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A general mechanism for tuning: Gain control circuits and synapses underlie tuning of cortical neurons

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Abstract

Tuning to an optimal stimulus is a widespread property of neurons in cortex. We propose that such tuning is a consequence of normalization or gain control circuits. We also present a biologically plausible neural circuitry of tuning.

This report describes research done at the Center for Biological & Computational Learning, which is in the McGovern Institute for Brain Research at MIT, as well as in the Dept. of Brain & Cognitive Sciences, and which is affiliated with the Computer Sciences & Artificial Intelligence Laboratory (CSAIL).

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1 Introduction

Across the cortex, especially in the sensory areas, many neurons respond strongly to some stimuli, but weakly to others, as if they were tuned to some optimal features or to particular input patterns. For example, neurons in primary visual cortex show Gaussian-like tuning in multiple dimensions, such as orientation, spatial frequency, direction, velocity. Moving further along the ventral pathway of primate cortex, V4 neurons show tuned responses to different types of gratings or contour features [8, 15], and some IT neurons are responsive to a particular view of a face or other objects [11, 13].

In other sensory modalities, neural tuning is also common. Olfactory neurons in the fly respond to particular mixtures of molecules, or odors [25]. Auditory neurons of a song bird can be tuned to sound patterns, or motif [9]. In the case of the motor system, the activity of a spinal cord neuron is related to a particular pattern of force fields or limb movements [16]. The tuning of a neuron may be sharp and sparse in some cases, or distributed and general in other cases [12], but despite qualitative differences, such tuning behavior seems to be one of the major computational strategies for representing and encoding information in cortex.

Consequently, tuning in cortex is often characterized and approximated with a multidimensional Gaussian function in many models. In [15], contour feature tuning in V4 is fitted with a Gaussian function in curvature and angular position space. In [2], a similar Gaussian function is used to characterize the response of the afferent cells to the IT neurons. In the model of visual object recognition by Riesenhuber and Poggio, which attempts to describe quantitatively the first few hundred milliseconds of visual recognition, the Gaussian function is one of the two key operations for providing selectivity [19].

Even though Gaussian-like tuning behavior in cortex is widely acknowledged, it remains a major puzzle in neuroscience: how could such multidimensional tuning be implemented by neurons? The underlying biophysical mechanism is not understood. In Hubel and Wiesel's model of V1, the tuning properties of simple and complex cells are explained in terms of the geometry of the afferents: for simple cells, the alignment of several non-oriented LGN afferents would give rise to the orientation selectivity (see [7] for a review, and [21] for a quantitative model). Although attractively simple and intuitive, this explanation is challenged by a competing theory that maintains orientation selectivity is enforced, if not created, by the recurrent neural circuitry within V1 [1, 6, 23]. The tuning along non-spatial dimensions such as velocity or color, however, can not rely on the geometric arrangements only. Furthermore, tuning in other sensory modalities (*e.g.,* auditory or olfactory neurons) and in higher visual areas where the tuning seems to be of a more abstract nature (*e.g.,* the complex shape tuning in IT) would require a more general mechanism.

In this paper, we propose a biophysically plausible solution to the puzzle of Gaussian-like tuning.

2 A general mechanism for cortical tuning

As mentioned in the introduction, many neurons show tuning, which is often described in terms of a multidimensional Gaussian function:

$$f(\vec{x}) = e^{|\vec{x}-\vec{w}|^2/2\sigma^2}. \tag{1}$$

The key operation in Eqn. 1 is $|\vec{x}-\vec{w}|^2$, the computation of similarity between two vectors, which determines a tuned response around a target vector $\vec{w}$. However, we do not have any obvious neural circuitry or biophysical mechanism for such operation. How, then, could Gaussian-like tuning arise in cortex?

