



# From shunting inhibition to dynamic normalization: Attentional selection and decision-making in brief visual displays



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## ARTICLE INFO

### Article history:

Received 18 June 2014

Received in revised form 25 October 2014

Available online 8 November 2014

### Keywords:

Attention

Normalization

Shunting equation

Saliency

Decision making

## ABSTRACT

Normalization models of visual sensitivity assume that the response of a visual mechanism is scaled divisively by the sum of the activity in the excitatory and inhibitory mechanisms in its neighborhood. Normalization models of attention assume that the weighting of excitatory and inhibitory mechanisms is modulated by attention. Such models have provided explanations of the effects of attention in both behavioral and single-cell recording studies. We show how normalization models can be obtained as the asymptotic solutions of shunting differential equations, in which stimulus inputs and the activity in the mechanism control growth rates multiplicatively rather than additively. The value of the shunting equation approach is that it characterizes the entire time course of the response, not just its asymptotic strength. We describe two models of attention based on shunting dynamics, the integrated system model of Smith and Ratcliff (2009) and the competitive interaction theory of Smith and Sewell (2013). These models assume that attention, stimulus saliency, and the observer's strategy for the task jointly determine the selection of stimuli into visual short-term memory (VSTM) and the way in which stimulus representations are weighted. The quality of the VSTM representation determines the speed and accuracy of the decision. The models provide a unified account of a variety of attentional phenomena found in psychophysical tasks using single-element and multi-element displays. Our results show the generality and utility of the normalization approach to modeling attention.

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## 1. Introduction

Normalization, or divisive normalization, models offer a simple and powerful formalism for characterizing a variety of visual phenomena, including the effects of covert attention. Normalization models have provided theoretical accounts of such diverse phenomena as lightness adaptation (Sperling & Sondhi, 1968), contrast sensitivity (Heeger, 1991, 1992) and contrast gain control (Geisler & Albrecht, 1997; Ross & Speed, 1991; Scholl, Latimer & Priebe, 2012; Wilson & Kim, 1998), pattern masking (Foley, 1994), efficient, decorrelated encoding of natural images (Schwartz & Simoncelli, 2001), and the psychophysics and neural correlates of attention (Boynton, 2005; Herrmann, Heeger & Carrasco, 2012; Herrmann, Montaser-Kouhsari, Carrasco, & Heeger, 2010; Lee, Itti, Koch, & Braun, 1999; Lee & Maunsell, 2009; Reynolds & Heeger, 2009). Carandini and Heeger (2012) surveyed the range of applications of normalization models and argued that normalization should be viewed as a “canonical neural computation.”

Computationally, the idea expressed in normalization models is that the response of a visual mechanism coding a target stimulus is modulated divisively by the sum of the activity in other mechanisms in its neighborhood. In normalization models of lightness adaptation and gain control, the divisive input depends on the contrast energy in the local surround; in models of masking and pattern vision, it depends on the activity in a local population of spatial-frequency and orientation tuned filters. Unlike traditional linear system models of vision (e.g., Campbell & Robson, 1968), in which one stimulus can influence the visual response to another stimulus only if their associated receptive fields have overlapping bandwidths, normalization models allow for a form of global influence that extends outside the classical receptive field (Foley, 1994; Heeger, 1991, 1992). They explain, for example, how the visual response to a grating stimulus can be influenced by the properties of a stimulus oriented at 90° to it.

In this article, we investigate the temporal dynamics of normalization and show how the scope of normalization models can be greatly expanded if they are formulated dynamically. The key theoretical insight provided by normalization models of attention is that the sensory representations of stimuli depend on nonlinear interactions between stimuli and their surrounds, and these

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interactions can be modulated by attention. We show how normalization models can be obtained computationally as the asymptotic or steady-state solutions of a class of biologically-plausible systems of differential equations known as *shunting equations* (Grossberg, 1980). Whereas normalization models characterize the steady-state properties of the system, the solutions of the associated shunting equations characterize its entire time course. Formulating a model dynamically makes it possible to view a wide range of attentional phenomena as expressions of a common set of processing mechanisms, of which normalization is one manifestation.

In the second part of this article, we review some of these phenomena and describe two models, one proposed by Smith and Ratcliff (2009) and the other proposed by Smith and Sewell (2013), to account for them. Both models use shunting equations to describe the formation of the stimulus representations that support perceptual decision making. Although the models and the experimental phenomena they seek to explain have been discussed in previous articles, our presentation here serves both to highlight the unity of the underlying theoretical and computational principles and to emphasize the relationship among what might otherwise seem a diverse and unrelated set of experimental findings. Some of these phenomena may not seem closely related to normalization, but we argue that they can all be viewed as manifestations of attentionally modulated shunting dynamics.

An additional aim of the article is to provide a partial reformulation of the Smith and Ratcliff (2009) and Smith and Sewell (2013) models in order to clarify the relationship between them and to make them consistent with one another. The reformulation also provides an explicit mathematical expression of a theoretical principle that was only represented implicitly in the previous published versions of the models, namely, that stimulus selection and stimulus identification are carried out by visual pathways that code different aspects of the stimulus. Our aim in elaborating the models in this way is to emphasize their relationship to other current normalization models in the literature.

