

## ***The Neural Control of Orienting Eye and Head Movements***

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*Abstract.* This paper reviews behavioral experiments concerned with the coordination of eye and head movements and studies examining the roles of the brain stem reticular formation and superior colliculus (SC) in the control of gaze. While there is evidence for at least two major types of linkage between eye and head movements, much remains to be learned about the physiological and morphological bases for the different modes of eye-head coordination.

### **INTRODUCTION**

The sudden onset of a novel stimulus usually triggers responses that orient the eyes, external ears, head, and/or body toward the source of the stimulus. These movements facilitate the reception of additional signals originating from the source and the sensory guidance of further limb and body movements. Combined movements of the eyes and head, in particular, have been studied extensively as an example of the coordination of different motor programs. This chapter summarizes the major findings of these behavioral studies as well as data concerning the neural control of coordinated movements of eye and head. This summary was greatly facilitated by four recent review articles (Berthoz and Grantyn 1986; Grantyn and Berthoz 1988; Guitton 1988; Roucoux and Crommelinck 1988).

### **BEHAVIORAL STUDIES**

#### **The Linear Summation Model**

During involuntary perturbations in head position, the vestibulo-ocular reflex (VOR) provides an automatic mechanism for controlling the interaction of eye and head movements. Images of the visual scene are stabilized on the retina by vestibularly induced rotations of the eye that are equal and *opposite* to head movements. However, voluntary shifts in gaze (the sum of changes in eye and head position) may require movements of the head and the eyes

in the *same* direction. Seemingly, the VOR would be disruptive during voluntary gaze shifts since it produces eye rotations in the opposite direction of the intended gaze shift.

Bizzi and colleagues studied the coordination of eye and head movements in a series of influential experiments conducted in the 1970s. During large gaze shifts made when the head was not restrained, they observed a stereotyped sequence of eye and head movements. Saccadic eye movements begin first, and then after 20-30 ms, the head starts to move in the same direction.<sup>1</sup> After a combination of eye and head movements bring the line of sight to the target, gaze position remains relatively constant even though the head continues to move. This occurs because the VOR is still active, causing the eye to counterrotate with a velocity that exactly opposes head velocity.

Based upon these and other findings, eye and head movements were considered to be programmed independently (Morasso et al. 1973), with any displacement of the retinal image resulting from continued head movements automatically pulled by the VOR. Accordingly, the commands required to generate saccadic eye movements were thought to be identical whether or not the head moved. If the head moves, vestibularly induced compensatory eye movements are added linearly to the saccade signal. This model of eye-head coordination is now known as the linear summation model.

The linear summation hypothesis is supported by other evidence. Gaze duration, amplitude, and peak velocity (for movements to targets between 10 and 40° in eccentricity) are almost identical (as predicted by the model) whether accomplished by combined eye and head movements or, when the head is restrained, by eye movements alone (Morasso et al. 1973). Also, saccades triggered *while the head is already moving* are smaller in amplitude, shorter in duration, and reduced in velocity when compared to similar saccades made with the head fixed (Morasso et al. 1973). Although these differences could be due to modifications of the central oculomotor program occurring when a head movement has already been initiated, this does not seem to be the case. Saccades of animals whose heads are unexpectedly restrained (assumed to have programmed head movements which they were prevented from making), are identical with those of the animals whose heads are continuously restrained (Morasso et al. 1973). This result would not be expected if commands for the impending (but prevented) head movement altered commands for the associated saccadic eye movement.

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<sup>1</sup> EMG records show that activation of the neck muscles precedes activation of the extraocular muscles by 20 ms. Thus, the overt sequence of eye and head movements does not reflect the order of neural commands. The delay between the onset of neck EMG activity and actual head movement is attributed to contraction time of the neck muscles and the inertial properties of the head (Bizzi et al. 1972).

Furthermore, differences in the metrics of saccades made with and without head movements are not present for several weeks after bilateral labyrinthectomy. In this condition, gaze overshoots the target because eye movements during head turning do not compensate for the ongoing head movements (Dichgans et al. 1973).