One possible answer to this puzzle is hinted by the following mathematical identity, which relates the Euclidean distance measure, which appears in the Gaussian function, with the normalized scalar product:

$$|\vec{x}-\vec{w}|^2 = -2\vec{x}\cdot\vec{w} + 1 + |\vec{w}|^2, \text{if } |\vec{x}| = 1. \tag{2}$$

In other words, the similarity between two normalized vectors, $\vec{x}$ and $\vec{w}$, can be measured with a Euclidean distance as well as a scalar product, or the angle between two vectors. Hence, Eqn. 2 suggests that Gaussian-like tuning can arise from a normalized scalar product operation.*

The advantage of considering normalized scalar product as a tuning operation is its biophysical plausibility. Unlike the computation of Euclidean distance or a Gaussian function, both normalization and scalar product operations can be readily implemented with a network of neurons. The scalar product or the weighted sum can be computed by the dendritic inputs to a cell with different synaptic weights. The normalization across the inputs can be achieved by a divisive gain control mechanism involving inhibitory interactions [3, 4, 10, 18]. The neural response may be subject to extra nonlinearities, such as sigmoid or rectification,

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*This relationship was pointed out by Maruyama, Girosi and Poggio in [14], where the connection between the multilayer perceptron and the neural network with radial basis function is explored. Their analysis is based on the exact form of this identity (*i.e.,* the input $\vec{x}$ to the Euclidean distance is normalized as well as the input to the scalar product). In this paper, we examine a looser connection between the Euclidean distance and the normalized scalar product (*i.e.,* the input to the Euclidean distance is not, but the input to the scalar product is normalized):

$$|\vec{x}-\vec{w}|^2 \leftrightarrow \frac{\vec{x}\cdot\vec{w}}{|\vec{x}|}.$$

in the soma or the axon. Together, the normalized scalar product with a nonlinear transfer function can give rise to a Gaussian-like tuning function, as shown in the next section.

While many neurophysiological experiments have found tuning behaviors in cortex, theoretical studies [16, 17] also indicate that a network based on radial basis functions (like Gaussian) indeed is a plausible computational scheme capable of learning. Here, learning is defined as a capacity for generalizing an input-output mapping from a finite number of data. In a learning neural network with radial basis functions, the "hidden" units show Gaussian-like tuning behavior to the input. More concretely, a computational model with a network of Gaussian template-matching units is shown to be capable of performing object recognition, while reproducing the shape selectivity and invariance properties of IT neurons [19, 20].

3 One plausible neural circuit for tuning

Eqn. 2 suggests that a crucial element for tuning is the normalization, which can be expressed mathematically as

$$R_i = \frac{x_i}{\sqrt{\sum_{j \in N} x_j^2}}. \tag{3}$$

Eqn. 3 can be implemented by a pool of neurons N, whose individual responses are divisively normalized by the collective response across the pool, giving rise to the following two important properties.

1. **Individual neural response is normalized:** The response of each neuron is divided by the total response of the pool that includes other neurons as well as itself. The normalization factor is always greater than the numerator in Eqn. 3. Hence, the neural response is upper bounded and operates within a well-defined dynamic range (*i.e.*, $R_i \in [0, 1]$).

2. **Collective response across the pool is normalized:** The sum of neural responses within the normalization pool is also normalized (*i.e.*, R_i can be thought of as the ith component of a normalized vector $\vec{R}$, with $|\vec{R}| = 1$). This aspect of normalization received less attention in the past, but it may be the underlying mechanism for cortical tuning, which is the focus of this paper.

How would a network of neurons accomplish such divisive normalization across the pool? In the past, several plausible neural circuits for gain control mechanism have been proposed and explored in various contexts. [18] considered forward and recurrent shunting inhibition circuits for gain control within fly's visual system. Many researchers have used the normalization mechanism to explain the contrast-dependent, saturating neural responses in primary visual cortex [3, 4, 10] and center-surround effects within receptive field [5]. In [22], similar divisive normalization scheme was shown to increase independence of neural signals, despite the dependencies in image statistics.

