

Simulations of Saccade Curvature by Models That Place Superior Colliculus Upstream From the Local Feedback Loop

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Walton, Mark M. G., David L. Sparks, and Neeraj J. Gandhi. Simulations of saccade curvature by models that place superior colliculus upstream from the local feedback loop. *J Neurophysiol* 93: 2354–2358, 2005. First published December 22, 2004; doi:10.1152/jn.01199.2004. When humans or monkeys are asked to make saccades to visual targets accompanied by one or more distractors, the two dimensional trajectory of the saccade will sometimes display significant curvature. Port and Wurtz used dual electrode recordings to show that this phenomenon is associated with activity at more than one site in superior colliculus (SC). The timing and initial direction of the curvature could be predicted by computing a weighted vector average of the normalized activity of the two neurons. As these authors noted, however, this approach does not result in correct predictions of the final direction of curved saccades. We show that the final direction of these movements can be predicted by taking into account the brain stem saccade generator and the local feedback loop. If the output of SC is computed as a weighted vector average of the saccades requested by the activated sites, and this collicular output is interpreted by downstream structures as desired displacement, existing models that place SC upstream from the local feedback loop can generate realistic saccade trajectories, including the final direction. We propose that saccade curvature is the result of a change in the relative level of activity at the two sites, which the brain stem saccade generator interprets as a change in desired displacement.

INTRODUCTION

When saccadic eye movements are studied in the laboratory, it is generally done by presenting a single target at a time. This approach has been extremely valuable because it allows the isolation of neural activity related to a single eye movement without complications related to competing stimuli. Outside the laboratory, however, many potential visual targets are often present at any one time. For this reason, the last few years have seen an increase in interest in studying the processes underlying the selection of saccade targets (for a recent review, see Schall 2002). The general experimental approach has been to monitor neural activity in oculomotor structures and the eye movements generated by monkeys performing behavioral tasks that utilize multiple targets (McPeck et al. 2003; Port and Wurtz 2003). In such studies, the two-dimensional trajectories of saccades sometimes display significant curvature as defined by Smit and Van Gisbergen (1990), and enhanced neural activity is observed at more than one site in the superior colliculus (McPeck et al. 2003; Port and Wurtz 2003).

In a recent study, Port and Wurtz (2003) presented monkeys with two targets with a small stimulus onset asynchrony while

recording from single neurons at the two activated collicular sites. To predict the instantaneous direction of the saccade, they used the weighted vector average equation

$$V_{\text{model}}^t = \frac{\frac{(f_a^t - b_a)V_a}{P_a}k_a + \frac{(f_b^t - b_b)V_b}{P_b}k_b}{2} \quad (1)$$

where V_{model}^t is the predicted direction of the saccade at time t , f_a^t and f_b^t are the firing rates for neurons a and b, respectively, b_a and b_b are the baseline firing rates, V_a and V_b are the preferred vectors for the two neurons, P_a and P_b are the peak saccade-related discharge associated with straight (control) saccades, and k_a and k_b are constants. The model did a good job of predicting the initial direction of the saccade as well as the timing of the curvature. However, these authors reported that the model did not correctly predict the final direction of their curved saccades. When activity at one site returns to baseline partway through the saccade, the equation predicts that the final direction will be the same as that of a hypothetical straight saccade that would result from the activation of the other site alone. This, however, is not the proper direction to reach either target, because the initial direction of the saccade has carried the eyes away from the straight path to the second target. Indeed, a close examination of the trajectories of real saccades shown in figures in various papers in the literature (see, e.g., McPeck et al. 2003; Fig. 2; Port and Wurtz 2003; Figs. 1, 2, 4, 5, and 7), indicates that the final direction is often close to what would be required to bring the eyes to one of the targets.