### Other Modes of Eye-Head Coordination

Despite the simplicity of the linear summation hypothesis, a single strategy for coordination of eye and head movements cannot be responsible for all types of gaze shifts. Self-paced eye and head movements between visual targets at fixed locations differ from gaze shifts made to targets appearing at unpredictable times and locations (Bizzi et al. 1972). During predictive movements, the head begins to move well before the eyes do. The head movement is achieved by a gradual increase in the activity of the agonist muscles instead of the sudden burst of neck muscle activity recorded from the agonist muscles when an unexpected stimulus is presented. That the interval between the onset of eye and head movements depends upon target eccentricity, predictability, and visibility (see Guitton 1988 for references) suggests that, temporally, command signals driving the eye are only loosely coupled with those driving the head.

The different patterns of eye and head movements produced by electrical stimulation of rostral and caudal regions of the SC also illustrate different modes of eye-head coordination. Electrical stimulation of neurons at a single site in *rostral* regions of the deep layers of the cat's SC produces saccades of approximately the same direction and amplitude, regardless of the initial starting position of the eye (Roucoux and Crommelinck 1976). In contrast, stimulation of neurons located in *caudal* regions of the SC evokes movements that bring the eye to a given position in the orbit even when the stimulation-induced movement begins at different initial positions. When these experiments were repeated in animals free to move their heads (Harris 1980; Roucoux et al. 1980), application of brief stimulation trains through electrodes in the *rostral* SC evoked gaze shifts consisting of eye movements only; evoked head movements were not observed.<sup>z</sup> Brief trains of electrical stimulation applied *caudally* evoked contralateral eye and head movements that produced gaze shifts of particular directions and amplitudes.

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<sup>z</sup> With the head fixed, however, longer stimulus trains applied rostrally can lead to activation of neck muscles after the staircase of saccades elicited by the stimulus causes the eyes to move past the midline to the side of the muscle whose activity is being recorded (Guitton et al. 1980). Thus, muscle activation depends on orbital position of eye in orbit. Also, microstimulation of the anterior SC in cats with the head free (Roucoux et al. 1980; and Harris 1980) produces a slow contralateral head movement if the stimulus is applied long enough to bring the eye beyond a position threshold.

The stimulation-induced head movements had short and constant latencies (25–30 ms) and were high velocity movements. Unlike those produced by stimulation at rostral sites, the saccades associated with these head movements were not modified by the VOR. Thus, there are at least two modes for controlling gaze: one produced by eye movements alone, and a second involving combined eye and head movements. In the first mode, movements of the head are compensated for by an active VOR. In the second mode, vestibular compensatory movements are absent.

Other experiments have been concerned with the issue of how gaze shifts are programmed when the target lies beyond the oculomotor range of the observer. The oculomotor range of cats ( $\pm 25^\circ$ ) is smaller than that of monkeys ( $\pm 45^\circ$ ) and, in cats with their heads free, almost all saccades larger than  $4^\circ$  are accompanied by rotations of the head (see Guitton 1988 for references). Moreover, highly motivated subjects (cats and humans) usually generate single-step, saccade-like gaze shifts when looking to targets beyond their oculomotor range. During the initial phase of these large gaze shifts, the eyes and head move in the same direction and may continue to do so until the eyes reach their oculomotor limit or until the line of sight is directed at the target. Usually the head continues to move and, at this point, the eyes move in the opposite direction, compensating for the still ongoing head movement. This pattern of eye and head movement suggests that initially the VOR is inactive, but is activated later, after the target is acquired.

