differences in the spatial properties of the VCR in cats tested under head-fixed conditions before and after decerebration. In both their alert and decerebrate cats, patterns of muscle recruitment exhibited many of the same features of recruitment observed in the head-fixed animals examined in our study. For example, CM was activated ipsilaterally, rather than contralaterally as is typical for alert, head-free cats.

Second, data presented here provide evidence that fixation of the head may have a greater effect upon the temporal patterning of muscle recruitment than decerebration. In this study, the fortuitous opportunity to release the head of one decerebrate cat (5) from restraint was immediately found to result in a set of EMG patterns more like those observed in intact cats, even though the resulting muscle activity was insufficient to produce appropriate compensatory movements of the head. For example, the phase of CM reversed, and SA became unmodulated in a pattern similar to that observed in one of the alert cats.

Peterson et al. (1985) have reported similar findings when they recorded discharge patterns in dorsal neck muscles: the phase relationships of OCI and SP were generally the same in decerebrate cats under head-fixed and head-free conditions, but a marked phase shift was seen in CM when the head was free. Peterson et al. (1985) interpreted this finding as evidence that CM was particularly responsive to stretch during rotations that were produced by other neck muscles. Such a stretch would be prevented in head-fixed preparations. Although it is possible that the cervicocollic reflex is particularly strong in this one muscle, it may also be the case that CM is recruited out of phase with other neck muscles in the alert animals in order to perform one of several possible biomechanical roles, including correcting off-axis motion, providing a braking force for the movement or restricting the motion at one or more cervical joints (cf. Thomson et al. 1994). Whatever the explanation, the counterphasic use of CM appears to be a consistent feature of horizontal head movements in unrestrained, alert or decerebrate cats (Akaike et al. 1989; Roucoux et al. 1989; Richmond et al. 1992; Thomson et al. 1994) but not head-fixed cats.

Present and previous studies suggest that head fixation tends to "homogenize" the phase relationships of output signals to neck muscles. Goldberg and Peterson (1986) have reported that EMG responses in a variety of neck muscles have more variable phase relationships when alert cats are free to move their heads than when their heads are fixed during whole-body rotation. In the present studies, neck muscles in alert, head-free cats also exhibited highly muscle-specific phase relationships, whereas decerebrate, head-fixed cats all had response phases that led platform position by about 15–60° (Table 2). These values are comparable to the mean phase of EMG signals (44±13°) reported previously for several neck muscles during the horizontal VCR at 0.2 Hz (Ezure and Sasaki 1978; Bilotto et al. 1982). Significantly, less synchronization was present in the phase relationships of the neck muscles when the head of the decerebrate cat was released from restraint in our study (Fig. 4).

Unfortunately, it is difficult to test directly whether head fixation influences the patterning of neck-muscle electromyograms. An appropriate experiment would require that compensatory head movements be elicited in alert cats under head-fixed and head-free conditions in the dark, to remove the confounding presence of a visual signal. However, it is hard to deliver a specific and repeatable vestibular stimulus to a cat that can be expected to move its head "whimsically" during the testing protocol. As a first approximation, Banovetz et al. (1995) recently compared the EMG patterns in neck muscles of alert cats during platform rotations, first under head-fixed conditions and then when the head was restrained only partially. In this latter condition, the head-holder was modified so that the cat could support the weight of its head but could not make any movements in yaw or roll. Banovetz et al. (1995) observed no significant difference in the VCR responses of neck muscles in these partially head-restrained cats compared with head-fixed cats, and concluded that head fixation has little effect on patterns of neck-muscle recruitment. However, it is unclear whether "freeing" the head in this manner is an acceptable substitution for removing restraints in all axes. Clearly, the relationship between decerebration, head fixation and patterns of neck-muscle recruitment needs to be worked out in more detail.

The nature of the vestibulocollic reflex

The differences in motor patterning seen during whole-body rotations in the alert, head-free cat, the decerebrate, head-free cat and the decerebrate, head-fixed cat raise questions about the appropriate definition of the vestibulocollic reflex. Vestibulocollic reflexes have been described classically under decerebrate, head-fixed (called open-loop) conditions (for review see Wilson et al. 1995). However, the reflex responses observed in our decerebrate, head-free cat had a different patterning, more like that observed in alert animals making compensatory head turns. The head of the decerebrate, head-free cat was not seen to move detectably during the testing, suggesting that the responses were still being elicited under open-loop conditions. Which set of muscle synergies then constitutes the real VCR? The emerging complexity of this "simple" behavior and its neural substrate provides both a caution in interpreting the results of previous studies on head-fixed animals, either intact or decerebrate, and an opportunity to identify the behavior's components more specifically. Because a variety of behavioral variants can be produced systematically, depending on easily modified experimental conditions, it should be possible to identify premotor pathways by associating their patterns of neural activity and the consequences of various ablations with the various EMG recruitment patterns.

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