Towards A Superior Colliculus-Only Saccade Control Model For Direct and Curved Saccade Trajectories

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Abstract—While a prominent model of the saccade system from Arai et al. successfully models and selects a single saccade target from multiple loci and mimics some of the observed averaged and slightly curved saccades in the authors' own monkey experiments, it is unable to produce the observed highly curved saccade trajectories for delayed two-target saccade tasks without supplemental control signals to the saccade burst neurons [1]. It is presently unknown the extent to which the saccade system is affected by signals outside of the superior colliculus (SC), so we need a more complex model for SC-only control logic in order to capture the full fidelity of observed saccades. We propose, validate, and test a simplified model of the saccade system and define a new control scheme that is able to generate averaged, slightly curved, and highly curved saccades similar to ones observed in monkey experiments. The success of our control scheme suggests that implementing a similar controller in a full saccade system model would allow it to produce realistic saccade trajectories from only the SC.

Index Terms—saccade, control, computational model

May 10, 2015

I. INTRODUCTION

Early distributed models of the saccade system have used lateral inhibition between neurons inside the superior colliculus (SC) and employed a winner-takes-all (WTA) strategy that guarantees only one target is present when the saccade system initiates a saccade. When multiple visual targets are present in visual working memory, experimental data shows that "averaging saccades" result where the saccade target is at a location determined by the spatial average of the salient visual stimuli [2]. Later models employed long range lateral inhibition within the SC so that visual stimuli clustered near enough to each other in the visual field would inhibit each other, but excite an area approximately near the their spatial average. These models are able to produce direct saccades to single targets and express average saccades to virtual targets. One experiment from monkeys performing express average saccade tasks finds that multiple loci are present in the SC rather than one locus corresponding to the average [3]. Experts are in disagreement about the existence of long range lateral inhibitory connections within the SC [4] [5], so it is unclear how to model the SC in the saccade system. Arai et al. offered a design to account for the multiple loci present in the SC and also the variety of saccade trajectories observed during the authors' own monkey experiments. In this model, long range lateral inhibition was hypothesized to not exist and the authors were able to simulate slightly curved saccades and express averaging saccades, but were unable to generate highly curved saccade trajectories, which were observed in their monkey experiments. With the addition of two parallel inputs to each of the horizontal and vertical saccade burst generator neurons, the model was found to be capable of producing highly curved saccades. Other researchers have reached a similar result and hypothesize that the parallel inputs may come from the cerebellum [6] [7]. Although the parallel inputs have been employed to great effect in these models, no physiologic experiments have verified the existence of these pathways for this purpose.

Our model implements a simplified version of the saccade system based on the model from Arai et al. [1] and makes three contributions:

- We show that the dynamic control model proposed by Arai et al. is equivalent to a feedback integral controller.
- We validate our model and control approach by comparing an integral-only feedback simulation to the results from Arai et al.
- We demonstrate that a SC control signal constructed from proportional error and derivative terms can reproduce slightly curved, average, and highly curved saccades.

II. FOUNDATIONAL SUPERIOR COLLICULUS CONTROL MODEL

Our model is based on the SC model presented by Arai et al. [1]. For the rest of the paper, we will refer to this model as the "foundational model". Arai et al. use the following equation to update the SC output signal:

$$\tau \frac{d\mathbf{x(t)}}{dt} = -\mathbf{x(t)} + \mathbf{Wz(t)} + \mathbf{v(t)} - \mathbf{f_p(t)} - \mathbf{f_v(t)}$$

For details of the model, readers are referred to the authors' article [1]. In this equation, $x(t)$ is the SC control signal, W is

a matrix of learned synaptic weights between each visual field neuron, $z(t)$ is the result of sending $x(t)$ through a sigmoid transfer function, and $v(t)$ is the input visual stimulus. The $f_p(t)$ and $f_v(t)$ terms are the eye position and eye velocity feedback signals, and after the model has been trained, these are approximately proportional to the actual eye position and velocity. Solving this ordinary differential equation yields:

$$\mathbf{x(t)} = $$
$$c_1 e^{\frac{-t}{\tau}} + e^{\frac{-t}{\tau}} \int_{-\infty}^{t} \frac{e^{\frac{\xi}{\tau}}(Wz(\xi) + v(\xi) - f_p(\xi) - f_v(\xi))}{\tau} d\xi$$