Equation 1, proposed to relate the discharge profiles of SC neurons to the instantaneous direction of saccade (Port and Wurtz 2003), implies that the SC must reside within the local feedback loop and, furthermore, incorporates the role of the saccadic burst generator. Another possibility is that SC may be upstream from the local feedback loop. If this is the case, Eq. 1 is inappropriate because the influence of the feedback loop on saccade direction is not taken into account. In this manuscript, we report simulations in which the SC resides upstream from and provides the input to a local feedback circuit (Fig. 1), analogous to various previous models of the saccadic system (Moschovakis 1994; Scudder 1988; Tweed and Vilis 1985). According to this view, the output of SC at any given point in time is interpreted by downstream structures not as instantaneous direction, but as *desired displacement with respect to when the resettable integrator is reset to zero*, which is equiv-

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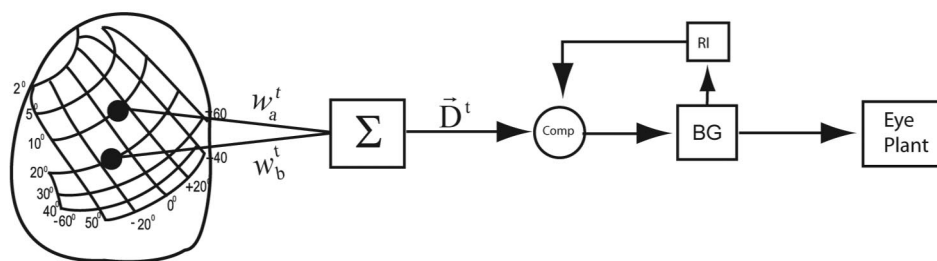


FIG. 1. Simplified schematic of the models. Two sites in superior colliculus are active. The center of the activated population at each superior colliculus (SC) site is schematically indicated by a black dot. The output of SC, a weighted vector average computed by Eq. 2, is the input to the local feedback loop. D^t , desired displacement; BG, burst generator; Comp, comparator; w'_a and w'_b are Gaussian weight functions; RI, resettable integrator.

alent to the initial positions of the eyes in the orbits. This model successfully predicts the final direction under various configurations of simulated activity at two SC sites. These findings have been published previously in abstract form (Walton et al. 2004).

MODEL

Figure 1 illustrates a schematized version of the model, which was implemented in Simulink (Mathworks). In accordance with the neural activity observed during asynchronous presentation of two targets (Port and Wurtz 2003), we simulated activity at two SC sites that encode different vectors from the same initial eye position. The temporal profiles of the activity were initially defined as Gaussians normalized to unity. The output of the SC, also called the desired displacement, was expressed as

$$D^t = \frac{w'_a}{w'_a + w'_b} V_a + \frac{w'_b}{w'_a + w'_b} V_b \quad (2)$$

where D^t is the desired displacement at time t , V_a is the vector requested by site A, V_b is the vector requested by site B, and w'_a and w'_b are Gaussian weight functions intended to represent normalized neural activity. These weight functions were intended to model population activity at the two activated sites.

The output of the SC, D^t , drove two two-dimensional, push-pull versions of the local feedback model, which were implemented in a previous study (Barton et al. 2003). These resemble the models of Grossman and Robinson (1988) ($\lambda = 0.9$) as well as Becker and Jürgens (1990) ($c = 0.05$ or 0.3).

Both performed equally well for the simulations reported in this study, and we report simulations only from the Grossman and Robinson (1988) model.

In the models tested, an external trigger signal is used to silence omnipause neurons (OPNs) and permit saccade initiation (Robinson 1975). The onset of the trigger is time-locked to the activity at the first activated locus (site A), and the offset is loosely associated with a reactivation of the OPNs. Unfortunately, there are no data to tell us how real OPNs respond on trials involving curved saccades. Because the purpose of this study was to examine the effect that the feedback loop has on the final direction, the OPNs were left off long enough to ensure that none of the saccades would be truncated before the curvature was completed.

SIMULATIONS

Neural activity recorded from SC neurons during multiple target presentation shows that, on some trials, one neuron returns to baseline or sharply attenuates its burst before the other neuron and is associated with a curved saccade directed toward the target encoded by the active neuron (McPeck et al. 2003; Port and Wurtz 2003). The sharp attenuation of activity at site A was modeled as a normalized Gaussian function multiplied by a negative ramp that returned the discharge rate to zero. Figure 2 shows the results of manipulating the relative time of offset of activity at site A. The initial saccade direction is an average of that requested by the two sites because the weight functions have the same height and onset times. However, when activity at site A is cut off prematurely, the saccade

