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Research Note

Horizontal Eye Position-related Activity in Neck Muscles of the Alert Cat*

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Summary. The activity of neck muscles was recorded in the alert, head-fixed cat together with the horizontal and vertical components of eye movements. Electromyographic activity of obliquus capitis cranialis and caudalis, and longissimus capitis, is closely related to horizontal eye position in the orbit both during spontaneous eye movements and vestibular nystagmus. The activity of splenius also shows this relationship but the coupling is less tight, probably because of the postural function of this muscle.

Key words: Eye-head coordination – Vestibular nystagmus – Visuo-motor system – Cat

It is well known that during rapid head and eye coordinated voluntary movements in the alert animal, eye and neck muscles are synergistic (Outerbridge and Melvill Jones 1971). In the monkey, Bizzi et al. (1971) have shown that, during rapid head and eye movements to a visual target, the onset of ipsilateral eye and neck muscle activity is synchronous. They suggested a parallel motor command to both types of muscles. In addition, following superior colliculus electrical stimulation (Guitton et al. 1980; Roucoux et al. 1980), or spontaneous orienting behavior (Roucoux et al. 1981), two modes of head-eye coordination were found. For gaze shifts limited to the oculomotor range (±25°), the neck EMG (Biventer cervicis) discharge onset depends upon eye position in the orbit: the head begins to turn only if the eye crosses an excentricity threshold. For gaze shifts larger than 25° the neck muscles discharge prior to the eye saccade independently of eye position.

By contrast, in most of the recent studies conducted in anesthetized or decerebrate animals, concerning the vestibular control of neck muscles (Berthoz and Anderson 1971; Wilson et al. 1979; Ezure and Sasaki 1978; Ezure et al. 1978; Peterson et al. 1981) the emphasis was put on the vestibular compensatory nature of dynamic characteristics of the neck muscle discharge (Vestibulo-collic reflex: VCR).

In the present work we have studied the activity of neck muscles in the head-fixed alert cat during both spontaneous eye movement and vestibular nystagmus. We have particularly focused our attention on those neck muscles (located in deeper layers) which have been shown to contain a large number of neuromuscular spindles, and have a putative proprioceptive function in motor reactions involving neck muscles (Richmond and Abrahams 1975).

The experiments were performed in alert unanesthetized cats. Horizontal and vertical components of eye angular position were recorded by the search coil technique. Search coils were implanted chronically around the eye ball. Calibration was performed by rotating the coils around the animal. Mid position of the eye was calculated by storing on the computer the eye movement recordings over a period of 2–3 h and calculating a mean value for both components of eye movement.

Electromyographic bipolar electrodes made with teflon-coated stainless steel wires (100 μm diameter) were implanted chronically in various neck muscles: Splenius, complexus, biventer cervicis, longus capitis, longissimus capitis, obliquus capitis cranialis and caudalis. The electromyographic (EMG) activity was integrated with a standard analog integrator (5–50 ms time constant). EMG of neck muscles and eye movements were recorded in two conditions: (a) during spontaneous eye movements in the light and (b) during vestibular nystagmus in complete darkness. For this purpose, the animal and recording set-up were placed on a turntable allowing a sinusoïdal

