

A mathematical model for resolution enhancement in layered sensory systems

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Abstract. Heiligenberg (1987) recently proposed a model to explain how the representation of a stimulus variable through an ordered array of broadly tuned receptors could allow a degree of stimulus resolution greatly exceeding the resolution of the individual receptors which make up the array. In his model, this “hyperacuity” is achieved by connecting the receptors to a higher level pool interneuron according to a linear synaptic weighting function. We have extended this model to the general case of arbitrary polynomial synaptic weighting functions, and showed that the response function of this higher level interneuron is a polynomial of the same order as the weighting function. We also proved that Hermite polynomials are eigenfunctions of the system. Further, by allowing multiple interneurons in the higher level pool, each of which is connected to the receptors according to a different orthogonal weighting function, we demonstrated that extended stimulus functions can be represented with enhanced precision, rather than just the value of individual point stimuli. Finally, we suggest a solution to the problem of “edge effect” errors arising near the ends of finite receptor arrays.

1 Introduction

Sensory systems have evolved to detect and analyze the parameters of external stimuli that vary over extremely broad ranges. Although stimulus parameters vary as continua, the sampling of stimulus functions by a nervous system is necessarily discrete, due to the finite number of sensory receptors available for any particular modality. Questions concerning the inherent limits of resolution in sensory systems have challenged researchers for decades. In particular, how is the ability of a sensory system to detect fine differences in a stimulus parameter constrained by the relative spacing or “density” of the receptors with respect to that parameter? How is this systematic resolution limited by the resolution or the width of the tuning curves of the

individual receptors that make up the primary sensory array? A somewhat surprising result that has emerged from studies of many different vertebrate and invertebrate sensory systems is that the degree of stimulus resolution observed at the behavioral level generally exceeds the resolution of the individual receptors by a substantial margin. The term “hyperacuity” was coined by Westheimer and colleagues (Westheimer 1975; Westheimer and McKee 1977) to describe such phenomenon in their investigation of the human visual system using the approach of psychophysics. They showed that humans could resolve two line stimuli with a spacing far less than the spacing of photoreceptors in the retina.

These studies have stimulated a great deal of work by neurophysiologists and engineers who would like to understand the biological circuitry underlying such hyperacuity phenomena. In numerous experimental studies, stimulus parameters such as the spatial location of a visual or auditory point source have been shown to be “mapped” continuously within layered arrays of neurons (see Konishi 1986; Knudsen et al. 1987 for recent reviews). Generally, in these neural maps, each neuron can be characterized in terms of 1) its peak tuning to the relevant sensory parameter (in the above case: the optimal spatial location of the point source) and 2) the width of its tuning curve (i.e., the distance away from the optimal spatial location at which a stimulus would elicit a response equal to some pre-defined fraction of the peak response). Adjacent receptors naturally have slightly different peak tuning points and generally have broadly overlapping tuning curves with respect to the inter-receptor spacing. As a consequence of this ordered representation of a stimulus variable in the neural map, the presentation of an extended stimulus (such as a visual image) will result in the generation of a corresponding unique spatial pattern of activity in the neural array. Therefore, higher level interneurons access information about the stimulus by virtue of 1) the location of their dendrites within this neural map, and 2) the relative synaptic strengths or “weights” of inputs from different afferent nerve endings in the map. For instance, Blasdel and Fitzpatrick (1984) demonstrated

that in the input layers $4C\alpha$ and $4C\beta$ of the monkey primary visual cortex, the resolution of the retinotopic map is much finer than the radius of arborization of individual afferent fibers from lateral geniculate nuclei, and that this degree of resolution is maintained for both types of afferents (parvocellular and magnocellular) despite the very different sizes of their terminal endings. It was thus suggested that “the precision of mapping might relate more directly to the arrangement and homogeneity of dendritic fields than to the terminal field sizes of the afferent axons”. With these general experimental results in mind, one aspect of the resolution questions stated above can be rephrased as follows: How does the sensitivity of a higher level interneuron to changes in a sensory parameter depend upon 1) the inter-receptor spacing, 2) the shape of the receptor tuning curves, and 3) the weighting function by which the synaptic strengths of different receptors in the array are coupled to the higher level interneuron?

The issue of this generalized “hyperacuity” was recently explored by Heiligenberg (1987). In his model, an array of receptors (with Gaussian-shaped tuning curves) were distributed uniformly along the entire range of a stimulus variable. Each receptor contributed excitation to a higher level interneuron, with the synaptic weight of each receptor’s input set proportional to its rank index in the receptor array. In other words, the synaptic weight between a receptor at one end of the array and the higher level interneuron would be relatively weak, but the weight of the synapses would increase in a linear fashion for the receptors progressively farther across the array. The receptor at the far opposite end of the array would have the greatest synaptic weight onto the higher level interneuron. Numerical simulation and subsequent mathematical analysis of this model (Baldi and Heiligenberg 1988) demonstrated that the response function of the higher level interneuron was monotone increasing and surprisingly linear, so long as the width of the receptor tuning curve is much greater than the inter-receptor spacing. The smoothness of this function could allow very precise values of a previously coarsely-coded stimulus parameter (at the receptor level) to be “interpolated” from the activity of the higher level interneuron, thereby offering a partial explanation of the general phenomenon of hyperacuity.

