Electromyographic Activity of Dorsal Neck Muscles in Squirrel Monkeys During Rotations in an Upright or Upside Down Posture

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Killian, J. Eric and James F. Baker. Electromyographic activity of dorsal neck muscles in squirrel monkeys during rotations in an upright or upside down posture. J Neurophysiol 93: 2587–2599, 2005. First published January 12, 2005; doi:10.1152/jn.01229.2004. Electromyographic (EMG) activity was recorded from occipitocipitalis, semispinalis, and splenius neck muscles in five alert squirrel monkeys during 0.25-Hz rotations about horizontal axes oriented at 22.5° intervals, including pitch, roll, and intermediate axes. The animals were oriented in either upright or upside down posture. In the upright posture, all monkeys exhibited compensatory EMG activity with maximal activation during rotations about axes between pitch in the pitch forward direction and contralaterally directed roll. Response timing varied across animals with EMG peaks ranging from near pitch forward head velocity to near pitch forward head position. When the head was upside down, response dynamics and directionality were altered to varying degrees in different monkeys. The greatest change in response to head inversion was seen in the monkey that had response phases closest to head position, the least in the animal with phases closest to head velocity. The monkey with EMG response peaks closest to position phase showed nearly 180° inversion of responses when the head was upside down, suggesting that in this monkey a righting reflex mediated by utricular signals was activated in the upright down posture. The monkey with EMG response peaks closest to velocity phase may have lacked a righting response and exhibited only a canal-mediated compensatory vestibulocervical reflex in both upright and upside down postures. The results suggest that reflex contraction of neck muscles in response to passive head rotation includes an interplay of compensatory and righting responses that varies from animal to animal.

INTRODUCTION

Both the vestibulocervical (or vestibulocollic, VCR) and vestibuloocular (VOR) reflexes compensate for head movement. In the case of the VOR, head movement produces opposing eye movement that keeps images still on the retina. In the case of the VCR, however, head movement produces opposing neck muscle activity that minimizes the head movement itself (Schor et al. 1988). Thus the VCR differs from the VOR in being a closed loop negative feedback system: its output directly affects its input and it does not rely on another system (the visual system in the case of the VOR) for calibration. Head-fixed animal preparations have been used to study the dynamics of the VCR under open loop conditions.

Previous work on the dynamics of the VCR has been done in decerebrate cats using electromyographic (EMG) recordings of neck extensor activity during horizontal (Berthoz and Anderson 1971; Bilotto et al. 1982; Ezure and Sasaki 1978), roll (Baker et al. 1985; Berthoz and Anderson 1971), and pitch (Baker et al. 1985; Dutia and Hunter 1985) sinusoidal rotations. Yaw data from Bilotto and colleagues (1982) over a frequency range of 0.1–5 Hz and lower frequency data from Ezure and Sasaki (1978) can be fit with a two-pole, two-zero, lead-lag transfer function. One pole and zero are provided by the central neural circuitry of the VCR, presumably to accommodate the load presented by the head (Bilotto et al. 1982). The remaining VCR EMG dynamics reflect the behavior of the semicircular canal input that drives the reflex.

The directions of rotation that maximally excite dorsal neck muscles in the VCR have been studied in both alert and decerebrate cats. Results from experiments in decerebrate (Baker et al. 1985; Banovetz et al. 1995) and alert (Banovetz et al. 1995) cats conducted at 0.25 Hz indicate that maximal activation directions for dorsal neck muscles including biventer cervicis, complexus cervicis, occipitocipitalis, splenius capitis, rectus major, and obliquus inferior are directed toward forward pitch and roll away from the side of the muscle. These muscle excitation directions are roughly opposed to the estimated pulling actions of the neck muscles (Wickland et al. 1991), although they need not be in direct opposition for the VCR to be compensatory, and the principles by which the central circuits set the directionality of neck muscle activation are a matter of debate (Pellionisz and Peterson 1988) as is true for the CNS control of muscle synergies in general (Buchanan et al. 1986; Holdefer and Miller 2002; Weiss and Flanders 2004).

While the VCR acts to prevent head instability (Baker et al. 1982; Fakhri et al. 1993; Schor 1974) whatever the position of the head in space, righting reflexes work to return the head to the upright position with respect to gravity. Righting reflexes are an elaborate sequence of behaviors drawing on visual and vestibular inputs and operating over the neck, shoulders, torso, and limbs. Head- and shoulder-righting reflexes are dependent on an intact labyrinth (Pellis et al. 1991). In blindfolded cats attempting to maintain upright posture during a brief fall, the initial neck muscle EMG activity is slightly altered by semicircular canal inactivation and completely abolished after subsequent otolith signal removal by labyrinthectomy (Watt 1976). The overall conclusion from neck muscle EMG studies is that semicircular canals provide the predominant neural signals for the VCR and head stability and otoliths the signals for righting and upright posture.

