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The role of spiking nonlinearity in contrast gain control and information transmission

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Abstract

Threshold and saturation are two nonlinear features common to almost all spiking neurons. How these nonlinearities affect the performance gain of the transfer function and coding properties of the neurons has attracted much attention. Here, we deduce basic analytical relationships among these nonlinearities (threshold and saturation), performance gain and information transmission in neurons. We found that performance gain and information transmission can be maximized by input signals with optimal variance. The threshold and saturation inside the model determines the gain tuning property and maximum coding capacity. This framework provides an understanding of some basic design principles underlying information processing systems that can be adjusted to match the statistics of signals in the environment. This study also isolates the exact contributions of the nonlinearities on the contrast adaptation phenomena observed in real visual neurons.

Keywords: Static nonlinearity; Contrast gain control; Information transmission; Gain tuning

1. Introduction

For an arbitrary visual stimulus, its fluctuations around the mean value are characterized by contrast (which we define as signal variance). When we double the amplitude of the signal while keeping the signal structures invariant, do neurons encode the signal in the same way? Experimental evidence has shown that visual neurons in the retina and visual cortex could effectively adjust the gain of their transfer functions to maintain a high sensitivity at varying luminance contrast levels (Ohzawa, Sclar, & Freeman, 1982, 1985; Shapley & Victor, 1978, 1979, 1980). This implies that there exists a contrast gain control mechanism (Ohzawa et al., 1982, Ohzawa, Sclar, & Freeman, 1985; Shapley & Victor, 1978, 1979, 1980), which provides the visual system's great flexibility to function well under varying external conditions.

In the last few decades, many different aspects of contrast adaptation in visual neurons have been discovered and observed in experiments. In the retina, it was found that the amplitude of the recovered linear transfer function of retina ganglion neurons decreases as the input contrast increases (Benardete & Kaplan, 1999; Shapley & Enroth-Cugell, 1984). It has been suggested that a power law relation may exist between the input contrast and the amplitude gain (Chander & Chichilnisky, 2001; Truchard, Ohzawa, & Freeman, 2000). The contrast gain, defined as the mean neuronal response divided by the stimulus contrast, was found to depend on both the contrast and frequency component of input signals: as contrast increases, the contrast gain of the neuron in response to the signals with low temporal frequencies decreases dramatically, and the frequency tuning curve shifts towards high frequency band. In the primary

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striate and extra-striate visual cortex, besides the instantaneous adaptation of transfer functions to input contrast, another slower type of adaptation phenomenon has been found: with the increase of the mean contrast level (averaged over a period of 40 s), the contrast–response functions of the neuron shift primarily to the right along the log-contrast axis, suggesting that the cortical neuron could adaptively adjust its limited response range to match prevailing contrast levels (Ohzawa et al., 1982, 1985). The slope of the contrast–response curve was found to change with the increase of the mean contrast level, displaying a divisive or multiplicative effect (Geisler & Albrecht, 1992). These phenomena have been widely observed in neurons of various cortical areas, including the primary visual cortex (e.g. Geisler & Albrecht, 1992; Ohzawa et al., 1982; Ohzawa et al., 1985; Sanchez-Vives, Nowak, & McCormick, 2000; Truchard et al., 2000), the fly H1 neuron (Brenner, Agam, Bialek, & de Ruytervan Steveninck, 2000; Fairhall, Lewen, Bialek, & de Ruyter van Steveninck, 2001), and even motion-sensitive extrastriate cortex (Kohn & Movshon, 2003).

There has been great deal of interest in discovering the factors and biophysical mechanisms accounting for contrast adaptation phenomenon, and in attempting to model underlying gain control mechanisms. Various factors and mechanisms have been studied to account for the adaptive change of the transfer function to the input contrast, including the rectifying mechanism (Heeger, 1992; Sakai & Naka, 1995), post-receptor control loop (Sakai et al., 1995; Smirnakis, Berry, Warland, Bialek, & Meister, 1997), and network interactions (Victor, 1987). It was also suggested that the active ionic channels inside the spiking generation (Kim & Rieke, 2001; Sanchez-Vives et al., 2000) might play an important role in controlling the changing of the transfer function. In order to clarify the contrast gain control mechanism underlying divisive contrast–response functions in the visual cortex, many models have been developed, such as the long-standing normalization model based on shunting inhibition (Carandini, Heeger, & Movshon, 1997; Heeger, 1992). However, a later study (Holt & Koch, 1997) indicated that shunting inhibition cannot produce a divisive effect on neuronal responses, only a subtractive effect. Subsequent modeling studies have focused on the synaptic modulations. These include the recently emphasized synaptic depression mechanism (Abbott, Varela, Sen, & Nelson, 1997; Carandini, Heeger, & Senn, 2002; Chance, Nelson, & Abbott, 1998), complex neuronal model with combination of shunting inhibition and synaptic noise (Chance, Abbott, & Reyes, 2002; Prescott & De Koninck, 2003), a Hodgkin–Huxley model with pure excitatory and inhibitory synaptic modulations (Murphy & Miller, 2003), and others. These simulation studies provide potential models of the real contrast gain control mechanisms in visual neurons. However, the true biophysical substrate of gain control is still unclear (for reviews see Carandini, Heeger, & Movshon, 1999; Meister & Berry, 1999). Multiple mechanisms and various factors might coexist to affect various aspects of contrast gain adaptation (for reviews see Demb, 2002; Priebe & Ferster, 2002; Salinas & Thier, 2000). Therefore, it is important and necessary to figure out the basic factors controlling the changing transfer function of the neuron and the shifting contrast–response curves, and the principles in the neurodynamics underlying these factors. Considering that contrast gain control may also serve as a basis for efficient information encoding of the visual system (Atick & Redlich, 1992; Barlow, Fitzhugh, & Kuffler, 1957; Schwartz & Simoncelli, 2001), it is also necessary to clarify the exact roles of each possible factor for information transmission.