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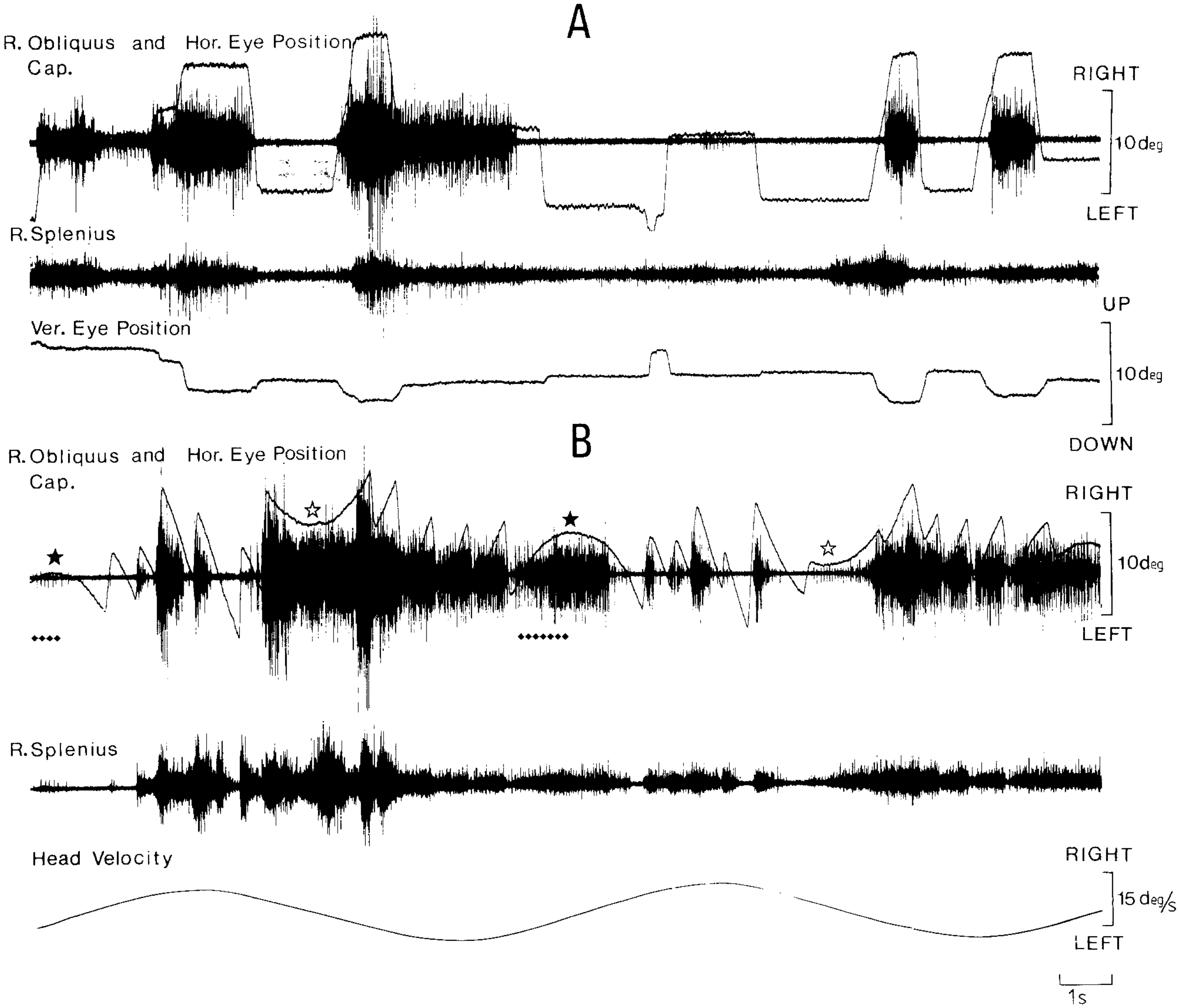

Fig. 1A, B. Comparison between obliquus capitis cranialis and splenius muscle activity with eye movements during spontaneous saccades or vestibular nystagmus. **A** Spontaneous eye movements. *Upper traces:* two signals were superimposed: horizontal component of the eye angular displacement and EMG activity of the right obliquus capitis cranialis. Calibration is for horizontal eye movement. *Middle trace:* EMG activity of the right splenius. *Lower trace:* Vertical component of eye angular displacement. **B** Sinusoïdal head rotation in darkness. *Upper and middle traces* are the same as in **A**. *Lower trace:* Head velocity

rotation around the vertical axis at a frequency of 0.1 Hz and about 90° peak to peak. During the recording the head of the cat was inclined at 21° forward to bring the horizontal semicircular canals into the horizontal plane. In all cases the head of the cat was fixed by bolts to a stereotaxic frame, and the body was firmly restrained to suppress or minimize any relative movement between body and head.

Neck Muscle Activity During Spontaneous Eye Movements

The records reveal a close relationship between EMG of obliquus capitis cranialis or caudalis, and longissimus capitis muscles with the horizontal component of spontaneous eye movement. Figure 1A illustrates this point. EMG of the right obliquus capitis has been superimposed onto the horizontal eye position trace. The approximate mid-horizontal position of the eye in the orbit has been aligned with the baseline of the EMG trace. The muscle discharges only when the eye is rotated horizontally in a position ipsilateral to the side of recording. The relationship is less clear for the right splenius in this particular case.