The main conclusion drawn from Heiligenberg’s model is that hyperacuity may be achieved provided that the receptors have sufficiently broad tuning to the stimulus. Does this conclusion depend on the particular choice of synaptic weighting scheme (linear weighting in this case)? Is the hyperacuity thus achieved limited to the localization and discrimination of point stimuli only? We address these two questions in the present paper. First, we consider the case of applying certain weighting functions as natural generalizations to Heiligenberg’s linear weighting model. We prove the validity of the model by showing that the response of the higher level interneuron, to which the receptors are connected via polynomial weighting functions, is also a polynomial function of the same order, but usually with

different coefficients. A logical question to ask, then, is what kind of polynomial weighting function would result in an identical response function for the higher level interneuron? This leads to the second point of the paper: we prove that when a Hermite polynomial is used as synaptic weighting function, the interneuron response would be the same Hermite polynomial. In other words, Hermite polynomials are “eigenfunctions” of the system, and the linear weighting function is simply the Hermite polynomial of order one. As a third point of the paper, we propose a scheme of resolution enhancement in representation of extended stimulus functions (stimulus patterns) instead of point stimuli as in Heiligenberg’s original model. We suggest that if the higher level pool contains several interneurons, each of which is connected to the receptors array via a different (yet mutually orthogonal) Hermite polynomial weighting function, then any extended stimulus may be uniquely and completely represented by the collection of higher level interneurons. Finally, we address the problem of “edge effects” errors introduced near the ends of a finite receptor array by considering alternative weighting functions that vanish at infinity.

2 Polynomial weighting functions

Following Baldi and Heiligenberg (1988), we consider a one-dimensional array of sensory receptors with Gaussian-shaped tuning curves distributed uniformly along the entire range of a stimulus variable x . The Gaussian width of the receptor tuning curves will be defined as d , the inter-receptor spacing as a , and the rank index of each receptor in the array as k . The weighting function $\omega(k)$ represents the synaptic strengths of the k -th receptor onto a higher level interneuron. We wish to express the response function $f(x)$ of the higher level interneuron in cases where the given weighting function $\omega(k)$ is non-linear in k .

We first consider the most natural generalization: the power weighting function $\omega(k) = k^p$, where p is any positive integer. Note $p = 1$ reduces to Heiligenberg’s original model. We follow their notations and, without loss of generality, assume $a = 1$ (i.e. simply choose a as the measuring unit).

Statement 1: For positive integer p , the sum

$$f(x) = \sum_{k=-\infty}^{\infty} k^p \left(\frac{1}{\sqrt{\pi d}} e^{-(x-k)^2/d^2} \right)$$

can be approximated by a polynomial of order p , provided that d is sufficiently large.

Proof. By applying the binomial expansion formula

$$\begin{aligned} f(x) &= \sum_{k=-\infty}^{\infty} (x + (k-x))^p \left(\frac{1}{\sqrt{\pi d}} e^{-(x-k)^2/d^2} \right) \\ &= \sum_{k=-\infty}^{\infty} \left(\sum_{j=0}^p \binom{p}{j} x^{p-j} (k-x)^j \right) \end{aligned}$$

$$\begin{aligned} & \times \left(\frac{1}{\sqrt{\pi d}} e^{-(x-k)^2/d^2} \right) \\ & = \sum_{j=0}^p (-1)^j \binom{p}{j} x^{p-j} A_j(x), \end{aligned} \quad (1)$$

where the auxiliary function $A_j(x)$ is defined by

$$A_j(x) = \frac{1}{\sqrt{\pi d}} \sum_{k=-\infty}^{\infty} (x-k)^j e^{-(x-k)^2/d^2}. \quad (2)$$

Since the summation over k is from $-\infty$ to ∞ ,

$$\begin{aligned} A_j(x+1) &= \frac{1}{\sqrt{\pi d}} \sum_{k=-\infty}^{\infty} (x+1-k)^j e^{-(x+1-k)^2/d^2} \\ &= \frac{1}{\sqrt{\pi d}} \sum_{k=-\infty}^{\infty} (x-(k-1))^j e^{-(x-(k-1))^2/d^2} \\ &= \frac{1}{\sqrt{\pi d}} \sum_{k=-\infty}^{\infty} (x-k)^j e^{-(x-k)^2/d^2} \\ &= A_j(x). \end{aligned} \quad (3)$$

That is, $A_j(x)$ has a period of 1.