Recently, dual modes for gaze control have been observed in monkeys. Tomlinson and Bahra (1986a, b) report that for movements of less than  $20^\circ$  in amplitude, gaze shifts are accomplished almost exclusively by movements of the eyes; however, for larger saccades, approximately 80% of the total change in gaze is due to head movement. The hypothesis that the VOR is inactivated during large gaze shifts has been tested in experiments in which the head is braked, suddenly and unexpectedly *during* a saccade. In the experiments of Tomlinson and Bahra (1986b), a torque pulse could be directed in the same direction as, or opposite to, the direction of the saccadic eye movement. Based upon their findings, the VOR appears to be inactive for most of the duration of large-amplitude ( $> 40^\circ$ ) gaze shifts. During quite small gaze shifts ( $< 10^\circ$ ), the VOR is clearly functioning; however, as the size of the gaze shift is increased, there appears to be a region where the VOR operates with reduced gain before it enters the large gaze shift region where the VOR is turned off entirely. In related experiments, Lauritis and Robinson (1986) reported that there was no compensation for mechanical perturbations in head position during gaze shifts larger than  $40^\circ$ . Guitton and Volle (1987) performed similar experiments and obtained mixed results. Results comparable to Tomlinson and Bahra (1986b) and Lauritis and Robinson (1986) were obtained from two subjects, but considerable

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variability in the interaction between the VOR and saccade signals was observed in the remaining two subjects.

Tomlinson and Bahra did observe an apparent interaction between the saccadic eye movements and head movements, even when the VOR was inactivated. As the velocity of head movements increased, there was a corresponding decrease in eye velocity, so that gaze velocity remained nearly constant throughout the gaze shift. Since, presumably, the VOR was turned off when this interaction occurred, they concluded that this represents an interaction between the motor programs for producing eye and head movements.

## NEURAL MECHANISMS FOR COORDINATING EYE-HEAD MOVEMENTS

### Motor Maps in the SC

Although frontal regions of the cerebral cortex are strongly implicated in the control of gaze (for references see Isa and Sasaki 1988; Alstermark et al. 1985; Guitton and Mandl 1978), the role of the SC in gaze control has been studied in much more detail. Indeed, many lines of evidence indicate that the SC is an important part of the neural substrate for generating orienting responses. This structure is involved in both the localization of sensory stimuli and the initiation of orienting responses (for recent reviews of this literature see Sparks 1986; Sparks and Hartwich-Young 1989). In animals with restricted ocular motility (such as cats), electrical stimulation of the SC produces short latency movements of the eyes and head as well as movements of the pinnae and vibrissae. In general, the direction and amplitude of all stimulation-induced movements (eyes, head, pinnae, vibrissae) depend upon the site of stimulation. Medial stimulation produces movements with upward components while lateral stimulation produces movements with downward components. In the anterior SC, relatively small movements are produced, whereas caudal stimulation produces larger movements (see Sparks and Hartwich-Young 1989 for references). Since, in most experiments, simultaneous measurements of the movements of the eyes, head, vibrissae, and pinnae are not obtained, it is not clear whether the SC contains several completely independent motor maps or a single motor representation that coordinates the various subcomponents of an orienting response. This issue needs to be reexamined, but early experimenters observing freely moving animals emphasized that collicular stimulation evokes a sequence of eye, pinna, head, trunk, and limb movements that resembles naturally occurring orienting movements (Hess et al. 1946).

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### Pathways for Collicular Control of Orienting Responses

Collicular control over orienting movements of the eyes, head, and pinnae may be exerted through *ascending* and *descending* pathways from the deep layers to motor and premotor areas in the brain stem and spinal cord (for references see Grantyn and Berthoz 1988; Sparks and Hartwich-Young 1989). It is currently thought that the most important *ascending* projections for generating gaze commands are those to the rostral interstitial nucleus of the medial longitudinal fasciculus (a structure which plays an important role in the generation of vertical saccadic eye movements (see Sparks and Hartwich-Young 1989 for references), and those to structures implicated in vertical and torsional movements of the head (the nucleus of the posterior commissure, the interstitial nucleus of Cajal, the periaqueductal grey, the supraoculomotor zone, and the Edinger-Westphal nucleus).