Although the object of a fair amount of study earlier in the century (Magnus 1926; Muller and Weed 1916; Roberts 1978),
righting reflexes have drawn less attention recently, and their
relation to the VCR has not been examined. Compensatory and
righting reflexes are synergistic when an animal is upright but
antagonistic when the animal is upside down. In this study, we
hold head-fixed monkeys in these two different body postures
and compare the resulting sets of neck muscle EMG responses
to try to separate the dynamics and spatial properties of
compensatory reflexes from those of righting reflexes.

**Methods**

**Animal preparation**

All procedures followed the principles of laboratory animal care set
forth by the National Institutes of Health in the *Guide for Care and
Use of Laboratory Animals* and were approved by the Institutional
Animal Care and Use Committee at Northwestern University. Two
male and three female squirrel monkeys were used. Under isoflurane
and nitrous oxide anesthesia (80% N₂0–20% O₂), the animals were
placed in stereotaxic position. A midline incision exposed the dorsal
cranial surface, and small stainless steel screws (0–80) were inserted
into the skull at six to eight locations to help anchor one or two
aluminum posts used to hold the head during an experiment. Each
rectangular post was lowered onto the skull and centered over the
midline so that its faces aligned with the stereotaxic coordinate planes.

During the experimental sessions of two of the monkeys, we com-
pared EMG activity evoked in the inverted posture when restrained by
one versus the other head post, one located ~20 mm rostral to the
other. No differences were apparent, and we concluded that differ-
ences in placement of the head holder could not account for variation
across animals.

After anchoring the head holder posts, or in a subsequent surgery,
the midline incision over the skull was continued caudally to expose
the dorsal neck musculature for chronic placement of EMG elec-
trodes. A rostral-to-caudal incision was made through the skin on the
midline, followed by further rostral-to-caudal incisions just to one side
of the midline through the muscle layers. Tissue was then blunt-
dissected along natural divisions between muscles. This approach
allowed suturing in layers to restore muscle placement as the wound
was closed. Superficially, trapezius was identified but delicate. Oc-
cipitocervicalis, splenius, semispinalis, and sternocleidomastoid were
identified, then electrodes were inserted in the muscles as described in
the following text, in a ventral-to-dorsal order, beginning with ster-
nocleidomastoid. Data from sternocleidomastoid that was not consistent
and are not reported here. Sternocleidomastoid was not instrumented
in later monkeys. Electrodes were also implanted in trapezius, but
signals were weak, and we were unconvincing that they were isolated
from other muscles, so those data are not reported here.

In initial experiments, we used bipolar silicone patch electrodes
(Microprobe) for neck-muscle EMG recordings. At the outset, these
electrodes recorded EMG activity that was qualitatively similar to our
later and much more extensive data set. However, the patches were
quite bulky compared with the squirrel monkey neck muscles, may
have interfered with muscle action, and stimulated tissue rejection
within weeks of implant. EMG signals became progressively weaker
over sessions, and signs of inflammation were seen when the dorsal
neck was dissected after electrode failure. Wire electrodes recorded
satisfactorily in past acute experiments, where distinctive spatial
properties for different muscles argued that crosstalk was not a
problem (Baker et al. 1985), so bipolar wires knotted in place in the
belly of the muscles were used to collect all the data reported here.

Bipolar wire electrodes were implanted into the left and right
splenius capitis, semispinalis, and occipectocervicalis. Electrodes were
made of insulated stainless steel wire (Cooner AS 631), which was
stripped of insulation in a 2-mm-wide bare spot several millimeters
from the end of the wire. To insulate the cut end of the wire that was
left in the neck, the Teflon insulation was melted, stretched over the
wire end, and fused. A small-gauge hypodermic needle was passed
through each muscle, the end of the wire was inserted into the sharp
end of the needle in the reverse direction, and the needle was
withdrawn, leaving the wire in the muscle. The electrode wire was
pulled through the muscle until the bare spot was inside the muscle
belly, and then the end of the wire was tied to itself, around the
muscle. Another such wire was also inserted and tied to the muscle
several millimeters away from the first wire. Led under the skin and
soldered to a connector that was cemented to the skull, these two
intramuscular wires made up the bipolar electrode for each muscle. At
least a week of recovery was allowed after each surgery. Electrode
placement was verified by postmortem dissection at the conclusion of
the experiments in one monkey. The other monkeys were kept for
other experiments for many months after the electrodes failed, and in
those animals, we could verify only that there was still a knotted lead
within the muscle mass in those muscles that still had unbroken leads.