We know that any periodic function can be expanded into its Fourier series. In the present case,

$$\begin{aligned} A_j(x) &= \sum_{m=-\infty}^{\infty} e^{i2\pi mx} \int_0^1 A_j(u) e^{-i2\pi mu} du \\ &= \frac{1}{\sqrt{\pi d}} \sum_{m=-\infty}^{\infty} e^{i2\pi mx} \\ & \quad \times \sum_{k=-\infty}^{\infty} \int_0^1 (u-k)^j e^{-(u-k)^2/d^2} e^{-i2\pi mu} du \\ &= \frac{1}{\sqrt{\pi d}} \sum_{m=-\infty}^{\infty} e^{i2\pi mx} \\ & \quad \times \sum_{k=-\infty}^{\infty} \int_{-k}^{-k+1} u^j e^{-u^2/d^2} e^{-i2\pi mu} du \\ &= \frac{1}{\sqrt{\pi d}} \sum_{m=-\infty}^{\infty} e^{i2\pi mx} \int_{-\infty}^{\infty} u^j e^{-u^2/d^2} e^{-i2\pi mu} du \\ &= \frac{1}{\sqrt{\pi d}} \sum_{m=-\infty}^{\infty} e^{i2\pi mx} \left(\frac{1}{-2\pi i} \right)^j \\ & \quad \times \frac{\partial^j}{\partial m^j} \int_{-\infty}^{\infty} e^{-u^2/d^2} e^{-i2\pi mu} du \\ &= \frac{1}{\sqrt{\pi d}} \sum_{m=-\infty}^{\infty} e^{i2\pi mx} \left(-\frac{1}{2\pi i} \right)^j \\ & \quad \times \frac{\partial^j}{\partial m^j} (\sqrt{\pi d} e^{-(m\pi d)^2}) \\ &= \sum_{m=-\infty}^{\infty} e^{i2\pi mx} \left(\frac{d}{2i} \right)^j H_j(m\pi d) e^{-(m\pi d)^2}, \end{aligned} \quad (4)$$

where the derivatives of the Gaussian function were expressed using the well-studied Hermite polynomials $H_j(x)$ (see Appendix):

$$H_j(x) = (-1)^j e^{x^2} \frac{d^j}{dx^j} e^{-x^2}. \quad (5)$$

Rearranging the terms of summation and taking into account $H_j(-x) = (-1)^j H_j(x)$ and that $H_j(0) = 0$ (for odd j) or $(-1)^{j/2} j! / (j/2)!$ (for even j), (4) then becomes

$$\begin{aligned} A_j(x) &= \left(\frac{d}{2i} \right)^j \left(H_j(0) + \sum_{m=1}^{\infty} e^{-(m\pi d)^2} H_j(m\pi d) \right. \\ & \quad \left. \times (e^{i2\pi mx} + (-1)^j e^{-i2\pi mx}) \right) \\ &= \left(\frac{d}{2} \right)^j \left\{ \frac{j!}{(j/2)!} \left(\frac{1+(-1)^j}{2} \right) + 2 \sum_{m=1}^{\infty} \right. \\ & \quad \left. \times e^{-(m\pi d)^2} H_j(m\pi d) \cos \left(2m\pi x - j \frac{\pi}{2} \right) \right\}. \end{aligned} \quad (6)$$

Now we take a closer look at the above expression. Since the absolute value of $H_j(m\pi d)$ is bounded by $1.086 \sqrt{j!} 2^{j/2} e^{(m\pi d)^2/2}$ (see Appendix), and the absolute value of $\cos(x)$ is bounded by 1, we can see that as d becomes sufficiently large, only terms of $m = 0$ with even j dominate in the curled bracket of (6). Therefore

$$A_j(x) \cong \begin{cases} \left(\frac{d}{2} \right)^j \frac{j!}{(j/2)!}, & j = 0, 2, 4, \dots, \\ 0, & j = 1, 3, 5, \dots, \end{cases} \quad (7)$$

implying that all A_j are, in the above limiting case, constants rather than functions of x . Substituting them into (1) proves our Statement 1.

Statement 2: The polynomial in Statement 1 must take the following form:

$$f(x) = \begin{cases} a_0 + a_2 x^2 + \dots + a_p x^p, & p = 2n, \\ a_1 x + a_3 x^3 + \dots + a_p x^p, & p = 2n + 1, \end{cases}$$

where a_j are constant coefficients.

Proof. This is obvious, in view of (7) in the proof of Statement 1. Alternatively, we can prove Statement 2 by noting the parity of $f(x)$ with respect to x :

$$\begin{aligned} f(-x) &= \sum_{k=-\infty}^{\infty} k^p \left(\frac{1}{\sqrt{\pi d}} e^{-(x-k)^2/d^2} \right) \\ &= \sum_{k=-\infty}^{\infty} (-1)^p (-k)^p \left(\frac{1}{\sqrt{\pi d}} e^{(x-(-k))^2/d^2} \right) \\ &= (-1)^p \sum_{k=-\infty}^{\infty} k^p \left(\frac{1}{\sqrt{\pi d}} e^{(x-k)^2/d^2} \right) \\ &= (-1)^p f(x), \end{aligned} \quad (8)$$

which means that, with respect to the argument x , $f(x)$ must be an even function for even integer p and an odd function for odd integer p .

Statement 3: If, instead of $\omega(k) = k^p$, we have the generalized weighting function

$$\omega(k) = a_0 + a_1 k + \dots + a_p k^p,$$

then

$$f(x) = c_0 + c_1 x + \dots + c_p x^p,$$

where a_j, c_j are all constant coefficients of the respective polynomials, and $a_j \neq c_j$ in general.