This equation shows us that the SC portion of the foundational model determines its output based on the integrated feedback signals. While Arai et al. have shown this to be helpful for generating direct and slightly curved saccade trajectories, they noted that this model was not able to handle highly curved trajectories without additional hypothetical parallel inputs into the SBGs. Although these parallel inputs have been suggested by other researchers [6] [7], there is as of yet no physiologic evidence to support them. We will show in the next sections that a different control equation will enable any of the aforementioned saccade trajectories to be produced without any additional SBG inputs.

III. Our Superior Colliculus Control Model

We employ a simplified model of the SC system. The foundational model successfully demonstrates that short-range lateral inhibition and selective (shunting) disinhibition from the SNr can turn a visual field with multiple loci into a single target appropriate for each type of saccade. We abstract this away and assume a selection process has already produced a single target at each time step. Figure 1 shows a block diagram of our simplified model, which we explain in more detail in the following paragraphs.
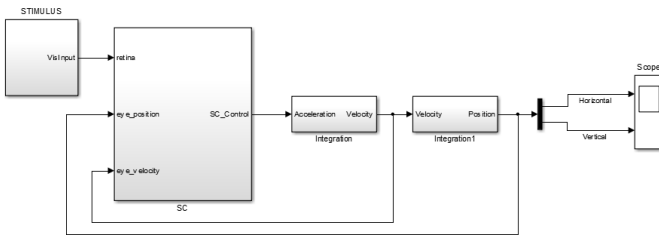

Fig. 1. A high-level block diagram of our simplified SC control model. A visual stimulus is provided to the SC which produces a control signal. The control signal is applied to generate a velocity and then a position, which is sent to the eye (or scope for simulation display). The velocity and position feed back into the SC.

We begin by using our model to simulate each of the three saccade experiments simulated by Arai et al. with the foundational model and we use realistic saccade peak accelerations and velocities [8]. Our model receives the same SC inputs, namely the horizontal and vertical eye positions, eye velocities, and the visual target. The SNr disinhibition is assumed to be applied at simulation start and released once

the error function converges to near zero, so we do not handle this input explicitly. Our error function is measured using a forward Euler approximation:

$$\mathbf{E(t)} = \mathbf{G(t)} - (\mathbf{f_p(t)} + \mathbf{f_v(t)}\mathbf{\Delta t}) \tag{1}$$

The error vector $\mathbf{E(t)}$ contains two components, one for the horizontal and one for the vertical elements corresponding to those axes in the visual field. $\mathbf{G(t)}$ is the goal or target location in the visual field, and $\mathbf{f_p(t)}$ and $\mathbf{f_v(t)}$ are the approximate eye positions and velocities. For our validation experiment, the control signal time step is given by:

$$\begin{cases} \mathbf{I(t)} & = \mathbf{I(t-1)} + \mathbf{E(t)}\mathbf{\Delta t}, \mathbf{I(0)} = \mathbf{0} \\ \mathbf{C(t+1)} = K_i \mathbf{I(t)} \end{cases} \tag{2}$$

$\mathbf{I(t)}$ accumulates the error over time and acts as the integral term from the original model. $\mathbf{C(t)}$ is the control signal analogous to the SC output signal, and K_i is a tunable parameter.

For our simulation where we attempt to reproduce all types of saccade trajectories observed in monkey trials [1], we use the following formulas:

$$\begin{cases} \mathbf{D(t)} & = \dfrac{\mathbf{E(t)} - \mathbf{E(t-1)}}{\Delta t} \\ \mathbf{C'(t+1)} = K_p \mathbf{E(t)} + \mathbf{K_d}\mathbf{D(t)} \end{cases} \tag{3}$$

$\mathbf{D(t)}$ is a simple approximation of the derivative of the estimated error, and the new $\mathbf{C'(t)}$ control signal is a linear function of the error and its derivative. Again, K_p and K_d are tunable parameters.