Recent experimental (Chander & Chichilnisky, 2001; Kim & Rieke, 2001) and theoretical studies (Paninski, 2003; Pillow & Simoncelli, 2003; Schwartz, Chichilnisky, & Simoncelli, 2002; Yu & Lee, 2003) indicated that earlier studies in mammalian retina (e.g. Arcas & Fairhall, 2003; Benardete & Kaplan, 1999; Brown & Masland, 2001; Shapley & Victor, 1978; Victor, 1987) which use traditional reverse correlation techniques, might fail to separate the effect of nonlinearities (threshold and saturation) from real adaptive behavior. That is, the change of the recovered transfer function due to input contrast observed in the experiments could emerge from two causes: nonlinearity and an unknown adaptive mechanism (Arcas & Fairhall, 2003; Chander & Chichilnisky, 2001; Kim & Rieke, 2001; Schwartz et al., 2002). New system identification techniques (Chander & Chichilnisky, 2001; Paninski, 2003; Pillow & Simoncelli, 2003; Schwartz et al., 2002) have been developed to recover the exact transfer functions by ruling out the effect due to nonlinearity. Moreover, our previous investigation (Yu & Lee, 2003) suggested that nonlinearities in the neuronal model might play an important role in the effect of the distribution of the input signal on the recovered transfer function. Thus, before we discover the real adaptive contrast gain control mechanisms, it might be necessary to make clear the exact contributions of static nonlinearities (e.g., threshold and saturation) on the observed contrast adaptation phenomena. In this paper, we will use a simple linear–nonlinear cascade model to give an analytical solution on the effect of the specific nonlinear factors on the changing gain of the apparent transfer function, and information transmission of the neurons to various inputs. The relations among nonlinearity, performance gain (the amplitude gain of the recovered linear kernel) and information transmission rate will be elucidated. In a sister paper (Yu, Potetz, & Lee, submitted for publication), we will make clear the additional adaptive mechanism accounting for contrast gain control under the principle of the maximal

information transmission. These studies seek to discover step by step the contributions of each necessary factor on contrast adaptation, and to provide a basic framework for understanding potential contrast gain control mechanisms, and helping experimental scientists to distinguish the nonlinearity induced "contrast adaptation" phenomenon from those induced by real contrast gain control mechanisms.

2. Model and methods

The neuronal model used here is a linear–nonlinear (LN) cascade model (see Fig. 1), i.e., a linear kernel function $h(t)$, followed by a static nonlinearity $g(\cdot)$, which has been widely used to decouple the linear kernels and the nonlinearity (see a review by Meister & Berry, 1999). Here, $h(t) = \sin(\pi t/\tau_a)\exp(-t/\tau_b)$ with $\tau_a = 80$ ms and $\tau_b = 100$ ms. $x(t)$ is given by

$$x(t) = \int_0^{+\infty} h(\tau)s(t-\tau)\,\mathrm{d}\tau. \tag{1}$$

The nonlinearity is specified by

$$g(x) = \begin{cases} 0, & \text{if } x < \theta, \\ x-\theta, & \text{if } \theta < x < \eta, \\ \eta-\theta, & \text{if } x \geqslant \eta, \end{cases} \tag{2}$$

where θ is the threshold and η is the saturation level.

Signals with Gaussian distributions are widely observed in nature and have been widely used as input signal to study neurons' response properties in experimental studies (e.g. Benardete & Kaplan, 1999; Chander & Chichilnisky, 2001; Kim & Rieke, 2001; Sakai et al., 1995; Smirnakis et al., 1997; Truchard et al., 2000). Here, Gaussian white noise stimulus $s(t)$ with mean 0 and SD σ is used as input signal. σ is considered to be the contrast of the signal. Its probability density function (PDF) is given by $p_s = \frac{1}{\sqrt{2\pi\sigma^2}}\exp\left(-\frac{s^2}{2\sigma^2}\right)$. The linear response $x(t)$ also has a Gaussian distribution with PDF $p_x = \frac{1}{\sqrt{2\pi\sigma_x^2}}\exp\left(-\frac{x^2}{2\sigma_x^2}\right)$, where σ_x is given by $\sigma_x^2 = \langle x^2(t)\rangle = \sigma^2\int_0^{+\infty} h^2(\tau)\,\mathrm{d}\tau$, where $\langle\cdots\rangle$ denotes time average.

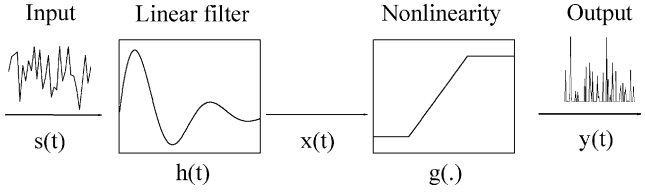

Fig. 1. The LN model consists of a linear filter $h(t)$ followed by a nonlinearity $g(\cdot)$. $x(t)$ is the convolution of the input signal $s(t)$ and the filter $h(t)$. The nonlinearity $g(\cdot)$ operates on $x(t)$ to generate the output $y(t)$.