Proof: This is immediately evident from Statement 1 and Statement 2 above, since $f(x)$ is linearly dependent on $\omega(k)$. That is to say, if

$$f_1(x) = \sum_{k=-\infty}^{\infty} \omega_1(k) \left(\frac{1}{\sqrt{\pi d}} e^{-(x-k)^2/d^2} \right) \quad (9)$$

and

$$f_2(x) = \sum_{k=-\infty}^{\infty} \omega_2(k) \left(\frac{1}{\sqrt{\pi d}} e^{-(x-k)^2/d^2} \right). \quad (10)$$

then, for $\omega(k) = \omega_1(k) + \omega_2(k)$,

$$\begin{aligned} f(x) &= \sum_{k=-\infty}^{\infty} \omega(k) \left(\frac{1}{\sqrt{\pi d}} e^{-(x-k)^2/d^2} \right) \\ &= f_1(x) + f_2(x). \end{aligned} \quad (11)$$

3 Hermite polynomials as eigenfunctions

Statement 3 says that if the synaptic weighting as a function of receptor index is a polynomial function $\omega(k)$, then the response of the interneuron as a function of stimulus location would also be a polynomial function $f(x)$ of the same order. However, the coefficients of the two polynomials may not be equal. Naturally we want to know what kind of the polynomial $\omega(k)$ will result in a polynomial $f(x)$ with identical coefficients. In a sense, we are looking for the "eigenfunction" of the system. The conclusion is provided by the following statement:

Statement 4. For $\omega(k) = H_p(k/\sqrt{2d})$, the sum

$$f(x) = \sum_{k=-\infty}^{\infty} H_p \left(\frac{k}{\sqrt{2d}} \right) \left(\frac{1}{\sqrt{\pi d}} e^{-(x-k)^2/d^2} \right)$$

can be approximated (when d is sufficiently large) by $H_p(x/d)$, where $H_p(x)$ is the p -th order Hermite polynomial.

Proof. Note the following formula for Hermite polynomials (see Appendix):

$$H_p(x+y) = 2^{-p/2} \sum_{j=0}^p \binom{p}{j} H_{p-j}(\sqrt{2}x) H_j(\sqrt{2}y) \quad (12)$$

We expand $H_p(k/\sqrt{2d})$ in this way:

$$\begin{aligned} f(x) &= \sum_{k=-\infty}^{\infty} 2^{-p/2} \sum_{j=0}^p \binom{p}{j} H_{p-j} \left(\frac{x}{d} \right) H_j \left(\frac{k-x}{d} \right) \\ &\quad \times \left(\frac{1}{\sqrt{\pi d}} e^{-(x-k)^2/d^2} \right) \\ &= 2^{-p/2} \sum_{j=0}^p (-1)^j \binom{p}{j} H_{p-j} \left(\frac{x}{d} \right) B_j, \end{aligned} \quad (13)$$

where

$$B_j = \frac{1}{\sqrt{\pi d}} \sum_{k=-\infty}^{\infty} H_j \left(\frac{x-k}{d} \right) e^{-(x-k)^2/d^2} \quad (14)$$

is a period function (of period 1) and expandable into Fourier series (c.f. Sect. 2):

$$\begin{aligned} B_j &= \frac{1}{\sqrt{\pi d}} \sum_{m=-\infty}^{\infty} e^{i2\pi mx} \int_{-\infty}^{\infty} H_j \left(\frac{u}{d} \right) e^{-u^2/d^2} e^{i2\pi mu} du \\ &= \frac{1}{\sqrt{\pi}} \sum_{m=-\infty}^{\infty} e^{i2\pi mx} \int_{-\infty}^{\infty} (-1)^j \frac{d^j e^{-u^2}}{du^j} e^{-i2\pi mud} du. \end{aligned} \quad (15)$$

Here we already made use of (5). Integrating by part in succession for j times, and keeping in mind that (see Appendix)

$$\left. \frac{d^j e^{-u^2}}{du^j} \right|_{-\infty}^{\infty} = (-1)^j H_j(u) e^{-u^2} \Big|_{-\infty}^{\infty} = 0,$$

we obtain

$$\begin{aligned} B_j &= \frac{1}{\sqrt{\pi}} \sum_{m=-\infty}^{\infty} e^{i2\pi mx} (-1)^j \int_{-\infty}^{\infty} (-1)^j \\ &\quad \times \left(\frac{\partial^j}{\partial u^j} e^{-i2\pi mud} \right) e^{-u^2} du \\ &= \sum_{m=-\infty}^{\infty} e^{i2\pi mx} (-i2\pi md)^j e^{-(m\pi d)^2}. \end{aligned} \quad (16)$$

For $j=0$, the value of B_0 is easily obtained as

$$\begin{aligned} B_0 &= \sum_{m=-\infty}^{\infty} e^{i2\pi mx} e^{-(m\pi d)^2} \\ &= 1 + 2 \sum_{m=1}^{\infty} \cos 2m\pi x e^{-(m\pi d)^2}. \end{aligned} \quad (17)$$

For $0 < j \leq p$, (16) then becomes

$$\begin{aligned} B_j &= (-2i)^j \sum_{m=1}^{\infty} e^{(-m\pi d)^2} (m\pi d)^j (e^{i2\pi mx} + (-1)^j e^{-i2\pi mx}) \\ &= 2^{j+1} \sum_{m=1}^{\infty} e^{(-m\pi d)^2} (m\pi d)^j \cos \left(2m\pi x - j \frac{\pi}{2} \right). \end{aligned} \quad (18)$$

