# Gravity Load Related Asymmetries in the Sagittal Vestibulo-collic Reflex

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EMG recordings of the neck muscles (biventer cervicis, complexus, splenius, longus capitis) of decerebrate cats were obtained during pitch and roll stimulations (sinusoidal stimulation: 30° p-p amplitude, 0.2 Hz frequency). Most of the EMG responses to pitch showed activation peaks leading the position stimuli by 56° and inhibition peaks leading by 11°. Conversely, in response to roll the activation peak led by 16° and the inhibition peak by 10°. The activation peaks of the pitch responses were, thus, more asymmetric and more leading than those of the roll responses. Consequently, the harmonic distortion coefficient was significantly higher in pitch than in roll. Moreover, when the vertical semicircular canals were activated in absence of otolithic modulation, the pitch and roll responses maintained the same difference in timing observed in the presence of otolithic coactivation. It appeared that the simultaneous stimulation of both anterior semicircular canals (pitch) induces a greater lead than that of combined anterior and posterior canals (roll). Thus the timing of neck muscle responses to vestibular stimulation depends on the pair of activated vertical semicircular canals. *Key words: vestibulo-collic reflex, vertical semicircular canals, vertical asymmetries and gravity.*

## INTRODUCTION

The influence of the head gravity load on the vestibulo-collic reflexes (VCR) differs strikingly according to the plane of stimulation. During sagittal plane stimulation (pitch), the gravity load opposes upward head movements and enhances downward ones. Conversely, during frontal plane stimulation (roll), the gravity effect is partly balanced and during horizontal stimulation, movements are not affected at all by the gravitational load. Thus, one can expect that in reflexes involving head posture adjustment, such as the VCR, different patterns of neck muscle activation will be utilized depending upon the plane of stimulation. The responses to pitch should be asymmetric, with upward responses being more powerful and dynamic than the downward ones, while no asymmetries should be seen in the roll responses. Previous studies have already revealed marked asymmetry in the vertical vestibulo-ocular reflex (VVOR), consisting of a greater compensatory slow phase velocity in the upward direction than in the downward one (1–5). On the other hand, no asymmetry was seen in the ocular reflexes evoked in other planes of stimulation (3). However, the upward preponderance in the VVOR was observed only in the side down position, i.e. when the vertical semicircular canals are activated alone without gravitational modification of otolithic receptors. As a matter of fact otolithic coactivation occurs in most vertical head movements and the eye responses are symmetric to maintain correct gaze stability (1, 3, 5). Thus we suggest that the asymmetry observed in the VOR reflects an intrinsic asymmetry in the vestibular system that could be directed to the vestibulo-collic reflex since a portion of the pathway leading from the vestibular system to the oculomotor nuclei is also used to carry vestibular impulses to neck motoneurons (6, 7).

Therefore we should expect different activation patterns of EMG of neck muscles to head pitch in the upward and downward responses and different dynamics compared to the other planes of stimulation. Furthermore this difference in the sagittal VCR should be not suppressed by otolithic receptor activation.

In order to verify this hypothesis EMG recordings were performed in neck muscles of decerebrated cats during whole body oscillations during pitch and roll stimulation. The animals were sinusoidally oscillated in the upright position to evoke combined maculo-collic and ampullo-collic reflexes and in the side-down and nose-down positions to evoke the ampullo-collic reflexes alone.

## MATERIAL AND METHODS

*Preliminary surgical procedures.* Experiments were performed on 6 cats. The animals were anesthetized with ketamine hydrocloride and diazepam. The head was held in a stereotaxic apparatus so that the horizontal semicircular canals lay in the horizontal plane (23° nose-down with respect to the stereotaxic 0°) and two head-restraining screws were secured with dental cement to smaller screws fixed to the skull. The animals were allowed to recover for at least 3 days before the eye movements were recorded.

Electromyographic recordings were performed in decerebrate cats. Under halothane-nitrous oxide anesthesia the trachea was cannulated and a craniotomy

was performed. Cerebral tissue was aspirated to de-cerebrate the animals by a transection in a coronal plane about 5 mm anterior to the superior colliculi. Animals were allowed to recover for at least 1 h before the electromyographic recording.

