# Infomax models of oculomotor control

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***Abstract*—From a Bayesian point of view, learning is simply the process of making inferences about the world based on incoming data. The efficiency of this learning is determined by the quality of the information provided by the sensors. Thus, a critical part of learning is the existence of a sensory-motor system designed to maximize the information required to achieve goals. Here we show that a wide range of primate eye movement phenomena can be elegantly explained from the point of view of infomax control. The proposed approach describes the velocity profiles of saccadic eye movements as well as previously existing models. In addition, the infomax approach explains phenomena that are beyond the scope of previous models: non-saccadic eye movements, and the difference in end point and velocity profiles observed in saccade-to-target and reach-to-target tasks. The results suggest that the occulomotor control system evolved to be a very efficient real time learning machine.**

## I. Introduction

From a Bayesian point of view, learning is simply the process of making inferences about the world based on incoming data. The efficiency of this learning is determined by the ability of the sensory-motor control system to maximize the information needed to achieve goals (infomax control).

Humans make over 150,000 saccades per day, spending about 2 hours in saccadic flight, during which useful vision is very poor. It is well known that the velocity profiles of primate saccadic eye movements are quite stereotyped and adhere to consistent relationships between amplitude, duration, and peak velocity. These relationships have been called the "main sequence" [1].

Recent models of oculomotor control have been successful at describing saccade velocity profiles using optimal control principles. Typically, these models focus on the relationship between motor commands and forces applied to the eyes, and postulate that the goal of the oculomotor system is to drive the eye to target locations as quickly and accurately as possible. Some models postulate that the eyes minimize the expected deviation from a target end point [2], [3]. Other models postulate that eye movements minimize the time required to reach the target point [4], which turns out to be mathematically equivalent. These models ignore the sensory properties of the eyes and assume that the goal of oculomotor control is to reach target points. How these targets are selected is beyond the scope of the models. A recent class of models has focused on explaining how the target points are selected using information maximization principles [5], [6]. Up to now these models have focused on the sensory properties of the eyes (e.g., the fall-off of sensitivity as a function of eccentricity) and have ignored their mechanical properties. Here, we show that by jointly examining the sensory and mechanical properties of the eyes it is possible to explain a range of new phenomena that were beyond the scope of the previous models. The approach shows that a wide range of primate eye movement phenomena reveal that the primate oculomotor system evolved to be a very efficient real-time learning machine.

## II. Infomax Model

To model oculomotor control, we first need to have a description of the system of the eye. We follow [2] in using a state-space model with signal dependent noise to describe the eye. We call the state of the eye at time $t$ as $X_t$, and describe its changes through time with

$$dX_t = \underbrace{AX_t dt}_{\textbf{drift}} + \underbrace{BU_t dt}_{\textbf{control}} + \underbrace{(C + U_t) dB_t}_{\textbf{noise}} \tag{1}$$

$$X_t = \begin{bmatrix} X_{e,t} \\ \dot{X}_{e,t} \end{bmatrix} \tag{2}$$

Where the matrix $A$ represents the passive dynamics of the system, $B$ describes the effects of the control inputs $U_t$ on the state, and $C$ describes the effect of the Brownian motion $B_t$ on the state. $X_t$ is the state matrix, which contains the eye position $X_{e,t}$ and velocity $\dot{X}_{e,t}$ Notice that the noise scales with the size of the control input, which gives rise to a tradeoff between controlling the system and being certain of the system's state. The values in the $A$ and $B$ matrices were found from human saccades in [7], and like [2] we use these values. These values were retrieved from horizontal saccades, and we model saccades similarly in only one dimension.

Although previous models have assumed that the endpoint of a saccade, which we will call $Z$, is known exactly, here we introduce target uncertainty by treating $Z$ as a random variable. Especially if this target is presented in the periphery, subjects will be unsure of the target's location due to sensory uncertainty. Here we model the belief of the target's location as a Gaussian distribution. Additionally, we assume target has its own dynamics described by

$$dZ_t = \eta_t dt + n dV_t \tag{3}$$

where $\eta_t$ is the model of the target's velocity, and $dV_t$ is Brownian motion, with magnitude determined by $n$. We assume the model of the target dynamics is known. The model could potentially be learned or estimated from the observations of the target, but we do not address this issue here. Even though the dynamics are known, $Z$ is not, so we need a model for how the eye learns about the location of the target.

