A Field Theory of Saccade Generation: Temporal-to-spatial Transform in the Superior Colliculus

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Recent models have placed the superior colliculus inside the local feedback loop that generates the pulse of innervation needed to make a saccade. Such closed-loop models need to take into account the different coordinate systems of visual and motor signals. This paper presents a computational model showing how the superior colliculus can bring the visual and motor information together in a common reference frame.

Saccade Superior colliculus Control systems Coordinate maps

INTRODUCTION

Robinson (1975) proposed that rapid eye movements, or saccades, were generated by a local feedback loop in the brain stem. The local feedback loop model compares a motor signal with a visual signal, to determine how far the eye has moved relative to how far the eye has to go. However, these signals have quite different representations in the brain. The visual signal is represented by the locus of activity on a logarithmically warped, retinotopic map in the superior colliculus (SC) (Cynader & Berman, 1972; Robinson, 1972). The motor signal is represented by the temporal activity of neurons in the brain stem, which are organized into horizontal and vertical populations (Henn, Hepp & Bütter-Enacver, 1982; Keller, 1974; King & Fuchs, 1979; Luschei & Fuchs, 1972). How can the brain compare visual and motor information when they have such different representations? Is the visual information transformed into a temporal signal, and then compared with the motor signal? Or, is the motor signal projected onto a spatial map, so that it can be compared with the spatial map of the visual signal? In the former case, the comparison mechanism can be on individual neurons that receive both visual excitation and motor inhibition. In the latter case, some mechanism would be needed for comparing two spatially distributed signals. This paper proposes a hybrid mechanism for performing this comparison: the motor signal is converted to a spatial map in the SC, and both the visual and motor spatial maps are converted to temporal signals and compared in the brain stem.

In Robinson's original model, the visual and motor signals were both encoded temporally, and there was no role for the SC. Subsequently, evidence for a second neural integrator led Jürgens, Becker and Kornhuber (1981) to modify the local feedback loop model by adding a displacement integrator (DI in Fig. 1). The model with a displacement integrator worked in retinotopic coordinates. Since that model's input, \( \Delta \), was a desired rotation of the eye in retinotopic coordinates, and the neurons of the SC were organized into a retinotopic map of visual space, it made sense to obtain \( \Delta \) as a temporally encoded signal from the output of the SC. However, the temporal characteristics of the cells in the SC do not fit well with this role. In the SC it is the locus of activity on the map that determines where the saccade will go (Robinson, 1972; Schiller & Koerner, 1971; Schiller & Stryker, 1972; Sparks, Holland & Guitton, 1976; Wurtz & Goldberg, 1972). Furthermore, the temporal activity of most saccade-related SC cells consists of a burst that is fairly uniform for all saccades (Sparks & Mays, 1980), and the spatial distribution of that activity covers a large population of SC neurons (Sparks et al., 1976). It is usually assumed that the collicular output signal is based on some average population code, such as the center-of-activity (the neural analog of the physical center-of-gravity), of the activity on the SC (Lee, Rohrer & Sparks, 1988). Thus, early models used a simple spatial-to-temporal transform to convert a locus of activity on the SC into a temporal signal in the brain stem (Robinson, 1973). The local
feedback loop closed in the brain stem, and worked entirely in motor coordinates. However, some experimental evidence suggests that the temporal course of activity in SC neurons is tightly coupled with saccadic movements (Waitzman, Ma, Optican & Wurtz, 1988, 1991). Indeed, many recent models of the saccadic system have placed the SC inside the local feedback loop (Arani, Keller & Edelman, 1994; Droulez & Berthoz, 1988, 1991a; Lefèvre & Galliara, 1992; Waitzman et al., 1991; van Opstal & Kappen, 1993).

