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Supplemental Information

Temporal Encoding of Spatial Information

during Active Visual Fixation

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Supplemental Inventory

1. Supplemental Experimental Procedures

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Probabilistic Estimation of the Power Spectrum

The model expressed by Eq. 1 relies on two assumptions: (a) the statistics of the observed images are spatially homogeneous; and (b) fixational eye movements do not depend on the stimulus. For notational simplicity, we consider one spatial dimension, but the analysis applies equally to two dimensions.

In general, given a zero-mean image I(x) and a trace of eye movements $\xi(t)$, the autocorrelation function of the retinal input is given by:

$$s(x,\tau) = \left\langle I(x_0 + \xi(t_0)) I(x_0 + x + \xi(t_0 + \tau)) \right\rangle_{x_0,t_0,I,\xi}$$

where the angle-bracket indicates averaging.

We specify the eye movement process by a conditional probability $p(\xi(t_0 + \tau) = x_2 | \xi(t_0) = x_1)$. The autocorrelation function can then be expressed as:

$$s(x,\tau) = \iint \left\langle I(x_0 + x_1) I(x_0 + x + x_2) p(\xi(t_0) = x_1) p(\xi(t_0 + \tau) = x_2 | \xi(t_0) = x_1) \right\rangle_{x_0,t_0,I} dx_1 dx_2.$$

Under the above two assumptions (statistical homogeneity of the images, and independence of fixational eye movements and the stimulus), we obtain:

$$s(x,\tau) = \int \left\langle I(y)I(y+x+\Delta x) \right\rangle_{y,I} \left\langle \int p(\xi(t_0) = x_1, \xi(t_0+\tau) = x_1 + \Delta x) dx_1 \right\rangle_{t_0} d\Delta x$$

where we substituted $y = x_0 + x_1$ and $\Delta x = x_2 - x_1$.

That is,

$$s(x,\tau) = c_I(x) \, \mathrm{a} \, q(x,\tau),$$

where $c_I(x)$ is the autocorrelation function of the observed images, $q(x,\tau)$ is the probability that the eye moved by x in the interval τ (averaged over all starting positions), and å is spatial convolution. The power spectrum of the retinal stimulus, $S(k,\omega)$, is given by the Fourier Transform of its autocorrelation $s(x,\tau)$. Since the Fourier Transform replaces convolutions by products,

$$S(k,\omega) = I(k)Q(k,\omega)$$
⁽²⁾

where $Q(k,\omega)$ is the Fourier Transform of $q(x,\tau)$.

In two dimensions, the same analysis holds, and the above equation applies, with the Fourier Transform variable k interpreted as a spatial frequency vector (k_x, k_y) .

Input Power Spectrum during Brownian Motion

Eq. 2 enables closed-form estimation of the input power spectrum when the eye movement process is two-dimensional Brownian motion. In this case, the probability distribution of retinal displacement obeys the diffusion equation:

$$\frac{\partial}{\partial t}q(x,y,t) = \frac{1}{2}D\nabla^2 q(x,y,t)$$
⁽³⁾

where D is the diffusion constant.

For the initial condition that q is concentrated at the origin at t = 0, the solution of Eq. 3 is well-known:

$$q(x, y, t) = \frac{1}{2\pi Dt} \exp\left(-\frac{x^2 + y^2}{2Dt}\right).$$
 (4)

This function has Fourier Transform

$$Q(k_x, k_y, \omega) = \frac{(k_x^2 + k_y^2)D}{(k_x^2 + k_y^2)^2 \frac{D^2}{4} + \omega^2}.$$
(5)

Substitution of $Q(k_x, k_y, \omega)$ from Eq. 5 into Eq. 2 gives the power spectrum of the retinal stimulus, as plotted in Figs. 2B - D. To obtain the value of D from the recorded eye movement data, we measured the empirical standard deviation of the eye displacement as a function of time, for intervals from 0 to 500 ms. We then chose the value of D for which the standard deviation of the probability distribution q(x, y, t) in Eq. 4, namely $\sqrt{2Dt}$, provided the least-squares best fit to the data. This yielded $D = 40 \operatorname{arcmin}^2/s$.

Influences of Fixational Eye Movements on Neural Responses

The maps in Fig. 4*B*, *C* summarize the influences of fixational eye movements on the contrast sensitivity functions of retinal ganglion cells. These functions are typically measured in physiological preparations which eliminate eye movements. Eq. 2 allows estimation of how sensitivity measured with a retinally-stabilized stimulus is affected by the presence of fixational eye movements.

Let $F_s(k,\omega)$ represent the contrast sensitivity function of a ganglion cell measured in the absence of eye movements. With presentation of a stimulus I(k), this cell produces a response with power spectrum:

$$R_{s}(k,\omega) = I(k) \left| F_{s}(k,\omega) \right|^{2}.$$
(6)

When the same image I(x) is examined in the presence of fixational eye movements, Eq. 2 gives the spectral density, $S(k,\omega)$, of the resulting input to the retina. Thus, the power spectrum of the cell's output will be given by:

$$R_D(k,\omega) = S(k,\omega) \left| F_S(k,\omega) \right|^2 = I(k)Q(k,\omega) \left| F_S(k,\omega) \right|^2.$$
⁽⁷⁾

Comparison between Eqs. 6 and 7 reveals that the impact of eye movements is summarized by the term $Q(k, \omega)$, which multiplies the neuron's contrast sensitivity function. Therefore, the contrast sensitivity of the neuron to any external stimulus I during normal fixational instability is fully described by the function:

$$F_D(k,\omega) = \sqrt{Q(k,\omega)} \left| F_S(k,\omega) \right|,\tag{8}$$

so that

$$R_D(k,\omega) = I(k) |F_D(k,\omega)|^2.$$

Thus, F_D represents the neuron's sensitivity to static external images when the redistribution of power caused by fixational eye movements has been taken into consideration. The maps in Fig. 4B and C were obtained by combining neurophysiological measurements of contrast sensitivity functions in macaques [24,31,32] with the eye movement function $Q(k,\omega)$ shown in Fig. 3B, as described in Eq. 8.