

Eye-Head Coordination

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Synonyms

Eye-head coupling; Gaze control; Eye-neck synergy

Definition

The control of the line of sight by the central nervous system is part of a larger visuomotor system allowing us to perceive, localize and recognize objects in the outside world. It is therefore an important research topic, and eye-head coordination further represents a good model for the study of the sensory-motor transformation mechanisms involved in the control of any multi-joint system. Eye-head coordination refers to the various mechanisms which contribute to orienting movements or to stabilization of the line of sight in space. This paper focuses on orienting movements and considers temporal and spatial coupling mechanisms, regulating respectively when and how much the ocular and cephalic body platforms move.

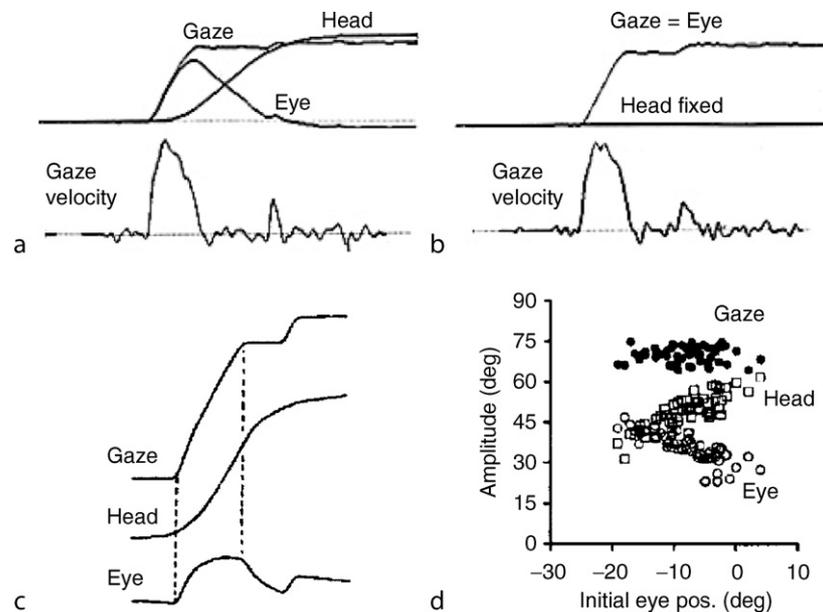
Characteristics

Upstream Event/Conditions

Orienting movements of the visual axis (gaze) are continuously required when animals visually explore their environment. A simple reason is that, in animals lacking panoramic vision, the visual field does not cover the whole surrounding space and furthermore, in higher mammals, the specialization of the central part of the retina (fovea) allows an optimal analysis of only a very small part of the central visual field. Thus, exploration of our visual environment requires frequent [▶gaze shifts](#) to foveate ([▶Foveation](#)) objects of interest, separated by periods of active gaze stabilization during which visual analysis is performed. The eyes and the head are the two main body effectors, sometimes assisted by the trunk, that contribute

synergistically to this gaze orientation and stabilization behavior. The low inertia eyeballs achieve fast and accurate orienting movements (saccades) to catch visual targets and to keep them in the foveal region of the visual field. As the desired amplitude of gaze movement increases, the amplitude of the eye saccade saturates and the contribution of the head becomes more prominent. The head is slower to move but has a larger operating range, allowing re-centering of the eyes in the orbit after each large [▶gaze shift](#). This eye-head coordination pattern varies quantitatively between species as a function of the possible range of eye movements in the orbit (e.g. the oculomotor range of a cat is smaller than that of primates, leading to a larger contribution of the head to the gaze shift), but its qualitative features remain constant across species. Thus, the motor behavior yielding appropriate analysis of our visual environment involves precisely controlled and coordinated eye and head movements, involving for each platform all three degrees of freedom and additionally for the eyes, both conjugate and disconjugate movements. For simplification, we will focus on conjugate 2-D eye movements combined with 2-D head movements.