Recent studies in the monkey also suggest that there are two types of neurons related to saccadic activity in the intermediate layers of the SC. One type is the classical saccade-related burst neuron, which bursts during saccades. The locus of activity on the SC map of the burst neurons carries the information about the desired ocular displacement (Munoz & Wurtz, 1995a; Robinson, 1972; Schiller & Kornbluth, 1971; Schiller & Stryker, 1972; Sparks et al., 1976; Wurtz & Goldberg, 1972). Another type is the buildup neuron, which begins firing before, and usually bursts during, saccades. Studies in the cat suggested that a "hill" of activity in the intermediate layer neurons (which are similar to primate buildup neurons) moved rostrally during a saccade (Munoz, Guittin & Pelisson, 1992a; Munoz, Pelisson & Guittin, 1991b). The interpretation of a moving hill in the cat was somewhat controversial (Sparks, 1993), and led to a similar study in the monkey. The results in monkeys showed that, rather than a moving hill of activity, a wave of activity spread rostrally across the buildup neurons during a saccade (Munoz & Wurtz, 1995a, 1995b). Although the spreading wave hypothesis is somewhat controversial (Gandhi, Keller & Hartz, 1994), recent models have attempted to find theoretical roles for such a spreading wave. Recently, Optican (1994) proposed a model of the saccadic system in which the buildup neurons act as a spatial integrator within the local feedback loop controlling saccades. The idea behind the spatial integrator is that the displacement integrator of Fig. 1 is represented by the distribution of activity across a neuronal map, rather than the average rate of firing of a population of neurons. Several models have been proposed that use the distribution of activity in the SC to effect a spatial integration, but these models have folded together the operation of displacement integration and visual-motor comparison so that the output of the SC was the dynamic motor error (v in Fig. 1) needed by the brain stem burst generators (Arani et al., 1993; Droulez & Berthoz, 1988, 1991b; Lefèvre & Galliara, 1992; van Opstal & Kappen, 1993). The new model by Optican performs the spatial integration in the SC, and the dynamic motor error is computed in the brain stem.

Models that combine the displacement integrator and the visual-motor comparator in the SC do not explain why there should be two types of neurons (burst and buildup) in the intermediate layer of the SC. To explain these two cell types, Optican (1994) proposed that the SC provided not one, but two output signals. One output was related to the desired ocular displacement (v, provided by the saccade-related burst neurons), and the other was related to the current ocular displacement (\( \Delta \), provided by the buildup neurons acting as a spatial integrator). In that model the required computation of the local feedback loop was achieved by first mapping both visual and motor signals onto the SC. Then both loci were converted into temporal signals, in motor coordinates, for comparison in the brain stem. In such a spatial integrator model, motor velocity feedback must generate a dynamically changing distribution of activity on an SC map, thus effecting a temporal-to-spatial transform. This paper presents a computational model that shows how activity in the SC can be spread across the buildup cells by the velocity feedback signal, so that the buildup neurons act as a spatial integrator, even when the visual and motor signals have different coordinate systems. This spread of activity is controlled by a vector field in the SC, which forms the basis of a field theory of the computational role of the SC in saccade generation.

RESULTS

Coordinate transformations

Two-dimensional saccades result from the generation of horizontal and vertical pulses. This is achieved in the model with two cartesian pulse generators (represented by the two-dimensional amplifiers, G, in Fig. 1). However, the visual and motor maps on the SC are not laid out in a cartesian grid (Robinson, 1972). To make this point more concretely, Fig. 2 shows an idealized mapping from visual space onto the SC. The graph of visual space uses polar coordinates, \((R, \theta)\), in degrees, and that of the SC uses cartesian coordinates, \((X, Y)\), in mm. In the anisometric version used here, the equations...
mappings retinotopic coordinates onto collicular coordinates are:

$$X = B_l \log \left( \frac{\sqrt{R^2 + 2AR \cos(\Theta) + A^2}}{A} \right)$$  \hspace{1cm} (1)

$$Y = B_r \arctan \left( \frac{R \sin(\Theta)}{R \cos(\Theta) + A} \right)$$  \hspace{1cm} (2)

The parameters \( A = 3.0 \text{ deg,} \quad B_l = 1.4 \text{ mm,} \quad B_r = 1.8 \text{ mm} \) were chosen by Ottes, Van Gisbergen and Eggemont (1986) to give the best fit to Robinson's (1972) stimulation map of the SC cortex. These equations can be inverted to convert from millimeters on the collicular surface to degrees in retinotopic space (Ottes et al., 1986):

$$R = A \sqrt{e^{x^2} - 2e^x \cos(y) + 1}$$  \hspace{1cm} (3)

$$\Theta = \arctan \left( \frac{e^x \sin(y)}{e^x \cos(y) - 1} \right)$$  \hspace{1cm} (4)

where \( x = X/B_l \) and \( y = Y/B_r \); \((x, y)\)-coordinates can be considered an isometric remapping of the anisometric \((X, Y)\)-coordinates.