Finally, we simulate the effects of running the chosen control signal through the MLBNs, neural integrators, and eye plants present in the foundational model using a symplectic Euler integrator:

$$\begin{cases} \mathbf{a_{eye}(t+1)} = \mathbf{C(t+1)} \\ \mathbf{v_{eye}(t+1)} = \mathbf{v_{eye}(t)} + \mathbf{a_{eye}(t+1)}\mathbf{\Delta t} \\ \mathbf{p_{eye}(t+1)} = \mathbf{p_{eye}(t)} + \mathbf{v_{eye}(t+1)}\mathbf{\Delta t} \end{cases} \tag{4}$$

Here the a_{eye}, v_{eye}, and p_{eye} vectors correspond to the eye acceleration, velocity, and position respectively. If either the acceleration or velocity vectors exceed the maximum horizontal or vertical maximums observed in humans, they are clamped. The maximums values used in our model are $\frac{3000°}{s^2}$ and $\frac{400°}{s}$ [8]. For each of the validation and simulation experiments, the K parameters are tuned by hand to produce realistic saccade trajectories and once tuned remain the same across all saccade tasks for the same experiment.

IV. Validation

In order to validate our model, we adopt the same experimental setup that Arai et al. used for the unpublished monkey experiments and for the foundational model simulations. They use a rectilinear 40x40 visual field and assume some topological mapping from this field to the retinotopic projection of the visual field into the SC. For each of the three saccade types, they simulate a visual stimulus at one or more locations in the visual field. We describe the exact setup for each of their experiments below and show our integral-term control function results for comparison.

saccade task. Both targets appear away from the current eye focus at the same time and one of the targets (the red one) has a higher reward value associated with it. Initially the saccade aims for a location somewhere between the two targets, then once the V4 visual cortex and inferotemporal cortex have processed the target colors and the reward value of each is determined, the saccade curves towards the higher valued target [9]. The upper left image in figure 2 shows the simulated result of this saccade task using the foundational model [1], and the figure in the upper right shows the results from our model using the integral controller. While difficult to see, our model's trajectory is very slightly curved and terminates acceptably near the target location. Our model qualitatively reflects the trajectory from the foundational model.
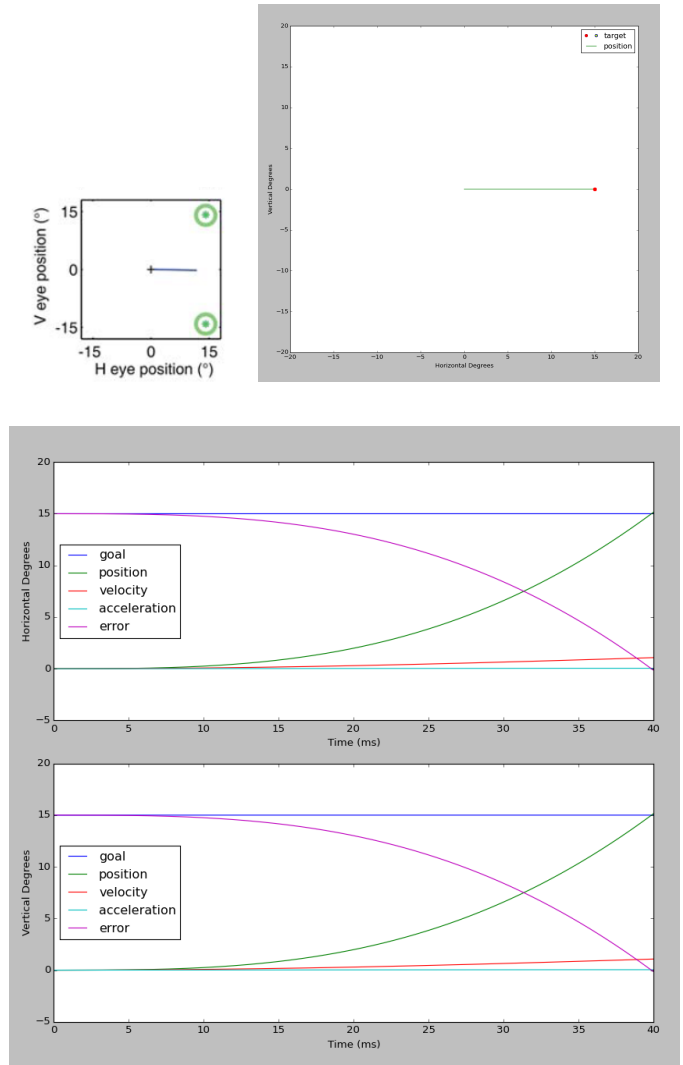