3. Results

3.1. Gain analysis

The linear kernels of real neurons are often estimated by neurophysiologists using white noise reverse correlation (e.g. Arcas & Fairhall, 2003; Benardete & Kaplan, 1999; Brown & Masland, 2001; Shapley & Victor, 1978; Victor, 1987). We will derive mathematically a gain factor to quantify the effect of the static nonlinearity $g(\cdot)$ on the recovered linear kernel $h'(t)$. According to Bussgang's theorem (Bendat, 1990), for any memoryless nonlinear system $y = g(x)$ with an input signal drawn from a Gaussian distribution, we can estimate a linear transfer function $K(f)$ (in Fourier domain, where f is frequency) for specifying the input and output relationship of such a nonlinearity by

$$K(f) = \frac{Y(f)X(f)^*}{X(f)X(f)^*} = \frac{\langle xg(x)\rangle}{\sigma_x^2}, \tag{3}$$

where $X(f)$ and $Y(f)$ are the Fourier transforms of signal $x(t)$ and output $y(t)$ respectively. Similarly, for the entire LN model, the optimal linear function $T(f)$ that describes the input–output relationship is given by

$$T(f) = \frac{Y(f)S(f)^*}{S(f)S(f)^*}, \tag{4}$$

where $S(f)$ is the Fourier transform of input signal $s(t)$. Combining Eqs. (3) and (4), and noting that $X(f) = H(f)S(f)$, we have

$$T(f) = H(f)K(f) = H(f)\frac{\langle xg(x)\rangle}{\sigma_x^2}, \tag{5}$$

where $H(f)$ and $T(f)$ are the Fourier transforms of the original linear kernel $h(t)$ and the recovered first order Wiener Kernel $h'(t)$, respectively. This indicates the entire effect of the static nonlinearity on the recovered kernel is simply introducing a gain scaling factor to the original linear kernel in the LN model. $\alpha = \frac{\langle xg(x)\rangle}{\sigma_x^2}$ is defined as the gain factor. Finally, from Eqs. (1) and (2), we got

$$\alpha = \frac{\int_\theta^\eta x(x-\theta)p_x\,\mathrm{d}x + (\eta-\theta)\int_\eta^{+\infty} xp_x\,\mathrm{d}x}{\sigma^2\int_0^{+\infty} h^2(\tau)\,\mathrm{d}\tau}. \tag{6}$$

Performing the integrations and simplifying yields

$$\begin{aligned}\alpha(\sigma) &= \frac{1}{2}\left[\mathrm{erf}\left(\frac{\eta}{\sigma_x\sqrt{2}}\right) - \mathrm{erf}\left(\frac{\theta}{\sigma_x\sqrt{2}}\right)\right] \\ &= P[x(t)\in[\theta,\eta]].\end{aligned} \tag{7}$$

Thus, the recovered linear kernel $h'(t) = \alpha\cdot h(t)$. The gain factor α quantifies how much the performance effectivity of the real linear kernel $h(t)$ can be affected by threshold θ, saturation η and stimulus standard deviation σ. Although we restrict ourselves here to the case of a Gaussian input signal, Eq. (5) can be easily

generalized to handle the non-Gaussian case using Scarano's generalization of Bussgang's theorem (Scarano, 1991). This generalization requires that the nonlinearity $g(\cdot)$ be smooth, such as a sigmoidal function. We have chosen the nonlinearity $g(\cdot)$ here to examine the exact effects of threshold and saturation (Eq. (2)). This static nonlinearity has been viewed as a good approach to model real neuron's nonlinearity.

It can be observed from the equation that α varies with σ^2 for a LN model with fixed values of θ and η. That means linear kernel recovered from conventional Wiener kernel method in the experiments should contain a distortion effect due to the nonlinearity. However, such a distortion effect reflects the preferred selectivity of the system to the distribution of the input signal. To illustrate this phenomenon, we fix $\theta = 5$ and $\eta = 40$, we compute the gain factor α for signals with different σ's. Fig. 2a shows that recovered or recovered linear kernel $h'(t)$ (the inverse Fourier transform of $T(f)$) is heavily dependent on the value of σ. Interestingly, we found that α is not monotonic, it increases with σ in the small range, reaches a maximum, and decreases with further increase in σ (the circles in Fig. 2b). The variance-gain curve demonstrates a gain tuning phenomenon. To confirm these analytical results, we applied Gaussian white noise $s(t)$ to the model and used the standard Wiener kernel method (Korenberg, 1988; Lee & Schetzen, 1965; Marmarelis, 1993) to recover the Wiener kernel for the whole LN model based on the input $s(t)$ and output $y(t)$ for each σ. The amplitude gain (which is equal to gain factor α) of the recovered kernel (triangles in Fig. 2b) matches perfectly with our analytical results. This result suggests the amplitude gain varying with contrast observed in neurophysiological experiments (Benardete & Kaplan, 1999; Shapley & Enroth-Cugell, 1984) should arise at least partly from the nonlinearity of the system. This does not reflect any underlying adaptive gain control of the system.