Figure 2A, which concerns the longissimus capitis muscle, shows that the firing of a single motor unit is nicely correlated with eye position above a certain

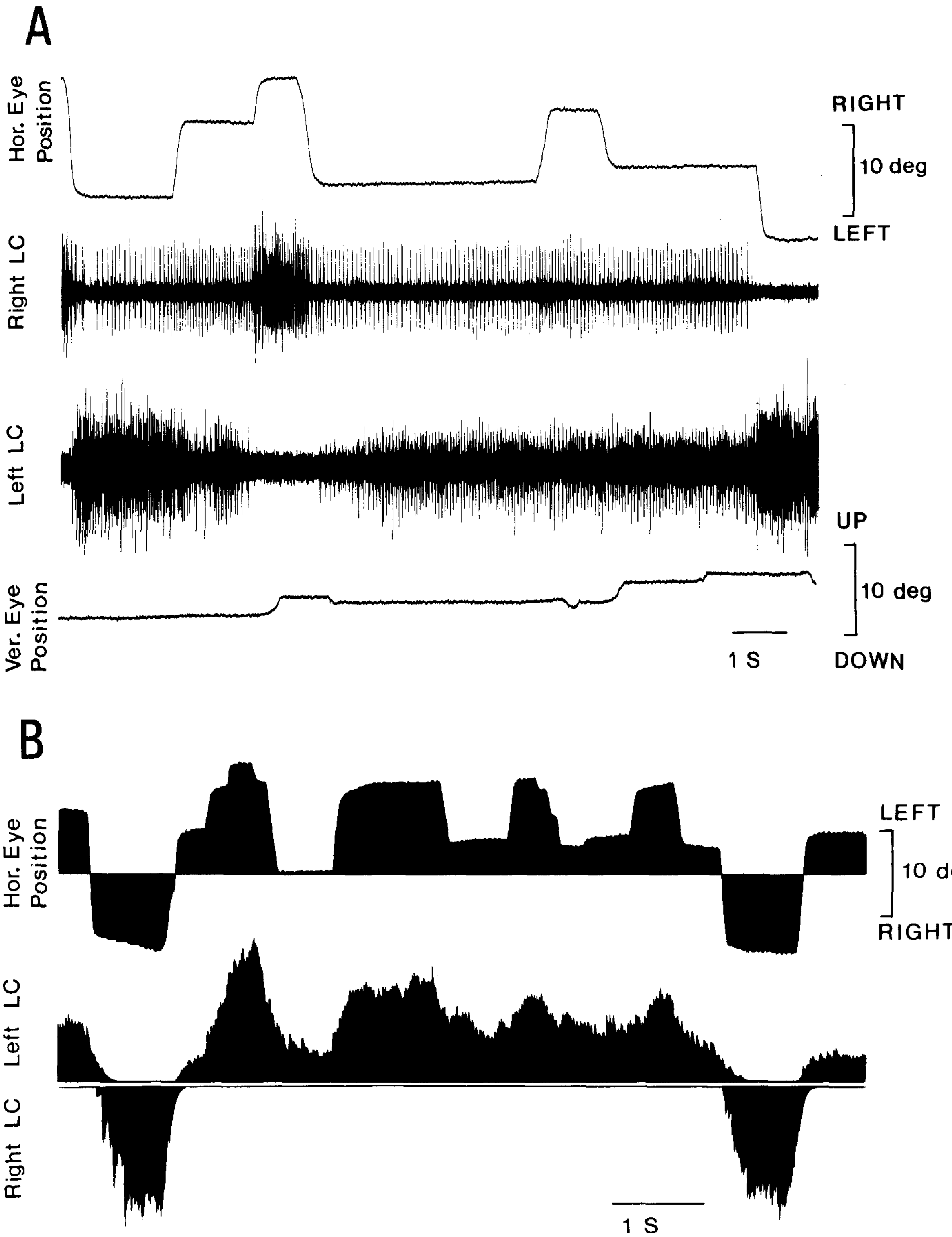

Fig. 2A–C. Comparison between left and right longissimus capitis (*LC*) activity and eye movements during spontaneous saccades or vestibular nystagmus. **A** EMG activity during spontaneous eye movements. *From top to bottom:* horizontal component of the eye position; EMG activity of the right *LC;* EMG activity of the left *LC;* vertical component of the eye position. **B** Integrated and rectified, EMG activity during spontaneous eye movements. *From top to bottom:* horizontal component of the eye position; EMG activity of the left *LC;* EMG activity of the right *LC* (this signal is shown upside down). **C** Integrated, rectified, EMG activity during sinusoïdal head rotation in darkness. *From top to bottom:* horizontal component of the eye position; EMG activity of the left LC; EMG activity of the right *LC* (this signal is shown upside down); head velocity