Fig. 2. The image in the upper-left shows the result of a simultaneous two-target saccade experiment from Arai et al. [1] using the foundational model. The saccade expressly begins moving to a location between the two stimuli and then once the visual cortex has processed the target colors and associated a value with each, the saccade curves towards the red one with higher value. Our model shown in the upper-right simulates this change in target location by moving the target from the mid-right to the upper-right corner during the simulation. We use an integral controller in our model. Note both images are qualitatively similar.

Figure 2 shows the results of a simultaneous two-target

Fig. 3. The figure in the upper-left shows the result of a simultaneous two-target saccade experiment from Arai et al. [1] using the foundational model and where both visual targets have equal value. The foundational model selects a target from the two loci that is midway between the two stimuli. Our model shown in the upper-right simulates a saccade to this average location using our integral controller. Both of these trajectories are similar.

Figure 3 shows the results of a simultaneous two-target saccade task where both of the visual targets are equal in value. During the foundational model simulation of this task, two loci are present in the visual field, but a single target is selected midway between the two visual stimuli. This "averaging saccade" is also reproduced in the right image by our model using integral-only control.
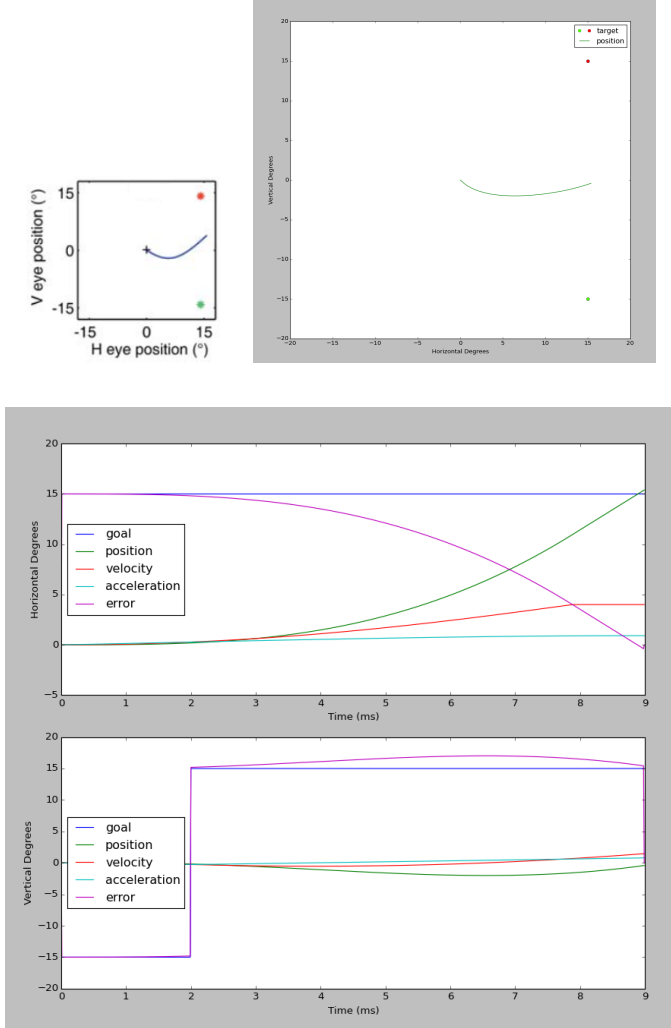

Fig. 4. The figure in the upper-left shows the result of a delayed two-target saccade experiment from Arai et al. [1] using the foundational model. First, the green target in the lower right is presented, then a small time later before the saccade to that target is complete, a second higher-valued target (shown in red) is presented. The saccade trajectory should curve away from the green target and converge on the red target. Our model shown in the upper-right simulates a very similar (incorrect) trajectory using an integral-only control signal.

