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Discharges of Superior Colliculus Neurons during Head and Eye Movements of the Alert Cat

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Summary. 452 single neurons from the superior colliculus were recorded in awake and non-paralysed cats. 75 neurons were obtained from cats with unrestrained horizontal head movements.

228 neurons remained unaffected by saccadic eye movements. Eye movement related discharge followed the onset of saccades in 156 neurons either only in the presence of a visual pattern (92 neurons) or in darkness, too (64 neurons). The latter reaction type probably depends on eye muscle afferents.

In 48 neurons eye movement related activity preceded the onset of eye movements. 12 neurons fired in synchrony with eye movements of any direction (type I). 30 neurons were excited during contralaterally directed eye versions within or into the contralateral head related hemifield. They were inhibited when the eyes moved within or into the ipsilateral head related hemifield (type II). 6 neurons with constant maintained activity during fixation were inhibited by ipsilaterally directed saccades, but remained unaffected by contralateral eye movements.

Head movement related discharge followed the onset of head movements in 20 neurons only in presence of a visual pattern and also in darkness in 6 neurons. Ipsilateral head movements or postures strongly suppressed maintained activity and visual responsiveness of some neurons.

15 neurons discharged in synchrony with and prior to contralateral head movements. Ipsilateral head movements inhibited these neurons. Activation or inhibition were usually related to movement *and* to posture, exceptionally to movement *or* to posture.

Electrical stimulation of recording sites of these neurons through the recording microelectrode elicits contralateral head movements.

Key words: Colliculus superior – Single neurons – Eye movements – Head movements – Cat

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Introduction

In recent years a considerable amount of evidence has accumulated, that the mammalian superior colliculus serves as a senso-motor integration center of the orienting response. Sensory stimulus parameter and drugs influence the behavioral response and collicular neuronal reactions in an analogous manner (isoparametric parallelism) (Horn and Hill, 1966; Straschill and Hoffmann, 1969). Electrical stimulation of the colliculus superior elicits motor components of the orienting reaction (Szyka and Radil-Weiss, 1971; Straschill and Rieger, 1973). Loss of orienting responses towards stimuli in the contralateral sensory field follows destruction of one colliculus superior (Sprague and Meikle, 1965). The results of the present study provide further evidence. They show, that discharges of some neurons of the cat superior colliculus accompany head or eye movements, which are main motor components of the orienting and searching program of the animal. An abstract of the present results has been previously reported (Straschill et al., 1974).

Methods

Preparation: Approximately 50 experiments were conducted on 10 chronically prepared cats. Surgery was performed under pentobarbital anesthesia about five days before the first experiment. A 10 mm trephine hole was made over the occipital cortex with its center at frontal and lateral zero (HC-stereotaxic coordinate system). A metal cylinder was fitted onto the opening and embedded in a surrounding mould of dental cement hardened on the skull. This cylinder served as basement for a hydraulic mirodrive. Silver silver-chloride portable electrodes were implanted subcutaneously at the outer canthi of the eyes for recording the electrooculogram (EOG) in the horizontal plane and at the upper and lower margin of the orbit for recording in the vertical plane. In a first series of experiments (6 cats), two steel tubes were placed transversely across the dorsal surface of the skull, fixed by dental cement with their ends left exposed. In a second series of experiments a vertically oriented bolt was implanted into the occipital bone at midline position. These methods of preparation were largely adapted from Noda et al. (1969), whose description should be consulted for further details. Guiding principles in care and use of animals were strictly observed.

