

The ascendancy of the cerebral cortex in mammals naturally raises questions about the role of the archetypal subcortical centres we share in common with other classes of vertebrates. For the optokinetic as well as the gaze and limb orienting systems, the ancient subcortical visuomotor control centres, the NOT/DTN and the superior colliculus, are not so much dominated by the cerebral cortex as served by it. We suggest that understanding the organization of cortical output to subcortical centres may be helpful in understanding the evolution and behavioural functions of different areas in the cerebral cortex.

## **Testing the predictions of different models of the saccadic system**

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A long standing problem in oculomotor research is the spatial-to-temporal transform: how the anatomical (spatial) code of saccade metrics (direction and amplitude) found in the superior colliculus is transformed into the temporal signals required by motor neurons for generating saccadic eye movements. The influential study by Robinson (1972) showed that electrical stimulation at a particular site in the superior colliculus always generates a saccade with a particular metric (spatial encoding). This led to construction of a topographic map depicting direction and amplitude of elicited saccades as a function of stimulation site in the superior colliculus. Neurophysiological studies in the following years have shown that the collicular neurons always encode a certain change in eye position rather than the final position of the eyes in the orbit. An impending saccade is signalled by the activity not of a single neuron but rather of an ensemble of neurons. It is predominantly the location of this population within

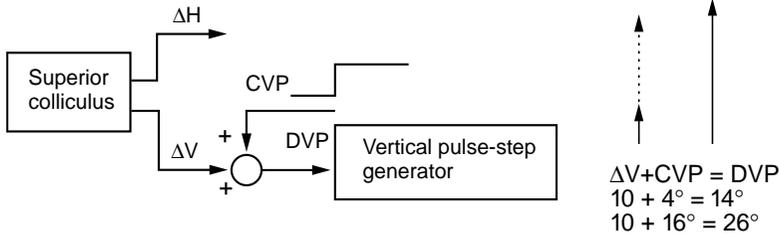
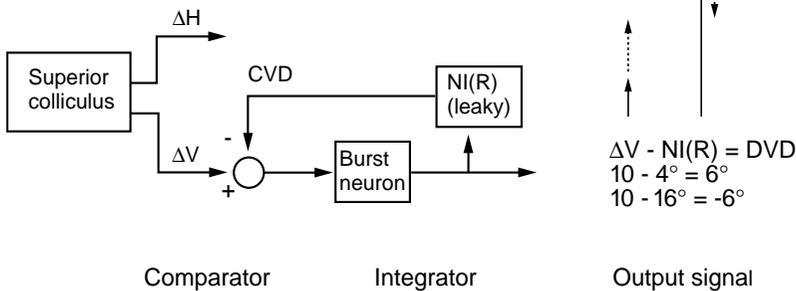
the topographical map that encodes the information about the saccade (Schiller and Koerner, 1971; Sparks, 1978, 1986; Sparks and Jay, 1986; Sparks and Mays, 1980).

This spatial coding seems to be inappropriate for generating the pulse–step signals required for saccadic rotations of the eyes. First, a pulse of activity in the eye-muscle motor neurons produces the phasic increase in muscle tension needed for overcoming the viscosity of the oculomotor apparatus (eyeball and eye muscles) and to move the eye at high velocity. Then a step of tonic activity causes the sustained change in muscle tension required to hold the eye in the new orbital position and to overcome the elastic properties of the orbital tissue. It is agreed that the signal for generating saccades coming from the superior colliculus is fed into two pulse–step generators in the pons and the rostral midbrain, one dedicated to generating horizontal, the other to vertical saccades.

Disagreement exists, however, as to how the pulse-step sequence is generated. Although numerous models have been developed to account for the spatial-to-temporal transform, there has been a paucity of critical experiments testing their differential predictions. Here I describe three experiments (the dissertation work of M.J. Nichols) designed to test the differential predictions of various classes of models of the saccadic system. The first tested *position* versus *displacement* models, i.e., whether the input into the pulse–step generator is desired position or desired displacement. The second compared the predictions of *common-source* models with those from *cross-coupling* models for the coordination of horizontal and vertical components of oblique saccades. The third set of experiments examined whether the probable feedback comparators are of *independent* or *vectorial* type.