Figure 4 shows the results of a delayed two-target task. First a green target is presented and then a higher-value red target is presented some small time later before the first saccade is able to converge on the first target. Monkey experiments have shown that a highly curved trajectory should result that bends away from the green target and converges on the red, but the integral control signal used in both the foundational model and

in our model results in a trajectory that curves somewhat and never converges to the desired target.

We have shown that our control model is able to reproduce results very similar to those simulated by the foundational model. This validates our simplified model and also our verifies our classification of the foundational model's SC controller as an integral controller. Next we show simulation results for these same saccade experiments using the proportional and derivative control equations described in section III.

V. Simulation Results

We run the same three saccade experiments from the previous section using the proportional and derivative control scheme presented in section III.
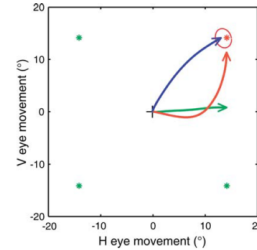

Fig. 5. This figure and the following caption are reproduced from (Arai et al. 2005) [1]: "Three distinctive variations of saccade trajectory produced by a monkey performing a visual search task. The small red and green asterisks represent locations of the target and three distractors, respectively. In the search task the animal was rewarded for making a saccade to the location of the odd-colored target. 1 slightly curved, on-target saccade (blue); 2 averaging saccade (green); 3 highly curved saccade (red). The light red contour around the target location shows the 95% confidence ellipse for single-target saccades made by the same animal to the upper-right target location. Arrowheads indicate saccade direction and endpoint."

The K_p and K_d parameters were hand tuned to perform the saccades without ringing or over-damping. For the slightly curved saccade task and the averaging saccade task, the chosen parameters lead to saccades with similar delay and durations as the simulations using the foundational model.

Figures 6, 7, and 8 show our simulation results using our controller. Figure 5 is reproduced from (Arai et al. 2005) [1] and shows a depiction of the types of saccades the researchers observed in their unpublished monkey experiments.

VI. Discussion

Two interesting and important observations stem from the simulation results:

- This proportional and derivative control scheme reproduces qualitatively the same results for both slightly curved and averaging saccades.
- Figure 8 shows that this new control scheme is capable of producing highly curved saccades that converge to the correct target as expected.

The success of the proposed proportional and derivative control scheme for each of the saccade tasks suggests that deploying a similar method of control in place of the integral controller used in the foundational model may allow that
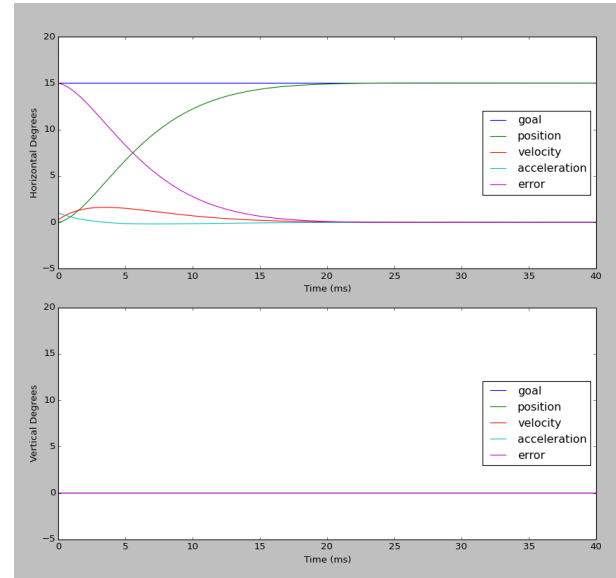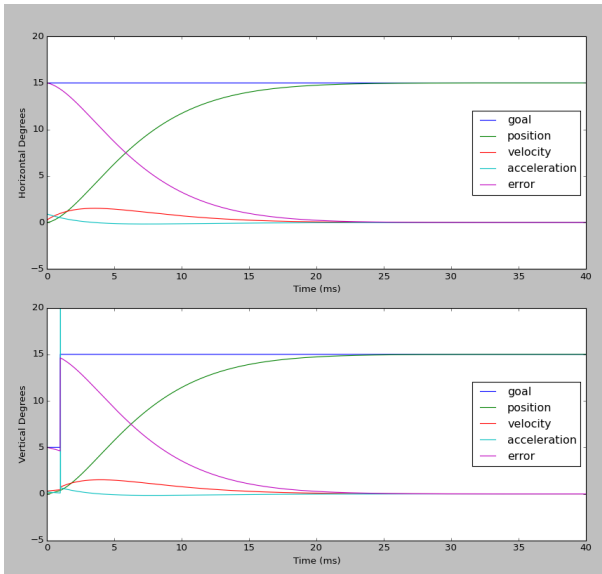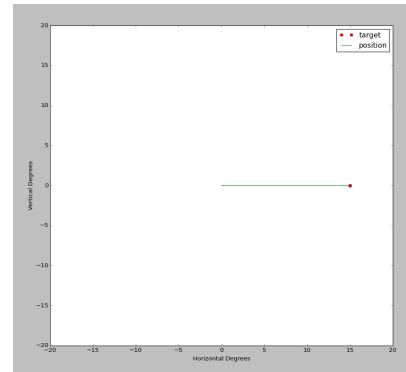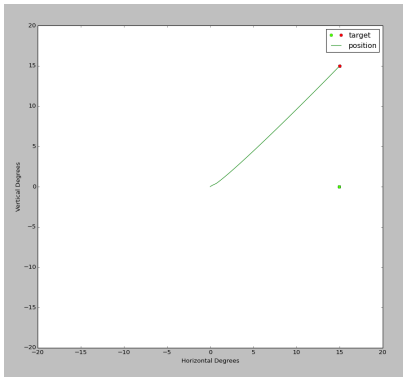
Fig. 6. Our model using the proportional and derivative control scheme performing the simultaneous two-target experiment with unequally valued targets. This produces a slightly curved saccade as expected.

