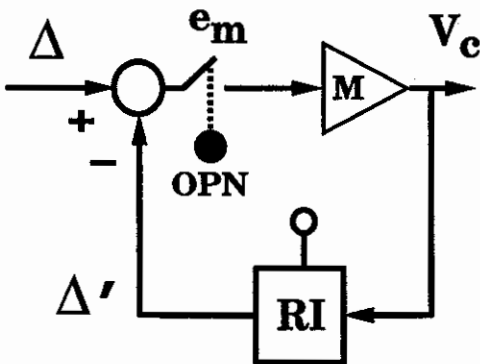


## Control of Saccade Trajectory by the Superior Colliculus

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### Introduction

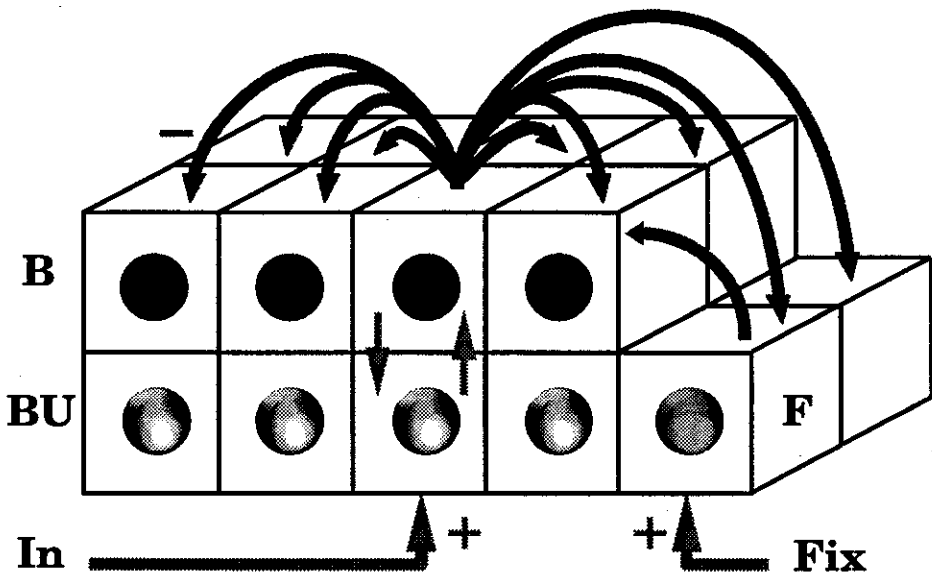
Central to our understanding of the saccadic system is a proposal by David A. Robinson (1975) that saccadic eye movements are controlled by a local feedback (LFB) loop. The basic LFB loop (Fig. 1), modified to work in retinotopic coordinates (Jürgens *et al.* 1981), generates a velocity command, or pulse, according to the difference ( $e_m$ ) between how far the eye needs to turn ( $\Delta$ ), and the amount it has already turned ( $\Delta'$ ). Early models of the saccadic system assumed that the feedback loop was in the brain stem, and that the input,  $\Delta$  came from neurons in the intermediate layer of the superior colliculus (SC). A resettable integrator was assumed to convert the efferent velocity command into  $\Delta'$ , although no site for this integrator has been proposed.



**Figure 1.** Basic model of local feedback loop.  $\Delta$  is desired displacement.  $\Delta'$  is the current displacement. The motor error is  $e_m$ .  $V_c$  is the velocity command. RI is an integrator that is reset to zero at the start of each saccade. OPN is the omnipause neuron that gates saccade activity. M is the medium lead burst neuron.

Since  $\Delta$  is a desired rotation of the eye, and the neurons of the SC are organized into a retinotopic map of visual space, it makes sense to obtain  $\Delta$  from the output of the SC. However, the temporal characteristics of the cells in the SC do not seem to fit well with this role. In the SC it is the locus of activity on the map that determines where the saccade should go (Schiller and Koerner 1971; Robinson 1972; Schiller and Stryker 1972; Wurtz and Goldberg 1972; Sparks *et al.* 1976). Furthermore, the temporal activity of most saccade-related SC cells consists of a burst that is fairly uniform for all saccades (Sparks and Mays 1980). Thus, a spatial-to-temporal transformation is necessary to convert the space/time characteristics of a collicular  $\Delta$  into the frequency-encode activity needed by the brain stem burst neurons (Robinson 1973).

