CURRENT VIEWS ON THE MECHANISMS OF EYE-HEAD COORDINATION

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ABSTRACT. Considerable evidence has now accumulated suggesting that the eye movement control system, which to date has been almost exclusively studied in animals whose heads are restrained, is but a special case of a more general gaze control system that controls displacements of the visual axis when the head is unrestrained. The gaze control system was viewed, originally, as being oculocentric in nature: i.e., the trajectory of the visual axis in space was thought to be independent of head motion. A mechanism was proposed whereby the head's contribution to a gaze shift could be subtracted out by the action of the vestibulo-ocular reflex. This view has been considerably modified in recent years and the gaze control system has now become an elegant example of how the brain controls and coordinates two independently moving body segments.

1. Introduction

Almost two decades ago, Bizzi and collaborators described how monkeys move their eyes and head simultaneously to acquire a visual target (Bizzi et al., 1971; Dichgans et al., 1973; Morasso et al., 1973). The fundamental feature of this hypothesized motor strategy is that the same saccadic eye movement is programmed to acquire the target irrespective of whether the head moves or not. If the head movement starts after the saccade has terminated, the gaze is maintained on target by the action of the vestibulo-ocular reflex (VOR) which moves the eye, relative to the orbit, with a velocity equal and opposite to that of the head. Normally, in monkey, a saccade starts only just slightly (40ms) before any visible head acceleration and it is hypothesized that any head movement occurring during the saccade attenuates, using the VOR, the saccade amplitude by an amount equal to the head.

displacement during the saccade. The influence of the cervico-ocular reflex is negligible (Bizzi, 1981; Dichgans et al., 1973). Therefore the head both adds and linearly subtracts its contribution to the motion of the visual axis and the gaze trajectory (= eye-in-space = eye-in-head + head-in-space) is the same irrespective of whether the head is restrained (head-fixed) or unrestrained (head-free).

This view of eye-head coordination was essentially an "oculocentric" one in that the presence or absence of head motion was considered irrelevant to gaze control. We now know that this view is only partly correct. The following 3 sections explain why.

2. Neural Limits to Ocular Motility

One way of experimentally demonstrating this strategy is to suddenly and unexpectedly brake the head just before it is to move (Bizzi, 1981; Dichgans et al., 1973; Morasso et al., 1973). In this condition, visual feedback is too slow (150-200 ms) to modulate the saccade and neck proprioceptive influences are negligible (Bizzi, 1981; Dichgans et al., 1973). Thus with the head suddenly immobilized, and neither vision, proprioception nor VOR to modulate the saccade, the resulting saccade amplitude, according to the oculocentric theory should be equal to the target offset angle.

To verify this we unexpectedly prevented head motion before gaze shifts of different amplitudes, and found that maximum saccade amplitude was limited neurally, not mechanically, to about 45° in humans and 15° in cats (Guitton et al., 1984; Guitton and Volle, 1987). For targets within these values, a saccadic eye movement alone can attain a target irrespective of whether or not the head moves. An analogous result has been found by Tomlinson and Bahra (1986) in the monkey. For target offsets beyond these values, the saccade would be of insufficient amplitude to reach the target.

3. Interaction Between the Saccade and Oppositely Directed Vestibularly-induced Slow Eye Movement

The manner in which the saccade signal is attenuated by head motion is of considerable interest. One way of experimentally investigating this problem is to brake the head suddenly and unexpectedly during the saccade. Again, in this condition, visual feedback is too slow to modulate