Arch Psychiatr Nervenkr (1981) 230:117–127

Archiv für Psychiatrie und Nervenkrankheiten
Archives of Psychiatry and Neurological Sciences

Vestibulo-Ocular Reflex (VOR), Cervico-Ocular Reflex (COR) and Its Interaction in Active Head Movements*

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Summary. In normal adults the vestibulo-ocular reflex (VOR) and the cervico-ocular reflex (COR) were investigated during passive and active head or body movements, respectively. Sinusoidal rotations around the vertical axis of the body at frequencies of 0.05, 0.1, and $0.2\,s^{-1}$ and total amplitudes of 20°, 40°, 60°, or 80° were employed.

The average eye deviations (Schlagfeld) during VOR were directed opposite to the direction of the head turning. During COR, however, slow eye deviations of higher amplitude were anticompensatory relative to the fixed head. During active head turnings the average eye deviations showed the same anticompensatory direction as in COR, but were still larger. They increased with stimulus amplitudes up to 60°.

At least a weak cervical nystagmus was elicited in all subjects, with its fast phases beating in the direction of the relative head movement. Its gain reached marked values up to 0.5, but only for peak stimulus velocities below 25°/s. The nystagmus gain during active head turnings was only slightly higher than during VOR.

With higher stimulus velocities, large anticompensatory saccades appeared just before the change of stimulus direction; these are typical for active head movements, but were also found during COR.

Key words: Vestibulo-ocular reflex – Cervico-ocular reflex – Active head movements

Zusammenfassung. Bei 10 gesunden Erwachsenen wurden Augenbewegungen während des passiven vestibulo-oculären Reflexes (VOR) mit cervico-oculären Augenbewegungen (COR) und solchen bei aktiven Kopfbewegungen verglichen. Gereizt wurde bei geschlossenen Augen mit sinusförmiger Drehung

* Supported by Sonderforschungsbereich Hirnforschung und Sinnesphysiologie (SFB 70) der Deutschen Forschungsgemeinschaft (DFG)

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0003-9373/81/0230/0117/$ 02.20

um die vertikale Körperachse mit Frequenzen von 0,05, 0,1 und 0,2 s^{-1} und Gesamtamplituden von 20, 40, 60 und 80 Grad.

Während die langsamen Schlagfeldverlagerungen beim VOR der Kopfbewegung kompensatorisch entgegengerichtet sind, bewegen sich die Augen beim COR (fixierter Kopf) während höherer Reizamplituden in antikompensatorischer Richtung, also entgegen der Schulterbewegung bei fixiertem Kopf. Auch bei aktiven Kopfbewegungen sind diese langsamen Augendeviationen antikompensatorisch, aber stärker ausgeprägt als beim COR und nehmen mit Reizamplitude bis 60 Grad zu.

Ein zumindest schwacher Halsnystagmus (rasche Phase in Richtung der relativen Kopfbewegung) überlagert bei allen Versuchspersonen die langsamen Schlagfeldverlagerungen. Sein Verstärkungsfaktor (gain) erreicht signifikante Werte bis 0,5 nur für maximale Reizgeschwindigkeiten bis 25 Grad/s. Der Verstärkungsfaktor des vestibulären Nystagmus erreicht Werte bis 0,6 und liegt bei aktiven Kopfbewegungen noch etwas darüber (0,78).

Typisch für aktive Kopfbewegungen, aber auch beim COR vorhanden, sind große antikompensatorische Sakkaden, die bei höherer Reizgeschwindigkeit kurz vor Wechsel der Reizrichtung auftreten.