Recording: During the experiment the cat was comfortably placed on a hammock in front of a semicylindrical screen. The head was fixed in the horizontal plane by mounting the transverse tubes on pairs of earbars fixed in the stereotaxic frame. In a second series of experiments, the vertically oriented, skull implanted bolt was inserted into the headholder via a joint which rotated frictionfree. This arrangement permitted the animal to perform head movements in a horizontal plane with the vertical bolt serving as rotation axis. Head movements were monitored by a low-torque potentiometer driven by the rotating bolt. Eye movements were recorded by electrooculography through DC-coupled amplifiers. Records of ocular pursuit movements to visual stimulus movements of known amplitude were used to calibrate the EOG. The right or left superior colliculus was stereotaxically reached after penetration of the intact dura and the overlying brain structures. The electrodes were lowered into the colliculus by means of a hydraulic micro drive, which was fixed to the headholder (first series of experiments). The appearance of visually driven activity at the arrival of the collicular surface served as landmark for depth determination during the experiments. Action potentials were recorded by means of tungsten electrodes, fed through cathode followers and amplifiers, displayed on oscilloscope and recorded on film together with EOG potentials.

Stimulation: Moving and stationary visual stimuli were projected onto a hemicylindrical screen by a projector, which could be rotated around its three axis. The projected stimuli consisted of bright discs and gratings of alternating black and white stripes. Unit activity was recorded together with eye movements during darkness and with each stationary and moving visual pattern. Approximate determination of receptive field position was attempted during periods of fixation in primary position.

Results

A. Neuronal Activity Associated with Eye Movements

Activity of 452 collicular neurons was recorded together with a sufficient number of spontaneous eye movements to exclude or verify a correlation between the two events. Activity was recorded in total darkness and in the presence of stationary stimuli such as a bright disc, or a grating filling the whole visual field. The same stimuli were moved through the receptive region with velocities up to 400 deg/sec. The localized stationary stimuli were projected into that region of the screen which consistently yielded a neuronal response to small stimulus movements or to flashed light spots. Under these experimental conditions the following neuronal reaction types could be distinguished.

I. Lack of Correlation between Neuronal Discharge and Eye Movement

228 neurons (55%) showed no alteration of their maintained discharge in darkness, or in the presence of the stationary pattern, when the cat made saccades. These neurons were usually direction-selective, unreactive to stimulus velocities higher than 50 deg and located in layers below the stratum opticum.

II. Eye Movement Related Neuronal Discharge Following Onset of Eye Movements

156 neurons discharged in synchrony with eye movements in the presence of a stationary visual pattern. The discharge followed the onset of eye movements after a variable latency. 92 neurons of this group were silent, or discharged independently of eye movements when the animal stayed in total darkness, but fired in synchrony with eye movements when a stationary visual pattern was presented. The latency of this discharge was fairly constant and ranged between 50 and 75 msec when the animal faced a visual pattern filling its whole visual field. In neurons with relatively small receptive fields the latency became more variable and the correlation between eye movements and discharge less strict when the whole field pattern was replaced by a small stationary object. The reaction was usually phasic consisting of a single burst of short duration, occasionally phasic tonic continuing throughout the fixation period. All neurons, which were directionally unselective when tested with moving visual stimuli, fired in synchrony with eye movements of any direction. 20 directionally selective units fired independently of eye movement direction, 16 direction-sensitive units discharged with eye movements opposite to the preferred direction. Lack of synchrony in the absence of a visual pattern, dependence of

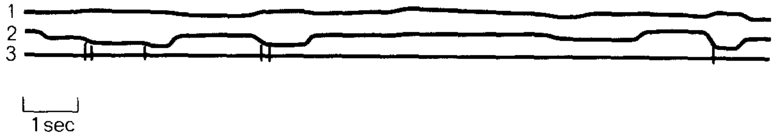

Fig. 1. Eye movement related reactions following onset of eye movements. *1* Vertical electrooculogram: Upward deflection corresponds to upward directed eye movements. *2* Horizontal electrooculogram: Downward deflection corresponds to contralaterally directed eye movements. *3* Neuronal discharge in total darkness

discharge latency on the extension of the visual pattern in the visual field and opposed direction selectively for stimulus and for eye movements suggest that these movement-detecting neurons discharge when retinal images of stationary objects are displaced by eye movements.

