Effect of Fixational Eye Movement on Signal Processing of Retinal Photoreceptor: A Computational Study

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SUMMARY The eyes are continuously fluctuating during fixation. These fluctuations are called fixational eye movements. Fixational eye movements consist of tremors, microsaccades, and ocular drifts. Fixational eye movements aid our vision by shaping spatial-temporal characteristics. Here, it is known that photoreceptors, the first input layer of the retinal network, have a spatially non-uniform cell alignment called the cone mosaic. The roles of fixational eye movements are being gradually uncovered; however, the effects of the cone mosaic are not considered. Here we constructed a large-scale visual system model to explore the effect of the cone mosaic on the visual signal processing associated with fixational eye movements. The visual system model consisted of a brainstem, eye optics, and photoreceptors. In the simulation, we focused on the roles of fixational eye movements on signal processing with sparse sampling by photoreceptors given their spatially non-uniform mosaic. To analyze quantitatively the effect of fixational eye movements, the capacity of information processing in the simulated photoreceptor responses was evaluated by information rate. We confirmed that the information rate by sparse sampling due to the cone mosaic was increased with fixational eye movements. We also confirmed that the increase of the information rate was derived from the increase of the responses for the edges of objects. These results suggest that visual information is already enhanced at the level of the photoreceptors by fixational eye movements.

key words: visual processing, information rate, hyper acuity, edge enhancement, spatial smoothing

1. Introduction

At the first stage of visual signal processing, external information is acquired at the retinal photoreceptors by moving the eyes and is converted into neuronal signals. Two types of eye movements, saccades and fixations, are engaged to acquire external information (visual sampling). A saccade is a ballistic eye movement in which a gaze position orients to the most salient point in a scene. During intervals of fixation between saccades, the gaze is roughly held at a certain point, but small fixational eye movements occur. The fixational eye movements consist of ocular drift, tremor, and microsaccades[1]–[4]. Thus, dynamic sampling of the visual scene continues during fixation, in which the visual system uses this “coarse” information for a stable perception.

For the last few decades, the knowledge regarding the functional roles of fixational eye movements has dramatically changed. At first, fixational eye movements were considered to be noise[5], or thought to be merely adjusting gaze position to the center of vision (null point), or a fixating on the target to adjust for a loss of focus[6]. Also, visual fading caused by continuous fixation is prevented by retinal motion evoked by fixational eye movements[2], [7]–[10] or head move[18], [24]. Recently, several lines of novel functional roles of fixational eye movements have been uncovered by vision research and associated computational studies. Microsaccades enhance low-frequency vision[11], [12], improve the visualization of high-spatial frequency components of scenes, such as edges and small targets[13]–[15] and shift foveal locus to highest acuity region[16]–[18]. Fixational eye movements also contribute to fine tuning of visual signal with shaping spatial-temporal characteristics to provide a stable vision[19]–[23].

In the retinal network, optical information for external scenes is converted into neuronal signals on retinal photoreceptors. It is known that cone cells in the photoreceptor layer form a particular mosaic-like alignment called the cone mosaic[25]–[27]. Furthermore, cone cells are packed around the foveal region and become sparse as a function of distance from the fovea[28]. That is, much information of the external scene is sampled around the fovea and less information is sampled in the periphery. However, the effects of the cone mosaic on visual functions caused by fixational eye movements is not understood.

Here we focus on the effects of cone mosaic and fixational eye movements on the input to the visual system, i.e., on the information encoded by retinal photoreceptors (cones). We integrate physiologically realistic models of fixational eye movements excepting tremor, eye optics, and responsiveness and spatial mosaics of the three cone types, showing that the information rate of the cone population is greatly increased by fixational eye movements.

2. Model

2.1 General Structure

Figure 1 A illustrates the constructed model. The structure of the model we used in the current study consists of an eye...
movement part, an eye optics part, and the retinal photoreceptors part. The constructed model allowed us to evaluate signal processing in the neuronal stream from eye movement generation to the photoreceptors without a missing link. Each of the parts, called sub-models in our framework, were separately constructed with parallelization, and then those were connected using the PLATO environment [29]. In brief, the PLATO environment provides a MPI-based model connection interface (Interface) and an agent system (Agent). Figure 1 B illustrates schematic diagram of an example of model integration in the PLATO environment. The Interface automatically connects sub-models based on XML-based model description codes with supporting multiple programming languages in the simulation. The XML-based model description code includes a sub-model connection pattern and data structure of the IO between sub-models and is prepared in advance for the development of each of the sub-models. The data file is accessed via the Interface during simulation. The Agent controls all models with consideration of the IO timing, access to the data file through the Interface, and the progress of each model. Therefore, the connected models work as one system in the PLATO environment.