Fig. 1a presents one simple and plausible neural circuitry for divisive normalization. This circuit is based on Heeger's model of gain control in simple cells, where the inhibitory (possibly of shunting type) feedback connections perform the pool normalization [10]. With a certain choice of nonlinearities, this model has a steady state solution that is close to Eqn. 3. The normalization is "close enough" in the sense that the denominator may contain a constant (related to the strength of shunting inhibition) or the nonlinearity may not exactly be the square root of summed squares (see Appendix A).

Another crucial operation for tuning according to Eqn. 2 is the scalar product, which can be directly accomplished by the synapses (neglecting dynamics). In $\vec{x} \cdot \vec{w}$, $\vec{w}$ corresponds to a vector of synaptic weights, and $\vec{x}$ to the presynaptic inputs, as shown in Fig. 1b.

Combined together, the circuits in Fig. 1 are the basic elements for a network that can compute normalized scalar product, which in turn would produce tuning behavior in a general multidimensional input space.

4 Comparison between the Gaussian function and the normalized scalar product

In this section, two different representations of tuning are compared. One is the Gaussian function, based on Euclidean distance measure, and the other is based on normalized scalar product (NSP). They are related to each other by Eqn. 2, and we show that both forms of tuning are qualitatively equivalent and can be made quantitatively close.

Mathematically, the Gaussian tuning function and the normalized scalar product with a sigmoid nonlinearity are represented as

$$R_{Gauss} = e^{|\vec{x}-\vec{w}|^2/2\sigma^2}, \tag{4}$$

$$R_{NSP} = \frac{1}{1 + e^{-\alpha(\frac{\vec{x}\cdot\vec{w}}{|\vec{x}|+c} - \beta)}}. \tag{5}$$

The sigmoid is a commonly-used transfer function for modeling the relationship between the presynaptic and postsynaptic activations or membrane depolarizations in neurons. It sharpens the tuning behavior created by normalized scalar product and allows a better approximation of the Gaussian function, as the parameters α and β are adjusted.[†]

[†] In our simulation, a nonlinear fitting routine (`nlinfit` in `Matlab`) was used to find the best α and β with fixed $c = 0.1$ in R_{NSP} for a given $\vec{w}$ and σ.

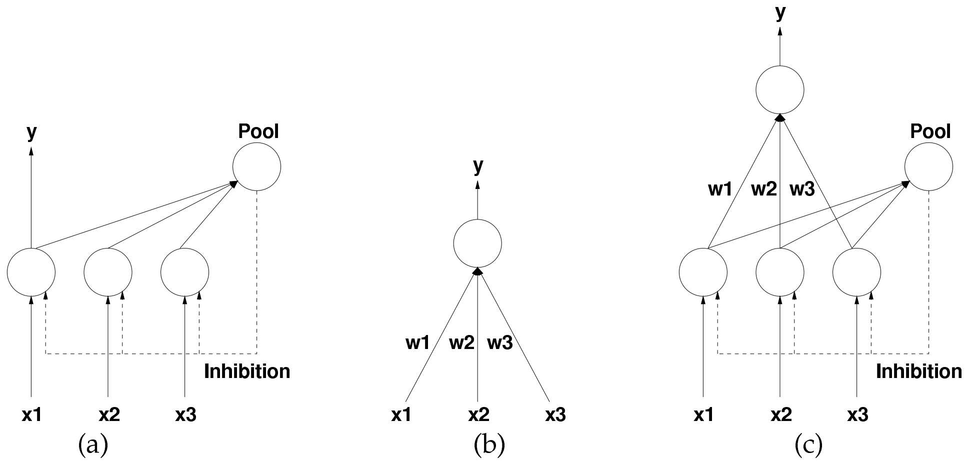


Figure 1: Simple neural circuits for: (a) Divisive normalization, $y = x_1/(c + \sqrt{\sum_j x_j^2})$ based on [10]. This circuit is just one possibility. Divisive normalization may be computed alternatively by feedforward (instead of feedback) inhibition at the dendrites as in [18]. (b) Scalar product, $y = \sum_j x_j w_j = \vec{x} \cdot \vec{w}$. (c) Normalized scalar product. This circuit can produce Gaussian-like tuning.