*Descending* projections leave the deep layers through two major pathways: the contralaterally directed predorsal bundle or tectospinal tract and the ipsilateral tectopontine-tectobulbar tract. The contralaterally projecting fibers of the predorsal bundle terminate within nuclei of the pontine and medullary reticular formation and the spinal cord. Most of the targets of the tectospinal fibers have been shown to be involved in the control of eye and/or head movements. For example, the majority of neurons within the nucleus reticularis tegmenti pontis (NRTP) of macaque monkeys burst or pause in association with saccadic eye movements of particular directions and amplitudes. Neurons projecting within the predorsal bundle terminate also in the nucleus reticularis pontis oralis (NRPO) which corresponds, in part, to the paramedian pontine reticular formation. This area of the brain stem is instrumental in the generation of horizontal saccades. Through their terminations within the medial accessory nucleus of the inferior olivary complex, contralaterally projecting collicular neurons gain access to the climbing fiber system and to visually responsive neurons in cerebellar lobules VI, VII, and VIII in the posterior vermis. It has been suggested that this tecto-olivo-cerebellar pathway is critically involved in the cerebellar control of head and eye movements. The deep layers of the SC are reciprocally connected to the nucleus prepositus hypoglossi (NPH), a structure that has efferent and afferent connections with numerous structures involved in movements of the head and eyes. Finally, descending crossed projections from the deep SC also terminate in the medial and descending vestibular nuclei, the nucleus intercalatus, and the spinal trigeminal nucleus.

In the monkey, only a few scattered axons of the predorsal bundle descend to the spinal cord. In the cat, however, deep collicular neurons send fibers to areas involved in the control of head movements; i.e., to the supraspinal nucleus (which then projects bilaterally to laminae VIII and IX of the first five cervical spinal cord segments) and to laminae VI-VIII of the first five

cervical segments of the spinal cord. However, even in the cat, only a small number of fibers reach the spinal cord so that most of the tectal neurons projecting in the tectospinal tract should be considered "tectobulbar" cells (Grantyn and Berthoz 1988). Most fibers travelling in the tectospinal tract are directed to the medial pontobulbar reticular formation. The regions of denser terminations coincide with the main sites of origin of reticulospinal tracts. Moreover, recent experiments indicate that even those neurons that project all the way to the spinal cord have collaterals that distribute signals to the pontobulbar reticular formation (see Grantyn and Berthoz 1988 for references).

Ipsilaterally directed fibers of deep collicular neurons project ventrolaterally to terminate on visually responsive neurons within the parabigeminal nucleus and the dorsal lateral pontine grey, as well as on oculomotor neurons within the mesencephalic reticular formation. In cats, the paralemniscal region of the lateral pontine tegmentum, an area involved in movements of the pinnae, also receives ipsilateral inputs from the deep collicular layers. Further targets of the ipsilateral descending pathway are the rostral pontine reticular formation, the dorsolateral wing of NRTP, and the NRPO. The NRPO, in turn, has projections to the spinal cord and is thus thought to function in the mediation of head movements.

### Physiological Studies

In this section, the evidence for linkages between motor programs for controlling eye and head movements obtained from simultaneous measurements of eye position and the activity of neck muscles is reviewed. The results of experiments recording from neurons in the SC or cells in regions receiving tectal signals are then summarized.

*Correlation of eye movement signals and neck muscle activity.* Simultaneous measurements of the activity of extraocular and neck muscles support behavioral evidence for tight eye-head coupling during orienting responses. Even when the head is immobilized, the tonic component of the activity of several dorsal neck muscles is highly correlated with the horizontal position of the eyes during spontaneous eye movements and during vestibular nystagmus (Vidal et al. 1982; Roucoux et al. 1982; Lestienne et al. 1984). The relationship between neck muscle activity and horizontal eye position is nonlinear. Very little, if any, muscle activity is observed until the eye reaches a threshold position in the orbit. Then, a linear relationship between muscle activity and eye position is observed out to approximately 15° eccentricity. The relationship beyond that position is unclear since recruitment of additional motor units makes it difficult to isolate individual units. Interestingly, during vestibular stimulation, muscle activity is correlated with

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eye position instead of head velocity, the signal carried by vestibular afferents. The relationship between tonic levels of neck muscle activity and eye position is greater when the head is fixed. When the head is free, neck muscle activity is usually related to head position; however, muscle activity is phasically modulated during saccadic eye movements and head accelerations.