Schlüsselwörter: Vestibulo-oculärer Reflex (VOR) - Cervico-oculärer Reflex (COR) - Aktive Kopfbewegung - Halsreflexe

Introduction

The existence of functional connections between proprioceptors in cervical structures and the oculomotor system was first observed by Barany in 1906 [1]. He found that reflectory coordinated eye deviations were elicited by trunk movements in rabbits. Later, similar cervically induced eye movements were reported in infants as well as in adults exhibiting certain pathological conditions [2, 7, 8, 11, 12, 14]. In healthy adults the presence of neck-to-eye reflexes can only be disclosed in the absence of visual feedback such as in darkness or with closed eyes [10, 18]. Under these conditions a tonic slow shift of eye position is directed opposite to the trunk movement, i.e., in the direction of the hypothetical head turning relative to the body, while the head is actually fixed in space [10]. These slow deviations depend on the level of arousal and, in contrast to VOR, increase with drowsiness [3]. Superimposed on the slow deviations, some saccades are also elicited toward the direction of the hypothetical head movements. With increased alertness, such as that required during mental arithmetic, the slow eye shifts attenuate, and cervically induced quick phases appear more frequently [3, 5, 19]. A neck-induced positional nystagmus was found only under pathological conditions, e.g., after cutting the second and third cervical dorsal roots or after vestibular lesions [6].

The following study was aimed at comparing eye movements induced passively by either vestibular stimuli or neck afferents with those during active head movements.

Methods

The subjects were healthy volunteers, three females and seven males, from 23 to 37 years of age ($\bar{x}$ = 28 years).

Horizontal eye displacements were recorded using direct-current electro-oculography with silver/silver chloride disk electrodes placed on the outer canthus of each eye.

The subjects sat on a rotation chair (Tönnies, Feiburg/Brsg.), which allowed rotations in a sinusoidal pattern. The head was immobilized by a head support that was either attached to the chair (VOR) or to the room (COR). After the fixation was unlocked, active head movements around this axis could be recorded by a potentiometer.

The test session contained sinusoidal rotations with frequencies of 0.05, 0.1, and 0.2 s^{-1} and total amplitudes of 20°, 40°, 60°, or 80° with peak angular velocities of 6°–100°/s.

For active head rotation the subjects were instructed to move the head as sinusoidally as possible at a given amplitude and period, indicated by a rhythmic sound. After a short practice session, the subjects were able to turn their heads with the indicated parameters. During the entire session, the eyes were closed. To get a comparably high level of alertness, the subjects had to perform mental arithmetic. As the whole session lasted for about 90 min, periods of low vigilance could not be avoided.

The recorded eye movements were analyzed by hand over five cycles with respect to average horizontal eye deviations (Schlagfeld) and nystagmus in comparison to the trunk or head movements.

All eye movements are related to head positions. Since in COR the head actually is fixed, the term 'relative head movement' is used to facilitate the comparison between the different modes of stimulation.

Results

Eye Movements During Vestibulo-Ocular Reflex (VOR), Cervico-Ocular Reflex (COR), and Active Head Movements

During sinusoidal *vestibular stimulation,* a nystagmus appeared in the direction of the movement. Besides this nystagmus, minor deviations of average eye position were elicited, mostly in the direction opposite the head movement during slow rotations. At higher peak velocities of rotation these deviations sometimes paralleled the head movement. They are accentuated in weak nystagmus (Fig. 1b).

During *cervico-ocular reflex,* slow eye deviations were superimposed on a nystagmus. At least some beats of a cervical nystagmus could be elicited in all subjects. Generally the nystagmus beats in the direction of the movement of the head relative to the trunk, but with a lower frequency than during VOR. The form of the single nystagmus resembled a staircase pattern more than a usual saw tooth nystagmus with alternating fast and slow phases (Fig. 1c). This was because both slow eye deviations and fast components of nystagmus were directed parallel to the relative head movements [5].