By arguments analogous to the proof of Statement 1, we have, for sufficient large d ,

$$B_0 \simeq 1, B_j \simeq 0. \quad (19)$$

It follows from (13) that $f(x)$ assumes the same Hermite polynomial form as in the weighting function:

$$f(x) \simeq 2^{-p/2} H_p \left(\frac{x}{d} \right). \quad (20)$$

That is to say, Hermite polynomials are the eigenfunctions of the system. However, it is noteworthy that in $f(x)$ the argument of the Hermite polynomial is x/d , and in $\omega(k)$ it is $k/(\sqrt{2d})$. The first five polynomials are given in the Appendix for reference.

4 Interneuronal representation of sensory patterns

Heiligenberg's model deals with the problem of two-point resolution, i.e. how a sensory system can resolve the location of a "point" stimulus with a precision exceeding the interreceptor spacing. A point stimulus has only a single stimulus value. A pure tone of a certain frequency, or a point of light in the visual space constitutes auditory or visual point stimuli, respectively. Heiligenberg's work and the results shown in

previous sections of this paper have demonstrated that: a) if the sensory receptors array is connected to the higher level interneuron via any weighting function discussed above, and b) if the tuning width of each sensory receptor is sufficiently larger than the inter-receptor separation, then the interneuron would indeed generate discernibly different responses to individually presented stimuli which are different by an amount less than the inter-receptor separation. The response as a function of stimulus location is sufficiently smooth and monotonous (i.e., without “ripples”) to allow reliable interpolation into regions between the locations of the two adjacent receptors (Heiligenberg 1987). Now we go one step further to ask how an extended sensory stimulus function (or sensory “pattern”) $g(x)$ could be encoded and represented beyond the receptor level with a solution exceeding the inter-receptor spacing. Here a sensory pattern refers to a collection of point stimuli distributed across the parameter range. A chord with multiple frequencies, or an image of a face are examples of such sensory patterns. We will show that if we have, instead of a single higher level interneuron, a group or “layer” of interneurons, each connected to the sensory receptor array using some different yet appropriately chosen weighting scheme $\omega_n(k)$, then the representation of the sensory pattern by this interneuron group is uniquely determined with enhanced resolution (see Fig. 1).

Suppose that 1) each interneuron in this higher level group receives input from the array of sensory receptors, with the synaptic weighting characterized by a Hermite polynomial $H_p(k)$, and 2) the order p of the Hermite polynomial is different for each interneuron in this group. We recall that the family of Hermite functions forms the basis function set (spanning the entire Hilbert space) into which any function $g(x)$ satisfying certain conditions can be expanded as (see Appendix)

$$g(x) = \sum_{n=0}^{\infty} c_n H_n \left(\frac{x}{d} \right) e^{-x^2/d^2}, \quad (21)$$

and is thus uniquely specified by the associated Hermite

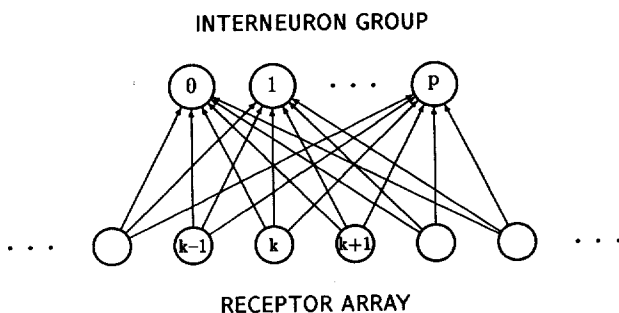


Fig. 1. A group of interneurons, each connected to the sensory receptors array via some different yet mutually orthogonal synaptic weighting function, are capable of encoding a sensory pattern with enhanced resolution. Here, the weighting function for interneuron p is the p -th order Hermite polynomial $H_p(k)$. It can be shown that the response of this interneuron R_p is proportional to the coefficient c_p of the Hermite expansion of any sensory pattern

expansion coefficients

$$c_n = \frac{1}{2^n n! \sqrt{\pi} d} \int_{-\infty}^{\infty} H_n \left(\frac{x}{d} \right) g(x) dx. \quad (22)$$

The response of the k -th sensory receptor r_k is

$$r_k = \int_{-\infty}^{\infty} g(x) \left(\frac{1}{\sqrt{\pi} d} e^{-(x-k)^2/d^2} \right) dx. \quad (23)$$

Therefore the response of the p -th interneuron R_p , whose weighting function is assumed to be $H_p(k/\sqrt{2}d)$, can be expressed as

$$\begin{aligned} R_p &= \sum_{k=-\infty}^{\infty} H_p \left(\frac{k}{\sqrt{2}d} \right) r_k \\ &= \int_{-\infty}^{\infty} g(x) \left(\sum_{k=-\infty}^{\infty} H_p \left(\frac{k}{\sqrt{2}d} \right) \right. \\ &\quad \left. \times \left(\frac{1}{\sqrt{\pi} d} e^{-(x-k)^2/d^2} \right) \right) dx \\ &= \int_{-\infty}^{\infty} g(x) 2^{-p/2} H_p \left(\frac{x}{d} \right) dx \\ &= \sqrt{\pi} 2^p p! c_p, \end{aligned} \quad (24)$$

which is proportional to c_p .