**Recording paradigms**

The alert, untrained squirrel monkey was placed in the primate
chair. The head was bolted to the chair so that, when the chair was at
rest, the horizontal stereotaxic plane of the head was aligned with the
earth-horizontal plane. Inside the chair, a horizontal plate at the level of
the animal’s waist separated the arms from the legs and divided the
chair into two compartments. Neither the arms nor the legs were
restrained. Also inside the chair was a horizontal bar, which the
monkeys often chose to hold during whole-body rotation. In total
darkness, the animal was rotated sinusoidally about a head-centered,
earth-horizontal axis through an angle of up to ±30°.

The main set of experiments was designed to determine which
earth-horizontal axis of rotation produced the maximal EMG re-
sponse. All rotation axes lay in the horizontal planes of both the earth
and the animal’s head. The different axis orientations were interaural
(pitch), anteroposterior (roll), and directed at 22.5° increments be-
 tween interaural and anteroposterior so as to total 16 axes evenly
spaced around a full 360° in the head’s horizontal plane. The largest
data set consisted of sinusoidal rotations through an angle of ±30°
and at a frequency of 0.25 Hz, but 0.125- and 2-Hz stimulus frequen-
cies were also used. Trials of different directions and frequencies were
interleaved to minimize order effects. Trials began with the monkey
either upright or upside down. When the monkey was held upside
down, part of its weight was supported by the thighs, which rested
against the horizontal waist plate. Upright and upside down trials were
interleaved so as not to hold the monkey inverted for too long. The
monkey was returned to the upright posture immediately if it strug-
gled visibly before a trial or audibly during a trial or had persistent,
high-amplitude, bursts of EMG activity suggestive of distress. Trails
in which there were bursts of apparently voluntary EMG activity were
terminated, and those data were not saved. All cycles of saved data
were included in the analysis.

**Data collection and analysis**

EMG signals were amplified differentially with a gain of 500 and a
200 to 1,500-Hz (–3 dB) band-pass filter, and then rectified, filtered
by a low-pass circuit with a 50-Hz corner frequency, and amplified
20–100 times more. The rectified and filtered signals, the EMG
responses of the VCR and righting reflexes, were then sampled at
1,000 Hz/channel by National Instruments data-acquisition hardware
(NB-MIO-16, NB-DMA-8-G) that was controlled by custom soft-
ware.

During off-line analysis, a single sinusoid of the stimulus frequency
was fit to the rectified EMG traces by an analytic least-squares
method. The fit was used to calculate the amplitude and phase shift of
the EMG response relative to head tilt. These were plotted against the
direction of the stimulus orientation for each trial. These plots were fit

*J Neurophysiol* • VOL 93 • MAY 2005 • www.jn.org
with an analytic least-squares model that assumed that all inputs to the EMG summed to produce cosine tuning like that of the vestibular afferents (Estes et al. 1975). That is, it assumed that the inputs could differ either in their directionality or in their dynamics, but not both.

The one-input, cosine-tuning model, shown by dashed lines in Figs. 2B and 3B is

$$G \cos (\rho) = A \cos (p_a) \cos (d - d_a)$$
$$G \sin (\rho) = A \sin (p_a) \cos (d - d_a)$$

where $G \cos (\rho)$ and $G \sin (\rho)$ are the rectangular coordinates corresponding to the polar coordinates of the gain ($G$) and phase ($\rho$) of the response, ($A, p_a, d_a$) are the gain, phase and direction of the single input, respectively, and $d$ is the stimulus direction in the animal’s horizontal plane.

In addition to the cosine-tuned fits, the amplitude and phase from all trials of the experiment were collectively fit using another analytic least-squares model. This model assumes two hypothetical inputs that sum together and produce all the amplitudes and phases at each stimulus direction. Each of these two inputs has an amplitude, a phase, and a preferred direction. The amplitude of each input’s response is a cosine function of the angle between the stimulus direction and the input’s preferred direction. The direction and phase of one input differ by 90° from those of the other. Thus the two components of the model are said to be in spatial and temporal quadrature. The component with the larger amplitude defined the major axis of the response directionality, and responses were normalized to this amplitude. The phase of the component along the other (minor) axis was 90° advanced from that of the major component.

The two-input, spatiotemporally convergent (STC) model (Baker et al. 1984b), shown by solid lines in Figs. 2B and 3B, is

$$G \cos (\rho) = A \cos (p_a) \cos (d - d_a) + B \cos (p_b) \cos (d - d_b)$$
$$G \sin (\rho) = A \sin (p_a) \cos (d - d_a) + B \sin (p_b) \cos (d - d_b)$$

where ($B, p_b, d_b$) are the gain, phase and direction of the second input and the other variables are the same as in the preceding text.

