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A Stochastic Feedback Model to Simulate Saccadic Eye Movement Variability ⋆

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Abstract: Variability is an important behavioral signature of biological movements that can be used as a tool to understand motor control. This study has modeled the inter-trial variability of very rapid eye movements called saccades by using a stochastic feedback model. The proposed model represents the brainstem saccade generation system with noise in the loop. Three types of noise signal namely visual noise, premotor noise and motor noise are considered in this model. The model can predict the inter-trial variability in the angular displacement of saccade trajectories. The accuracy of the predictions of the model has been verified using experimental data of horizontal saccades. It is observed that the presence of all the three noise components is important for the prediction of the dynamic evolution of the inter-trial variability during eye movement. This work provides a way to better understand the control of the saccadic system.

Keywords: Saccade control, Signal-dependent noise, Visual noise, Oculomotor Noise, Inter-trial Variability, Internal feedback.

1. INTRODUCTION

Noise is a key factor in biological systems. The motor system is also affected by noise during the process of generating a movement. This noise could enter the system at various levels of a motor act, ranging from sensory to execution. The reasons for the noise could be ripples in the force generated in muscle fibres or the cellular noise in motor neurons or even the stochastic nature of the action potential which is due to the randomness in the biochemical cascade causing it (Faisal et al. (2008)). There have been numerous studies that try to understand the types of noise that affect the motor system. The study by Van Beers (2007) has suggested that the motor system is affected by different types of noise like sensory and motor noise. Sensory noise arises due to errors in target localization and motor noise could be getting generated at the motor planning stage or the execution stage. Various studies (Van Beers (2007), Harris and Wolpert (1998)) have shown that the noise could be constant, signal-dependent or temporal. The inherent noise in the system reflects in the behavior of humans and other animals in the form of variability in their movements. In spite of this variability, the movements made by humans and other primates are very accurate and stereotypical. This suggests that the brain might be employing an online control on the system such that the variability is maintained minimal. So studying the variability in movements is very important in understanding the motor system.

A very simple and well-understood system that can be used for studying the variability in movements is saccadic eye movements. *Saccades* are very fast eye movements that increase the acuity of vision by bringing the target image near to the fovea in the eye. There is extensive literature that studies the brainstem control circuit for the generation of saccades. Robinson (1973) used a local feedback model to simulate horizontal saccades. Several modified versions of this original model (Robinson (1973)) have come up with the explanation for saccadic control. A well accepted model was proposed by Scudder (1988). The model used the error between target displacement signal and eye displacement to provide an input to the excitatory burst neurons in order to produce a saccade.

All the models of saccade generation (Robinson (1973), Scudder (1988)) have investigated the ideal scenario of a motor system without any noise and have tried to predict the main sequence relationship observed in the saccades. These studies have investigated only the mean behavior of the saccadic system. But it is imperative to study the variability in these movements to completely understand their control. All the optimal control modelling studies (Van Beers (2008), Harris and Wolpert (1998)), which investigated the variability, have restricted themselves to modeling the variability at the endpoint of the saccadic eye movement or the variability in the main sequence parameters like amplitude, duration and peak velocity of saccades. They have completely ignored the information that may be contained in the dynamic evolution of inter-trial variability of the trajectories.

A few recent studies by West et al. (2009), Wu et al. (2014) and Eggert et al. (2016) have suggested the importance of dynamic evolution of variability. West et al. (2009) investigated

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the dynamic nature of variability to suggest that saccade trajectories may be receiving online correction. Wu et al. (2014) have shown the temporal structure of variability to be dynamically regulated and that it could predict motor learning ability. Eggert et al. (2016), in their work tried to model the inter-trial variability in saccades made by monkeys using a simplified model of saccade generation to investigate the effect of different types of noise like accumulating and premotor noise that corrupt the system upstream of the oculomotor neurons. This study has generated the main sequence saccade trajectory by using a linear saccade generator model. But many studies ((Scudder, 1988), Van Gisbergen et al. (1981)) have suggested that the non-linearity in kinematics of the saccades may be due to the presence of non-linearity upstream of the plant. They have used a saturating burst generator in the system to account for this non-linearity. The model in Eggert et al. (2016) did not consider this non-linearity. Hence, there is a need for studying evolution of the inter-trial variability of saccade trajectories of humans using an appropriate saccade generation model in the presence of noise.