Especially with higher velocities, large saccadic eye movements occurred at the beginning of trunk movements and in the direction of the relative head movements (Fig. 2). As compared to vestibular eye movements, the slow shifts of average eye position in COR were larger, and in contrast to VOR were parallel to the relative head movements, but often irregular and asymmetric. The phase relation to the stimulus varied much more than in VOR. Only exceptionally slow shifts were found to be compensatory with respect to the relative head movement, as described

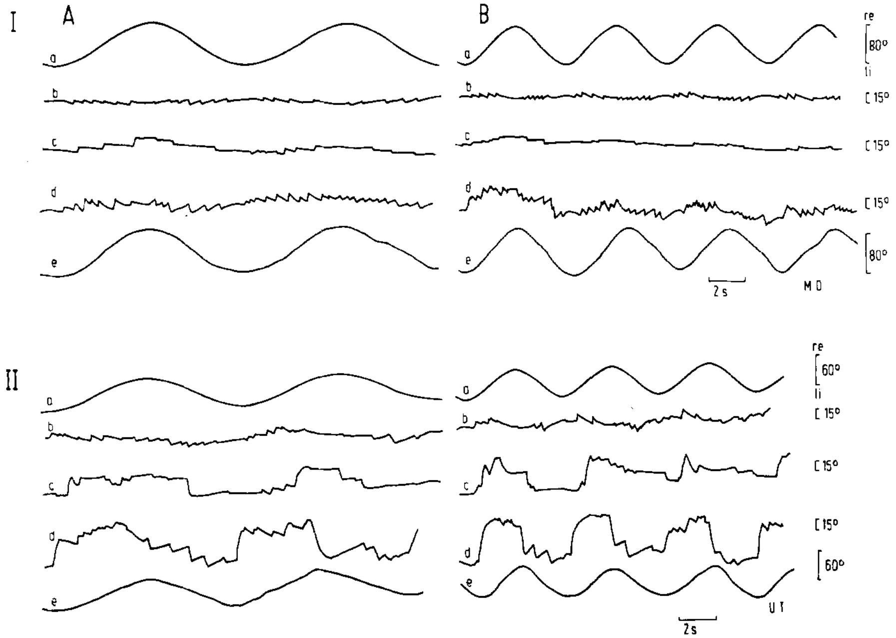

Fig. 1. Recordings of vestibulo-ocular reflex (b), cervico-ocular reflex (c), and eye movements during active head turning (d) in two subjects (I, II). Turntable position (a) and head position during active head movement (e). Stimulus frequencies are $0.1\,s^{-1}$ (A) and $0.2\,s^{-1}$ (B)

by Meiry [15]. Again these slow deviations were fewer in marked nystagmus. In the same subject they varied considerably, depending on the level of attention. During mental arithmetic nystagmus was more pronounced and slow shifts were diminished.

During *active sinusoidal head movements (V + COR)* the effects of vestibular and neck stimulation were combined. The nystagmus was activated with respect to slow phase velocity and amplitude. The most prominent effect was the increase of the large saccadic eye movements already described in COR (Fig. 1d). Although there was no constant phase relation to the stimulus signal, these large saccades seemed to be more phase-advanced than in COR and often started with or even just before the onset of the head movement. Slow deviations of average eye position reached much higher amplitudes than with VOR and COR. They often were asymmetric and not sinusoidal. As in COR, when tested in isolation, their direction was parallel with the direction of head movements. Often they were combined with large saccades but could also occur without saccades (Fig. 3).

Quantitative Analysis of Nystagmus

The distribution of averaged nystagmus *slow phase velocities* over a period of head movement followed the sinusoidal input signal for velocity. In COR the slow phase velocities were much smaller than in VOR, and the highest velocities were found during active head movements (Fig. 2).