For R_{Gauss}, $\vec{w}$ specifies the center of the Gaussian function in a multidimensional space. The Gaussian width σ determines the sharpness or sensitivity of tuning (σ need not be the same along different dimensions). For R_{NSP}, $\vec{w}$ specifies the direction of the feature vector along which the response is maximal, and the parameters α and β determine the sharpness of the tuning. In both cases, the response is maximal if the input $\vec{x}$ is matched to the target $\vec{w}$.

Fig. 2 shows a few direct comparisons between R_{Gauss} and R_{NSP}. Although not identical, R_{NSP} and R_{Gauss} exhibit comparable tuning behaviors. Because of the normalization, the dimensionality of R_{NSP} is one less than that of R_{Gauss}. With the same number of afferents n, the Gaussian tuning function may be centered at any points in $\mathcal{R}^n$, whereas the normalized scalar product is tuned to the direction of the vector in $\mathcal{S}^n$ or $\mathcal{R}^{n-1}$. An obvious way of avoiding such limitation is to assume a constant dummy input and to increase the dimensionality of the input vector, which was the approach taken here as in [14]. Then, the normalized scalar product may be tuned to any arbitrary vector $\vec{w}$, just like the Gaussian function (see Appendix B for more discussions on this issue).

5 Discussion

In this paper, we described how the normalized scalar product can account for the tuning of neural responses. We also sketched a plausible neural circuit.

The normalization for tuning provides some new insights and predictions. For example, along the ventral pathway of primate visual cortex, the receptive field size on average increases, and neurons show tuning to increasingly complex features [11]. In order to build a larger receptive field and to increase feature complexity, the neurons may be pooling from many afferents covering different parts of receptive fields. The afferent cells within the pool would interact via normalization operation, whose interaction may appear as a center-surround effect as observed in V1 [5]. If indeed a general mechanism for tuning, normalization would be present in other cortical areas, where similar center-surround or interference effects may be observable.

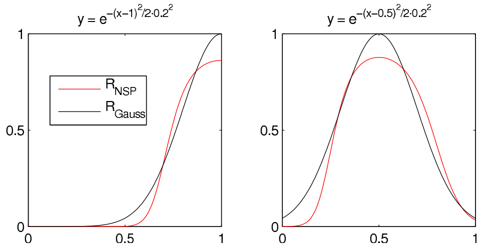
The effects of normalization may also appear whenever the response of one afferent in the normalization pool is modulated (for example, an attentional mechanism through a feedback connection). Change in one neuron's response may affect not only the output of the network, but the response of other afferent neurons in the normalization pool.

We also note that this scheme for cortical tuning has implications for learning and memory, which would be accomplished by adjusting the synaptic weights according to the activation patterns of the afferent cells.

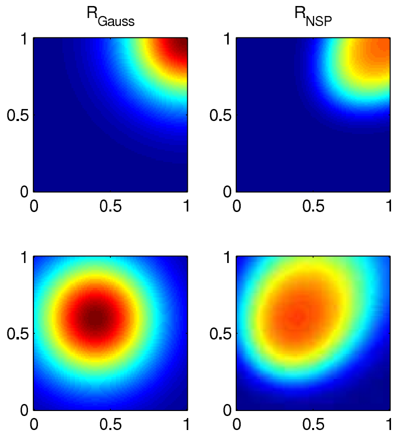
Interestingly, similar neural circuits may be involved in increasing the invariance properties of neurons. It has been observed that IT neurons show certain degree of translation and scale invariance [2, 13], and so do the V4 neurons [15]. One way of producing invariance is the maximum operation, whose approximate implementation may involve a form of pool normalization [26]. A computational model [19, 20] has shown that Gaussian-like tuning and maximum operations were sufficient to capture object recognition processing in visual cortex. We claim here that similar inhibitory neural circuits with different nonlinearities (see Appendix C) may accomplish both operations.