Fig. 7. Our model using the proportional and derivative control scheme performing a virtual two-target saccade task with equally valued targets. The resulting averaging saccade mimics results observed in monkey experiments.

model to generate highly curved saccades obviating the need for the parallel SBG inputs. Since no physiologic evidence has confirmed the presence or absence of parallel SBG signals contributing to saccades, it remains unknown whether this improved controller is better suited for modeling the saccade system. Still, we hope that this serves as an example of a situation where more complex control dynamics may be necessary when modeled neural module connectivity is insufficient to support the fidelity demands.

VII. CONCLUSION

In this paper, we have presented an alternative formulation of the SC control mechanism for the saccade system. Borrowing from the efforts of Arai et al., we built a simplified model of the saccade system and validated it against simulation results and qualitative experimental results. We proposed and employed our improved control scheme and demonstrated that it was capable of producing slightly curved and averaging saccades comparable to simulation and experimental results. We also showed that the new control scheme could simulate highly curved saccade trajectories which have been observed

in monkey experiments [1], but have not been simulated successfully by models using only SC control. We are in the process of migrating our successful controller to the original model proposed by Arai et al. to obviate its need for hypothetical parallel SBG signals to generate highly curved saccade trajectories. The reader is referred to the appendix for details regarding this future work in progress.

ACKNOWLEDGMENT

APPENDIX

This section depicts work in progress integrating the improved SC control model into the original SC model proposed by Arai et al. [10]. In a real neural implementation of this model, some recurrent loops in the SC would be necessary to remember and accumulate feedback signals. The model is currently being implemented in MATLAB's® Simulink®.
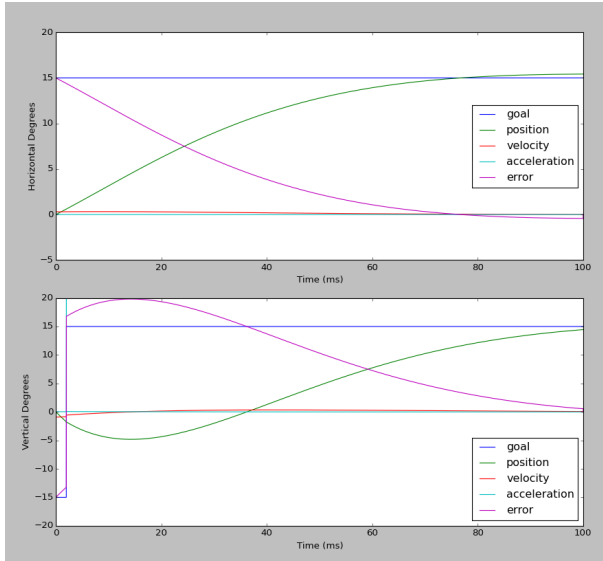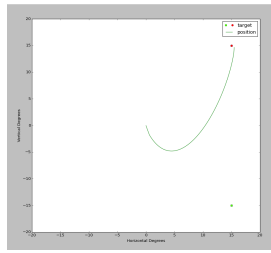
Fig. 8. Our model using the proportional and derivative control scheme on the delayed two-target task. A highly curved saccade results, which matches expectation.