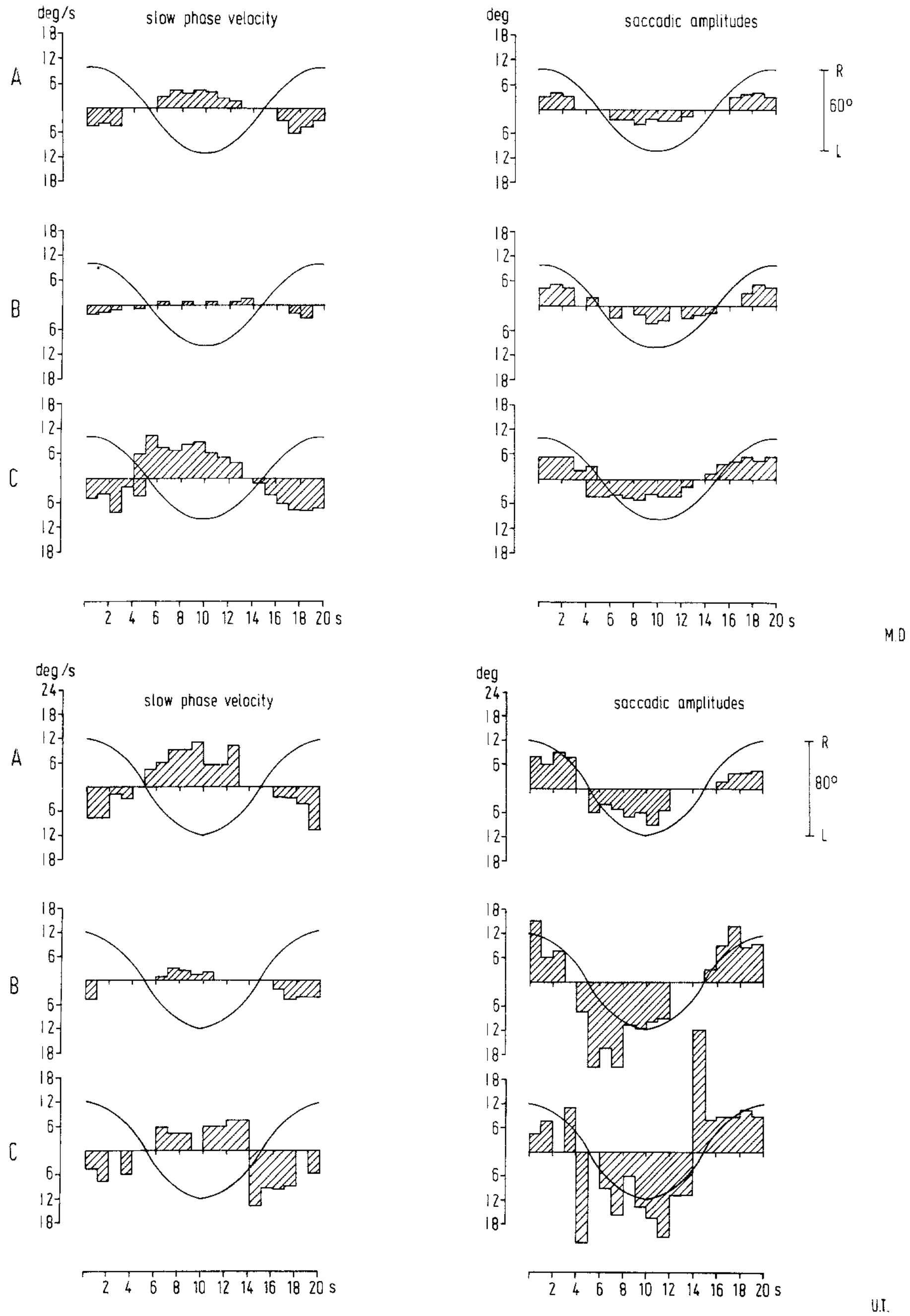

Fig. 2. Distribution of nystagmus slow phase velocities and saccadic amplitudes averaged over five periods for VOR (A), COR (B), and active head turnings (C). Stimulus velocity is given by the sinus signal. Same two subjects as in Fig. 1

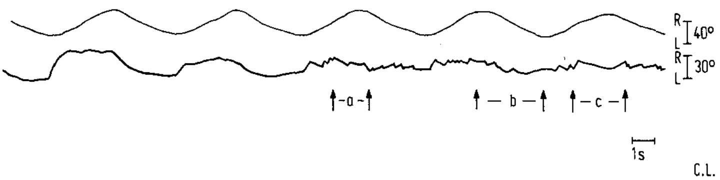

Fig. 3. Eye movements (lower trace) during active head turning (upper trace). Mental arithmetic beginning with the third cycle. Peak amplitudes of overall eye deviation (a), change of nystagmus direction (b), and maximum nystagmus slow phase velocity (c)