We choose the two inputs so that they are in spatial and temporal quadrature, which constrains the system of equations to give an easily solved finite solution set. These then become ($A, p_a, d_a$) and ($B, p_b + \pi/2, d_b - \pi/2$). After substitution into the previous equations and simplification, the STC model becomes

$$G \cos (\rho) = A \cos (p_a) \cos (d - d_a) - B \sin (p_b) \sin (d - d_b)$$
$$G \sin (\rho) = A \sin (p_a) \cos (d - d_a) + B \cos (p_b) \sin (d - d_b)$$

Multiple component pairs from the two-input STC model from different experiments were averaged by first adding their projections onto the spatial $x$ and $y$ axes to produce a new component pair, which is in spatial but not necessarily temporal quadrature. This new pair was then converted into a component pair which is in both spatial and temporal quadrature using Eqs. 5–10 of Angelaki (1991). The amplitude of this component pair was then divided by the number of pairs in the sum, to produce the average fits shown by solid and dashed lines in Figs. 4–7.

**RESULTS**

Sinusoidal tilt of the head produced regular contractions in the three dorsal neck muscles, as shown by the traces of EMG activity in Fig. 1. Each trial consisted of seven cycles of 0.25-Hz rotation about an axis that lay in both the earth’s and the monkey’s horizontal plane. The axis used in the trial shown in Fig. 1 rotated the monkey forward and slightly to its right and was located 22.5° from the pitch axis that rotates the animal directly forward. This rotational direction was near the direction that best stimulated left semispinalis and splenius in this monkey (monkey D). EMG response peaks occurred near the point of maximal forward head velocity as was typical for this monkey. The response in each of the muscles studied in all monkeys was well-modulated during particular directions of rotation.

One common pattern of modulation can be seen in Fig. 2. EMG responses of occipitoscapularis from monkey A during a single trial have been cycle-averaged and displayed next to the corresponding axis of rotation in Fig. 2A, and a plot of the amplitude and phase of the EMG responses as a function of stimulus direction can be seen in B. The strongest response, indicating the muscle’s preferred direction, occurred during rotation about the axis directed at 112.5°, seen in the Fig. 2A, top left, next to the roll axis labeled 90°. Another peak response can be seen at −67.5°, which is the same axis as 112.5° but with opposite phase convention. As the stimulus moved away from this axis, the amplitude of the modulation fell off in a cosine-like fashion, especially visible in the plot of amplitude in Fig. 2B. The phase of the EMG response stayed nearly constant as the stimulus moved away from the muscle’s preferred direction. After passing the directions of minimal response, near pitch at 22.5 and −157.5°, the phase of the response abruptly changed by 180°. The direction of rotation that maximally activated this muscle can easily be seen in the polar plot of model amplitude versus direction of rotation in Fig. 2C. The axis of rotation that best stimulated the muscle is given by the dotted line, which represents the major component of the model fit. Perpendicular to this direction, shown by the short dotted line representing the minor component of the model fit, the amplitude fell to near zero. The amplitude, phase, and direction of the major component of the fit were 1 (by normalization), 21°, and 118°, respectively, and those of the minor component were 0.07, −69°, and −152°. This simple EMG response was closely fit by the cosine-tuned, single-input model, which is shown as dashed lines in Fig. 2B.
An EMG response pattern that is not cosine-tuned can be seen in the responses of a semispinalis muscle from monkey E, shown in Fig. 3. Rotation about the axis directed at $112.5^\circ$, near roll to the monkey's left, resulted in a well-modulated but relatively weak muscular contraction. As the rotation axis was moved away from the $-112.5^\circ$ axis toward the pitch backward (0°) direction (counterclockwise from the bottom in Fig. 3A and to the right along the x axis in Fig. 3B), the amplitude of the EMG response gradually increased. Its timing also gradually changed so that the response shifted from slightly leading (phase $= -163^\circ$) rightward head position (phase $= -180^\circ$) to slightly lagging (phase $= -103^\circ$) forward head velocity (phase $= -90^\circ$). The lack of a direction that produced a response of near-zero amplitude and the gradually shifting phase are hallmarks of a significant STC response pattern (Baker et al. 1984a,b). An STC response pattern is produced by a linear summation of signals, each of which has a cosine-tuned profile like that shown in Fig. 2, but which have different

![Diagram](image-url)
preferred directions and temporal phases. The solid lines in Fig. 3, B and C, are a fit to the data and represent one kind of STC response pattern. By contrast, the dashed lines are a poorer fit to the data and are from the non-STC, cosine-tuned model.

