# Extracting Motion Information Using a Biologically Realistic Model Retina

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**Abstract**. We show that neither linear nor static nonlinear operations in computational models are capable of precisely reproducing the observed characteristics of retina ganglion cells (RGCs) responding to dynamic stimuli. In particular, velocity tuning of single cells stimulated by uniform motion and the signaling of motion starts and stops by a RGC population are considered. In both cases, the consideration of a dynamic non-linear feedback loop originally introduced to explain contrast gain control effects brings the temporal properties of the model into agreement with experimental findings from multielectrode recordings.

#### 1 Introduction

In biological visual systems, complex image processing is known to occur as early as on the retinal level. The result of this processing is the spiking activity of retinal ganglion cells (RGCs), which is transmitted to higher visual centers via the optic nerve. Since the corresponding firing rates are always positive, a spatio-temporal convolution of the visual scene followed by a static rectification appears to be the simplest appropriate choice for mapping retinal function onto a mathematical model [6].

However, there are additional non-linearities that contribute to retinal processing [5]. For example, a major characteristic of retinal responses is the saturation at high stimulus contrast. There is general agreement that this contrast dependence is not, as one could expect, mediated by a static non-linearity, but by a dynamical feedback loop. This discovery dates back to 1978, when Shapley and Victor [8] found that stimulus contrast modulated the time course of retinal responses in a non-trivial way. Despite the fact that this contrast gain control (CGC) mechanism is now well-characterized in terms of mathematical modeling, its function for image processing is still unclear. In this paper, we use mathematical modeling and extracellular multi-electrode recordings of RGC activity to show that dynamical CGC is a key factor in the processing of motion patterns, and conclude that one of its major functions is to enable a representational tracking of stimulus movement.

#### 2 Computational Retina Model

In order to study the effects of dynamical CGC on the responses of RGCs, we used the following model of retinal response generation. The spatiotemporal stimulus contrast pattern  $s(\mathbf{r}, t)$  is first convolved with a kernel function  $K(\mathbf{r}, t)$  that resembles the receptive field properties of individual RGCs,

$$u(\mathbf{r}, t) = g(\mathbf{r}, t) \left[ K(\mathbf{r}, t) * s(\mathbf{r}, t - \delta) \right].$$
(1)

 $g(\mathbf{r},t)$  is a modulation factor to be specified below,  $\delta$  is the response latency, and "\*" denotes a convolution. From the activation  $u(\mathbf{r},t)$ , the firing rate pattern of the RGCs,  $f(\mathbf{r},t)$ , is obtained by rectification,

$$f(\mathbf{r},t) = \tilde{\alpha} \left[ u(\mathbf{r},t) + \Theta \right]_{+}$$
(2)

where  $\tilde{\alpha}$  and  $\Theta \geq 0$  determine scale and baseline value, respectively,  $[x]_+ := xH(x)$  is the rectification operator, and  $H(\cdot)$  is the Heaviside step function. The kernel function  $K(\mathbf{r}, t)$  in (1) is assumed to factorize into a spatial and a temporal part,  $K(\mathbf{r}, t) = K_{\rm s}(\mathbf{r}) K_{\rm t}(t)$ , where the former exhibits a spatial "difference of Gaussians" profile, and the latter acts as a high-pass filter [6]:

$$K_{\rm s}(\mathbf{r}) = \frac{g_+}{2\pi\sigma_+^2} \exp\left(-\frac{\mathbf{r}^2}{2\sigma_+^2}\right) - \frac{g_-}{2\pi\beta^2\sigma_+^2} \exp\left(-\frac{\mathbf{r}^2}{2\beta^2\sigma_+^2}\right), \qquad (3)$$

$$K_{t}(t) = \delta(t) - \alpha H(t) \exp(-\alpha t).$$
(4)

The parameters  $g_+$  and  $g_-$  determine the relative weights of center and surround, respectively, while  $\sigma_+$  and  $\beta \sigma_+$  (with  $\beta > 1$ ) are their diameters. In the temporal part,  $\alpha^{-1}$  is the decay time constant of the response, and  $\delta(t)$  denotes the Dirac delta function. The numerical values for the parameters  $\delta = 100$  ms,  $g_+ = 3$ ,  $g_- = 0.8g_+$ ,  $\sigma_+ = 80 \,\mu\text{m}$ ,  $\beta = 3$ , and  $\alpha = 4 \,\text{Hz}$  could be determined by matching the model to other experiments [9, 3, 1].

Berry II et al. [1] suggested a CGC feedback loop involving a low-pass temporal integration of the activation,

$$v(\mathbf{r}, t) := B u(\mathbf{r}, t) * [H(t) \exp(-t/\tau)], \qquad (5)$$

transformed into a local modulation factor  $g(\mathbf{r}, t) \in [0, 1]$  for the activation via

$$g(\mathbf{r},t) = \frac{1}{1 + \{[v(\mathbf{r},t)]_+\}^4}.$$
 (6)

Strength and time course of the CGC modulation are determined by the parameters B and  $\tau$ , respectively. Incorporating this feedback loop into our retina model generates a delayed suppression of high, sustained activation, thus altering the temporal characteristics of RGC firing. Choosing  $\tau = 170 \text{ ms}$  and B = 85 Hz yields good agreement with the results of Ref. [1].

