Adaptive contrast gain control and information maximization ☆

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Abstract

Contrast gain control is an important mechanism underlying the visual system's adaptation to contrast of luminance in varying visual environments. Our previous work showed that the threshold and saturation determine the preferred contrast sensitivity as well as the maximum information coding capacity of the neuronal model. In this report, we investigated the design principles underlying adaptation behavior in contrast gain control by an adaptive linear–nonlinear model. We found that an adaptive rescaling mechanism predicted by information transmission maximization can explain a variety of observed contrast gain control phenomena in neurophysiological experiments, including the divisive input–output relations, and the inverse power-law relation between response gain and input contrast. Our results suggest that contrast gain control in visual systems might be designed for information maximization.
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1. Introduction

The visual systems exhibit great flexibility in adapting their input–output functions to the variance or the contrast [6,9,10,12] of light signal in the visual environment. The amplitude gain of the transfer function of visual neurons was found to decrease with input variance [9], and even displays an inverse power-law relation [12] (see Fig. 2). In addition, the contrast response function in visual cortical neurons was found to shift along the log contrast axis to adaptively match the prevailing input signals [6]. These contrast adaptation phenomena have been widely observed in the retina [9], striate [6], and extrastriate visual cortex [5] of mammals, and fly H1 neurons [1,3] suggesting the existence of an contrast gain control mechanism. However, the biophysical factors and computational rules governing its operation remain elusive. How to understand these phenomena? Why do visual neurons behave in this way?

We have shown that classical neuronal model with nonlinearities of threshold and saturation can display an apparent adaptation in the recovered transfer function to the variance of the input signal [13,14]. However, we found that the mutual information in those system, as well as the kernel gain, exhibit a bell-shape as a function of the input variance [6]. There is only one optimal variance that can induce the maximal information transmission of the system. That means nonlinear dynamics due to static nonlinearity alone cannot maintain a neuron's information transmission rate at the highest level with the variation in signal variance. Here, we explored theoretically a possible extra adaptation mechanism that might restore information maximization for any input variance in neurons. We introduce an additional gain rescaling to the static model, while keeping all other parameters (thresholds, saturation levels, membrane time constants) constant. We found it sufficient to produce information maximization that is consistent with some neurophysiological findings [1,3].

2. Model and results

We use the similar standard linear–nonlinear (LN) cascade model as in Ref. [14] except that we introduce an additional scaling factor $\beta(\sigma)$. See Fig. 1. β scales the
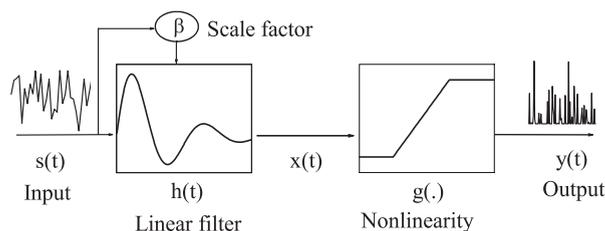

Fig. 1. The adaptive LN model consists of a linear filter $h(t)$ followed by a nonlinearity $g(.)$. The amplitude of the linear filter $h(t)$ is controlled by β, which acts as an adaptive mechanism. $x(t)$ is the convolution of the input signal $s(t)$ and the filter $h(t)$. The nonlinearity $g(.)$ operates on $x(t)$ to generate the output $y(t)$.

amplitude of the linear kernel according to the variance of the input signal as an adaptive mechanism. Linear kernel is given by $h(t) = \beta(\sigma)A\sin(\pi t/\tau_a)\exp(-t/\tau_b)$ with $A = 1$, $\tau_a = 80$ ms and $\tau_b = 100$ ms. The output of linear kernel $x(t)$ is given by $x(t) = \int_0^{+\infty} h(\tau)s(t-\tau)\,d\tau$. The nonlinearity $g(.)$ is specified by

$$g(x) = \begin{cases} 0 & \text{if } x < \theta, \\ x - \theta & \text{if } \theta \leqslant x < \eta, \\ \eta - \theta & \text{if } x \geqslant \eta, \end{cases} \tag{1}$$

where θ is the threshold and η is the saturation level. Without loss of generality, we use a Gaussian white noise stimulus $s(t)$ with zero mean and SD σ as the input signal. Its probability density function (PDF) is given by

$$p(s) = \frac{1}{\sqrt{2\pi\sigma^2}}\, e^{-s^2/2\sigma^2}.$$

The linear response $x(t)$ also has a Gaussian distribution with PDF

$$p(x) = \frac{1}{\sqrt{2\pi\sigma_x^2}}\, e^{-x^2/2\sigma_x^2},$$

where σ_x is given by

$$\sigma_x^2 = \langle x^2(t) \rangle = \sigma^2 \int_0^{+\infty} h^2(\tau)\,d\tau,$$

where $\langle \cdots \rangle$ denotes time average. β is determined computationally by maximizing the mutual information between $s(t)$ and $y(t)$ with respect to β, for signals of a given σ. This is the adaptive LN model.