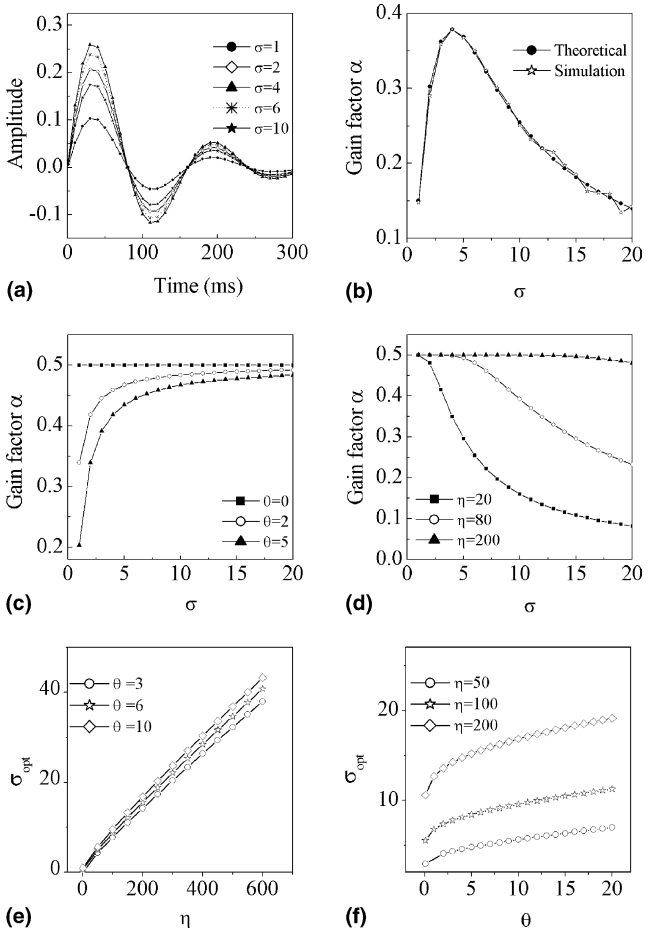

Fig. 2. (a) The theoretical kernels recovered from stimuli of different σ for threshold $\theta = 3$ and saturation $\eta = 50$. (b) The gain factor α as a function of σ. (c) The gain factor α as a function of σ for three threshold values with $\eta = 1000$. (d) The gain factor α as a function of σ for three saturation values with $\theta = 0$. (e) The σ where α reaches maximum is called σ_{opt}. σ_{opt} increases linearly with saturation level η for different threshold values ($\theta = 3$, 6 and 10). (f) For fixed saturation levels ($\eta = 50$, 100 and 200), σ_{opt} increases monotonically, but not linearly, with threshold θ.

The threshold θ and η are responsible for producing this bell-like gain tuning curve, which indeed belongs to the coherence resonance (CR) phenomenon observed in various physical areas (e.g. Gammaitoni, Hanggi, Jung, & Marchesoni, 1998; Hu, Ditzinger, Ning, & Haken, 1993; Pikovsky & Kurths, 1997). A common feature of CR is that the coherence measure or response property in the output of a complex system can be maximized by the fluctuating signal with optimal variance. Our results provide a basic framework for the CR phenomenon in a static nonlinear system. That is, for any system with threshold and saturation, it can potentially display coherence resonance.

To understand why the gain factor α increases with σ in the small σ range, we fix the saturation η to 1000 and vary threshold θ. The very large η essentially represents infinite saturation. Fig. 2c shows that for $\theta = 0$, the system behaves like a half-rectification device, α does not change with an increase in σ, staying at 0.5. At higher values of θ, α increases with σ, displaying a rising phase in the gain tuning curve. The results indicate that threshold plays a decisive role in determining the gain sensitivity of the neuron in the rising phase of the gain tuning curve.

To understand the influence of saturation in gain control, we set $\theta = 0$ and vary the value of η of the system. Fig. 2d demonstrates that for different η, the gain factor decreases with an increase in σ. The rate of decrease is larger for smaller saturation values (e.g. $\eta = 20$). At large η (e.g. $\eta = 200$), the decrease is slow, resulting in high gain across all σ. The saturation level therefore determines the falling slope of the gain tuning curve.

This gain tuning curve determines the neuron's preference to the distributions of different σ. The optimal

σ_{opt} in which gain is maximum can be obtained by differentiating Eq. (7), which gives

$$\sigma_{opt}^2 = \frac{\theta^2 - \eta^2}{2(\ln\eta - \ln\theta)\int_0^{+\infty} h^2(\tau)\,d\tau}. \quad (8)$$

The obtained σ_{opt} increases with saturation η (see Fig. 2e). It also increases slightly with an increase in threshold θ (Fig. 2f). This might provide a mechanism and rules for a neuron to adjust its transfer function and gain tuning curve according to the statistical context of the input signals. However, the range of adjustment of the optimal σ by changing η and θ is rather limited. Fig. 3 shows gain factor as a function of threshold, saturation and σ. Larger saturation values and smaller threshold values are accompanied by larger gains over a greater region of stimulus variance. For any given saturation level and threshold, there is an optimal σ where the gain factor is maximum.