In the last few years there have been several papers that proposed a new role for the SC as the spatial-to-temporal translator. Waitzman *et al.* (1988) hypothesized that the SC was inside the LFB loop, and functioned as its summing junction. The temporal activity at one locus on the SC would thus generate the motor error signal,  $e_m$ . Droulez and Berthoz (1988), Lefèvre and Galiana (1992), van Opstal and Kappen (1993), and Arai *et al.* (1993) (see also Keller, this volume) have all suggested that the SC is inside the loop, acting as the integrator of an eye velocity feedback signal and providing  $e_m$  as its output.

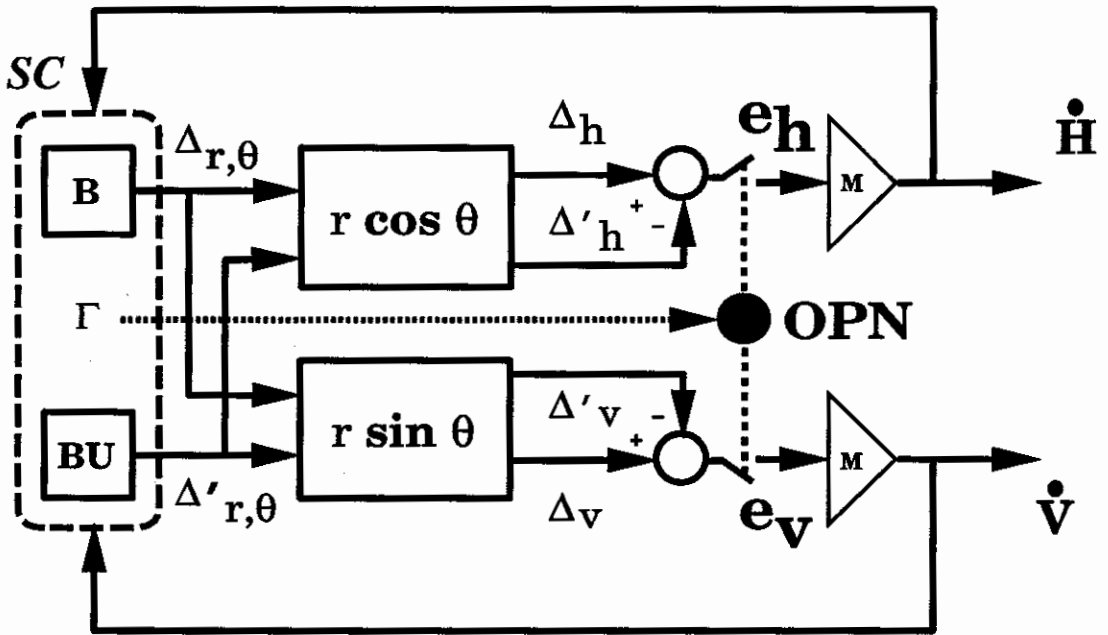


**Figure 2.** Superior colliculus model is organized into three compartments. Vertical modules span burst (B) and buildup (BU) layers. Neurons in the rostral fixation zone (F) receive a command to fixate (Fix), and inhibit other modules. (Light arrows show excitatory, and dark arrows inhibitory, connections.) Buildup neurons (BUNs) receive cortical inputs (In) reflecting target eccentricity. The BUNs act as the resettable integrator of the local feedback loop. Burst neurons (BNs) receive excitatory input from the BUNs, and are strongly inhibited by lateral connections among themselves. Thus, the BNs act as a winner-take-all network that selects the locus of peak activity among the BUNs. This selected locus determines the desired eye rotation,  $\Delta$ . Both BUNs and BNs receive velocity feedback signals from brain stem.

Although these newer models combine the motor map of the SC with the LFB loop of the saccadic pulse generator, they do not account for the results in recent neurophysiological studies of the superior colliculus. This paper presents a new hypothesis of SC function that reconciles these later neurophysiological findings with a two-dimensional extension of Robinson's one-dimensional LFB loop. The ability of the new model to make straight, oblique, saccades will be demonstrated as an example of an emergent property of the new model.

### New Structure

The structure of the new model is motivated by certain experimental results that elucidate the role of the SC in saccades. Recent neurophysiological studies have differentiated three types of neurons in the intermediate layers of the SC (see Wurtz and Munoz, this volume): fixation neurons (FNs), burst neurons (BNs) and buildup neurons (BUNs). Furthermore, evidence is accumulating, in both cat (Munoz *et al.* 1991a; Munoz *et al.* 1991b) and monkey (Wurtz and Munoz, this volume), that activity in the buildup neurons spreads rostrally during a saccade. Correspondingly, the new model divides the SC into three compartments, B, BU, and F (Fig. 2), and explains how the three cell types might function within the local feedback loop during a saccade.



