“Collective coding” of correlated cone signals in the retinal ganglion cell

(signal/noise ratio/cone density/statistics of images)

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ABSTRACT The signals in neighboring cones are partially correlated due to local correlations of luminance in the visual scene. By summing these partially correlated signals, the retinal ganglion cell improves its signal/noise ratio (compared to the signal/noise ratio in a cone) and expands the variance of its response to fill its dynamic range. Our computations prove that the optimal weighting function for this summation is dome-shaped. The computations also show that (assuming a particular space constant for the correlation function) ganglion cell collecting area and cone density are matched at all eccentricities such that the signal/noise ratio improves by a constant factor. The signal/noise improvement factor for beta ganglion cells in cat retina is about 4.

The receptive field center of a ganglion cell in cat retina represents the spatially summed responses of many cones. The responses are not summed evenly but with a dome-like weighting that peaks at the middle of the field and declines toward the edge (refs. 1 and 2; Fig. 1A). The shape of the weighting function is constant across the visual field, but the collecting area of the ganglion cell and the distribution density of the cones vary markedly. In central retina, cone density is high and ganglion cell dendritic field is narrow (3–5), so the weighting profile represents relatively few, closely spaced cones (refs. 6–8; Fig. 1B, field a). In peripheral retina, cone density is low and ganglion cell dendritic field is broad, so the weighting profile represents many, widely spaced cones (Fig. 1B, fields b and c).

The relation between these three fundamental aspects of ganglion cell functional architecture (the number, spacing, and weighting of cones converging for the receptive field center) has never been explained. Here we describe how these biological factors are related to a physical factor, the local correlation of luminance in the visual scene. Our computations show that the dome-shaped weighting of cone signals in the ganglion cell optimally improves the signal/noise (S/N) ratio compared to the S/N ratio in a single cone. Further, the S/N improvement achieved by collecting signals from a few, closely spaced cones or many, widely spaced cones is apparently the same. The computations suggest that evolution may have tuned certain basic features of retinal circuitry to match the statistics of natural images.

METHODS

If the signals in neighboring cones were identical and if the ganglion cell collected them with equal weight, the S/N ratio in the ganglion cell would improve (compared to the S/N ratio in a single cone) as the square root of the number of cones[†] (9, 10). Such signals are generally not identical, but

they do tend to be strongly correlated (11, 12). The correlations stem partly from optical blurring but mainly from spatial autocorrelation in the visual scene. Intuitively, therefore, the S/N ratio should improve when partially correlated signals are summed and weighted, not evenly, but according to the strength of their autocorrelations.

To determine the optimal weighting for summing partially correlated signals, we assumed a square array of equally spaced cones and assigned autocorrelation coefficients to all pairs as a function of distance (Fig. 1C). Cone responses were summed linearly according to individual weighting coefficients. We defined the S/N ratio in the ganglion cell as the square root of the ratio of the expected signal power $E\{S^2\}$ to the expected noise power $E\{N^2\}$:

$$E\{S^2\}/E\{N^2\} = f^2(s/n)^2,$$

where s/n is the S/N ratio of a single cone and also

$$f^2 = \sum_{i=1}^m \sum_{j=1}^m a_i a_j r_{ij} / \sum_{i=1}^m a_i^2. \quad [1]$$

The S/N ratio of the ganglion cell is given by $f(s/n)$, where f is a “signal-to-noise improvement factor,” (S/N ganglion cell)/(S/N cone).

Derivation: We assume that a sequence of cone signals is “wide-sense stationary” (12), with its mean at each adaptation level. Autocovariance of signals between two cones i and j is expressed as

$$E[s_i s_j] = s^2 r_{ij} \quad (0 \leq r_{ij} \leq 1),$$

where $s^2 = E[s_i^2]$ is the variance of the cone signal and r_{ij} are autocorrelation coefficients characterized by $r_{ij} = r_{ji}$. The variance of the noise is $E[n_i^2] = n^2$. Noise sources are assumed to be independent of each other and also of signals, as shown by

$$E[n_i n_j] = 0 \quad (\text{for } i \neq j)$$

and

$$E[n_i s_j] = 0 \quad (\text{for all } i \text{ and } j).$$

The expected signal power is given as

$$E\{S^2\} = E\left[\left(\sum_{i=1}^m a_i s_i\right)^2\right] = s^2 \sum_{i=1}^m \sum_{j=1}^m a_i a_j r_{ij}.$$

Abbreviation: S/N, signal/noise.

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[†]Signal is defined here as the deviation of the voltage response from its spatial mean over an integration time. Noise is variation in the voltage due to Poisson fluctuation of photons, transduction processes, membrane channels, synaptic vesicles, etc.