Based on the above kernel analysis, we conclude that in the discovering contrast adaptation phenomena by the classical Wiener Kernel method (Korenberg, 1988; Lee & Schetzen, 1965; Marmarelis, 1993), the nonlinear effect should not be avoided. Nonlinearity introduces a contrast gain tuning phenomenon, which is an intrinsic property of the nonlinear systems. This tuning property determines the preferred contrast sensitivity of the system to the input signals with various statistical distributions. However, note that the relationship between effective kernel gain and input variance in this LN model is non-monotonic in the general case (Fig. 2b). This is inconsistent with recent experimental findings, which showed that the gain of the recovered linear kernel decreases monotonically with the input contrast (Benardete & Kaplan, 1999; Shapley & Victor, 1978, 1979, 1980), and even displays an inverse power law relationship (Chander & Chichilnisky, 2001; Smirnakis et al., 1997; Truchard et al., 2000). Thus, the static LN model cannot explain the contrast adaptation observed in experiments in a complete way. To isolate gain change due to adaptive change in the system, one must factor out the effect due to static nonlinearity. Additional adaptive mechanisms may exist accounting for the interesting power law relationship. In another paper (Yu et al., submitted for publication), we will discuss that in detail.

In sum, the above results demonstrate that the threshold and saturation of the system play a functional role in shaping the basic contrast–response gain tuning for various stimulus statistics, serving as a substrate for contrast adaptation.

3.2. Effective nonlinearity

In neurophysiological experiments, an unknown system is usually studied by its recovered linear kernel (i.e., $h'(t) = \alpha * h(t)$) and recovered nonlinearity $g'(x)$ (e.g. Chander & Chichilnisky, 2001; Kim & Rieke, 2001; Meister & Berry, 1999). In above sections, we studied the effect of the static nonlinearity on the properties of recovered linear kernel $h'(t)$. What will the recovered nonlinearity look like? Given the recovered kernel $h'(t)$, we can estimate the linear response $x'(t)$ as

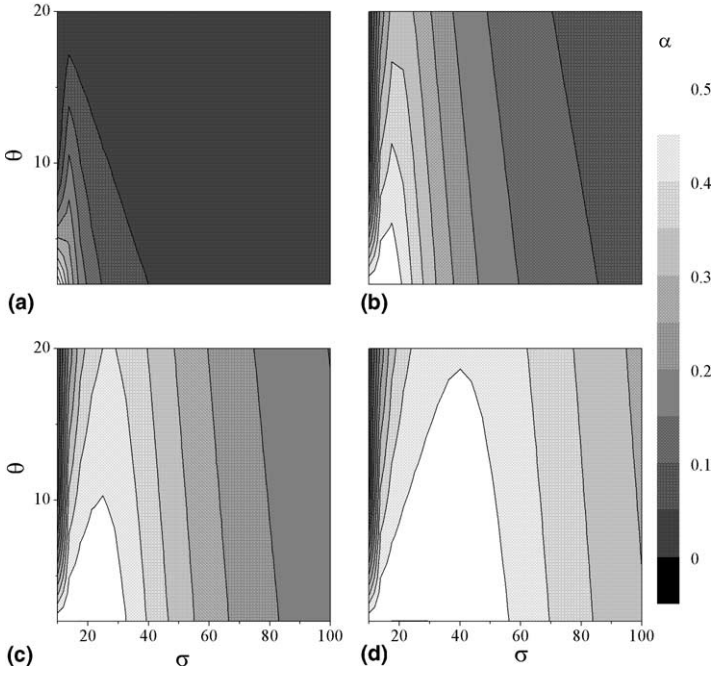

Fig. 3. Gain factor $\alpha(\sigma,\theta)$ for $\eta = 20$ (a), $\eta = 100$ (b), $\eta = 200$ (c), and $\eta = 400$ (d) respectively.

$$x'(t) = \int_0^{+\infty} h'(\tau)s(t-\tau)\,\mathrm{d}\tau. \quad (9)$$

By plotting the input–output relations of $x'(t)$ and $y(t)$, the recovered nonlinearity $g'(x)$ for each stimulus variance is shown in Fig. 4a. As a comparison, the original nonlinearity $g(\cdot)$ is plotted by the thick line. Noted that $g'(x)$ is dependent on the signal variance. The shift of the input–output relations here reflects the changing sensitivity of the system to the changing input signal. When we scale the linear projection response $x'(t)$ by the gain factor α from Eq. (6), all the recovered nonlinearities $g'(x)$ and the real nonlinearity $g(\cdot)$ overlap (see Fig. 4b).

In the experimental situation, if the contrast adaptation is entirely due to the static nonlinearity, when we divide $x'(t)$ by a scale factor α' that can collapse $g'(x)$ to $g(x)$, $h_r = h'(t)/\alpha'$ should be equal to intrinsic linear function $h(t)$ regardless of σ. However, in recent experimental studies (Chander & Chichilnisky, 2001; Kim & Rieke, 2001), it was found that h_r is not invariant to σ (for example see Fig. 4 in the paper by Chander & Chichilnisky, 2001), suggesting that there exists an additional adaptive mechanism accounting for temporal contrast gain control. Our results therefore provide a theoretical framework for interpreting their results.