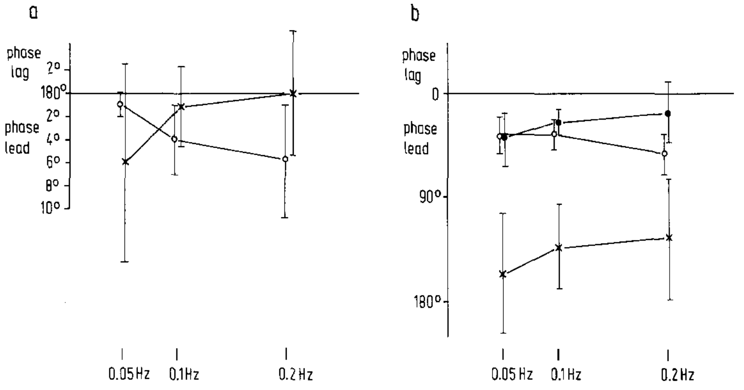

Fig. 4. Phase relation of change of nystagmus direction and stimulus direction (a) and of the peaks of average eye position and stimulus position (b) for VOR (+), COR (●), and active head movements (○)

The *phase relation* between change of nystagmus direction, that is, change of cumulative eye position and the stimulus position, showed a very small lead for vestibular nystagmus (6°) during slow frequencies. During active head movements, however, the phase lead increased slightly with higher stimulus frequencies (Fig. 4a). The direction of the slow phase of vestibular nystagmus was opposite and compensatory to the direction of the stimulus.

Because of staircaselike cervical nystagmus and the low frequency, an analysis of phase relationship was not possible for COR.

The *gain* defined as the relation between peak slow phase velocity to peak stimulus velocity, decreased with increasing stimulus frequency and increasing velocity. For all frequencies tested, the gain fell with higher amplitudes. It was always lowest for COR (0.05–0.54) and highest for active head movements (0.33–0.78). The vestibular gain ranged between 0.23 and 0.62. With increasing stimulus velocities the gain of COR decreased more than that of VOR or of active head movements (Fig. 5).

In general the distribution of *averaged saccadic amplitudes* followed the stimulus velocity, but as already described, the largest saccades were elicited at the maximum acceleration.

In contrast to slow phase velocities, the saccadic amplitudes in certain subjects were sometimes higher in COR than in VOR, but as a rule they were highest in active head movements.

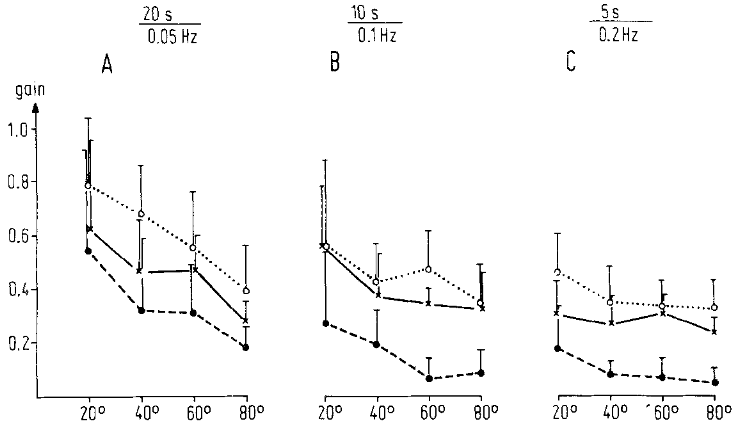

Fig. 5. Gain of peak nystagmus slow phase velocity to peak stimulus velocity of VOR (+), COR (●), and active head turnings (o). Stimulus amplitudes are indicated in the abscissa

