Eye-Head Coordination Obeys Minimal-Effort Rule

Andreas A. Kardamakis¹ and Adonis Moschovakis¹
¹Institute of Applied and Computational Mathematics, FORTH, Crete, Greece

Gaze shifts are combined eye-head movements consisting of coordinated eye saccades and rapid head movements. These two-segment movements have an extra degree of freedom that allows the gaze system additional flexibility when programming eye and head commands for reorienting the line of sight. However, behavioral observations show that the eye and head contributions are systematically constrained in that larger gaze shifts rely on larger head components, whereas smaller ones consist mainly of eye movements. Furthermore, eye contributions do not exceed amplitudes of 30-35° even for gaze shifts as large as 75° and eye velocity profiles are less and less symmetrical as the amplitude of the gaze shifts increases. Optimal control theory suggests that these data could be accounted for if the brain followed the principle of minimal effort to program horizontal gaze shifts. The optimal set of control signals is obtained by relating the dynamics of the controlled eye/head components to the criterion function. The performance objective is to minimize the squared sum of eye/head torque signals, integrated in time for each coordinated movement (minimal-effort). By applying Pontryagin’s Maximum Principle, we obtained analytical expressions for eye/head control signals and from these we acquired the optimal trajectories of the eyes and the head by solving the deterministic two-point boundary-value problem. To qualitatively represent extraocular muscle length-tension curves we introduced an eye position-varying weight expressed as a polynomial function. This accounts for the active elastic restoration forces that pull the eye towards the central position. A second weight corresponding to the optimal head control signal was used to express the large inertial difference relative to the eye. In this context, eye/head commands are programmed to follow a performance trade-off between viscoelastic and inertial forces.

Optimal trajectories were obtained for rightward horizontal centripetal and centrifugal gaze shifts ranging from 5° to 75° while initial eye positions varied from 30° to the left to 10° to the right of straight ahead. Our model accurately predicted the amplitude of eye and head components relative to the amplitude of the gaze shifts as well as the fact that oculor movements do not exceed 30°. Furthermore, the model accounts for the quantitative relationships between eye and head contributions as a function of initial eye positions. The head contributed progressively less (and the eyes more) to gaze shifts of the same size as initial eye position deviated further in the contralateral direction. The greater the size of the gaze shift, the steeper the slope of these relationships. Perhaps the most striking feature of the model is its ability to generate eye velocity profiles that closely match those of animals. Lower peak velocities and dual-peak velocity profiles emerge as a result of the minimal-effort principle. Simulations of optimal head-restrained saccades also show realistic unimodal velocity profiles with shorter acceleration and longer deceleration phases, and provide an explanation of the main sequence relationship. Reproduction of the major kinematic features of head-fixed and head free movements implies that the time course of force development was successfully modelled. Ultimately, the motoneuronal commands sent to the eye and the head must in turn be consistent with the signals predicted by the minimal-effort rule. Our results suggest that the minimal-effort rule provides a rationale for the adoption of the cross-talk mechanism between eye and head control signals, which belongs to the independent eye/head control class of neural models.

Acknowledgments
Financial support of grant 03ED803 from the Secretariat of Research and Technology is gratefully acknowledged. We deeply thank Dr. Tsakiris for his valuable assistance.