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FIG. 1. (A) Dome-like sensitivity profile in the center of ganglion cell receptive field and the broad, shallow surround. (B) Number and density of cones collected by beta ganglion cells at different eccentricities (3–8): field a, 0.3 mm in area centralis; field b, 2.5 mm; and field c, 5.8 mm. (C) Scheme of collective coding. For a square array of cones of size $\sqrt{m} \times \sqrt{m}$ (labeled sequentially 1 to m), autocorrelation coefficients (r_{ij}) are assigned to all pairs ($i = 1, 2, \dots, m; j = 1, 2, \dots, m$) as a function of distance. All responses in this array are assigned weighting coefficients (a_i) and summed linearly in a ganglion cell. (D) S/N improvement factor in cat retina versus eccentricity. Over the region considered, the number of cones converging on a ganglion cell increases 5-fold, but the spacing between cones widens (see B). These factors balance for an autocorrelation function with a space constant of 30 μm so that S/N improvement is constant across the visual field. The points a, b, and c represent the values for the collecting areas shown in B.

The expected noise power is given as

$$E[N^2] = E\left[\left(\sum_{i=1}^m a_i s_n\right)^2\right] = n^2 \sum_{i=1}^m a_i^2.$$

End.

By taking the derivative of Eq. 1 with respect to a_i , one finds that maximal improvement occurs when

$$a_i = \sum_{j=1}^m a_j r_{ij} / f_o^2 \quad (i = 1, \dots, m), \quad [2]$$

where f_o^2 is the maximum of f^2 . Thus, the optimal weight of each cone is proportional to weighting coefficients (a_j) and correlation coefficients (r_{ij}). The latter are simply functions of intercone distance. The improvement factor, f , for the S/N ratio can be maximized by adjusting the cone weighting coefficients for each set of autocorrelation coefficients. The family of equations represented by Eq. 2 was solved numerically.

ically. Derivation:

First derivative of Eq. 1 with respect to a_i :

$$\begin{aligned} \partial f^2 / \partial a_i &= \left[\left(\sum_{k=1}^m a_k^2 \right) \left(2 \sum_{j=1}^m a_j r_{ij} \right) \right. \\ &\quad \left. - 2 a_i \left(\sum_{j=1}^m \sum_{h=1}^m a_j a_h r_{jh} \right) \right] / \left(\sum_{k=1}^m a_k^2 \right)^2 \\ &= 2 \left(\sum_{j=1}^m a_j r_{ij} - a_i f_o^2 \right) / \sum_{i=1}^m a_i^2, \end{aligned}$$

where we use the relation as follows:

$$\begin{aligned} \sum_{i=1}^m \sum_{j=1}^m a_i a_j r_{ij} &= a_i^2 r_{ii} + a_i \sum_{j=1, j \neq i}^m a_j r_{ij} + a_i \sum_{h=1, h \neq i}^m a_h r_{hi} + \text{others} \\ &= a_i^2 r_{ii} + 2 a_i \sum_{j=1, j \neq i}^m a_j r_{ij} + \text{others} \quad (\because r_{hi} = r_{ih}). \end{aligned}$$

FIG. 2. Effect of weighting function on S/N improvement. For a cone array (*Upper left*) and an exponential autocorrelation function with a space constant of $30\ \mu\text{m}$ (*Upper right*), both chosen arbitrarily, the optimal weighting was computed by using Eq. 2. Its one-dimensional profile (O; *Lower left*) along the diagonal line (●●●) of the top array is shown to be dome-shaped. S/N improvement factors (*Lower right*) were calculated by using Eq. 1 for this weighting function (O) and also for flat (F) and exponential (E) functions.

FIG. 3. Effect of collecting area on S/N improvement. The number of cones increases with collecting area. S/N improvement factors were computed for arrays of various sizes by using the optimal weighting function and the autocorrelation function with a $30\text{-}\mu\text{m}$ space constant. The three points on the curve represent the values for the arrays illustrated.

Therefore,

$$(\partial/\partial a_i) \sum_{i=1}^m \sum_{j=1}^m a_i a_j r_{ij} = 2 \sum_{j=1}^m a_j r_{ij}.$$

We get Eq. 2 by setting $\partial f^2/\partial a_i = 0$. Next, the second derivative of Eq. 1 at $f^2 = f_o^2$ proves that the extreme value f_o^2 is maximal:

$$\partial^2 f^2/\partial^2 a_i = 2(1 - f_o^2)/\sum_{i=1}^m a_i^2 < 0 \quad (\because f_o > 1).$$

End.

RESULTS AND DISCUSSION

The set of optimal weighting coefficients computed by using Eq. 2 turned out to form a dome-shaped function. For the example illustrated in Fig. 2 (array size, cone density, and autocorrelation function all arbitrary), the S/N improvement factor is 6.1 for the dome-shaped weighting function, whereas for other weighting functions it is less: 5.9 for the flat and 5.5 for the exponential. The differences between the various weighting functions seem modest, particularly as compared to the other three determinants of S/N improvement (collecting area, cone density, and autocorrelation function; Figs. 3, 4, and 1D). Yet, since the S/N ratio is what limits the ganglion cell's contrast sensitivity over a wide range of luminance (13) and since natural scenes are mostly low contrast (14), even a modest improvement to the S/N ratio will improve ganglion cell performance. Therefore, the advantage achieved by the dome-like weighting may be biologically significant.