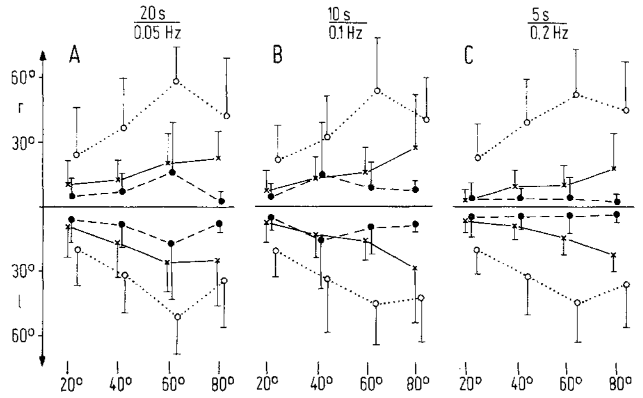

Fig. 6. Total saccadic amplitudes averaged over five periods. Symbols as in Fig. 5

The total *saccadic amplitudes,* averaged over five periods, increased with stimulus amplitudes up to 60° for all stimulus frequencies. For active head movements and COR there was a decline in total amplitude at 60°–80° of stimulus amplitude that was not found in VOR. The total amplitudes during active head movements were much higher than the simple addition of VOR and COR would have predicted (Fig. 6).

Quantitative Aspects of Slow Deviations of Average Eye Position

These eye movements were variable and differed for each individual. Therefore, a quantitative analysis with respect to the gain gave no systematic results. Generally, these slow eye deviations were smallest in VOR and highest during active head movements. They increased with stimulus amplitudes up to 60°. Similar to the total of saccadic amplitudes, there was a decline at 60°–80° (Fig. 7), at least for active head movements.

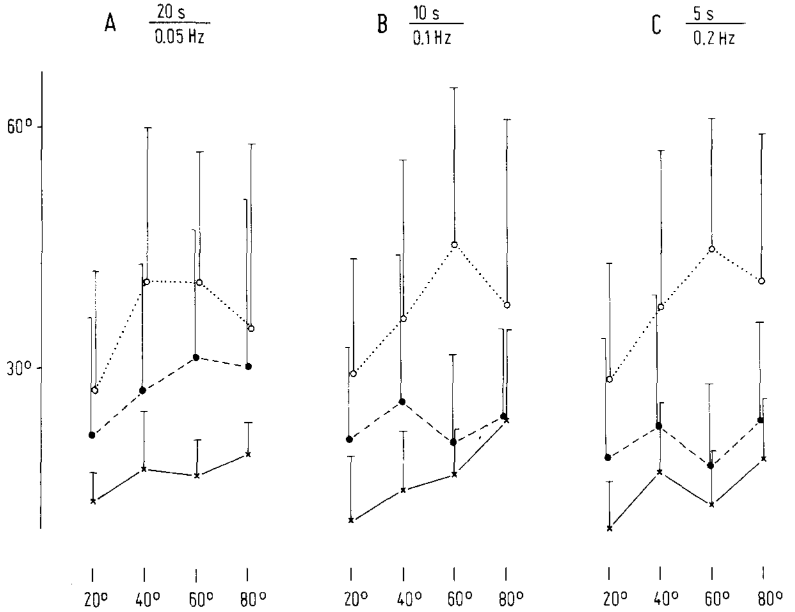

Fig. 7. Maximum amplitudes of overall eye deviations averaged over five periods with mean values and standard deviations (symbols as in Fig. 5)

The phase relationship showed a large phase lead for VOR (about 130° for higher frequencies and 160° for the lower frequencies used). A relatively small phase lead of 20°–50° was found in COR and during active head movements. In COR there was a tendency to be phase-locked with stimulus position in higher frequencies, whereas during active head movements the phase lead increased (Fig. 4b).

Discussion

Slow Eye Deviations

In the analysis of neck-induced eye movements, most attention was paid to slow eye deviations because cervical nystagmus in man was considered to be very variable and difficult to analyze [3, 4, 15, 19]. Slow deviations of average eye position were found with all modalities of stimulation. They are very small in VOR, increase in COR, and are largest with active head movements. They increase with drowsiness and become smaller with increasing vigilance. These contrast with nystagmus, which is stimulated by attention. The dependence on mental alertness restricts the possibility of a quantitative analysis (Fig. 3).