Similar to [8], who use a POMDP framework to examine hand-eye coordination, we model the observations $Y$ that the eye collects about the target. These observations change through time as

$$dY_t = (X_{e,t} - Z_t) g(X_{e,t}, Z_t, \dot{Z}_t) dt + dW_t \tag{4}$$

If the observations were noiseless and accurate, they would give the eccentricity of the target with respect to the location of the eye. However, the observations are contaminated by noise, $dW_t$, and the signal-to-noise ratio (SNR) is defined by the visual acuity function $g$. We choose the following form of the visual acuity function

$$g(X_t, Z_t, \dot{Z}_t) = e^{-\left[\underbrace{\frac{1}{\rho}((X_{e,t} - Z_t)\beta)^{\rho}}_{\textbf{eccentricity}} + \underbrace{\frac{1}{2}(\dot{X}_{e,t} - \dot{Z}_t)^2 \gamma}_{\textbf{velocity}}\right]} \tag{5}$$

where $\rho$ and $\beta$ define the shape and width of the falloff in SNR due to the target's eccentricity, and $\gamma$ defines the width of the falloff in SNR due to the relative velocity of the eye. For computational simplicity, we restrict $\rho$ to be an even number so we can avoid using an absolute value on $(X_{e,t} - Z_t)$. For example, if we assume the velocity term is zero, and $\rho = 4$, Figure 1 shows a schematic of how the SNR would decrease as the eccentricity (on the x-axis) diverges from zero in either direction.

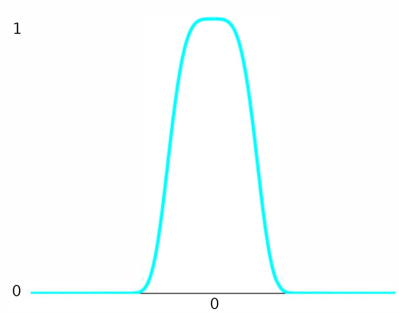


Fig. 1. Schematic figure of how the SNR decreases as the eccentricity (x-axis) differs increasingly from zero.

A similar shape would hold for the velocity term of the visual acuity function as well. The velocity term models the cost of moving the eyes rapidly. In humans, saccadic suppression masks high-frequency visual information during fast eye movements. Similarly, in the model, a high velocity of the eye with respect to the target reduces the SNR of the observations. This sets up another tradeoff. If the eye is far from a stationary target, the controller must decide whether it is better to make slow movements that generate more reliable observations, or fast, unreliable movements to decrease the eccentricity of the target. The optimal action will depend on the values of the parameters $\rho$, $\beta$, and $\gamma$, and the relative cost of action and uncertainty. Taken together, (1), (3), (4), and (5) describe the system to be controlled. What remains is to find a control policy that can generate the actions $U_t$ from times 0 to final time horizon $T$ such that the system is driven to a desired state.

### A. *Learning the control policy*

To find the optimal policy, we first need to define an objective function. Here we use a quadratic objective function, and use iterative Linear Quadratic Gaussian (iLQG) [9] control, which will require dealing with both the partial observability and the non-linearity from (5). In this paper, we will model eye movements in three tasks (target-directed saccades, smooth pursuit, and eye-hand coordination). Objective function in (8) will be modified based on task goals.

For the moment, we will focus on target-directed saccades. In this task, we use data collected from horizontal saccades in humans [10]. The participants were asked to saccade from a central fixation point to a flashed target at different amplitudes. Because the task involves positioning the eyes as close as possible to the target, we start with a term for minimizing the squared error between eye and target. Additionally, we include a term to model the cost of action. Let the cost function take the form

$$(X - Z)^2 + U^2 Q \tag{6}$$

where $Q$ is a scalar that captures the tradeoff in cost related to being far from the target point and making actions.