Reaction properties of a second subgroup comprising 64 neurons suggest convergence of visual and eye muscle proprioceptive excitatory inputs. Eye movements synchronous discharge persisted in total darkness in these neurons (Fig. 1). For the same neuron, latency varied from 25–125 msec depending upon the initial eye position. In agreement with the findings of Rose and Abrahams (1975) each neuron required a certain minimal displacement of the eyes from the primary position to be excited. This displacement threshold ranged from 5–15 deg. In 49 neurons the fixed point which had to be transversed, was situated in the contralateral visual hemispace, in 15 neurons ocular deviation from the midline in either direction led to discharges. If a neuron was direction-sensitive for both stimulus and eye movements, the preferred directions agreed. In presence of a visual pattern 36 neurons gave a phasic tonic response in synchrony with eye movements. 18 neurons discharged phasically with a brief burst. In darkness all reactions were phasic.

III. Eye Movement Related Activity Preceding Onset of Eye Movements

48 neurons discharged or paused in synchrony with slow and saccadic eye movements in darkness and in presence of a stationary pattern. The onset of discharge (pause) preceded the onset of eye movements. In neurons tested in animals with mobile head only searching (scanning) or orienting (stimulus triggered) saccades and pursuit movements were accompanied by neuronal reactions. These neurons remained unaffected during rapid and slow phases of nystagmus following passive horizontal head movements. Three reaction types could be distinguished. Type I (12 neurons) discharged in synchrony with eye movements of any direction or amplitude (Fig. 2A). Discharge preceded onset of eye movements by 150 msec and continued up to 500 msec into the postsaccadic fixation period. Asymmetry of responses to contralateral eye movements was observed in 4 neurons of this type. Contralateral saccades evoked stronger responses. Type II (30 neurons) discharged only in synchrony with contralaterally directed eye movements. Ipsilaterally directed eye movements

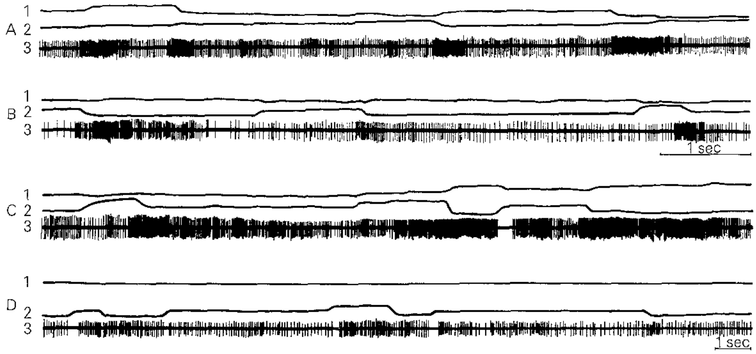

Fig. 2A–D. Types of eye movement related reactions preceding onset of eye movements. **A** Direction unspecific reaction (type I). **B, C** Direction specific reaction (type II): Neurons are activated with contralaterally directed saccades and are unresponsive (B) or inhibited (C) with ipsilaterally directed saccades. **D** Inhibition associated with ipsilateral saccades (type III). Constant maintained activity during fixation and during contralateral saccades. Registration as in Figure 1