*Activity of reticulospinal neurons.* Reticulospinal neurons demonstrate both physiological and morphological characteristics implicating them in the control of eye-head movements. Vidal and colleagues (1983) recorded from the periabducens area of the pontine-medullary reticular formation, a region containing the cells of origin of the reticulospinal pathway. They isolated neurons with activity related to the tonic and/or phasic components of the activity of dorsal neck muscles as well as to ipsilateral horizontal eye position. While these findings supported the notion that reticular neurons may mediate the synergistic activity of eye and neck muscles, the recordings were not from identified reticulospinal cells. Grantyn and Berthoz (1987a, b) recorded from reticulospinal cells identified by stimulation of the cervical spinal cord and used intra-axonal horseradish peroxidase (HRP) injections to describe their anatomical connections. Based upon their findings, many reticulospinal cells burst in synchrony with the phasic components of ipsilateral neck EMG and ipsilateral saccades. Bursts are often followed by a prolonged discharge, but the frequency of this tonic activity decays even though eye and head position remain constant. The firing rate of reticulospinal cells also depends on eye position: if the eyes are deviated contralaterally, reticulospinal cells do not discharge during saccades in the on-direction. The burst magnitude and frequency of tonic discharges, however, are proportional to ipsilateral eye position for on-direction saccades initiated when the eyes are directed ipsilaterally.

Morphologically, reticulospinal neurons issue many collaterals on their route to the spinal cord. The major targets are the abducens and facial nuclei and the dorsal gigantocellular tegmental field. The dorsal gigantocellular tegmental field is a source of direct excitatory and inhibitory inputs to cervical motoneurons.

In summary, the findings of Grantyn and Berthoz provide a physiological and morphological basis for *synergistic* movements of eyes and head during orienting responses. Signals carried by reticulospinal neurons are related to *both* neck muscle activity and eye position. Accordingly, these signals distribute not only to the spinal cord, but also to structures closely concerned with the control of eye movements.

*Activity of tectoreticulospinal neurons.* Grantyn and Berthoz (1985) recorded the activity of tectoreticulospinal (TRSN) axons in cats with fixed heads

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during saccades to visual targets. Cells were classified as TRSNs on the basis of short-latency (0.3-0.5 ms) orthodromic responses to SC stimulation and antidromic activation by stimuli applied at C1 or C2 levels of the spinal cord. Some of these cells have visual and motor properties. They are activated by a moving visual stimulus even when the animal fails to orient to the stimulus. These cells do not discharge before spontaneous saccades in the dark but display strong bursts before visually guided saccades within their movement fields. The motor burst begins before the saccadic eye movement and the onset of the phasic neck EMG discharge, but, typically, the bursts are of short duration and coincide only with the initial, phasic component of muscle contractions. The pattern of axonal collaterals in the brain stem was reconstructed by filling TRSNs with HRP. A "diffuse" pattern of collaterals is observed, but Grantyn and Berthoz note that, in fact, collicular signals are distributed to regions of the brain stem known to be involved in the initiation or guidance of eye and head movements.

Grantyn and Berthoz (1985) concluded that TRSNs contribute to the facilitation of neck motoneurons only during the initial part of phasic muscle contractions and that the signals needed to complete the motor response must be generated in circuits acting in parallel with TRSNs. They emphasize, also, the conditional linkage between TRSN bursts and neck EMG. For example, the intense activity recorded from TRSNs is completely decoupled from the neck muscles when the eyes are directed in the ipsilateral hemifield. Also, the high frequency bursts generated in response to visual stimuli are never translated into neck muscle activity.

Munoz and Guitton (1985) studied TRSNs in head-free cats. During spontaneous eye and head movements, neither saccade-related nor neck EMG-related discharges were observed. TRSNs did not discharge in relation to either the slow or quick phases of vestibular nystagmus. However, before orienting movements to visual targets, many of the cells display a sustained low frequency discharge followed by a high frequency burst. The sustained discharge of these cells is related to the angular separation between the target and the visual axis (gaze position error). Control observations indicate that this activity is not related solely to target position with respect to the head or to the position of the eye in the orbit. TRSNs discharge high-frequency bursts of action potentials prior to visually triggered gaze shifts made in the head-fixed or head-free conditions (Munoz and Guitton 1986). These high-frequency presaccadic bursts are weak or absent when the cat generates gaze shifts to nonvisible remembered targets. Presaccadic bursts were also well correlated with bursts of EMG activity recorded from neck muscles. Munoz and Guitton (1985) emphasize that TRSNs were never observed to discharge, either tonically or phasically, during spontaneous gaze shifts made in the light or dark. Thus, cats can make saccadic gaze shifts even when their TRSN pathway is silent.