That the response of any interneuron to a stimulus pattern as given above is proportional to the Hermite expansion coefficient c_p implies that any $g(x)$ can be uniquely represented by the response of this set of interneurons $\{c_p\}$. Note that the precision of representation at this stage is not limited by the receptor separation, but by the total number of neurons available in this interneuron group. This number then determines the highest order of Hermite polynomial weighting function required.

5 Weighting functions without “edge-effects”

There are some intrinsic difficulties associated with polynomial weighting schemes. A serious problem is the so-called “edge-effect” described as follows. Since any biological receptors must actually be finite in number, truncation of the summation series at some finite index results in severe degradation of the interneuronal representation of stimulus values near boundaries of the receptor array. For instance, near either end of the receptor array, the interneuron response $f(x)$ in Heiligenberg’s linear model would no longer be monotonous and would have regions of degeneracy where adjacent stimulus locations would yield identical responses. The problem of edge-effects is well recognized by the original authors (Heiligenberg 1987; Heiligenberg and Baldi 1988). This problem is unavoidable, so long as the weighting function does not vanish at infinity. There are at least two possible ways of handling this for biological systems. In some situations, the stimulus variations as well as the peak tuning points of the receptor array “wrap around” into a circular configuration so that the summation of the receptor array is

a periodic function. There are no edge-effect errors associated with the truncation of this summation series, since receptor rank index may be considered as infinite. An example of such a circular configuration is the cricket cercal sensory system (Jacobs and Miller 1988; Jacobs et al. 1986), in which the peak tuning points of mechanoreceptors are distributed across the whole 360° range of wind stimulus orientations.

Alternatively, edge-effect errors could be eliminated if synaptic weighting functions vanish at infinity. This corresponds to the fact that dendritic spreads of real neurons are never infinite. Therefore, while inputs from all receptors can be thought of as being included in the summation, the contributions from receptors farther away are in fact negligibly small. Here we consider weighting functions $\omega(k)$ which approach zero relatively rapidly as $k \rightarrow \pm\infty$. Technically, $\omega(k)$ is required to be square-integrable, so that its Fourier transform exists. For the interneuron's response given by

$$f(x) = \sum_{k=-\infty}^{\infty} \omega(k) \left(\frac{1}{\sqrt{\pi d}} e^{-(x-k)^2/d^2} \right), \quad (25)$$

its Fourier transform is

$$\begin{aligned} \hat{f}(u) &= \sum_{k=-\infty}^{\infty} \omega(k) \int_{-\infty}^{\infty} \left(\frac{1}{\sqrt{\pi d}} e^{-(x-k)^2/d^2} \right) e^{-i2\pi ux} dx \\ &= \left(\sum_{k=-\infty}^{\infty} e^{-i2\pi ku} \omega(k) \right) e^{-(\pi u d)^2} \\ &= \bar{\omega}(u) e^{-(\pi u d)^2}, \end{aligned} \quad (26)$$

where $\bar{\omega}(u)$ denotes a one-periodic function. For $|u| \gg 1/d$, $\hat{f}(u) \simeq 0$ due to the exponentiation fall-off in (26). On the other hand,

$$\begin{aligned} \bar{\omega}(u) &= \sum_{k=-\infty}^{\infty} e^{-i2\pi ku} \omega(k) \\ &\simeq \int_{-\infty}^{\infty} e^{-i2\pi ux} \omega(x) dx \\ &= \hat{\omega}(u), \end{aligned} \quad (27)$$

where $\hat{\omega}(u)$ is the Fourier transform of $\omega(x)$. Note that the above approximation, which essentially replaces the summation over finite step size $\Delta k = 1$ with an integration over infinitesimally small step size dx , is valid only when the following two conditions are met. First, $\omega(x)$ must be smooth varying on the scale of $\Delta x = 1$. Second, u must be small enough such that $u \Delta k|_{\Delta k=1} \ll 1$. The second condition can actually be relaxed or ignored, since $\hat{f}(u) = 0$ anyway for large u as argued above. Therefore, for smoothly varying $\omega(x)$ and sufficiently large d ,

$$\hat{f}(u) = \hat{\omega}(u) e^{-(\pi u d)^2}. \quad (28)$$

If we further require that $\hat{\omega}(u)$ is band-limited by $1/b$ (i.e., $\omega(x)$ varies only on the scale of total input range b of the interneuron, with $b \gg d \gg 1$), then

$$e^{-(\pi u d)^2} \simeq e^{-(\pi d/b)^2} \simeq 1,$$

or

$$\hat{f}(u) \simeq \hat{\omega}(u). \quad (29)$$

Performing the reverse Fourier transform gives

$$f(x) \simeq \omega(x). \quad (30)$$

This implies that the interneuronal response also varies smoothly and on the scale of the total input range b . Note that no "edge-effects" are present, simply because $f(x)$ approaches zero as $x \rightarrow \infty$.