### ***Position versus displacement models***

Position and displacement models and their outputs predicted to produce a change in vertical position of the eye are compared in

**Position model****Displacement model**

**Figure 42.** Comparison of position and displacement type models for the input to the pulse-step generator, the output of which drives the oculomotor neurons. Signals from the superior colliculus specify the change in both horizontal ( $\Delta H$ ) and vertical ( $\Delta V$ ) position of an ensuing saccade. The two signals are converted in separate circuits, each involving a comparator and an integrator, which generate the pulse and step signals required by the extraocular muscles responsible for the horizontal and vertical rotations of the eyes. Only the circuit for the vertical component is shown here. CVP, current vertical position of eye in orbit; DVP, desired vertical position. For further explanation, see text.

Figure 42. Position models (Robinson, 1975; van Gisbergen *et al.*, 1981) assume that the collicular signal of the desired change in eye position ( $\Delta H$ ,  $\Delta V$ ) is combined with a signal of the current position of the eye in the orbit to generate a signal of the desired position of the eye. In contrast, displacement models (Jürgens *et al.*,

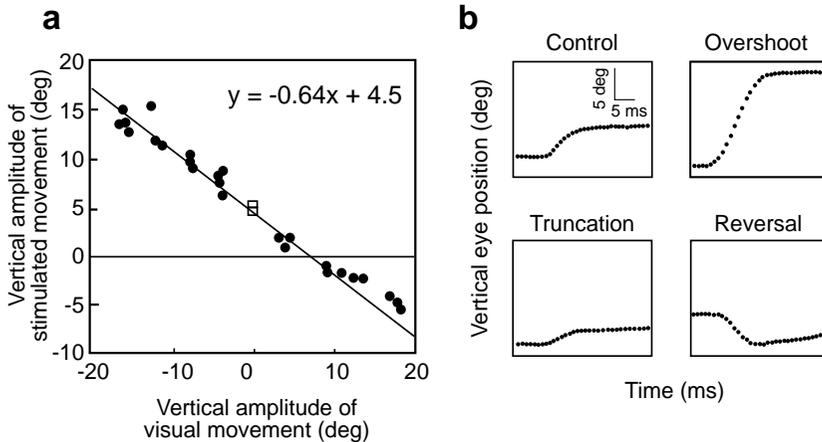
1981) assume that a desired displacement rather than a desired position signal is used as the reference signal for the comparator that controls the duration of the pulse. The desired displacement reference signal is compared, movement by movement, to a signal of the displacement that has already occurred during the saccade. The signal of actual displacement is produced by a neural integrator circuit that is reset at the end of each saccade. The integrator may be reset actively or, as illustrated in Figure 42, passively because it is leaky. As the time required for the integrator to reset is assumed to be less than the 200-300 ms interval between saccades, the presence of this integrator may go unnoticed.

If this resettable integrator really exists and decays gradually during intersaccadic intervals, then the two classes of models make dramatically different predictions about the consequences of stimulating the superior colliculus immediately after a visually guided saccade. The response of the pulse-step generator will differ depending on when the saccadic command arrives during the integrator's decay period. Any residual value of the integrator will automatically be subtracted from the next displacement command at the comparator. In contrast, the position models predict no relationship between onset of stimulation and saccade amplitude.

Assume that stimulation of a site in the superior colliculus under control conditions produces a saccade with a  $10^\circ$  upward component. What happens if the site is stimulated immediately after a  $4^\circ$  upward visually guided movement? According to position models, the desired displacement signal of  $10^\circ$  upward would be combined with a signal of the current vertical eye position ( $4^\circ$  upward) to produce a signal of  $14^\circ$  upward, the desired vertical orbital position. The displacement model predicts that, if stimulation occurs exactly when the visually guided movement ends, the current value of the resettable integrator ( $4^\circ$ ) will be subtracted from the stimulation-induced desired displacement of  $10^\circ$ , resulting in a stimulation-induced movement of  $6^\circ$ . Similarly, if stimulation

occurs after a  $16^\circ$  upward visually guided movement, position models predict that a  $10^\circ$  upward saccade will move the eyes  $26^\circ$  upward, whereas with displacement models a  $6^\circ$  degree downward saccade is expected. Thus, if the displacement model is correct, truncation, overshoot or even reversal, depending on the preceding saccade, should be seen. The position model, on the other hand, predicts that the amplitude will be independent of the size of the preceding saccade.

