Model: Brainstem control of saccades

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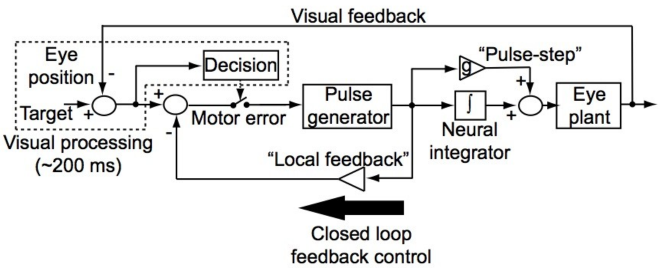
Brief Description *	Saccades are thought to be controlled in flight by means of "local feedback control". Conceptually, this means that a desired eye displacement is input to a control system, which drives the eye until the "error" between the desired and actual eye displacement is eliminated. Neurobiologically, such control is achieved by several groups of neurons distributed throughout the brainstem. This model attempts to simulate these groups of neurons to demonstrate that their concerted efforts can achieve the function of "feedback control". One of the key contributions of this model is that it shows how distributed populations of neurons can functionally appear to implement negative feedback control. The model also exemplifies the concept of "push-pull" interaction in controlling eye movements.
Narrative *	Several groups of neurons distributed throughout the brainstem are believed to contribute to saccade control, and in a manner consistent with the general local, feedback scheme of Fig. 1. These are often described aggregately as the â€˜brainstem burst generatorâ€™, and they comprise: 1) the final oculomotor neurons that innervate the eye muscles, as well as 2) the pre-motor neurons that drive these motor neurons by compiling the pulse-step commands for saccades. Fig. 2 summarizes the different classes of neurons in the brainstem burst generator and shows examples highlighting their discharge characteristics around the time of saccades. Some of these neurons appear directly correlated with specific control elements in the model of Fig. 1, whereas the contribution of others to saccade control is less clear.Oculomotor neurons (MNâ€™s) (Fig. 2) innervating the eye muscles exhibit pulse-step discharges for saccades in their on-direction and pauses for saccades in their off-direction. For example, for a horizontal saccade in one direction, the motor neurons innervating the contracting muscle will burst to pull the eye in the desired direction, and the neurons innervating the antagonist (relaxing) muscle will pause to relax it. This suggests that oculomotor control in the brainstem occurs in a push-pull manner where â€˜excitatoryâ€™ drive to one set of muscles is complemented by â€˜inhibitoryâ€™ drive to the antagonist set. This observation is important because it has resulted in revised â€˜push-pullâ€™ versions of the local, feedback models of Fig. 1 to more accurately reflect the brainstem circuitry (Fig. 2) . After the saccade, MNâ€™s (for all muscles) maintain a tonic discharge rate, and this rate is different from that before the eye movement, because such rate reflects the new eye position in the orbit. Thus, MNâ€™s implement the pulse-step command necessary to rapidly drive a saccade (Fig. 1), and existing models implement this command through a scheme like that in Fig. 2.Excitatory burst neurons (EBNâ€™s) and inhibitory burst neurons (IBNâ€™s) are thought to provide the eye â€˜velocityâ€™ command to the MNâ€™s, and they most directly correlate with the â€˜pulse generatorâ€™ in Fig. 1. For a given saccade, EBNâ€™s drive the MNâ€™s innervating the contracting muscle needed to pull the

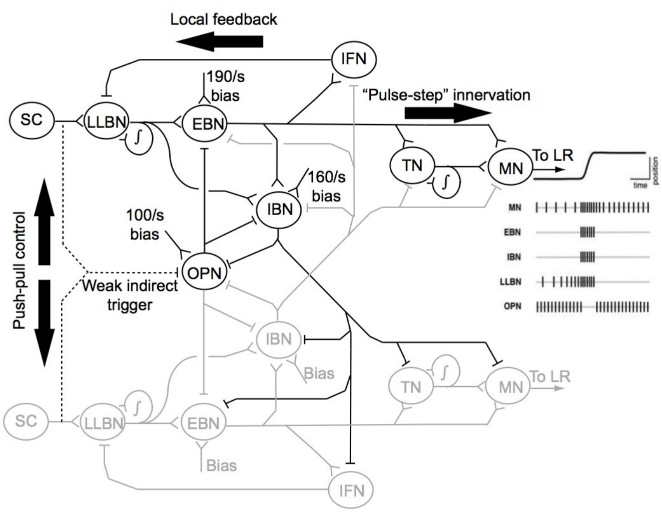
	eye, and IBNâ€™s have cross projections that inhibit the (other) MNâ€™s of the antagonist eye muscle, which should relax. Thus, for a given MN, the (mathematical) difference between EBN excitation and IBN inhibition that it receives from the other side may be thought of as specifying the eye â€˜velocityâ€™ command (Van Gisbergen, et al., 1981), and this organization is again consistent with the idea of â€˜push-pullâ€™ control evident at the MN level. As shown in Fig. 2 (Scudder, 1988), such a mathematical difference is also often the way that push-pull models of the brainstem burst generator are implemented. For example, instead of the pulse generator of Fig. 1, a push-pull version might look like that included in the complete circuit of Fig. 2 (Scudder, 1988).Tonic neurons (TN's) are thought to reflect eye position, and thus may correspond to the neural integrator element in Fig. 1 (which integrates the velocity command to provide the position command for the eye muscles).Omnipause neurons (OPN's) are tonically active and pause during saccades. They may play a role of the "switch" in Fig. 1, which triggers saccades.This distributed biomimetic model is an example of how to simulate saccade generation and local feedback but in a manner consistent with the known neurobiological realization of it in the burst generator.
Tags	brainstem, burst generator, local feedback, saccade