It is also possible to show the mapping from the motor coordinates of the brain stem burst burst neurons \((H, V)\) onto the SC. Recall the transformation from cartesian to polar coordinates:

$$R = \sqrt{H^2 + V^2}$$  \hspace{1cm} (5)

$$\Theta = \arctan(V/H).$$  \hspace{1cm} (6)

Equations (1)-(4) and the transformation in equations (5) and (6) let us solve for the \((X, Y)\) coordinate frame of the SC in terms of \((H, V)\):

$$X = \frac{B_l}{2} \log \left[ \frac{(H + A)^2 + V^2}{A^2} \right]$$  \hspace{1cm} (7)

$$Y = B_r \arctan \left( \frac{V}{H + A} \right).$$  \hspace{1cm} (8)

The corresponding inverse transform from collicular to visual space is given by:

$$H = A e\cos(y) - A$$  \hspace{1cm} (9)

$$V = A e\sin(y)$$  \hspace{1cm} (10)

where \( x = X/B_l \) and \( y = Y/B_r \). The mapping onto the SC from polar coordinates (Fig. 2) is more natural for visual information, whereas the mapping from cartesian coordinates (Fig. 3) is more natural for motor information.
Spatial integration

To create a spatial integrator in the buildup layer of the SC, a conversion from feedback velocity, $\hat{H}, \hat{V}$, to velocity of spread on the SC, $(\hat{X}, \hat{Y})$, is needed. In the original model (Jürgens et al., 1981), the displacement integrator started at zero and integrated the velocity feedback up to the desired displacement, $\Delta = (H, V)$. In Optican’s (1994) model, the displacement integrator started at $\Delta$, and integrated down to zero. This choice of initial conditions was necessary because the displacement integrator was represented by a spatial integrator, whose initial locus of activity was at a site corresponding to the desired ocular displacement.

If the buildup neurons are to act as the spatial version of the displacement integrator, the activity across the population of buildup neurons must spread under the influence of the velocity feedback, $(H, V)$. Let the current ocular displacement be $\Delta = (H(t), V(t))$. Then the distribution of activity in the SC must follow the trajectory:

$$X(t) = f(H(t) - H(t))$$

$$Y(t) = g(V(t) - V(t))$$

where $f$ and $g$ are the functions that convert from motor cartesian coordinates to collicular curvilinear coordinates.

The time derivatives of $X$ and $Y$ are:

$$\dot{X} = \frac{\partial X}{\partial H} \dot{H} + \frac{\partial X}{\partial V} \dot{V}$$

$$\dot{Y} = \frac{\partial Y}{\partial H} \dot{H} + \frac{\partial Y}{\partial V} \dot{V}$$

Using the transformations in equations (7) and (8) in equations (13) and (14) gives:

$$\dot{X} = -\frac{B}{A} e^{-x} \cos(y) \dot{H} + \sin(y) \dot{V}$$

$$\dot{Y} = -\frac{B}{A} e^{-y} \sin(y) \dot{H} - \cos(y) \dot{V}$$

where $x = X/B$, and $y = Y/B$.

$\hat{X}$ and $\hat{Y}$ define a vector at every point on the colliculus. This vector field specifies how the activity in the buildup neurons at every point on the SC must spread if it is to reflect the motion of the eye. In Fig. 4, sample vectors are drawn for rightward movements with different elevations (from down 90 deg to up 90 deg). Each arrow along a given meridian (dashed lines) shows how the activity on the SC must spread during the
saccade, so that the new point reflects the reduction in motor error during the saccade. As a saccade progresses, the dynamic motor error declines, and the activity in the buildup neurons spreads rostrally. As the activity reaches the rostral SC, the vectors rotate so that they are always tangent to the meridian at their base. The length of the arrow (corresponding to a fraction of eye velocity) also increases as the activity spreads rostrally, because of the logarithmic warping of the SC map. Thus, equations (15) and (16) provide a computational scheme for spreading the activity in the intermediate layers of the SC during a saccade so as to form the displacement integrator.

Simulation
A simple model of the saccadic system (Fig. 1) was made that incorporated the visual and motor maps represented in Figs 2 and 3. Rather than simulate the activity of individual neurons, this simple model simulated movement of the center-of-activity of the buildup neuron activity during the saccade. What is important to consider here is how the coordinate transformations are achieved in the temporal-to-spatial transform, and this only requires that the simulation show how the center-of-activity moves. Simulations of a more physiologically detailed model of the superior colliculus will be presented in a later paper.

First-order differential equations in cartesian coordinates were used for the eye movement, and equations (15) and (16) were used for the spread of activity across the buildup neurons. Euler integration was used to solve the differential equations using a MATLAB program (The Mathworks, Mass.). The integration step size was 0.5 msec (one-tenth the smallest time constant in the SC model). The trajectories of the eye movement and the spread of the center-of-activity across the buildup neuron population during an oblique saccade are shown in Fig. 5. The trajectory for the oblique eye movement is straight, whereas the corresponding trajectory for the spread of activity in the SC is curved, because of the nonlinear coordinate transformations.