**Figure 3.** Nonlinear polar integrator model of two-dimensional saccades.  $\Delta_{r,\theta}$  and  $\Delta'_{r,\theta}$  are the desired and current displacement in the nonlinear polar coordinates used by the superior colliculus.  $\Delta_h$ ,  $\Delta_v$ , and  $\Delta'_h$ ,  $\Delta'_v$  are the desired and current displacements in cartesian coordinates after transformation by long lead burst neurons. Neurons in the SC encode the amplitude ( $R$ ) and direction ( $\theta$ ) of the desired eye displacement in a nonlinear movement map. However, rather than  $R$  itself, the nonlinear map sends a compressed signal,  $r$ , downstream. For example, large saccades are represented by activity in the caudal SC, whereas small saccades are represented by activity in the rostral SC. A set of static weights, with  $r \cos(\theta)$  and  $r \sin(\theta)$  relationships, link each position in the SC map to the horizontal and vertical long lead burst neurons. Separate motor error signals,  $e_h$  and  $e_v$ , are then computed in the brain stem to drive the medium lead burst neurons ( $M$ ) that generate the velocity commands ( $\dot{H}$  and  $\dot{V}$ ).

The most important structural difference between this model and previous models is that the SC provides three outputs, rather than just one. In previous models the SC was either upstream from the LFB loop and provided the saccade goal,  $\Delta$ , or it was inside the LFB loop, and provided the motor error signal,  $e_m$ . The new model provides three outputs (Fig. 3): the balance,  $\Gamma$ , of the activity of the fixation neurons and the burst neurons, which is used to control the omnipause neurons (OPNs) in the brain stem. The burst neurons are also used to select the desired displacement,  $\Delta$ , from all the input activity. Finally, the new model uses the buildup neurons (which show the spread of activity during a saccade) as the resettable integrator, providing  $\Delta'$ .

Collectively, the BUNs act as a spatial integrator of saccade velocity, as suggested by Droulez and Berthoz (1988; 1991) and Lefèvre and Galiana (1992). However, instead of motor error, the BUNs send a signal to the long lead burst neurons that is related to the current displacement of the eye,  $\Delta'$ , but in nonlinear polar coordinates. The motor errors that drive the horizontal ( $e_h$ ) and vertical ( $e_v$ ) bursters are then calculated as the differences of the appropriate signals in the brain stem (Fig. 3).

The BNs act as a winner-take-all network that selects the saccade goal ( $\Delta$ ). During the saccade, the BNs integrate the same velocity feedback signal as the BUNs. However, this feedback causes the activity of BNs to decay during the saccade, rather than to spread. Thus, the decay in the activity level of the BNs is related to  $e_m$ , as seen by Waitzman and colleagues (1988; 1991), and as modeled by van Opstal and Kappen (1993). In the models of Waitzman et al. and of van Opstal and Kappen, this decay is, in fact,  $e_m$ . However, in the new model this decay determines the signal  $\Gamma$ , the balance between the fixation and burst neurons, which inhibits the OPNs during a saccade. It is important that the BNs decay during the saccade, because the FNs and the BNs reciprocally inhibit each other. If the BNs did not decay during the saccade, the FNs would not be able to resume firing until some time after the saccade was over. This delay would introduce an instability into the saccadic system, because the high gain of the brain stem burst neurons would not be countered by the onset of OPN activity.