The dotted lines in Fig. 3C represent the preferred directions of one possible set of signals that would produce this pattern. The major and minor component axes do not necessarily reflect signals from two afferent populations but do offer a more precise description of the EMG behavior in this case than does the cosine-tuned fit. An infinite set of different signals can sum to give a particular STC response pattern (Schor and Angelaki 1992). In the model as applied here, the set is a pair of inputs, axes or components, which are said to be in spatial and temporal quadrature: their preferred directions are separated by 90° and their phases also differ by 90°. The amplitude, phase, and direction of the major component of the fit are 1, 65°, and 166°, respectively, and those of the minor component are 0.34, −24°, and 76°. In contrast, because the amplitude of the minor component of the fit from Fig. 2 was so small (only 0.07), it is considered cosine-tuned, not STC.

For each monkey, each muscle’s response to rotation had a characteristic pattern, whether cosine-tuned or more spatiotemporally convergent. Figure 4 shows the results from one muscle, semispinalis, from all experiments across all monkeys.

Responses to rotation when the monkey was in the normal upright posture are in the first column. Sample data points from Figs. 2B and 3B, which show an experiment from the left semispinalis of monkeys A and E, respectively, are consistent with the results from other experiments within that same animal, as seen in Fig. 4, left. Superimposed on the data in Fig. 4, left, are — representing the average of the individual fits to each day’s experiment. (An individual fit to a day’s experiment is shown by the solid lines in Figs. 2B and 3B.) Seven to twelve experiments were performed in each of the five monkeys.

Semispinalis had a cosine-tuned response pattern in monkeys A, B, and D, in which the minor component of the fit was only 0.01, 0.04, and 0.10 times as large as the major component, respectively. By contrast, semispinalis in monkeys E and F showed a more spatiotemporally convergent pattern; in these cases the respective ratio of the size of the minor component to that of the major component was 0.37 and 0.30.

The monkeys were turned and held upside down and subsequently rotated about the same earth-horizontal axes as described previously. Like the rotations starting from an upright posture, these rotations resulted in a characteristic response pattern for a particular muscle in a particular monkey, as can be seen in Fig. 4, middle. The - - - in the middle is the average of the individual fits to each day’s experiment when the monkey was held upside down and is re-plotted on the right panel.

**Fig. 4.** Spatiotemporal properties of semispinalis. Each panel is a plot of amplitude and phase of EMG response as a function of the direction of the earth-horizontal axis of rotation. Numbering convention of axis direction, which forms the x axis of each panel, is the same as in Figs. 2 and 3: 0° is pitch backward, 90° is roll rightward, etc. Left and middle: the responses to rotation when the monkey was upright or upside down, respectively. Each row shows results from 1 monkey. Units for amplitude are arbitrary and are only for comparison of responses from the same muscle in the same monkey. Phase is relative to head rotational position. — and - - -, the average of the fits to all the experiments for that monkey in the upright and upside down postures, respectively. Right: these averages are re-plotted and rescaled to have the same amplitude for comparison.
along with the average fit from left from the rotations performed when the monkey was upright. In four of five animals (monkeys A, B, D, and F), the direction of rotation that maximally activated the muscle was the same for both upright and upside down postures. This can be seen in the upper half of each of the panels in Fig. 4, right, in which the peaks of the - - - and — of the amplitude plots are located close to each other along the x axis. On the other hand, in monkeys A, B, and F, there was a large change in the phase of the response when the monkeys were rotated in the upside down position (Fig. 4, bottom half of each panel, right). Only in monkey D were both the spatial and temporal properties of the semispinalis response largely the same for the two different postures.

The EMG responses for splenius and occipitostacapularis in Figs. 5 and 6 show a similar mix of cosine-tuned and spatiotemporally convergent patterns. The average fits for all the muscles have been summarized for comparison in Fig. 7. As in semispinalis, responses in splenius (Fig. 7, middle) and occipitostacapularis (Fig. 7, right) differed somewhat from monkey to monkey. Spatial properties of responses were largely the same for upright and upside down rotations in monkeys A, B, and D, whereas in monkeys E and F, there was a substantial change in the direction of rotation that maximally excited the muscles when the monkey was held upside down. The phase of the response shifted greatly during upside down rotations of monkeys A, B, E, and F. Thus only in monkey D were both spatial and temporal properties of the response largely the same for the two different postures.

Another perspective on the consistency of EMG responses across experiments can be seen in Figs. 8 and 9, which show for each experiment one vector representing the direction of rotation that maximally activated the muscle, the maximal activation direction (MAD) vector. This direction is the direction of the major component from the simultaneous fit to all the amplitudes and phases of EMG responses from 1 day’s experiment, equivalent to the longer dotted line in Figs. 2C and 3C. Results from rotations about an upright posture are shown in Fig. 8 and those from rotations about an upside down posture in Fig. 9. The direction of rotation that maximally activated each muscle was broadly consistent across experiments, tending for all muscles toward pitch forward rotation with some component of contralateral roll. The one major exception can be seen in the first row of Fig. 9, in which the vectors in monkey A are shifted almost 180°, due to a shift in the phase of the response by almost 180°. This can be seen better in Table 1.