In this paper, a model is proposed for brainstem control of saccade generation in the presence of noise that can affect the motor system. The model incorporates the presence of a saturating burst generator in the system which can account for the non-linearity in the saccade main sequence. It also includes three types of noise in the loop namely visual noise, burst neuron noise and oculomotor noise. Unlike the general models of saccade generation that predict the mean trajectory of the saccadic eye movement, this model can simulate multiple trials of saccades. Thus, the model allows the investigation of variability that is existing in the eye movements, on a trial-to-trial basis. In this work, the evolution of the inter-trial variability of the angular displacement of saccade trajectories in the presence of different types of noise is studied. The predictions of variability by the model have been validated using experimental data of horizontal saccades made by humans.

2. PROCEDURE FOR EXPERIMENT AND MODELLING

2.1 Experimental Details

A total of seven participants were part of the study (addressed as S1-S7 in this paper). All of them were between 23-26 years of age and had normal or corrected to normal vision. The data presented here is part of the dataset previously published in Gopal and Murthy (2015). All subjects have given their informed consent in accordance with the guidelines of institutional human ethics committee of the Indian Institute of Science. Subjects were monetarily rewarded for their participation.

Design of the Experiment The paradigm (see Fig. 1) had a central white fixation box. At the beginning of each trial the subjects had to fixate their gaze on this fixation box. After a fixation period of 300 $\pm$ 100ms, a peripheral green target appeared either on the right or left of the fixation box at an eccentricity of 12°. The square boxes in Fig. 1 shows the stimulus appearing on the screen during the experiment in each trial. The dashed arrow shows the timing sequence of appearance of each stimulus. The small white arrow inside the square box represents an ideal saccadic eye movement. Subjects were instructed to make a saccade to the green target, as quickly and accurately as possible. The trial was aborted if the subject failed to make a response within a time limit of 600 ms.

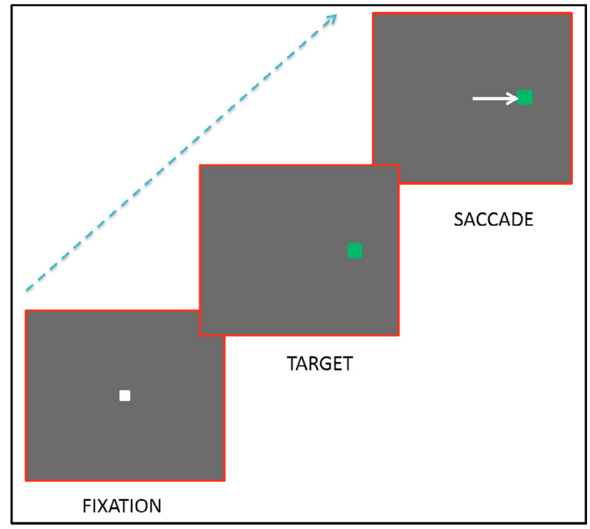

Fig. 1. Experimental paradigm

Setup for Data Acquisition The stimulus was shown to the subjects using TEMPO/VDOSYNC software. The TEMPO system acquired data in real time at a resolution of 1 ms. The monitor used to display the stimulus was mounted on a customized wooden stand. The subject sat on a chair in front of the wooden housing with the chin resting on the chin-rest and the head restrained by two temple locks on either sides. The reflection of the stimulus was viewed on the plane mirror when the stimulus appeared on the monitor mounted above the mirror. The eye movements were recorded by tracking the pupil by using a camera-based eye tracking system from ISCAN. The tracker was mounted on a spectacle frame and it acquired the position of the eye at a sampling frequency of 240 Hz.

2.2 Details of the stochastic saccade generation model

The proposed model is a modified stochastic version of the desired displacement model of saccade generation (Scudder (1988)). A model without any noise in the loop can only generate the mean saccade trajectories. The major difference in the proposed stochastic model is the presence of various types of noise affecting the system at the input level, the burst generator level and the pulse-step generator level. The gray colored blocks with dashed outline in Fig. 2 shows the noise incorporated blocks. All the noise signals used in the model are drawn from a Gaussian distribution. It is possible that in smaller structures like molecules or single neurons, the noise may be discrete in nature (Faisal et al. (2008)), but in this case, we are modelling neuronal signals of a population of neurons. Hence, the noise may be approximated by a Gaussian process in continuous time (Ditlevsen and Samson (2013)). Such a stochastic model is required for predicting the inter-trial variability of the saccade trajectories.

The input to the model is the firing rate corresponding to the desired displacement which is thought to be encoded in the superior colliculus. A visual noise (Eggert et al., 2016) is added to the input before it enters the comparator module. This noise accounts for the possible error in target localization. This noise is a Gaussian random variable which is constant for a particular amplitude of saccade.