In the past, various neural micro-circuits have been

(a) Comparison in 1-dimension



(b) Comparison in 2-dimension



(c) Comparison in higher dimensions ($d = 5, 10, 20$)

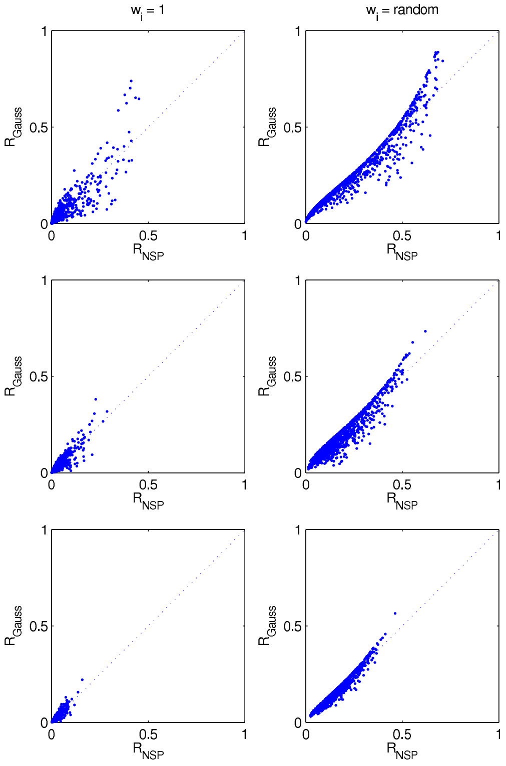


Figure 2: Comparison of R_{Gauss} and R_{NSP} in several dimensions. Note that in all cases, the Gaussian tuning function can be approximated by the normalized scalar product followed by a sigmoid nonlinearity. The parameters α and β in the sigmoid are found with nonlinear fitting, while c was fixed at 0.1. As pointed out in Appendix B, a dummy input was introduced to obtain tuning to an arbitrary $\vec{w}$ (*i.e.*, R_{NSP} is in S^{n+1}). (a) Comparison in 1-dimension: R_{Gauss} (black) with $\sigma = 0.2$ and R_{NSP} (red) are shown for $w = 1$ (left) and $w = 0.5$ (right). (b) Similar comparisons in 2-dimension: $\vec{w} = (1, 1)$ (top) and $\vec{w} = (0.4, 0.6)$ (bottom). (c) Comparisons in higher dimensions. Since the visualization of the entire function is difficult for high dimensions, 1000 random points are sampled from the space. The same nonlinear fitting routine was used to find the parameters in R_{NSP}. The width of Gaussian is scaled according to $\sigma = 0.2\sqrt{d}$, where d is the dimensionality.

proposed to implement a normalization operation. The motivation was to account for gain control. We make here the new proposal that another role for normalizing local circuits in brain is to provide the key step for multidimensional, Gaussian-like tuning. In fact this may be the main reason for the widespread presence of gain control circuits in cortex where tuning to optimal stimuli is a common property.

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Appendix A: Normalization circuit

The model in Fig. 1 is based on [10], and the steady-state responses of the neurons (neglecting dynamics) are determined by the following:

$$G = \sqrt{\sum_j R_j^2}, \tag{6}$$

$$R_i = x_i \cdot \left[\frac{1-G}{c}\right]_+ . \tag{7}$$

The inhibitory signal G depends on the pooled responses. The particular choice of nonlinearity (square root of summed squares) yields a mathematically convenient form of normalization. Other choices can produce tuned responses, although they are not as easy to track analytically. The response R_i is proportional to the input x_i, subject to an inhibitory signal operating multiplicatively. Such multiplicative interaction may arise from the inhibition of shunting type, as noted in [24]. The rectification operation for ensuring positive neural response is denoted by $[\,]_+$. With a little algebra,

$$R_i = \frac{x_i}{c + \sqrt{\sum_j x_j^2}}, \tag{8}$$

which is the same as Eqn. 3, except for the positive constant c, related to the strength of inhibition. Because of c, the above equation is not the true normalization in a mathematically rigorous sense, but as shown in Appendix B, this approximate normalization is enough to create Gaussian-like tuning.