Increasing the collecting area causes the S/N ratio at first to rise sharply (Fig. 3). However, since the autocorrelation function declines exponentially, the improvement due to adding cones at the edge of the array decreases rapidly, and the S/N improvement factor soon asymptotes. Increasing the cone density improves the S/N ratio in proportion to the square root of the density and with a slope that depends on the autocorrelation function (Fig. 4). When cone signals are identical (flat autocorrelation function), the optimal weighting is also flat, and the slope of the S/N improvement is one. When cone signals are only partially correlated, the optimal weighting is always dome-shaped, no matter what the cone density, and the slope of the S/N improvement is less than one.

We considered next how the cone weighting function, cone density, and ganglion cell collecting area might interact to influence the S/N improvement in beta ganglion cells of the cat at different eccentricities. The results of computations involving these three factors depend on the value selected for the fourth factor—i.e., the autocorrelation function. This in turn probably depends on what scene a cat most needs to view and on the viewing distance, neither of which are known for sure. It is known, however, that the average spatial autocorrelation in a natural scene is nearly exponential (11, 14, 15). Therefore, we performed the appropriate computations by using a family of exponential autocorrelation functions to see what would happen (Fig. 1D). For large space constants, the effect of increased collecting area dominates, so the S/N improvement factor rises with eccentricity. For small space constants, the effect of decreased cone density dominates, so the S/N improvement factor falls with eccentricity. However, for one particular space constant, 30 μm , the increased collecting area and decreased cone density

FIG. 4. Effect of cone density on S/N improvement. (Upper) Three arrays with the same spatial extent but increasing cone density are illustrated. As density rises, signals in neighboring cones become more strongly correlated. For three functions of autocorrelation (cases a, b, and c; Lower left), optimal weighting (Lower center), and S/N improvement (Lower right) were computed. When the autocorrelation is flat (case a), the optimal weighting is also flat. When the autocorrelation is exponential (cases b and c), signal correlation between cones is less than one, so the optimal weighting is dome-shaped. In all cases, S/N improvement is proportional to the square root of the cone density, but the slope decreases with shorter space constants of autocorrelation.

balance precisely so that the S/N improvement is constant for all eccentricities.

This striking result suggests, at least as one possibility, that the function served by the reciprocal shifts in cone density and receptive field collecting area is to achieve (for static images) the same improvement in the S/N ratio in all beta cells across the visual field. Although, *a priori*, there may be no reason to hold the S/N ratio constant with eccentricity, one can imagine that the task of wiring the cortex would be simpler if the signal in all cells of the beta array had a similar degree of reliability.

This reasoning would hold only if the cat retina had evolved to view scenes whose average autocorrelation function has a space constant of 30 μm . This function must arise primarily from the scene itself, rather than mainly from optical blurring, because the space constant of the cat's optical line spread function (16, 17), at 11 μm , is much narrower than the postulated autocorrelation function. Fourier transformation shows that the postulated function cuts off at about 7.4 cycles per degree and that below this cutoff all frequencies are represented at 70–100% amplitude. It follows that the smallest ganglion cell aperture should have about the same cutoff as the autocorrelation function and that there should be a family of ganglion cells with larger apertures tuned to the lower frequencies in the scene. This resembles what has been found by physiological measurement: central beta cells with cutoff not much above 7 cycles per degree and peripheral beta cells whose apertures increase with eccentricity (7, 8). Thus, the idea that evolution has tuned the cat retina to view scenes with a particular set of statistical properties is both reasonable and consistent with empirical measurements.

The overall structure of a ganglion cell receptive field embodies two distinct coding procedures. The *surround*, which is broad and shallow (Fig. 1A), represents a process termed "predictive coding" (14). Many cone signals correlated only weakly are summed over a wide area to predict the signal at the center. The prediction is subtracted from the center response, leaving only the difference to be amplified. This compresses the signal by removing the redundant components, permitting greater amplification of the nonredundant components, and thereby protecting them from corruption at subsequent stages by noise (18).

The *center* of the receptive field, which is narrow and tall, apparently serves the complementary operation, which we term "collective coding." A relatively few cone signals, correlated strongly, are summed over a small area and weighted so as to optimally improve the S/N ratio. The match

of collecting area to cone density apparently ensures that all beta cells have the same S/N ratio. While predictive coding compresses the signal variance so as not to exceed the dynamic range of an axon, collective coding expands the signal variance to fully exploit the available dynamic range. Both coding schemes apparently cooperate to match retinal output to the fixed-channel capacity of the optic nerve. In short, the ganglion cell's overall sensitivity profile may be appreciated, as Barlow (19) suggested, as the neatest way to package the greatest amount of useful information.

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