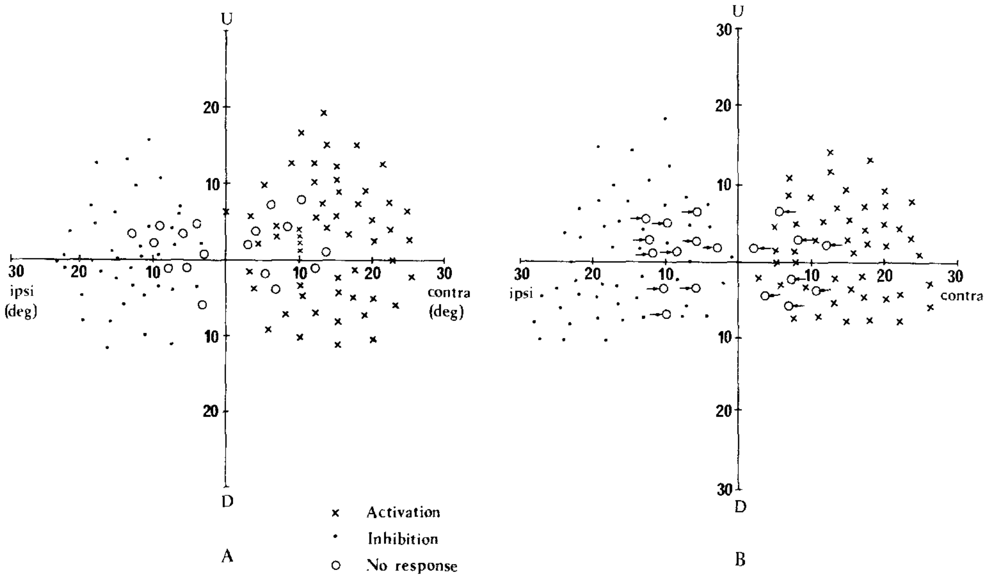

Fig. 3A and B. Graphical representation of target point of saccades associated with neuronal reactions of type II. Zero position corresponds to initial eye position prior to saccades (**A**) or to primary position of the eyes (**B**). Abscissa: Horizontal deviations (deg.) from zero position. Ordinate: Vertical deviation from zero position. Arrows in B denote direction of saccades without a response. Figure 3B demonstrates, that only contralaterally (resp. ipsilaterally) directed saccades with target points in the contralateral (resp. ipsilateral) hemifield are associated with activation (resp. inhibition)

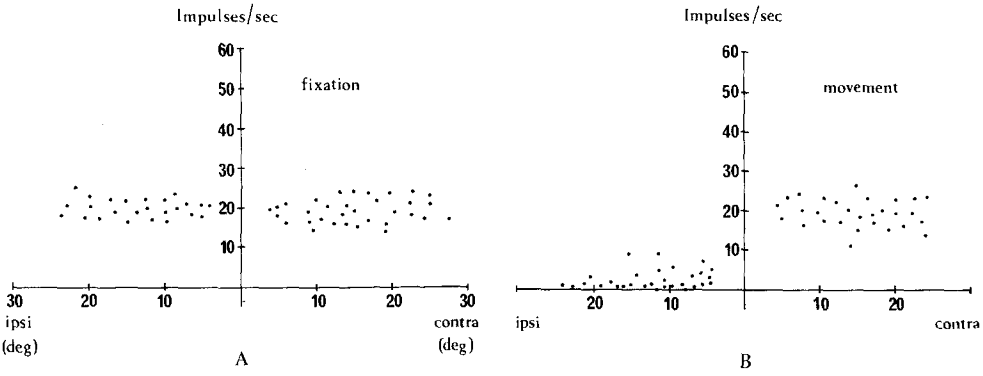

Fig. 4A and B. Graphical representation of discharge properties of reaction type III during fixation **A** and during eye movements **B**. Zero position: Initial eye position prior to saccades. Abscissa: Horizontal deviation of postsaccadic fixation points. Ordinate: Number of impulses/sec during fixation period (A) and during the actual eye movement (B)