3.3. Invariant input–output relationship

The contrast response curve or the input–output relationship is useful for probing the contrast gain control phenomena (Geisler & Albrecht, 1992; Ohzawa et al., 1985). Gaussian white noise signals, while useful for deriving the recovered linear Wiener kernel, are inappropriate for estimating the input–output relationship of the system. This is because the temporal variation of the signal is faster than the convolution window of the cell's kernel, resulting in a many-to-one input–output (I/O) mapping, and thus a fuzzy I/O curve. To recover the input–output relationship, experimenters typically use a stimulus that keeps an input attribute constant for a period of time Δt, and obtain the output by averaging the response of the neuron during that period (Geisler & Albrecht, 1992; Ohzawa et al., 1982, 1985). For example, a spatial sinewave grating of a particular luminance contrast (the input attribute) will be drifted across the receptive field of the measured neuron. The temporal frequency of the sinewave grating is typically about two cycles per second. Gratings of several contrast values are presented for $\delta t = 4$ s each, for a total of 10 times. These contrast values are chosen to be within one octave of a given mean contrast value. This experiment is then repeated several times, with different mean contrast values (see Fig. 1 in the paper by Ohzawa et al., 1985). For each mean value, a contrast sensitivity curve is plotted which gives the neural response for each contrast value. The response of the neurons was found to adapt to the mean contrast of the signals, causing the contrast sensitivity curve to shift to the right as the mean contrast is increased (see Fig. 3 in the paper by Ohzawa et al., 1985). This adaptation of the contrast response function to mean contrast is a hallmark of contrast gain control.

Can static LN model produce the shifting contrast response curves? To answer this question, we simulated this experiment with our cascade LN model using

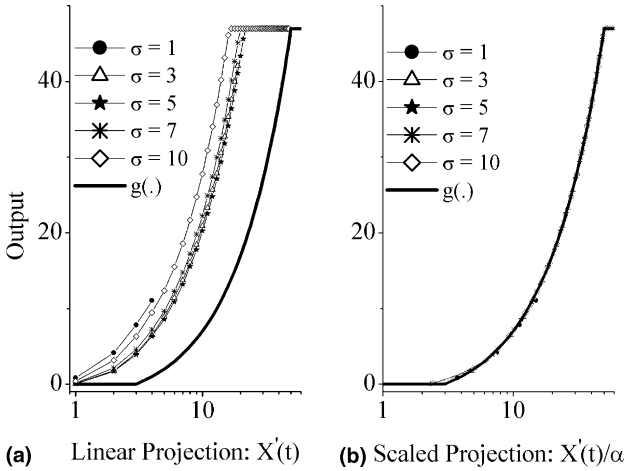

Fig. 4. (a) The recovered nonlinearities for various values of σ in the case of $\theta = 3$ and $\eta = 50$. (b) Scaled nonlinearities by gain factor α for various values of σ in the case of $\theta = 3$ and $\eta = 50$.

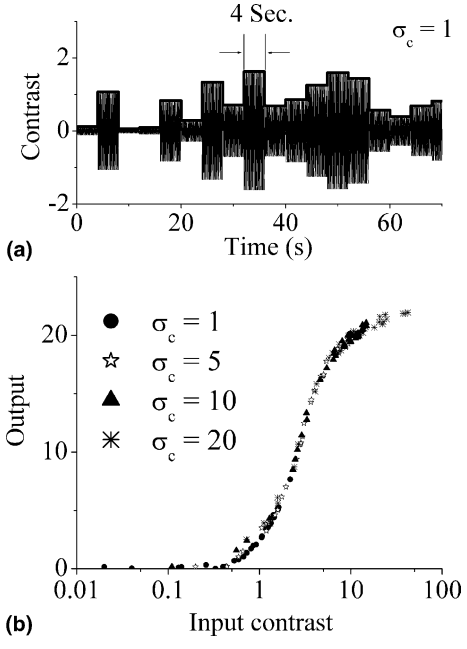

Fig. 5. For the model with $\theta = 5$ and $\eta = 50$: (a) A example of input contrast signal with sinewave modulation (temporal sine frequency is 10 Hz). The standard deviation of contrasts is $\sigma_c = 1$. (b) Input–output relations for various input contrast signals with $\sigma_c = 1$, 5, 10 and 20, respectively.

similar input. We use one dimensional temporal sinewave gratings of different contrasts (see the dark black line in Fig. 5a) as the stimulus to the neuron. Here, the sinewave grating with a temporal frequency of 10 Hz is a carrier, while the amplitude modulation is the input contrast signal $c(t)$. Each contrast value of $c(t)$ is presented for $\delta t = 4$ s. These contrast values are drawn from a Gaussian white distribution with standard deviation σ_c. This standard deviation σ_c determines the mean contrast level of each sequence, which lasts for 1000 s. The input–output curves are obtained from sequences of four different mean contrast levels, with $\sigma_c = 1$, 5, 10, and 20 respectively. To plot the input–output curve, the model's response for each time bin δt is averaged to get a mean value for each contrast value. Fig. 5b shows the resulting input–output curves for four mean contrast levels. The perfect overlapped curves show that there is no adaptive behavior in the investigated system, i.e., the model is static. The slope of input–output relation is independent of mean contrast level, and is unaffected by the nonlinearity. (It should be noted that the time bin δt used here should be larger than the character time scales τ_a and τ_b of linear kernel. Otherwise, the input–output relation will be distorted heavily.) Hence, the shifting input–output curves of cortical neurons observed in experiments (Geisler & Albrecht, 1992; Ohzawa et al., 1982, 1985) cannot be attributed to the static nonlinearity.