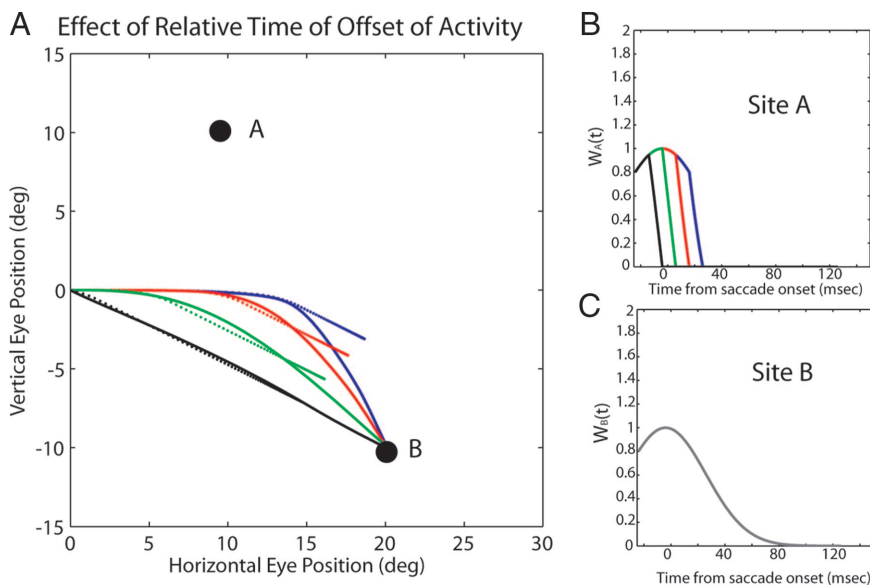


FIG. 2. Simulations manipulating the relative time of offset of activity at site A. The Gaussians in B correspond to the traces in A of the same color. The Gaussian in C is gray because the Gaussians for site B were the same for all simulations in this figure. A: \cdots , saccade trajectories predicted by Eq. 3. —, trajectories simulated in this paper, using Eq. 2. If activity at site A declines faster than activity at site B (B and C), the saccade curves toward target B.

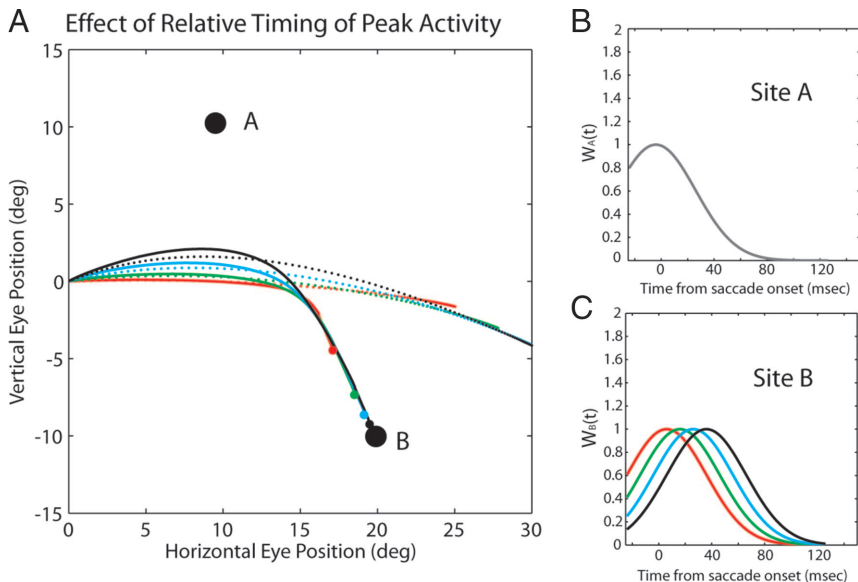


FIG. 3. Simulations manipulating the relative timing of the Gaussians. Same format as Fig. 2. Colored dots indicate the endpoints of each saccade. The later the onset of activity at site B with respect to site A (B and C), the more the initial direction of the saccade is biased toward A (A). Once A returns to baseline, however, the saccade curves toward target B, because site B is still active.

immediately curves toward target B. Note that the final direction is, for each trial (—), that which would be required to bring the eyes to target B, not the direction of the saccade that is requested by site B, which is the only site still active.