Architecture

Diagrams



This figure shows a systems-level model of the saccadic system. For a given visual target, the error between target and eye position is the desired eye displacement needed to acquire the target. This desired eye displacement is the input to the control system. Once a decision to make a saccade is made (the switch element), the desired displacement is subtracted from a "local feedback" signal estimating current eye displacement. The difference ("motor error") is input to a pulse generator which generates an eye velocity command. The velocity command proceeds forward to the eye plant both directly and through a neural integrator. Thus, the eye plant receives a pulse (velocity command) and a step (integral of velocity command) to keep the eye on target after the saccade. The local feedback loop takes a copy of the pulse generator command (velocity commands) and feeds a transformation of it back as an "internal estimate" of how far the eye has moved.



This figure shows a neural network model of the control system shown in Fig. 1. The superior colliculus (SC) projects to long-lead burst neurons (LLBN's) and then to excitatory burst neurons (EBN's). the EBN's provide the velocity command which is fed forward to tonic neurons (TN's) and motor neurons (MN's). Local feedback is believed to be achieved by feeding back a copy of the EBN output (filtered through IFN's and LLBN's). EBN's and LLBN's also excite inhibitory burst neurons (IBN's) which project to the other side so that they suppress the antagonist eye muscle. Thus, the control scheme is symmetric, where one side is active while the other is suppressed. Omnipause neurons (OPN's) have strong inhibitory connections between burst neurons and are thought to trigger saccades (the switch element of Fig. 1). The depiction on the right demonstrates the discharge properties of the different classes of neurons simulated by the model.

Inputs

Name	**Data Type**	**Description**
Desired displacement	angle	The model receives a desired displacement of the eye from the superior colliculus

Outputs

Name	**Data Type**	**Description**
Eye displacement	angle	The model outputs a realistic trajectory of the eye by inputing the motor neuron (MN) output to a simple mathematical model of the eye plant.

Submodules

Name	**Description**
IFN	inhibitory feedback neurons - these are a prediction of the model and they are thought to be part of the local feedback pathway to implement closed loop control of saccades.
MN	Motor neurons - these are neurons that innervate the eye muscles. They exhibit a pulse-step discharge during saccades. The pulse is thought to reflect the "velocity" command coming from burst neurons, and the step is believed to reflect the "position" command that keeps the eye at the new position after the saccade.
TN	Tonic neurons - these are neurons that are tonically active in a manner that is proportional to eye position. They thus might correspond to the neural integrator element of Fig. 1.
OPN	Omnipause neurons - these are neurons that are tonically active during fixation. They pause during saccades. They are thought to trigger saccades by releasing inhibition from the burst neurons when they pause.

IBN	Inhibitory burst neurons - these are neurons that burst with saccades, like EBN's. However, they inhibit motor neurons for the antagonist eye muscle, thus implementing push-pull control.
EBN	Excitatory burst neurons - these are neurons that exhibit saccade-related bursts. They provide a "velocity" command that is then fed forward to MN's and TN's to drive the eye muscles. As the eye approaches its target, the "motor error" decreases and the burst neurons decrease their activity. This decreases eye velocity. Note that the output of EBN's involves an inhibition from IBN's on the other side. This is the push-pull element of control.
LLBN	Long-lead burst neurons - these are brainstem neurons that exhibit a saccade-related burst plus long prelude activity (giving rise to the name "long-lead"). According to the model, they might integrate a local estimate of the burst command from EBN's (the velocity command). This gives rise to the "actual eye displacement" which can be compared with the desired eye displacement during the course of a saccade.

Submodule: IFN

Brief Description *	inhibitory feedback neurons - these are a prediction of the model and they are thought to be part of the local feedback pathway to implement closed loop control of saccades.
Tags	

Submodule: MN

Brief Description *	Motor neurons - these are neurons that innervate the eye muscles. They exhibit a pulse-step discharge during saccades. The pulse is thought to reflect the "velocity" command coming from burst neurons, and the step is believed to reflect the "position" command that keeps the eye at the new position after the saccade.
Tags	

Submodule: TN

Brief Description *	Tonic neurons - these are neurons that are tonically active in a manner that is proportional to eye position. They thus might correspond to the neural integrator element of Fig. 1.
Tags	

Submodule: OPN

Brief Description *	Omnipause neurons - these are neurons that are tonically active during fixation. They pause during saccades. They are thought to trigger saccades by releasing inhibition from the burst neurons when they pause.
Tags	

Submodule: IBN

Brief Description *	Inhibitory burst neurons - these are neurons that burst with saccades, like EBN's. However, they inhibit motor neurons for the antagonist eye muscle, thus implementing push-pull control.
Tags	

Submodule: EBN

Brief Description *	Excitatory burst neurons - these are neurons that exhibit saccade-related bursts. They provide a "velocity" command that is then fed forward to MN's and TN's to drive the eye muscles. As the eye approaches its target, the "motor error" decreases and the burst neurons decrease their activity. This decreases eye velocity. Note that the output of EBN's involves an inhibition from IBN's on the other side. This is the push-pull element of control.
Tags	

Submodule: LLBN

Brief Description *	Long-lead burst neurons - these are brainstem neurons that exhibit a saccade-related burst plus long prelude activity (giving rise to the name "long-lead"). According to the model, they might integrate a local estimate of the burst command from EBN's (the velocity command). This gives rise to the "actual eye displacement" which can be compared with the desired eye displacement during the course of a saccade.
Tags	