elicited either no response (Fig. 2B) or active suppression of maintained activity (Fig. 2C). Saccades of a wide range of amplitudes (Fig. 3A, B) were accompanied by neuronal activation or inhibition. Location of the saccade's target in the contralateral hemifield (related to primary position of the eyes) as well as contralateral direction of the saccade were necessary conditions of neuronal activation (Fig. 3B). Hence saccades starting from the ipsilateral resp. contralateral hemifield must traverse primary position to evoke an excitatory resp. inhibitory response (Fig. 3B). Neurons were activated prior to and during the saccadic movement. Discharge extended into the fixation period for 200 msec to 2 sec. There was no consistent relationship between durations of fixation periods and durations of neuronal activations. Saccade synchronous inhibition was usually confined to the period of actual saccadic movement. Type III neurons (6 neurons) exhibited an essentially constant maintained discharge rate during fixation (Fig. 4A). Prior to or coincident with a saccade in the ipsilateral direction the unit ceased firing (Figs. 2D, 4B). The suppression of activity lasted for the duration of the rapid eye movement. Two units of this type showed a burst-like postsaccadic activation following contralateral saccades in addition to the suppression with ipsilateral saccades. Recording sites of type I, II and III neurons were restricted to the stratum medium or stratum profundum. The majority of reaction types I, II or III was responsive to visual stimulation. Units discharging with saccades of any direction (type I) were usually not direction-sensitive when tested with moving visual stimuli. Saccade direction selective units of type II usually preferred contralaterally directed stimulus movements.

B. Neuronal Activity Associated with Horizontal Head Movements

In a second series of experiments the cats were able to perform eye movements as well as horizontal head movements. The limit of head movements was

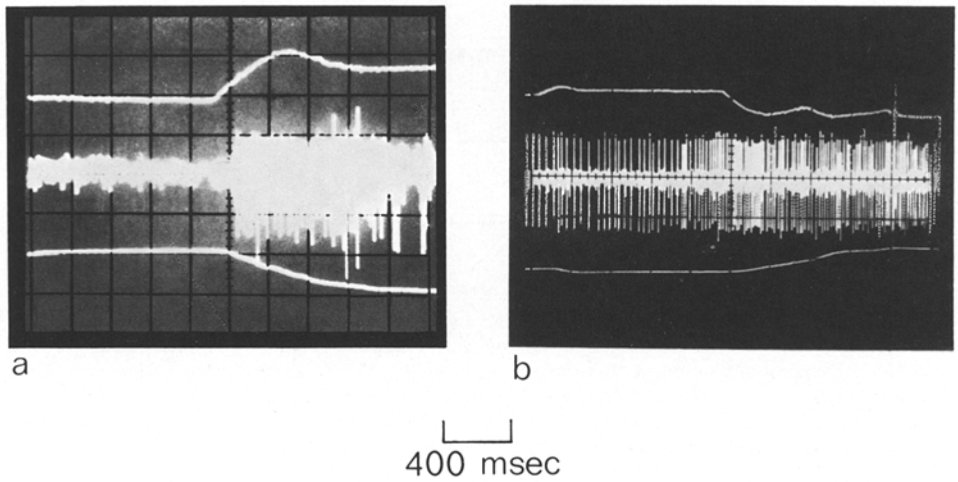

Fig. 5a and b. Patterns of eye-head movement coordination and head movement related neuronal reactions. **a** A single large saccade is followed by a slow eye movement of opposite direction, while the head is still moving. Neuronal reaction follows onset of head movement in total darkness. **b** The head movement is accompanied by a series of saccadic and slow eye movements. Neuronal activation precedes onset of head movement. Registration: a: Upper trace: Horizontal EOG. Upward deflection in a and downward deflection in b correspond to contralateral eye movements. Middle trace: Head movement. Downward deflection in a and upward deflection in b correspond to contralateral head movement

45 deg to either side. Velocities of head movements ranged between 40 and 100 deg/sec. During orienting and searching movements two patterns of sequences of eye-head coordination were observed.

1. A large saccadic eye movement precedes the onset of a head movement of equal direction by 30–50 msec. After termination of the saccade the eyes move slowly in opposite direction to maintain fixation, while the head is still in process of motion (Fig. 5A). This pattern was observed when the animal made orienting movements towards visual or acoustic stimuli.

2. The head movement is accompanied by a series of saccades and slow eye movements. The saccades are made in direction of the head movement, the slow eye movements in opposite direction. The initial, usually largest saccade of the series begins before or simultaneous with the head movement. This pattern was observed when the cat scanned its visual environment (Fig. 5B).