Our results suggested that there should exist an adaptive mechanism, which is beyond static nonlinearity, which controls the contrast gain for adapting to various contrast distributions. In a sister paper (Yu et al., submitted for publication), we will discover the necessary factors and principles for the potential adaptive mechanism.

3.4. Impact on information encoding

Static nonlinearity affects not only the performance gain of the neuron to input signals, but also the information coding property. We next studied the relationship between performance gain and the information encoding of the system. We do this by deriving a relationship between the mutual information and the system parameters. Shannon information theory (Shannon & Weaver, 1949) provides a measure to quantify the ability of a system or a communication channel to convey information. Generally, for a communication channel with an input signal $s(t)$ and an output response $y(t)$, the total output entropy

$$H(y) = -\sum_{y} p(y)\log_2 p(y) \tag{10}$$

is used to measure its theoretical information transfer capacity, while mutual information

$$\begin{aligned} I_m &= H(y) - H(y|s) \\ &= -\sum_{y} p(y)\log_2 p(y) + \sum_{s,r} p(s)p(y|s)\log_2 p(y|s), \end{aligned} \tag{11}$$

measures how much of that capacity is actually used to encode the input signal. $H(y|s)$ can be defined as 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 $H(y|s) = 0$. In this case, the mutual information is simply equal to the output entropy $I_m = H(y)$. The probability distribution of the output response $y(t)$ can be derived from Eqs. (1) and (2). We can derive the entropy of $y(t)$ directly from this distribution using Eq. (11) in the discrete form (Dayan & Abbott, 2001, chap. 4).

Fig. 6 shows how mutual information I_m varies as a function of threshold, saturation and stimulus σ. Note that I_m goes through a maximum as σ varies, in accord with previous studies of similar nonlinear systems (Bell & Sejnowski, 1995). This pattern displays a coherence resonance phenomenon (e.g. Gammaitoni et al., 1998; Hu et al., 1993; Pikovsky & Kurths, 1997). For a fixed σ, I_m increases with an increase in saturation value or with a decrease in the threshold. This result indicates that the nonlinearity determines the information transmission tuning curve of the system. That is, only those signals with intermediate variance can be processed by the system in a way that maximizes information transmission, while those with smaller or larger variance cannot be well encoded and transmitted. Considering that nonlinearities (threshold, saturation) can change the gain tuning curve (see Fig. 2b) and information tuning curve (see Fig. 6), they might provide a potential mechanism for a neuron to adjust itself to match the statistical context of the input signals by changing threshold θ and saturation η, although the adjustment range is rather limited. For various parametric conditions, mutual information I_m is roughly proportional to the gain factor α (see Fig. 7). This implies that the information encoding property and the gain performance of the linear transfer function are correlated in static nonlinear systems.

Thus, for the static LN model in response to signals with various statistical distributions, there only exists one optimal contrast, for which the model can respond with maximal information transmission. While for other stimuli, the model cannot process them efficiently. However, recent experimental studies in fly H1 neurons indicate that the information transmission rate could remain relatively constant for various input contrasts, implying an adaptive property for varying environments. Therefore, there must be a real adaptive gain control mechanism beyond the static nonlinear effect. Indeed, as shown by Bell and Sejnowski (1995), the nonlinearity

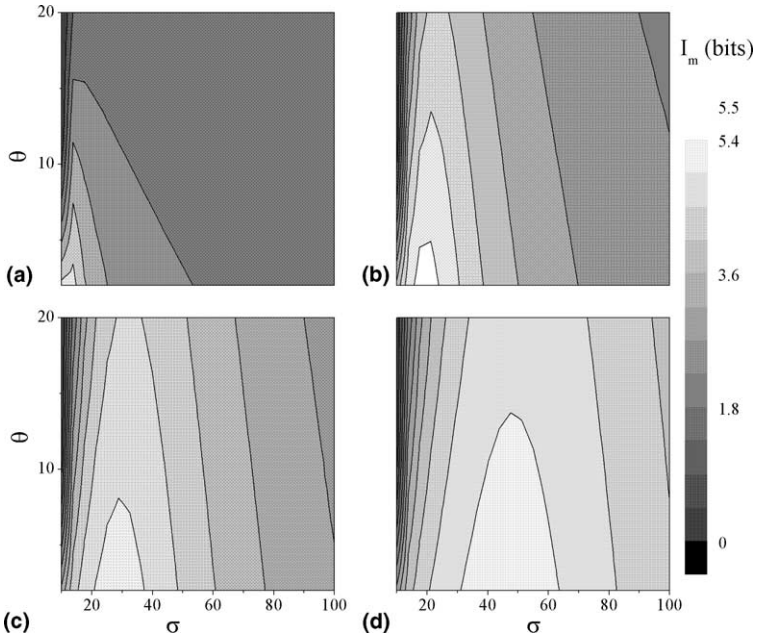

Fig. 6. Mutual information $I_m(\sigma,\theta)$ for $\eta = 20$ (a), $\eta = 100$ (b), $\eta = 200$ (c), and $\eta = 400$ (d) respectively.