We have shown the amplitude gain of the recovered linear kernel of the static model is a function of the input signal variance σ^2 [3]. The ratio α between the amplitude gain of the recovered linear kernel $h'(t)$ and the original linear kernel $h(t)$ is given by

$$\alpha = \frac{\int_\theta^\eta x(x-\theta)p(x)\,dx + (\eta-\theta)\int_\eta^{+\infty} xp(x)\,dx}{\sigma^2 \int_0^{+\infty} h^2(\tau)\,d\tau}. \tag{2}$$

That is, for an input signal with Gaussian white distribution, we have $h'(t) = \alpha.h(t)$, where gain factor α quantifies how the performance of linear function $h(t)$ is affected by the static nonlinearity (threshold θ, saturation η) and stimulus standard deviation σ. Mutual information [8] quantifies the ability of a system or a communication channel to convey information and is given by

$$\begin{aligned} I_m &= H(y) - H(y \mid s) \\ &= -\sum_y P(y)\log_2 P(y) + \sum_{s,y} P(s)P(y \mid s)\log_2 P(y \mid s), \end{aligned} \tag{3}$$

where $H(y)$ is the total entropy of the response, $H(y \mid s)$ is noise entropy, accounting for the variability in the response that is not due to variations in the stimulus, but comes from other noise sources. For simplicity, we consider the noiseless case, where

$H(y \mid s) = 0$. In this case, the mutual information is simply equal to the output entropy $I_m = H(y)$.

We are interested in computing the entropy of the output y. The distribution function of y (also refereed to as the cumulative density function) is

$$D(y) = P[Y \leqslant y] = \begin{cases} 0 & \text{if } y < 0, \\ \int_{-\infty}^{y+\theta} p(x)\, \mathrm{d}x & \text{if } 0 \leqslant y < \eta - \theta, \\ 1 & \text{if } y \geqslant \eta - \theta. \end{cases} \tag{4}$$

In order to compute the entropy of y, we approximate y by a discrete random variable $\hat{y}$, which we define by $P[\hat{y} = i\Delta y] = P[y \in [(i-1)\Delta y, i\Delta y]]$, where Δy is the quantization resolution of y, and i is an integer from 0 to $\lceil (\eta - \theta)/(\Delta y) \rceil$. Note that $P[y \in (a, b]]$ can be computed analytically as $D(b) - D(a)$. The mutual information, which is equal to entropy for the noiseless case, is then computed as in Eq. (3). It can be shown that changes in Δy affect the entropy of $\hat{y}$ only by an additive constant [2]. Since we are only interested in comparing the values of mutual information I_m as we change σ, θ, and η, our choice of Δy does not affect our results. Here, we set $\Delta y = 1$.

What is the effect of different amplitude of β on the information transmission? Fig. 2a shows that there is a non-monotonous relation between β and I_m for each given σ. There exists an optimal value of β, named β_{opt} where information I_m is
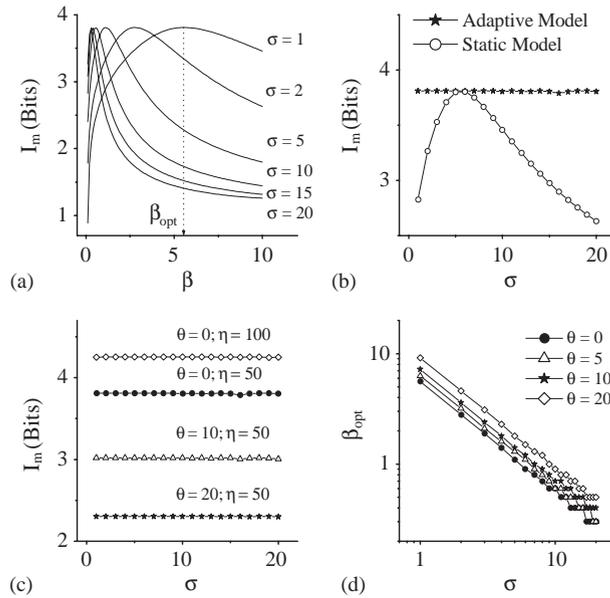