*Experimental apparatus and stimulations.* The animals were firmly secured inside a cradle placed on a servo-controlled triaxial turn-table (3M 3000 Mangoni, Italy). The head was secured to a stereotaxic frame by means of head restraining screws. Vestibular stimulation was delivered by rotating the animals in their sagittal (pitch) and frontal (roll) planes. Cats were also pitched 90° side-down and rolled 90° nose-down. In these positions, modulation of the otolithic input by the gravity vector is eliminated and the response can thus be attributed to the stimulation of the vertical semicircular canals alone.

*Electromyographic recording.* After cutting the skin, neck muscles were exposed. The edges of incision were anesthetized with lidocaine to prevent skin pain. Pairs of insulated stainless steel wires were inserted into the complexus, splenius and biventer cervicis muscles (extensor and torsional muscles) and in the longus capitis (flexor muscle). Mineral oil at body temperature was employed to prevent cooling and evaporation. The electrode position was verified at the end of experiment. Multiunitary activities were recorded from a neck muscle during each experimental session (8–10 recordings).

The electromyographic activity was differentially amplified and filtered (bandpass filter 10–3000 Hz). Then the electromyographic recording and table position were stored on a magnetic tape recorder (Store 4DS, Racal, UK).

*Data analysis.* Signals were digitalized off-line using an integrated hardware and software package (ISC-16-E), Computerscope EGA-A System, Electronic Inc., USA) mounted on an AT compatible personal computer (Vectra ES-12, Hewlett Packard, USA).

Signals were digitalized with a sample period of 640 μs. High-amplitude artifactual responses were rejected. The data were rectified and 20 cycles were averaged. Then 84 points/cycle histograms were computed and a least square procedure was used in order to obtain the first and the second harmonics. The amplitude of the sum of the first and second harmonics was measured from the baseline to determine the activation and inhibition peak values. These amplitudes were divided by turn-table angular position amplitude and then further divided by the mean (DC)/$\frac{1}{2}$ EMG level of activity to obtain percent modulation of EMG per degree of table rotation (8). The response timing was determined by combining the first and second harmonics and measuring the peaks

of the response with respect to table position. Harmonic distortion was calculated as the ratio of the second to the first harmonic.

## RESULTS

### *The vertical and torsional vestibulo-cervical reflexes (VVCR and TVCR) in the upright position*

*Extensor and torsional muscle study.* Multiunitary electromyographic activity of the biventer cervicis, complexus and splenius muscles were recorded (8–10 recordings for each muscle) during sinusoidal pitch and roll stimulations (30° p-p, 0.2 Hz). On the basis of the different torque vectors of the muscles (9–10) the biventer cervicis responded to pitch, the splenius to roll stimulations, and the complexus muscles to both roll and pitch. Regardless of the muscle or recording site being considered, the responses to pitch were characterized by an asymmetry in the activation and inhibition timing. In fact, the EMG activity of most of the recordings (more than 70%) increased steeply during activation phase and decreased gradually during inhibition phase: the activation peak led the stimulus position by about 56° ± 14°, while the inhibition peak led it by 11° ± 8° (Fig. 1). The harmonic analysis showed a higher degree of harmonic distortion, as the amplitude of the second harmonic was 35% ± 13 of the first, and the second harmonic max peak led the first by 35°–55°. As for the intensity of the response, the amplitude of activation peak, evaluated from the baseline activity, was 3 times greater than the inhibition peak.

The EMG responses to roll stimulation showed more symmetric behavior. In most cases the responses were sinusoidal with less than 10% harmonic distortion. The phase of peak activation was 16° ± 5° and peak of inhibition was 2° − 10° (Fig. 1). When distortion was greater than 10% (34% of the cases), the time relationship between the first and second harmonics differed from that observed during pitching, with the max peak of the second harmonic leading that of the first by 75°–90°. In terms of amplitude, the roll response was also more symmetric, with an activation peak only 1.2 times higher than the inhibition peak.