The expression in (6) will be the cost function if the target location $Z$ is known. However, because the location $Z$ is unknown, we cannot use this cost directly. Instead, we need to take the expected value of (6), which leads to

$$(X - \hat{Z})^2 + \sigma_Z + U^2 Q \tag{7}$$

where $E[Z] = \hat{Z}$ and $\sigma_Z$ is the variance of the estimate of the target location. With (7), we have a quadratic cost function. Notice that even in a situation where the task is to move to a specified location, there is still pressure to find a solution that maximizes the information about the target location.

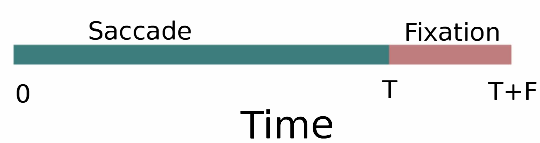


Fig. 2. The two segments of the finite horizon used for control. First, from time 0 to time $T$, there is no penalty for the distance from the eye to the target. Second, during fixation (from time $T$ to time $T + F$), the penalty on the eye position is enforced. The penalty on the magnitude of the action $U$ is enforced for the entire horizon.

In this target-directed task, the entire eye movement in one trial includes first a saccade and then a short fixation period at the target. To apply the cost function (7) to the entire movement, we also separate the movement control into these two segments, as shown in Figure 2. The first segment, which we will call the saccade, only contains penalties on the actions. The second segment, from time $T$ to time $T+F$, which we call the fixation, also includes the penalty on the state of the eye. With this, the complete minimization objective becomes

$$\int_T^{T+F} ((X_t - \hat{Z})^2 + \sigma_Z)dt + \int_0^{T+F} U_t^2 Q dt \tag{8}$$

Following [9], we include $\hat{Z}$ and $\sigma_Z$ in the state $X$, and plan according to the belief state. Using an extended Kalman-Bucy filter, we can find the dynamics of $\hat{Z}$ and $\sigma_Z$. The extended Kalman-Bucy filter equations are as follows

$$d\hat{Z}_t = \eta dt + K_t dI_t \tag{9}$$

$$dI_t = (dY_t - f(X_t, \hat{Z}_t, \dot{\hat{Z}}_t))dt \tag{10}$$

$$K_t = \sigma_{Z,t} \frac{\partial}{\partial \hat{Z}_t} f(X_t, \hat{Z}_t, \dot{\hat{Z}}_t) \tag{11}$$

$$d\sigma_{Z,t} = -K_t^2 dt + n_t^2 dt \tag{12}$$

where we've defined

$$f(X_t, \hat{Z}_t, \dot{\hat{Z}}_t) = (X_{e,t} - \hat{Z}_t) g(X_t, \hat{Z}_t, \dot{\hat{Z}}_t) \tag{13}$$

and $g$ is as in (5). Using the product rule, we can find

$$\frac{\partial}{\partial \hat{Z}_t} f(X_t, \hat{Z}_t, \dot{\hat{Z}}_t) = g(X_t, \hat{Z}_t, \dot{\hat{Z}}_t)(1 - \beta(X_{e,t} - \hat{Z}_t)^\rho) \tag{14}$$

Using the above equations, we can incorporate the observation process $Y$ with the estimate of the target location and give the dynamics of $\hat{Z}$ and $\sigma_Z$ in relation to time.

The final step is to augment the $A$ and $B$ matrices from (1) to include the dynamics of $\hat{Z}$ and $\sigma_Z$ in relation to changes in the other state variables. We can find the necessary terms in the augmented matrices by taking the partial derivatives of (12) with respect to $X_{e,t}$, $\dot{X}_{e,t}$, $\hat{Z}$, and $\sigma_Z$. This will allow us to linearize the dynamics of the system around a given state or sequence of states.

With the linearized dynamics, the belief state $\hat{Z}$, and the quadratic cost function, we can now solve for a control policy using iLQG. The policy learned by iLQG is a closed-loop policy. This means the optimal action at a given time can depend on the state rather than just the time; in other words, the optimal policy can react to changes in the environment. This feature of the policy is interesting, and differs from previous models, and its implications are discussed in more detail in Section V. Once the control policy has been learned, it can be applied to a noise-free simulation to give an the expected trajectory of the eyes for a set of parameters.