Table 1 summarizes the average values of the components of the fits to all experiments. Each fit is made of two components. Each component has an amplitude, a direction, and a phase.
The directions of the two components are perpendicular to each other, and each can be thought of as a spatial axis. The component of the fit that has a larger amplitude is said to lie along the major axis of the response. The phase of the component along the minor axis is by convention 90° greater than the phase of the major component. In monkey A, the average phase of the major component of the response when the monkey was inverted was roughly 180°, almost 180° different from the phase when the monkey was upright. To make comparisons easier between responses during upright and inverted postures in monkey A, 180° was subtracted from both the phase and the direction of the average values of the major component of the fit for the responses of this animal in the inverted posture. The resulting values are shown in Table 1. In characterizing the change in the response in monkey A when the animal was inverted, one can say either that the directionality of the response was largely the same but the phase was shifted by almost 180° or that the directionality was reversed but the phase was roughly the same. Other monkeys showed less of a change in response when inverted than monkey A. In monkeys B and F, the phase shifted roughly 90 and 120°, respectively. Monkey D showed little change in phase.

A comparison of the average maximum activation direction from these squirrel monkeys with previous data in the cat can be seen in Table 2. The appropriate vector components from Table 1 of the cat study (Banovetz et al. 1995) have been converted to the convention used in this study to indicate direction of rotation in the horizontal plane. The values for biventer cervicis and complexus cervicis in the cat have been averaged to compare with semispinalis in the squirrel monkey. The maximum activation direction for semispinalis and splenius in the squirrel monkey were closer to forward pitch (180°) than in the cat. However, the maximum activation direction for occipitocervicalis in the squirrel monkey was closer to contralateral roll (90°) than in the cat.

DISCUSSION

Nature of the variation in VCR EMG responses

Reflexes are distinguished by rapid, autonomous, and predictable action, all presumed to originate in simple, fixed neuronal circuitry (Sherrington 1898). However, even the simplest of neural pathways are subject to control by other neural systems, to adaptation or habituation, and to alteration of action in response to stimulus context (Pearson and Gordon 2000). The cervical muscle activity studied here in response to vestibular stimulation may be subject to such influences, and responses might vary from one experimental session to the next. The nature and extent of these variations could provide...
clues to the functions and limitations of the VCR. The VCR is a coordinated action of synergistic and antagonistic muscle groups, which introduces the further problem of the criteria by which the nervous system organizes motor synergies (Pellionisz and Peterson 1988; Peterson 2004). Many such criteria have been suggested (Weiss and Flanders 2004), and the nervous system may be able to choose among them. At one extreme, responses of the three studied muscles could vary unpredictably from trial to trial, with amplitude, directionality, and timing of EMG activity differing from one moment to the next. This would suggest that there are many ways to serve the basic VCR goal of head stability (Keshner et al. 1992) or that there are multiple possible VCR goals, and the neural substrate is free to choose among the alternatives. At the other extreme, the directionality and dynamics of a given muscle’s EMG might be precisely repeatable across all trials with the same stimulus, and across all animals of the same species, suggesting that the biomechanical constraints (Crowninshield and Brand 1981) of the head and neck leave only a single optimal pattern of VCR responsiveness for each muscle.

**VCR EMG directionality in the upright posture**

The idea that VCR activity in our tests varies unpredictably can be rejected with confidence. Directionality vectors and response phases of each muscle were closely clustered across experimental sessions not randomly distributed. Dorsal neck muscles in the squirrel monkey were most active during contralaterally directed rotations about axes intermediate between pitch and roll with differing degrees of roll sensitivity from those reported by previous studies in alert and decerebrate cats (Banovetz et al. 1995) in which occipitoscapularis response vectors were more closely aligned with the pitch axis, and splenius and semispinalis response vectors more closely aligned with the roll axis. The cat VCR directionality may have been specific for the prone posture (Keshner 1994; Statler and Keshner 2003) or might reflect biomechanical differences in the way the head relates to the neck and torso in primates versus felines. In the cat, as in the primate, the head rests atop a cervical spinal column that is normally oriented vertically with respect to gravity (Vidal et al. 1986), so it is likely that any biomechanical influences on VCR directionality in the two species relate to the quadrapedal stance of cats rather than the orientation of the cervical vertebrae.