The predictions of the displacement model have all been reproduced experimentally (*Fig. 43*; Nichols and Sparks, 1995). Stimulation at exactly the same site in the superior colliculus using constant stimulus parameters led to saccades of different sizes and even direction, dependent on the size and direction of



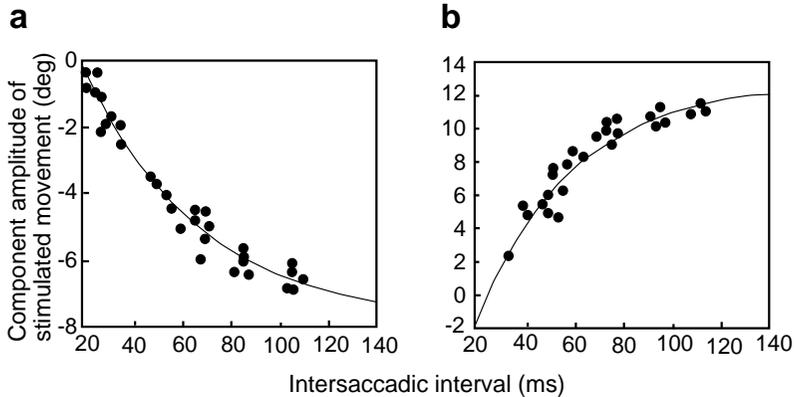
**Figure 43.** Experimental testing of models for the input to the vertical pulse-step generator. **a**, the amplitude of saccades elicited by stimulation at a single collicular site are plotted as a function of the amplitude of the preceding visually guided saccade. The strict linear relationship fits with the predictions of the displacement model. Open squares indicate the amplitude of the control saccade. **b**, four examples of stimulated saccades showing overshoot, truncation and reversal, as predicted by the displacement model. Reproduced with permission from Nichols and Sparks, 1995.

the preceding visually guided saccade. The activity of superior colliculus neurons thus should be considered to be a request signal for an impending saccade rather than a command signal that is inexorably obeyed. The movement that is actually executed depends upon the state of other neural elements in the saccade-generating circuit, not just the locus and level of collicular activity.

The slope of the plot in Figure 43a depends on the amount of integrator discharge that has occurred before the onset of the stimulation-induced movement. As the leaky integrator has an inherent time constant, the displacement model predicts a maximum effect of, for instance, truncation directly at the end of the saccade and an exponentially decreasing effect depending on the time constant of the integrator. This was verified experimentally by maintaining the size of the preceding saccade constant but varying the time of onset of the train of microstimulation pulses. The non-stationary effect, i.e. the resettable neural integrator, was found to decay gradually over about 150 ms (*Fig. 44*). An exponential function with a time constant of about 45 ms provides the best fit and accounts for 97% of the data variance (*Fig. 44a*). This time constant also explains why, with a normal temporal separation of 200-300 ms between saccades, a first saccade does not alter the performance of the following one.

### ***Common-source versus cross-coupling models***

Saccade-generator models also differ in how they account for the coordination of the horizontal and vertical components of oblique saccades. For purely horizontal or purely vertical saccades, the duration increases linearly with saccade amplitude. For oblique saccades, so-called component stretching occurs: the peak velocity of each component is reduced from the value it would have for a purely horizontal or vertical saccade of the same amplitude and the durations of the components are prolonged. Two competing classes of models account for this phenomenon: common-source models, in which the ratio of synaptic weights at each point in the collicular



**Figure 44.** Time constant of the leaky integrator in the displacement model. The amplitudes of the elicited saccades are plotted as a function of the interval between the visually evoked and electrically stimulated saccades for two data sets (**a**, **b**). The exponential function fitting the data points represents the decay of the leaky neural integrator, with a time constant of about 45 ms. In naturally occurring saccades the integrator should decay to zero within the average intersaccadic interval of 200-300 ms. Reproduced with permission from Nichols and Sparks, 1995.

map between the horizontal and vertical pulse-step generator circuits is held to dictate component velocity; and cross-coupling models, which assume that component stretching occurs because of inhibitory interactions between the horizontal and vertical pulse-step controllers.