Fig. 2. (a) For an adaptive LN model with threshold $\theta = 0$ and saturation $\eta = 50$, mutual information I as a function of rescaling factor β for signals of different σ's. (b) The mutual information I as a function of σ for the adaptive LN model and the static LN model. (c) Mutual information I as a function of σ for various model parameters with β chosen to maximize I for each σ. (d) Optimal β as a function of σ for four given values of threshold in a log–log plot exhibits an inverse power law.
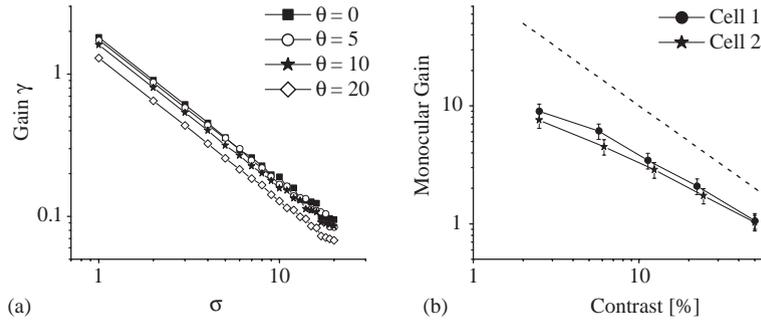
Fig. 3. (a) Gain γ as a function of σ for four given values of threshold with β optimized for information transmission. (b) Monocular gain in two cat simple cells as a function of stimulus contrast (from 2.5% to 50%) in the log–log axes; for comparison, a line with slope of -1 is plotted in dashed line. Adapted from Fig. 5. of Ref. [12].

maximized. Let's now assume that the biological goal of an adaptive neuron is to maximize information transmission. That is, for any input σ, the neuron will adjust its linear function amplitude to get β_{opt}. Fig. 2b shows that the information transmission Imax for such an adaptive LN model is maintained at the highest level for any given variance. Note that for the static LN model with $\beta = 1, I_m$ varies with σ, with only one global maximum I_{max} at a particular σ (see Fig. 2b). The signal with nonoptimal value cannot be efficiently processed by the system with high transmission rate. However, the adaptive model can ensure that signal with any distribution σ can always be processed with highest information transmission rate. The highest value of information transmission is constrained only by the threshold and the saturation of the model itself [8,9]. The lower (or higher) is the threshold (saturation), the higher the maximum information rate can be reached (Fig. 2c). The adaptation factor β_{opt} decreases monotonously with an increase in σ. Interestingly, in the log-log plot, β_{opt} and σ displays a inverse power law relationship, the fitting slope is -1 (Fig. 2d).

The response gain γ, i.e., the amplitude of the recovered kernel, now equal to $\alpha * \beta$ (see Eq. (2)), also displays a scale invariant power-law relationship with a scale -1 with σ (Fig. 3a). Note that without gain rescaling, i.e., $\beta = 1$ is fixed, the gain γ varies with σ, displaying a bell-like tuning curve, which emerges simply from static-nonlinearity. Gain rescaling is crucial for maintaining mutual information constant with variation in σ. This power law finding matches the experimental observation (see Fig. 3b) very well, thus implying that the contrast gain adaptation observed in experiments may reflect an underlying efficient encoding process. Fig. 3b is adapted from Fig. 5a in Ref. [12], which shows that response gain of cat simple cell varying with the contrast of monocular input also in power-law relationship in the log-contrast plot. A contrast gain slope of -1 indicates that the gain control system is 100% effective, whereas a slope of 0 indicates that the system is completely ineffective. The cells in Fig. 3b showed a slope around -0.75 suggesting the neurons might be trying to re-scale gain adaptively in order maximize information transmission.

3. Discussion

The power-law relationship observed experimentally and the theoretical findings of this paper suggests that there might exist an intrinsic adaptation mechanism in single neurons or network to maximize the information encoding. Such an adaptation, which is independent of static nonlinearity, involves mainly changing of the amplitude of the linear transfer function. Biophysically, a single neuron itself is a circuit, whose transfer function is controlled by the ionic conductances and capacitances. Recent experiments showed that the activation of Na^+-activated and Ca^{2+}-activated K^+ currents inside single cells [4,7] or the adjustment of voltage-dependent conductance might play an important role in contrast adaptation [11]. These mechanisms might serve to control the gain of the linear kernel part of the LN cascade.

In summary, the contrast adaptation phenomena observed in neurophysiological experiments can potentially be factored into a component due simply to the static nonlinearities of the neurons [6,9] and another component due to an adaptive rescaling of the gain in the linear transfer function in the LN cascade for the purpose of information maximization.

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