The neural control of combined eye-head gaze saccades is less well understood than the control of saccadic eye movements performed when the head is restrained [1,2]. A first issue of eye-head coordination concerns the relative timing between eye and head movement initiation [3]. Behavioral investigations have revealed that this eye-head temporal coupling can vary according to experimental conditions. However, on average, for gaze shifts larger than 15°–20°, the head starts to move close to the eye saccade onset and therefore contributes significantly to the gaze shift. Note that the nearly concomitant initiation of eye and head displacements is the best strategy in terms of overall response time, but puts higher constraints on the neural processes controlling eye-head coordination. A second issue then concerns mechanisms by which the central nervous system regulates the size of each eye and head motor command in an appropriate way to bring gaze accurately onto the target [4]. This spatial coupling problem, involving a neural decomposition of a desired gaze displacement signal into eye and head motor commands, is complex because it must take into account both the very different mechanical properties of



Au2 **Eye-Head Coordination. Figure 1** Kinematics of combined eye-head gaze shifts. (a–c) typical horizontal movement trajectories for 40° gaze shifts recorded in man. (a) head free, (b) head fixed, and a 100° gaze shift in monkey (c). (d) effect of initial eye position on the coordination between eye and head for gaze shifts of nearly 70° in the monkey. The plot shows the amplitude of gaze shifts (filled circles), and of their eye (open circles) and head movement (open squares) components against initial eye position. Panels (a) and (b) are redrawn from Pelisson et al. JNP (1988), panel (c) from Guitton TINS (1992) and panel (d) from Freedman and Sparks JNP (1997).

the eye and head platforms and the possible reflex interactions between them. Particularly, it supposes that the two antagonistic oculomotor responses – eye saccade and ►vestibuloocular reflex (VOR) – are precisely coordinated. Indeed, the gaze shift phase must be followed by perfect gaze stabilization as soon as the fovea is aligned with the target. This stabilization is due to the VOR which compensates for any residual head movement by producing a counter-rotation of the eyes. The accuracy of gaze shifts thus requires a very precisely timed switch between saccadic activity and VOR response.

Downstream Event/Conditions

Temporal Coupling of Eye and Head Movement Initiation

The general pattern of eye-head temporal coupling can be predicted from the different properties of the ocular and the cephalic mechanical systems. Indeed, the larger inertia of the head relative to the eye can account for the 10–20 ms average lag of the head in the initiation of natural orienting movements, since the same lag has been observed for movements evoked experimentally by electrical microstimulation of gaze-encoding structures like the ►superior colliculus (SC). However, on top of this average head lag, a number of factors have been shown to affect the precise temporal synchronization of eye and head movement initiation (sensory modality of the target, target predictability, size and

direction of gaze shift, initial eye and head positions, verbal instructions, see [3]): the head lag tends to decrease or even reverses to a head lead for non visual or highly predictive targets, for vertical as compared to horizontal gaze shifts, when the head is initially deviated away from the intended gaze shift direction, and when subjects are specifically asked to align their head with the target. These changes in eye-head initiation pattern imply significant variations in the relative timing of eye and head neural commands (due in large part to variations of the latter), which in turn can be accounted for by the fact that the motor systems controlling each of the two platforms are not simply gated by a common mechanism. More specifically, head motor commands, including task-dependent intentional signals, can be sent to the spinal cord level while the pre-oculomotor neurons are still gated off by the omnipause neurons in the brainstem reticular formation, or conversely can be delayed – or suppressed – relative to the triggering of pre-oculomotor neurons.

Spatial Coupling

A central question has been how the two antagonistic ocular responses – the orienting saccade and the compensatory VOR response – combine during the gaze shift. Stated differently, the problem is whether the VOR continuously operates, despite being counterproductive, during the orienting gaze shift. A first hypothesis

postulated that the continuously operating VOR led to the central cancellation of the physical head contribution to the gaze shift. It is now quite firmly established that this ►[linear summation hypothesis](#) [5] does not hold, and that the VOR is inhibited during the gaze shift by the saccadic commands. Data to refute the summation hypothesis have been provided both by behavioral and neurophysiological experiments. The former demonstrated that head-unrestrained gaze shifts are faster than gaze shifts of the same size performed with the head fixed, which indicated that the head movement contribution is not cancelled centrally by the VOR. In addition, specific head perturbation paradigms have been used to show that the modifications of the head trajectory during a gaze shift also affect gaze trajectory but not gaze final accuracy, owing to an ocular compensation unrelated to VOR. These observations indicate first that the VOR response does not adequately compensate for the head perturbations, signaling a momentary reduction of its gain during the gaze shift, and second that a central control of desired gaze displacement, independent of the status of the VOR, is involved in maintaining gaze terminal accuracy [6,7]. Thus, both the speed and the accuracy of gaze shifts can be optimized, leading to a performance compatible with the high functional value of orienting gaze shifts in everyday life. This conclusion is also supported by neurophysiological data. On the one hand, recordings from the so-called position-vestibular-pause (PVP) neurons, which constitute the intermediate link of the VOR 3-neurons arc, have shown a specific reduction of these neurons' head sensitivity during the saccadic part of gaze shifts in monkey [8]. Earlier data have indicated that a similar class of vestibular neurons in the cat are inhibited by saccadic burst neurons. On the other hand, several categories of neurons previously known to discharge in relation to saccadic eye movements in the head restrained condition have been shown to actually encode the total displacement of gaze (eye + head) in space: this has been shown for some saccadic burst neurons and omnipause neurons of the reticular formation, and for all burst neurons and fixation neurons of the superior colliculus. Although these findings are consistent with the ►[gaze feedback hypothesis](#) that was initially proposed to account for the maintenance of gaze accuracy despite VOR inhibition, the existence and neural implementation of such gaze feedback is still highly debated [9].