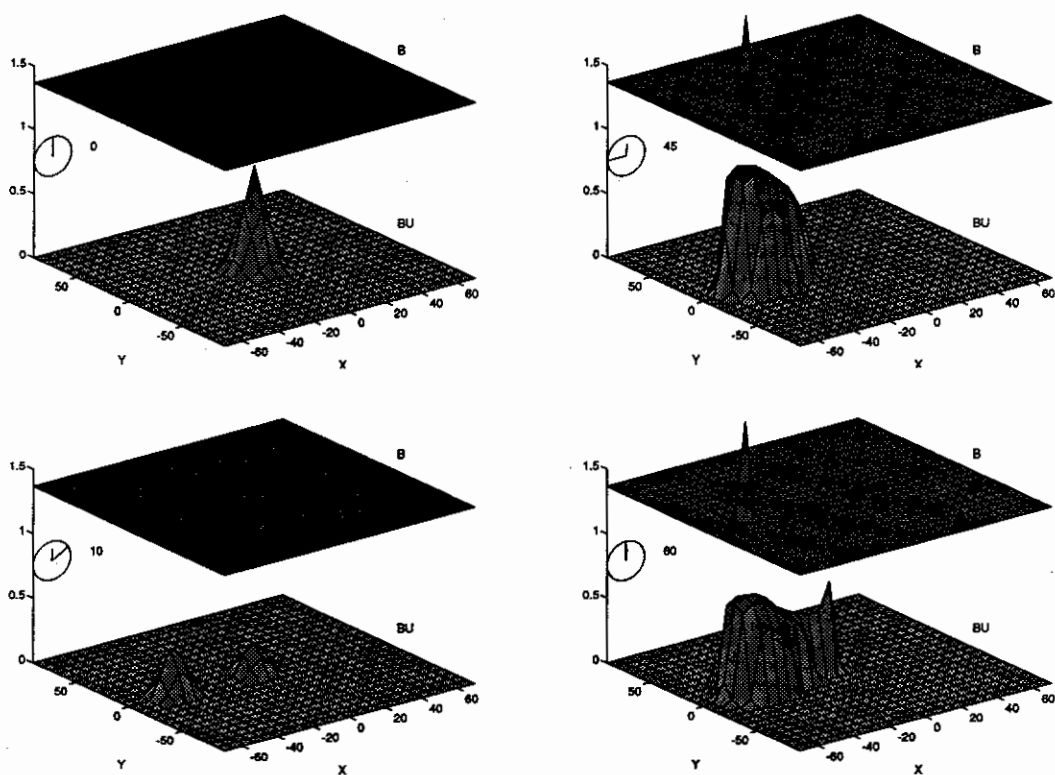
### Simulation

A preliminary version of the new model was simulated using MATLAB/Simulink software (The MathWorks, Inc.). Figure 4 shows the activity in the Burst layer (upper surface, B) and the Buildup layer (lower surface, BU). Each surface is the conjunction of a right and left superior colliculus, so the rostral fixation zone is in the center of the lower grid. In this simulation, the target location information reached the BU layer five msec into the simulation. Simultaneously, the fixation command was withdrawn from the fixation neurons. The sequence of figures shows the decay of activity in the FNs, with a simultaneous growth of activity in the BUNs. A burst starts in the BNs, and is followed almost immediately by the shut off of the OPNs. This starts the saccade, and the velocity feedback to the SC causes the BUNs to burst. The velocity feedback also causes the activity in the BU layer to spread toward the rostral pole of the SC (in the middle of the grid) during the saccade. Even though the cells in the BU layer excite the cells in the B layer (cf. Fig. 2), the activity in the B layer does not spread rostrally along with the spread of activity in the BU layer. The locus of activity in the B layer stays constant because of the strong lateral inhibition among the BNs. Note the start of a burst in the FNs in the last frame (when the saccade is nearly over).

### Oblique Saccades

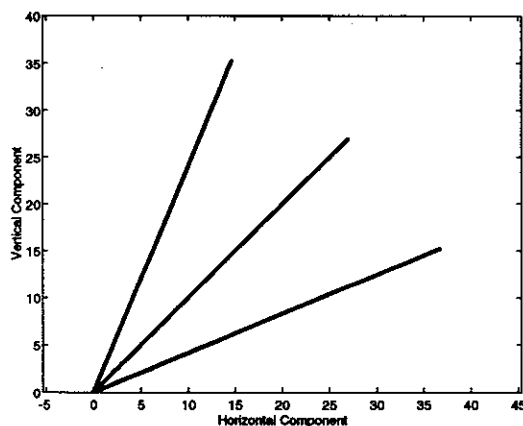
It has been known for some time that extending Robinson's local feedback loop model from one to two dimensions presented some difficulties. If two independent 1-D models are used, the oblique saccades will not be straight. For example, a saccade to a target  $30^\circ$  to the right and  $10^\circ$  up would be strongly curved, because the duration of the  $10^\circ$  vertical component is shorter than that of the  $30^\circ$  horizontal saccade (Guitton and Mandl 1980; Evinger *et al.* 1981).

Van Gisbergen et al. (1985) proposed solving this problem by making a 2-D model with a polar burster. In this model, a common velocity command in polar coordinates was decomposed into horizontal and vertical components. One consequence of there being a single burster in this model is that it can make only perfectly straight saccades whose vertical and horizontal components start and end together. Physiological recordings, however, show that oblique saccades can be curved. Furthermore, the horizontal and vertical components of a saccade do not always start and stop together, suggesting that there must be more than one burster population (King *et al.* 1986). Indeed, the brain stem burst neurons appear to be organized into horizontal and vertical groups.



