New model of gaze tracking: Novel architecture with parallel gaze and head controllers

Pierre M. Daye[1,2,*], Lance M. Optican[2], Gunnar Blohm[3], Philippe Lefèvre[1]

[1]ICTEAM and IoNS, Université catholique de Louvain, Louvain-la-Neuve, Belgium

[2]Laboratory of Sensorimotor Research, National Eye Institute, NIH, DHHS, Bethesda, MD, USA

[3]Centre for Neuroscience Studies, Queen's University, Kingston, ON, Canada

Introduction

From **behavioral experiments and electrophysiological recordings** (Dodge, 1903; Westheimer, 1954; Rashbass, 1961; Becker and Fuchs, 1969), researchers started to build mathematical models of the saccadic system. Those models are used to test assumptions about the functions of neural areas during saccades. They can also be useful to demonstrate the feasibility of a control structure. Robinson (1975) published a model with **an internal feedback loop** that controls eye position. However, that model was based on a **small amount of physiological data** and therefore needed to be updated. One of the most important alterations was to change the feedback from an efference copy of position to an efference copy of velocity through the inclusion of a **resettable integrator** (Jürgens et al., 1981).

With **head-unrestrained behavioral recordings** (Bizzi et al., 1971), authors created models of eye-head coordination during saccades. Laurutis and Robinson (1986) proposed a head-unrestrained gaze saccade model with an internal **feedback loop of gaze**.

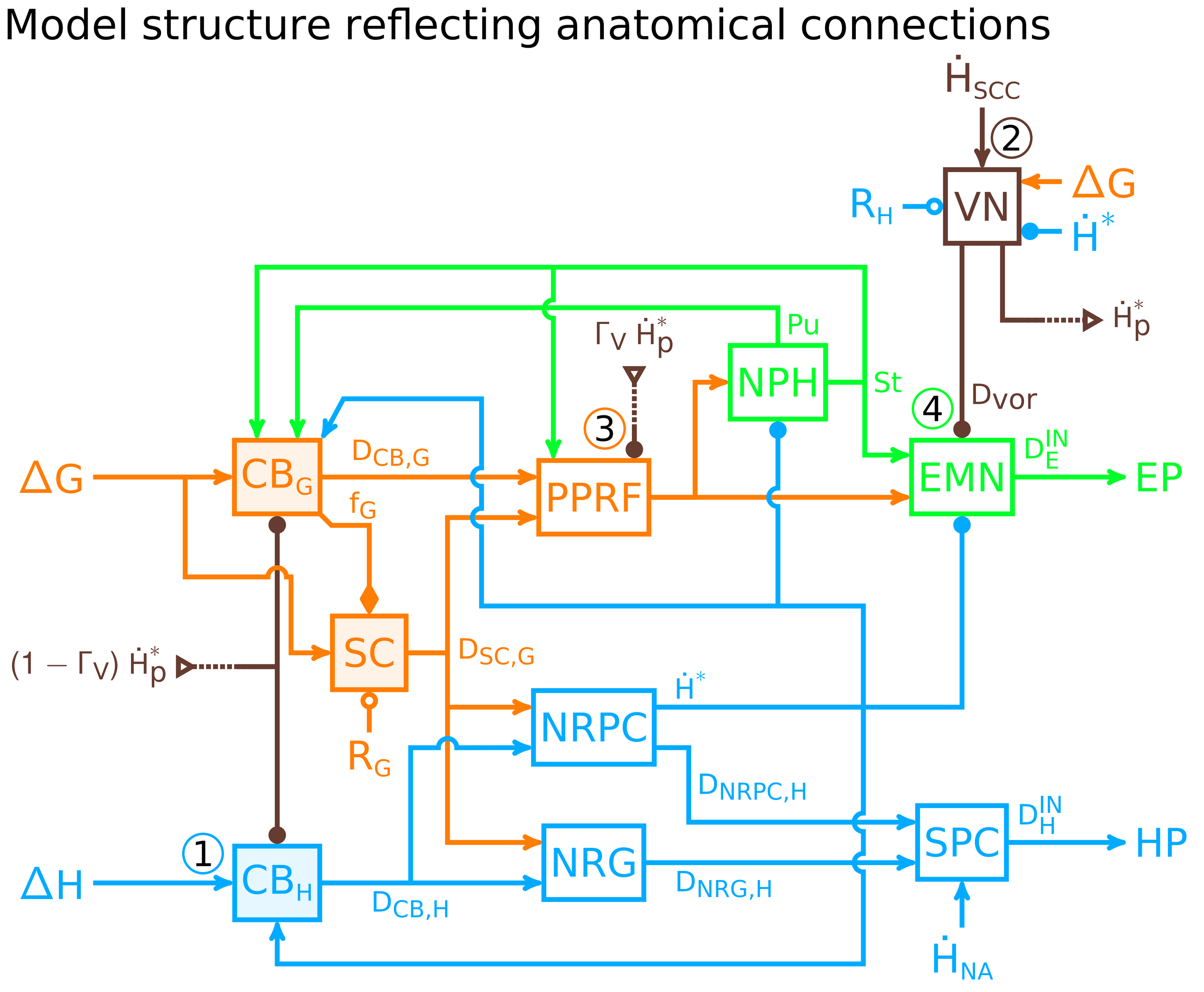
Based on the observed **tight coupling** between eye and head (Guitton et al., 1990), the **key role of the superior colliculus** during head-unrestrained saccades (Stryker and Schiller, 1975; Roucoux et al., 1980) and the accuracy of gaze saccades following a head perturbation, Galiana and Guitton (1992); Lefèvre and Galiana (1992) proposed a **colliculocentric model** of head-unrestrained gaze saccades with gaze feedback to **control both gaze and head** trajectories and to **reject perturbations**.