#### **3** Contrast Gain Control and Tuning Properties

Time-averaged response properties of single RGCs are conventionally summarized in tuning curves. In order to quantify the effect of CGC on the timeaveraged response of RGCs, we therefore studied their tuning properties with respect to stimulus contrast and velocity with and without CGC. Fig. 1a shows



Figure 1: Tuning curves of model retinal ganglion cells with and without dynamical contrast gain control. (a) Mean response firing rate with (solid) and without (dashed) gain control as a function of the contrast of a continuously moving dark bar (velocity  $0.44 \,\mu\text{m/ms}$ , width 133 ms) in front of a white background. (b) Mean response firing rate of a model RGC with (solid) and without (dashed) gain control as a function of the velocity of the bar from (a) at 100 % contrast. Inset: same data in a log-log plot.

that the CGC feedback yields the expected contrast saturation of the response. In addition, it exerts a non-trivial effect on the velocity tuning, as shown in Fig. 1b. In contrast to the tuning curve for RGCs without CGC, the CGC model cell exhibits a velocity tuning that is closer to a power law (straight line in the log-log plot) with exponent  $\approx 0.3$  over a wide range of velocities. Power-law velocity tuning of this type has been reported frequently in studies of RGC response properties, e.g. [4, 7]. Thus, CGC contributes to the empirically encountered form of time-averaged contrast and velocity tuning of RGCs.

## 4 Role of Dynamic Contrast Gain Control in Motion Processing

Since the CGC feedback loop implemented in our model involves a temporal integration, it also alters the time course of RGC responses. This effect was

demonstrated by a study that investigated the response of individual RGCs to a continuously moving bar, which led Berry II et al. [1] to the conclusion that CGC is involved in retinal motion processing. They found that the peak of retinal activity is shifted in the direction of stimulus motion, so that a "motion anticipation" effect results. This suggests that retinal CGC may be responsible for the psychophysical flash lag effect, which, however, turned out not to be the case [2]. Thus, the function of dynamical CGC is still controversially discussed.

Here we pursue the idea that CGC plays a role in the formation of a population code for stimulus motion patterns. As a stimulus, we used a white light bar (0.1 mm wide) performing a stepwise motion perpendicular to its orientation: Continuous movement with a speed of  $0.44 \,\mu\text{m/ms}$  lasted for 500 ms. The bar was then stopped but still visible for another 500 ms before it started moving again for another 500 ms, and to on. This stepwise motion stimulus was used as input to our retina model, and also applied in a multi-electrode recording experiment with an isolated turtle retina. In the experiment, we acquired action potentials from a population of RGCs, which were pooled over many stimulus repetitions to find a population firing rate at each time step. The experimental preparation, the recording setup, and the data processing are described in detail in another publication [10].

We will demonstrate that the CGC loop is necessary for the generation of the reponse characteristics found empirically. This is achieved by comparing the full model with CGC loop to a version without CGC loop (B=0). The free parameters  $\tilde{\alpha}$  and  $\Theta$  (and B for the full model) were determined by minimizing the mean squared deviation between model and measured activity. Fig. 2 shows the population response to a succession of movement steps together with the predictions of the different model versions. Periods of stimulus movement were from t = 0 ms to t = 500 ms and from t = 1000 ms to t = 1500 ms. The response latency of about 100 ms is clearly visible, after which the motion onset is signaled by a sharp 300% rise in retinal population discharge rate. Following motion offset, the retinal activity exhibits an equally steep drop. Thus, the retinal population signal closely follows the movement pattern. The plot clearly shows that only the model with CGC loop is capable of reproducing the steep rise of the population activity upon motion onset. The onset response of the model without CGC is too slow, since it is governed by the time constant of the linear kernel,  $\alpha^{-1} = 250 \,\mathrm{ms}$ .

Even though the high value of  $\alpha^{-1}$  is found in several independent measurements [9, 3], it is an interesting question whether a model without CGC but with a smaller time constant could yield a better agreement with the experimental data. This turns out not to be the case: Allowing  $\alpha$  to be adjusted in the model without CGC does indeed yield a smaller time constant  $\alpha^{-1} = 41.7$  ms, but no better agreement with the experiment. This is shown in Fig. 2 (dotted line), which demonstrates that this model version fails to exhibit the relatively slow decay of the retinal activity following the stop of stimulus motion.



Figure 2: **Upper panel:** Population response of turtle retinal ganglion cells (solid, 219 RGCs, 450 stimulus repetitions) to stepwise motion (500 ms movement, 500 ms pause) of a bright bar (width 100 µm) as a function of time. Shaded area indicates standard error. Corresponding output of the retina model with contrast gain control loop (dashed), without contrast gain control (dot-dashed), and without contrast gain control but with adjusted linear time constant  $\alpha$  (dotted). Lower panel: Deviation of the mean experimental population response from the three model scenarios as a function of time.

### 5 Summary and Conclusions

In summary, we find that CGC has a profound impact on the response characteristics of RGCs. First, the retina model with CGC feedback describes the experimentally observed time-averaged contrast and velocity tuning of RGCs better than a corresponding model without CGC. To investigate the effect of CGC on the temporal course of responses, we used a stepwise motion pattern of a bar stimulus. Multi-electrode recordings of a RGC population responding to this stimulus exhibited an extremely steep rise of activity shortly after motion onset, and an equally steep drop after the stimulus stopped its motion (Fig. 2). A comparison with several variants of our retina model lead to the conclusion that CGC is a key ingredient in the formation of the movement pattern population code. Models without CGC do either not reproduce the fast onset response (for  $\alpha$  fixed to biologically plausible 4 Hz), or yield a reponse decay that is too fast (for adjustable  $\alpha$ ). Thus, we have demonstrated that retinal responses to moving stimuli can only be explained by computational models that include a contrast gain control operation, i. e., negative feedback of lowpass filtered recent activity. This result suggests that one of the functions of CGC could be to allow the retina to accurately follow changes of stimulus motion despite the relatively high time constant in its linear operation.

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