## III. Evaluation Methods

To evaluate the suitability of the infomax model for describing oculomotor control, we looked at three different eye movement paradigms. The first is in describing the velocity profiles of horizontal saccades, as was described earlier. Second, we examined the qualitative suitability of our model for predicting smooth pursuit in amenable situations in simulation. We also examined a task where the eye played a supportive role to the hand, which had to reach a target.

### A. Saccades

To learn the parameters of the system that describes the eye's movement and observations, we perform a pattern search to minimize the root squared error between the velocity profiles of 5, 10, 20, 30, 40, and 50 degree saccades generated by the optimal controller under the fixed set of parameters and the behavioral data from [10]. We allow the saccade duration $T$ to change with each amplitude, but all other parameters are held constant across amplitudes.

To compare the infomax model to other models, we use a cross-validation paradigm, where each amplitude saccade is held out in turn. The parameters for each model are set from the remaining amplitudes, and an optimal movement for the held-out amplitude is generated with the learned parameters. Then, the error is calculated, and averaged across the amplitudes.

### B. Smooth pursuit

To model eye movements other than saccade, we need only make minimal changes to the objective function (8). Rather than considering the task where the eyes are required to move to a particular location (as was the case in our model of the saccade task from [10]), here we only consider the goal of minimizing the variance of the estimate of the target location. As such, the objective comes closer to pure information maximization, and is defined as

$$\int_T^{T+F} \sigma_Z dt + \int_0^{T+F} U_t^2 Q dt. \tag{15}$$

Although we have tried the following experiments with an objective function closer to (8) with similar results, it is more compelling to show that even without a strict penalty on the location of the eyes, we can generate qualitatively similar behavior to smooth pursuit, so we will focus on this case.

### C. Hand-eye coordination

We model eye movements in a rapid reaching task (data collected and described by [11]) in two conditions: Eye+hand, in which the reward is given based on the endpoint of hand movement; Eyes only, in which the reward is given based on the endpoint of saccadic eye movement. In the experiment, subjects were instructed to reach the target at a distance of 20 cm (25 degree visual angle) from the starting location either with hand (Eyes+hand) or eye (Eyes only) movement at a time window of 600 ms. For the former, subjects can freely move their eyes and thus eye movements only serve to guide hand movements. For the latter, subjects' reward will be based on the endpoints of eye movements and thus eye movements contribute directly to the task goal. We used Eyelink1000 system to track eye movement and Phasespace motion capture system to record hand movement in the experiment.

We model the hand as a point mass, and used the dynamics for the hand as described in [4].

For Eyes+hand condition, without constraint on eye movement to the target, the objective function for eye movement is

$$\int_{T}^{T+F}((X_{h,t}-\hat{Z})^2+\sigma_Z)dt+\int_{0}^{T+F}U_t^2Qdt \qquad (16)$$

where $X_{h,t}$ is the position of the hand at time $t$.

For Eyes only condition, with the task goal of moving eyes to the target, similar as the target-directed saccade task, the objective function for eye movement is (8).

## IV. Results

### A. Predictions of optimal saccades for static targets

Figure 3 compares the infomax model prediction of saccade velocity profiles over a range of amplitudes. Optimal velocity profiles (Fig 3b) captured the important shape features shown in behavioral data (Fig. 3a) (i.e. symmetric for low amplitudes and asymmetric/left-skewed peak for high amplitudes). The optimal positions (Fig. 3c) also show similar trajectories as in the observed behavior.

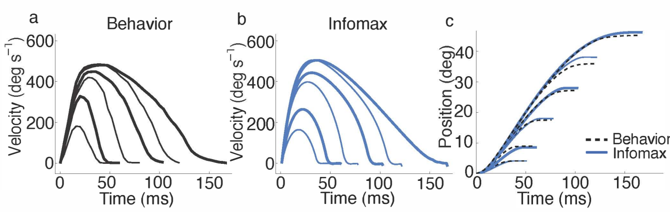


Fig. 3. Comparison of behavioral result and infomax predictions. a. Observed velocity profiles of horizontal saccades when the target is at $5°$, $10°$, $20°$, $30°$, $40°$ and $50°$ ([10]). b. Optimal saccadic velocity profiles for corresponding amplitudes shown in a. c. Optimal eye positions (solid blue line) and observed eye positions (dashed black line) for the amplitudes shown in a.