Even though strong coupling between eye and head has been observed, there are numerous situations in which they can have an uncoupled behavior, e.g. (Goossens and Van Opstal, 1997; Freedman and Sparks, 1997). Based on those observations, Freedman (2001) proposed a new architecture for the control of head-unrestrained saccadic movements based on **prior decomposition of the desired gaze displacement into its eye and head components**.

New results that require a new model. Currently, no head-unrestrained gaze saccade model includes a representation of the neurophysiology of **head control pathways** ① (Isa and Sasaki, 2002). Additionally, Roy and Cullen (2004) demonstrated that **passive, not active head movements are compensated by the VOR** ②. Finally, no model can explain why the **PPRF activity is sensitive to head perturbations** ③ for small amplitudes (Sylvestre and Cullen, 2006) while the **eye trajectory remains insensitive to head perturbations** ④ during large gaze shifts (Tomlinson and Bahra, 1986).

Model description

Model structure reflecting anatomical connections



Gaze-related area/drive

Head-related area/drive

Eye-related area/drive

Vestibular-related area/drive

Neural areas:

- CB_G: Gaze cerebellar controller
- CB_H: Head cerebellar controller
- *EMN*: Eye motoneurons
- *EP*: Eye plant
- *HP*: Head plant
- *SC*: Superior colliculus
- *NPH*: Nucleus prepositus hypoglossi
- *NRG*: Nucleus reticularis gigantocellularis
- *NRPC*: Nucleus reticularis pontis caudalis
- *PPRF*: Paramedian pontine reticular formation
- *SPC*: Spinal cord
- *VN*: Vestibular nuclei

Signals:

- ΔG: Desired gaze displacement
- ΔH: Desired head displacement
- $D_{CB,G}$: Gaze cerebellar drive
- $D_{CB,H}$: Head cerebellar drive
- D_E^{IN}: Eye plant drive signal
- D_H^{IN}: Head plant drive signal
- $D_{NRG,H}$: NRG head drive
- $D_{NRPC,H}$: NRPC head drive
- $D_{SC,G}$: Gaze collicular drive
- D_{VOR}: Vestibular drive
- f_G: Cerebellar facilitation
- $\dot{H}^*$: Head-in-space velocity internal estimate
- $\dot{H}_{NA}$: Head-on-trunk velocity neck afferent
- $\dot{H}_{SCC}$: Head-in-space velocity from semicircular canals
- $\dot{H}_p^*$: Head-in-space perturbation velocity
- Γ_V: VOR gain=f(ΔG)
- *Pu*: Eye pulse signal
- R_G: Gaze reset signal
- R_H: Head reset signal
- *St*: Eye step signal