*Flexor muscle study.* EMG responses of the longus capitis to pitch were weak and showed a high degree of harmonic distortion ( >30%). However, in contrast to extensor muscle behaviour, the inhibition was steeper than the activation. The former led the stimulus by 52° ± 15°, while the activation peak led by only 19° ± 13° (Fig. 2). Harmonic analysis reflected this difference revealing an opposite time relationship between the first and second harmonics compared to the extensor responses.
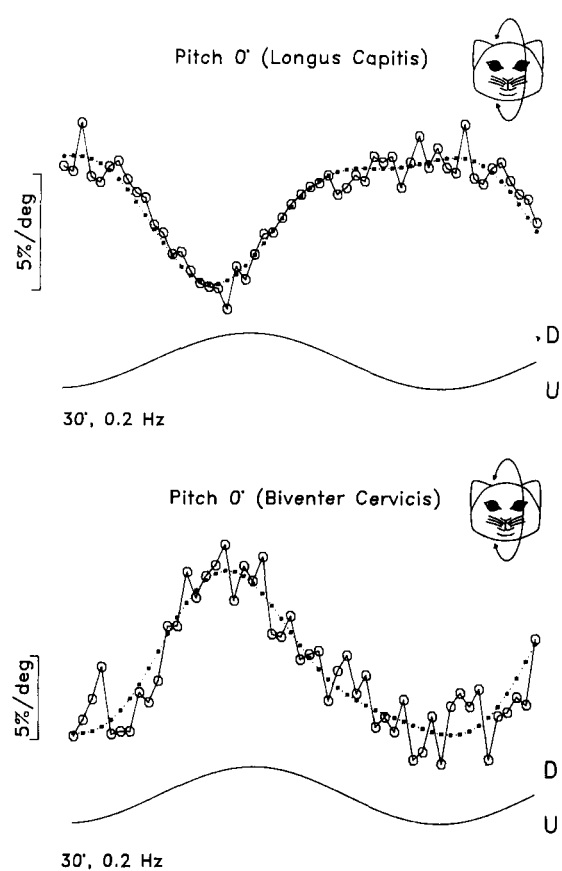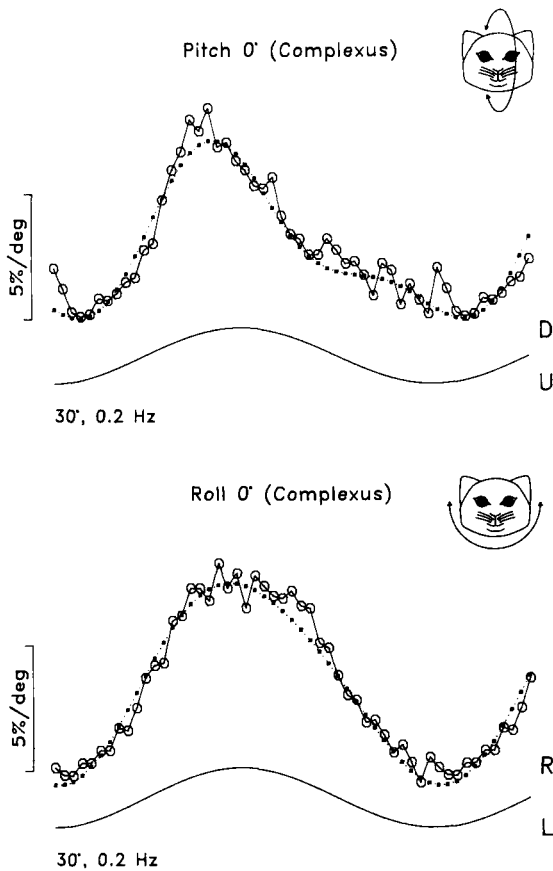
Pitch 0˚ (Complexus)



30˚, 0.2 Hz

Roll 0˚ (Complexus)



30˚, 0.2 Hz

Pitch 0˚ (Longus Capitis)



30˚, 0.2 Hz

Pitch 0˚ (Biventer Cervicis)



30˚, 0.2 Hz

*Fig. 1.* Averaged (10 cycles) rectified electromyographic responses (*circles*) in the complexus muscle during pitch and roll vestibular stimulation, in upright position. The sum of first and second harmonics (*dotted line*) is superimposed to the EMG trace. At the bottom of each panel the table position is shown. *D*: down, *U*: up, *R*: right, *L*: left.

*Fig. 2.* Averaged (10 cycles) rectified EMG responses (*circles*) in the biventer cervicis (extensor muscle) and the longus capitis (flexor muscle). The sum of the first and second harmonics and table position are indicated as in Fig. 1.