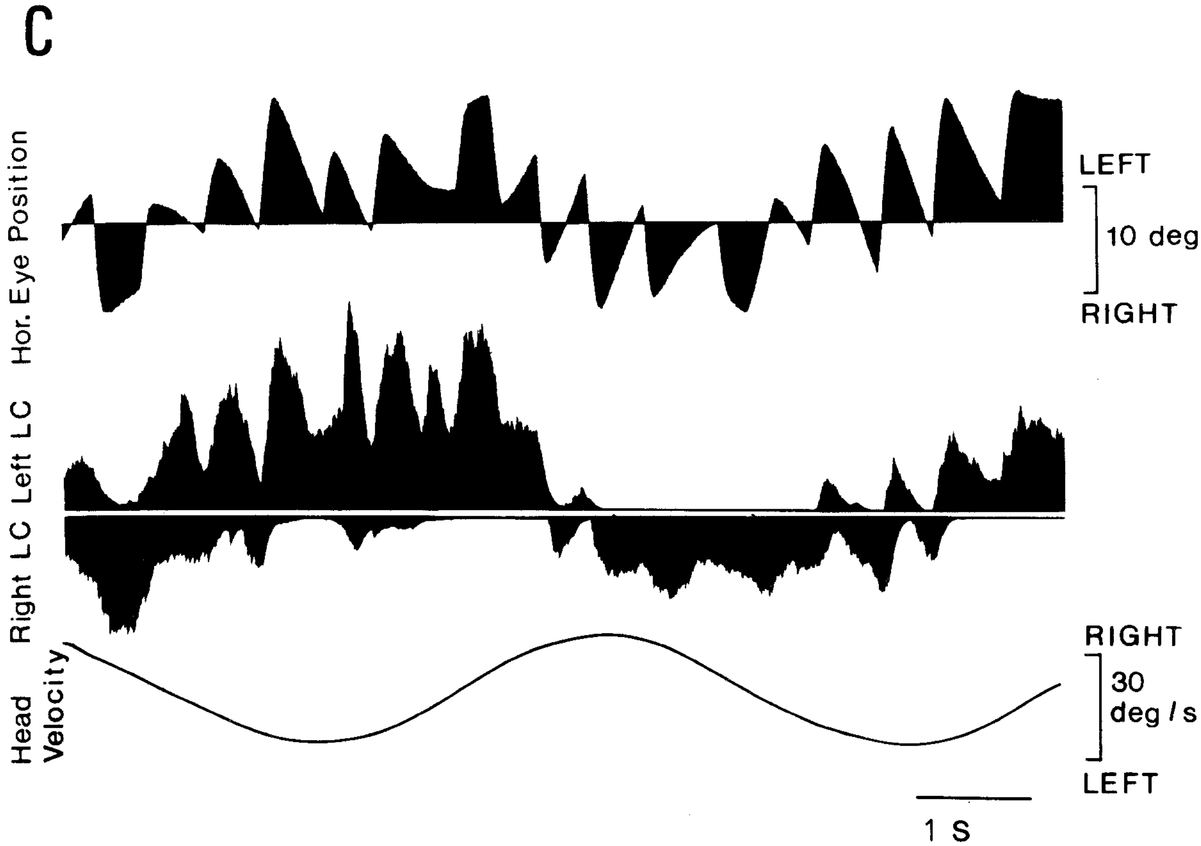

Fig. 2C

threshold of excentricity in the ipsilateral direction. When the eye reaches an excentric position other motor units are recruited. This recording also shows the behavior of the contralateral longissimus capitis in which activity is reciprocal. In Fig. 2B the EMG has been integrated with a 50 ms time constant. The activity of right and left longissimus can be compared with the horizontal eye position trace. A line has been drawn on the horizontal eye position trace to indicate approximately the mid eye position. The total pattern of the two muscles replicates the variations of horizontal eye movements. Preliminary quantification of these records (by calculation of the correlation between horizontal eye displacement component and integrated EMG), visual inspection of the records obtained in two cats with eight muscles implanted, and of one cat in which 26 neck muscles were implanted leads to the following conclusions: (a) Obliquus capitis cranialis, obliquus capitis caudalis and longissimus discharge exclusively when there is an ipsilateral horizontal eye movement component; (b) the activity of antagonistic pairs (right and left) is reciprocal with respect to eye position in the orbit. A certain degree of overlap exists around mid eye position; (c) the muscle discharge increase is due both to the increase of the firing frequency of individual motor units and/or to recruitment; (d) this increase is essentially related to eye position and not apparently to eye velocity; (e) the threshold of EMG discharge varies depending upon the state of alertness of the animal. Apparent habituation during long-term recordings seems to be only due to these changes in threshold.