As an example, we consider the Gaussian weighting function whereby the strength of synaptic weighting is given by $\omega(k) = \exp(-(k/b)^2)$, $b \gg d \gg 1$. In this case, the response of the interneuron to a point stimulus at x is

$$\begin{aligned} f(x) &= \sum_{k=-\infty}^{\infty} e^{-k^2/b^2} \left(\frac{1}{\sqrt{\pi d}} e^{-(x-k)^2/d^2} \right) \\ &= \frac{1}{\sqrt{\pi d}} e^{-x^2/(b^2+d^2)} \left(\sum_{k=-\infty}^{\infty} e^{-(1/b^2+1/d^2)(xb^2/(b^2+d^2)-k)^2} \right). \end{aligned} \quad (31)$$

By a calculation analogous to the calculation of A_j in (4), the summation in the last parenthesis becomes

$$\begin{aligned} &\sum_{k=-\infty}^{\infty} e^{-(1/b^2+1/d^2)(xb^2/(b^2+d^2)-k)^2} = \\ &= \sum_{k=-\infty}^{\infty} \sqrt{\frac{\pi b^2 d^2}{b^2+d^2}} e^{i2\pi k(xb^2/(b^2+d^2))} e^{-(k\pi b d)^2/(b^2+d^2)}, \end{aligned} \quad (32)$$

and therefore

$$f(x) = \frac{b^2}{\sqrt{b^2+d^2}} \sum_{k=-\infty}^{\infty} e^{i2\pi k(xb^2/(b^2+d^2))} e^{-(k\pi b d)^2/(b^2+d^2)} \times e^{-x^2/(b^2+d^2)}. \quad (33)$$

The contributions of $k \neq 0$ terms are characterized by the factor $\exp(-(k\pi b d)^2/(b^2+d^2))$, or 4×10^{-18} , for $k=1$, $d=2$, and $b=10$ (remember that the inter-receptor separation is 1 according to our convention). The dominant contribution therefore comes from the $k=0$ term

$$\begin{aligned} e^{-x^2/(b^2+d^2)} &= e^{-(x^2/b^2)/(1+d^2/b^2)} \simeq e^{-x^2/b^2(1-d^2/b^2)} \\ &= e^{-x^2/b^2} e^{x^2 d^2/b^4} \simeq e^{-x^2/d^2} \left(1 + \frac{x^2 d^2}{b^4} \right), \end{aligned}$$

which differs from $\omega(x) = \exp(-x^2/d^2)$ only by a factor of $x^2 d^2/b^4$, or 0.04 (even if we take the very unfavorable value of $x=10$). This shows that indeed $f(x)$ can be well approximated by $\omega(x)$.

6 Conclusion and discussion

Heiligenberg's model, which employs an array of orderly arranged and broadly tuned receptors to enhance the pointwise resolution, can be extended in a number of ways. We first proved the general results that the model works for any polynomial weighting functions. We further demonstrated that Hermite polynomials are the eigenfunctions of this system. This leads to a new

scheme of stimulus representation, i.e., a group of higher level interneurons can encode any generalized stimulus function with enhanced resolution if they adopt appropriately chosen weighting schemes. Finally we discussed possible ways of eliminating or reducing the "edge-effects".

Note that the problem we attempted to solve in this paper is the same problem Heiligenberg and colleagues intended to solve—namely the hyperacuity problem. It should be clear that we are not here providing a new model or an alternative approach to the solution of this problem. Rather, we have shown that Heiligenberg's model is not restricted to his simplified choice of *a*) the linear synaptic weighting scheme and *b*) the single-valued point stimulus. In a sense, we have extended the applicability of Heiligenberg's model with respect to synaptic weighting and stimulus type. Our analysis implies that as long as receptors are sufficiently broadly tuned, hyperacuity may always be achieved in the representation of the sensory stimulus at the interneuron level.

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Appendix

If we expand $\phi(x, z) = e^{-z^2 - 2xz}$ in a power series of z , we have

$$\begin{aligned} e^{-z^2 - 2xz} &= e^{x^2} e^{-(z+x)^2} \\ &= e^{x^2} \sum_{n=0}^{\infty} \left[\frac{d^n e^{-(z+x)^2}}{dz^n} \right]_{z=0} \frac{z^n}{n!} \\ &= e^{x^2} \sum_{n=0}^{\infty} \frac{d^n e^{-x^2} z^n}{dx^n n!} \end{aligned} \quad (\text{A1})$$

The differentiation of e^{-x^2} produces a polynomial, defined as Hermite polynomial, multiplied by the exponentiation factor:

$$\frac{d^n}{dx^n} e^{-x^2} = H_n(x) e^{-x^2}, \quad (n = 1, 2, \dots); H_0(x) = 1. \quad (\text{A2})$$

therefore

$$\phi(x, z) = e^{-z^2 - 2xz} = \sum_{n=0}^{\infty} \frac{H_n(x)}{n!} z^n. \quad (\text{A3})$$