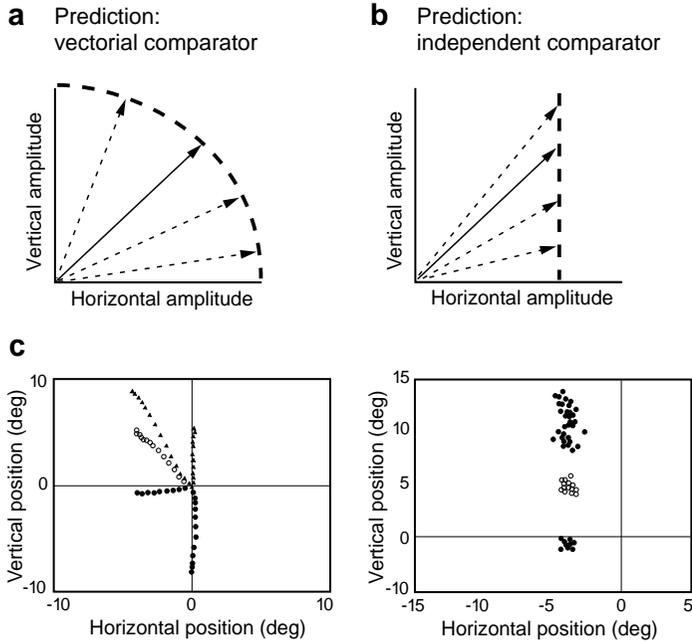
We tested the predictions of these two types of models using the experimental approach outlined above. Sites in the superior colliculus were stimulated electrically immediately after either vertical or horizontal visually guided saccades. Under these conditions, the amplitude of the component that corresponds to the direction of the preceding visually-guided movement varies systematically, while the other 'constant-amplitude' component remains essentially constant. As with visually guided saccades, the peak velocity of the constant-amplitude component in stimulation-evoked saccades decreased as the amplitude of the

orthogonal component increased (Nichols and Sparks, 1996). The component stretching effect in stimulation-evoked saccades was qualitatively indistinguishable from component stretching in matched, visually guided movements even though the locus of stimulation-induced activity in the superior colliculus was fixed from one stimulation-evoked saccade to the next. Because the component stretching in stimulation-evoked oblique saccades does not depend on the locus of activity in the collicular motor map, these results are inconsistent with the predictions of common-source models. They are, however, consistent with the predictions of cross-coupling models.

### ***Vectorial-comparator versus independent-comparator models***

In a third set of experiments (Nichols & Sparks, in press), we tested the differential predictions of two classes of models with different types of comparator: vectorial and independent. Vectorial comparator models assume that a single comparator controls the amplitudes of both horizontal and vertical components of the movement for a desired oblique displacement. The comparator receives feedback from both horizontal and vertical displacement integrators but does not maintain separate representations of horizontal and vertical dynamic motor error, i.e., the discrepancy between the desired and the accomplished displacements. If, for example, feedback from the vertical channel were increased or decreased, the horizontal component of a movement should be modified accordingly, because the movement would terminate when the sum of feedbacks from the horizontal and vertical channels matched the desired displacement vector. Collicular stimulation following various perturbations of the vertical feedback should thus influence both components of the ensuing stimulation-evoked saccade and result in saccades all with the same vectorial amplitude (*Fig. 45a*).

In contrast, independent-comparator models assume that separate signals for the desired horizontal and vertical displace-



**Figure 45.** Comparison of models with vectorial or independent comparators in the generation of oblique saccades. **a**, **b**, predictions of the two models. The oblique saccade resulting from collicular stimulation (control) is shown as a solid line; the dotted lines represent the results of perturbations predicted by the two models. **c**, experimental data are consistent with separate and independent horizontal and vertical comparators. Upward-directed (filled circles) or downward-directed visually guided saccades (filled triangles) were followed by saccades evoked by collicular stimulation at a single site. The vertical amplitude is affected by the preceding saccade, whereas the horizontal amplitude is not. Open circles: control saccades.

ments are used as references for independent and separate horizontal and vertical feedback comparators. As the two components do not influence each other, this model predicts the independent manipulation of the horizontal and vertical amplitudes of oblique stimulation-evoked saccades (Fig. 45b).

For every stimulation site tested, the amplitude of the horizontal or the vertical component (depending on the direction of the

preceding saccade) of stimulation-evoked saccades varied systematically but the amplitude of the orthogonal component was roughly constant (*Fig. 45c*). Thus, the horizontal and vertical amplitudes of oblique stimulation-evoked saccades can be manipulated independently, an effect that can be readily accounted for by independent comparator models but not by vectorial-comparator models.

### ***Towards simplicity***

The numerous modifications and extensions of Robinson's original feedback model of saccadic control (Robinson, 1975) make many different assumptions about what types of signals are required as inputs to a pulse-step generator circuit and the types of feedback comparators used, among other things. Because they have rarely faced certain empirical tests, they all remain viable and so it is no longer certain exactly which transformations of collicular signals are needed for generation of the motor signal. Progress in understanding how collicular signals are transformed into those required by the motor neurons involved in the control of saccadic eye movements will be greatly facilitated by more experiments that, like those reported here, reduce the number of competing models.