I. Neuronal Reactions Following Onset of Head Movements

20 out of 62 visually responsive units discharged in synchrony with head movements in presence of a visual pattern but not in total darkness after a latency of 50–100 msec. In 6 out of 75 neurons head movement synchronous discharge persisted in absence of a visual pattern. Ipsi- and contralateral head

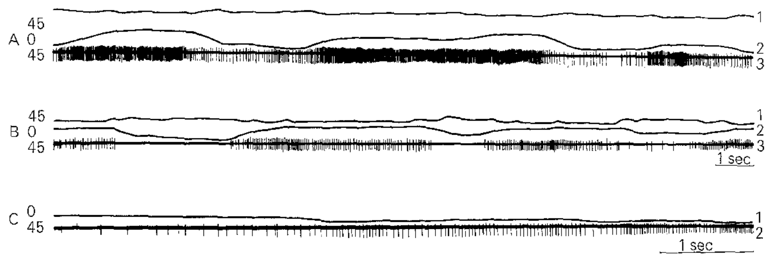

Fig. 6A–C. Types of head movement related reactions of collicular neurons. **A, B** Direction specific activation during contralateral head movements and head postures (phasic-tonic reaction). **C** Dependence of maintained discharge rate on contralateral deviation from primary head position (tonic reaction). Registration: **A, B** Upper trace: Horizontal EOG. Upward deflection corresponds to ipsilateral eye movement. Middle trace: Head movement: Upward deflection corresponds to contralateral head movement. Lower trace: Neuronal reaction. **C** Upper trace: Head movement. Downward deflection corresponds to ipsilateral head movements. Lower trace as in A and B

turning was accompanied by neuronal activation after a latency of 10–25 msec (Fig. 5A).

In 30% of visually responsive units visual responsiveness and spontaneous activity was strongly suppressed, when the head moved to the ipsilateral side or when it was kept in a maintained position of ipsilateral abduction. The suppressive effect increased with increasing head deviation from the midposition. Ipsilateral head movements or posture suppressed also excitations due to eye muscle proprioceptive input. During ipsilateral head movements two tonically firing neurons with eye movement related activity of type II were completely silent.

II. Neuronal Activity Preceding Onset of Head Movements

From 75 units, which were recorded in animals with unrestrained horizontal head mobility, 15 discharged in synchrony with contralateral head movements (Fig. 5B, Fig. 6A, B). Ipsilateral head turning evoked partial or complete suppression of discharge. Activity of these neurons was neither affected by eye movements nor by passive head movements. Most units fired during the period of head movements and when the head was maintained in a posture of contralateral abduction (Fig. 6A, B). Discharge rate increased with increasing speed of head movements. Three neurons discharged only when the head was actually moving but not during phases of maintained contralateral abduction. Two neurons were little influenced by head movements but exhibited a maintained discharge, whose rate was proportional to the amount of horizontal contralateral deviation from primary head position (Fig. 6C). 10 neurons responded directionally sensitive to moving visual stimuli. Preferred stimulus and head movements agreed. Multimodal convergence of visual, somatosensory and acoustic inputs was observed in 8 of these units. Recording sites of units with head movement related activity were restricted to the medium or profound collicular layers. Electrical stimulation at the recording sites of such neurons evoked contralateral head turning, whose amplitude depended upon the duration of the electrical stimulus. Threshold current intensity was 2 μA. With increasing current strength the speed of head movements increased.

Discussion

The results of the present study demonstrate that a considerable proportion of tectal movement-detecting neurons remains unaffected when retinal images of stationary objects are displaced by eye movement. These neurons probably correspond to those preferring low or medium stimulus velocities (Dreher and Hoffmann, 1972). A smaller proportion responds to saccade-induced image shifts as well as to rapidly moving stimuli. In agreement with the findings of Abrahams and Rose (1975), neurons with properties suggesting eye muscle proprioceptive input were observed here. Their functional significance remains obscure. Since eye muscle afference excites tectal neurons mostly after completion of the saccadic movement, it can contribute little to the latter's execution. Theoretically, it might be involved in eye-head coordination augmenting activity of cells of origin of the tectospinal tract. Projection of extraocular afferents to cells of origin of the tectospinal tract has been demonstrated (Abrahams and Rose, 1975). In our sample, however, cells suggestive of receiving eye muscle afference were not involved in head movements whereas neurons, whose activity was clearly related to head movements, were not influenced by eye movements.