In Figure 4, we compare infomax with previous models (Internal Model from [12]; Minimum Variance Model from [3]). RSE comparison (Fig. 4c) suggests there is no significant difference (summed over all velocity profiles between behavior and model predictions) between those 3 models (p>0.1).

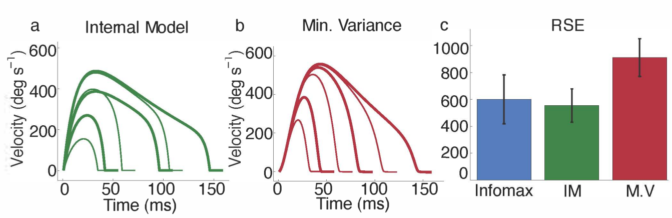


Fig. 4. Comparison of infomax and previous models. a. Internal Model from [12]. b. Minimum Variance Model from [3]. c. Mean RSE over all the amplitudes, error bars show the standard error of the mean.

### B. Prediction of saccadic and smooth pursuit eye movement for moving targets

Figure 5a and 5b show infomax prediction for eye movements when the target moves at 20 deg/s with no location difference between initial fixation and the onset of the moving target. Eye velocity trace in Fig. 5a suggests the eye will increase velocity rapidly and continuously until reaches the target velocity ($\sim$ 40 ms after target onset), and then track the target using pursuit eye movements. Eye position trace in Fig. 5b shows eye positions closely match target locations.

Figure 5c and 5d shows model prediction of eye movement when the moving target is initially located 5 deg to the right of fixation, and then moves to the right at 10 deg/s. Eye velocity trace in Fig. 5c shows the eye will first make a quick catch-up saccade-like movement to the target ($\sim$150 ms after target onset) and then track the moving target at a matching speed. The eye position trace in Fig. 5d suggests the eye will reach the target at the end of the first quick movement and then track the target position.

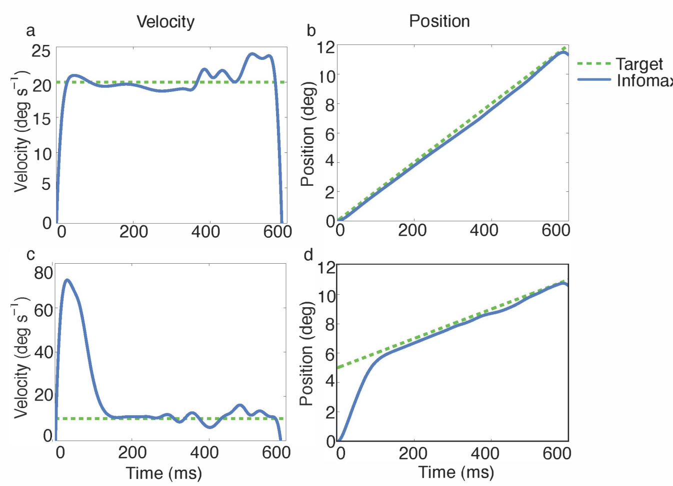


Fig. 5. Representative eye movement responses to moving targets. Top row: a. Eye velocity trace (solid blue line) and b. corresponding eye position and target position in response to a zero-offset target moving rightward at 20 deg/s (dashed green line). Bottom row: c. Eye velocity trace (solid blue line) and corresponding eye position and target position in response to a moving target initially located at 5 deg in the right visual field and then moves rightward at 10 deg/s (dashed green line).

### C. Prediction of eye movement in Hand-eye coordination

Figure 6a shows model predictions of eye movement in hand-eye combination (solid blue) and eyes only (solid red) conditions. Comparing with behavioral data (dashed blue, dashed red lines) observed in the experiment (Figure 6b), eye movement endpoints in the task show that subjects undershoot target with saccadic eye movements when the task goal is to reach the target with the hand (top panel in Figure 6b). However, the undershooting disappeared when the task goal was to fixate the target with eye movements (bottom panel in Figure 6b). Infomax predictions (Fig. 6a) of optimal eye positions for the hand-eye condition (solid blue) and eye only (solid red) are consistent with this observation from the behavioral data (dashed blue and red).