In VOR, the slow deviations in average eye position lead between 130° and 160° relative to the head position, but this is only true for the velocities used here. For higher velocities, there is a strong anticompensatory oculomotor response mainly consisting of large saccades during the initial phase of head movements [16].

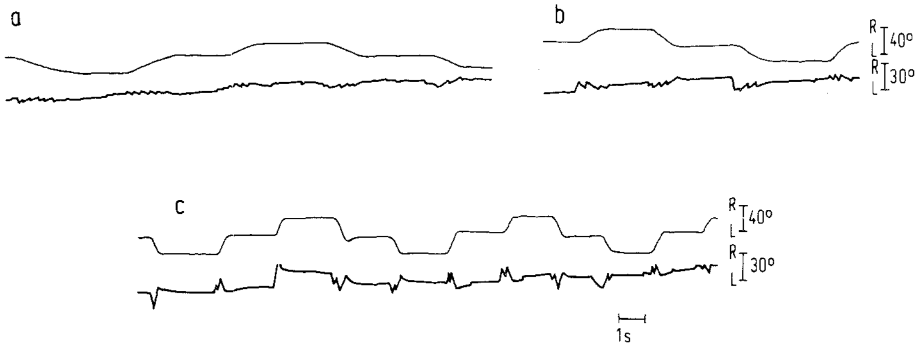

Fig. 8. Trapezoid active head turnings (upper trace) at different velocities and resulting eye movements (lower trace)

A similar anticompensatory pattern is found in COR and active head movements at lower stimulation velocities. The large saccades are typical for active head movements and often appear just before the onset of head turning. They resemble saccadic eye movements found in persons who have to move head and eyes to fixate a new target [13, 17]. An important difference is that the saccades clearly appear before the head is moved. During slow head turnings, several nystagmus beats are seen instead of one or few larger saccades during fast head movements (Fig. 8).

It seems, therefore, that neck afferent mechanisms facilitate tracking of a visual target. These mechanisms seen during passive neck stimulation are enhanced and much more effective during active head movements. Together with the findings of Melvill Jones [16], it may be assumed that vestibular and neck reflexes work together for this purpose and may also be modulated by the central command to move head and eyes. Saccades are not generated by vestibular mechanisms alone, as stated by Barnes [4].

There are probably two ways through which VOR and COR interact and finally determine the average eye position, depending on the stimulation velocity or frequency. During fast movements there is a summation between VOR and COR with the effect of a large eye advance relative to the head movement. Because of the phase difference during slow movements, however, both mechanisms may compensate. These compensatory interactions of COR and VOR during slow head movements resemble the functional interaction between cervical and vestibular mechanisms for spinal motor systems, as demonstrated in the cat [20, 21].

Nystagmus

In contrast to earlier reports [3, 5], we could elicit cervical nystagmus in all of our subjects. Its intensity varied considerably and it could be very strong in some subjects. Barnes and Forbat [5] classified neck-induced nystagmus into three types and stated that only one is found in each subject. Our data, however, show a high degree of intraindividual variation, depending mostly on the level of attention.

The gain of slow phase velocity of the cervical nystagmus depends reciprocally on stimulus velocity and is only effective (> 0.2) for peak stimulus velocities below 25°/s.

For higher stimulus velocities the gain of COR is negligible. It may be concluded that neck afferents contribute to the nystagmus elicited by active head turnings only during slow head movements. With higher stimulus velocities, the gain of active head movements is mainly determined by the vestibular input.

In contrast to the above-described phase difference of slow eye deviations, there is no significant phase difference of nystagmus slow phase velocities between active head movement and vestibular stimulation.

The saccadic activity of VOR and COR is similar for amplitudes up to 60°. During active head movements it reaches higher values than the simple addition of both, probably due to the large saccades in the beginning of the head movement. Comparable to the very small gain of slow phase velocities for COR, the saccadic activity of COR becomes negligible for high stimulus velocities.

During active head turnings and COR, but not during VOR, there is a decrease in saccadic activity with stimulus amplitudes above 60°. This may be interpreted as saturation in the working range of neck proprioceptors.

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Received November 24, 1980