The diagram shown in figure 9 depicts the SC control loop. Figure 10 shows a detailed view of the SC module. Pictured modules and supporting code are available upon request.

REFERENCES

[1] K. Arai and E. L. Keller, "A model of the saccade-generating system that accounts for trajectory variations produced by competing visual stimuli," *Biological Cybernetics*, vol. 92, pp. 21–37, 2005.

[2] I. H. Chou, M. a. Sommer, and P. H. Schiller, "Express averaging saccades in monkeys," *Vision Research*, vol. 39, pp. 4200–4216, 1999.

[3] J. a. Edelman and E. L. Keller, "Dependence on target configuration of express saccade-related activity in the primate superior colliculus." *Journal of neurophysiology*, vol. 80, no. 3, pp. 1407–1426, 1998.

[4] D. P. Munoz and P. J. Istvan, "Lateral inhibitory interactions in the intermediate layers of the monkey superior colliculus." *Journal of neurophysiology*, vol. 79, no. 3, pp. 1193–1209, 1998.

[5] G. Özen, M. C. Helms, and W. C. Hall, *The Superior Colliculus: New Approaches for Studying Sensorimotor Integration*. CRC Press, 2003, ch. 6: The Intracollicular Neuronal Network, pp. 147–158.

[6] P. Dean, "Modelling the role of the cerebellar fastigial nuclei in producing accurate saccades: the importance of burst timing." *Neuroscience*, vol. 68, no. 4, pp. 1059–1077, 1995.

[7] C. Quaia, P. Lefèvre, and L. M. Optican, "Model of the Control of Saccades by Superior Colliculus and Cerebellum Model of the Control of Saccades by Superior Colliculus and Cerebellum," pp. 999–1018, 2012.

[8] J. a. Van Gisbergen, J. a. Van Gisbergen, D. a. Robinson, D. a. Robinson, S. Gielen, and S. Gielen, "A quantitative analysis of generation of saccadic eye movements by burst neurons." *Journal of Neurophysiology*, vol. 45, no. 3, pp. 417–42, 1981. [Online]. Available: http://www.ncbi.nlm.nih.gov/pubmed/7218009

[9] S. N'guyen, C. Thurat, and B. Girard, "Saccade learning with concurrent cortical and subcortical basal ganglia loops." *Frontiers in computational neuroscience*, vol. 8, no. April, p. 48, 2014.