Neural activity recorded during simultaneous and asynchronous target presentations does not always show a rapid attenuation of activity at one of the two SC sites (McPeck et al. 2003; Port and Wurtz 2003). Modification of neural responses were noted in terms of the relative timing and level of activities at the two sites. Figure 3 shows the effects of manipulating the relative timing of the Gaussians for the two sites. The later the onset of activity at site B, the more the initial saccade direction is biased toward A. On the other hand, with longer delays in the onset of activity at site B, site A returns to baseline before B does, and the saccades curve toward B. When the relative height of the weight functions was manipulated with activity at the two sites having the same onset and offset times, the result was a group of straight averaging saccades (data not shown). In these simulations, the relative height of the Gaussians determined the endpoints. Because the focus was on saccade curvature, we also ran these simulations with a 20-ms difference

in time of peak activity. This resulted in various initial directions, determined by the relative weights, and a late onset of curvature, determined by the 20-ms difference in offset times (Fig. 4).

To emphasize the effect of the feedback loop, the model's simulations were compared with the trajectories predicted by Eq. 1. The weight functions in Eq. 2 were substituted for the normalized firing rate terms in Eq. 1, resulting in

$$V'_{\text{model}} = \frac{w'_a V_a k_a + w'_b V_b k_b}{2} \quad (3)$$

We set $k_a = k_b = 1$ for simplicity. The results, shown as dotted traces in Figs. 2–4, resemble the model responses evoked by Port and Wurtz (2003; see their Fig. 4A) but differ from both our simulations and observed behavior.

DISCUSSION

We simulated a model that places the SC upstream from the local feedback loop and that computes collicular output as a weighted vector average defined by Eq. 2. Using Gaussian-like

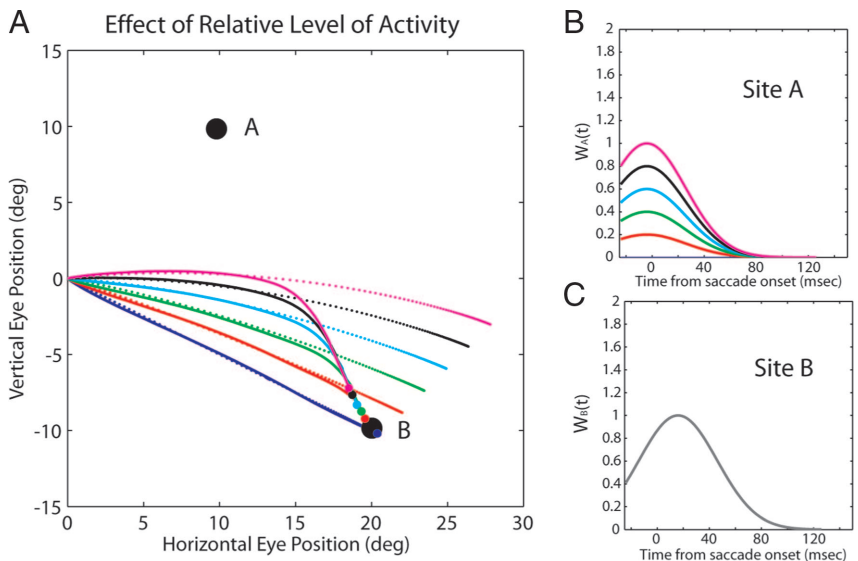


FIG. 4. Simulations manipulating the weight factor. Same format as Fig. 2. Colored dots indicate the endpoints of each saccade. The initial direction of the saccade is determined by the weight factors for the 2 sites and the difference in timing of the Gaussians (20 ms for all trials in this figure), both of which affect the relative weights at any given point in time during the saccade. As observed for other groups of simulations, once activity at site A returns to baseline, the saccade curves toward target B.

waveforms as substitutes for activity observed in SC neurons, the model is able to generate curved saccades that resemble eye movements associated with observed neural activity (McPeck et al. 2003; Port and Wurtz 2003). [It is even able to simulate the more extreme examples of saccade curvature, such as the right angle saccades reported by Port and Wurtz (2003); see Supplemental information.¹] When the relative level of activity at the two sites changes during the saccade, this desired displacement signal also changes, inducing curvature in the saccade trajectory. When activity at one site returns to baseline, the desired displacement signal becomes equal to that encoded by the other site as though the first site had never been active. Because the feedback loop interprets desired displacement with respect to the eye position *when the resettable integrator was set to zero*, i.e., the initial positions of the eyes in the orbits, the simulated saccade curves and heads directly toward the other target. This simply reflects the reaction of the feedback loop to changing input.