Neck Muscle Activity During Vestibular Nystagmus

Figure 1B shows an example of typical recordings obtained during vestibular stimulation in the horizontal plane. In this case, as in Fig. 1A, the horizontal eye position trace has been superimposed onto the EMG of the right obliquus capitis. EMG of the right splenius and head velocity are shown for comparison. All the records obtained so far show a close relationship between horizontal component with eye movement and EMG, and *not* with head velocity. Two cycles of head oscillation are shown here; EMG amplitude can therefore be compared during two successive identical values of head velocity. For instance, the two filled black stars indicate two successive times at which peak head velocity was near to zero. The phase of the vestibulo-ocular reflex at this oscillation frequency (0.1 Hz) is such that eye velocity is nearly zero. Although the vestibular signal is identical at these two instants, the EMG intensity is clearly different. A similar comparison can be made at the times indicated by the two empty stars. The black dots indicate approximately the time during which the VCR is maximum. Splenius muscle activity also follows horizontal eye position. The behavior of longissimus capitis during vestibular nystagmus is very similar (Fig. 2C).

All the above results were obtained when the cat was fully alert. Drowsiness induced two types of pattern. On the one hand, cocontraction of the antagonistic muscle unrelated to eye movement. On the other hand, occasionally, a VCR-like pattern (particularly in the large muscles). It is also important to note that our findings were also obtained even during the first two to three trials of newly prepared cats and were therefore not due to training.

In conclusion, in the head-fixed alert cat the activity of obliquus cranialis, caudalis and longissimus capitis muscles is tightly coupled with the horizontal component of eye displacement in the orbit. This coupling is apparently more complex for splenius, complexus and longus capitis. The cat is known to make large head saccades whose velocity is close to eye velocity (Collewijn 1977; Roucoux et al. 1981), and the relationship obtained in the present results probably reveals the existence of a circuitry linking specifically horizontal head and eye movements in the plane of the horizontal semicircular canals.

The most surprising result is the apparent absence of a "vestibulo-collic" reflex during sinusoïdal oscillation in the horizontal plane with the phase predicted by experiments performed on decerebrate animals. The observed pattern is in fact out of phase with what was predicted for the VCR.

The following hypothesis could be proposed to interpret these results. Two extreme "strategies" of head-eye coordination could exist. In a first case, only observed in very alert animals, the cat directs its gaze in the direction of head motion ("Look where you go"). This induces an eye displacement ipsilateral to head displacement and EMG activity in ipsilateral neck muscles, (together with active inhibition of contralateral muscles) through a specific circuitry which is the same during vestibular nystagmus and spontaneous saccades. For example, during passive head rotation the quick phases of vestibular nystagmus tend to bring the beating field ("Schlagfeld") in the direction of head rotation. If for instance the head rotates to the right, the right eyeball beats in the right corner of the orbit and the right neck muscles, driven by an "eye position signal", discharge proportionally to eye excentricity. VCR is therefore suppressed by the active inhibition of the contralateral muscles. In a second case, the animal counteracts the head movement and maintains a fixed eye position in space ("Keep looking where you start from"). This is the classical compensatory type of eye movement in which the eye is moving contralaterally to the direction of head rotation. During rotation to the right, e.g., the right eye beats in the left corner of the right orbit and the left eye in the left corner of the left orbit. Right neck muscles are silent and left neck muscles discharge. In this last case the VCR and the eye position related neck muscle activity are synergistic. EMG seems therefore to depend upon the location of the eye in the orbit indicated by, presumably, a central "eye position" craniotopic signal such as is known to be coded in some prepositus hypoglossi neurons (Baker and Berthoz 1975; Lopez-Barneo et al. 1979) or even vestibular second order neurons (Berthoz et al. 1981; Yoshida et al. 1981). We believe that this finding could modify a number of current concepts of head-eye coordination and may also have an importance for the relationship between the understanding of the organisation of equilibrium and body goal-directed movements.

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