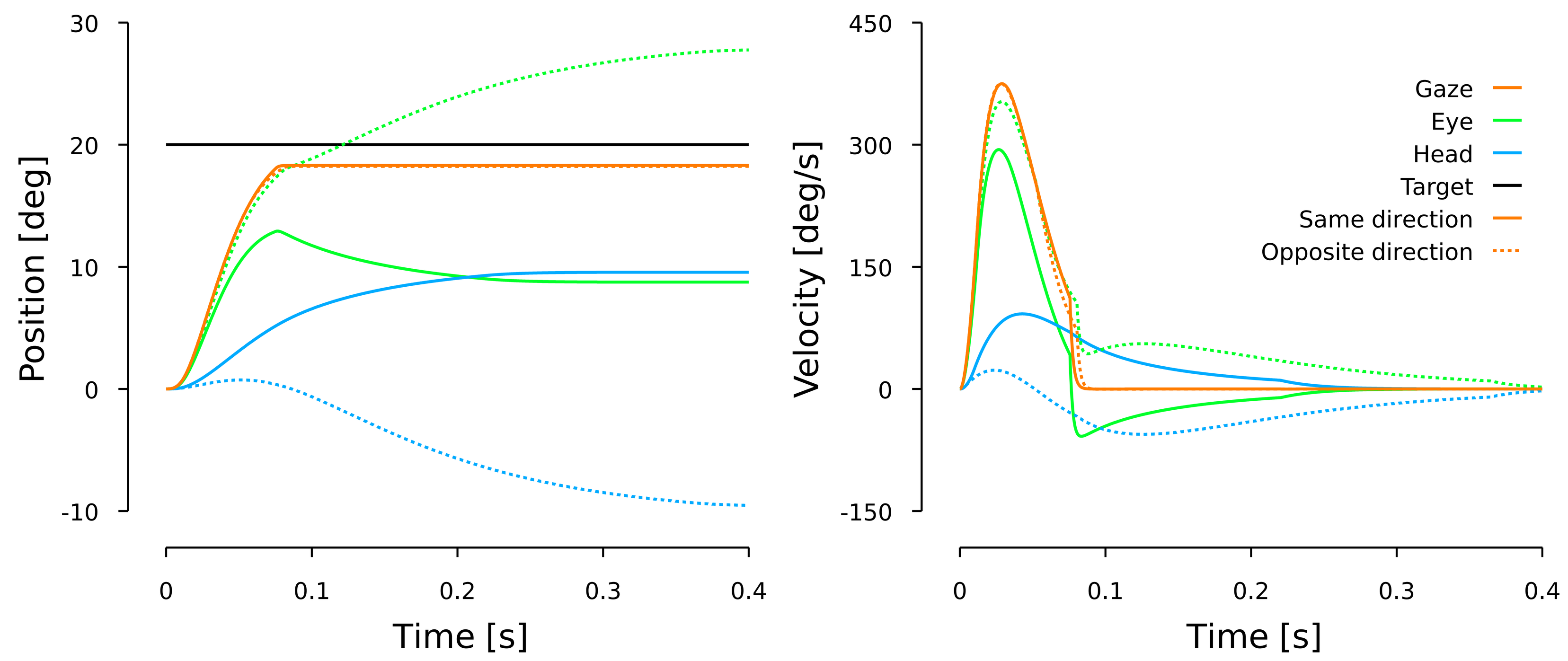
Model properties

Two inputs: desired gaze (ΔG) and head (ΔH) displacements
Two outputs: eye (D_E^{IN}) and head (D_H^{IN}) motor drives

Four pathways:

1. Gaze control structures
   - **CB_G**: Cerebellar gaze feedback controller to control gaze trajectory.
   - **SC**: Supplementary drive in the gaze direction modulated by CB_G.
   - **PPRF**: Includes gaze velocity saturation and oculomotor range.
2. Head control structures:
   - **CB_H**: Cerebellar head feedback controller to control head trajectory.
   - **SC**: Deviates the head in the gaze direction.
   - **NRG**: Includes a saturation on head velocity.
   - **NRPC**: Includes a saturation on head velocity.
   - **SPC**: Stabilizes the head at the end of the movement.
3. Eye structures:
   - **NPH**: Computes the step and the pulse of innervation.
   - **EMN**: Computes the motor drive sent to the eye.
4. Vestibulo-ocular reflex:
   - **VN**:
     (a) Computes the vestibular drive. The gain of the VOR is function of ΔG.
     (b) Computes the unexpected head velocity from an internal estimate of the head velocity and the measurements of the semicircular canals.
   - **Action**: The VOR signal acts at 3 different levels in the model: eye motor neurons, cerebellar controllers and PPRF → responses with different time constants.