*Vestibulocollic reflexes evoked in the side-down and nose-down positions*

The VCR was also studied by yawing the animals 90° side-down. In this condition the muscle responses were induced by sagittal activation of the vertical semicircular canals alone as also occurs in pitch, but in the side-down yawing, there is no otolithic stimulation. Under this experimental condition the EMG peak responses showed a greater lead compared to that in upright position (activation peak phase = 78° ± 13 and inhibition peak phase = 38° ± 11) (Fig. 3).

Conversely, by yawing the animals 90° nose-down, the responses were elicited by stimulating vertical semicircular canals alone, as also occurs in roll, but without otolithic modulation. In this case the activation peak of the EMG response led the stimulus by 45° ± 15, and the inhibition peak led it by 35° ± 8°, showing a remarkable increase in phase lead as compared to that of upright roll responses (Fig. 3).
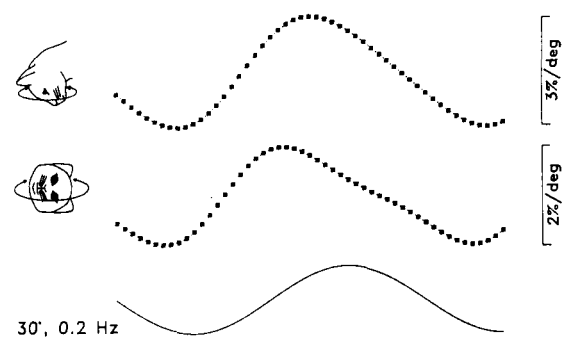


30˚, 0.2 Hz

*Fig. 3.* Sum of the first and second harmonics of the averaged (10 cycles) rectified electromyographic responses to 90° nose-down (*upper trace*) and 90° side down (*lower trace*) yawing, in the complexus muscle. At the bottom the stimulus is reported (30°, 0.2 Hz).

However, comparison of these pure canal-induced responses revealed a constant phase lead increase of about 30° in the activation peaks of the pitch with respect to roll responses.

## DISCUSSION

The EMG responses of the extensor muscles (complexus and biventer cervicis) to pitch stimulation were characterized by an asymmetric pattern. This asymmetry was seen in the timing and amplitude of the responses. In fact the peak of activation was higher and showed a greater lead than those of the inhibition peak. In addition, the activation pattern of a flexor muscle (longus capitis) was weak and opposite to those of the extensors. Conversely, the activity of the complexus and splenius in response to roll stimulation was more symmetric in timing and amplitude. Moreover, roll induced a delayed activation peak compared to that seen with pitch.

On the basis of these EMG observations we can infer that the motor command for upward reflex head movement has a greater lead and intensity than that for downward head movement. In addition, the motor command for the torsional reflex has a more symmetric and delayed pattern with respect to that of pitch.

It is likely that these differences represent a reflex accommodation to counteract different loads. In fact, on the basis of physical considerations, the head load can be expected to depend on the direction and the plane of the VCR. Hence this reflex introduces greater phase lead and intensity in the upward reflex movements, because the gravity load counteracts only upward responses, while it facilitates downward responses and has only limited effects on the torsional ones.

To analyze the mechanisms responsible for these differences, we distinguished the relative contributions of ampullar and macular inputs to the VCR. Our data show that the VCR evoked in the absence of otolithic modulation maintained the relative timing differences observed in upright position. This suggests that activation of the semicircular canals alone is responsible for the asymmetric motor command that compensates different gravity loads. This is not surprising since, at the level of the eye reflexes, it has been already shown that the upward preponderance in the vertical vestibulo-ocular reflex is caused by vertical semicircular canal activation alone, while the otolithic system serves to suppress the asymmetry (3).

In conclusion, it appears that the differences in phase between the vertical and torsional commands for the VCR are introduced by canal activation and are not suppressed by otolithic modulation. This compensates for the gravity load in sagittal plane stimulation to achieve head stability. On the other hand, in the VVOR, where there is no gravity load opposing eye movements, otolithic modulation abolishes the asymmetric command which would be detrimental to proper gaze stabilization.
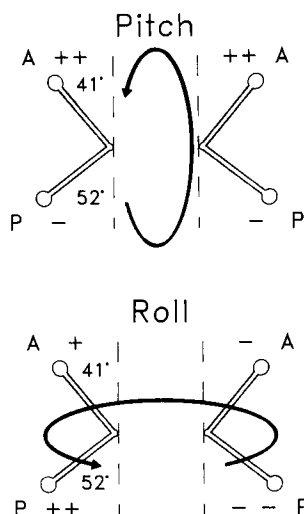


*Fig. 4.* Schematic drawing of spatial arrangement of the semicircular canals and their activation during pitch and roll. The relative amount of semicircular canal activation is indicated by sign + and the inhibition by sign −. *A*: anterior, *P*: posterior semicircular canals.