**Monkeys versus muscles**

The extent to which VCR EMG response vectors were aligned with the pitch axis appears to vary across animals in Fig. 8, raising the possibility that the VCR of the five monkeys...
tested was not constrained by the biomechanical action of each muscle but instead idiosyncratic to a response pattern adopted by each animal. An example of the latter for the data collected in the upright posture would be different degrees of tolerance for pitch instability in the different subjects that could result in a systematic deviation of the maximal activation direction vectors toward pitch in monkeys less tolerant of pitch instability. Systematic differences across animals may be more likely for data collected with the head inverted. A monkey might adopt the strategy of righting its head, but do this preferentially by rolling, or might avoid backward pitch righting, or even attempt to remain stable without righting at all so that visual fixation can be maintained.

In addition to the response vectors for each neck muscle in each monkey, Figs. 8 and 9 show the response vectors for a given muscle superimposed across all five monkeys (bottom rows), and for comparison, the vectors for a given monkey superimposed across the three muscles (rightmost columns). The total dispersion of the vectors for splenius and semispinalis in Fig. 8, bottom row, is greater than the total dispersion of the vectors from all three muscles in each monkey, right column, suggesting that behavior specific to an individual monkey was at least as important as muscle biomechanics in the determination of response vectors. The very narrow dispersion of vectors of all three muscles for monkey A is further support for the importance of factors that vary by subject rather than by muscle. Response vectors obtained in the inverted posture were more closely clustered by monkey (Fig. 9, rightmost column) than by muscle (Fig. 9, bottom row) in all cases, also consistent with the importance of the individual subject in neck muscle reflex directionality.

Canal and otolith signals in VCR EMG responses

Modulated canal and otolith signals are both available to command reflexive neck contractions during vertical rota-

**FIG. 8.** Maximum activation direction (MAD) vectors of semispinalis, splenius, and occipitotrapecularis during tilts from an upright body posture. Each of the 1st 5 rows shows results from 1 monkey, and each of the 1st 3 columns shows results from 1 muscle. Each vector represents the preferred direction of the major component of the fit to the amplitudes and phases from 1 experiment, equivalent to the longer dotted line in Figs. 2C and 3C. The direction of rotation represented by each vector is given by the right-hand rule: when the right thumb is aligned with the direction of the vector and the fingers are flexed, the fingers curve in the direction of rotation that maximally activated the muscle. The rightmost column displays the vectors for all 3 muscles combined for each monkey. The bottom row displays the vectors for all 5 monkeys combined for each muscle.
tions about a horizontal axis, and at the 0.25 Hz frequency used in this study, the two signals are thought to contribute about equally to the VCR (Peterson et al. 1988). The stimulus to the canals, angular acceleration, is independent of initial starting position, whereas otolith responses are due to changes in the direction of the gravitational vector with respect to the head and depend on the head’s angle with respect to the vertical (Loe et al. 1973). Behavior mediated by simple canal pathways might be expected to be invariant for different initial postures, while simple otolith pathways should be linked to gravity and are expected to carry very different signals when the head is upside down. For example, a chin-to-chest tilt of the head excites anterior canals no matter what the starting posture. However, a chin-to-chest tilt excites posteriorly located utricular hair cells when the starting position is upright but inhibits them when the starting position is upside down.

VCR versus righting reflex

The canal signal independence from head position is appropriate to the stabilizing function of the VCR, but this stabilizing action acts counter to any attempt at head righting from a nonupright head posture. Utricular otolith signals, in contrast, depend on posture in exactly the manner required by righting reflexes, which could operate by neuronal circuitry that opposed any stimulus to the utricle to maintain its upright orientation. If this was true, then the otolith component of neck muscle EMG excitation should be compensatory and synergistic with canal signals in the upright head posture, but anticompen-
satory and opposing canal signals when the head is inverted and a righting reflex activated. Clearly anticompen-satory EMG activity was seen in monkey A, where the directionality of EMG response vectors with the head upside down (Fig. 9) is nearly opposite that in the upright posture (Fig. 8), and differs

FIG. 9. MAD vectors of semispinalis, splenius, and occipitoscapularis during tilts from an inverted body posture. Layout of figure is identical to that of Fig. 8. Each row shows results from 1 monkey, and each column shows results from 1 muscle. Each vector represents the preferred direction of the major component of the fit to the amplitudes and phases from one experiment, equivalent to the longer dotted line in Figs. 2C and 3C. The direction of rotation represented by each vector is given by the right-hand rule: when the right thumb is aligned with the direction of the vector and the fingers are flexed, the fingers curve in the direction of rotation that maximally activated the muscle. The rightmost column displays the vectors for all 3 muscles combined for each monkey. The bottom row displays the vectors for all 5 monkeys combined for each muscle.
from the directionality of the responses of the other monkeys in the upside down head position. At another extreme, monkey D showed little change in EMG directionality when the head was upside down. The intermediate behavior of the other three monkeys suggested an interplay of stabilizing and righting reflexes. This behavior was not well captured by the response vector representation, and spatial temporal convergence analysis was required to more accurately summarize their responses.