Neurons, whose eye movement related activity changes precede onset of eye movements, were previously described in the brainstem of monkeys and cats (Luschei and Fuchs, 1972; Cresty and Baker, 1976) and in the colliculus superior of monkey (Schiller and Koerner, 1971; Wurtz and Goldberg, 1972) and cat (Straschill and Hoffmann, 1970; Arduini et al., 1974). We are unable to explain the high percentage of collicular eye movement related neurons (80%), as reported by Arduini (1974) in contrast to our previous and present results. It cannot be due to the fact, that their eye movement related population includes neurons with eye muscle afference, since the latter require higher eye movement velocities than the encéphale isolé preparation can achieve (Arduini et al., 1974; Rose and Abraham, 1975). Collicular neurons of the monkey discharged prior to saccades of certain amplitudes and directions (Schiller and Koerner, 1971; Wurtz and Goldberg, 1972), whereas feline analogues of our present study were independent of the saccade's amplitude, but required saccades of certain directions made within or into the contralateral hemifield (related to primary position of the eyes) to be excited or suppressed.

The functional significance of the monkey's collicular eye movement related neurons is not clear. Some authors suggest involvement in the mechanisms subserving object localization onto the fovea (foveation) (Schiller and Koerner, 1971; Robinson, 1972), others conclude from their findings, that these neurons contribute to the execution of oculomotor components of the orienting response (Wurtz and Goldberg, 1972).

In the cat a certain degree of specificity of collicular eye movement related function is suggested by the observation that only spontaneous or stimulus triggered saccades but not rapid phases of vestibular nystagmus were accompanied by neuronal discharges. Since these discharges were not specifically associated with eye movements of a certain amplitude, they cannot control foveation. But they may initiate contralateral orienting or searching eye movements, whose precise execution is determined by other parts of the oculomotor system.

Patterns of eye-head coordination of the cat resembled closely those observed in monkeys during triggered or scanning head movements (Bizzi et al., 1972). The analysis of the role of central programs and peripheral vestibular feed back in eye-head coordination of the monkey (Bizzi et al., 1972) may thus well apply to the cat.

Head movement synchronous activation or inhibition following onset of active and passive head movements may result from neck muscle afferents or from vestibular input. The existence of neck muscle afferents to cat collicular neurons has been convincingly demonstrated (Abrahams and Rose, 1975).

The few studies on a possible vestibular influence on collicular neurons yielded contradictatory, negative (Potthoff et al., 1967; Rieger and Straschill, 1973) or positive (Bisti et al., 1972) results.

In contrast to eye movement related neurons, discharge of head movement related units reflected closely the parameters of head movements or postures. Analogous to oculomotor neurons of the brainstem (Luschei and Fuchs, 1972), these directionally selective neurons fired with contralaterally directed head movement and did not require contralateral version movements within or into the contralateral hemifield (related to primary head position) as did collicular eye movement related units. The good correspondence between discharge parameters of collicular head movement related neurons and motor execution suggests to regard the deeper layers of the colliculus superior as a premotor center of spinal neck muscle motoneurons. The existence of many monosynaptic tectospinal connections to neck muscle motoneurons mediated through the tectospinal tract (Anderson et al., 1971) and the fact, that electrical stimulation of cat's deep collicular layers elicits easily head movements (Szyka and Radil-Weiss, 1971), support this hypothesis. From the absence of head movement related neurons in the monkey colliculus superior Robinson and Jarvis (1974) conclude that in the primate this structure is not the site for the generation of head movements.

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