Head and gaze displacements in opposite direction ①

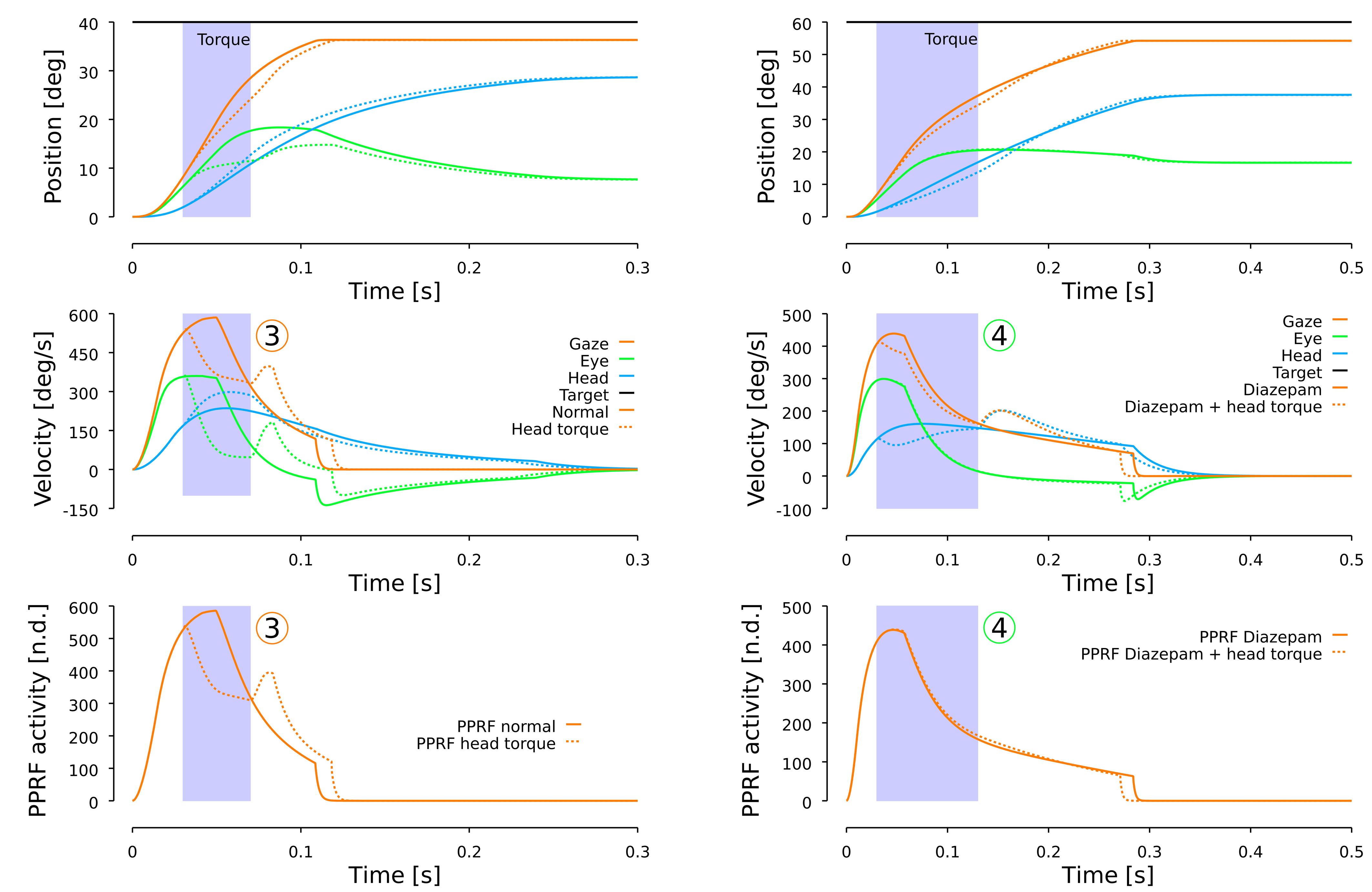


Gaze and the head pathways are coupled.

⇒ The head acts as a perturbation for the gaze feedback loop.

⇒ The gaze acts as a perturbation for the head feedback loop.

Head perturbations during gaze saccades ②



When the VOR is active (left column), the vestibular input principally affects the PPRF activity to quickly compensate for the perturbation (Sylvestre and Cullen, 2006). When during large gaze saccades (right column), when the VOR shuts off, the vestibular input principally affects the gaze and the head controllers to compensate for the perturbation without affecting the eye trajectory (Tomlinson and Bahra, 1986).

Conclusions

A new model for the control of head-unrestrained gaze saccades based on **separate gaze and head controllers** is proposed. This model simulates (1) gaze and head desired displacements in opposite directions and (2) rejection of perturbations on the gaze trajectory with the same architecture.

The proposed gaze control structure is the first to explicitly include a **head control scheme based on previously reported anatomical and neurophysiological observations**.

The model integrates an **explicit representation of the VOR** that opposes only unexpected head movements. The vestibular signal acts at three different places to ensure that the compensation of the perturbation is correctly done. For small amplitudes (short durations), the action through the PPRF and the EMN quickly corrects the eye trajectory. For large amplitudes (long durations), both gaze and head controllers have enough time to negate the perturbation using the projection at their inputs.

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