2.2 Eye Movement Model

The detail of the model for the generation of fixational eye movement is described elsewhere in Inagaki et al. 2011 [30]. Figure 1 C illustrates the network architecture of the eye movement model utilized in the simulation. In brief, the model consists of a tonic neuron (TN), an excitatory burst neuron (EBN), an inhibitory burst neuron (IBN), omnipause neuron (OPN), an integrator neuronal network formed by recurrent connections of 15 integrator neurons, and an eye plant for generating horizontal and vertical fixational eye movements (microsaccade and drift) without tremor. Each of the neurons in the model is described by a conductance-based spiking neuron model. The model size (number of neurons) is comparable to 25 to 40 neurons found in the goldfish oculomotor integrator network [31].

The tonic neuron is activated by a constant current input to replicate the resting activity of vestibular neurons. To generate a saccade-related burst, the EBN and the IBN are activated by a constant current input that corresponds to the signal from the superior colliculus. Also, the EBN and the IBN receive inhibitory input from OPN during fixation when fixational eye movements are generated. The integrator neuronal network is formed by recurrent excitatory synaptic connections of the 15 integrator neurons, and an eye plant for generating horizontal and vertical fixational eye movements (microsaccade and drift) without tremor. Each of the neurons in the model is described by a conductance-based spiking neuron model. The model size (number of neurons) is comparable to 25 to 40 neurons found in the goldfish oculomotor integrator network [31].

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The non-uniform spatial distribution of the cones was generated by a stochastic algorithm. To reproduce the non-uniform spatial distribution of cones, we approximated the cone \((d_{cone})\) and rod density \((d_{rod})\) distribution [28] using following equation, where \(\theta\) is the visual angle from the fovea:

\[
d_{cone} = \frac{19900}{1+2.32\theta} + 1200
\]

\[
d_{rod} = 0.0516\theta^2 - 0.8586\theta^4 + 56.08\theta^5 - 1793.33\theta^6 + 26858.3\theta + 8901
\]

The cone mosaic was generated on a 36 million cell array (6000x6000) in which photoreceptor types \((type_{cell})\) are assigned to each cell array according to the following equations:

\[
p_{cone} = \frac{d_{cone}}{d_{cone} + d_{rod}}
\]

\[
type_{cell} = \begin{cases} 
\text{cone} & \text{if} \ (p_{rand} < p_{cone}) \\
\text{rod} & \text{elsewhere}
\end{cases}
\]

\[
type_{cone} = \begin{cases} 
S & \text{if} \ (p_{rand} < p_s) \\
M & \text{if} \ (p_{rand} < p_s + p_m) \\
L & \text{elsewhere}
\end{cases}
\]

\(p_{cone}\) is existence probability of the cone in the cell array. \(p_{rand}\) is the uniform random number ranging from 0 to 1. \(p_s\) and \(p_m\) denote the existence probability of the S type cone and M type cone, and are set at 0.1 and 0.45, respectively. The light response of cones is modeled by ordinary differential equations of the membrane dynamics [37], where the spectrum sensitivity of cones also implemented based on the physiological evidence [38]. For the details of the calculation of the light response with consideration of the spectrum sensitivity, refer to van Hateren and Snippe, 2007 [37] and Baylor et al., 1987 [38].

2.5 Model Simulation

The fixation of stationary images was simulated by means of the constructed model. The stationary images comprised 8 various scenes including human, texture, natural image, etc. The simulation was run on the K-computer (SPARC 64 VIII fx 88128 Cores), or on the RIKEN Integrated Cluster of Cluster in RIKEN (Intel Xeon 8000 Cores). We simulated fixation of the stationary image with or without fixational eye movements to understand its roles in photoreceptor signal processing. Fixational eye movements were added after a 1 second simulation to avoid a transient response of the photoreceptors. Fixation was simulated for 4 seconds by which time the information rate mentioned in the following section had reached a plateau. Also, we simulated the same fixational eye movements due to the thought that variability in generated fixational eye movements might affect the information rate analysis. The duration of the simulation step of each of the models were the following: 0.1 ms in the eye movement model, 30 ms in the eye optics model, and 0.1 ms in the photoreceptor model. Here fine simulation step was utilized in the eye movement model and the photoreceptor model.
model due to the accurate calculation of neuronal spike and membrane potential. The variations in the simulation step time were automatically adjusted by PLATO.