The desired displacement input is compared with the instantaneous displacement at the comparator junction. The instanta-

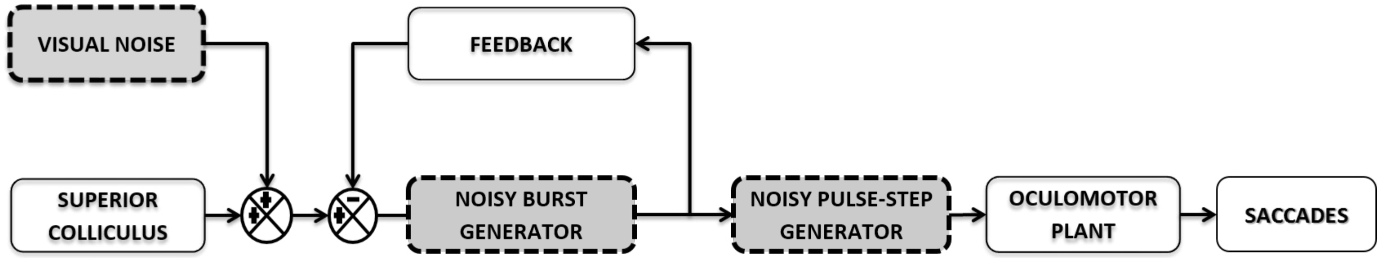

Fig. 2. Block diagram of the stochastic feedback model for saccade generation

neous information of the displacement is obtained through the internal feedback loop connected to the output of the noisy burst generator, which is the next block. The noisy burst generator is modelled as a non-linear transformation ($f(\cdot)$) as in Van Gisbergen et al. (1985) with an additive noise component called the burst neuron noise (ε_{bn}). It is a signal-dependent noise that has been modelled to scale up with the firing strength of neurons (Harris and Wolpert (1998)). It is modelled as a Gaussian random variable with mean zero and standard deviation proportional to the amplitude of the signal it is corrupting.

$$f(e) = a\Big(1 - exp(-e/e_0)\Big) + \varepsilon_{bn}. \tag{1}$$

Here, e is the motor error generated at the comparator. The scaling constants, a and e_0 are free tuning parameters of the model.

The output of the noisy burst generator goes to the feedback block as well as to the noisy pulse step generator. The feedback block consists of a resettable integrator which converts the velocity information, thought to be encoded at the output of the burst generator, into an instantaneous displacement signal for generation of motor error at the comparator junction. This block is affected by the noise that leaks in from the output of the burst generator.

The noisy pulse generator block produces a pulse signal followed by a step signal with an added noise disturbance. The pulse part is responsible for the rapid movement of the eye to the target and the step signal maintains the eye at the target position. This pulse-step signal is generated by adding the output of the noisy burst generator output signal to itself after passing through an integration block. This pulse-step is corrupted by a signal-dependent noise called oculomotor neuron noise. This noise scales proportionally with the output of the pulse-step generator. It is added just before the control signal enters the oculomotor plant and is similar to the motor noise suggested in (Eggert et al., 2016). The output of this block is fed into the oculomotor plant to generate saccadic eye movements.

Oculomotor Plant Dynamics A lumped third order model is used for the oculomotor plant (Shadmehr and Wise (2005)). Robinson et al. (1986) studied the mechanical response of human eyes and approximated the system using a third order linear system with three time constants. It consists of a second order spring mass damper model which is preceded by a low pass filter (see Fig. 3). This lumped model provides a good approximation of the saccade-generating oculomotor system. The dynamics of the eyeball in the eye socket, that is filled with fluid, is modelled as a spring mass damper system.

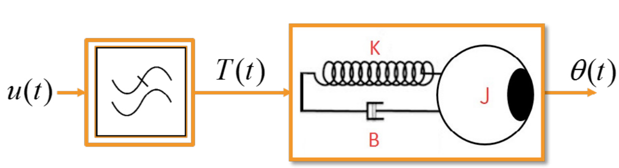

Fig. 3. Oculomotor plant lumped model

$$J\ddot{\theta}(t) + B\dot{\theta}(t) + K\theta(t) = T(t). \tag{2}$$

Here, J is the moment of inertia of the eyeball, B is the viscosity coefficient and K is the elasticity coefficient of the viscoelastic eyeball system. Here, if we set $K = 1$, then $J = \tau_1\tau_2$ and $B = \tau_1 + \tau_2$. Thus, Equation (2) can be written as a second order transfer function $G_1(s)$.