**STC in VCR EMG responses**

STC models have been used extensively to characterize central vestibular neuron responses in rats (Angelaki et al. 1992), cats (Baker et al. 1984b, 1988; Perlmutter et al. 1999), and rhesus monkeys (Angelaki and Dickman 2000). Similar studies of neck EMG responses in cats have been conducted previously (Baker et al. 1985, 1988; Peterson et al. 1988). As demonstrated in Fig. 3, STC models capture two important features of neck EMG responses: the dependence of response dynamics on stimulus direction and the lack of a stimulus direction that produces no response.

One goal at the outset of this study was to try to determine, during rotations about earth-horizontal axes, the relative contribution to the VCR of signals from the semicircular canals versus signals from the otolith organs. Rotation of the head about an earth-horizontal axis produces vestibulocervical reflexes that may be driven by several different central signals of vestibular origin, including signals derived from the semicircular canals related to head rotational velocity, and signals derived from the otolith organs related to rotational head velocity or related to static head tilt with respect to gravity. For instance, Angelaki and Dickman (2000) found that the majority of central otolith neurons in the rhesus monkey peaked in phase with head velocity during linear translation $<0.5$ Hz. Correlates of the otolith signals are found in the vestibuloocular reflex, where static tilt signals correlate with ocular counterrolling and tilt of Listing’s plane (e.g., Furman and Schor 2003), and velocity estimator signals correlate with bias in eye velocity during sustained head rotations about earth-horizontal axes (e.g., Killian and Baker 2002). That certain control signals are shared by the VOR and VCR is supported by the projection of many vestibular neurons to both oculomotor nuclei and the spinal cord (Boyle et al. 1992; Isu et al. 1991; Minor et al.

<table>
<thead>
<tr>
<th>Monkey</th>
<th>Semispinalis</th>
<th>Splenius</th>
<th>Occipitoscapularis</th>
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**TABLE 2.** Comparison of direction of maximum activation in dorsal neck muscles of squirrel monkey and cat

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<tr>
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<td>160</td>
<td>150</td>
</tr>
<tr>
<td>Occipitoscapularis</td>
<td>140</td>
<td>164</td>
<td>166</td>
</tr>
</tbody>
</table>

*Semispinalis* values in the cat are averages of values from biventer cervicis and complexus cervicis. Cat data from Banovetz and colleagues (1995).
1990; Perlmutter et al. 1998a,b). Within the spinal cord, a single cat vestibulospinal axon typically branched among the motor pools of multiple muscles (Perlmutter et al. 1998a), consistent with the overlapping response directions of neck muscles reported here in monkeys.

VCR phase in this study when the head was upright was comparable to the range found previously in alert and decerebrate cats and is consistent with multiple VCR control signals. During rotation at 0.25 Hz, the phase ranged from near tilt velocity (99° phase lead re head position, monkey D, Table 1) to position (15° phase lead, monkey A) in the MAD. The phase of the VCR in alert cats in response to yaw rotations about an earth-vertical axis was closer to head rotational velocity (75°) (Banovetz et al. 1995). Other studies in decerebrate cats showed phases more intermediate between head velocity and head position (Berthoz and Anderson 1971; Bilotto et al. 1982; Ezure and Sasaki 1978). Extrapolating from the data of Dutia and Hunter (1985), at 0.25 Hz in decerebrate cats biventer cervicis EMG has a phase lead of ~40–45° with respect to forward head tilt during pitch. This falls within the range observed in this study. The average phase lead of pitch response in semispinalis in alert monkeys found here was 17, 30, 98, 74, and 44° for animals A, B, D, E, and F, respectively.

The spatial and temporal properties of the VCR in each animal were related. Monkey A, as previously mentioned, had a response with phase near position in the upright posture and showed the largest change in the preferred direction of its response, nearly reversing the action of the reflex, when the animal was in the upside down posture. On the other hand monkey D, in which the phase was closest to tilt velocity when upright, showed the smallest change in the preferred direction of its response. These differences are consistent with the idea that neck muscle EMG in response to head rotation is a combination of stabilizing and righting reflexes, with stabilizing mediated by canal signals that are most clearly evident in the upright head posture and with righting mediated by utricular signals that are most clearly evident with the head upside down. Neck muscle reflex activity appears to reflect varying degrees to which an animal relies on stabilizing versus orienting reflex systems. The challenge for future experiments is reliable isolation of neck muscle reflex components so that righting reflexes can be characterized in detail and their relation to overall control of the head better understood.

GRANTS

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R E F E R E N C E S