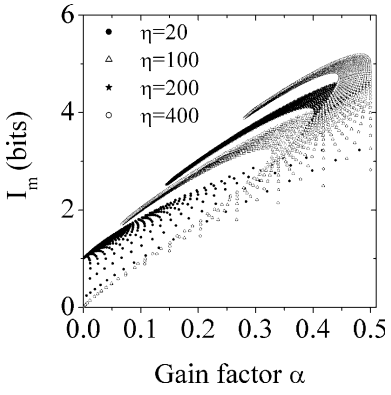

Fig. 7. $I_m(\sigma,\theta)$ as a function of $\alpha(\sigma,\theta)$ for various values of σ and θ. Each point corresponds to a value of $\alpha(\sigma,\theta)$ from Fig. 3 and a value of $I_m(\sigma,\theta)$ from Fig. 4.

of a neuron can be adjusted to maximize information transmission for various external conditions. Our further study (Yu et al., submitted for publication) will indicate that the linearity of a neuron can also be adjusted so as to maximize information transmission for various external conditions. Those studies may shed a light on the mechanisms underlying real adaptation behavior for maximal information transmission in the neurons.

4. Discussion and conclusion

In summary, dependence of performance gain and information coding property on the signal variance or contrast is a basic property of any nonlinear system with threshold and saturation. However, it does not reflect any real adaptation behavior intrinsic the system. Each fixed pair of threshold and saturation values determines a particular gain tuning curve and an information encoding tuning curve. These curves are typically characterized by a rising phase at small σ and a falling phase at large σ, with gain and mutual information being maximized at an intermediate range of σ. By manipulating these two parameters, one may potentially steer the system to optimize neural response amplitude and information encoding efficiency for specific stimulus environments. The general principle of steering is that by increasing the saturation level or by lowering the threshold, the region of high mutual information and gain will expand and the optimal contrast value will increase. There is therefore a pressure to push the saturation up and the threshold down to maximize information transfer and encoding over a larger range of stimuli. However, this might be balanced by a pressure to minimize energy expenditure, which may tend to push the threshold up and saturation down. It is interesting to note that young neurons have higher thresholds and lower saturation than adult neurons (Rust, Schultz, & Movshon, 2002). Our results suggest that this might be because young neurons are more limited in their energy resources.

This basic framework may be helpful in understanding an important property of neurons in brain, i.e., their capacity to adjust the gain of their responses according to the statistics of the input stimulus. In different statistical environments, sensitivity and information processing can be optimized by adaptively adjusting a neuron's

threshold and saturation level via cellular and molecular mechanisms or synaptic modifications from network interactions. Considering that threshold and saturation are common features of nonlinear systems in the natural world, the dependency of gain and information transfer tuning on these properties may be universal in all nonlinear threshold systems. Our results therefore not only illuminate the connection between static nonlinearities, performance gain and information transfer in neurons, but also provide insights to some rules governing the design of nonlinear information processing systems that can be adjusted to match the stimulus statistics in the environment.

However, the real contrast gain control mechanism should go beyond the effect of the static nonlinearity. At least, static nonlinearities cannot account for two important observations concerning contrast gain control phenomena. (1) The divisive shifting of the contrast–response relations as a function of mean contrast level (Geisler & Albrecht, 1992; Kohn & Movshon, 2003; Ohzawa et al., 1982, 1985; Sanchez-Vives et al., 2000). By using methods similar to those of the experiment, we constructed the input–output curves of our static LN model in response to various mean contrast levels. It is clear that various contrast–response curves of the LN model in response to different mean contrast levels are completely overlapped. No shifting effect is observed as that observed in experiments (Geisler & Albrecht, 1992; Kohn & Movshon, 2003; Ohzawa et al., 1982, 1985; Sanchez-Vives et al., 2000). This means that the shifting contrast response curves along the log-contrast axis in cortical neurons does reflect an underlying intelligent contrast gain control mechanism, which is beyond the effect of the static nonlinearity. (2) Experiments showed that there exists a power law relation between the amplitude gain of the transfer function and the input contrast in the real neurons (Chander & Chichilnisky, 2001; Truchard et al., 2000). However results from our static LN model, and from the complex Hodgkin–Huxley neuronal model, demonstrated that nonlinearity only produces a bell-shape curve between the amplitude gain of the transfer function and the input contrast. These differences indicate the existence of an intelligent gain control mechanism underlying visual adaptation behavior in the real neuron, which is absent in the popular neuronal models such as leaky integrate-and-fire and Hodgkin–Huxley models. In another paper (Yu et al., submitted for publication), we will discover what kind of adaptive factors and principles need to be considered to account for the adaptation phenomena in contrast gain control behavior, especially the contrast-dependent shifting (or divisive) input–output relationships.

In summary, our results clarify the exact contributions of the static nonlinearity to the observed adaptation phenomena in neurophysiological experiments. We also make clear the difference between the nonlinear effect and real adaptation phenomena, which has confused experimental scientists. We have shown that the static nonlinearity determines the optimal performance gain of the linear function in fluctuating environments. This performance gain of the linear kernel and the information transmission of the system go through a global maximum as the input contrast changes, showing an apparent ''adaptation effect''. Indeed, this is a type of coherence resonance phenomenon widely discussed in the physics literatures (e.g. Gammaitoni et al., 1998; Hu et al., 1993; Pikovsky & Kurths, 1997). Our results show that any nonlinear system, with threshold and saturation, may have the potential to display a coherence resonance phenomenon.

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