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## SUMMARY AND CONCLUSIONS

Behavioral studies indicate that eye-head coordination is not achieved by a single motor program. At least two major modes of operation are observed. When the desired gaze shift is small, this may be accomplished by movements of the eyes alone; voluntary or involuntary movements of the head are countered by the VOR. Very large gaze shifts are accomplished by moving both the eyes and head toward the target. During the initial phase of these movements, the VOR is switched off but later, after the line of sight is near the target, the VOR is reactivated. Strategies for achieving intermediate amplitude gaze shifts are not as clear, however there is the suggestion that the VOR may be still active, but with reduced gain. Other behavioral studies emphasize the flexibility of the temporal linkage between eye and head movements. The interval between the onset of neck muscle activity and extraocular muscle activity is variable, depending upon stimulus conditions and the attentive state of the subject.

In their early experiments, Bizzi and colleagues noted that, except in the special case in which the eyes are centered in their orbits, there is no fixed relation between the location of the retinal image of a visual target and the amplitude of the head movement required to look to the target. Thus, the neural system controlling head movement must have access to information about the position of the eye in the orbit. In this context, it is interesting to note that almost all of the neurons found in the pontine and medullary reticular formation with activity related to movements of both the eye and head display eye-position thresholds, i.e., a relationship between firing rate and neck muscle activity is not observed until the eye reaches a certain threshold position in the orbit.

Results of microstimulation and recording experiments suggest that the SC may be involved in the coordination of eye and head movements during large gaze shifts. This is consistent with anatomical findings. TRSNs send extensive collaterals to brain stem regions involved in the control of head and eye movements. Moreover, Munoz and Guitton (1987) suggest that the characteristics of the burst may determine the velocity profile of eye and head movement trajectories. This implies that the same signal is sent to eye and head premotor circuits. The suggestion that the SC contains a single signal of gaze motor error, rather than separate signals of eye motor error and head motor error, raises a number of questions. Since there are major differences in the mechanical properties of the eyes and head, how can a single signal be used to control both? Where is this common signal transformed into the ones needed specifically by the extraocular muscles and into those needed by neck muscles? If at the level of the SC, gaze (rather than eye or head) shifts are being organized, how and where are separate eye and head motor error signals formed? Also, since the eye and

head components of a gaze shift may differ in both onset and duration, how is this accomplished with a single signal?

As noted by Grantyn and Berthoz (1987a), there are interesting differences in the properties of cells with gaze-related neural activity found in the brain stem reticular formation and tectal cells projecting to this area. These differences represent one level of transformation of the signals used for controlling eye-head movements. TRSNs respond to visual stimuli even when orienting eye movements are not made to the stimulus. Reticulospinal cells do not. TRSN cells do not discharge during "spontaneous" gaze shifts, but reticulospinal cells do. The burst activity of TRSNs is independent of eye position while reticulospinal cells are activated only when the eye is in certain orbital positions. Reticulospinal cells develop slowly decaying tonic activity roughly proportional to ipsilateral eye position, but TRSNs lack tonic activity when tested under identical behavioral conditions.

As several authors have noted, the finding of distinctive modes for coordinating eye and head movements raises questions. For example, are the different modes of coordination organized in different brain areas? How is switching from one mode to another accomplished? The finding of Tomlinson and Bahra that the horizontal VOR, but not the vertical VOR, is active during large vertical saccades suggests independent gates for horizontal and vertical circuits. Experiments ongoing in several laboratories can be expected to resolve some of these issues and to add to our understanding of the neural bases for coordinated eye and head movements.

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