## 2. Normalization and shunting dynamics

Normalization models have provided successful descriptions of visual processes at different levels of analysis, ranging from the contrast sensitivity of single neurons to behavioral responses in perceptual judgment tasks. Normalization describes how the response,  $R_i$ , of one of a set of mechanisms,  $i$ , to a stimulus depends on the responses of other members of the set to the components of the stimulus, denoted  $I_j$ . In a typical normalization model, the response is described by an equation of the form

$$R_i = \frac{I_i^p}{a_i + \left(\sum_j b_j I_j\right)^q}. \quad (1)$$

In this equation,  $a_i$  is a constant that depends on the mechanism but is independent of the stimulus and the exponents  $p$  and  $q$  characterize the nonlinearities of the response. Typically they are power functions of low order (e.g., around 2), which may be equal to each other or different, depending on the setting.

Probably the simplest normalization model is the ubiquitous Naka–Rushton/Michaelis–Menton model of contrast gain control (Albrecht & Geisler, 1991; Albrecht & Hamilton, 1982; Kaplan, Lee & Shapley, 1990; Ross & Speed, 1991; Sclar, Maunsell & Lennie, 1990; Scholl, Latimer & Priebe, 2012),

$$R(c) = \alpha \frac{c^2}{c_{in} + c^2}. \quad (2)$$

In this equation,  $c$  is stimulus contrast and  $R(c)$  is the associated perceptual response. The gain control model states that the contrast response is a nonlinear, saturating function of contrast power or energy,  $c^2$ . The constant  $\alpha$  determines the saturation point and the constant  $c_{in}$ , which represents the aggregated effects of inhibition, determines the horizontal position of the function on the log-contrast axis. The inhibitory constant can be written as  $c_{in} = c_{0.5}^2$ , where  $c_{0.5}$  is a semisaturation constant that characterizes the contrast at which  $R(c)$  attains half its maximum value.

Heeger (1991, 1992) proposed a normalization model of cortical simple and complex cell responses of the form of Eq. (1). The general form of the equation in Heeger's model is

$$R_i(t) = \frac{E_i(t)}{a_i + \sum_j E_j(t)}, \quad (3)$$

where  $E_i(t)$  is the time-varying response of a spatiotemporally tuned mechanism. In Heeger's model simple cell,  $E_i(t)$  is the amplitude response of a half-squared linear operator with a specified spatial frequency and orientation tuning and a specified phase. (We have simplified Heeger's notation a little for ease of exposition.) The half-squared operator behaves like a half-wave rectifier in that the mechanism responds selectively to either positive or negative contrast excursions, depending on its phase, consistent with the fact that neurons only respond either to contrast increments or decrements. The use of a half-squaring operator instead of a half-wave rectifying operator means that the response to low-intensity stimuli is less than would otherwise be the case, which is consistent with both the physiology (Heeger, 1991, 1992) and the psychophysics (Laming, 1986).

The sum in the denominator of Eq. (3) is over a set of four mechanisms whose phases vary in steps of  $90^\circ$ . The sum is proportional to the Fourier energy in the stimulus, which means the amplitude response of the model simple cell in Eq. (3) is normalized by stimulus energy. Heeger's model complex cell is obtained by summing four simple cells with orthogonal phases ( $0^\circ$ ,  $90^\circ$ ,  $180^\circ$  and  $270^\circ$ ). The response of the model simple cell depends on the amplitude of the stimulus and is sensitive to its phase or contrast polarity; the response of the model complex cell depends only on the overall stimulus contrast energy.

Foley (1994) proposed a masking model influenced by Heeger's work, which is related to Eq. (1). Foley's Model 2 has the form

$$R = \frac{(|E|^+)^p}{Z + \left(\sum_j |I_j|^+\right)^q}, \quad (4)$$

where  $E = \sum_k S_{E,k} c_k$ , and  $I_j = \sum_k S_{I,j,k} c_k$  are weighted sums of the  $k$  components of the stimulus, which individually have contrast  $c_k$ . The weights characterize the sensitivities of excitatory and inhibitory mechanisms:  $S_{E,k}$  is the excitatory sensitivity to the  $k$ -th stimulus component and  $S_{I,j,k}$  is the inhibitory sensitivity of the  $j$ -th divisive input to this same stimulus component. The notation  $[\cdot]^+ = \max(\cdot, 0)$ , denotes half-wave rectification, which has similar properties to the half-squaring operator in Heeger's model, except that the response is a linear rather than a nonlinear function of the stimulus strength. Models related to Eq. (4) continue to be influential in contemporary accounts of masking (e.g., Meese & Holmes, 2010).

### 2.1. Normalization models of attention

The effects of attention can be incorporated into normalization models in a very natural way by assuming that the excitatory and inhibitory components of the normalization equation are weighted by attention in some way, where the weights depend on the allocation of attention in space (or feature space). Lee et al. (1999) pro-

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