2.6 Analysis

The quantitative analysis of the sampling of external information by the cone mosaic was performed with respect to the information rate [39]. We applied information rate analysis for the simulated cone responses during fixation of stationary scenes with/without fixational eye movements. In the present study, information rate is calculated using entropy. The details of the calculation of the information rate is referred to Garrigan et al. 2010 [39]. In brief, the entropy of the response is calculated as taking the entropy of noise from entropy of response. Then, the entropy between the cone mosaic response \( S \) and the external input \( E_{in} \) can be estimated as follows:

\[
I_{E}(S, E_{in}) = - \sum_{s \in S} p(s) \log_2[p(s)] \tag{7}
\]

\( s \) denotes a particular cone mosaic response level in the band of whole response \( S \). Here we utilized the membrane potential of the cones’ response to the input of the stationary external image for \( s \). The probability of \( s \) is \( p(s) \). The entropy is also related to the noise level. However, we did not calculate entropy for the noise due to the fact that it was negligible than the response of cones in our simulation.

3. Simulation Results

3.1 General Structure General Response of Eye Optics and the Cone Mosaic

First, we checked the responses of the eye optics and the outputs of the photoreceptors for the stationary external image. Figure 1 E summarizes the input of the stationary external image, output of the eye optics model, and the response of the cones. For visualization, the output of the eye optics and the response of cones were normalized from 0.0cd to 100.0 cd and from 0 mV to 32 mV, respectively. Also, the output of the eye optics and the response of cones were represented using pseudo-color and grayscale, respectively. We confirmed the reproduction of the cone mosaic—the responses of the cones were packed around the foveal region while they became sparse with increasing distance from the fovea. Note that the blank response area in the cone mosaic due to nonexistent of cones.

3.2 Effect of Fixational Eye Movement in the Fixation of the Stationary Scene

To evaluate the effect of fixational eye movements in visual sampling by the cone mosaic, fixation of the stationary scene was simulated by the constructed model. We simulated 4 seconds of fixation of a stationary scene either with fixational eye movements or without them. The image sampled by the cone mosaic \( I \) was calculated as the temporal average of the membrane potential of each cone with the following equation:

\[
I(x, y, T) = \frac{1}{T} \int_0^T s(x + x_p, y + y_p, t) \, dt \tag{8}
\]

\( s_i \) represents the membrane potential of each cone. \( x \) and \( y \) represent the coordinates for the world axis of the sampled image by the cone mosaic. \( x_p \) and \( y_p \) represent the displacement of the sample positions due to fixational eye movements. To evaluate the effect of fixational eye movements on the visual sampling by the cone mosaic, a difference image between the sampled image with fixational eye movements and one without fixational eye movements was calculated.

Figure 2 summarizes the differences in the image sampled by the cone mosaic during the 4 seconds of fixation of the stationary scene with and without fixational eye movements. The sparse response in the sampled image was improved with fixational eye movements (Fig. 2 A) though the response still existed without fixational eye movements (Fig. 2 B). In particular, the sparse response near the foveal region was dramatically improved. Enhancement of the edges in the stationary scene was also clearly observed in the difference image between average response of cones with fixational eye movements and average response of cones without fixational eye movements (Fig. 2 C).

3.3 Analysis of Information Rate on Sampling by the Cone Mosaic

To quantitatively analyze effect of fixational eye
movements, we utilized the information rate as an index. The information rate of the sampled image was estimated at every simulation step in 8 different stationary scenes. Figure 3 illustrates the fixational eye movements and the changes in the information rate during fixation of the 8 scenes with/without fixational eye movements. An elevation of the information rate was observed when fixational eye movements were added, whereas it decayed to the plateau level when no fixational eye movements were present. Specifically, the large elevation of the information rate was found when the microsaccade occurred, whereas a gradual elevation was observed during ocular drifts. Note that the information rate was saturated in the 4-second fixation.

Next, we calculated significance of the information rate for the external scene sampled by the cone mosaic with/without fixational eye movements, and separately calculated amount changes in information rate for microsaccades and drift. We used a value for the information rate at the 4-second in each of sampled images. The significance was evaluated using Wilcoxon signed rank test. Figure 4 summarizes the changes in the information rate for the 8 stationary images with and without fixational eye movements. A significant increase of information rate with fixational eye movements was confirmed \( (p < 0.01, n = 8) \). Moreover, amount of changes in information rate caused by microsaccades is significantly larger than one caused by drifts \( (p < 0.01, n = 8) \). This indicates that microsaccades is the main player for enhancement of information rate.