**Figure 4.** Simulation showing activity in Burst and Buildup layers during a saccade. The upper grid is the Burst layer (B), and the lower grid is the Buildup layer (BU). Each grid represents both Left and Right superior colliculi, so the rostral locus of the Fixation Neurons (FNs) is in the center of the lower grid. The small clock and number on the left give the time (0, 10, 45, and 60 msec) during the simulation. Target location reached the BU layer five msec into the simulation. The fixation command was simultaneously withdrawn from the FNs. The sequence of figures shows the decay of activity in the FNs, the growth of activity in the BUNs, the start of the burst in the BNs, and the spread of the BU layer activity toward the rostral pole of the SC (middle of the grid). In the last frame, activity in the FNs restarts. Note that, even though the activity in the BU layer is spreading rostrally, the activity in the B layer stays fixed in place because of the strong lateral inhibition among BNs.

To account for these findings, Grossman and Robinson (1988) suggested a model that cross-coupled independent horizontal and vertical bursters. By adjusting the gain of the cross-coupling, saccades could be made either straight or curved. However, this model also has a flaw, in that all oblique saccades are slow. Consider a saccade at  $45^\circ$ . This saccade needs no cross-coupling to remain straight. Nonetheless, the cross-coupling would be in effect, making the oblique saccade at  $45^\circ$  slower than a horizontal saccade of the same amplitude.



**Figure 5.** Three oblique saccades made by the nonlinear polar integrator model. Saccades were at angles of  $22.5^\circ$ ,  $45^\circ$ , and  $67.5^\circ$  to the horizontal. Although the horizontal and vertical bursters are independent in his model, coupling through the nonlinear polar integrator in the SC keeps the saccades straight. (Axis units in degrees.)

The new model generates straight saccades with normal velocities because its structure puts the SC, which has a more-or-less polar organization, into the feedback loop. Thus, the new model has two independent horizontal and vertical bursters, which are coupled through a polar integrator with a nonlinear output. Saccade speed is constant with angle of elevation,  $\theta$ , and the trajectories are straight. Three oblique saccades made by the model are shown in Fig. 5. Note that they are almost perfectly straight. The peak radial velocities of these saccades were nearly equal. Thus, this model produces oblique saccades with straight trajectories, and with peak velocities that are independent of their angle.

(Normal saccades are often a little curved, and so the perfectly straight saccades of this model are a bit unrealistic. Noise in the horizontal and vertical bursters, or imperfections in the SC spatial integrator, might be sufficient to make the simulated saccades curve more realistically, but such extensions to the model have not yet been studied.)

## Conclusions

The new model places the superior colliculus inside the local feedback loop of the saccadic system. Different roles are proposed for each of the three cell types seen in the intermediate layers of the SC. The fixation neurons prevent saccades by exciting the omnipause neurons in the brain stem. The buildup neurons integrate the velocity feedback signal to measure the current eye displacement. The burst neurons select the goal of the saccade from the peak activity in the buildup layer.

The buildup cell layer plays the role of a spatial integrator. Thus, the integrator for the local feedback loop is in a polar coordinate reference frame. The projection from the superior colliculus to the long lead burst neurons in the brain stem converts the collicular signal into the cartesian coordinate frame used by the medium lead burst neurons that generate the saccadic velocity command. Thus, the motor error signal can be considered as being in polar coordinates. However, the output of the superior colliculus is a nonlinear function of eccentricity, approximately logarithmic (Ottes *et al.* 1986). Thus, the output ( $r$  in Fig. 3) can be considered a saccadic velocity command in polar coordinates. When this polar command is distributed to the independent cartesian bursters, it results in oblique saccades that are straight. Since the polar command is velocity, and not position, the nonlinearity does not affect saccade accuracy. However,

saccade velocity will grow logarithmically with saccade amplitude. But such a nonlinear growth is just what is seen in the relationship between saccade amplitude and peak velocity (Fuchs 1971; Bahill *et al.* 1975).

In the one-dimensional local feedback loop, the current eye displacement is fed back and compared with the desired eye displacement. That comparison allows the loop to automatically compensate for variations in eye velocity and make accurate saccades. The model proposed here attempts to preserve this compensatory behavior in a two-dimensional model by feeding back an eye velocity vector to the SC. The SC then generates a vector signal related to errors in the trajectory of the saccade. With the SC inside the local feedback loop, the loop minimizes a vectorial error signal, rather than independent horizontal and vertical errors. Thus, the loop compensates automatically for perturbations in saccade trajectory as well as making accurate saccades.

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