DISCUSSION
A theoretical understanding of the saccadic system requires full, two-dimensional models that work in physiologically realistic reference frames. Even a simple model that deals with the problem of coordinate transformations (e.g., Fig. 1) points up a novel approach to performing the spatial-to-temporal transformation needed to saccade to a visual target. In this case, the
novel mechanism is the spatial integration of velocity feedback, which, as others have pointed out (Droulez & Berthoz, 1988; Lefèvre & Galiana, 1992), is a simple way to convert from the temporal firing of brain stem neurons to a spatially distributed map in the SC. van Opstal and Kappen (1993) pointed out that if the SC is inside the local feedback loop, a temporal-to-spatial transform may be needed to convert from the coordinate system of the motor signals to the coordinate system of the SC. In their model, they used a static weight field to compute the temporal-to-spatial transform (van Opstal & Kappen, 1993). In the field theory model, equations (15) and (16) dynamically compute the temporal-to-spatial transform the saccadic system needs to include the SC inside the local feedback loop. Other two-dimensional models have not dealt explicitly with the problem of coordinate transformations (Arab, Keller & Edelman, 1994; Droulez & Berthoz, 1988, 1991b; Lefèvre & Galiana, 1994; van Opstal & Kappen, 1993), although its importance was pointed out in one of the first closed-loop models of the SC (Potts & McCulloch, 1947). In this paper it has been shown that the usefulness of spatial integration is maintained when the nonlinear coordinate transformations are taken into account, and that the temporal-to-spatial transform can be computed dynamically.

Classically, the SC has been regarded as possessing a single map, the one from visual coordinates shown in Fig. 2. It was assumed that the motor signals in the intermediate layers of the colliculus used the same visual-based mapping. However, the results in this paper suggest that for the SC to cause activity to spread across the buildup neurons under the control of eye velocity feedback requires an additional collicular map, shown in Fig. 3. The two maps discussed here should not be confused with the separate populations of burst and buildup neurons. The mappings referred to are the sensory-to-SC and motor-to-SC coordinate transformations. One map brings sensory information, and the other map brings motor information, into a common, collicular, reference frame. The need for the second map arises because the new model places the SC inside the saccadic local feedback loop, and thus the colliculus must keep track of both sensory and motor information.

Other modalities of sensory information, such as auditory signals, are also transformed as they project onto the SC (Jay & Sparks, 1984), which require more sensory-to-colliculus mappings. Since the SC is also involved in the control of head movements, mappings for head or gaze movements are also required. Thus, the classical concept of one collicular map (visual) must be
extended to allow for multiple maps (motor, auditory, etc.).

These ideas give rise to the general hypothesis that the role of the SC is to act as an intrinsic reference frame for saccadic eye movements. Why would such a specialized structure be necessary? The vestibuloocular reflex, for example, has no such spatial map. However, the sensory information coming from the semicircular canals is already encoded temporally in the firing rates of the vestibular neurons. As the oculomotor neurons also encode eye movements temporally, all that is needed to transform from sensory to motor coordinates is a rotation from the canal axes to the muscle axes. In contrast, the sensory information needed to make a saccade has many different representations. Auditory signals are in craniootic coordinates, whereas visual signals are in retinotopic coordinates. Also, these sensory signals are represented not by temporal activity, but rather by the distribution of activity across cortical maps. Thus, there might be a significant advantage to the saccadic system if all its inputs were transformed into an intrinsic reference frame. The obvious choice would be to have all the spatially mapped signals transformed into temporally encoded signals. However, in cases where the spatial sensory mappings are highly nonlinear, this would give rise to very noisy signals. For example, converting from the logarithmic mapping of the visual system to the superior colliculus would require an exponentiation of the locus of activity. A more robust system would result if the temporally encoded motor signals were logarithmically mapped onto the SC. This general hypothesis might be tested by comparing the effects of lesions in the SC and the model on trajectories of saccades, and on saccades to auditory targets. One result of the SC being inside the feedback loop that suggests itself is that saccades after a lesion should be curved, which is consistent with several physiological studies (Aizawa & Wurtz, 1994; Hikosaka & Wurtz, 1985, 1986).

Many other control systems in the brain also need to compare sensory and motor signals from different coordinate systems (cf. Zambarberi, Beltrami & Verasdo, 1995). Perhaps the role described here for the SC, of converting both sensory and motor signals into a common reference frame, is the function of many brain maps that use sensory signals to control motor responses.

REFERENCES


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