From (A2) follows immediately

$$H_n(-x) = (-1)^n H_n(x). \quad (\text{A4})$$

Differentiating (A3) with respect to x yields:

$$(-2z) e^{-z^2 - 2xz} = \sum_{n=1}^{\infty} \frac{H'_n(x)}{n!} z^n. \quad (\text{A5})$$

The left-hand side of (A5), after inserting into (A3), can be written as

$$(-2z) e^{-z^2 - 2xz} = \sum_{n=0}^{\infty} \left[-2 \frac{H_n(x)}{n!} \right] z^{n+1}. \quad (\text{A6})$$

Comparing (A5) with (A6) yields

$$H'_{n+1}(x) = -2(n+1)H_n. \quad (\text{A7})$$

Similarly, differentiating (A3) with respect to z will result in the following recurrence formula:

$$H_{n+1}(x) + 2xH_n(x) + 2nH_{n-1}(x) = 0. \quad (\text{A8})$$

The first five Hermite polynomials are shown here:

$$\begin{cases} H_0 = 1, H_1 = -2x, H_2 = 4x^2 - 2, \\ H_3 = -8x^3 + 12x, H_4 = 16x^4 - 48x^2 + 12. \end{cases}$$

In general, the following formula gives the explicit form of higher order H_n 's:

$$H_n(x) = (-1)^n \sum_{k=0}^{[n/2]} (-1)^k \frac{n(n-1)(n-2) \cdots (n-2k+1)}{k!} (2x)^{n-2k} \quad (\text{A9})$$

where $[n/2]$ denotes the largest integer $\leq n/2$. We note for $x = 0$

$$H_{2n}(0) = (-1)^n \frac{(2n)!}{n!}; H_{2n+1}(0) = 0. \quad (\text{A10})$$

From the generating function $\phi(x, z)$, we obtain

$$e^{-(z\sqrt{2})^2 - 2((x+y)/\sqrt{2})(z\sqrt{2})} = e^{-z^2 - 2xz} e^{-z^2 - 2yz} \quad (\text{A11})$$

whence by (A3)

$$\sum_{n=0}^{\infty} \frac{2^{n/2}}{n!} H_n\left(\frac{x+y}{\sqrt{2}}\right) z^n = \left(\sum_{r=0}^{\infty} \frac{H_r(x)}{r!} z^r \right) \left(\sum_{s=0}^{\infty} \frac{H_s(y)}{s!} z^s \right). \quad (\text{A12})$$

Multiplying the two series on the right and then identifying coefficients of like powers of z , we obtain

$$\frac{1}{n!} 2^{n/2} H_n\left(\frac{x+y}{\sqrt{2}}\right) = \sum_{r=0}^{\infty} \frac{1}{r!(n-r)!} H_r(x) H_{n-r}(y), \quad (\text{A13})$$

or

$$2^{n/2} H_n\left(\frac{x+y}{\sqrt{2}}\right) = \sum_{r=0}^n \binom{n}{r} H_r(x) H_{n-r}(y). \quad (\text{A14})$$

The asymptotic behavior of $H_n(x)$ for large x is $e^{x^2/2}$; in fact the following inequality can be derived:

$$|H_n(x)| < 1.086435 \sqrt{n!} 2^{n/2} e^{x^2/2}. \quad (\text{A15})$$

Therefore $H_n(x) \exp(-x^2) \rightarrow 0$ as $|x| \rightarrow \infty$.

The Hermite polynomials satisfy the following orthogonal condition (note the weighting e^{-x^2}):

$$\int_{-\infty}^{\infty} e^{-x^2} H_n(x) H_m(x) dx = 0, \quad (n \neq m), \quad (\text{A16})$$

$$\int_{-\infty}^{\infty} e^{-x^2} H_n^2(x) dx = 2^n n! \sqrt{\pi}, \quad (n = 0, 1, 2, \dots), \quad (\text{A17})$$

and therefore they form the basis function set for series expansion of an arbitrary function $g(x)$. Indeed, let

$$h_n(x) = e^{-x^2} H_n(x), \quad A_n(x) = \frac{e^{-x^2/2} H_n(x)}{\sqrt{2^n n!} \sqrt{\pi}},$$

then $g(x)$ may be decomposed into one of the followings:

$$\sum_{n=0}^{\infty} \mu_n H_n(x), \quad \sum_{n=0}^{\infty} \nu_n h_n(x), \quad \sum_{n=0}^{\infty} \lambda_n A_n(x), \quad e^{\sum_{n=0}^{\infty} \sigma_n H_n(x)},$$

which are respectively called type H, h, A, C Hermite polynomial expansion, with

$$\mu_n = \int_{-\infty}^{\infty} \frac{e^{-x^2} H_n(x) g(x)}{2^n n! \sqrt{\pi}} dx, \quad \nu_n = \int_{-\infty}^{\infty} h_n(x) g(x) dx,$$

$$\lambda_n = \int_{-\infty}^{\infty} \frac{H_n(x) g(x)}{2^n n! \sqrt{\pi}} dx, \quad \sigma_n = \int_{-\infty}^{\infty} \frac{e^{-x^2} H_n(x) \log g(x)}{2^n n! \sqrt{\pi}} dx.$$

More properties of Hermite polynomials can be found in standard mathematical textbooks, such as Sansone et al. (1959).

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