$$G_1(s) = \frac{1}{(\tau_2 s + 1)(\tau_1 s + 1)}. \tag{3}$$

A low-pass filter is used to approximate the muscle dynamics which is similar to an actuator. The firing rate required to produce an angular displacement is the input to the low-pass filter block. The firing rate is represented as a function of time, $u(t)$. The output of the block represents the torque required to generate the movement of the eyeball. Then, the system dynamics of this actuator model of muscle can be written as

$$\tau_3\dot{T}(t) + T(t) = u(t). \tag{4}$$

Equation (4) gives a first order transfer function $G_2(s)$

$$G_2(s) = \frac{1}{(\tau_3 s + 1)}. \tag{5}$$

Now the entire system can be represented by a third order model given as

$$G(s) = G_1(s)G_2(s)\frac{1}{(\tau_3 s + 1)(\tau_2 s + 1)(\tau_1 s + 1)}. \tag{6}$$

As per the information in Harris and Wolpert (1998), the values of the time constants are taken as $\tau_1 = 223$ ms, $\tau_2 = 14$ ms and $\tau_3 = 4$ ms.

3. RESULTS

3.1 Experimental Data Analysis

The data was collected by the method described in detail in Section 2.1. All the analyses and results are based on data of saccades made to the target on the right because no difference was found between right and left saccades. Since the data was collected at 240 Hz, there were only a few data points available for analysis, sampled once every 4 ms in the short time during which a saccade happened. Hence, the data was interpolated using cubic interpolation to a sampling frequency 1 kHz. The cubic interpolation was used as it was observed to give the best fit when a curve fit analysis was done on the experimental dataset. The saccade beginning was marked at the time point where the velocity either exceeded 25 degree per second or 10% of peak velocity, whichever was greater and the saccade end was marked where the velocity fell below this cut-off. Stringent outlier removal criteria was employed on the dataset in the same way as in Vasudevan et al. (2016).

The average number of trials that were recorded was around 140 per subject. Each trial gives displacement data corresponding to a single saccade, based on the design of the experiment. It was observed that there is variability in the saccade trajectories made repeatedly by the same subject to the same target at 12° eccentricity. Since each saccade happens with different duration, time binning had to be done to calculate the variance across trials. The time between 0% to 100% of completion of saccade was divided into 30 bins. So each time bin would mark the completion of approximately 3.3% of the movement. The variance of the displacement values at each of these time bins was calculated across trials.

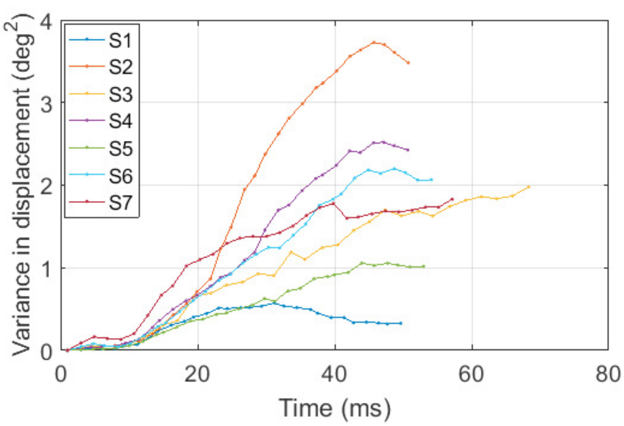

Fig. 4. Variability in angular displacement across population

The inter-trial variance observed in the angular displacement for 7 subjects is shown in Fig. 4. It can be observed that the variance is small at the start of the saccade, then increases during the movement and typically saturates towards the end of the movement. Large differences were observed in the variability in movements among the subjects depending on their performance. But, the average variability that was observed in the population is only 1.8753 deg^2 and is similar to variance observed in other literature (Van Beers (2008)).

3.2 Model Simulation Results

The model with noise in loop, described in the Section 2.2, was used to simulate multiple trials of saccades. In order to remove the variability effects that arise due to the difference in duration of each saccade, the model also simulated saccades of the same duration equal to the mean duration of the experimental data. The saccade generation circuit can have variations across individuals. So, the parameters of the non-noisy version of the model were tuned to match the mean angular displacement trajectory of each individual subject. In Fig. 5, the mean angular displacement of subject S2 obtained from experimental data is shown along with the mean angular displacement predicted by the tuned model.