To summarize, gaze orientation towards a target of interest is based on a desired gaze displacement command, which has to be decomposed in separate commands for eye and head. The VOR response is inhibited during the saccadic part of the gaze shift and the gaze trajectory is controlled by internal feedback. The termination of the saccadic pulse generator activity, due to this feedback control, and the resumption of a unity VOR gain are both involved in the accurate

termination of the gaze shift on the target, and in the subsequent gaze stabilization independently of any residual head movement.

Involved Structures

To a large extent, the search for mechanisms responsible for eye-head coordination has so far focused on the brainstem, the superior colliculus and the cerebellum. As already stated above, a candidate neural substrate of the intra-saccadic VOR inhibition has been found at the brainstem level, involving an inhibition of PVPs neurons during saccades, likely arising directly from saccadic burst neurons. Note also that another pathway, this time excitatory and running in the opposite direction (from the vestibular complex to saccadic burst neurons), has been suggested in the cat to contribute to the triggering of an eye saccade and/or the acceleration of the eyes during head movement. Although these particular burster-driving neurons have not yet been found in monkey, this type of excitatory, anticomensatory, vestibulo-ocular pathway is probably required in all animals for the triggering of saccade during head movements when there is no explicit target (quick phases of vestibular nystagmus). The superior colliculus is another brainstem structure that has been intensively investigated in different animal species. Since nearly 40 years ago, we have known that saccadic eye movements produced by head-restrained animals are topographically encoded at the level of the deeper collicular layers. More recently, studies in the head-unrestrained cat or monkey have shown that this collicular motor map in fact encodes the saccadic shift of gaze in space rather than the displacement of the eyes in the orbit. Indeed, unit recording, electrical microstimulation and anatomical studies have demonstrated that the SC contains a gaze motor map, and proposed that the SC provides the brainstem pre-motor centers with a desired gaze displacement command [4,10,11]. A remaining question that has not yet found a consensual answer is how and where in the cerebello-reticular network this collicular gaze displacement drive is decomposed into separate commands for the eyes and head. Does this decomposition occur downstream from a gaze pulse generator controlled by a single gaze feedback loop, as postulated in the original gaze feedback hypothesis, or does it occur ahead of two separate (eye and head) generators each controlled by its own feedback loop? Does it occur before or after the level of the spatio-temporal transform (i.e. of the transformation between the neuronal population code used by the SC to represent the desired gaze displacement and the frequency code used by motoneurons)? Gaze-related SC output neurons have been shown to project to the reticular formation both to the eye-related bursters and to the ►[reticulo-spinal neurons \(RSNs\)](#). RSNs in turn

send collateral projections to the eye-related premotor neurons and to the spinal pre-cephalomotor neurons. Thus, RSNs are ideally suited to carry this eye-head decomposition process, but additional research is necessary to understand what the specific role of the different sub-types of RSNs is [12]. In any case, the SC is viewed as a major sensory-motor interface between cortical centers, where the appropriate goal for gaze is selected and encoded topographically in gaze coordinates, and the brainstem reticular formation, where different neuronal populations use a frequency code to represent the individual eye and head components in their respective coordinate frames.

Methods to Measure This Event/Condition

The neurophysiological description of eye-head coordination mechanisms has long been hampered by the difficult task of recording unit neuronal activities in the head-unrestrained animal; thus, although increasing recently, the amount of data collected in this condition is still modest relative to the vast amount of information on the oculomotor and the vestibular systems collected in the head restrained condition. The situation is even worse for human subjects, since the available neurophysiological methods (neuroimaging and transcranial magnetic stimulation) all require firm stabilization of the subject's head. At the behavioral level, however, several methods are now available to record eye and head movements simultaneously. Beyond describing natural eye-head coordination, behavioral approaches have allowed the development of mechanical head perturbation tests which constitute a privileged way to investigate eye-head coordination. These tests are now increasingly associated with neural recordings in animal studies, allowing us to resolve important issues like the saccade-related inhibition of vestibulo-ocular neurons, and the frame of reference used by oculomotor centers to encode saccadic commands.

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