4. Discussion

Several research groups have elucidated the functional roles of fixational eye movements in vision through vision research and related computational studies. For instance, it was revealed that fixational eye movements prevent visual fading caused by continuous fixation [2], [7]–[10]. Microsaccades, one component of fixational eye movements, improve vision among wide spatial frequency band [10]–[15], [40]. It has been suggested that microsaccades are correlated with attentional shifts to peripheral objects [41]–[43]. Moreover, fixational eye movements also contribute coarse to fine tuning of visual signal with shaping spatial-temporal characteristics to provide a stable vision [19]–[23].

As described, many visual functions related fixational eye movements have been unveiled. However, the mosaic like alignment of cones (the cone mosaic) has not been considered, and the effects of the cone mosaic on visual signal processing mentioned above are not fully understand.

In the present study, we explored the impact of fixational eye movements on the signal processing in photoreceptors, the first stage of visual input to the brain, during visual sampling. A mathematical model composed of eye movement generation, eye optics, and photoreceptors was developed based upon anatomical and physiological characteristics and integrated by the PLATO system. The constructed photoreceptor sub-model also reflected the specific alignment pattern of cone cell known as the cone mosaic. Consequently, the integrated model can simulate responses from eye optics and photoreceptors with consideration of fixational eye movements without a missing link.

4.1 Function of Fixational Eye Movements

In the past, fixational eye movements were considered to be an artifact [5]. In the past few decades, several lines of novel functions of fixational eye movements in vision have been gradually uncovered by vision research due to the evolution of technology for the measurement of eye movements and computational studies. It is reported that microsaccades enhance low-frequency vision [11], [12], improve the visualization of high-spatial frequency components of scenes, such as edges and small targets [13]–[15] and shift foveal locus to highest acuity [16]–[18]. Furthermore, fixational eye movements also contribute coarse to fine tuning of visual signal with shaping spatial-temporal characteristics to provide a stable vision [19]–[23]. However, those fixational eye movements related functions have been missing the effects of the cone mosaic on visual sampling.
In the present study, we evaluated the function of fixational eye movements by a computer simulation of sparse sampling with the cone mosaic during fixation using information rate analysis. From the computer simulation of stationary scene fixation, we confirmed that fixational eye movements enhance information for edges in a scene and spatially smooth information sampled by the cone mosaic, especially around the foveal region. As a result, the information rate for the external scene sampled by the cone mosaic during fixation is significantly increased by fixational eye movements. Furthermore, most of the increasing of information rate corresponding edge area in Fig. 2C is originated by microsaccades. At this process, visual fading is counteracted by ocular drift in our computer simulation as reported in Kuang et al. [18] and Poleti and Rucci [19].

Our results first found the functional roles of fixational eye movements on retinal photoreceptors and demonstrated that the photoreceptors have rich capacities of visual signal processing, as represented by the increased information rate, especially edge enhancement and smoothing, associated with fixational eye movements.

4.2 Roles of Microsaccade and Drift

The sampling of clear external information, particularly for key scene components such as the edges of objects, is important for perception and recognition. It was reported that temporal modulation caused by fixational eye movements contribute coarse to the fine tuning of visual signal with shaping spatial-temporal characteristics to provide a stable vision [19]–[23]. Our computer simulation for visual sampling by the cone mosaic showed that the information rate is gradually increased during ocular drifts, whereas it is largely elevated by the initial few microsaccades (Fig. 3 A). Namely, the initial few microsaccades that cause edge enhancement are more effective on the elevation of information rate, whereas the gradual elevation of the information rate is caused by the smoothing of corrupted sample information due to the cone mosaic by ocular drifts as shown in especially foveal/parfoveal area (Fig. 3 A). Furthermore, a large portion of the increase information rate is originated by microsaccades (Fig. 4). The large elevation of the information rate for the sampled external scene related to the enhancement of edges (Fig. 2 C). Those results imply that large amplitude of fixational eye movement (microsaccade) potentially more effective than smaller one (drift) on the increase of information rate. In this process, a clear relationship between the amplitude of the microsaccade and the increase of information rate are not found. One of the possibilities, the direction of the microsaccade and/or edge pattern of the scene might be contributed to the process of the increase of information rate, and those need to be clarified in the future simulation works. In the model, the sampled information by the cone mosaic is temporally accumulated into a response of each photoreceptor. Therefore, our results also support that temporal modulation accompanied by fixational eye movements contribute to shaping the spatial characteristics [19]–[23].

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