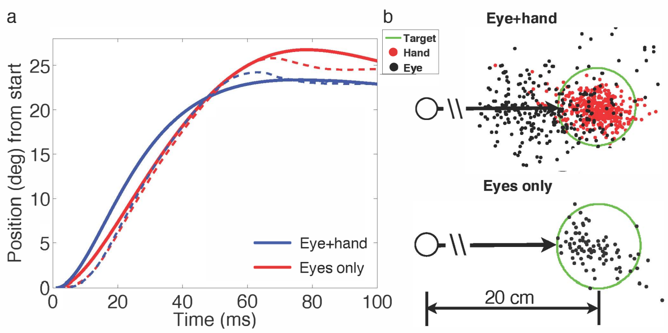


Fig. 6. Eye movements in the reaching task. a. Comparison between infomax prediction of optimal eye positions (solid lines) and behavioral data (dashed lines). b. Eye movement endpoints in Eye+hand condition (top panel) and in Eyes only condition (bottom panel). Green circle is the target; red dots are hand endpoints in Eye+hand condition; black dots are eye endpoints.

## V. Discussion

We showed that saccadic eye movements emerge as the solution to an information maximization problem with sensors that have a limited field of view and limited temporal resolution. The information maximization principle explains the velocity profiles observed in saccadic eye movements as well as previous principles, including minimum end-point variance [2] and minimum time [4]. More importantly, information maximization explains eye movement phenomena that were beyond the scope of previous models. We showed that, for moving targets, infomax generates both saccades and smooth pursuit eye movements. When target onset location is close to the initial eye fixation (foveal), infomax predicts smooth pursuit eye movement which closely tracks target positions. When the target appears in a peripheral location, infomax predicts a catch-up saccade followed up by smooth pursuit eye movement. Qualitatively, this behavior was observed in empirical studies [13], [14]. While previous models [15] explained smooth pursuit from the point of view of minimizing tracking errors, here we explain both saccadic movements and smooth pursuit from the point of view of maximizing information about the location of a target.

We designed an experiment in which target tracking and information maximization make different predictions. Subjects were instructed to reach a target with their hands (Hand condition) or with their eyes (Eye condition). Subjects were rewarded based on the endpoints of hand movements or eye movements, respectively. For the Eye condition, subjects made eye movements as predicted both by the infomax approach and by the target tracking approach. However, for the Hand condition, eye movements undershot the target by $\sim$2.5 degrees. This result was predicted by the information maximization approach but contradicted the target tracking models. According to the infomax model, the reason why people undershoot in the Hand condition but not in the Eye condition is that moving the eyes close to the target does not improve the accuracy of the hand motion.

It should be noted that the infomax model generates closed-loop control policy for the eyes. At first glance, this might seem an undesirable feature since saccades are widely believed to be open-loop, ballistic movements. However, due to the limited temporal bandwidth of our eye model, when the eyes move quickly they provide very little visual information, and thus virtually operate in open loop mode. The decision to move slowly in closed loop mode, or quickly in open loop mode, can be seen as the result of optimizing a common information maximization principle.

## VI. Conclusions

From a Bayesian point of view, learning is equivalent to making inferences based on the information gathered by the sensors. Efficient learners are thus those that control their sensors so as to maximize the expected value of information. Here, we showed that a wide range of properties of the oculomotor system, including the velocity profiles of saccades, the transition between smooth pursuit and saccadic movements, and eye hand coordination in reaching tasks can be explained from the point of view of information maximization. In summary we showed that, by considering that the occulomotor system has evolved to be a very efficient real-time learning machine, one can make sense of a wide range of phenomena that were previously addressed using different principles or that were beyond the scope of previous models.

It should be noted that our work is agnostic with respect to brain implementation issues. For example, while we show that saccadic movements and smooth pursuit movements serve a common goal (information maximization) it is perfectly plausible for the two forms of movements be controlled by different brain systems. It is also possible that, as recently suggested [14], [16], saccades and pursuit are two outcomes of a single sensorimotor system. Regardless, our work suggest that the brain systems involved in oculomotor control have evolved to serve a common computational principle: efficient, real-time learning.

## VII. Acknowledgments

This research was supported by NSF IIS 0968573 and NSF IIS 0808767.

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