The denominator terms in *Eqs. 1* and *2* create a fundamental dissociation in the predictions of the two models. This difference has important consequences that may be best understood by considering what the output of each equation would be after activity at one collicular site has gone to zero ($f_a^t - b_a = w_a^t = 0$). In *Eq. 1* (Port and Wurtz 2003), as the firing rate for the second site declines during the latter part of the saccade, the normalized firing rate term gets smaller ($V_{\text{model}}^t \rightarrow 0$), and the small changes are in the direction of V_b relative to the instantaneous eye position. As a result, the predicted saccade slows, as noted by the closeness of consecutive time points in Fig. 4A of Port and Wurtz (2003). In essence, this equation predicts that the instantaneous firing rate of collicular neurons determines saccade velocity (i.e., the correlation between the firing rate for the neuron and the predicted instantaneous velocity will be approximately 1). Therefore this equation is appropriate only if one starts from the premise that SC is within the local feedback loop, but even then it fails to predict the final direction (Port and Wurtz 2003). Had we treated *Eq. 1* as SC output that is upstream from the local feedback loop, then the model would produce a looping trajectory that brings the eyes back to the initial position at the end of the movement, which is not the observed behavior.

In the implementation of *Eq. 2*, once $w_a^t = 0$, the SC output becomes constant, even as activity at the second site is decreasing ($w_b^t \rightarrow 0$). This configuration implies that the desired displacement is encoded by the locus of activity, not the instantaneous firing rate at site two after activity at site one has returned to baseline. In contrast, when activity is present at both sites, the SC output is determined by the relative activity at the two sites. It should be stressed, however, that the final direction of the curved saccade is determined by the feedback loop not by *Eq. 2*. In the scenario described in the preceding text, only one collicular site is active during the latter portion of the movement. This site continues to generate the same desired displacement command that it would have if it had been the only active site all along. The saccade curves only because the downstream comparator measures the difference between the changing desired displacement signal and the actual displacement readout of the resettable integrator.

As discussed in the preceding text, the model we simulated assumes that the SC is upstream from the local feedback loop that controls saccade *dynamics*. Consistent with this hypothesis is the observation that the firing rate of collicular neurons is not a good predictor of dynamic motor error in studies involving saccade perturbation (Goossens and Van Opstal 2000; Keller and Edelman 1994; Keller et al. 2000). Our assumption, however, does not preclude the SC from receiving *static* feedback information (Gandhi and Sparks 2004) that could update the metrics of the desired saccade (Keller and Edelman 1994; Keller et al. 2000) or the duration of the collicular burst (Soetedjo et al. 2002) but does not determine the direction and velocity of the saccade (Lefèvre et al. 1998; Quaia et al. 1999). Such feedback could be mediated through the cerebellum (Lefèvre et al. 1998; Quaia et al. 1999) and/or other regions (Soetedjo et al. 2002; Waitzman et al. 1996).

In a recent model of saccade control (Lefèvre et al. 1998; Quaia et al. 1999), the SC is placed upstream from the local feedback loop and the cerebellum is placed within the local feedback loop. In this model, there is no cross-coupling between the horizontal and vertical premotor burst neurons. Instead, the trajectory of oblique saccades is controlled by the dynamic pattern of activity in the oculomotor region of the fastigial nucleus. This mechanism gives the system some ability to compensate for unexpected deviations of the saccade from the optimal (straight) trajectory. For oblique saccades, this means that differences in the timing of activation of the horizontal and vertical premotor burst neurons can result in curved oblique saccades that still land on target, even without cross-coupling. It is important to note, however, that this type of curvature is associated with activity at only a single SC site. More to the point, the curvature of oblique saccades to single targets results from the normal action of the feedback loop in a situation in which desired displacement remains constant throughout the saccade. In contrast, the curvature that we are concerned with is associated with more than one competing visual target and activity at two SC sites. In this situation, the curvature occurs because the desired displacement command changes during the saccade. Thus the curvature is often much larger than the curvature reported for oblique saccades to single targets.

In the Lefèvre et al. (1998) model, as in the models we tested, it is the local feedback loop that controls the direction of the saccade not the SC. In both models, the SC is placed upstream from the local feedback loop that controls saccade dynamics. Thus although some of the details differ, we believe that any model in which saccade dynamics are controlled downstream from SC would make similar corrections.

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¹ The Supplementary Material for this article (a figure) is available online at <http://jn.physiology.org/cgi/content/full/01199.2004/DC1>.

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