The errors were quantified as the sum of squared errors between the experimental mean angular displacement and its model

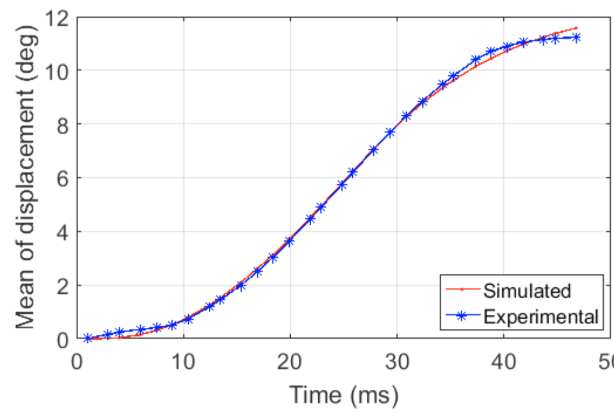

Fig. 5. Mean angular displacement predicted by the non-noisy model for subject S2. Similar results were obtained for other subjects as well.

prediction at each time point. Let $err(\theta)$ denote the error corresponding to the angular displacement θ.

$$err(\theta) = \frac{\sqrt{\sum_{j=1}^{m} [\theta_{exp}(t_j) - \theta_{pred}(t_j)]^2}}{\sqrt{\sum_{j=1}^{m} \theta_{exp}(t_j)^2}}. \quad (7)$$

Here, j represents each time-bin (representing 3.3% of the movement) at which data was available, θ_{exp} is the mean of experimental data of angular displacement and θ_{pred} is the mean angular displacement predicted by the model. The errors

Subject	S1	S2	S3	S4	S5	S6	S7
Error(%)	1.51	1.98	1.84	1.61	1.38	1.85	2.81

Table 1. Errors in mean angular displacement prediction by non-noisy model

in the model fitting of mean angular displacement for each subject is shown in Table.1. The errors in the prediction of mean angular displacement of the non-noisy model after tuning was below 3% for all subjects.

The individually tuned model was then simulated multiple times with noise added to generate as many trials of saccadic eye movements as the experimental data for each subject. The inter-trial variability of the simulated saccades were calculated as described in Section 3.1. The three noise components namely visual noise, burst neuron noise and oculomotor noise were tuned to match the variance profiles calculated from the experimental data. This was also done for each subject individually because there could be physiological differences in the noise affecting the system in each person. The best model predictions of inter-trial variance were obtained only when all three noise components were included. The total variability predicted by the model, for the subject S2, when all the three types of noise were present is shown in Fig. 6 (bottom right panel). It was observed that it is not possible to explain the observed experimental variability completely by simulating the model separately with each of the individual noise in the loop. But the model with all the three types of noise was able to completely match the experimental data. Individually, each noise component was observed to capture only part of the variance profile characteristics. This can be seen in Fig. 6. The plots in the first three panels show the contribution of each noise component

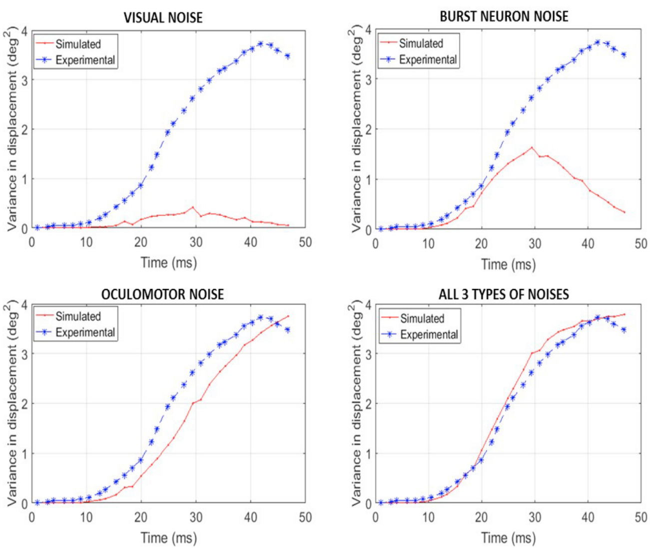

Fig. 6. Model prediction of inter-trial variability in angular displacement. (Top panels and the bottom left panel show the variability predicted by the model with each type of noise and the bottom right panel shows the model prediction in the presence of all the three types of noise.)

to the total variability predicted by the model for an example subject S2.

The model with all three types of noise incorporated was able to predict the variances for all the subjects with high correlation. The correlation between the model prediction and experimental data of inter-trial variance in angular displacements were above 90% for all subjects.

4. CONCLUSION

The inter-trial variability in saccadic eye movement trajectories was modelled using a stochastic feedback model. The model captured the noisy brainstem control circuit for saccade generation compared to ideal models which do not consider the noise in the loop. It was observed that the time profile of the variability in angular displacement is due to the presence of both signal-dependent and constant noise. The model was able to predict the variability profiles across the population with high correlation.

All biological systems are inherently noisy and hence this is a more realistic approach for understanding the computations underlying the production of accurate voluntary movements by the motor control system in humans. The model can be used to understand how different sources of noise contribute to the movement profiles of saccades. The work also suggests that understanding variability in movements is a powerful tool to investigate movement control.

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