[10] K. Arai, S. Das, E. L. Keller, and E. Aiyoshi, "A distributed model of the saccade system: Simulations of temporally perturbed saccades using position and velocity feedback," *Neural Networks*, vol. 12, no. 10, pp. 1359–1375, 1999.
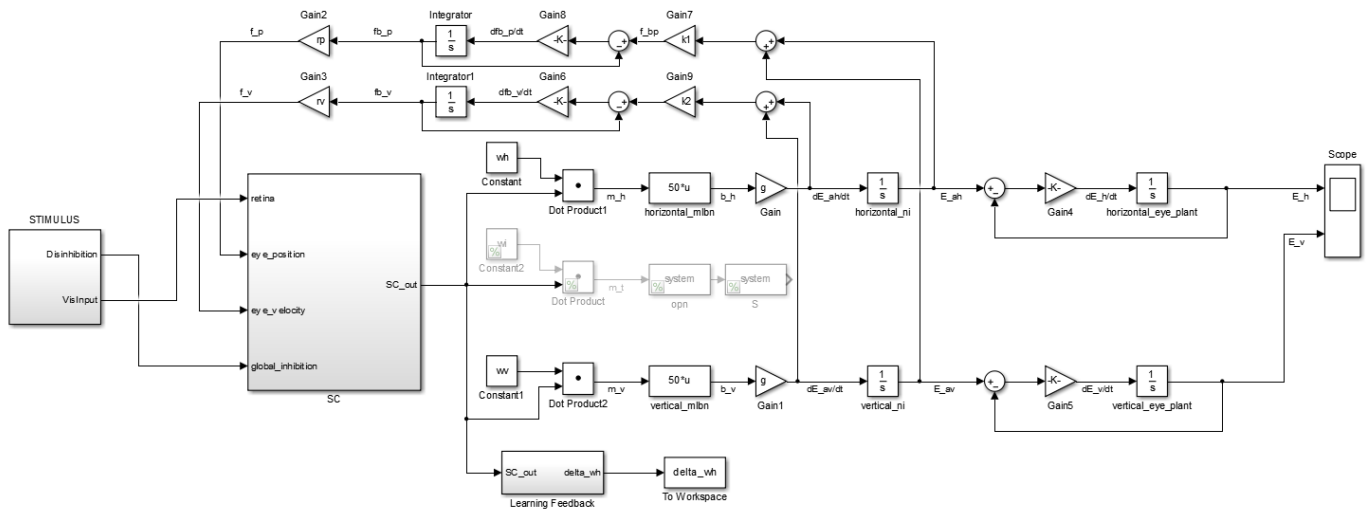
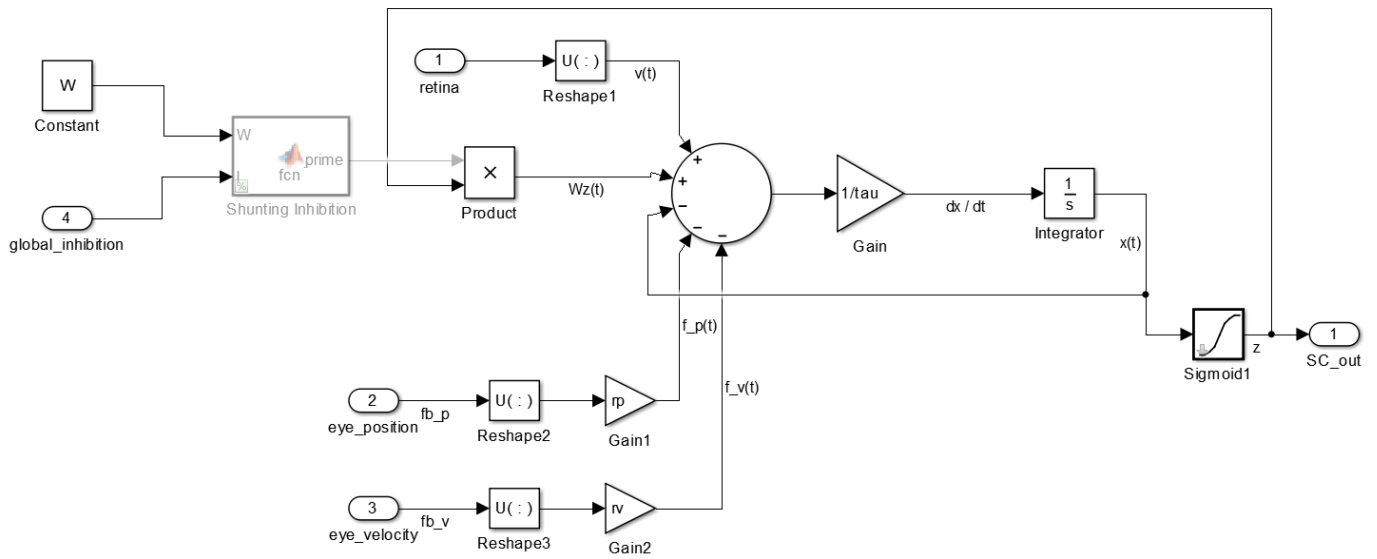Fig. 9. A Simulink® reproduction of the saccade system model proposed by Arai et al. [10].

Fig. 10. A detailed view of a Simulink® reproduction of the SC module proposed by Arai et. al. [10]