To explain the canal induced differences we suggest various mechanisms involving peripheral input and central network. The diversity of the central structures involved in upward, downward and torsional reflexes (11, 12) supports the possibility of different central processing of pitch and roll reflexes.

As for peripheral mechanisms, in the literature there is no evidence for differences between the anterior and posterior canals in term of threshold or sensitivity of the ampullar receptors. However, there are reports of a particular spatial orientation of the vertical semicircular canals that could explain our observations (13–15). In fact the anterior canals are more closely aligned with the sagittal plane, and the posterior canals with the frontal plane. This arrangement would enhance the responsiveness of both anterior canals during pitch and only of one of them during roll stimulation (Fig. 4). The enhancement of both anterior canal activations increases the receptor activation, in particular that of the dynamic receptors, and in turn, should give rise to a lead phase shift and to a gain increase in the upward responses.

## ACKNOWLEDGMENTS

## REFERENCES

1. Anderson JH, Precht W, Pappas C. Changes in the vertical vestibulo-ocular reflex due to kainic acid lesion of the interstitial nucleus of Cajal. Neurosci Lett 1979; 14: 259–64.

2. Darlot C, Lopez-Barneo J, Tracey D. Asymmetries of vertical vestibular nystagmus in the cat. Exp Brain Res 1981; 41: 420–6

3. Pettorossi VE, Errico P, Ferraresi A, Draicchio F, Santarelli RM, Bruni R. Vestibular and optokinetic asymmetries in the ocular and cervical reflexes. In: Berthoz A, Graf WM, Vidal PP, eds. The head-neck sensory motor system. Oxford: University Press, 1991: 419–31.

4. Snyder LH, King WM. Vertical vestibuloocular reflex in cat: asymmetry and adaptation. J Neurophysiol 1988; 59: 279–98.

5. Tomko DL, Wall III C, Robinson FR, Staab JP. Influence of gravity on cat vestibulo-ocular reflex. Exp Brain Res 1988; 69: 307–14.

6. Denise P, Darlot C, Wilson VJ, Berthoz A. Modulation by eye position of neck muscle contraction evoked by electrical labyrithine stimulation in the alert cat. Exp Brain Res 1987; 67: 411–9.

7. Uchino Y, Isu N. Properties of vestibulo-ocular and/or vestibulocollic neurons in the cat. In: Berthoz A, Graf WM, Vidal PP, eds. The head-neck sensory motor system. Oxford: University Press, 1991: 266–72.

8. Baker J, Goldberg J, Peterson BW. Spatial and temporal response properties of the vestibulo-collic reflex in decerebrate cats. J Neurophysiol 1985; 54: 733–56.

9. Keshner EA, Baker JF, Banovetz J, Peterson BW. Patterns of neck muscle activation in cats during reflex and voluntary head movements. Exp Brain Res 1992; 88: 361–74.

10. Wickland CR, Baker JF, Peterson BW. Torque vectors of neck muscles in the cat. Exp Brain Res 1991; 84: 649–59.

11. Fukushima K, Fukushima J, Terashima T. The pathway responsible for the characteristic head posture produced by lesions of the interstitial nucleus of Cajal in the cat. Exp Brain Res 1987; 68: 88–102.

12. Wilson VJ, Peterson BW. Vestibular and reticular projections to the neck. In: Peterson BW, Richmond FJ, eds. Control of head movement. Oxford: University Press, 1988: 129–40.

13. Blanks RHI, Curthoys IS, Markham CB. Planar relationships of semicircular canals in the cat. Am J Physiol 1972; 223: 55–62.

14. Ezure K, Graf W. A quantitative analysis of the spatial organization of the vestibulo-ocular reflexes in lateral- and frontal-eyed animals. I. Orientation of semicircular canals and extraocular muscles. Neuroscience 1984; 12: 85–93.

15. Mazza D, Winterson BJ. Semicircular canal orientation in the adult resting rabbit. Acta Otolaryngol (Stockh) 1984; 98: 472–80.

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