Finally,

$$y = \sum_i w_i R_i, \tag{9}$$

resulting in normalized scalar product, capable of producing tuning behavior.

Appendix B: Optimal templates in normalized scalar product

Since the scalar product $\vec{x} \cdot \vec{w}$ measures the cosine of the angle between two vectors, the maximum occurs when those two vectors are parallel. Because it is also proportional to the length of the vector, a simple scalar product is not as flexible as Gaussian function which can have an arbitrary center. We may assume that both vectors $\vec{x}$ and $\vec{w}$ are normalized ($\vec{x}$ by pool normalization and $\vec{w}$ by Oja's rule [6], for example), so that only the direction within the input space is relevant. However, a more flexible, simple workaround is to assume a constant dummy input, which introduces an extra dimension and allows tuning for any $\vec{w}$ [14]. This constant may be the resting activity of a neuron.

Using the result of derivation from the previous section and assuming such dummy unit (indexed with d in w_d and x_d), the response of the normalizing neural circuit is given by

$$y = \frac{\sum_{j=1}^{n} w_j\, x_j + w_d\, x_d}{c + \sqrt{\sum_{j=1}^{n} x_j^2 + x_d^2}}, \tag{10}$$

which can be viewed as a normalized scalar product in $(n+1)$-dimension. Then, using elementary calculus, it is easy to verify that by choosing w_d and x_d, the maximum response occurs when $\vec{x} = \vec{w}$, for arbitrary w_i.
Let's take the partial derivative:

$$\frac{\partial y}{\partial x_i} = \frac{w_i}{c + \sqrt{\sum_{j=1}^{n} x_j^2 + x_d^2}} - \frac{\sum_{j=1}^{n} w_j\, x_j + w_d\, x_d}{\left(c + \sqrt{\sum_{j=1}^{n} x_j^2 + x_d^2}\right)^2} \cdot \frac{\frac{1}{2}\, 2\, x_i}{\sqrt{\sum_{j=1}^{n} x_j^2 + x_d^2}}. \tag{11}$$

Setting $\frac{\partial y}{\partial x_i} = 0$,

$$0 = w_i \left(c + \sqrt{\sum_{j=1}^{n} x_j^2 + x_d^2}\right) \sqrt{\sum_{j=1}^{n} x_j^2 + x_d^2} - x_i \left(\sum_{j=1}^{n} w_j\, x_j + w_d\, x_d\right). \tag{12}$$

Setting $x_i = w_i, \forall i$ and simplifying the expression,

$$w_d = c\sqrt{\frac{\sum_{j=1}^{n} w_j^2}{x_d^2} + 1} + x_d. \tag{13}$$

As long as the above condition is met, any arbitrary $\vec{w}$ can serve as an optimal template, and since w_d and x_d can be freely chosen, it is easily satisfied. In particular, set $x_d = 1$ and $w_d = c\sqrt{\sum_{j=1}^{n} w_j^2 + 1} + 1$, as done in the simulations for Fig. 2.

Appendix C: Maximum-like operation

With slightly different nonlinearities in normalization, similar gain control circuit could be used to perform maximum-like operation on the inputs to a neuron [26]. Consider the following divisive normalization (compare with Eqn. 8):

$$R_i = \frac{x_i^{q+1}}{c + \sum_j x_j^q}. \tag{14}$$

For sufficiently high q,

$$R_i = \begin{cases} x_i, & \text{if} \quad x_i = x_{max} \\ 0, & \text{if} \quad x_i \neq x_{max} \end{cases} \tag{15}$$

With $y = \sum_i w_i R_i$ where $w_i = 1$, the final output is the maximum of the inputs.